Insect Resistance in Crop Plants

by

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INSECT RESISTANCE IN CROP PLANTS
Fig. 1. Differences such as these in the damage done to adjacent strains of corn by the supposedly omnivorous grasshoppers (Melanoplus spp.) lead one to expect that resistance to other insects may be more common than is now evident. Left, Kansas hybrid 2234; right, U.S. hybrid 35. (Courtesy R. W. Jugeheimer and Dept. of Agronomy, Kansas State University, Manhattan.)
To My Wife

Elizabeth May Painter

without whose help and encouragement
this work could scarcely
have been done.
"... It is one of the attractions of the attempt to develop an applied branch of genetics that the stimulus of practical needs opens up lines of enquiry of wide theoretical interest."

Hutchinson, J. B.—Jour. of Genetics 40:282. 1940.
PREFACE TO PAPERBOUND EDITION

While the first printing of *Insect Resistance in Crop Plants* has been out of stock several years, requests for it have not diminished. Universities offering courses on the subject are increasing. The need for increased agricultural production at this time, particularly in developing countries, requires that all possible means of insect control be explored and used. Resistant varieties of crop plants provide protection and insurance against insect damage at no extra cost in materials or labor, and with no danger from chemicals or chemical residues.

Theories and ideas developed when this book was first printed, despite the little information available, have been confirmed and are proving valuable guides in a number of insect resistance studies. A second printing makes the information available, and also provides an opportunity to correct the relatively few typographical errors in the first printing.

This publication should long remain the place to start in any study of resistance. It outlines the possible complexities of components of resistance and suggests possible bases and factors that affect the expression and permanence of resistance. Methods used in study of resistance have been detailed along with early examples in a number of crops. The bibliography was as complete as possible at the time of the first printing and remains the foundation for further studies in insect resistance.

Since the first printing, increased interest and attention have been given to the study of plant resistance to insects, with considerable success. The increased interest was prompted primarily by: problems associated with toxic insecticidal residues with animals, other than the target pest, in national and international trade; the increasing quantities of insecticides required for adequate control of insects on many crops, with the accompanying increase in human hazards and cost; widespread accumulation of insects resistant to insecticides; and, in developing countries, the difficulties associated with the cost and lack of farmers' knowledge of more sophisticated insect control methods.
The use of resistant varieties is outstandingly successful in several crops. In Kansas the use of hessian fly-resistant wheat varieties provides excellent protection wherever these varieties are used. Over a period of at least fifteen years the insect was eliminated as a problem across the center of the state where for many previous years it had been highly destructive. In the Monerzuma hills region of California the use of resistant wheat varieties has made hessian fly a rare insect. In all major winter wheat-growing areas of the United States, adapted hessian fly-resistant wheat varieties are now available to control this insect at no cost to the farmer.

Five years after the discovery of the spotted alfalfa aphid in the United States, four adapted resistant alfalfa varieties were available to farmers for control of this insect in several regions. Now several additional varieties are in use. Other less striking examples could be cited.

A feared development in insect resistance was the selection of biotypes able to feed on resistant varieties. To date, only six such plant-insect relationships are known. These occur primarily where resistance is the result of a single genetic factor, and "lock and key" relationships with the biological strains have developed. In other cases, especially where examples of insect resistance have complex bases, no difficulties with biotypes have occurred.

In contrast to the use of insecticides, where results are sudden and there is decreasing effectiveness unless reapplied, insect-resistant varieties are more permanent and cumulative in effectiveness. This is especially true of low levels of insect resistance, which have not received the attention they deserve. The use of insect-resistant varieties should be of increasing value around the world in the coming development of integrated insect control.

Andrew H. Painter

August, 1968
PREFACE

The spectacular successes of the newer types of insecticides that have been developed during and after World War II have tended to obscure the fact that there are many other ways by which insects may be controlled. Information on these other ways is not broadcast by highly paid advertising staffs. Yet there are large areas where certain crops could not be grown profitably because of insects without the use of biological or cultural control measures. It is hoped that this volume will aid in keeping the proper balance between various methods so that insect control may have the greatest effectiveness for the least cost to both grower and ultimate consumer.

The literature on the resistance of crop plants to insects has been widely scattered even for individual crops. One purpose of this book has been to bring together the references to work of this nature and to summarize that work in certain crops as an indication of what has and can be accomplished by this means of insect control. A cooperative study of insect resistance in crop plants has been the major project of which I have been a leader at Kansas Agricultural Experiment Station since 1926. At the time that the project was established it was the only one of its kind in any experiment station. While the major work involved wheat, resistance to a variety of insects was studied wherever found in corn, sorghums, and alfalfa. Partly as a result of this study of insect resistance the following improved varieties carrying insect resistance have been distributed to the farmers of Kansas: Atlas sorgo, resistant to chinch bugs; Kawvale and Pawnee wheat, partially resistant to hessian fly; Ladak alfalfa, resistant to pea aphids; and the corn hybrid Kans. 2234, which carries some resistance to grasshoppers. Since 1937 I have taught an advanced course in the Department of Entomology dealing with insect control by host-plant resistance. For courses of this nature and for those in crop improvement this book may serve as a text or reference book.

As a result of these personal experiences and a study of the literature it has been possible to draw some general conclusions regarding insect resistance. These are presented as tentative and
subject to modification when more evidence is available. Some of the suggestions are of wide biological interest in connection with the relationship between insect and host plant and in the evolution of this relationship. For all of the conclusions presented the basic data are at present inadequate. If such ideas stimulate further research along these lines, they will have served their purpose. I believe that much of the information collected by economic entomologists may have notable general biologic importance if collated and studied. Conclusions presented here are offered as an example.

Because the literature on insect resistance has been so widely scattered, the results of the combined efforts of entomologists and plant breeders are not generally known. The evidence presented here indicates that, in a number of cases, control by host-plant resistance as measured by yield compared favorably with control by insecticides, even where the latter is quite satisfactory. Such insects as the hessian fly on wheat, the grape phylloxera, and the woolly aphid may be satisfactorily controlled by host-plant resistance, but, so far, not by insecticides. In most problems involving phytophagous insects, the use of insecticides will remain an emergency control measure and, as such, emphatically necessary. It is equally necessary that we attempt to use more permanent control methods that are less costly to growers. The use of insect resistance belongs to such a control program.

The information presented in the chapters on specific crops will be of interest principally to entomologists and plant breeders who can study insect resistance in those crops; to entomologists who are conducting general projects in the control of the insects concerned; and to administrators, because it serves as an indication of what can be done with other crops and other insects. The general chapters should be of use to any persons who are interested in insect biology. As these chapters bring together scattered information on plant-insect relationships, it is hoped that they will be of use to graduate students since these chapters deal with a subject which is inadequately covered in existing texts. For plant breeders working in crop improvement some new viewpoints regarding insects may be presented, which, it is hoped, will prove of use in their consideration of employing insect resistance in their programs.

Insect resistance has proved especially valuable where the unit value or margin of profit of a crop is small and the acreage large.
It also should be of particular value in those parts of the world where
the individual land holdings are too small to permit the economical
use of insecticides and where growers are not familiar with their use.

An attempt has been made to find references to, and read either
in the original or as abstracts, all of the literature on insect resistance
in crop plants that has been published up to 1949, together with a
few of the more recent papers. References to literature found
during the time the book was in press have been inserted in Chapter
X. The general subject of insect resistance is not indexed either in
Biological Abstracts or in the Review of Applied Entomology. The
regular indices for the more recent volume of Plant Breeding Ab­
stracts have not been published. It has been necessary to go
through these abstract journals page by page, and when a reference
to insect resistance was found, to check any references given in it.
By such means and the use of bibliographies in the general papers
recorded in Chapter I, it is hoped that few important papers have
been missed. While the data reviewed here deal primarily with
field crops, the results in studies of resistance to other insects, espe­
cially to woolly apple aphid and resistance to phylloxera, have been
used as illustrative material in the general chapters where applicable.

The chapters on specific crops deal with those field crops in
which the resistance to insects have been studied in the greatest
detail. They are intended as examples of the possibilities and the
extent of the work that has been done in this field. Under each
crop and each insect an attempt has been made to give enough in­
formation on plant breeding and insect biology so that those familiar
with one but not the other field could have a better understanding of
the information on insect resistance. It is not expected that the
general material on either crop or insect would be complete. The
common names and scientific names of North American insects used
are those listed in the Common Names of Insects Approved by the
American Associations of Economic Entomologists (Jour. Econ.
Ent. 39:427-448. 1946). Likewise, Standardized Plant Names,
Second Edition (Harrisburg, Pa., McFarland, for American Joint
Committee on Horticultural Nomenclature, 1942), has been used
for plant names except, as in cotton, where a more recent
monograph was available.

In the chapters dealing with general principles the examples
have been selected, where applicable, from crops and insects not
treated elsewhere. Since this has not always been possible, some duplication has been necessary. Additional examples will be found in the chapters on specific crops.

The viewpoint of the biological phenomena described in this volume is primarily that of an entomologist. An attempt has been made to give equal emphasis to both the entomological and the plant-breeding phases. For a better understanding of various features of plant breeding as applied to insect resistance I have been indebted to discussions with my associates in agronomy and botany at Kansas State College, particularly to John H. Parker, Louis P. Reitz, C. O. Johnston, A. M. Brunson, and R. W. Jugenheimer.

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I wish also to call attention to the several illustrations loaned by individuals and organizations and acknowledged specifically in various places. Illustrations not otherwise acknowledged are from the files of Kansas State College; many were taken by the college photographer, Floyd Hanna.

Manhattan, Kansas.
May, 1951
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CHAPTER I
INTRODUCTION

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    plant breeder; fields involved; cooperation.

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Differences in the responses of plant varieties to insect attack
and the interrelations of plants and insects have been on record for
more than a hundred years. Thus the information on this subject
is coextensive with the study of economic entomology.

More than one hundred years ago (Lindley 1831) an apple
variety, Winter Majetin, was first reported to be resistant to the
woolly aphid, *Eriosoma lanigerum* (Hausm.). From time to
time other varieties of apples have been found to show this character and, according to recent experimental work, they still retain it.

The hessian fly, *Phytophaga destructor* (Say), was supposed to have been introduced into the United States in about 1776, and we find the first mention of the possibility of resistance to its attack in a winter wheat in 1785. Additional reports found throughout the literature can sometimes be shown to pertain to varieties which still are resistant in some localities. The first extensive observations were reported by Wickson (1886), Woodworth (1891), and Kellner (1892), who were working in California. Some of the wheat varieties which they reported still retain the same relative rank as to resistance or susceptibility in that state.

About the middle of the nineteenth century it was found that some of the American species of grapes were highly resistant to the grape phylloxera, *Phylloxera vitifoliae* (Fitch), while the European species, *Vitis vinifera* L., was very susceptible. This fact formed the basis for a method of control which is still the most important one today. Thus a number of early evidences of the importance and value of resistant varieties and their use in insect control have been confirmed by recent research.

**THE RELATION OF RESISTANCE STUDIES TO ECONOMIC ENTOMOLOGY**

Generalizations on a subject where much of the information is as new as it is in the case of insect resistance in plants must necessarily be tentative and based on present evidence as it can now be interpreted. In the first and most important place it should be acknowledged that insect resistance is not a cure-all, but must be fitted carefully to the control of specific insects and into the plant-improvement programs of particular crops. The development of resistant varieties usually requires a long period of controlled experiments and plant breeding. Hence insecticidal control and, to a lesser extent, other means must remain the first line of defense against injurious insects. On the other hand, results already secured indicate that the possibility of using plant resistance to insects richly deserves careful study for each major insect pest and many minor ones.

The intensity of resistance varies widely from crop to crop with
the associated insects. As a result of these differences in resistance
the use of resistant varieties falls roughly into three groups, namely,
(1) as the principal control method, (2) as an adjunct to other
measures and, (3) as a safeguard against the release of more
susceptible varieties than exist at the present time.

Resistant varieties as a principal control method. There are, in
the first place, cases in which insect resistance offers a major means
of control. Insects of which this is true sometimes have been those
that are practically plant parasites with high host specificity. This
is true in the case of some aphids and scales, and a few others.
That high host specificity is not a necessity for a high degree of
insect resistance is suggested by such examples as the relationships
of grasshoppers to corn and sorghums (Brunson and Painter 1938),
which has been repeatedly observed during grasshopper outbreaks
since 1878.

If sorghums are almost entirely avoided as food by such a
supposedly omnivorous insect as the grasshopper, is it surprising
that within a single host species important differences can be found?

An outstanding example of insect resistance as a major means
of control is the well-known case of the grape phylloxera, Phylloxera
vitifoliae (Fitch). Phylloxera-resistant grape vines were sent
about eighty years ago from this country to France. These vines
still form an important means of control for this insect. Dr. L. O.
Howard (1930) in his "History of Entomology" has reported
in dramatic detail the damage which the Phylloxera did in France
and the swiftness of economic recovery after resistant vines were
introduced.

"The alarm caused in France by the Phylloxera is difficult to
exaggerate. It had many disastrous effects. Aside from the abso-
late destruction of the vines as early as 1884 over a territory com-
prising 1,200,000 hectares, a monetary damage which was esti-
mated at 7,200,000,000 francs, there must be added the conse-
quent necessary importation of wine and of dried grapes to make
wine, which cost France over 2,800,000,000 francs, and the total
loss by 1884 of ten billion francs (two billion dollars).

"That this catastrophe should have occurred just when it did
was particularly insupportable. The Franco-German War began
in 1870, monopolized the whole strength of the French Empire,
and left the nation at its conclusion enfeebled to such an extent
and burdened with such a debt that this added crippled condition of one of her most flourishing industries was crushing.

"The whole world marveled at the rapidity of France's recuperation. Enormous indemnity to Prussia was paid in a marvelously short time, and it is safe to say that the discovery of the means of repairing the damage done by the Phylloxera and of restoring French wine culture to its former prosperous condition helped greatly not only to pay the enormous debt but to restore the confidence of the people, politically experimenting as they were with their new republican form of government." (Howard 1930.)

While the Phylloxera is one of the best examples of resistance as a major method of insect control, other examples are less well known or are being developed. Cotton is grown over thousands of acres in parts of Africa only because of the selection of a single plant that was resistant to leafhoppers of the genus Empoasca (Parnell 1935). The increase from this plant later became the variety U 4, which has not only made possible the growing of cotton in these localities but also led to further study and the development of other resistant, but better adapted, varieties there and elsewhere. The development of wheat varieties resistant to hessian fly in California, Kansas, and Indiana through the cooperation of state and federal entomologists and agronomists gives promise of removing this insect from the list of important pests (Annand 1947; Painter and Jones 1948).

Resistance as an adjunct to other control measures. It is as an aid to other control measures that insect resistance is most important and may be most commonly used. This use of resistant varieties involves careful coordination with other control measures on the one hand and with the crop-improvement program on the other. In the case of chinch bugs we apparently shall always need barriers, or other means where usable, for the protection of young sorghum and corn plants, but resistant varieties of these crops furnish almost the only practical defense against the second and third brood bugs as well as against the few that get by the barriers (Snelling et al. 1937; Holbert et al. 1933). Used in this way as a control measure, resistant varieties affect a period in the life history of the chinch bug that can be reached economically in no other manner.

Resistant varieties may have their use in connection with companion crops or cover crops in orchards. Crops of wheat, oats, or
other plants are sometimes used as protection for young legume
seedlings and such companion crops may provide a source of infe-
tation for commercial fields of the same crops nearby. A hessian
fly resistant wheat variety will make an important contribution in
this regard. Balbo rye, because of its near-immunity to the same
insect may be used where adapted for early fall and spring pasture
in place of wheat. Certain kinds of cover crops, because of their
lower susceptibility or attractiveness to plant bugs (Miridae) of
the genus Lygus, are better cover crops for orchards than others
(Venables and Waddell 1945). These fields of use have not been
sufficiently exploited.

In addition to resistance to insect attack as an adjunct to other
means of insect control there is an excellent possibility that it may
aid in the control of some of the diseases that are carried by insects.
In the breeding for the resistance to the aphid, which carries mosaic
of raspberries (Schwartz and Huber 1939), a measure of control
of the disease has been obtained as well as control of the insect.

Reducing chance of release of susceptible species or varieties of
plants. A third group of possibilities for the use of resistant
varieties consists of studies which serve to prevent the distribution
of new varieties and species that are more susceptible to various
insects than those currently grown. Insects concerned in this group
are often those capable of feeding on a wide range of hosts which
sometimes show only a low level of resistance.

All corn varieties thus far studied can be destroyed by grass-
hoppers if these insects are sufficiently plentiful; yet there are differ-
ences in extent of injury by grasshoppers to corn varieties and
hybrids which are highly significant and may under many circum-
stances mean the difference between good yield and crop failure
(Brunson and Painter 1938). Surely there are places where it is
worthwhile to consider resistance to grasshoppers, where such in-
formation is available, in the choice of inbreds and hybrids for in-
crease and distribution, even though we may not list grasshopper
resistance in corn as a control measure of value comparable to
poison bait or other insecticides.

Grasshoppers as well as most other insects always take a small
toll, perhaps 10 per cent, of a crop before it becomes profitable
to use chemical control. Resistant varieties even of a very low
level of resistance may be used to prevent or reduce this small
amount of injury or to reduce the number of years in which it occurs.

In the field of soil conservation many new varieties and species are being introduced or studied, including strains of native grasses. It appears highly important that these should be tested with at least the more important insects to which they might be susceptible in order that species and varieties of plants that will increase our troubles from these pests may not be recommended. Some such information on native grass species is available for a few insects (Jones 1939; Hays and Johnson 1925) but more is needed.

In the use of crops which show only a low level of resistance instances may occur in which insecticidal and other means of

Fig. 2. Comparative defoliation of two strains of a Eurasian species of bromegrass *Bromus inermis* Leyss., by grasshoppers principally *Melanoplus mexicanus* (Sauss.), Manhattan, Kansas, August 1949. Left, the variety Martin, from Minnesota, that has the leaves stripped from the stems; and right, the variety Lincoln, from Nebraska, which does not have the leaves stripped from the stems. (Courtesy Dept. Agronomy, Kansas State College, and K. L. Anderson.)
control might be successful with moderately resistant varieties but not with susceptible ones.

**RESISTANT VARIETIES AND OTHER PHASES OF ENTOMOLOGY**

Relationship of resistant varieties to general population levels of insect involved. In addition to the three groupings discussed above there are several other points at which the use of insect-resistant plant varieties touches the field of economic entomology. For instance, it has been shown that varieties on which insects feed may exert a large influence on their fecundity and on other phases of their life history (Painter 1936). Chinch bugs raised on various kinds of seedlings laid about 18 times as many eggs on Dwarf Yellow milo, a variety of grain sorghum, as on Atlas sorgo, a variety of forage sorghum, and about 25 times as many on Manchuria barley as on Kanred wheat (Dahms et al. 1936). Differences such as these, although known to be less pronounced on more mature plants, may easily affect the general population level of an insect when a resistant variety becomes sufficiently abundant. Atlas sorgo was released by the Kansas Agricultural Experiment Station in 1928 and, because of its chinch bug resistance and other desirable qualities, has largely replaced other sorghums in eastern Kansas. One might, therefore, expect an effect on the chinch bug population level. But in this same period the winter barley acreage has likewise increased, and two wheat varieties, Kawvale and Tenmarq, which may be more susceptible to chinch bugs than are older varieties (Jones 1937), have been distributed. Thus the possible effect of Atlas sorgo on the level of chinch bug population may have been largely counteracted by other known crop and varietal shifts. This illustrates the complexities of the problem and also its possibilities. Not only may one crop and one insect be controlled but where alternate hosts are involved, there is a possibility of influencing the insect-population level in one crop by planting resistant varieties of an alternate host. The use of crops to fight chinch bugs is a well-known means of control (Flint and Burlison 1920). Isely (1935) has pointed out the relation of hosts to abundance of bollworm, and Sanderson (1939) has studied the relation of different crops to the abundance of the grasshopper, *Melanoplus differentialis* (Thos.). In a study of the relation of
hosts to abundance of the bollworm, *Heliothis armigera* (Hbn.), in South Africa, Parsons et al. (1938) found that larvae, bred on a purplish-flowered variety of chick pea (*Cicer arietinum*), gave rise to small lightweight pupae and small moths that produce few eggs. Those reared on the ordinary white-flowered variety of the same crop are large and prolific and the larval survival is high. This crop is one source of the bollworms that infest cotton. The possibilities in influencing the population of the bollworm are evident. Eichmann and Webster (1940), in a study of the relationship of pea aphids to alfalfa and canning peas, pointed out that severe infestations of the latter crop are derived from alfalfa. It was found that Ladak alfalfa was resistant in Washington as had previously been reported to be the case in Kansas (Painter and Grandfield 1935), where this variety was released for use by farmers in 1937. Eichmann and Webster suggest the use of resistant varieties of alfalfa for the control of pea aphids on peas. Studies in Kansas and at other stations have resulted in the isolation of several strains much more resistant in laboratory tests than is Ladak (Dahms and Painter 1940), and progress in this control of an insect on two crops by the use of resistant varieties on one may become an actuality in the future.

**Relationship of resistant varieties to biological control.** There appear to be only a few cases on record in which a study has been made of the influence of plant host on insect parasites or predators by way of the insect host. Landis (1937) working with the insect predators *Podisus maculiventris* (Say) and *Perillus bioculatus* (F.) (Hemiptera, Pentatomidae), reared on four different insect hosts, found wide differences in the rate of development and mortality depending on the insect host used. One of these hosts, the Colorado potato beetle, *Leptinotarsa decemlineata* (Say), was reared on six different species of *Solanum*. Mortality of both species of the pentatomid nymphs was greatest when the beetle larvae fed on *S. carolinense*. Beetle larvae fed on *S. atropurpureum* appeared more toxic to *Podisus* than to *Perillus*.

Diverse effects are reported in the available data concerning relationships between plant and insect parasite by way of the intermediate host insect. The behavior response of a parasite to the food plant of its host in finding that host is well known (Thorpe and Caudle 1938), but little information appears to be available
INTRODUCTION

concerning the parasite's reaction to different plant varieties used by the host. Simmonds (1944) has shown that the lemon, in comparison with the orange, as a host for the California red scale, Aonidiella aurantii (Mask.), has an inhibiting effect on the development of the parasite Comperiella bifasciata How. A similar situation is involved in the relationship of the Sago palm and citrus to these same insects (Flanders 1942) and contributed to the failure to establish the parasite in California for 35 years. In this and an earlier paper Flanders (1940) discussed other and similar cases. Bradley and Arbuthnot (1938) record the observation that variations in host habits may produce life cycles of Chelonus annulipes Wesmael of several different durations. Seams and McMillan (1935) have shown that on unfavorable food plants parasitized larvae of the pale western cutworm died before pupation.

The information available indicates that the relationship between resistant varieties of plants and the insect parasites of the pests affected by the plant resistance may take two or more trends. First, reduction in the population level of the insect hosts might make it difficult for the parasites to find them and, thus, would have an adverse effect on biological control by parasites. Second, the profound effect on the physiology of the host which may result from feeding on resistant plants might affect the establishment of insect parasites favorably, or unfavorably. Again the effect of resistant plants on host size would influence the prolificacy, size, and perhaps sex of the insect parasite (Flanders 1936, 1939, 1940). Thus any relationship between resistant plant varieties and insect parasites cannot be predicted with certainty beforehand but will need to be worked out in each individual case.

Relationship of resistant varieties to chemical control. There has been a growing volume of evidence of the relationship between food, including resistant plant varieties, and the efficacy of chemical control measures. It has been reported (Phillips and Swingle 1940) that mosquito larvae vary from almost complete susceptibility to complete resistance to rotenone and nicotine in accordance with their previous diet. Compton and Kearns (1937) have stated that "great variation in the susceptibility of red spider to certain sprays has been shown to be closely correlated with the species of plant infested." Swingle (1939) has reported that the percentage of kill by lead arsenate in the case of a leaf-feeding
insect varied from 0 to 98 per cent in accordance with the previous diet of the insect.

Malenotti (1935) has reported that the mortality of the coccid *Epidiaspis leperii* from three different insecticides was lower on pear than on peach. Markos and Campbell (1943) studied the effect of host plant on the susceptibility of the southern armyworm to calcium arsenate and showed that the high mortality from the insecticide when the insect was fed on rhubarb might be concerned with the presence of oxalic acid in the cells of this plant. The mortality resulting from the insecticide was much lower when the insect had been fed on squash, corn, or soybean than when it had been fed hollyhock, kale, rhubarb, or cranberry bean. McGowan and Gendorff (1945) reported that the mortality of flies when treated with insecticides containing DDT and pyrethrum varied according to the food on which they had been reared. Some recent papers (Sleesman and Bushnell 1945, Wilson and Sleesman 1947, and Linn, Apple, and Arnold 1948) suggest that leafhoppers may be easier to control, when necessary, on host potatoes that are resistant to leafhoppers than on those that are susceptible. These effects do not concern the equally important character of pilosity of the plant and its relation to the adherence of dusted arsenicals, as has been studied in cotton by Dunnam (1936). These various data strongly suggest that the combination of chemical control and resistant varieties may prove more effective when control cannot be obtained by either method alone. Such control may come about either through the independent, though cumulative, effect of the two methods or through some effect of the resistant variety on the physiology of the insect, making it more easily killed by the insecticide. Such many-sided aspects of the relation of plant varieties to entomology indicate that they should be studied more widely. The rearing of herbivorous insects for the study of their biology should be done primarily on known varieties of plants. Not to do so is in the same class as is not giving the correct scientific name of the insect being studied. With somewhat less emphasis, the same may be said of some aspects of chemical control. Furthermore, no well-rounded control program for an important plant-feeding insect is complete unless it includes the search for and the study of resistance to the insect concerned.

1 The Italian pear scale, *E. piricola* (Del Gue).
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RELATION OF INSECT RESISTANCE TO OTHER PLANT-BREEDING PROBLEMS

The position of the study of insect resistance in relation to plant breeding is comparable to that of its relation to insect control.

**Where insect resistance takes precedence over other breeding problems.** There are occasions in which breeding for insect resistance takes precedence over breeding for yield or other agronomic qualities. These are mostly cases in which the insect is the limiting factor in the distribution of a crop. Until recently, for example, the commercial production of sweet corn in the south was prevented because of the severe damage done by the corn earworm, *Heliothis armigera* (Hbn.), to ears of varieties being grown at the time. New sweet corn varieties which have recently become available as a result of insect-resistance studies can be grown commercially in the southern states because these strains have resistance to this insect. While some of these sweet corns do not have as high a quality as the best northern sweet corns, the major step in improvement has been taken (Magoon *et al.* 1945).

In a like manner chinch bugs are a limiting factor in the commercial production of spring barley and of milo and related sorghums in eastern Kansas and neighboring states. The crops named are mainly confined to the western section of the state because of the frequent abundance of chinch bugs in the eastern part (Snelling *et al.* 1937, see maps p. 7). This problem presents the possibility of solution by means of resistant varieties because although barley varieties are known to differ in their susceptibility to chinch bugs, no sustained attempt has been made so far to use this method of control in this crop. In the case of the sorghums some progress has already been made toward more chinch bug resistant types.

Insects may often be an unsuspected factor in curtailing yield in a crop. The recent use of the new insecticides against the leafhoppers on potato has been an important factor in the increased potato yield in 1947 and 1948; but data presented in a paper by Linn, Apple, and Arnold (1945) have shown that in parallel tests a resistant variety, Sequoia, had almost as good a yield as did some of the susceptible potato varieties when these were protected by insecticides. Yet Sequoia appears to be only a moderately resistant
variety compared to unnamed strains that have been studied. It is frequently impossible to assess the damage done, especially by a sucking insect, unless the crop can be grown almost or completely free from insects or damage, side by side with injured plants. If such examples were better known perhaps there would be more cases where insect resistance would become of major concern to plant breeders.

Insect resistance as a normal part of a plant-breeding program.

More frequently insects are only one of the limiting factors in preventing high yields, high quality, or both, in a crop. As such they deserve a consideration along with plant disease, susceptibility to drought, cold, or other factors in the environment. If resistance to these other factors is considered in a breeding program resistance to insects should also be sought in the plant-breeding program. There are two ways in which this has been done. A definite breeding program may be set up in which world-wide collections of varieties and related species are examined for the presence of genes conferring resistance to insects. These genes, when found, may be incorporated into the commercial crop by standard plant-breeding methods. This type of a program, involving resistance to hessian fly in wheat in Kansas and elsewhere, has produced varieties and hybrids that are used by farmers and by plant breeders of neighboring states. This type of a program often should involve all the major insects of a crop rather than a single one.

The second and more common approach has been a testing program concerned with material in use by the plant breeder in connection with other problems. From the standpoint of insect resistance such a testing program has less promise and therefore is of less interest to the entomologist. It should provide information to prevent the distribution to farmers of varieties more susceptible than those now grown, but unless appropriate genes happen to be in the material being studied, there is little likelihood of achieving much insect control. The work on earworm resistance at the Kansas Agricultural Experiment Station has been such a testing program. In 1939, after 15 years of such testing all the hybrids Experiment Station in the corn-performance tests had less earworm injury than any out-of-state or commercial hybrid in the test. But it is believed that a higher degree of resistance could have been secured through the study of a wider range of corn types than were currently available. Most plant breeders to some extent do select
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for insect resistance, either unconsciously because the insect affects the yield, or consciously from a knowledge of conspicuous differences in injury among strains being studied. With the help of a properly trained entomologist such a selection program can be systematized and accelerated. A testing program should, however, be set up in connection with new varieties before they are offered to farmers. A crop variety highly desirable in other respects may have hidden susceptibility to an insect heretofore of little consequence. Such a variety may reflect adversely on the organization sponsoring it. The distribution during the 1940's in the central United States of rust-resistant oat varieties, which later proved to be highly susceptible to the then little-known Victoria Blight, suggests what might occur if an insect replaced a disease as the pest to which a new variety was susceptible. The breeding of plants for resistance to insects deserves consideration in any well-thought-out program of crop improvement.

THE NATURE OF THE PROBLEMS AND THE RELATIONSHIP OF ENTOMOLOGIST AND PLANT BREEDER

In plant breeding the pursuit of any one genetic character such as insect resistance, without continual attention to others, may quickly make a strain of little use. Obviously the entomologist is poorly equipped to consider all these other characters by himself. Likewise, the complexities of insect life history, behavior, physiology, and taxonomy render the task of breeding for insect resistance a difficult one for the plant breeder alone. Such research, as has been pointed out in connection with the woolly apple aphid, is "A Case for Team Research" (Hatton et al. 1937). The plant breeder, agronomist or horticulturist, and entomologist, are the basic members, but for an understanding of the mechanism of resistance, the plant and insect physiologists and biochemists should also be members of the team. This will necessitate cooperation between these groups, a matter which has been discussed by Parker and Painter (1937), Snelling (1941), and by others. Despite the human problems involved in team research many of the outstanding accomplishments in breeding for insect resistance have come as a consequence of it. Especially notable, but not the only cases, have involved the woolly apple aphid, corn insects, and wheat insects.

Formal written agreements can facilitate such team work and
may be administrative necessities, but real success depends on sharing work as well as credit, and on the true meeting of minds in the field plot, the laboratory, or greenhouse as well as about the conference table. The workers require a broad biological background with particularly an understanding of the problems and possibilities in the others' field of work. For the plant breeder this includes not only some appreciation of insects and their possible destructive-ness, but also some understanding of the interrelationships of insects in their various stages with plants. For the entomologist it involves particularly a genetic point of view, that is, the ability to appreciate the genetic possibilities of events seen in field and laboratory. The average entomologist, who usually is better trained in ecology than genetics, has been prone to explain variations in injury to plants in terms of the environment when a genetic explanation is equally possible. Only progeny tests and experiments will determine which is correct. This lack of genetic viewpoint on the part of entomologists has been one reason for the slow acceptance of insect resistance as a means of insect control.

REVIEWS AND BIBLIOGRAPHIES ON RESISTANCE TO INSECTS

Reviews have been published of various fields of insect resistance in plants and related subjects. Some of these contain bibliographies of importance. These include papers by Bigger et al. (1943), Brues (1946), Csenokov (1940), Dahms and Fenton (1939), Drain (1944), Felt and Bromley (1931), Flint (1936), Flint and Bigger (1938), Forbes (1909), Graham (1929), Hunter and Leake (1933), Imms (1937), Isely (1941), Koch (1933), Leach (1940), Lees (1926), Lockhead (1918), Malenotti (1935), Martin (1940), McColloch (1924), Mumford (1931), Painter (1936), Parker and Painter (1932), Platt and Farstad (1941), Roemer et al. (1938), Snelling (1941), Snelling et al. (1941), Sweetman (1936), Trehener (1917), Trouvelot (1939), Vavilov (1935a, 1935b), Wardle (1929), and Wardle and Buckle (1923).

The paper by Snelling (1941) and the bibliography "Insect Pest Resistance in Plants," published in 1944 by the Imperial Bureau of Plant Breeding and Genetics, contain many of the references to papers on the subject. Together they represent well over 800 references that are not duplicates. The bibliographies and some of
DEFINITIONS

Some of the terms used in describing kinds and degrees of resistance have been defined (LePelley 1927; Wardle 1929; Mumford 1931; Painter 1936, 1941; Snelling 1941) and some of the ideas expressed have been used in the definitions given below. Such terms are bound up with the classifications and causes or factors responsible for resistance. The latter will be treated in detail later. Two points, however, need to be emphasized. In the first place, resistance is a phenomenon concerned with the interaction of the plant and insect, and may be examined or defined from the standpoint of either or both. In the second place, in most cases studied resistance has been relative. The resistance of a variety is definable only in terms of other and usually more susceptible varieties. Any division in respect to the level of resistance or susceptibility usually is purely arbitrary.

Resistance of plants to insect attack may be defined as the relative amount of heritable qualities possessed by the plant which influence the ultimate degree of damage done by the insect. In practical agriculture it represents the ability of a certain variety to produce a larger crop of good quality than do ordinary varieties at the same level of insect population.

The degree of resistance in general, as applied to the interrelation between a specific insect and varieties of a particular species or group of species of host plants, may be classified as follows:

Immunity. An immune variety is one which a specific insect will never consume or injure under any known condition. Thus defined, there are few, if any, varieties which are immune to the attack of any specific insect known to attack varieties of the same plant species. A few varieties which approach this degree of resistance will be discussed later.

High resistance. A variety with high resistance is one which possesses qualities resulting in small damage by a specific insect under a given set of conditions.

Low level of resistance. A low level of resistance indicates the possession of qualities which cause a variety to show less damage or infestation by an insect than the average for the crop under consideration.
Susceptibility. A susceptible variety is one which shows average or more than average damage by an insect.

High susceptibility. A variety shows high susceptibility when much more than average damage is done by the insect under consideration.

The terms indicate the way in which they are used by most workers in insect resistance and as seen in the field, without analysis of the mechanisms involved. An intermediate level of resistance is sometimes spoken of as moderate resistance. This may result from one of at least three situations. A variety which is called moderately resistant may have such a level because it consists of morphologically similar plants, some of which have high and others low resistance because of differences in physiological characteristics. In contrast a moderately resistant variety may be made up of plants derived from a single clone, which is heterozygous for incompletely dominant genes that confer high resistance when homozygous. Moderately resistant plants also may be homozygous for genes which under given environmental conditions produce such a level of injury or infestation. Thus, the wheat variety Pawnee shows moderate resistance to the hessian fly, *Phytophaga destructor* (Say), in central Kansas and this level of resistance can be recovered in hybrids involving this variety as one parent.

Certain phenomena which are related to resistance may be defined and classified as follows:

Pseudoresistance. This term may be applied to apparent resistance which is the result of transitory characters in potentially susceptible host plants. Varieties or crops showing pseudoresistance are of considerable importance in economic entomology but should be distinguished from varieties which show resistance throughout a wider range of environment. Three types may be distinguished.

1. Host Evasion. Under some circumstances a host may pass through the most susceptible stage quickly or at a time when insect numbers are reduced. Some varieties evade insect injury by early maturity and this factor has been made use of to good advantage in economic entomology. Late planting of an early maturing variety or other special experiments will indicate whether true resistance is present.

2. Induced Resistance. This term may be used for the temporarily increased resistance resulting from some condition of
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plant or environment, such as a change in the amount of water or soil fertility. Such induced resistance may be of great value, especially in the field of horticulture, but should not be confused with inherent differences in resistance which exist between varieties or individual plants.

(3) Escape. Escape refers to the lack of infestation of, or injury to, the host plant because of transitory circumstances such as incomplete infestation. Thus the finding of an uninfested plant in a susceptible population does not necessarily mean that it is resistant. Even under very heavy infestations susceptible plants will occasionally escape and only studies of their progenies will establish their true relationship.

The definitions given above are equally applicable to other animal pests of plants, such as mites and nematodes. However, the analyses given in the two chapters which follow are only partially applicable to such animals.

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CHAPTER II
THE MECHANISMS OF RESISTANCE

I. Introduction.
A. The "why" of resistance always excites comment.
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C. The threefold basis of resistance as seen in the field; definitions.

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   (1) Insects with mouth-parts fitted for chewing.
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IV. Tolerance.
A. General vigor and heterosis in relation to tolerance.
B. Replacement, regrowth, and repair of tissue.
   (1) To injury of biting insects.
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C. The strength of plant tissues in relation to tolerance.

V. Unclassified resistance mechanisms.

VI. Criteria for evidence of cause of resistance.
A. Introduction: Usually not one but several causes.
B. Evidence must be provided of an intimate relation between cause of resistance and plant and insect physiology or insect behavior.
C. The assigned cause must show complete association with a given genetic factor wherever found and especially in segregating populations.
   (1) Possible genetic relationships between cause and resistance.
D. Statistical evidence of the cause of resistance.
E. Breeding for insect resistance has been done successfully without knowing cause.

VII. Bibliography.

Insect resistance as defined in the preceding chapter is that which is observed in the field. This is also in parallel with the usage of the plant pathologists (Reddick et al. 1940) who have developed the study of plant disease resistance. Visiting administrators, entomologists, or plant breeders when shown plots demonstrating the effectiveness of insect resistance, most frequently ask: “What is the cause of this resistance?” In answer it can only be said that progress is being made in finding out the cause of resistance but that, so far, experimenters have been able to utilize insect resistance in crop improvement and insect control without complete knowledge of the reasons why the plants are resistant. While first studies sometimes indicate a simple explanation of resistance, later ones are likely to point toward a more complex relationship between plant and insect, especially when all resistant varieties are studied. The hairiness of legumes and other plants, for instance, was early indicated as a basic factor in resistance to leafhoppers (Hollowell et al. 1927) but later investigations have shown that, in some cases at least, hairiness accounts for only part of the resistance (Jewett 1932; Poos and Smith 1931; Johnson and Hollowell 1935). Hence, one must frequently deal
with a number of causes or mechanisms which result in resistance rather than with a single factor, and in attempting to breed resistant varieties a knowledge of these mechanisms may sometimes be of little use. Even if the cause of resistance is a single compound the chemical analysis of a thousand individual plants probably would take longer than a properly designed entomological test on a larger number of plants. The insect involved must always be the final judge of whether a new variety, selection, or hybrid is really resistant.

Attempts to classify cause of resistance. There have been several attempts to classify the reported causes of resistance. The classification by Mumford (1931) as "epiphyaxis" and "endophylaxis" is of little practical use. The 15 categories used by Snelling (1941) in classifying the plant characteristics suggested in the literature as having an influence in resisting insect attack indicate the wide variety of factors that may be involved. Painter (1936, 1941) has attempted to work out a classification of those items suggested as "cause" of resistance so as to emphasize the insect-plant interrelations that are a feature of insect resistance. This classification is indicated in the accompanying diagram. The various environmental factors may act primarily on the insect, the plant, or the insect-plant relationship (Fig. 3).

The threefold basis of resistance as seen in the field. The analysis that has been of maximum usefulness, however, has been one which divides the phenomena of resistance as seen in the field into three bases or mechanisms. Of these, one or a combination of any of the three is present in most cases of resistance that have been studied sufficiently. The three bases are interrelated as indicated in the diagram:
Fig. 3. The insect-plant interrelations of various items that have been suggested as "causes" of resistance. The various environmental factors may act primarily on the insect, the plant, or the insect-plant relationship.
If a variety is not preferred, lower degrees of tolerance and antibiosis are required; if a variety carries low preference and considerable antibiosis, less tolerance is required.

Preference or non-preference is used to denote the group of plant characters and insect responses that lead to or away from the use of a particular plant or variety, for oviposition, for food, or for shelter, or for combinations of the three. Anthropomorphic connotations should not be read into this terminology.

The term antibiosis is here used in its usual sense as the tendency to prevent, injure, or destroy (insect) life. It was proposed (Painter 1941) for those adverse effects on the insect life history which result when the insect uses a resistant host-plant variety or species for food. The effects on the insect take the form of reduced fecundity, decreased size, abnormal length of life, and increased mortality. The latter appears usually in the first instar or in those stages just preceding the adult stage. Various combinations of these effects result from feeding on different resistant varieties.

Tolerance is a basis of resistance in which the plant shows an ability to grow and reproduce itself or to repair injury to a marked degree in spite of supporting a population approximately equal to that damaging a susceptible host. This basis of resistance frequently is present along with other types of resistance in a single variety; in such cases it is evident under an extremely heavy insect infestation, upon changed environmental conditions which obscure other types of resistance, or upon genetic analysis of hybrids between the resistant variety and a susceptible one.

This basic triad of resistance relationships usually has been found to result from independent genetic characters which, however, are interrelated in their effects. A variety that is not preferred does not require the degree of antibiosis or tolerance that must be present in a preferred variety of the same level of resistance. A plant that exhibits high tolerance and low antibiosis toward a given insect may show the same level of resistance as one that has a high degree of antibiosis and an average degree of tolerance. In any given variety genes for one or more of these characteristics may be present but sometimes others will be found in other varieties. The possibility of cumulative resistance by recombinations of genetic factors for different types of resistance thus is introduced. This type of recombination is in addition to possible multiple genetic factors in the plant which may lie at
the basis of any one of the three characteristics. The expression of the genetic factors resulting in these three characteristics is frequently modified by various ecological conditions and by other genes. A discussion of the insect and plant bases of preference, antibiosis, and tolerance will be attempted in this chapter in the light of our present, often scant, knowledge. An analysis of some of the ecological and genetic factors modifying resistance will be given in a later chapter.

The separation of pseudo-resistance from true genetic resistance, and the determination of the approximate proportion of resistance due to each of the three characteristics indicated above is of early and primary importance in any serious study of resistance.

PREFERENCE AND NON-PREFERENCE

A knowledge of the ways in which insects locate plants for shelter, food, or oviposition involves a study of the behavior of such insects in the presence of various stimuli derived from the plants. The finding of food plants sometimes may involve only chance (Broadbent 1949), but choice of plants from a distance by insects ordinarily is at first a result of trial and error, or the chance happening within range of the stimuli from the preferred host. Such stimuli are usually not single but take the form of chains of conditioned responses (Kennedy 1927; Richardson 1925; Uvarov 1933), each corresponding to a separate stimulus. Any break in the chain throws the insect back on chance as a means of finding food. The lack of such stimuli or the presence of counteracting repellent or distracting stimuli constitutes the phase of resistance referred to above as "preference and non-preference."

Insect behavior as a basis for preference. Insects have been favorite subjects for the experimental or observational study of behavior but for the most part these studies have had only indirect bearing on insect resistance in plants. The most suggestive studies have concerned the reaction of insects to closely related species of plants rather than varieties. Interpretations of preference therefore must be made with the aid of only meager knowledge and are suggested as bases for future study rather than as complete interpretations.

Factors conditioning preference. The finding by insects of plants for food or for oviposition may be a response to the same stimuli or to different ones. In the case of most insects with incomplete
metamorphosis and also in the case of many beetles the same plant serves as food for both young and adult. Hence the attraction of the adult for food or oviposition may result at least in part from the same stimuli. This is rarely true of those insects belonging to the Orders Lepidoptera, Hymenoptera, and Diptera. Here the adult generally feeds on nectar and other plant juices, quite different from the food of the larvae. With the maturing of the gonads the adults, particularly the females, respond to a different set of stimuli, which result in bringing them for oviposition near the plants on which the young will feed.

The use of parts of plants for shelter, largely in response to mechanical stimuli, may modify results from other stimuli. The onion thrips, *Thrips tabaci* Lind, shows a preference for varieties of onions with flat leaves, which offer shelter for the insect where the leaves come together (Jones et al. 1934). A number of insects, such as the walnut caterpillars and other species of *Datana*, normally feed in groups or colonies. This gregariousness may modify other responses, including those to food plants. Other behavior patterns affect the food-finding of insects. Many leaf-feeding insects show a negative geotaxis, climbing upward whenever they are removed from their food plant. Caterpillars and some other insects show reactions to shapes or forms of objects (Fraenkel and Gunn 1940) orienting in the direction of fairly distinct dark-light boundaries. Both these reactions often serve to place the insects on or in the neighborhood of their food but have little to do with resistance mechanisms.

Responses to color and intensity of light, to contact with surfaces of the plant, and to chemical constituents of the plant are the chief means by which insects find their plant host. As such they are the chief characteristics of the plant which may be modified genetically and hence give rise to resistance by way of a lack of response to the plants possessing the modification.

**Preference differences as a response to colors or intensity of light.**

One of the most common observations concerning insects is that they respond to light in various ways. Cockroaches scuttle into dark corners when a light is turned on at night. Many moths, leafhoppers, and other insects congregate at various lights. But when the behavior of insects with respect to light is analyzed carefully, different responses are found to the different physical attributes of
light: direction, intensity, wavelength or color, and in some cases the direction of the oscillations of polarized light (von Frisch 1949).

Weiss (1943, 1944, 1945) has reviewed the available information on the responses of insects to color. Much work on color responses has been done in studying the relation of insects to flowers (Clements and Long 1923; Knoll 1921-1926). The experimental studies have involved the training of certain species of insects to associate color with food (von Frisch 1937) and recording responses to direct light of different wavelengths (Milne and Milne 1944). In contrast, response of insects to plants involves reflected light and the character of the surface from which it is reflected.

Insects as a group react positively to a wide range of wavelengths from about 3600 Å. (ultraviolet) to 7200 Å. (red). Weiss and his co-workers (Weiss et al. 1944) have tested in the laboratory the responses to different wavelengths of over 15,000 insects in more than 50 different species from several orders. They found generally that under equal physical intensities the peak sensitivity is produced by stimulation by wavelengths in the ultraviolet of about 3650 Å. Insects also responded somewhat less strongly to the stimulus of wavelengths from 4920 to 5150 Å. (blue-blue-green). The other wavelengths were relatively unattractive under conditions of the tests; the yellow and red parts of the spectrum caused the least response. Certain species of insects often did not distinguish between red and black.

Differences have been shown by various species of insects in respect to the specific wavelengths to which they will respond. The response also changes with the physiological state of the insect. Götz (1938) states on the basis of his own and others' experiments that lepidopterous larvae tend to depend on sight and differentiation of shapes rather than smell or taste as a means of finding food. He also reports (Götz 1936) that caterpillars of the butterflies Vanessa io (L.), V. urticae (L.), and Pieris brassicae (L.) are attracted to green pieces of paper during the feeding period but fail to respond in that manner when they are ready to pupate. Ilse (1937) reported that during the egg-laying period females of Pieris brassicae (L.) flew to leaves of various plants and gave a drumming reaction with the first pair of legs. This same reaction, often a prelude to oviposition, is elicited by cards of certain colors ranging from emerald green to greenish blue, but not by yellow.
cards. During its egg-laying season a species of hawkmoth is attracted by green, visits yellow as well, but neglects the bluish-green cards. Knoll (1921–1926) reported that the hawkmoth *Macroglossa stellatarum* L., when feeding, could be attracted to paper flowers of various colors. When ready to lay eggs the female could be attracted to green paper and would oviposit on green objects moistened with sap from the food plant. Thus in this case at least a color stimulus and a chemical stimulus are required for the completion of oviposition.

Chopra (1925), working with a moth, *Glyphipteryx fischeriella* Zell., that in the larval form feeds on seeds of *Dactylis glomerata*, cocksfoot, or orchard grass, found that strains of the grass native to the British Isles were infested more heavily than strains from other countries. The differences appeared to result from differential oviposition, which may have been correlated with differences in foliage color.

In the development of effective traps for the adult Japanese beetle, reactions to color as well as to odors and repellents have been studied. Japanese beetle traps consist of a container for the trapped beetles, surmounted by a funnel. In the center above the funnel is placed the attracting bait, consisting largely of geraniol. Above the funnel are placed two baffle plates, set at right angles to each other so that beetles flying toward the bait strike the baffles and fall through the funnel into the container. Langford *et al.* (1940) reported that such traps in Maryland in 1939 caught more than 1,737 barrels, or 104 tons, of beetles. The effect of differences in color on the number of beetles caught in the traps has been studied (Fleming *et al.* 1940). These men report that with traps painted different colors about the same number of beetles was attracted to each, but that with some of the colors more of the beetles avoided flying into the baffle. This suggests that a beetle is better able to discern and avoid obstacles of some colors than of others. The average seasonal indices of effectiveness for traps covered with various paints were: aluminum, 50.6; red, 78.4; dark blue, 88.6; white, 97.0; yellow, 150.8. These figures indicate something of the relative reaction to colors by this beetle.

The yellow-green varieties of peas are more resistant to the pea aphid than the blue-green varieties (Searls 1935; Cody 1941). Fewer aphids are found on the yellow-green varieties. Red-leafed cotton has been reported (Isely 1928) to be more resistant to the
boll weevil than at least some of the green-leafed varieties. From what is known of the lack of response of insects to yellow and red, it seems quite possible that in these cases the insects concerned simply do not "see" the yellow-green or red-leafed varieties, finding them partly by chance; if that is so, leaf color in these cases is a part of the mechanism of resistance. On the other hand, Harrison and Brubaker (1943) report that in each of three years the infestations of both the cabbage looper, _Trichoplusia ni_ (Hbn.) ( _Autographa brassicae_ (Riley)) and the imported cabbageworm _Pieris rapae_ (L.) were higher on the red- and purple-leaf varieties of cabbage as a group than on the green varieties. There are no critical data in any of these experiments regarding the real importance of the color.

A chlorophyll-deficient "golden" mutant strain of corn and a red-leafed strain of corn have been tested for resistance to migrating chinch bugs (Call 1927). Both proved highly susceptible, the susceptibility being due to a lack of tolerance. Celery varieties with green leaves and stems have been observed (MacLeod 1933) to be more resistant to injury by the tarnished plant bug than varieties with yellow color. This case of susceptibility, like that of the chinch bugs and corn, probably is a case of lack of tolerance rather than of differences in response of the insect to color.

Evidence presented by Weiss (1943, 1945) and the work of others which he reviewed indicates that the responses of insects to different wavelengths may in reality result largely from response to differences in light intensity or to differences in the absorption of light by the primary photosensitive substance of the visual sense cells. While there are differences in the precise color, including ultraviolet, reflected from leaves of species and varieties of plants, there may be wider differences in intensity of light resulting from variations in the surface of the leaves (Popp and Brown 1936; Shull 1929). Hairs, waxes, resins, etc., on the surface of leaves may or may not increase the reflection from such leaves. Moore (1937) in studying the attraction of aphids to sprayed surfaces by means of experiments and special apparatus, showed that _Myzus persicae_ (Sulz.) was sensitive to changes in light intensity which result from spraying potatoes with Bordeaux mixture. The aphids tended to increase on the sprayed plants. In another series of experiments, cabbage was sprayed with lead arsenate treated with various dyes. The aphid, _Brevicoryne brassicae_ (L.) was found in greatest num-
ber (653) on the cabbages sprayed with uncolored, white insecticide. The smallest number of aphids (275) was found on plants treated with an insecticide that was black because of mixture with charcoal. Untreated cabbage had 429 aphids. Spray materials colored red and green had 507 and 623 aphids, respectively. The least significant difference was 66.9. Differences in intensity of light reflected from the sprayed leaves is considered to be the cause of the variation in the number of aphids.

Hairy varieties of legumes and cotton frequently have been reported to carry fewer leafhoppers than non-hairy varieties, and the relationship sometimes has been considered to be a mechanical one. It is possible that in some cases differences in the intensity of light reflected from the hairy and glabrous leaves may account for differences in the numbers of leafhoppers attracted to the respective varieties. The fact that there are fewer aphids on glabrous cotton than on more hairy kinds (Annand 1946) may likewise be the result of differential attraction of the aphids because of differences in light intensities reflected from the two sorts of leaves.

Preference differences as responses to mechanical stimuli from the physical structure and surfaces of plants. While differences in the surface structure of leaves result in differences in light intensities reflected and, on some occasions, differences in the responses of insects, such surface structures also elicit responses through mechanical stimuli. The mechanical stimulation is perceived chiefly through the effect on articulated spines and hairs which occur on many parts of the insects' bodies. The antennae and ovipositor, or structures connected with the ovipositor, usually bear a considerable number and variety of these hairs and setae. The continual palpitation of the antennae of many species of insects appears to be a part of the means by which they learn about their surroundings. Many structural differences in plant varieties have been reported to be concerned with resistance, but data presented are usually inadequate to show the relation of these plant-structural differences to the behavior of the insect.

The presence or absence of shelter for the insect has sometimes been of importance in resistance. Negative photokinesis may be concerned in the reaction but insects also tend to find shelter by bringing all possible parts of the body into contact with nearby surfaces. In connection with the resistance of onions to thrips it has been shown (Jones et al. 1934) that a small angle of contact
of leaves between which these insects prefer to live contributes to­ward an increase in the thrips population of the varieties possessing such leaves. Varieties with round leaves had smaller populations

![Image of onion fields and resistant varieties](image1.jpg)

**Fig. 4.** The resistance of onions to the onion thrips (*Thrips tabaci* Lind) is partly related to the angle of divergence of the two innermost leaves, and the distance apart of the leaf blades on the sheath column. In the suscep­tible Australian Brown (right) there is better shelter for the insects than is true of the resistant variety White Persian (left). (Jones, Bailey, and Em­sweller 1934; courtesy California Agricultural Experiment Station.)

which, however, could be increased by fastening the round leaves together to cause more extensive contacts between them (Fig. 4).

The varieties of sorghums differ greatly in the tightness with which the leaf sheaths cling to the stem. Chinch bugs congregate in numbers behind the loose-fitting leaf sheaths of the milo varieties,
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and this character contributes to the susceptibility of these varieties (Snelling et al. 1937). Such plant characters as these affect the behavior of the insect and in so doing the total resistance or susceptibility of the plant.

Entomologists are prone to consider, probably correctly, that odor is the principal character through which insects find their host plants. In connection with the importation of insects into Australia for the control of prickly pear many cactus-infesting insects have been tested for ability to feed on numerous species of economic plants. The results have been largely negative, but those who have done this work believe that the choice of a food plant by a prickly-pear insect has been governed neither by botanical relationship nor chemical characteristics, but by physical similarity (Hamlin 1932; Dodd 1936). The fruit of peaches, tomatoes, and other plant parts that correspond in general texture to that of the prickly pear were the structures picked by the cactus insects for feeding or oviposition if such occurred at all.

The hardness of plant tissue often has been cited as a cause of resistance. The relationship has been thought of as a mechanical prevention of feeding. The data have usually consisted of a small but significant correlation between resistant varieties and firmer tissue. There is considerable reason to doubt whether differences in tissue hardness between varieties of one plant species are large enough to affect the degree of feeding (Painter 1943) of an insect accustomed to feed on the species concerned. There is a possibility, however, that differences in attractiveness of surfaces associated with plant hardness or toughness may account for part of the correlations observed. Studies of insect behavior on varieties differing in such a manner appear to be lacking.

It is in the egg-laying response that reaction to mechanical stimuli is most likely to be a factor in resistance. The chain of reactions that end in the oviposition of an insect on a plant is often made up of reactions to reflected light or odor, or both, the terminal stimulus being contact of the ovipositor with the right kind of surface. If this final contact stimulus is not of the right kind, oviposition does not occur or is erratic. Currie (1932) has studied the stimuli which result in the oviposition of the cocklebur seed fly, Euaresta aequalis Loew, in the bur of Xanthium sp., its normal host. He found that the females would not attempt oviposition on burs of Xanthium from which the characteristic hooked spines had
been removed. On the contrary, in the absence of *Xanthium* they would attempt to oviposit in an artificial bur made from rubber and bent pins. The females would not oviposit on a flat surface, even when it was studded with hooked spines. Evidently the shape and size of the bur as well as the spines are required to elicit oviposition. The odor of the host only appears to keep the flies in the neighborhood of the plant.

Insects rather commonly place their eggs within the tissues of the plant host; hence the structures beneath the surface of the plant may enter into the oviposition response. Fulton (1925) has described two races of the snowy tree cricket, *Oecanthus niveus* (De-Greer), which differ in song, habitat, and manner of oviposition.

One race, which lives in trees, lays eggs singly in the cortex of twigs. The females of the other race in some way choose stems of bushes of such a structure that they are able to lay eggs in rows in the pith at the center of the small stems. Since numbers of different species of plants are used in each case, the stimulus for oviposition for the most part must be through contact.

There are a few cases recorded in which mechanical stimulus related to oviposition appears different in different plants or varieties. McColloch (1920) has recorded that corn plants with glabrous leaves received fewer eggs of the corn earworm than did corn with hairy leaves. In studies on resistance of oat varieties to *Oscinella frit* (L.) it has been found (Cunliffe and Hodges 1946) that resistant varieties received about one-third as many eggs as did susceptible ones. In a study of the stimuli affecting oviposition the authors found no evidence of response to light, and studies with an olfactometer were negative. They did find, however, that the amount of separation of the coleoptile from the young plant affected the number of eggs deposited, this being a response to a mechanical stimulus.

Preference differences as responses to chemical stimuli. The response of insects to chemical attractants and repellents in plants generally has been thought to constitute the chief mechanism of preference as a part of insect resistance. The book by Dethier (1947), "Chemical insect attractants and repellents," presents in thorough detail the available information on the general subject. It should be consulted by those working in insect resistance. There remains only the necessity of relating Dethier's information to this field. Most of the available studies concern insects known for their
strong attraction to specific highly odorous substances found in a
group of species of plants. Such have been the studies on the at­
traction of the butterfly *Papilio ajax* L. to the essential oils present
in certain umbelliferous and other plants, and the attraction of
species of cabbage butterflies (*Pieris*) to mustard oil in different
species of the mustard family (Brassicaceae). Even with these
favorable subjects our knowledge is far from complete. There is
less information available on substances responsible for differences
in odors between plant varieties differing in attractiveness to insects.
However, because of the behavior of the insects these are presumed
to exist. Plant breeders have produced cabbages and marigolds
without their distinctive odor, thus indicating the possibilities of the
production of plant varieties lacking odors that attract insects.

Organs suitable for the reception of odors are known to occur
on various parts of the insects' bodies but are most common on the
antennae and, to a less extent, on the maxillary and labial palpi.
Organs of taste are located about the mouth, especially on the palpi,
but also on the tarsi of the front legs and less often on the antennae.
As a result of experiments, the locations of parts sensitive to both
taste and smell are known to differ in different species of insects
(Wigglesworth 1947).

The reaction to odors often does not include a wide variety in any
individual species of insect, but in the case of those substances to
which the sense organs are attuned the preception may be remark­
ably acute. Somewhat the same may be said of reaction to taste.
Sometimes single substances, or groups of related ones, are con­
cerned, but in nature mixtures and blends of odors of several sub­
stances are usual. The insects apparently orient to gradients of the
odorous substances. Currents of air carry odors and in some cases
the first orientation of the insect is toward the air current. This
helps to account for the long distances over which insects may be
attracted in finding food or a mate.

Among the most extensive observations on olfactory response
of a plant-feeding insect are those concerned with geraniol or other
materials and the Japanese beetle. Geraniol, a constituent of
sassafras, apple, and other favorite food plants, has been used as an
attracting substance (Richmond 1927; Langford, Muma, and Cory
1943). It has been found that extracts from various plants immune
to attack by the beetles act as repellents (Metzger and Grant 1932).
Some relationship also has been shown among 97 species and varie-
ties classified for susceptibility, reducing sugar content, and odor of the clarified extract (Metzger, Meulen, and Mell 1934). Generally the susceptible species showed a high sugar content and a fruity odor of the extract, but there were conspicuous exceptions. The few varieties of the species studied were essentially alike in the three respects. Langford and Cory (1949), however, have recorded considerable differences between varieties of grapes and apples in respect to injury by the Japanese beetle. In the case of grapes they associate the tomentose covering of leaves with lack of preference but indicate that this is only one of the possible factors. The attraction of the corn earworm, *Heliothis armigera* (Hbn.) to corn silk or possibly the ability to discriminate between varieties of corn is almost certainly in part an olfactory response (McCulloch 1920). Peat (1935) has reported significant differences in the oviposition of the cotton bollworm (*Heliothis armigera* (Hbn.)) on different strains of cotton in Southern Rhodesia. Fennah (1939) showed that the difference in attractiveness to *Tomaspis saccharina* Dist., the sugarcane froghopper, was the chief basis for the classification of varieties of cane as resistant or susceptible. In olfactometer tests comparing leaves of two varieties 55.3 per cent of the insects were attracted to B.H.10 (12) (susceptible), 28.3 per cent were attracted to Co. 213 (resistant), and 16.2 per cent did not react. The extract of leaves of B.H.10 (12) was highly attractive also, as were solutions of sucrose. In laboratory tests Folsom (1931) showed that there were differences in the attractiveness of four varieties of cotton for the cotton boll weevil. Of those tested Pima cotton was the most attractive and Mexican tree cotton the least. Two of the attractive substances were ammonium hydroxide and trimethylamine, both known to be present in the cotton plant and most attractive to boll weevils at concentrations of about 1 part per million.

The resistance of *Solanum polyadenium* to the potato flea beetle has been shown to be partly the result of the odor of an oil which occurs on the leaves (Sleesman 1940). The evidence is discussed in the section on resistance to insects in the potato. The odor, or other characters of a plant which attract the adults for oviposition, does not always correspond with the suitability of the attractive plant for larval food. The clearest case is that of the Colorado potato beetle, regarding which details are given in the section on resistance of potato to this insect. McIndoo (1935)
showed that odor was a primary reason for difference in attractiveness of various host plants of the beetle. Of the species being used for plant breeding in Europe, *Solanum demissum* is almost as attractive as the common potato *S. tuberosum*, but the former species is highly unsatisfactory as food for either adults or larvae (Trouvelot 1939). Other species of *Solanum* were non-attractive to the adults but were satisfactory food for the larvae. The choice of larval food plant by the adult female is by no means unerring. The bean weevil, *Acanthoscelides obtectus* (Say) and the cowpea weevil, *Callosobruchus maculatus* (F.) both lay eggs on bean species and varieties on which the larvae cannot mature. The bean weevil does not oviposits on some beans on which the larvae can readily mature (Larson and Fisher 1938).

In a number of cases insects appear unable to distinguish between plant species and varieties without tasting them. This is true, for instance, of the Colorado potato beetle larvae, there being no orientation of the larvae toward the plant from a distance. Raucourt and Trouvelot (1936) were able to isolate but not to identify the chemical in *S. tuberosum* and other *Solanum* species that attracts the larva through the taste reaction. Disks of pith, on which alcoholic extracts of *Solanum tuberosum* had been absorbed, were eaten readily by larvae of the beetle. Similar disks soaked in extracts from resistant *Solanums* were not eaten or barely tasted. Thus there exist in the genus *Solanum* chemicals that are attractive by odor to adults but not larvae, materials that are attractive to larvae by taste, and other materials that are repellent to the larvae by taste. Response to taste or to taste and smell appears to be a part of the explanation of grasshopper resistance in corn, sorghums (Brunson and Painter 1938), and wheat, and is discussed in the chapters on those crops. When resistant plants of sorghum or Maiz Amargo are small, the bite that serves as a taste may destroy the plant which, when larger, would show little damage. Thus there is an appearance of age resistance where actually no difference may exist in attractiveness between younger and older plants.

Horovitz and Marchioni (1942) in Argentina have shown that resistance to grasshoppers and locusts was the result of a single recessive gene carried on the first chromosome. The resistance was derived from Maiz Amargo and, as far as is known, is a preference phenomenon. If so, theirs is the only report in which this type of
resistance has been placed on a genetic basis. In studies at the Illinois Agricultural Experiment Station there was some evidence that antibiosis is also involved in the resistance of North American strains of corn to grasshoppers.

It has been shown (Thorpe et al. 1947; Crombie and Darrah 1947) that wireworm larvae (Agriotes spp.) tended to aggregate in areas moistened with aqueous extracts of plant tissues or with certain substances found in plants. Some of these latter substances also called forth the biting response but others did not. The larvae did not respond to odors but to substances dissolved in the soil water. There are thus two distinct kinds of responses in the food-finding of these insects, an orientation response and a biting response.

Among insects that suck the juices of plants, there may be an ability to distinguish between species and varieties of plants. But there certainly exists an ability to distinguish tissues on the inside of plants. Many of these aphids and other true bugs of the Orders Hemiptera and Homoptera feed by thrusting the stylets of their mouth-parts into the phloem. In the case of the beet leafhopper, Eutettix tenellus (Baker), it has been shown (Fife and Frampton 1936) that the phloem is located by the insect as a result of a pH gradient, the phloem sap being more alkaline than the other tissues. It is not known if this is the only means of finding the phloem tissue that is used by these great groups of plant feeding insects. Since the phloem tissue transports various organic food materials and many other substances, other gradients probably also exist. Likewise it is not known whether these gradients differ between varieties that are resistant and susceptible to sucking insects but such differences could be a possible basis for resistance. It also
has been shown (Carter 1927) that the beet leafhopper tends to congregate on plants having low osmotic concentration rather than those of the same species with high concentration. Presumably the insect can distinguish between the two by taste (Fig. 5).

In a continually growing list of plants and insects, preference has been shown to exist as one of the bases for resistance. In these cases the exact stimulus resulting in preference or non-preference is not known. Among those for which good experimental evidence is available are the resistance of corn to European corn borers and chinch bugs, the resistance of sorghums to chinch bugs, the resistance of certain legumes and of potatoes to the potato leafhoppers, the resistance of cranberries to leafhoppers (Wilcox and Beckwith 1933), the resistance of sugarcane to moth borers (Holloway 1935), and the resistance of cacao to thrips (Callan 1943). In most, if not all, of these studies, other mechanisms of resistance were found to exist side by side with preference.

The possibilities of preference as a resistance mechanism. In all cases so far thoroughly studied, other mechanisms as well as preference have been a part of resistance as observed in the field. The resistance of oats to the frit fly, *Oscinella frit* (Linn.), was shown to follow primarily from a differential oviposition (Cunliffe and Hodges 1946) as a result of preference. Although some oat varieties have some ability to recover from attack, no evidence of antibiosis has been discovered.

Generally it is considered that non-preference can give rise to only a low level of resistance. However, available data are as yet too few to be able to judge. In the resistance of *Solanum demissum*, and *S. tuberosum* × *demissum* hybrids, the material repellent to the larval taste did not drive the larvae or adults away but merely limited their feeding to tiny nibbles. Thus some starve to death in the presence of plenty. The existence of any poison in *S. demissum* other than the repellent, has been questioned (Busnel and Chevalier 1938; Muller and Sellke 1941). If this is the situation and since colonies of Colorado potato beetle cannot be maintained on *S. demissum*, then non-preference alone in this case would become a powerful resistance mechanism.

As indicated earlier the finding of a host plant for shelter, food, or oviposition involves a chain of reactions to a varying number of stimuli, depending on the insects and plants involved. The first movements of an insect stimulated by hunger or other physiological
state are random ones. On coming within range of odors from the host, the rate of insect movement or turning, or both, are speeded up. The turnings occur often at the outer limits of the stimulus perception and result in keeping the insect within the neighborhood of the host. In the presence of a current of air carrying an odor or a gradient of the odor, or in the presence of a particular color or intensity of light, directed orientation toward the host will occur. The final links in the chain of stimuli are brought about by contact, or taste, or both.

There appear to be two general ways in which resistance may occur through non-preference: (1) A resistant variety may lack one, or more, or a measurable amount of the qualities which provide the attractive stimuli present in a susceptible variety, or (2) a resistant variety may possess repellent qualities which take the place of, or successfully compete with, or mask the attractant stimuli. In the first situation the break in the chain of stimuli leaves the insect with chance or random trial and error as the means of finding the resistant host. Success in this regard will depend on the size or character of the break and the density of the insect population. Compared to directed response, the chance method of host-finding would be wasteful of the short lifetime available to the insect and of the stored food reserves in its body. This may partly account for the reduced insect populations often characteristic of resistant varieties. Some insects die without depositing eggs if a suitable host is not present. Larson and Fisher (1938) found that the cowpea weevils, *Callosobruchus maculatus* (F.), did not oviposit when placed in empty vials, or when placed on young vines females invariably died without being seen to lay eggs. In vials with bean seeds many eggs were deposited.

The presence of repellent characteristics has been postulated for a number of resistant varieties. Often neither the material nor the behavior basis for such characteristics has been satisfactorily demonstrated. The repellency in the resistance to the Colorado potato beetle discussed earlier appears to have a sound experimental basis. The repellent action of various chemicals to insects has been discussed by Dethier (1947) but few of these repellents involve differences between varieties of plants. The resistance of the wood of certain trees to termites is perhaps a related subject. Lists of resistant woods and a discussion of some of the chemical constituents that confer resistance are available (Oshima 1919; Snyder...
1921; Dadswell and Dadswell 1931; Wolcott 1946). Hardness of tissue in no way constitutes resistance in these woods but the repellent action of chemical constituents is the usual explanation.

The repellents and the lack of preference are definitely part of the resistance mechanism but often these factors are considered to be of less importance than are antibiosis and tolerance. This is perhaps the result of the widespread belief that while preference may exist when groups of susceptible and resistant varieties are grown together, such resistance will be lacking when the non-preferred varieties are grown alone. Data supporting such a belief are not available in any case of resistance so far studied. This is particularly true when due weight is given to changes in the age of plants, differences in size of insect population, and other changes in the situations compared. Populations of insects on non-preferred varieties may actually decrease. Parnell, King, and Ruston (1949) reported that a field of cotton resistant to leafhoppers may be practically free from adults or nymphs, while a patch of susceptible cotton not far away may be “shimmering with adults on the wing.” Studies on the resistant cottons, like those on other insect-resistant crops, have been made in plots containing both susceptible and resistant types where heavy populations have built up on susceptible plants. The authors state further that a “resistant type grown by itself in general cultivation, exposed only to its own build-up of population, will be more effectively resistant than the experimental results indicate.” Since the first cotton, partially resistant to leafhoppers, was produced by Parnell and distributed for general production in South Africa about 1928, and other types with improved resistance were released subsequently, the statement made above has been based on a long period of practical experience.

ANTIBIOSIS

The use of the term antibiosis was proposed for those adverse effects on the insect life history which result when a resistant host-plant variety or species is used for food. Some workers on insect resistance in crop plants would restrict the term “resistance” to those varieties showing antibiosis. However such a procedure would leave no term available for the varietal differences in insect injury and infestation as seen in the field and for which the bases are unknown. At present this form of resistance appears to be...
more desirable and possibly has the more permanent basis. Varieties with the highest value for insect resistance are those on which a specific insect is unable to maintain a population. A considerable number of such varieties are known.

**Examples of antibiosis as a factor in resistant plant varieties.** The concept of the importance of the food of insects as a possible frequent explanation of the mechanism of resistance was first advanced in 1936 (Painter). At that time information was available in entomological literature to show that grasshoppers, the pale western cutworm, the cotton bollworm (or corn earworm), greenbugs, grape phylloxera, Colorado potato beetle, and cotton boll weevil did not thrive equally well on different but related species of plants. Information was similarly available to show that varieties or individual plants of varieties of the same species of a host plant had vastly different values as food for the woolly apple aphid, the gooseberry witchbroom aphid, a raspberry aphid, the pea aphid on alfalfa, chinch bugs on sorghum, and the hessian fly on wheat. Attention was directed to the physiological irrelevancy of host-plant lists and of the classification of insects as monophagous and polyphagous.

Antibiosis appeared to be at least part of the resistance phenomena in the following insect-plant relationships: *Aphis rumicis* L. on bean (Davidson 1922); *Aphis gossypii* Glov., the melon aphid on cantaloupe (Ivanoff 1945); *Macrosiphum pisi* (Klb.), the pea aphid on peas (Harrington 1941); *Selenothrips rubrocinctus* Giard, the cacao thrips on cacao (Callan 1943); *Diatraea saccharalis* (F.), the sugarcane borer (Mathes and Ingram 1942); *Acanthoscelides obtectus* (Say), the bean weevil, and *Callosobruchus maculatus* (F.), the cowpea weevil (Larson and Fisher 1938). The following, which likewise showed antibiosis as a part of the resistance phenomena, are discussed in detail elsewhere: the European corn borer, southern corn rootworm, and corn earworm on corn; the potato leafhopper on potato; and the wheat stem sawfly on wheat and barley.

**The inheritance of resistance resulting from antibiosis.** The inheritance of this type of insect resistance has been studied in several crops. The resistance to the woolly apple aphid, *Eriosoma lanigerum* (Hausm.), apparently has existed in the heterozygous condition in the apple varieties Northern Spy and Winter Majetin
since the origin of those varieties 100 years or more ago. It has been shown that resistance in the form of antibiosis was inherited as a dominant in crosses involving Northern Spy (Crane et al. 1936). Crosses between Northern Spy and other resistant apple varieties gave a varying percentage of susceptible plants, depending on the variety and indicating the possible presence of several, chiefly dominant, genes for resistance. Differences in resistance in the hybrids ranged all the way from practical immunity to complete susceptibility. A few crosses between susceptible parents gave rise to a small number of highly resistant progeny, indicating the presence of recessive genes for resistance. Thus in the apple, there are several different genes, and each pair, when present, results in seedlings similar in their inability to support woolly apple aphid colonies.

Rasmuson (1914) reported that crosses between phylloxera-susceptible species of grapes yielded susceptible offspring while crosses between phylloxera-resistant species gave both susceptible and resistant offspring, with the latter dominant. Apparently more than one genetic factor may be involved in resistance to *Phylloxera vitifoliae* (Fitch).

The aphid-resistant red raspberry variety, Lloyd George, is reported to carry two or more genetic factors for resistance, both of them in a heterozygous condition (Schwartz and Huber 1939). Crosses indicated that the resistant condition was dominant to the susceptible and that plants which were somewhat resistant might carry only a single factor. The aphid, *Amphorophora rubi* Kalt., when caged on the resistant variety Lloyd George and resistant hybrids derived from it, died without reproducing. The female chinch bugs, *Blissus leucopterus* (Say), when caged on resistant sorghum plants, lay far fewer eggs than when caged on plants of susceptible varieties. Dahms and Martin (1940) reported data indicating that, as measured by egg-laying capacity, resistance was inherited as a dominant character in F1 plants and that there was evidence of complementary cumulative genetic factors for resistance. Under field conditions two or more times as many eggs were laid when females fed on susceptible varieties or hybrids as they did when fed on resistant ones. Both preference and tolerance as well as antibiosis are involved in chinch bug resistance in sorghums.

Ivanoff (1945) reported that the melon aphid, *Aphis gossypii*
Glov., maintained populations on resistant strains of cantaloupe only for short times under conditions in which susceptible plants were killed by the aphids. Plants of F₁ hybrids between resistant and susceptible plants were resistant and the F₂ progeny segregated in a typical Mendelian ratio of three resistant to one susceptible, indicating a single factor difference between resistant and susceptible varieties. The aphid-resistant cantaloupe “Texas Resistant No. 1” has been used extensively in the melon-growing sections of that state and also has had satisfactory aphid resistance under Kansas conditions. Hughes (1947) also has reported that in a cross between the cantaloupe varieties Smith’s Perfect (aphid-resistant) and V-1 (a strain of Hale’s best; aphid-susceptible) the resistance was inherited as a Mendelian dominant, there being in the F₂ generation 158 resistant and 63 susceptible plants.

In the resistance of wheat to the hessian fly, six or probably more different pairs of genetic factors are involved. Some are recessive and some are dominant. Details have been given in the chapter on the resistance of wheat to insects. The degree of effect of the plants possessing these genes ranges from some that are effective against only part of the hessian fly population to a combination of two pairs of genes which totally prevent the growth of fly larvae under all conditions so far tested. Under usual field conditions in Kansas several of these pairs of genes give almost the same amount of protection to the wheat plants possessing them. The genetic differences actually present have been demonstrated both by special experiments and by genetic analysis.

The fact of inheritance has been demonstrated for a number of other cases of insect resistance in plant varieties resulting from antibiosis, but fewer of the details are known. The antibiotic effect of a resistant variety on an insect varies all the way from some varieties on which particular insects live only a short time and do not reproduce, to those in which careful experimental procedure and statistical analysis are necessary to detect significant differences (Harrington 1941; Patch, Holbert, and Everly 1942; and other papers).

**Effects of antibiosis in the insect and on its life history.** The lower populations observed on resistant plant varieties may result either from non-preference and a food value equal to susceptible varieties, or equal preference and a difference in food value as measured by survival, reproductive capacity of the insect, or other effects. Ex-
experimental procedures are usually necessary to determine whether differences seen in the field are caused by preferences or antibiosis. If an insect population is measured in relation to varying sizes of the plants, tolerance also may give the appearance of antibiosis or preference by spreading a population of the same size over a larger tolerant plant in contrast to a smaller susceptible one.

The death of insects on resistant plants frequently takes place during the first instar. This is perhaps the most common and most easily observed characteristic of antibiosis. This death of the very young nymphs or larvae has been observed on resistant plants in several species of aphids; in the hessian fly; the European corn borer; the Colorado potato beetle; the bean weevil on Windsor bean, lima bean, and soybean; the cowpea weevil in various beans; chinch bugs on sorghums; and wheat stem sawfly in wheat. The small size of the insects at this stage makes a study of their physiology difficult. In some of these insects the early instars feed on a type of plant tissue different from the kind used by later instars of the same insect. The killing of young larvae and eggs by proliferation of tissue in the case of the cotton boll weevil (Hinds 1906) and a few other insects possibly should be included with this type of resistance.

Abnormal length of life of the insect when feeding on a resistant variety compared to a susceptible one has been observed in the chinch bugs feeding on sorghums (Dahms 1948). The number of days during nymphal life was generally longer on resistant varieties and shorter on susceptible ones. The length of life of the female during oviposition was generally longer on susceptible varieties and shorter on resistant ones. Essentially the same thing was true of the length of life and development of the pea aphid on peas (Harrington 1941). On a partially resistant variety the aphids required longer to reach maturity and lived for a shorter time during adult life than on a susceptible variety. There is some evidence that a second critical period may be present as indicated by a high death rate at the end of the nymphal or larval life. Such increased mortality has been reported by Isely (1935) for the corn earworm reared on various host plants and is suggested in some other studies.

A consistent restlessness of the insect is sometimes observed when it is feeding on resistant varieties. This is often true of aphids. In the Colorado potato beetle, the larvae went into a kind of stupor after feeding on resistant species of *Solanum*. The larvae also
reacted differently to stimuli such as to vibrations and light (Busnel and Chevalier 1938). There was a lack of secretion from subcutaneous glands; some of the larvae vomited after feeding on resistant plants; there was a reduction in the rate of heart beat. It is not certain how many of these effects may be the result of starvation because of refusal to feed on the non-preferred plant and how many may be the result of poisonous substances in the plant.

After feeding on resistant plants the Colorado potato beetle also showed a lack of formation of proper food reserves and, as a result, an inability to hibernate successfully (Brues 1940). Hill (1946) has shown that wide differences exist in the numbers of adults of the tuber flea beetle (*Epirus tuberis* Gentner) emerging the year following that on which the larvae had fed on different species of food plants. When study has been given to this phase of the biology of insects on resistant plants, other differences will almost certainly be found.

With rare exceptions the feeding of insects during developmental stages on resistant plants results in individuals that are smaller and have less weight. Such differences have been observed for length and weight in the hessian fly on Pawnee wheat (Painter and Jones 1945), for length in the chinch bug on sorghum varieties (Dahms 1948), and for weight of the European corn borer (Botger 1950) on different strains of corn. Such differences are useful in demonstrating antibiosis in insect-plant relationships where there is little mortality resulting from feeding on resistant plants.

The differential in size is often reflected in a lower fecundity of the females which have been reared on resistant hosts or have fed on such hosts during the period of oviposition. A reduction in number of young produced is a characteristic reaction of aphids when placed on resistant plants. This lowered fecundity may vary from the 12.5 per cent reduction reported by Harrington (1941), when the pea aphid is reared on resistant peas, to an almost complete prevention of any reproduction, when the same insect is reared on resistant alfalfa (Dahms and Painter 1940). Chinch bugs likewise lay fewer eggs when fed on resistant than on susceptible sorghums (Dahms 1948). Many Lepidoptera and some other insect adults do not develop additional eggs after emerging from the pupal stage. Among these insects the food of the immature forms determines the fecundity of the adults. Differences in egg production of females reared or fed on different species of plants...
are fairly well known. Isely (1935) has reported on such differences when the cotton bollworm (or corn earworm) was reared on different species of plants or even on different parts of the same plant. Considerable differences have been reported in the number of eggs laid by females of *Melanoplus bivittatus* (Say), the two-striped grasshopper, when fed during the oviposition period on different wild and cultivated plants (Tauber *et al.* 1945). These authors generally do not state the crop varieties used. When adult females of the tuber flea beetle, *Epitrix tuberis* Gentner, were fed on various species of food plants, widely different numbers of eggs resulted. When fed on potato (Bliss Triumph) the largest number of eggs were laid. When females were changed from an unfavorable food plant to potato, an increase in the number of eggs laid usually was recorded within two or three days following the change (Hill 1946).

The general result of these adverse effects of a resistant variety should be a reduction in the over-all population of the insect resisted. Painter and Jones (1948) reported such an effect on the hessian fly population as a result of wide-spread planting of the partially resistant wheat variety Pawnee. Mathes and Ingram (1942) suggested that there is a relationship between the resistance or susceptibility of sugarcane varieties and the infestation of the sugarcane borer in surrounding fields.

Possible physiological explanations of antibiosis. It is possible only to suggest explanations of antibiosis because the nutritive requirements of insects that feed on green plants is virtually unknown. One may suggest that resistant varieties provide a new tool for such a study. Apparently only one green-plant-feeding caterpillar, the European corn borer, has been raised on a synthetic diet (Bottger 1942; Beck *et al.* 1949). Practically all available data on nutritional requirements of insects have come from a study of stored products insects or others easily reared on synthetic media. Diversity in nutritive requirements among different species of such insects has been a common observation and may also be expected with insects that feed on green plants. In view of scarcity of facts, any suggestions of the possible physiological basis of antibiosis must be regarded as tentative.

The deleterious effect of *specific chemicals* has sometimes been suggested as a possible basis for the high mortality and other phenomena occurring when insects feed on resistant plants. The
presence of compounds with insecticidal properties is well known. McIndoo (1945) finds records of 1,180 different species of plants that have been investigated for possible commercial use against insects. The toxicity of the various strains of insecticide-producing plants shows considerable diversity not only from variety to variety but in different environments and in different parts of the same plant. Roach (1937) has recorded some success in attempts to isolate specific substances responsible for the immunity of Northern Spy to the woolly apple aphid (Eriosoma lanigerum (Hausm.)). The aphids were reared on artificial media prepared from the barks of immune and susceptible trees. The number of young produced was smaller and their life shorter on the media from the immune than on those from the susceptible trees. Studies of the extracts suggest that the cause of immunity or susceptibility is carried by a chemical substance insoluble in alcohol and ether and only slightly soluble after prolonged boiling in water. This is perhaps the nearest that anyone has come to isolating such a material.

The lack of specific food materials, including vitamins or materials analogous to vitamins, could be a source of the adverse effects of the feeding of insects on resistant plants. The need for various accessory growth factors has been shown for a number of insects, mostly for those that feed on stored food products (Trager 1947). Presumably the same statement would apply to insects that feed on green plants, but little information is available. Carotene is known to differ in amount in different inbred lines of corn, and a correlation has been shown between the amount of carotene in such inbreds and resistance to the corn leaf aphid (Coon, Miller, and Aurand 1948). Hodge (1933) has reported that the adverse characteristics in the differential grasshopper, Melanoplus differentialis (Thomas), resulting from feeding on certain foods are suggestive of vitamin deficiencies. Pepper and Hastings (1943) have found that a low percentage of linoleic acid in certain food plants of the sugarbeet webworm, Loxostege sticticalis (L.), was associated with infertility of females developing from larvae that have fed on these plants such as sugarbeets and sage (Artemisia spp.). Larvae that had fed on lambquarters, Chenopodium album L., which contained a much higher percentage of linoleic acid gave rise to fertile females. The similar lack of specific proteins or minerals may also be the basis for some cases of insect resistance in plants.
Differences in quantities of food available either in total amount or in respect to certain kinds may be associated with antibiotic effects. Plant-feeding insects frequently feed or begin their feeding on meristem tissues of plants which are richer in certain proteins than are other parts of the plant. It was found that reproduction of the pea aphid on flowering stems of alfalfa was greater than when aphids were fed on vegetative branches of the same plant (Dahms and Painter 1940). The increased survival of the European corn borer larvae when fed on the tassel or pollen of the corn plant, as discussed in detail elsewhere, is perhaps a similar phenomenon. The higher survival and faster growth associated with plant-reproductive structures occur also in the corn earworm (Isely 1935), codling moth (Heriot and Waddell 1942), and other insects that can feed on both reproductive and vegetative plant structures. Beck and Lilly (1949) report that the growth and survival of newly hatched larvae feeding on 4- and 6-inch corn can be improved by supplementary diet with glucose or sucrose. Such occurrences suggest that amounts and kinds of food materials may be important in antibiosis.

Certain foods may be present in a plant but not available. The "big bud" of black currants in England is a gall-like growth resulting from the feeding of a mite, *Eriophyes nibis* Nal. A certain strain of the host plant appears to be resistant because on this strain the mite, feeding in the bud, kills the tissue instead of causing it to develop into the gall-like structure (Lees 1918). The death of the plant tissue cuts off the food supply from the mite, which then dies. Such hypersusceptibility and the resulting apparent resistance is not reported in any insect-plant relationship as an explanation of resistance but it may occur especially in regard to the insects with sucking mouth-parts. A somewhat similar situation, however, was reported (Hamlin 1932) when the scale insect, *Dactylopius tomentosus* (Lamarck), was transferred from one species of *Opuntia* to another. Establishment of the young nymphs was retarded by the formation of thickened brownish corky areas by the plant about the points of insertion of the stylets. Only a few of several thousands of such young nymphs survived. A part of the resistance to the wheat stem sawfly of wheat varieties with solid straw, discussed in detail elsewhere, may be the result of a lack of available food. Eggs laid in the pith of solid-stemmed wheat hatched but the larvae seemed unable to use the pith for food or to tunnel through it to
their usual feeding area near the vascular bundles. Hence complete inability to reach the necessary food may be associated with antibiosis.

Methods of insect feeding in relation to antibiosis. The essential problem among the plant-feeding insects is to get through the cell wall of the plant in order that the cell contents may be digested. Insects solve this problem by the mechanical chewing up of cell tissues, by the piercing of cells, and by the action of enzymes through the cell wall. Enzymes capable of digesting cellulose have rarely, if ever, been produced by insects feeding on living plants (Wigglesworth 1947).

The plant cells of particles of leaves, taken in by some insects with chewing mouth-parts, appear to pass unchanged through the digestive system unless the cells are broken open. Other insects seem to extract the cell contents through the unbroken cell wall.

The food requirements of insects for growth and reproduction differ greatly among different species, but include, in addition to carbohydrates and proteins, certain elements, especially phosphorus and potassium and certain of the vitamins or vitamin-like substances. The absence or inaccessibility of any of these substances may be related to resistance.

Insects feeding on plants have mouth-parts of either the chewing or the piercing-sucking type. The mandibles of the chewing insects are of a great variety of patterns and are sometimes adapted to special uses correlated with the plant structure to be attacked (Isely 1944) (Fig. 6). Some caterpillars feed at the edge of a leaf, others normally on the surface; some use only the upper surface of the leaf, others only the lower. Connected with the mandibles of these insects is a large muscle attached broadly to the exoskeleton, making possible considerable pressure at the cutting edge of the jaw. The power of such muscles is shown by the ease with which some insects tunnel through the hardest wood. Hardness of plant tissue has frequently been cited as a "cause" of resistance of various insects. Later research has sometimes shown that physiological relationships were of greater importance. The degree of development of fiber and hardness of rind were cited early as causes of the resistance of sugarcane to the sugarcane borer, Diatraea saccharalis (Fab.) (Rosenfeld and Barber 1914). Such fiber has been mentioned often as a cause of resistance to various borers in sugarcane. Yet later studies have shown no relation between hardness of rind and
resistance to *Diatraea* (Mathes and Ingram 1942). This is particularly fortunate since high fiber content is generally undesirable.

A consideration of insect structures and abilities leads one to question whether differences in hardness of tissue of the order of those occurring between varieties of a plant species are sufficient to explain many of the cases of resistance. For instance, during the grasshopper outbreaks of 1934 the grasshoppers near Manhattan, Kansas, ate much of the corn, chewed the bark off certain trees and the labels off the stakes in the experimental sorghum nurseries, but only nibbled at the sorghum leaves (Fig. 7). Certainly a difference in hardness of tissue did not explain these choices and still less would such an explanation be probable in the case of differences found in amount of injury among different corn hybrids and varieties. The tetraploid plants of corn produced by doubling the chromosomes of the variety Colorado Kline had thicker and more coriaceous leaves than the original diploid plants. Yet these tetraploids showed no
increased resistance to the grasshoppers, *Dichroplus* sp. and *Chromacris miles* Drury (Andres and Saura 1944).

Differential toughness of pericarp has been cited as one cause for differences in extent of injury by corn earworm to young corn kernels. In Kansas later generations of this insect tunnel through the hardened kernels, and here also differential injury is shown by various hybrids. Those with softer, starchy kernels and also the hard, flinty types occur both among hybrids with low and with
THE MECHANISMS OF RESISTANCE

high degree of injury by corn earworm. Evidently, hardness of kernels is not a deciding factor in late injury by corn earworm. It is still less likely to be a factor when the kernels are in the milk or dough stage.

Among the insects with piercing and sucking mouth-parts, the mandibles and maxillae are formed into four needle-like stylets held within a jointed beak. The inner surfaces of the maxillae are grooved and, when pressed together, form two canals connected with muscular pumps in the head (Fig. 8). Through one of these channels salivary fluid is forced into the plant; through the other, plant fluids which sometimes may be partially digested, are drawn back into the insect. These stylets are inserted into the plant by pushing first one and then the other forward while the base is held within the beak. Among some of the Hemiptera, such as the chinch bug, the stylets are thrust through the cells; among many of the other insects, including particularly the aphids, the setal path is between the cells. Some species of insects employ both methods. Around the stylets within the plant there is formed a stylet sheath apparently coming mostly from the insect salivary glands (Fig. 9). The punctures of these insects usually reach the phloem tissue, although in other species of insects,
even in some species belonging to the same genus (*Empoasca*), the required food comes from mesophyl tissue only. In the case of the sugarbeet leafhopper (Fife and Frampton 1936), the stylets are apparently guided to the phloem tissue by the hydrogen-ion gradient, which tends to be more acid near the epidermis and more alkaline near the phloem.

Fig. 9. Three stylet sheaths which had formed about stylets of chinch bugs, *Blissus leucopeterus* (Say), in tissues of Dwarf yellow milo sorghum between two vascular bundles. The stylets entered tissue from the opposite side and some branches of each sheath reach the vascular tissue. (From Snelling, Painter, Parker and Osborn 1937.)

Again in this connection the statement sometimes made that hardness of tissue is often a cause of resistance to sucking insects is open to question. Some of these insects normally feed on or send their stylets through or between cells of branches of trees where lignification is heavier than in most crop plants (Fig. 10). The mechanism of piercing of these species of insects is not known to differ from related species feeding in softer tissue. It appears doubtful, for instance, if differences in thickness of epidermis to be found between the leaves of two varieties of a crop plant would be
enough to encourage an aphid to feed on one and prevent it from feeding on the other. Differences in plant structure may be found, however, to be genetically linked with resistance and hence prove to be useful marks in searching for resistance. What has been said

FIG. 10. The large sycamore aphid *Longistigma caryae* (Harr.) and many smaller species of aphids and scale insects feed on lignified branches of trees and not on leaves. The mouth-parts of these aphids apparently pierce these tissues with ease.

regarding the relation between resistance, hardness of tissue, and feeding may not apply to resistance to oviposition.

The thrips (*Thysanoptera*) contain another group of plant feeders with sucking mouth-parts that differ in many details from the aphids and other true bugs. In these minute insects the lower
part of the head is drawn out into a cone containing three piercing stylets. A hole is made by the mandible through a single cell of the epidermis of the plant. Only a few cells near the point of puncture of the epidermis can be reached by the stylets and from these cells the plant fluids are drawn up by the insect (Wardle and Simpson 1927; Barnhart 1943). There is no clear evidence of any injection of salivary fluid. Considering the anatomical evidence, it appears possible that in this case a differential thickness of the wall of the epidermal cells may be of importance in resistance. Cases where this appeared to be true have been reported in onions (Jones et al. 1934; Peterson and Haber 1943) (Fig. 11).

Two other types of mouthparts should be mentioned in connection with insect resistance. Among the beetles, the true weevils (Rhynchophora) differ from most other insects in having the head prolonged into a downward-curving beak or snout. At the end of the snout minute but typical chewing mandibles are located. In a number of forms this snout is used in making the opening in the plant tissue into which the egg is inserted. Some feeding takes place at the same time. Hence, in the true weevils, preference may be affected since oviposition and feeding are intimately related in a manner not often found among other insects.

Among the flies, the higher or Muscoïd diptera have larvae or maggots in which the feeding organs are different from all other insects. The house fly or the blowfly maggot is typical of the group but most of the plant-feeding forms are much smaller in size. In insects with chewing mouthparts the mandibles are situated on each
side of the mouth and move laterally. In fly maggots the head and extremely rudimentary mouth-parts are retracted into the thorax, and two "mouth hooks" that move vertically and function as substitute jaws have developed from the neck region. These mouth hooks act with a tearing, rather than a cutting action. Ordinarily the plant-feeding larvae of this group are found on young plant tissue, in galls, or in cavities in plants. Such larvae often employ the forepart of the body as a lever in connection with the tearing action of the jaws.

The morphology of the mouth-parts of herbivorous insects affects the responses of insects to plants which they utilize as food, but even more profoundly the type of mouth-part affects the type of damage for which such insects are responsible.

TOLERANCE

Tolerance differs from preference and antibiosis in the predominant part played by the plant. The other two divisions of resistance require an active insect response or lack of response. They are essentially insect-plant relationships. The use of tolerance in resistance studies does require, however, a thorough understanding of the ways in which insects may injure plants as well as the ways in which plants may repair the damage done. Tolerance response is perhaps more subject to variation as a result of environmental conditions than are preference and antibiosis. The age or size of plant and size of insect populations strongly influence the degree of tolerance exhibited by one variety in comparison with others. A variety well adapted in respects other than to insects may perform better under infestation than a variety that is tolerant to insects but poorly adapted in other respects. For instance, corn strains that are tolerant to chinch bug infestation under the moisture conditions of Illinois may not show as much tolerance under drier conditions in Kansas. For this reason it may be difficult to identify tolerance, even when present, in unadapted, exotic varieties of crop plants.

General vigor and heterosis in relation to tolerance. The general vigor of a plant greatly affects its tolerance to insect attack. This is perhaps best exemplified in the tolerance to chinch bugs resulting from hybrid vigor or heterosis shown by first-generation hybrids between varieties of sorghums or between inbred strains of corn (Fig. 12). First-generation hybrids between two susceptible vari-
Fig. 12. A plot of Dwarf yellow milo sorghum showing many plants killed or stunted by chinch bugs, Blissus leucopterus (Say). The few vigorous plants are F₁ hybrids in which hybrid vigor confers a high degree of tolerance. Manhattan, Kansas, 1933.
eties of sorghums have been green and flourishing long after the parents have been killed by chinch bugs (Snelling et al. 1937). The first-generation hybrids of susceptible parents that failed to show heterosis also failed to show any tolerance to chinch bugs. Similar differences occur in comparisons of inbred lines and hybrids of corn (Painter et al. 1935). Hybrid vigor is not the only factor in the tolerance or the resistance of corn to chinch bugs, for a considerable range of difference exists both between inbred lines and between hybrids. All corn inbreds tested have been more susceptible than the most susceptible hybrid tested under the same conditions.

More vigorously growing corn is usually more attractive to the ovipositing European corn borer moths but in hybrid corn the average yield reduction per borer, per stalk, is less than it is in open-pollinated corn. A part of this greater tolerance of hybrids may be the result of hybrid vigor. The lack of vigor of the glabrous soybeans in comparison with pubescent types may be a part of the greater susceptibility of the glabrous strains to the potato leafhopper, *Empoasca tabae* (Harris) (Johnson and Hollowell 1935). In general, most observations of the relation of general vigor or heterosis to tolerance have been concerned with the host of an insect with sucking mouth-parts.

Replacement, regrowth, and repair of tissue. The insects with chewing mouth-parts, as a rule, destroy the plant part attacked so completely that the only type of tolerance that can be developed is that concerned with replacement or regrowth. Such regrowth is often conditioned by the relative stage of maturity during which destruction of plant parts takes place. A typical example is that of resistance of soybean varieties to the Japanese beetle (Coon 1946). Although some varieties showed moderate resistance to feeding of the adult beetle, the final yield of both hay and grain showed a greater relationship to recovery, which, in turn, was to a considerable extent influenced by the maturity of the variety. Later maturing varieties showed some replacement of the foliage destroyed.

The larva of the frit fly, *Oscinella frit* (L.), feeds on and destroys the growing point of the central and sometimes the side tillers of the young oat plants. Cunliffe (1925) artificially destroyed the growing points of oat plants of the two varieties Sir Douglas Haig and Potato and compared the resulting yields and the number
of culms which developed. Normally Haig develops fewer tillers than does Potato. But after damage which simulated that caused by the frit fly, the oat variety Potato showed a significant reduction in yield of 58 per cent while Haig showed a non-significant reduction in yield of 19 per cent. Thus in this case recovery power could not be forecast from a knowledge of tillering capacity.

Com, wheat, and other crop-plant varieties differ in their recovery power after attacks of underground insects. This ability to replace a destroyed root system is not the same thing as having a well-developed root system; the two may or may not be associated. There are required, in addition to the presence of adventitious buds, the ability to produce the necessary growth hormone, suberin or callus to heal the wound, and at least an ordinary degree of resistance to disease organisms that may be accidentally introduced. These are all complicated processes (Bloch 1941). They are possessed to a varying degree by different strains of plants but are of greater usefulness when combined with a well-developed root system. As reported in detail elsewhere the inbred strains of corn differ greatly in respect to recovery from the attacks of the southern corn rootworm larvae (Fig. 13). The outstanding inbred in resistance to this insect, Ind. 38-11, possesses the ability to transmit to hybrids a good root system as well as tolerance, and the inbred itself shows antibiosis (Bigger 1943, and other papers). Differences that may include tolerance are also reported for the resistance of corn to white grubs and of wheat to wireworms. Some strains of sugarcane show varietal resistance to cane grubs through their ability to replace roots rapidly after root pruning has taken place. Other strains of sugarcane have such an extensive root system that the grubs do not destroy all the roots (Mungomery and Butacott 1940).

The effects of the feeding of insects with chewing mouth-parts is usually only too apparent, but the effects of the feeding of sucking insects (Hemiptera and Homoptera) may not be measured so easily. Sometimes little damage is done and large numbers of such insects as aphids must be present before the results can be assessed. A part, sometimes a principal cause of injury, results from the clogging of conducting vessels of the plant by sheath material secreted by the insect about the piercing mouth-parts or stylets (Johnson 1934, Painter 1928). These stylet sheaths remain permanently in place in the plant tissue. Some insects, notably
the tarnished plant bug and its relatives (family Miridae), inject toxic fluids into the plant, which result in considerable disintegration of cells, destruction of chloroplasts, and swellings or holes, especially where the injury takes place in a bud. It is perhaps sig-

![Image](image.png)

**Fig. 13.** Roots of inbred lines of corn (A and B) grown at Columbus, Ohio, 1937, in soil heavily infested with southern corn rootworm larvae, compared with one strain (C) grown at Wooster, Ohio, 1937, under light infestation. Inbred Ohio 56 (A) suffered 40% reduction in dry weight, Ohio Ox (B) lost 90%. At Wooster, Ohio, Ox (C) gave normal root growth. (Courtesy Ohio Agr. Expt. Sta., and L. L. Huber.)

ificant that there have been no extensive studies or successful use of plant varieties resistant to species of the family Miridae. This subject of the relation of plants to insect toxins has been reviewed by Carter (1939). The host plants of members of many of the
other families of Hemiptera and Homoptera show some evidence of the toxic action of material injected into the plant. This toxic material has sometimes been shown to consist of enzymes or to have been accompanied by enzymes. Some method of inactivation of the enzymes or the toxic material is possibly a basis for tolerance. In the case of resistance to psyllid yellows in potatoes, the resistance consists only of tolerance.

Various growth effects often follow the feeding of sucking insects, especially aphids. A stunting of the plant is often a characteristic result from this feeding. Such stunting occurs in alfalfa plants that are susceptible to the pea aphid, but plants that are tolerant do not show it. Went (1940) has suggested that aphids remove a proportion of the auxins along with the sap that they take up and that all growth due to auxins is decreased. A possible explanation of the greater tolerance of some plants may lie in the production of more auxins or a greater sensitivity of the tissues to those that are left. Allen (1947) has reported that it is possible by use of plant hormones to suppress some types of insect injury such as that caused by the tarnished plant bug, Lygus abineatus (Say). The invisible repair of internal tissues injured by sucking insects may be just as real in tolerant varieties as the more easily demonstrated repair of injuries done by chewing insects. Beside a reduction in auxins there is often a marked decrease in carbohydrates, proteins, and other constituents of the plant, as found by Evans (1941) in the case of the cabbage aphid, Brevicoryne brassicae (L.), feeding on cabbage. Such losses may contribute to the stunting or other types of injury (Fig. 14).

Perhaps the best known growth effects related to the feeding of insects are the production of galls. Some galls are large and conspicuous structures but many represent only minor changes in the cells. A few result from a stimulus provided by the ovipositing female (Carleton 1939) but most galls require a continual stimulus from the enclosed insect for the gall development. Minor growths more or less like insect galls are often associated with damage by non-gall-forming insects. Here also something similar to a plant hormone is involved (Nicolas 1946). The relation of tolerance to insect damage and plant hormones should repay further investigation.

The tolerance to hessian fly exhibited by certain wheat varieties appears to be a complex phenomenon. As is true of the tolerance
of oats to the frit fly, there are differences in the abilities of wheat varieties to tiller after fly infestation. This recovery is not the same as general tillering ability. The injury by the hessian fly results from the passage of enzymes or toxins through the plant cells in the neighborhood of the larva. When feeding begins these cells are small and on contact with the secretions from the insect they immediately cease their growth while those cells farther away con-

Fig. 14. Kansas common alfalfa plants on left severely stunted by pea aphids *Macrosiphum pisum* (Kltb.). The plant at right showed tolerance, and probably also antibiosis. Such resistant plants present in alfalfa fields in 1934 in Kansas, when tested for antibiosis during the following years (Dahms and Painter 1940) showed to different degrees the ability to prevent the maintenance of aphid populations. (Painter and Grandfield 1935.)

continue to grow. This forms a pocket in which the large larva and later the flaxseed is found. On highly susceptible plants the larval secretion may affect the neighboring tillers and if the winter wheat plant is small, it may be killed during the fall, or weakened and killed later by cold. On plants that are tolerant to the fly, evidence of the secretion is confined to fewer cells. There appears to be some means by which the secretion is inactivated or cell walls rendered less permeable to it. The plant therefore undergoes nearly normal growth despite the presence of well-developed fly larvae. Genetic factors for this type of tolerance are different from those resulting in other types of resistance (Fig. 15).
In wheat which carries the gene $H_s$, for fly resistance derived from the variety Ill. No. 1 W38, small underdeveloped larvae and flaxseed occasionally develop, especially under greenhouse conditions. Such plants show only small local lesions and usually the

![Image](image_url)

**Fig. 15.** Rows of two different wheat hybrids, both with 100% of plants infested by hessian fly in the fall, show differences in recovery and tolerance to that infestation the following spring, Manhattan, Kansas, April 1942.

infested tiller grows, pushing the flaxseed out of the leaf sheath. This type of tolerance is governed by the same genetic factor that controls antibiotic resistance (Caldwell, Cartwright, and Compton 1946). This is a different type of tolerance from that outlined in the preceding paragraph.

Probably the best known damage done by the hessian fly occurs
when straws fall over at harvest time because of the feeding of the fly at the base of the culm. There have often been observations indicating that varieties differ in respect to lodging as a result of hessian fly infestation, but few data have been published. Gossard and Houser (1906) reported on the infestation and percentage of fallen straws in 59 varieties grown in Ohio in 1904. The percentage of fallen straws varied from 1 to 20 per cent. The size and strength of straw of the different varieties were classified as "small," "medium," and "large." Two varieties, the only ones in the test with small straw, had the highest percentage of lodging, 11.6 and 20 per cent. But the 14 varieties with large straw ranged from 9.6 to 1 per cent and averaged 4.24 per cent. The 17 varieties with medium straw ranged from 8.0 to 1.5 per cent and averaged 4.79 per cent. It appears therefore that while there might be some general relationship with size and apparent strength of straw, there was a considerable range of variation within each group of varieties classified on the bases given. One would expect the degree of lodging to depend more on the amount of damage done to the straw by each individual larva than on the gross size and structure of the stem. This has been the case in some of the hard red winter wheats I have studied.

Strength of tissues as associated with tolerance to insect injury. The activities of insects that damage plants by boring into the stem is frequently accompanied by stalk breakage. The European corn borer, the southwestern corn borer, and the wheat stem sawfly are examples of such insects. Plant varieties tolerant to the first and the last insect have been reported. The last two insects cause the stalks to break over because, before hibernation, the single larva present cuts a V-shaped notch around the inside of the stalk just above the ground. The stalk thus girdled internally breaks over easily. Breakage of stalks by the European corn borer results from the general boring and feeding activities of many larvae. One would expect that tolerance to the two types of damage might result from the strength of quite different tissues.

Patch (1948) reported that stalk breakage in 16 single-cross corn hybrids in the absence of the European corn borer was highly correlated with the breakage that occurred in another set of the same 16 hybrids that had been artificially infested with the borer. This is probably as would be expected. One would also expect that corn hybrids selected for equal ability to stand without break-
age in the absence of the borer would show considerable variation in breakage under heavy borer infestation. Holbert (1946) has reported that corn hybrids differ in their ability to wall-off the feeding areas of the borer. The same thing occurs in corn stalks infested early in the season by the southwestern corn borer, *Diatraea grandiosella* Dyar. Sometimes in this latter case lignified tissue is laid down by the plant about the tunnels of the larvae, actually strengthening the stalk. Tolerance to insect damage may be greater in a tough, resilient stalk than in a large, hard but brittle one, although each may stand equally well in the absence of insect damage. There are thus other elements besides mechanical stiffness of stalk that can condition tolerance to stalk damage by insects.

Tolerance has sometimes been considered to be synonymous with yielding ability in the presence of the insect tolerated. This is not true, even though a high correlation between yielding ability and tolerance will be found for obvious reasons. If a normally high-yielding variety drops to the bottom of the list when grown in the presence of an insect, a lack of tolerance is to be suspected. If a usually low-yielding variety shows high yield in the presence of an injurious insect, it may be that the variety is highly tolerant in comparison with the others in the test. Thus yield comparisons in variety tests grown in the presence of an insect may suggest further studies of resistance but, except in special cases, yield is the result of too many factors to be of use as a measure of either tolerance or other types of resistance. The yields of corn hybrids containing inbred Ind.P.8 were at least a third more per European corn borer per plant than would have been expected on the basis of the usual amount of injury to other hybrids (Deay *et al.* 1949). This inbred line evidently confers tolerance on hybrids of which it is one parent. Tolerance mechanisms may be of considerable economic importance in insect control. A considerable part of the value of the partially resistant wheat variety, Pawnee, in use against the hessian fly lies in its high tolerance to attack. Hessian fly infestation in the fall rarely results in the death of plants of Pawnee, which also show good recovery after infestation both in the fall and spring.

**UNCLASSIFIED RESISTANCE MECHANISMS**

There are several reported bases of resistance that are governed by genetic factors and that cannot be classified under the three
THE MECHANISMS OF RESISTANCE

general relationships discussed previously. For the most part these bases serve as barriers to certain insects. Perhaps they do not belong with the mechanisms of resistance at all but rather should be classified as environmental factors.

The long husks on corn (Zea mays L.), when unpierced by holes made by emerging earworm larvae, serve as a barrier against the rice weevil, *Sitophilus oryza* (L.). There is a difference of opinion regarding the value of the husk. Certainly other mechanisms of resistance, such as preference and antibiosis, also may be present. Long husks have also been reported as contributing to the resistance of corn to corn earworm (*Heliothis armigera* (Hbn.)). Here the long silk channel does not serve as a barrier but rather it confines the larvae so that their cannibalistic habits take full effect and some of the insects are destroyed in this way. This may not be the only effect. If the silks contain antibiotic substances, the long silk channel would compel the feeding of the larvae on such substances to the benefit of the plant. As indicated in the section on resistance to corn insects, there is also a difference of opinion regarding the effectiveness of the long husks. Such differences may arise because of differences in the particular strains of corn studied or the environments under which the work was done.

A difference in the injury done by plant bugs (*Lygus* spp., family Miridae), to beans has been reported (Shull and Oakland 1931; Shull 1933). Besides differences during the blossoming period, there were differences in injury to the bean seeds. The least injured variety Butternut had thick-walled pods which were thought to prevent the stylets of these Mirids from reaching the developing seeds. In the variety Great Northern, which was the most injured, such a barrier was not present since the pod wall in this variety was thin.

Among rice the poor-quality Sathia varieties carry resistance to *Leptocorisa variicornis* F. (Hemiptera, Coreidae), the rice bug, because the panicle remains enclosed in an extension of the leaf sheath (Sethi et al. 1937). In crosses which were made between one of these varieties and economically desirable varieties of rice, the usual emerged condition was dominant in *F*1. Segregation in later generations showed that the enclosed panicle was controlled by three pairs of genetic factors. By the sixth generation some true-breeding hybrids had been secured that were resistant and of con-
siderable economic promise. The resistance appeared to be the result of the mechanical barrier of the leaf sheath in this plant-insect relationship.

CRITERIA FOR EVIDENCE OF CAUSE OF RESISTANCE

To the question frequently asked, "What is the cause of resistance?" the answer which must be made is that there are many possible causes of resistance. The commoner mechanisms by which these causes operate can be classified under the three headings of preference, antibiosis, and tolerance. The three are usually the result of separate genetic factors but are interrelated in their final effects on the insect-plant relationship. Preference may be dependent on one or more of a series of characteristics present in the plant which stimulate the insect receptors concerned with sight, touch, or the chemical senses. Here several genetic factors in the plant may be involved. At different stages of its life history an insect may feed on different parts of the plant. Deleterious effects on the life history of the insect may occur at each of these points of contact between the plant and the insect. The genes governing the lack of necessary food material for the insect, or the presence of deleterious substances may be the same in the different parts of the plant on which the insect feeds, or they may be different. The first generation of the corn earworm feeds in the whorl of the corn plant, later generations of the same insect in the ear. It has been shown that resistance at these two points is governed by different genetic factors (Painter and Brunson 1940). It is not yet certain whether this resistance is the result of preference or antibiosis, or both, but in either case the physical basis of resistance to the two kinds of damage probably is different.

In the same way if the insect causes various kinds of damage, different kinds of tolerance may result, each in response to separate genes or groups of genes. For example, in the resistance of wheat to the hessian fly certain varieties possess a tolerance which leads to fewer dead plants in the field. Other varieties have a type of tolerance that results in less stalk breakage from hessian fly attack in the spring. It is thus possible that separate resistance is exerted against each phase of insect damage done to a crop. In addition to this, the effect of the gene in causing resistance may differ in strength of expression at different times in the life history of the plant. In most analyses of occurrences of insect resist-
ance so far made, one or two insect-plant relationships have been the predominant, but not the only, mechanisms of resistance.

Many of the citations of the cause of resistance made in the past have been based on insufficient evidence. Very frequently the single point of evidence has been a significant positive correlation coefficient. Even a high correlation coefficient is only suggestive and by itself does not constitute proof. Sometimes the correlation has even been the result of a few particular varieties that happened to have been present in the test and hence does not hold for a larger group of strains.

Evidence presented for the cause of resistance should concern, primarily, the character and degree of insect-plant relationships in each of the fields of preference, antibiosis, and tolerance. Negative evidence that one or two of these relationships are not involved may be of importance also. There are at least three lines of evidence which should be presented: (1) experimental evidence of an intimate relation between the supposed cause and the insect physiology, plant physiology, or insect behavior; (2) evidence of complete association between an assigned cause and a given genetic factor wherever this factor occurs, but particularly in segregation following crosses between resistant and susceptible plants; and (3) statistical evidence in field tests in the form of high correlation between the assigned cause and resistance. Of these, the first two are the most important.

Evidence must be provided of an intimate relation between cause of resistance and plant and insect physiology or insect behavior. The study of the relation between insect resistance and plant morphology, physiology, or chemical composition must be concerned with the exact portion of the plant under attack by the insect. Such a plant study will be usable more or less in proportion to the localization of the area being studied. Most of the attempts in the past to correlate total plant analyses of resistant and susceptible strains with resistance have not been suggestive of possible causes. If an insect bores into the stalk through the terminal bud, a test for resistance by means of the weight necessary for puncturing an internode half-way down the stem probably is irrelevant. This is particularly true if, as is often the case, resistance operates in the form of antibiosis which brings about the death of the larvae in the first instar. On the other hand, the presence of certain digestive enzymes in a grown larva or nymph
constitutes only presumptive evidence that these same enzymes may be present in the first instar when resistance mechanisms concerned with digestion are often effective. Thus the ability of half-grown larvae or nymphs to feed on resistant plants is not evidence that they could do so when placed on the plant immediately after hatching. The presence of a substance or structure in resistant plants and its absence in susceptible ones, or the reverse, is not in any way evidence of cause, unless the substance or structure is shown to be physiologically vital to the insect.

The assigned cause must show complete association with a given genetic factor wherever this factor is found, especially in segregating populations. Some of the best evidence concerning the cause of resistance comes from a study of segregating populations in crosses between resistant and susceptible plants. Entomologists have tended to neglect this source of information; plant breeders to overemphasize it. Any association between an assigned cause and resistance should be complete. It is necessary, however, to be cautious in assigning an inherited factor as the cause in a case of resistance to insect attack.

Present genetic knowledge indicates that such an apparently causative factor may be:

(1) The actual modus operandi of resistance.

(2) One of the multiple effects of a gene (pleiotropic) operating to cause resistance in some other way. That is to say, the actual cause of resistance may be one effect of a gene, which is also visible in some character inherited parallel with resistance.

(3) A gene which is closely linked with the one causing resistance.

(4) One of a group of genes giving the same phenotypic reaction but not all connected with resistance.

(5) A gene which compensates for or modifies one of the effects of another gene that is actually the cause of resistance.

The examples of multiple effects on an organism, inherited as if resulting from a single gene, are frequently met with in genetic studies. Usually a gene has a single obvious inherited effect, but when sought, other less obvious effects have been found. Sometimes such multiple effects have been explained as the results from a group of very closely linked genes. Often data indicating which is the correct explanation are difficult to obtain.

Theoretically, in a population which shows random mating,
selecting for one gene does not provide any certainty of getting thereby another gene that is linked with it. However, the plant breeder rarely deals with populations showing random mating. The effects of linkage are always more evident in the earlier segregating generations. Anderson (1949) has pointed out the common experience of corn breeders (Brown and Anderson 1947) that in crossing two inbred lines it is much easier to select from the progeny true-breeding segregates like either parent rather than those combining the characters of the two. Linkage provides the best explanation of this effect. In crosses between two species, segregates like either parent are always more easily obtained than segregates combining the characters of both. Hence, selecting for a genetic factor closely linked with resistance may in some cases result also in securing resistant plants.

It also should be remembered that resistance and its cause may result from multiple factors, only one of which may be associated with the cause assigned. Different genetic factors may possibly achieve the same result through different means. In resistance of wheat to the hessian fly there are at least six genetic factors concerned with resistance that are evident in the death of the young larvae. Some of these genetic factors result in the death of all larvae under all conditions where the infested plants carrying the genetic factors have been tested. Genetic factors derived from Ill. No. 1 W38 and Marquillo result in the death of more larvae at low temperatures than at high ones. Other genes are effective by causing the death of young larvae of only part of the population of the fly. It seems probable that the chemical or physical properties of the wheat plant which result in the inactivity of the larvae to live and grow are not the same in the case of these different genetic factors. Genetic analysis can therefore contribute considerably to an understanding and an analysis of the cause of resistance.

Statistical evidence of the cause of resistance. Statistical evidence in the form of correlation between a structure of the plant and resistance has been widely used as evidence for cause of resistance. It is probably the least valid of any lines of evidence unless the correlation is absolute. In this field of study I would agree with the viewpoint of Anderson (1944): "It is a fundamental principle, too often ignored, that before a biological phenomenon is to be investigated on the mathematical level it must first be thoroughly
analyzed on the biological level. . . . Statistical analysis has a useful place in biology but it must be preceded by biological analysis.” In the study of the cause of resistance a scatter-diagram is often more illuminating than a correlation coefficient. It should be emphasized that any valid exception to a trend indicating the relationship between resistance and some other character is generally clear-cut evidence that the character assigned as cause is not actually operating as such. A scatter-diagram brings out these exceptions clearly.

The statements regarding the cause of resistance which are given above are not to be taken to mean that structures showing high correlation with resistance are not of use in breeding for resistance. This is especially true when adequate populations of the insect cannot be maintained on the breeding material. There are two examples in which a morphological structure correlated with resistance has been successfully used in breeding and has resulted in the introduction of new varieties. These are the use of solid-straw wheats in breeding for resistance to the wheat stem sawfly (Cephus cinctus Nort.) in Canada (Platt and Farstad 1946) and the breeding of hairy varieties of cotton for resistance to the leafhopper (Empoasca fascialis (Jac.)) in South Africa (Parnell et al. 1949). A visible character correlated with insect resistance is of particular value in forestry. Such a character has been used in selecting ponderosa pine (Pinus ponderosa Dougl.) for resistance to the resin midge (Retinodiplosis sp.) (Austin et al. 1945). If a plant character is followed too closely in breeding without frequent recourse to insect tests, other less obvious but equally important characters may be missed.

Breeding for resistance has been done successfully without knowing the exact cause. In most of the studies made in the United States concerning the use of resistance in insect control the exact cause of resistance has been unknown. The genetic characters for resistance have been handled by growing the test material under controlled infestations. These projects usually have been successful in bringing resistance into association with desirable agronomic characters. A knowledge of the cause of resistance is highly desirable but it may or may not be of use in breeding operations. If the determination of resistance requires a complicated chemical technique that must be used on each individual plant
in a segregating population, the maintenance of controlled insect population would probably be more economical of time and funds. The agronomist does not demand a full knowledge of the causes of high yield before breeding for this character in field crops. It is no more necessary to know the exact cause in breeding for insect resistance.

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CHAPTER III

FACTORS THAT AFFECT THE EXPRESSION OR THE PERMANENCE OF RESISTANCE

I. Introduction.
   A. Some factors affect the size of the insect population or degree of infestation, others affect the amount of damage per insect.
   (1) These two situations must be clearly differentiated.
   B. The genetic factors that are inherited consist of the ability of the plant to influence population or damage under a particular environmental condition.
   (1) If this environment is changed the plant-insect relationship, called resistance, may or may not also be changed.
   C. The importance of microenvironments.

II. Factors primarily concerned with the plant.
   A. Edaphic and climatic factors.
      (1) Relationship of soil and insect by way of food plant.
         (a) Soil nutrients.
         (b) Soil moisture.
      (2) Temperature.
   B. Biological factors.
      (1) Secondary effects of edaphic and climatic factors; adaptation.
      (2) Age resistance.
      (3) Hybrid vigor.
      (4) Effects of plant disease.
      (5) Insect evasion by genetic earliness.
      (6) Mutation.

III. Factors primarily concerned with the insect.
   A. Instar and size of population; fluctuations in populations.
      (1) Relation to preference.
      (2) Relation to tolerance.
   B. Importance of correct insect identification; specific differences in food habits of closely related species.
   C. Biotypes or biological strains of insects in relation to resistance.
      (1) Kinds, sources, identification of biotypes.
   D. Learning in insects; pre-imaginal olfactory conditioning and related phenomena.
   E. Changes by insects from one host to another.
   F. Relative permanence of physiological characters in insects.
IV. Limitations of the use of insect resistance.
   A. Use is dependent on the finding of mutant plant forms carrying the necessary resistance.

   B. Relation of resistance to insect habits and taxonomy.
      (1) Is resistance to be found more often among the host plants of insects of specialized habits?

V. Bibliography.

The preceding chapter has dealt with the mechanisms or causes of resistance without reference to the modifications of the expression of hereditary characteristics of plants and insects that may and sometimes do occur. In this chapter some of these modifications will be discussed briefly. Some of these might come under the headings of host evasion and induced resistance. Research in insect resistance in plants requires a knowledge of the possible plasticity of insect behavior and of the possible rate of change of insect biotypes and species. We must also appreciate the possibility of changes in the expression of genes in plants.

In dealing with the plant-insect relationship various environmental factors working directly or through the plant may affect the number of insects present or the amount of damage done per insect. These two are difficult to distinguish, for an increase in numbers of insects usually is accompanied by an increase in damage. Dry weather is usually associated with high populations of chinch bugs, partly because of a decrease in the effectiveness of the chinch bug fungus. But dry weather is usually also associated with increased damage not only because of the increased population of chinch bugs but also because of the withdrawal of needed liquids from the plant by the insects. Severe winter weather usually is accompanied by an increased killing of hessian fly infested wheat plants in certain wheat varieties. Hence some wheat strains will appear more tolerant to hessian fly after mild winters than after severe ones. The numbers of these insects are little affected by winter temperatures.

What is meant by the inheritance of resistance factors? For simplicity of treatment the genetic factors used as examples in simple genetics are mainly those that are affected imperceptibly by the
Geneticists and plant breeders have long known that what is inherited is not a specific character but rather the tendency of an organism to react in a particular way in a certain environment. Applied to insect resistance the genetic factors that are inherited consist of the ability of the plant to influence the insect population or withstand damage under a particular environmental condition. If this environment is changed, the plant-insect relationship called resistance may or may not also be changed.

Yarnell (1942) has given many examples of the effects of the environment on the expression of genetic factors. Two of the examples which he cites may be mentioned. In *Primula sinensis*, the Chinese Primrose, there is one genetic type in which the flowers are red when grown at 20°C, but white at 30°C. A different genetic strain had white flowers at both temperatures. In hessian fly resistance there is a comparable case. Wheat varieties carrying certain genes for resistance show a higher infestation at higher temperatures. Other genes for resistance to hessian fly in wheat are less affected by temperature variations. The several genes concerned ordinarily result in the inability of the fly larvae to begin feeding and to grow on the resistant variety. Hence they are antibiotic in character. Yarnell (1942) points out that onions grown on soils containing much peat are twice as pungent as those grown on sand, and that under comparable conditions some varieties are three times as pungent as others. If an insect were attracted or repelled by a certain degree of onion odor, it is evident that both environment and heredity must be considered in studying the preference of the insect for certain onions. Hairiness of leaves of cotton has been shown to be associated often with resistance to leafhoppers (*Empoasca* spp.) in that crop. Afzal and Ghani (1949) have shown that hairiness in the resistant variety 4 F was decreased significantly with later dates of sowing while the same character was increased in later dates of sowing of a susceptible variety, Victory. However, the amount of change was not sufficient to affect materially the leafhopper populations.

The importance of microenvironments. A highly important reason for the success and dominance of insects as a group lies in the fact that many of them are small enough to fit into environmental niches that are too small for many other animals. Anyone dealing with insect resistance in plants must be aware of the importance of these microenvironments, for the insect in them is exposed to con-
ditions very different from those surrounding the plant. Hence environmental conditions that speed up the life history of a plant may have little effect on the insect feeding within its stalk. Allen and Painter (1937), studying the wheat stem maggot, *Meromyza americana* Fitch, in wheat varieties in relation to dates of planting, found that differences in infestation during three years were the result of different effects of climatic factors on the life history of the plant and the life history of the insect. The insect in the pupal stage within the stem was affected to a slight degree by periods of drought and rain that greatly affected the wheat plant. Insects living near the stomata of leaves may be in an area of higher relative humidity than can be measured near the plant. The presence or absence of hairs will affect the relative humidity in such micro-environments.

FACTORS AFFECTING THE EXPRESSION OR PERMANENCE OF RESISTANCE WHICH ARE PRIMARILY CONCERNED WITH THE PLANT

**Edaphic and climatic factors.** The direct effects of ecological factors on insect populations and distributions have received much study, as have similar problems of the direct effect of ecological factors on plants. Entomologists have long known from observation that various climatic and edaphic factors could affect insect life histories and damage indirectly or by way of a primary effect on the plant. Little actual data are available to support some of the statements that have been made on this subject of the relation of soil fertility to insects, and only relatively few scattered papers recording experimental work are available. Some aspects of the problems of induced resistance have been reported by Felt and Bromley (1931). The idea that more vigorous plants or those growing in fertile soil were attacked less by insects probably originated in observations of the groups of bark beetles and wood borers that normally attack dying or injured trees and shrubs. Here the concept appears to be true (Keen 1936). The extension of the idea as a generalization to insects that can feed on young or healthy plants is open to question. The principal papers containing experimental evidence on these cases of induced resistance that have come to my attention during this study of insect resistance have been analyzed in the accompanying table (Table 1). These data give little support to the idea prevalent among entomologists as well as
others that high soil fertility is conducive to resistance in plants to insects. Each species of insect and often each host-plant species or variety constitutes a separate problem. With the present limited knowledge no other general conclusion can be advanced.

This complicated situation is not surprising since three complex “organic systems” are interacting in various ways. The soil situation affects the plant and the material taken from the plant affects the insect. In return, the increased insect population influences food materials present in the plant and probably also nutrients withdrawn from the soil. West (1945) has examined some of these interrelations in a study of infestation of *Macrosiphum solani folii*

### Table 1 Some References on the Relations of Soil Elements to Insects by Way of Host Plants

<table>
<thead>
<tr>
<th>Category</th>
<th>Observation</th>
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<tbody>
<tr>
<td><strong>A. High fertility</strong></td>
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<tr>
<td></td>
<td>(1) Davidson (1925) <em>Aphis rumicis</em> L. on beans (slight increase).</td>
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<td></td>
<td>(2) Huber et al. (1928) <em>Pyrausta nubilalis</em> (Hbn.), on corn (preference).</td>
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<td></td>
<td>(3) Bigger et al. (1938) Southern corn rootworm, <em>Diabrotica duodecimpunctata</em> (F.), larvae on corn.</td>
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<td></td>
<td>(4) Haseman (1946) <em>Macrosiphum solani folii</em> on petunia.</td>
</tr>
<tr>
<td></td>
<td>(5) Haseman (1946) <em>Toxoptera graminum</em> (Rond.) (on wheat?).</td>
</tr>
<tr>
<td><strong>B. High fertility</strong></td>
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<tr>
<td></td>
<td>(1) Hawkins (1930) <em>Melanotus</em> sp. (tolerance).</td>
</tr>
<tr>
<td></td>
<td>(2) Roach (1939) Leafhoppers on apple.</td>
</tr>
<tr>
<td></td>
<td>(3) Thompson (1941; 1942) Purple scale, <em>Lepidosaphes beckii</em> (Newman.).</td>
</tr>
<tr>
<td><strong>C. High nitrogen content</strong></td>
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<tr>
<td></td>
<td>(1) Dadd (1936) <em>Catoblathis</em>, on prickly pear.</td>
</tr>
<tr>
<td></td>
<td>(3) Bergman (1940) Silkworm, <em>Bombyx mori</em> (L.), on mulberry.</td>
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<tr>
<td></td>
<td>(4) Dahms and Fenton (1940) Chinch bugs, <em>Blissus leucopterus</em> (Say), on sorghums (tolerance).</td>
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<tr>
<td></td>
<td>(8) Haseman (1946) Greenbug, <em>Toxoptera graminum</em> (Rond.), on wheat (?).</td>
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<tr>
<td></td>
<td>(9) Dahms (1947) Chinch bugs, <em>Blissus leucopterus</em> (Say), on sorghums (antibiosis).</td>
</tr>
</tbody>
</table>
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(Ashmead) on tomatoes raised on different nutrient solutions. The effects found were more sudden in their results in the case of plants growing in solutions deficient in any one of the following nutrient elements: calcium, magnesium, potassium, phosphorus, and nitrogen. The complex relations are further exemplified by the findings of Frew (1924) in a study of Chlorops taeniopus Meig., the gout fly, that makes a gall-like growth on barley. The type of distortion caused depends on the stage of growth of the plant at the time of attack, and the amount of distortion depends on the rate of growth at the time of attack. Both stage and rate of growth can be influenced by fertilizers. The addition of superphosphate reduces

Table 1 continued

<table>
<thead>
<tr>
<th>D. Low nitrogen content</th>
<th>increased insect injury or population (or high nitrogen content decreased insects)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1) Bogdanova-Katrova (1918) Cabbage fly, Phorbia brassicae Bch., on cabbage.</td>
<td></td>
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<tr>
<td>(2) Jepson and Gadd (1926) Shot-hole borer, Xyleborus fornicatus Eichh., in tea (tolerance).</td>
<td></td>
</tr>
<tr>
<td>(3) Shchepkina (1930) Frit fly, Oxinella fri (L.), on barley.</td>
<td></td>
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<tr>
<td>(4) Mathur (1941) White fly, Aleurolobus fornicatus Mask., on sugar cane.</td>
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</tr>
<tr>
<td>(5) Haeman (1946) Chinch bugs, Bliszus leucopeterus (Say), on corn.</td>
<td></td>
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<tr>
<td>(6) Wittwer and Haeman (1945, 1946) Greenhouse thrips, Heliothrips haemorrhoidalis (Bouché), on New Zealand Spinach (preference).</td>
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<thead>
<tr>
<th>E. High phosphorus content</th>
<th>decreased insect injury or populations.</th>
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</thead>
<tbody>
<tr>
<td>(1) Shchepkina (1930) Frit fly, Oxinella fri (L.), on barley.</td>
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<tr>
<td>(2) Dahms and Fenton (1940) Chinch bugs, Bliszus leucopeterus (Say), on sorghums (tolerance).</td>
<td></td>
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<tr>
<td>(3) Dahms (1947) Chinch bugs, Bliszus leucopeterus (Say), on sorghums (antibiosis).</td>
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<thead>
<tr>
<th>F. High potash content</th>
<th>increased insect injury or populations.</th>
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<tbody>
<tr>
<td>(1) Davidson (1925) Aphis rumicis L. on beans.</td>
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<tr>
<th>G. High potash content</th>
<th>decreased insect injury or populations.</th>
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<tbody>
<tr>
<td>(1) Andrews (1914, 1919, 1921, 1923) Tea mosquito, Heliopeltis theivora Wth. (Miridae), on tea.</td>
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<tr>
<td>(2) Frew (1924) Gout fly, Chlorops taeniopus Meig., on barley.</td>
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<th>H. Effects of minor elements</th>
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<tbody>
<tr>
<td>Various—Creightoon (1938); Thompson (1941).</td>
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<tr>
<td>Calcium—Carter (review of frog hopper blight) (1939); Emery (1946); Wittwer and Haeman (1945, 1946).</td>
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<tr>
<td>Copper—DeLong (1934).</td>
</tr>
<tr>
<td>Selenium—Hurd-Harrer and Posa (1936); Mason and Phillips (1937); Fox (1943); and other papers.</td>
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<tr>
<td>Magnesium—Thompson (1942).</td>
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</table>
infestation in summer barley. A small amount of nitrogen may also reduce the infestation but a large amount added will not reduce it and may have a tendency to retard growth of the plant and so increase the infestation.

Each species of insect in relation to its host plant may be affected by soil conditions in respect to one or more of the factors of resistance, i.e., preference, antibiosis, or tolerance. Tolerance probably is the effect most frequently mentioned but increases or decreases in insect populations may give the appearance of tolerance. The effect of the soil on resistance may come about through an effect on plant cell constituents or on cell structures such as those described by Lutman (1934). In the relation of chinch bugs to sorghums excess nitrogen decreased the tolerance of plants of both resistant (Atlas) and susceptible (Dwarf Yellow milo) varieties (Dahms and Fenton 1940). In the majority of cases tolerance was increased by the addition of superphosphate. It was also found (Dahms 1947) that chinch bugs laid more eggs on both resistant and susceptible plants growing in solutions high in nitrogen or low in phosphorus than on the same varieties growing in solutions that were low in nitrogen or high in phosphorus. The difference between oviposition on plants of the two varieties growing in a particular solution was much greater than that resulting from the fertilizer treatments. These results concerning chinch bugs and sorghums are exactly the reverse of those reported by Haseman (1946) in regard to the relationship of chinch bugs and corn. Haseman does not give detailed data, however, nor does he state the variety of corn used. Care in the latter regard is important since strains of corn are known to differ in chinch bug resistance and in ability to take up certain nutriments (Harvey 1939). Some other reports with various insects have shown preference differences resulting from differences in fertilizer treatments (Huber et al. 1928; Whittwer and Haseman 1946). Related species of insects also differ in their sensitivity to the effects of soil conditions on host plants. Parnell (1927) during three years' tests found little difference in the effect of the leafhopper, *Empoasca fascialis* (Jac.), on cotton growing on various fertilizer plots. On the other hand Sloan (1938), working with *Empoasca terra-reginae* Paoli in Queensland, found that cotton showed increased susceptibility when produced on soils in which the supply of nitrate nitrogen exceeded the requirements of the cotton plant. Plants grown on certain red soils...
that may be deficient in potassium and phosphorus were also more susceptible to this insect. Thus soil-plant-insect relationships are a source of variation in resistance.

Plant varieties and species sometimes differ considerably in their abilities to utilize particular nutrients from the soil. Goodall and Gregory (1947) in reviewing this subject stated that these differences in many cases were too large to be disregarded. Hansen (1945) found seasonal variation in the mineral and vitamin content of certain green-vegetable crops. Harvey (1939) working with about 21 inbreds and hybrids of corn and 20 strains of two species of tomatoes found considerable differences in the efficient utilization of the nitrogen available in the soil. These relationships may also represent a mechanism of resistance by which different varieties and species of plants, when grown in the same kind of soil, may differ through differing abilities to utilize the chemicals present.

Soil moisture frequently has been reported to be of importance in increasing or decreasing insect resistance in plants. Lees (1926) and Mumford and Hey (1930) have reviewed this aspect of induced resistance. Most of the evidence available is circumstantial rather than experimental. Plants attacked by insects with sucking mouth-parts are the ones so far shown to be most influenced by soil moisture. Priesner (1939) considers that variations in available soil moisture and nutrients act through differences on osmotic pressure in their food. The resistance of sugar-cane plants to "frog-hopper blight," caused by the feeding of *Monechphora (Tomaspi)* saccharina Dst., has been shown to be concerned especially with water balance (Withycombe 1926). The cane variety Uba appears to be tolerant to attack but soil conditions affect all types of cane. With many plant-insect relationships either an excess or a deficiency of soil moisture may cause the plant to tend toward susceptibility to the insects but such effects often will be superimposed on varietal differences.

Light sometimes affects insects through an effect on the plant. Davidson (1925), working with *Aphis rumicis* L. on beans, found that reproduction on beans grown in semidarkness was about half of that taking place on beans in the light. Evans (1938) in a study of the cabbage aphid, *Brevicoryne brassicae* (L.), under similar conditions found that those aphids on plants grown in the light reproduced about five times as fast as those grown in semidarkness. In this case the effect on the insect was shown to result from the
changed chemical condition of the plant. As discussed in the section on resistance to wheat insects, it proved impossible to study resistance of certain strains to wheat stem sawfly under cage conditions because resistance is greatly reduced when the amount of light is slightly decreased. Yet genes from one of these strains are responsible for the resistance of the wheat variety Rescue, which occupied about 1½ million acres in 1948.

Temperature may affect the insect through its influence on the speed of plant growth. As is shown in the section on resistance of wheat to the hessian fly, varieties carrying certain genes for resistance to this insect have a larger infestation when the infestation develops in the greenhouse under high temperatures than when it develops under conditions of low temperature. In this case the increased temperature may affect infestation through speed of plant growth rather than a direct effect on the insect. This would appear to explain many of the minor fluctuations in resistance that have been observed in the field in these varieties from year to year. In all experiments the susceptible and resistant varieties retain their relative positions but at higher infestation levels and sometimes with less difference between the two classes. The effect of high temperature, however, appears to be greater in plants that are heterozygous for hessian fly resistance. The F₁ between a susceptible wheat and one carrying the Ill. No. 1 gene for resistance (H₁) is susceptible in the warm greenhouse but generally resistant in the field in the cool autumn. Dahms and Painter (1940) in a study of the rate of reproduction of the pea aphid, Macrosiphum pisi (Kltb.), on different alfalfa plants found that the aphid mortality on resistant plants was much greater at moderate temperatures than at low ones. Hence some of the resistant plants appear to be more susceptible at these lower temperatures but others, notably No. 5 Turkestan 19316 (of which progeny have been grown in alfalfa nurseries under the numbers K138 or CI04), retained their resistance at a range in mean temperature of from 78 to 57°F. Albrecht and Chamberlain (1941) also reported that low temperature may have resulted in a change in the apparent resistance status of some strains of alfalfa.

Emery (1946) has studied some of the factors not related to temperature that cause known aphid-susceptible alfalfa plants to appear to be resistant.

Biological factors. The edaphic and climatic factors discussed above sometimes have secondary effects. Plant breeders and grow-
ers, aided by a certain amount of natural selection, have picked strains that are adapted to producing good yields under a particular set of environmental conditions. The combination of characters that make up "adaptation" sometimes includes a degree of tolerance or other form of resistance to insects. Adaptation for other characters also may affect resistance. Crop varieties that are resistant to insects, such as leafhoppers that have sucking mouth-parts, often appear to be more drought-resistant than susceptible varieties. There appears to have been less agreement in regard to chinch bug resistance in corn inbreds, hybrids, and varieties than in regard to many other cases of insect resistance in corn. This may be because chinch bug outbreaks often occur during dry periods and the drought resistance of strains of corn influences their status in chinch bug resistance.

Differences in resistance at different stages of growth of a plant have been matters of common observation; yet differences in age at testing may result in conflicting statements regarding the status of varieties. If grasshoppers must taste a strain of corn before showing non-preference for it, one bite may destroy a seedling, while a half-grown plant provides many "tastes." This may be the explanation why greater differences in grasshopper resistance in corn have been observed in mature plants than in seedlings. In tests with seedlings the results secured before and after complete absorption of the material stored in endosperm may not agree. Such differences between young and old plants have been found in studies of chinch bugs on sorghums (Dahms 1948a). The differences in antibiotic effects of resistant compared with susceptible plants in regard to mortality, fecundity, and length of life were greater in seedlings than in older plants. The average number of eggs laid by females fed on seedlings of Dwarf Yellow milo was 99.4 and on seedlings of Atlas Sorgo 3.9. The average number of eggs laid on older plants of the same two varieties was 188.8 and 97.9, respectively. One variety, Feterita, reversed its position with regard to effects on biology of the chinch bug when tested as a seedling and as an older plant. In contrast to this marked antibiotic effect of the resistant plant seedlings, such young plants of all varieties are far more easily killed by chinch bugs in the field and progressively increase in tolerance as they increase in size (Snelling et al. 1937). In the Kuban region of the northern Caucasus the resistance of grapes to Phylloxera was reported to differ greatly in accordance with age, the
younger vines being more susceptible (Makarov-Kozhukhov 1931). Corn is generally more attractive to European corn borer moths near the time that the plant is in flower. The number of larvae surviving are also fewer in young corn plants and there are increases in the numbers surviving as the plant approaches time of silking. Viale (1950) was unable to maintain colonies of the corn leaf aphid, *Aphis maidis* Fitch, on either susceptible or resistant varieties of corn until the seedlings were several weeks old.

Some aspects of the relation of hybrid vigor to tolerance have been discussed in the preceding chapter. While this relationship has not been commonly reported in the literature on resistance, it is a prominent feature of the chinch bug resistance of corn and sorghums. In the latter case the tolerance resulting from heterosis interferes with the field classification of plants in early segregating generations for genes for other forms of resistance.

The presence of non-lethal infections of plant diseases undoubtedly often will affect the tolerance of plants to insect attack. Smith (1939) has reported a high correlation between the percentage of stem rust in wheat varieties and the percentage of wheat heads cut off by *Melanoplus mexicanus* Sauss. There were some exceptions to this preference exhibited by these grasshoppers. In the discussion following a paper by Schaper (1938) it was reported that Colorado potato beetles, *Leptinotarsa decemlineata* (Say), prefer to lay eggs on leaves of plants that are in poor condition and also that plants that have virus infections furnish better food for the insect. Thus it is necessary to be alert to the possibility that plant diseases may influence the expression of all three types of resistance: preference, antibiosis, and tolerance.

Genetically early or late strains of commercial plants have been utilized fairly often in the control of insects on crop plants. Perhaps the case that is best known to entomologists is that concerned with the boll weevil, *Anthonomus grandis* Boh., of cotton. This insect caused plant breeders to make a complete change in the time of maturity of the cotton varieties used in the area occupied by this insect (Ware 1936). The host evasion resulting from the early varieties that finally were grown reduced the damage caused by the boll weevil, but possibilities are still available for improvement in resistance to boll weevil in cotton. In connection with differences in maturity one should remember that the part used by an insect for food may mature at a different rate from that part used by man.
as a criterion of maturity. Snelling and Hoener (1940) have discussed the relationships between some measures of maturity in maize, pointing out that while there are correlations between various measures of maturity there also are differences in this respect among strains. Insects do not react alike in response to the different maturities of even one species of plant. Huber et al. (1934) have given an excellent example of this in a study of the relation between the silking date of 150 corn hybrids and varieties and infestation by the earworm, *Heliothis armigera* (Hbn.), and the European corn borer, *Pyrausta nubilalis* (Hbn.). The correlation with maturity was positive in the case of the earworm, negative in the same varieties when the borer was studied (Fig. 16). Preference for a certain part of the plant or stage of development, or ability to thrive only on certain parts are the factors usually involved together with the synchronization of plant and insect life histories. Day length and other environmental conditions affect the expression of maturity as varieties are moved from place to place so that a variety that exhibits host evasion in one place may not do so in another. This situation may be particularly disturbing if both host evasion and resistance occur in the group of varieties under study.

The factors discussed above are those which affect the expression rather than the permanence of resistance. As mutations resulting in resistance have occurred in the past, so reverse mutations resulting in susceptibility may be expected on rare occasions. In horticultural varieties that are propagated vegetatively, there are several instances in which the genes for insect resistance are dominant and appear to have been carried for a long period of time in the heterozygous condition. This has been particularly true of the resistance of apple to the woolly apple aphid, *Eriosoma lanigerum* (Hausm.) (Crane et al. 1936) and the resistance of raspberry to the aphid, *Amphorophora rubi* Kalt. (Schwartze and Huber 1939). There have been some records of apple varieties that were resistant in one area or country and susceptible in another. Among the possible explanations of such reports is that of a reverse somatic mutation resulting in susceptibility. Bud mutations have been well discussed by Shammel and Pomeroy (1936) who point out that most combinations of characters that may be brought about by cross-pollination are also likely to be found as bud sports. In dealing with resistance which results from plant mutations it is necessary to remember that different mutations may give the same final result so far as resistance
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**Fig. 16.** Infestations of the same varieties, hybrids and inbreds by corn earworm, *Heliothis armigera* (Hbn.), lower, and by European corn borer, *Pyrausta nubilalis* (Hbn.), upper, are correlated differently with maturity as measured by days from planting to silking. The positions of various strains is indicated by the numbers, circles or crosses. (After Huber, Polivka and Savage 1934. Courtesy Ohio Agr. Expt. Sta.)
in the field is concerned but may reach it through very different means; these means may be modified differently by the same environmental factors.

FACTORS PRIMARILY CONCERNED WITH THE INSECT

In addition to the group of factors that modify the expression of resistance in the plant there are groups of factors which modify the responses of the insect to the plant or which affect the final results. These modifiers of the expression or permanence of resistance are not all present in each insect-plant relationship but all merit consideration in each problem studied.

Instar and size of population; fluctuation in populations. The nymphal and larval stages of insects differ from each other and from the adult in various ways in respect to food. At one extreme are those species and groups of species in which the adult is morphologically incapable of taking food, e.g., the silkworm moths. Here the female usually emerges from the pupa with all eggs well developed and ready to be laid soon after fertilization. At the other extreme are those forms in which both adults and young use the same food and more or less development of the eggs occurs after the adult appears. Between these extremes are those in which there is a difference in the food of the adult and young, and considerable variation in the amount of development of the eggs. When the adult takes little or no food, the effect of the larval food plant on the fecundity of the adult may be measured directly. When eggs are developed over a longer period of adult life, the food of both young and adult must be considered in looking for any antibiotic effect of the food plant.

The amount of food consumed by various larval or nymphal instars differs greatly. Wolcott (1925), in a study of both plant- and animal-feeding insects, found that the ratio of the weight of the insect to the weight of food required to produce the adult varied from 1:3 to 1:9. Davis and Satterthwait (1916) have shown graphically the average amount of corn foliage eaten by the armyworm, *Spodoptera exigua* (Haworth), in each instar. Of a mean total of 41.39 square inches more than 34 square inches were eaten in the last instar, over 5 square inches in the 5th, and a little more than 1 1/2 during the other 4 instars. Where large populations of leaf-consuming insects are feeding on a group of varieties, the rela-
tive status of injuries to such varieties will change from day to day, fluctuating with the amounts of leaf surface consumed. Likewise, such insects as aphids increase in numbers under favorable conditions at an alarming rate. Each female greenbug, *Toxoptera graminum* (Rond.), can give birth to 2 or 3 young a day and lives for 20 to 30 days; the young begin to reproduce at an age of about 10 days. During the growing seasons only females are produced.

Estimates of numbers and of injury by these insects under some conditions are subject to change almost over night.

Among some insects the kind of food used or required changes with the different instars. This has been especially marked in the European corn borer, whose early instars of the first or the single generation strip off the upper surface of the young leaf or make holes in it. Later instars burrow into the midribs, leaf sheaths, etc., and only the last few instars are stalk borers. Genetic characters for resistance in the plant related to differing food habits of the several larval stages may be expected.

The insect populations in the field normally fluctuate widely from year to year and from place to place. If there are several generations a year, the early populations are usually smaller than the later
ones. Preference for certain sorghum varieties by chinch bugs is more easily recognized in the field when numbers of bugs are few than when they are many (Snelling et al. 1937). Some factor other than the number of insects may be the basic reason for this situation. The relation of numbers of insects to tolerance is a commonly observed one but the relationship may have unexpected results. For example, at Lawton, Okla., in 1934 a hundred F\textsubscript{1} lines of a cross between a resistant and a susceptible sorghum variety were exposed to chinch bug infestation in the field. In counts of dead plants and in a visual classification of the rows as to susceptibility made at about the middle of July, susceptible strains were in the minority, indicating a dominance of resistance. Later in the summer a classification of the same plants on a somewhat different basis put the majority of the strains in the susceptible groups, indicating the dominance of susceptibility. During the intervening days the chinch bugs had continued to feed and to increase in size and numbers (Snelling et al. 1937). The effects of these increases in the insects probably affected mostly the plants that were heterozygous for the resistance gene or genes.

Importance of correct insect identification; specific differences in food habits of closely related species. The importance of correct identification and separation of effects of the insect or insects concerned in resistance studies cannot be overemphasized. Because of inaccurate identifications an appreciable amount of the observations on insect resistance is open to question. Likewise, mixtures of species cannot be studied together unless it is first shown that the species concerned are identical in kind of injury done, in food plant varieties preferred, and in effect of different plant varieties on the insect. The fact that two or more insects belong in the same family or genus is a totally insufficient basis for assuming—as has been done sometimes—that plant varieties will react in the same way to the several insect species. Information on resistance to "thrips," "leafhoppers," "aphids," "cutworms," or "borers" is of questionable value unless species involved have been correctly identified or unless there is little possibility of more than one species being present. Some of the discrepancies in reports on insect resistance undoubtedly stem from misidentifications of the insects concerned.

Some groups of insects have been notoriously difficult to identify because of their superficial similarity. As a good example, the small green leafhoppers of the genus \textit{Empoasca} may be cited.
Many species can be distinguished only on the basis of the internal male genitalia. Females ordinarily can be separated only by rearing male progeny. This method of study was worked out first by DeLong in 1931 for the United States and has been employed in later studies by others (for example, Smith and Poos 1931; Poos and Wheeler 1943). These later studies have shown that species of *Empoasca* distinguished in this manner may differ in biology, host plant preference, and method of feeding.

The aphids are another group that require microscopic study for certain identification. Here the problem is somewhat different, for the species are frequently polymorphic, migrating between a summer and a winter host, on which their superficial difference in appearance may be considerable. The forms of the common species are fairly well known but among less studied aphids some of the different forms of a species may not have been described. Related species often differ in respect to host plants and feeding habits. It has been found that in some species of aphids the piercing mouth-parts or stylets usually pass between the cells while in other species the stylets are thrust through the cells of the plant (Smith 1926). When studying the aphids on raspberry, Winter (1929) found that the variety Herbert was resistant to *Amphorophora rubi* (Kalt.) but not to *Aphis rubicola* (Oestlant).

About 85 per cent of all insects, those with complete metamorphosis, pass through a larval stage that is completely different from the adult in appearance and sometimes in habitat and food (Peterson 1948). In some genera the adults are much alike, while the larvae are strikingly different in structure and appearance. This has come about because the two stages are exposed to different environmental conditions and may evolve at different rates. Hence sometimes related adults are easily separated taxonomically but the larvae are scarcely distinguishable. There are, for example, in the United States, three species of *Diatraea* that may bore into corn: *D. saccharalis* (Fab.), the sugar cane borer; *D. crambidoides* (Grote), the southern cornstalk borer; and *D. grandiosella* Dyar, the southwestern corn borer. All differ in their habits and in injury done. While the adults are distinct, the larvae can be separated only by the relative positions of three setae on the head (Peterson 1948). Differences in respect to food extend also to taxonomic and biologic categories below the rank of species. Hovnitz (1944, 1948a, 1948b) in studies of
the sulphur butterflies found that *Colias philodice philodice* showed marked preference for red clover as a food plant. *Colias philodice eurytheme* and *Colias philodice hageni* both prefer alfalfa. The first two subspecies are interfertile but when larvae of either are reared on the non-preferred host, they show retarded development, high mortality, sterility, and sexual apathy. Some intermediate *F₁* hybrids between *eurytheme* and *philodice* are fertile when the larvae are reared on either alfalfa or white clover (*Trifolium repens*).

**Biotypes or biological strains of insects in relation to resistance.**

There are situations when it may be necessary to look further than specific or subspecific differences for insect factors that influence the expression or permanence of resistance. Many biological strains of insects have been described that are concerned with a diversity of physiological reactions but which usually show no morphological distinctions (Thorpe 1930, 1940; Hayes 1935; Smith 1941).

Although a number of biotypes of insects connected with host-plant species are known, including possibly the grape phylloxera on grape, only one or two concerned with host-plant varieties have been worked out in considerable detail. Evidences of a few others have been presented in the literature. Dahms (1948b) has secured some evidence that greenbugs (*Toxoptera graminum* (Rond.)) from Oklahoma and Mississippi differed in the length of time they required to kill Reno barley and Tennex oats. Significant differences were also found in the number of nymphs produced by bugs from the two areas when grown on Denton wheat. The strains of European corn borer present in the United States (Arbuthnot 1944) may have other qualities with respect to food plants (Beall 1944) associated with their primary characteristics of single and multiple generations. Harrington (1943) working with pea aphids on peas found clear-cut differences among lines isolated from different localities in respect to their abilities to reproduce on three varieties of garden peas. Those lines producing the largest progenies were also largest in size. Later studies (Harrington 1945) showed that the pea aphid, *Macrosiphum pisi* (Kalt.), was made up of a complex of at least five races as measured by comparative feeding injury, rates of reproduction on different varieties of peas, and body size. A total of 31 different parthenogenetically pure lines was analyzed...
in detail. The strains giving higher reproductive rates appear to be more vigorous in general.

The first study of biotypes in connection with insect resistance was made by Painter (1930; Painter et al. 1931) in seeking an explanation for differences in hessian fly (Phytophaga destructor (Say)) infestation of the same wheat varieties in eastern and in central Kansas. Details are given in the section on the resistance of wheat to this insect. The hessian fly populations in the central part of Kansas were shown to consist of a mixture of at least two types, one of which was similar to that found in the soft-wheat-growing area of eastern Kansas and states farther east. The test variety Illini Chief sel. 223415, a winter wheat, was resistant in central Kansas but susceptible in the soft-wheat belt. The fly strain able to infest Illini Chief appeared to be genetically dominant to the biotype that could not infest this variety. The strain able to infest Illini Chief also appeared to be easier to handle in the greenhouse at that time and in tests since that time. Walkden (1945) found a somewhat smaller number of eggs in females of the fall generation collected in the hard-wheat area in comparison with those collected in the soft-wheat areas farther east. Chesnokev (1939) found similar differences in two geographic regions in the U.S.S.R. regarding the ability of populations of hessian fly to infest the variety Illini Chief. Thus the suggestion of a separate introduction into Kansas (Painter et al. 1931) may be correct, but this merely changes the locality and does not solve the problem of origin of the strains.

Cartwright and Noble (1947) published data that supported and considerably extended the original information on biotypes of hessian fly. They showed that Dawson and a number of other winter wheats were resistant to hessian fly in California but susceptible in Indiana. Fly populations from the two localities retained their respective infestation abilities under cages in the same greenhouse. Certain spring wheats, including Ill. No. 1 W38, were resistant at both places. For six years, in spite of continuous attempts involving many thousands of insects, it was impossible to find fly from Indiana that would survive beyond the second generation on Ill. No. 1 W38 or similar varieties. In 1943, however, a population was selected from the general population of Indiana flies which gave a markedly higher infestation on Ill. No. 1 W38 and similar varieties that were usually
resistant and which apparently also carry the same gene for resistance. It is notable that certain other spring-wheat varieties carrying other genes for resistance were not heavily infested by the population able to infest Ill. No. 1 W38. In this situation the insect biotype has been attuned to a particular genetic expression in the plant.

There appear to be two general types of biological races in insects so far as resistance in plants is concerned. One type, such as is represented by the aphids on peas, is merely a larger, more vigorous strain. The other type, illustrated by the Ill. No. 1 W38 strain of hessian fly, is adjusted in some way to the particular conditions resulting from the presence of a particular gene (Hs) in the plant. In this case certain elements of the insect physiology must fit specific elements of the plant physiology as a key fits a lock. The same situation has occurred in the development of strains of insects that are resistant to insecticides. Generally the resistant strain represents one that is more vigorous in various ways and therefore resistant to several insecticides (Smith 1941; Quale 1943). There appears to be one or more cases (Knipling 1942; Persing et al. 1942) in which the resistance to insecticides was more specific. In nature both types of biological races might be found in a single population.

In the resistance of the California red scale, *Aonidiella aurantii* (Mask.), to HCN fumigation the trait was found to be an incompletely dominant sex-linked character (Dickson 1941; Yust et al. 1943). There is no reason to doubt that at least most cases of biological strains, whether they concern resistance to insecticides or abilities to infest or damage insect-resistant plants, are basically the result of individual genes or groups of genes. Such genes, especially those involving general vigor, are part of the concealed variability carried by plant and animal species and are selected out as survivors from particularly rigorous situations. Such situations often give a high mortality, with the few individuals which are less affected by the adverse conditions surviving out of a population. These are characteristics which, if found in an experiment, should lead one to suspect the presence of biological strains.

Both the biotypes resistant to insecticides and the insect biotypes able to feed on resistant hosts have been relatively few in comparison with the total number of insects under observation in these fields. They may be expected to occur on some occasions and
should be planned for in any project on insect resistance in plants. Such biotypes have affected the expression of resistance and caused discrepancies in results with the same varieties in different localities. They also can affect the permanence of resistance by replacing a previously dominant biotype.

There is evidence that such a change may take place in connection with the distribution of the wheat variety Pawnee, which is resistant to only part of the hessian fly population. Information on this variety is given in the chapter on resistance to insects in wheat. It is now the most commonly grown variety in certain parts of the hard red winter-wheat area and has considerably reduced the fly population in those parts of the area where it is resistant. Whether the strain, able to feed on Pawnee, will replace the present mixture of strains is dependent on at least the following variables, some of which are unknown:

1. The original proportion of the population capable of feeding on the resistant variety.
2. The genetic relationships of the strain of fly to other strains.
3. The ecological adaptations of the strain of fly feeding on the resistant wheat.
4. The number of genetic factors and resistance characters involved in the resistance of wheat.
5. The purity of the resistant variety as grown on farms.
6. The proportion of acreage of resistant to susceptible varieties in a given area.
7. The thoroughness with which other control measures are practiced, especially the plowing under of stubble and volunteer plants.

Many of these variables apply equally in similar cases involving biological strains.

Under the most unsatisfactory conditions with respect to permanence of resistance the question resolves itself into one of whether the plant breeder and entomologist will be able to keep satisfactorily ahead of nature. In the similar field of breeding for resistance of plants to disease the answer has certainly been in the affirmative. The variety Pawnee apparently has already prevented an outbreak of hessian fly in central Kansas and paid for its cost of production (Painter and Jones 1948). It continues to show satisfactory resistance. As a defense against such a shift in the fly population wheat hybrids that are resistant to the entire fly population are now being tested for agronomic quality and
have given favorable records. A change in genetic factors for resistance or a combination of several genetic factors constitutes a valid defense against biological strains. Biotypes may be concerned either with preference or antibiosis but particularly with the latter in the examples studied so far.

Learning in insects; pre-imaginal olfactory conditioning and related phenomena. Insects are generally thought of as creatures of instinct with highly fixed behavior patterns. They do have a certain amount of plasticity in their behavior, which in some forms represents a simple form of learning according to Thorpe (1943, 1944), who has reviewed our knowledge on this subject. As in other studies of insect behavior the principal observations and experiments on learning have concerned the ants, bees, and wasps, where complex behavior patterns are more common than in other insects. Relatively few exact studies of plant-feeding insects have been made although the unsupported statement or idea that a particular insect “learned to use a new host plant” is not infrequent in the literature. In regard to modifications of resistance, learning in insects concerns primarily preference or non-preference and not antibiosis. In plant-feeding insects, so far as our information goes, learning concerns those types which Thorpe (loc. cit.) includes under habituation, trial and error, or associative learning, and latent learning, including pre-imaginal olfactory conditioning. Thorpe reviews several experiments in which the natural repellent effect of an odorous substance could be transformed into a high degree of tolerance or indifference by exposing the adults soon after emergence to an air stream bearing the odor. The experiments were those of Thorpe (1938, 1939) and Cushing (1941). Presumably the same kind of habituation can occur when the non-preference for a resistant variety is the result of a repellent odor or taste. It appears that this kind of learning would occur in nature only when there was almost universal planting of the resistant variety. No clear-cut examples have been reported.

Trial and error or associative learning may be concerned in the non-preference type of resistance. Mayer and Soule (1906) found that larvae of the monarch butterfly, Danaus plexippus (L.), persisted in a negative reaction to certain leaves other than those of the milkweed, Asclepias, if these were offered again within about 1½ minutes following a previous tasting experience. If
offered after that period, the larva would always take a few bites, then withdraw, snapping its mandibles and thrashing from side to side. Apparently some kind of associative memory persisted for this short period. All the experimental evidence quoted by Thorpe (1943, 1944) regarding associative learning is concerned with “avoidance of punishment” rather than learning associated with a reward. Both types could be concerned in modifying the status of a resistant variety. In connection with learning to run mazes a comment is made that individual cockroaches and individual ants exhibit wide differences in learning ability. Such differences, if they occur in phytophagous species, could be a source of variation in resistance.

The first experimental evidence on pre-imaginal olfactory conditioning was derived from a study of Nemertis canecenis (Grav.), a hymenopterous parasite of larvae of Ephesia kuhniella Zell., the Mediterranean flour moth (Thorpe and Jones 1937). The parasite finds its prey by odor but can be induced to oviposit on the larvae of Meliphora grisella (F.), a small wax moth, if the latter is contaminated with the odor of Ephesia. When parasites reared on the two host insects are separately tested in an olfactometer, those reared in Ephesia show no reaction to the odor of Meliphora. Those reared in Meliphora showed an increased reaction to this host of about 20 per cent. This new preference status did not increase after rearing for eight generations on the new host. On several occasions Thorpe has pointed out the possible relation of this type of latent learning to the problem of the origin of host-plant races in insects. Cushing (1941) has furnished some confirmatory evidence in experiments on Drosophila reared on various media. The possibility of these conditioned responses being passed on from larva to adult has been discussed by Uvarov (1933), who points out that the nervous systems of insects are unaffected, or practically so, by metamorphosis. Thorpe (1938) considers that the pre-imaginal conditioning is the association of the given constituent (odor) with a favorable environment as a whole rather than with a particular part of it. There have been a number of experiments reported in the literature of plant feeding insects that could be interpreted as examples of this type of learning, but no clear experimental evidence is available in most of them.
Changes by insects from one host plant to another. Entomologists record a considerable number of insects that have changed from their known or supposed native hosts to cultivated plants. The term food plant or host plant is here used only for those plants on which the insect can maintain a population apparently indefinitely under the conditions of study. If we omit those insects that apparently have always had rather general feeding habits, such as the armyworm and certain species of cutworms and grasshoppers, the number of insect species that have been recorded as changing hosts is relatively small compared to the total number of economic insects that have been studied. We rarely have exact observations, still less experimental evidence, of exactly what has happened when insects have changed hosts. The study of insect resistance in plants may shed some light on these occurrences and any information we can gather about the changes these insects have made may likewise be of interest to workers in insect resistance.

Experiments on insect resistance have provided evidence that differences between plants used as hosts and those that are not may be considered to be combinations of two groups of factors: (1) the behavior pattern by which the insect exhibits a preference for certain plants through reaction to a certain characteristic, or characteristics, of those plants, and (2) the effects on the insect that follow after an insect uses a particular plant for food. As is indicated in the accompanying table (Table 2) these two groups of factors by their interactions make possible a wide range of plant-insect relationships from full susceptibility to immunity. Since there may be many degrees of preference, repellance, and antibiosis, further subdivisions beyond those indicated in the table also exist. Moreover, different combinations of behavior reactions and antibiotic effects may apparently achieve the same results. A change to a new host plant should involve some change in either preference or antibiosis, providing the new host is not already within the behavior pattern and digestive capabilities of the insect. The latter was presumably the situation when the Colorado potato beetle transferred from the buffalo bur, *Solanum rostratum*, to the cultivated potato, *Solanum tuberosum*. Both plant species are attractive to the beetle and, judging from experiments reported in the section on insect resistance in potato,
both serve equally well as food for adults and young. The trans­fer to plant species and varieties originally within the physiological possibilities of the insect undoubtedly has been the most frequent situation among those host-plant changes that entomologists have observed.

Changes to a non-preferred host that has remained unchanged must involve some form of learning, probably pre-imaginal olfac­tory conditioning, or a mutation affecting the insect's nervous mechanism concerned with response to the plant characteristics. Any change to a host plant that causes antibiotic effects in the insect apparently must involve mutations in the insect physiology either at the time of the change or during the past history of the insect. Changes to a host which is both non-preferred and also causes antibiosis must involve complex changes unless the cause of both types of resistance is basically the same. So far, no situations of this latter kind have been analyzed unless it is true of the resistance of *Solanum demissum* to the Colorado potato beetle.

**Table 2** **EFFECT OF ANTIBIOSIS AND INSECT BEHAVIOR PATTERN ON THE AMOUNT OF PLANT RESISTANCE AND ON THE DEVELOPMENT OF BIOLOGICAL STRAINS**

<table>
<thead>
<tr>
<th>Amount of antibiotic effect on the next generation</th>
<th>Behavior reaction</th>
</tr>
</thead>
<tbody>
<tr>
<td>Normal development</td>
<td>Preference</td>
</tr>
<tr>
<td>Slow development often small size, some morta­lity or reduced fe­cundity</td>
<td>Low resistance</td>
</tr>
<tr>
<td>High mortality but de­velopment near nor­mal among a very small percentage of individual insects</td>
<td>Resistance, but development of biotypes likely</td>
</tr>
<tr>
<td>Little or no develop­ment of eggs or young</td>
<td>High resistance</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Amount of antibiotic effect on the next generation</th>
<th>Behavior reaction</th>
</tr>
</thead>
<tbody>
<tr>
<td>Normal development</td>
<td>Non-preference random infesta­tion</td>
</tr>
<tr>
<td>Slow development often small size, some morta­lity or reduced fe­cundity</td>
<td>Resistance</td>
</tr>
<tr>
<td>High mortality but de­velopment near nor­mal among a very small percentage of individual insects</td>
<td>Resistance, de­velopment of biotypes less likely</td>
</tr>
<tr>
<td>Little or no develop­ment of eggs or young</td>
<td>High resistance</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Amount of antibiotic effect on the next generation</th>
<th>Behavior reaction</th>
</tr>
</thead>
<tbody>
<tr>
<td>Normal development</td>
<td>Repellance</td>
</tr>
<tr>
<td>Slow development often small size, some morta­lity or reduced fe­cundity</td>
<td>Resistance</td>
</tr>
<tr>
<td>High mortality but de­velopment near nor­mal among a very small percentage of individual insects</td>
<td>Resistance, de­velopment of biotypes un­likely</td>
</tr>
<tr>
<td>Little or no develop­ment of eggs or young</td>
<td>Immunity</td>
</tr>
</tbody>
</table>
Most of the experimental studies on changes in insect food plants have been made in connection with attempts to demonstrate the inheritance of acquired characters or in connection with studies of Hopkins’ host-selection principle. Good reviews of studies along these lines have been written by Larson (1927), Imms (1937), Thorpe (1930, 1940), and Simmonds (1944), and most of the work need not be reviewed again here. There seems to be every reason to accept the conclusion of these reviewers that the inheritance of acquired characters need not be invoked to explain the results. The studies by Craighead (1921) in connection with the host-selection principle have been among the most comprehensive experimental studies of the change in host plants by insects. The principle as defined by Hopkins and quoted by Craighead is that “an insect species which breeds in two or more hosts will prefer to continue to breed in the host to which it has become adapted.” The experiments mentioned above were done with 11 species of Cerambycid or round-headed wood boring beetles on dead wood. In this latter respect the subject matter is different from the living plant material otherwise considered here.

Throughout Craighead’s experiments attention is frequently called to the high mortality of young larvae that occurred when a beetle was forced to oviposit on a new host. There were experiments in which a few surviving individuals served to establish a new strain on a host plant species, previously resistant to the insect. This type of selection of what are apparently mutant strains out of a general population is the same type of result as has been found in the study of hessian fly resistance in wheat. In other experiments described by Craighead, the results appear similar to those described above as pre-imaginal olfactory conditioning.

Larson (1927) after five years of study reported that the host-selection principle did not apply to the cowpea weevil, Callosobruchus maculatus (F.). In his experiments no evidence of a more or less permanent change of host was noted. This species normally breeds in Vigna sinensis but has been reared on certain varieties of other species of beans. On some of these, such as soybeans, Soja max, not more than three generations could be raised, and the population gradually died out. Hence no evidence was secured, either of the formation of biological strains or of pre-imaginal olfactory conditioning.
Thus changes in host plants appear likely to occur more frequently in some species and perhaps some groups of insects than in others. An examination of the fragmentary data on other species of insects that have changed their host plants since records have been kept or which have been studied experimentally during such a change, seems to show that they fall into three general patterns: (1) The old and the new hosts were both within the range of behavior reactions and physiology of the insect, (2) a change has occurred in the behavior pattern of the insect by way of some form of learning or by mutation, and (3) a change has occurred, by way of mutation and selection, in the physiology of the insect so that it can utilize the new host plant as food. It is best to consider the possibility of change to be a species characteristic and in resistance problems to study each case separately.

Relative permanence of physiological characters in insects. The permanence of resistance as an insect-control measure is concerned often with the permanence of mutant characters both in the plant and in the insect but particularly in the latter. It is essentially a problem in experimental evolution, the development of host relations, rate of mutation, selection, etc. Any answer to the question of permanence depends to a considerable extent on the mechanisms of resistance involved and will differ in different cases. The three basic characteristics involved in resistance, namely, preference, antibiosis, and tolerance, frequently are concerned with physiological characters either in the insect or in the plant or in both. Physiological characters frequently have been considered less stable than morphological ones. Kinsey (1929) has shown that, in the gall wasp genus *Cynips*, physiological characters are fully as stable phylogenetically as morphological ones. There are many cases where physiological characters of orders and families of insects are quite as characteristic as are morphological ones and are probably as old (Brues 1939). The division between the order Homoptera, leafhoppers, aphids, etc., and the order Hemiptera, containing the bed bug, chinch bugs, assassin bugs, etc., occurred in the early geologic history of insects since Homoptera of Permian age are known. The species of Homoptera all feed on plant sap, the other order contains both plant- and animal-feeding forms. The distinction between the plant- and animal-feeding forms must have arisen long ago. Hence there seems to be no reason for thinking that physiological characters concerned with food, such as those that form the basis
of most resistance, may be any less permanent than the morphologi­
cal characters with which the entomological taxonomist deals. Both are subject to mutation and the laws of inheritance and natural
selection.

LIMITATIONS ON THE USE OF RESISTANCE AS
AN INSECT CONTROL MEASURE

The use of resistance is dependent on the finding of mutant plant
forms carrying the necessary resistance. There may be various
causes that decrease the advisability or the possibility of the use of
resistance in insect control. The lack of plants or varieties that
carry an adequate degree of resistance would render its use im­
possible. In some of the literature on insects or plant breeding an
immune plant or variety has been considered necessary. Varieties
that are immune to particular insects are exceedingly rare but a con­
sideration of achievements in insect resistance shows that immunity,
however desirable, is not necessary. The search for resistant strains
of plants must not be considered as hopeless until all available germ
plasm has been carefully surveyed. Other things being equal the
chance of finding resistant types will be proportional to the number
and multiformity of the plants studied. If satisfactory resistance
is found only in species related to the crop plant, transfers of the
genes concerned are more difficult and take longer but often can be
made. As a general rule the ease of incorporating genes for re­
sistance into a commercial crop depends partly on the available
knowledge of genetics in the crop and partly on the possibility of
maintaining an insect population by which resistance may be tested.

There may be occasions in which the mechanism of resistance
is completely incompatible with characters desired in a crop plant.
So far no examples of these are available but a few possibilities may
be discussed. We know little of what causes the phenomenon of
antibiosis in resistant plants. If man and an insect feed on precisely
the same part of a plant, it is conceivable that varieties deleterious
to the insect might also be deleterious to man. Usually this ques­
tion does not require our consideration because the insect is not
feeding on a part of the plant eaten by man or uses only a segment of
the part used. The same considerations apply to domestic animals.
Here again clear-cut examples of these relationships are lacking.
The resistance to certain stalk borers in sugar cane has been asso­
ciated with high fiber content of the cane, a character which may
be undesirable when excessive. If the relation between resistance and fiber is an obligatory one, it may be necessary to decide between the cost of handling the extra fiber and the cost of the injury done by the insect, or of controlling it by other means. Conditions of this kind may require a choice of the alternatives.

The relation of resistance to insect habits and taxonomy. It has been common observation that insects differ in the range of diversity of their food plants. A few are confined to a single species of plant, others utilize a number of species of a single plant genus or a family, still others are recorded as feeding on many kinds of plants scattered throughout the higher plant orders. The question naturally arises whether resistance is to be expected commonly in insects with restricted or more inclusive food habits. On the basis of current theories it would be expected that resistance to monophagous insects would be more common than resistance to oligophagous species and that it would be almost a waste of time to look for resistance to polyphagous insects in any of their many host plants. A review of the food habits of the individual insects for which it has been possible to find resistant plants shows that the likelihood of finding such varieties is not related to the number of plant species on which the insect has been recorded as feeding. It is more likely to be influenced by the number of plant varieties available for study. This is encouraging because many insects of economic importance would be classified as polyphagous. Few species of insects have a wider range of food plants than the corn earworm, *Heliothis armigera* (Hbn.); yet considerable progress has been made in breeding corn resistant to this insect.

There may be, however, some relation between the taxonomic classification to which an insect belongs and the possibility of success in using resistance as a control measure. So far, little progress has been reported in breeding for resistance to any species of the plant bug family Miridae. However, there have been no extensive studies of any of these. The fact that Andrews (1923) found it possible to use induced resistance by soil treatment against the tea mosquito bug (*Helioptilus theivora* Waterhouse), which belongs to this family, suggests that genetic resistance is also possible.

In contrast, the plant lice, or Aphididae, have been the most frequent group for which resistance in plants has been reported. This may have occurred because of their ubiquity as plant pests and the ease of studying them. However, no trend in relation to the
number of reported hosts is discernible. Miss Patch (1938) in her catalog of the food plants of aphids gives the information utilized here for representative species to which plant resistance has been studied. Several varieties of raspberry have been reported as resistant to the aphid, *Amphorophora rubi* Kalt. (Winter 1929; Huber and Schwartze 1938), which has been reported to feed on ten species of plants all in the genus *Rubus*. Resistance to the pea aphid, *Macrosiphum pisum* (Kalt.), has been reported in garden peas (Searles 1935; Maltais 1936) and in alfalfa (Dahms and Painter 1940). Patch (1938) records this aphid from 58 species in the *Leguminosae* and six in other plant families. The greenbug, *Tettix* *optera graminum* (Rond.), is likewise recorded from 62 species of grasses (Gramineae) and six species of plants in other families. High resistance to greenbugs has been reported (Atkins and Dahms 1945) in barley varieties, medium resistance in wheat, and low resistance in oats. The degree of resistance in this case is quite closely proportional to the diversity of varieties available for study in the three crops. *Aphis gossypii* Glov., the melon or cotton aphid, has one of the longest lists of host plants recorded for any aphid—more than 280 plant species scattered through many families of the Angiospermae. Despite this impressive list, a high degree of resistance to *A. gossypii* has been found in varieties of cantaloupes (Ivanoff 1944) and some resistance has been reported among strains of cotton (Annand 1943), the two most important economic hosts of this insect. Thus the available information from a study of plant resistance to insects gives no suggestion of why some insects utilize many plants as food while others can use only one or two. This situation may change when more is known of the details of the mechanisms of resistance. Also we cannot forecast at present the possible speed with which resistance to an insect is likely to be found in a particular crop.

A multiplicity of factors in the environment may affect the expression of resistance. These may be effective either through the plant, or the insect, or both. Results have been reproducible in studies of insect resistance when care has been taken to reproduce a similar environment. These various factors that affect the expression of resistance have often been responsible for a part of the discrepancy in results sometimes secured by various investigators under different environmental conditions. That they do occur does not change the fact of the inheritance of resistance that must form
the basis of any plant breeding. A lesser number of factors affects the permanence of resistance. These mainly concern changes in the genes of either plant or animal. Processes are possible by which changes in the behavior of an insect may affect the permanence of resistance. While these possibilities exist and should be recognized, experimental evidence of loss of resistance has been very scarce.

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INSECT RESISTANCE IN CROP PLANTS


120 INSECT RESISTANCE IN CROP PLANTS


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CHAPTER IV
RESISTANCE TO INSECTS IN WHEAT

I. Introduction and information about the crop and insects to which resistance has been reported.

II. Resistance to hessian fly in wheat.
   A. Life history of the hessian fly.
      (1) Feeding and injury done by the fly.
      (2) Food plants.
   B. Early citations of resistance.
   C. Studies of resistance in wheat varieties at the Kansas Station and elsewhere.
   D. Biological strains of the hessian fly.
   E. The breeding and inheritance of resistance to hessian fly from sources in commercial winter wheats.
      (1) Development of Fuso 42 and Big Club 43 in California.
      (2) Information on inheritance of resistance to hessian fly in winter wheat at the Kansas Station, and production of Pawnee wheat.
      (3) Behavior of Pawnee under nursery conditions and in farmers' fields.
   F. Hessian fly resistance in spring wheats, foreign plants introductions, and in species other than *Triticum aestivum* (vulgare).
   G. Breeding for higher fly resistance from the spring wheats for use in hard red winter wheats.
   H. Breeding for fly resistance from the spring wheats for use in soft red winter wheats.
   I. The inheritance of resistance derived from spring wheats.

III. Resistance to the wheat stem sawfly, *Cephus cinctus* Nort., and related species.
   A. Biology of the wheat sawflies.
   B. Sources of resistance to wheat stem sawfly, and basis and inheritance of resistance.
   C. Production and characteristics of the wheat variety Rescue.

IV. Resistance to other insects in wheat.

V. Bibliography.
Wheat is the leading bread grain of the world and is grown wherever climatic and soil conditions are favorable in the temperate zone, especially in North America, Europe, China, Northwest India, Argentina, and Australia. The genus *Triticum*, to which wheat belongs, contains a number of species but from the commercial standpoint the most important are the bread wheat, *Triticum aestivum* L. (vulgare Vill.) and the durum or macaroni wheat, *T. durum* Desf. A varietal survey (Clark and Quisenberry 1948) made in 1944 shows 216 recognized varieties of wheat grown in the United States. The species of *Triticum* fall into three groups with vegetative cells of 14, 28, and 42 chromosomes respectively. Crosses between species with the same chromosome numbers are often fertile while crosses between species belonging to different groups show more or less sterility. However, more than half the acreage of hard red spring bread wheat now planted in the United States consists of varieties derived from interspecific crosses between parent species with 28- and 42 chromosomes, respectively. The varieties of wheat planted in the fall and ripening the following summer are called winter wheat; those planted in the spring and ripening the following summer or fall are spoken of as spring wheat. Ordinarily, winter-wheat varieties planted in the spring will not head while spring wheat planted in the fall is killed by the winter. Grains of either spring or winter wheat may be either "soft" or "hard," depending on the texture of the kernel and the relative amounts of protein and starch contained in it. The grain texture or quality is dependent in part on environment and in part on a number of genetic characters. The color red, amber, or white refers to the kernel and may be governed by one, two, or three genes, depending on the cross. Wheat is largely self-pollinated although the slight amount of cross-pollination varies somewhat with environmental conditions and the variety involved.

Major studies on resistance in wheat have been concerned with *Phytophaga destructor* (Say), the hessian fly, and *Cephus cinctus* Nort., the wheat stem sawfly. More or less detailed studies have been made concerning resistance or varietal differences to at least thirteen additional species or groups of species listed below (Packard 1941; Jones 1943).
RESISTANCE TO INSECTS IN WHEAT

Acrididae
Melanoplus spp. and others (Grashoppers)

Lygaeidae
Blissus leucopterus (Say) (Chinch bug)

Pestalotioidae
Chlorochroa uhleri Stahl (Green grain bug)

Aphididae
Toxoptera graminum (Rond.) (Greenbug)

Elatidae
Ludus aeripes Kly. (Northern grain wireworm)

Itonididae
Contarinia tritici (Kirby) (Wheat blossom midge)

Stodilphosis (= Clinodilphosis) mosellana (Geh.) (Wheat midge)

Chloropidae
Mermicys americana Fitch (Wheat stem maggot)

Chlorops pumilionis Bjerk. (= taeniopus Meig.)

Ocicnella frit (L.) (Frit fly)

Anthomyiidae
Hylemya (Phorbia) genitalis Schn.

Chalcidae
Harmolita grandis (Riley) (Wheat straw-worm)

Harmolita tritici (Fitch) (Wheat jointworm)

RESISTANCE TO HESSIAN FLY IN WHEAT

Life history of the hessian fly. The life history of the hessian fly is briefly summarized in Table 3.

Table 3 SUMMARY OF LIFE HISTORY OF HESSIAN FLY
(Adapted from McCollough 1923)

<table>
<thead>
<tr>
<th></th>
<th>Average Length</th>
<th>Minimum</th>
<th>Maximum</th>
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</thead>
<tbody>
<tr>
<td>Adult</td>
<td>42.6 hours</td>
<td>4 hours</td>
<td>147 hours</td>
</tr>
<tr>
<td>Eggs</td>
<td>4.8 days</td>
<td>3 days</td>
<td>12 days</td>
</tr>
<tr>
<td>Larval feeding period</td>
<td>11.4 days</td>
<td>9 days</td>
<td>17 days</td>
</tr>
<tr>
<td>&quot;Flaxseed&quot; larval and pupal resting period</td>
<td>11.7 days</td>
<td>7 days</td>
<td>26 days</td>
</tr>
<tr>
<td>Total</td>
<td>29.0 days</td>
<td>20 days</td>
<td>61 days</td>
</tr>
</tbody>
</table>

1 At 70°F. In the field the winter (about 5 months) is occasionally passed in the larval stage.
2 At 70°F and 70 per cent humidity. In the insectary this stage has been found to last as long as 4 years.

According to McCollough (1923) the average number of eggs laid was 97 per female and the maximum number, 320. In more recent work as many as 485 eggs have been laid by a single female. The eggs are usually laid on the upper surface of the leaf blade, the
larvae, upon hatching, migrating to the base of the leaf sheath. This migration requires from 12 to 25 hours and a mortality of 23 to 55 per cent has been recorded under favorable environmental conditions. Under unfavorable conditions the mortality may be 100 per cent. At the end of the larval feeding period the skin hardens and turns brown, and a new one forms beneath. The insect usually passes the winter in this stage which is known as the “flaxseed,” or puparia. When brought under suitable conditions of temperature and moisture the larva changes to a pupa within the “flaxseed.” Under favorable conditions most adults emerge in from 8 to 36 days, the average being about 19 days (Fig. 18).

In Kansas there may be as many as five broods each year. In the eastern United States and in other countries two or three broods appear to be the more usual number, one in the fall and two in the spring. On the Pacific coast there is usually no fall brood and frequently only one spring brood. The minimum length of life cycle recorded has been about 20 days.

Fig. 18. A hessian fly adult, *Phytophaga destructor* (Say).

*Feeding of the larvae.* The hessian fly belongs to the family Itonidae (Cecidomiidae), many of whose members cause the formation of galls. It is therefore not surprising that the injury by the larva of this insect is somewhat similar. The larvae appear unable to rupture the cell walls of the plant but secrete enzymatic or toxic substances, which in the case of susceptible varieties penetrate through several layers of plant cells and arrest the growth of the cells immediately beneath the developing larvae. The surrounding cells continue their growth about these immature forms, leaving a depression within which the larvae develop and finally change to “flaxseed” (puparium). The larvae feed on materials which come through the cell wall of the plant by diffusion but which is taken normally into the alimentary tract through the very minute mouth (Fig. 19).
In the fall the first evidence of infestation is the dark green appearance of the central leaf which is also shortened and appears broad and flat instead of round at the place where it emerges from the leaf sheath below. This is so because on susceptible plants elongation of the central leaf stops completely in about 48 hours after the larvae reach the normal feeding position. On resistant varieties elongation of the leaf occurs more or less normally but some chlorotic areas or lesions may appear after the leaf grows out. Later, in susceptible plants, the infested tiller usually dies though sometimes, in moderately resistant plants, it may recover in spite of the presence of the fly. Some plants of susceptible varieties are killed by the developing larvae, others form new tillers, obscuring the presence of infestation until the insects of the next generation damage wheat in the following spring. The relative numbers of plants killed by fall infestations depends on many factors, principally the variety involved, the intensity of infestation, the amount of moisture and fertility in the soil, and other conditions of growth during the late fall. Many plants are killed before winter sets in but there is clear evidence that infestation weakens the plants, resulting in greater winter killing than is normal for the variety.

In the spring the infestation may occur on any internode of the plant. Where there are two generations of fly, the flaxseed of the first generation are to be found on the basal internodes, those of the second generation on the upper one or two internodes. The larvae are usually to be found just above the point where the leaf sheath

FIG. 19. A cross section of stem of Kanred wheat (susceptible) and of a 5 day old hessian fly larva in place. Note the lack of growth of cells for several layers immediately below the larva.
joins the culm (Fig. 20). The injury is sometimes similar to that taking place in the fall. Some culms are prevented by the infestation from maturing heads, the internodes of others are more or less shortened and heads are produced, though frequently with much lowered yield. This lowered yield consists of a reduction in both the number and average weight of kernels and may amount to 25 or 30 per cent reduction in the average weight of grain of heads from infested stalks even when these are not broken. The damage most usually noticed by farmers is caused by the breaking over of the culm just before the time of harvest. This break takes place at the point where the stem is weakened by the feeding of the larvae (Fig. 21).

This insect hence does several kinds of injury both in the fall and in the spring, and resistance or tolerance may be developed to each kind.

_Food plants._ The hessian fly is able to feed on many different species of grasses of the tribe Hordeae, but the principal food plant of economic importance is the common bread wheat (_Triticum aestivum_). The insect will develop on certain varieties of barley (_Hordeum_) and rye (_Secale_). The rye variety Balbo, however, is practically immune.

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**Fig. 20.** Flaxseed of the spring generation of hessian fly in place above the nodes on wheat culms. The feeding of the larvae has resulted in various degrees of shortening of the internodes.
to fly. It has also been reared on most species of *Triticum* and one or more species of *Agropyron, Agrostis, Aegilops, Bromus, Elymus, Hordeum, Lolium, and Phleum*. It is very important to notice, however, that where a sufficient number of species, or varieties of species, of these genera have been tested, there is a wide variation in the amount of infestation on strains pres-

<table>
<thead>
<tr>
<th>YIELD FROM HEADS OF 75 TENMARQ WHEAT CULMS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Uninfested by hessian fly.</td>
</tr>
</tbody>
</table>

![Image of wheat stalks showing yield comparison](attachment:image.png)

**FIG. 21.** The reduction in yield which follows the feeding of one or more hessian fly larvae on a wheat culm often amounts to as much as 25% but passes unnoticed by the wheat grower. There is a decrease in both number and weight of kernels. The lodging of some of the stalks following infestation results in a greater decrease in yield even if the heads are picked up in harvesting.
ent in comparable tests (Jones 1936, 1938, 1939). There are a few records in the European literature of oats being infested by hessian fly but these records almost certainly refer to the similar and closely related species *Phytophaga avenae* (Marchal) rather than to *P. destructor* (Say), which never infests oats. Hessian fly has also been reared at Manhattan, Kansas, on several strains of the interspecific hybrids, *T. durum* × *T. aestivum* (vulgare), *T. dicoccon* × *T. vulgare*, and of the intergeneric hybrid *Triticum × Secale*.

**Early citations of resistance.** At the present time the hessian fly occurs in most parts of the holarctic region where winter wheat is grown and in many localities where spring wheat occurs. It has also been introduced into New Zealand. Most of the evidence of origin points to Europe and Asia, where other species of the same genus occur, and it seems that this species was introduced into North America on Long Island in 1776 and on the Pacific coast sometime before 1879. It is probable that other separate introductions into North America have occurred.

The first reference to a resistant variety of wheat was made in 1785 by an unknown writer in a farm paper. The name of the variety is not mentioned. During the early years after the introduction of the fly to North America the following ten varieties were repeatedly mentioned as being resistant to the hessian fly: Lawler, Underhill, Lancaster, White Flint, Red Chaff, Clawson, China, Fultz, Red May, and Mediterranean. All trace of some of the first named varieties has apparently been lost, but in tests at Manhattan, Kansas, and elsewhere one or more selections bearing the same names as the last five on the list have been tested and found resistant.

The first extensive studies of varietal resistance in wheat, rye, and barley to hessian fly were made in California by Wickson (1881), Woodworth (1891), and Kelner (1892), during the years of 1886, 1887, 1889, and 1892. Seed from over a hundred varieties was secured from various places all over the world and planted in special tests for the study of resistance to hessian fly, which by that time had begun to do much damage in California. The reports of results were given in three different tabulations in which was recorded a descriptive classification of the varieties in respect to resistance. The notations regarding the several varieties varied from "killed" to "not infested" and a number of intermediate classifications were also made. Additional information was given regarding yield and various other characteristics of the varieties. In
the second report Volo (durum) and Washington Glass were reported as remaining free of fly in all tests. Eight varieties (Forelle, bearded wheat from Missouyen, Palestine, Polish, Bluegrass, Common March, Diamond, and Egyptian Imported) were listed as “especially free from fly” and twelve others as “never having fly in abundance.” Many of the varieties on the list are now apparently unknown but it is interesting to find that among the list of resistant wheats were many varieties of durums, a fact that was noted by the authors. Woodworth (1891) also furnished a table indicating that more of the resistant varieties were found among the early than the late maturing ones. This, however, was not universally true. The hessian fly on the Pacific coast has only one main brood, which occurs in the spring during the period when the wheat is growing rapidly. This may have an important bearing on the relationship to maturity, although it must be remembered that infestation can take place on the upper node until about the time the head begins to emerge and, on minor late tillers, for a considerable length of time afterwards. Apparently nothing further was done in the study of resistance of wheat varieties to hessian fly in California until the work of Packard in 1921 (Packard 1928).

The next detailed report on hessian fly resistance was made in 1901 (Roberts, Slingerland, and Stone 1901). The variety Dawson’s Golden Chaff (now known as Dawson) was reported to be resistant to fly in six counties in New York. No actual data in the form of infestation counts were given but some convincing statements, yield data, and a picture of contrasting varieties under fly infestation were given. Five other varieties (Prosperity, No. 8, Democrat, Red Russian and White Chaff Mediterranean) were mentioned as being not appreciably affected by the fly. The authors reported that varieties with large coarse strong straw were less injured than weak-strawed and slow-growing varieties. They also reported that “the autumn brood of larvae was abundant in Dawson while it has been difficult to find indications of their presence in fields of this variety this summer.” They reported that in Ontario, Canada, where Dawson originated, it had at times been nearly destroyed by fly. As a result of recent studies in other localities, we can now suggest several explanations of these latter conflicting statements. Earliness may have been involved in the difference between autumn and spring infestation in New York, though Dawson is not particularly early at Manhattan, Kansas, in compari-
son with other susceptible varieties. Tests in Central Kansas have shown Dawson to be resistant both spring and fall. Another possible explanation would lie in the presence of different strains of fly in Ontario as compared with New York.

Important records on infestation of varieties of wheat were made in Ohio by Gossard and Houser (1906). In this bulletin there occurred the first actual records of counts of infested plants. The percentage of stalks infested was given for about 80 varieties, covering a period of three years. The common bread wheats varied in infestation from 32 per cent of the stalks infested to 62 per cent in the year 1905, in which the most counts were made. Dawson had an infestation of 53 per cent. A variety of Emmer had no infestation and “Wild Goose Spring Wheat,” which may be a durum variety, had 4 per cent. The authors concluded that their observations “give but little support to the idea that there are immune varieties,” with the possible exception of Emmer and “Wild Goose Wheat.” They also found no relation between different kinds of fertilized wheat plots and either the percentage of infestation or the amount of fallen straws. They stressed the importance of large stiff straws in preventing lodging after hessian fly infestation.

From Missouri (Haseman 1916) relatively small differences were reported between three varieties of wheat, Fultz, Fulcaster, and an unnamed one. The ash content varied directly in amount (percentage not given) with the infestation. Variety testing and study of resistance have been continued at the Missouri Station and results have been reported in several short articles (Haseman et al. 1921, 1931). An interesting feature of this long-time study has been the apparent change in the infestation rating of Illini Chief and some other varieties, although the reports do not give information concerning the time of year in which some of the counts were made.

Studies of resistance in wheat varieties at Kansas Station and elsewhere. Field tests with the fly-resistant variety Illini Chief were begun in Kansas in 1914. The testing of resistant varieties has been continued to the present date whenever the insects were available and were conducted cooperatively by the Departments of Agronomy and Entomology, Kansas State Agricultural Experiment Station. Since 1934 a considerable enlargement in the project has been made possible as a result of a cooperative agreement with the Federal Bureau of Entomology.

In 1915 and 1916 three large-scale field tests of Illini Chief gave
Fig. 22. Results of hessian fly infestation, Manhattan, Kansas, 1931–1932, on Tenmarq (left, 73% of plants infested in the fall), and Dawson (right, 10% of the plants infested). The thinning of the four-foot row of Tenmarq, a high yielding variety in the absence of fly, is the result of both fall and spring infestation.

The following percentage of plants infested (McColloch and Salmon 1918).

<table>
<thead>
<tr>
<th></th>
<th>Illini Chief</th>
<th>Turkey</th>
</tr>
</thead>
<tbody>
<tr>
<td>1st test, Manhattan</td>
<td>1</td>
<td>100</td>
</tr>
<tr>
<td>2nd test, Winfield, Kansas (spring)</td>
<td>10</td>
<td>95</td>
</tr>
<tr>
<td>3rd test, 1916</td>
<td>3 to 5</td>
<td>95 to 100</td>
</tr>
</tbody>
</table>

In the fall of 1916, 87 varieties of small grains were planted for the purpose of studying infestation by the hessian fly. Counts were recorded of the number of eggs laid, the percentage of plants with eggs, the average number of flaxseeds and the percentage of plants infested. The four varieties of durum represented in this
test had a smaller number of eggs laid on them as a group than were laid on any of the common bread wheats. Oats, winter barley, einkorn, Spring Emmer, and Spelt—all carried a smaller number of eggs than the ordinary winter wheats, which showed no material

![Image](image-url)

**Fig. 23.** Results of hessian fly infestation, Manhattan, Kansas, 1931–1932, on Illini Chief 223415 (left, 1% of the plants infested in fall); Kawvale (right, 4% of the plants infested in fall) and Kanred x Hard Federation, Kans. sel. 2672 (center, 64% plants infested in fall). The Kanred hybrid would normally yield as much or more than either of the other varieties in the absence of hessian fly.

It is interesting to note that while a few eggs were laid on Spring Emmer and none of the plants were later infested, a large number of eggs were laid on Winter Emmer which had 50 per cent of the plants infested when counts were made of the flaxseed. The range in the percentage of infested plants on
which the fly reached the flaxseed stage was from 0 to 65. There were 5 per cent or less of the infested plants in the varieties Illini Chief, Beachwood hybrid, Currell sel., and Dawson. Since these data were taken in the fall of the year, the resistance of Dawson appears to be real and not the result of early maturity, as it might have been in the case of the New York tests (Roberts et al. 1901) (Fig. 22, Fig. 23).

In a later progress report (McColloch and Salmon 1923) the average percentage of infestation on a number of wheat varieties was given. These included the average for up to ten tests for the fall infestation and up to four tests for the harvest infestation. The averages for the fall infestations ranged from 32.5 per cent for Kharkof to 1.3 for Illini Chief, while the harvest infestation ranged from 58.7 for Turkey and 59.5 for Michigan Bronze to 0 for Dawson. It is interesting to note that while in most cases the harvest infestation was in accord with the fall infestation, there are a few cases in which it was markedly different. This difference may indicate that a different set of genetic factors was responsible for the spring and fall infestation, respectively, in some of these varieties.

In addition to the points mentioned the authors drew the following conclusions from their tests:

"(1) There is practically no discrimination by adult fly in ovipositing, since eggs are deposited in large numbers on all varieties.

"(2) There is a great difference in the subsequent infestation, and certain varieties exhibit marked resistance.

"(3) Since several varieties, such as Illini Chief, Dawson Golden Chaff, Beechwood Hybrid, Currell Selection and Dietz, have had very few plants infested in the fall, they may be classed as resistant.

"(4) Other varieties as Turkey, Kharkof, Ghirka, Zimmerman, and Marquis, have been very susceptible under all conditions.

"(5) A few varieties as Kanred, Clark's Blackhull, and Fullcaster, have been erratic, being apparently resistant in one test and very susceptible in another.

"(6) The soft wheats, as a class, have been more resistant than the hard wheats, although one variety of hard wheat (Red Winter 2132) has shown a marked tendency toward resistance.

"(7) Under abnormal conditions, such as greenhouse tests, the
plants in general maintain their same relative position with regard to resistance."

In a study of the cause of resistance a high mortality occurred between the time of hatching and the time the larvae reached the base of the plant on all varieties. There was also a marked difference in the percentage of larvae getting down on the different wheats, but in all cases there were enough larvae to have injured the plants seriously, had they developed. The investigation also failed to demonstrate any marked relation between gross morphological characters and resistance, with the possible exception of the height of the ligule, which character may be associated with the percentage of larvae reaching the base of the plant. "It was also found that in the case of the resistant varieties, when larval development did take place, it was usually high in the stem and not at the base of the plants. Growth of the larvae was slow on these varieties, and in some cases one-fourth grown larvae were still active and moving about instead of assuming the normal sedentary habit. Undeveloped larvae were generally found at the base where the leaf sheath has its origin. The results of these observations indicated that resistance resulted from physiological conditions and was located at the base of the plant." The authors mentioned that some evidence has been secured, which indicated that resistance was in some way associated with the presence and utilization of silica by the different varieties of wheat. The silica has been considered to be related to resistance through the strengthening of the cell walls. It might also act through compounds that adsorb the digestive enzymes from the insect.

In a study of resistant varieties Packard (1928) reported on the infestation of 24 varieties of wheat of which Dawson, Illini Chief, and Prohibition showed considerable resistance under California conditions. The percentage of plants infested were 3, 11, and 8, respectively, while among 10 other varieties 100 per cent of the plants were infested. It was noted that more eggs were laid on these three resistant varieties than on the others tested and that "large numbers of the larvae successfully reached their normal feeding position under the leaf sheaths. Some internal character of the plants, not yet ascertained, prevented most of these larvae from maturing." Packard also tested 10 other varieties which had proved resistant in tests in Kansas and Missouri. All except one
of these “showed decided resistance to the hessian fly.” Many eggs were laid on all varieties but “a very small proportion of the larvae made any appreciable growth, however, substantiating the evidence already cited that the resistant varieties possess some histological or biochemical peculiarity, detrimental to the development of the larvae.” Packard was also able to select one fly-resistant strain out of a commercial field of the ordinarily susceptible variety Baart.

The data secured from 1922 to 1929 at the Kansas Station on the resistance of varieties of winter wheat to hessian fly were published by Painter, Salmon, and Parker (1931). The result of detailed counts on the fly infestation of about 400 varieties, selections, and hybrids were analyzed in several tables. As a result of these studies the following classifications were made for resistance to fly in the hard-winter-wheat belt:

<table>
<thead>
<tr>
<th>Resistant varieties</th>
<th>Varieties with medium infestation</th>
<th>Susceptible varieties</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dawson</td>
<td>Blackhull</td>
<td>Turkey</td>
</tr>
<tr>
<td>Honor</td>
<td>Superhard</td>
<td>Kharkof</td>
</tr>
<tr>
<td>Illini Chief Sel.</td>
<td>Early Blackhull</td>
<td>Kanred</td>
</tr>
<tr>
<td>Fulhard</td>
<td>Harvest Queen</td>
<td>Oro</td>
</tr>
<tr>
<td>Kawvale</td>
<td>Red Winter</td>
<td>Cheyenne</td>
</tr>
<tr>
<td>Michigan Wonder</td>
<td>Fulcaster (Kan. 317)</td>
<td>Minturki</td>
</tr>
<tr>
<td>Red Rock</td>
<td></td>
<td>Tennmarq</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Zimmerman</td>
</tr>
</tbody>
</table>

These comprised only a few of the more important varieties in each of these classes. For these, descriptions and agronomic characters were given. The above classification was purely arbitrary since the complete list of varieties showed every degree from high resistance to complete susceptibility. The varieties with low or medium infestation may have carried genetic factors for resistance different from those in the varieties having higher resistance. On the other hand, they may have represented heterogeneous mixtures of strains so far as resistance to fly was concerned. This was shown to be true in the case of Fulcaster and certain other varieties. The evidence that varieties may be homoygous for agronomic characters but heterozygous for resistance to fly is an important fact in the understanding of insect resistance. In the variety Kawvale there was an approach toward the objective of the investigation, which is the production of wheat varieties adapted to Kansas that would be
equal or superior in agronomic characters to those grown now and, in addition, resistant to the hessian fly. When Kawvale was distributed to farmers in 1931, it met with a very favorable reception because of its high yield and other valuable characters. In some counties the percentage of the acreage devoted to Kawvale reached more than 85 per cent before it began to decrease in popularity and to be partly replaced by Pawnee and other varieties. Kawvale is fairly susceptible in eastern Kansas and western Missouri, where it is best adapted, but under severe infestation (Painter et al. 1940) it has had the least injury of any commercial winter wheat. In farmers' fields severe injury has been observed but no cases of complete destruction such as occur with other varieties have been recorded (Etheridge and Helm 1938, p. 8).

In the publication (Painter et al. 1931) attention is called to five characteristics which affect the resistant qualities of wheat varieties. These may be listed as follows:

1. A decided difference in the number of flies which are able to develop on the several varieties.
2. Tolerance as found in Blackhull, sometimes permitting fly to develop without material damage to the plants.
3. Difference in rate of development of fly on different varieties.
4. Ability of wheat to produce tillers after infestation. Tenmarq is better than Turkey in this respect although both are susceptible.
5. Stiffness of straw.

It is also shown that infestation may be measured equally well on the basis of percentage of plants infested, percentage of tillers infested, or the total fly on a given number of plants. With heavier infestations the latter two measures are better.

It was again found that there was no close association between fly resistance and morphological characters or characters of agronomic importance. There appeared to be some association between resistance and purple straw or soft grain texture. It was believed, however, that this apparent association was caused by the particular varieties used in the tests rather than to any connection with insect resistance. In more recent tests involving hybrids between resistant and susceptible varieties no genetic association has been found. Experiments since 1931 in Kansas have tended to confirm most of the results cited above and also the relative degrees
Resistant to insects in wheat

of resistance of varieties insofar as resistance to the hard-wheat-belt fly is concerned. In later tests, however, there has been an increase in the level of infestation of varieties listed above as resistant (Painter and Jones 1945).

In western Oregon, Rockwood and Reeher (1933) reported that Illini Chief remained "practically immune" during a three-year test and that Prohibition was lightly infested for two years.

Data gathered at Nebraska (Kiesselbach, Anderson, and Suneson 1933; Suneson and Kiesselbach 1934) during the hessian fly outbreak of 1931-32 agreed in general with the results for the same varieties at Manhattan, Kansas. In a three-year average Kawvale had 7 per cent of the plants infested both spring and fall, Blackhull had 58 per cent of the plants infested in the fall and 70 per cent in the spring. Eight hard red winter-wheat varieties had 76 to 95 per cent of the plants infested in the fall and 82 to 91 per cent in the spring as an average for the three years. It is pointed out that Cheyenne and certain other wheats are tolerant to the fly, producing fair to good yields in spite of having heavy infestations. Two other effects were noted: "(1) The spring survivals of such normally hardy varieties as Nebraska 60 and Minturki were on a plane with those of the less hardy Blackhull hybrids. (2) Susceptible varieties that were weakened by the fall brood of hessian fly were subject to much greater infestation and damage by the spring brood of fly than the same varieties planted after October 1." The September 26 planting which had been heavily infested in the fall showed an average spring infestation of 14 puparia per plant while the October 6 planting showed 9 flaxseed per plant as an average for 20 varieties. The damage accompanying this difference in the number of puparia affected the yield.

At Michigan in 1932 and 1933, Anderson and Brown (1936) studied the results of an infestation on over a hundred strains of soft winter wheat. The infestation ranged from 7 to 75 per cent and 5 to 75 per cent, respectively, of the culms infested in the two years. The varieties involved were not named but the authors found a significant interannual correlation (0.30) in regard to the percentage of fly infestation. The breaking strength, and weight and diameter of culm were measured but the correlation coefficients between these characters and the percentage of fly infestation indicated that there was no significant relationship between these structural characters and the resistance to fly infestation. Likewise,
these characteristics were measured on infested and uninfested culms. In nearly every strain the varietal group average was higher for the uninfested culms, and a statistical analysis showed the difference to be significant. The authors state: “An explanation of these seemingly contradictory results may be that there is no association from strain to strain between hessian fly infestation, on the one hand, and breaking strength, culm weight, or culm diameter, on the other hand, but when culms are infested with puparia the result of such infestation on the individual culm is such that it becomes, on the average, a weaker, lighter, and smaller culm than does the puparia-free culm of the same strain.” The lodging in the field resulting from fly infestation was found to be highly significantly and positively correlated with the percentage of fly infestation. No data, however, were given on the important problem of whether infested varieties with larger, stronger culms showed less lodging than would be expected on the basis of their infestation.

At Saanichton, British Columbia, a hessian fly infestation in 1934 was reported by Foster and Jeffery (1937). The data were given on 29 varieties with a spring infestation which ranged from 0 to 100 per cent. Among the varieties with lower infestation were Egyptian Amber, Imperial Amber, two selections of Dawson, Red Rock, O.A.C. 104, and Triplet, all of which had less than 1 per cent infestation while Yeoman and Sun had 100 per cent. A lighter infestation in 1936 gave a somewhat similar ranking of the varieties. A comparison is made between the number of days to maturity, the height of plants on April first, and the percentage of culm infestation. Foster and Jeffery state that “the high positive correlation \((r = + 0.84)\) between number of days to maturity and infestation, and the negative correlation \((r = - 0.63)\) between height of plants on April 1 (about the time the hessian fly begins to emerge and lays its eggs on winter wheat) and infestation, indicate that stage of growth may account for the differential resistance of winter-wheat varieties at Saanichton.” They also reported that three different fertilizers, nitrate of soda, superphosphate, and a complete fertilizer applied in two different ways, had no effect on the yield of Sun wheat which was heavily infested with hessian fly. It should be pointed out, however, that the high positive correlation between stage of maturity and fly infestation may not be caused by an actual relationship, at least as it concerns the extremes of the infestation range. It may have merely originated from the particular varie-
ties represented in the test. Certain of the data given in the paper do not agree with the correlation. For instance, variety Ridit, with over 90 per cent of the culms infested, had the same number of days to maturity as Egyptian Amber with 0 infestation, was approximately of the same height on April 1, and had approximately the same days to maturity as O.A.C. 104 and Triplet, which had 0.4 per cent of the culms infested. Two other considerations tend to make one question the validity of the correlations given. From a knowledge of the biology of the fly it is questionable whether the wheat had reached a sufficient maturity by April 1 to reduce the infestation, since eggs can be laid on the flag leaf and larvae will mature on the upper internode of the culm, or infestation may occur on a small tiller. In addition it is known that Dawson and several other varieties which were resistant in British Columbia to the spring generation of fly were also resistant to the hard-wheat-belt fly of Kansas in the fall and in California in early spring when stage of maturity could hardly be a factor. At Manhattan, Kansas, and in experiments elsewhere susceptible spring-wheat varieties, and to some extent winter-wheat varieties, have shown differences correlated with maturity when the second spring generation was involved and when differences in maturity were wide.

Biological strains of hessian fly. The data so far given have emphasized certain differences and similarities in the infestation standing of varieties in different localities. Painter (1930) has shown that the infestation of certain varieties by fly from the hard-wheat belt of Kansas differed materially from the infestation of the same variety by fly from the soft-wheat belt of Kansas and from states farther east. The evidence given in that paper and in the paper by Painter, Salmon, and Parker (1931) is summarized in the latter paper as follows:

1. Observations on Kansas farms indicate that in the hard-wheat belt the soft wheats are less injured by fly than the hard wheats. In the soft-wheat belt frequently the reverse is true.
2. There is a lack of agreement in the literature in regard to the fly infestation of some varieties in different localities.
3. Identical varieties or strains give infestation data for the soft-wheat belt that are very different from those for the hard-wheat belt of Kansas.
4. The relative rank of a variety is changed very little under the wide range of infestation intensities studied. In the study of a resistant
and a susceptible variety in a series of infestations of different intensities, each additional increment of fly adds to the per cent of infestation of the resistant variety as the susceptible variety approaches 100 per cent plant of tiller infestation; meanwhile no material change occurs in these data for the susceptible variety. Under these conditions the difference between the varieties shows in the total fly present on each variety and these data show the usual differences.

(5) When brought into the greenhouse to infest wheat, under uniform conditions, fly from the several localities retained their characteristic infestation abilities.

(6) The ability of the fly from the hard-wheat belt to infest varieties in a differential manner is not materially affected by a wide range of natural and artificial soil conditions.

(7) It is possible to select, individually or in mass, from the normal fly populations of the hard-wheat belt a group of individuals which have a different infestation ability from the original or natural population of fly.

(8) The relationships with pure lines of wheat and the individual breeding experiments with the fly indicate that these biological or physiological strains are genetically distinct. The evidence available also indicates that the population of fly in any one locality consists of a mixture of two or more strains which differ in their ability to infest the several varieties of wheat.

An attempt was made to study the number and interrelations of biological strains by means of pure lines. This was found to be difficult because of the frequent occurrence of unisexual progenies from individual pairs of hessian fly (Painter 1930; Metcalf 1935). The presence of biotypes of hessian fly has been confirmed and much additional data were presented by Cartwright and Noble (1947). The relationship of biotypes to the breeding of resistant wheats will be discussed later.

Chesnokov (1939a), in Russia, found that Illini Chief and some other varieties were infested in the neighborhood of Leningrad but not by the southern (Kuban) population of hessian fly, thus suggesting that biotypes of fly occur in that region.

The presence of biological strains apparently does not explain all occasions when otherwise resistant varieties are infested, although it does account for a number of them, especially among the winter wheats. Cartwright et al. (1946) have demonstrated that high temperatures increase the infestation of resistant wheats in the greenhouse. This will explain some of the higher infestations of re-
sistant varieties under some of the tests at Manhattan, Kansas, and in the greenhouse. At the present time it is possible to suggest on the basis of relatively meager data a few other possible accessory explanations. The relative vigor of plants, especially of seedlings, appears to condition the percentage of larval establishment and eventual infestation. At the Kansas Station it has been found that seedlings from shriveled seed are on the whole more easily infested. There is some evidence that a varying amount of water or fertility of the soil may have some effect, though this has never been ade­quately demonstrated in publications. The relationship of maturity to infestation has been pointed out. Suneson and Kiesielbach (1934) have given some evidence that susceptible varieties which were weakened by the fall brood of fly were subject to greater in­festation and damage by the spring brood than were the same varieties planted after the fly-free date. The stage of growth of the leaf on which eggs were laid influences infestation (Painter 1930). The presence of a large number of larvae with their increased secre­tion may perhaps break down the factors responsible for resistance to some extent. At the Kansas Station it has been impossible to demonstrate clear-cut differences in infestation of wheat plants in­fected with several wheat diseases. In some varieties, for example, those of the Blackhull group, it appears that resistance may be more easily conditioned or influenced temporarily by environmental fac­tors than in other varieties. These statements perhaps will indicate the complexity of the situation and some factors still requiring study.

The inheritance and breeding of resistance to hessian fly from various sources in commercial winter wheat. In breeding for hessian fly resistance in Kansas and in California use has been made of American winter-wheat varieties, especially Dawson and Kaw­vale, which have been resistant in those areas. Cartwright and Wiebe (1936), working on the resistance to hessian fly of the spring generation in California, have published one of the first papers to place a case of insect resistance on the basis of genetic factors. Their publication deals with the inheritance of resistance between Dawson (resistant) and Big Club and Poso (susceptible). The resistant parent always had 1 per cent of the plants infested or less; the susceptible parents ranged in infestation from 94 to 100 per cent. The F1 plants were not tested for fly reaction. In the F1 generation 13.7 per cent of the hybrid plants of Dawson x Poso were infested and 18.4 per cent of the Dawson x Big Club. For the
purpose of genetic interpretation the F₁ plants were classified on the basis of their behavior in F₁ rows, each of which came from a single F₂ plant. The data from both F₂ and F₁ indicated the dominance of factors for resistance. When classified on the basis of an assumed arbitrary minimum at 77.5 per cent infestation, there was a 15 to 1 theoretical genetic ratio which agreed within the limits of experimental error in the case of both crosses. This would indicate that there are two dominant factors for fly resistance in Dawson which are complementary and perhaps cumulative. The wide spread within the more resistant class may indicate the presence of modifying factors or greater variability in infestation of plants heterozygous for resistance. The authors state that "the interpretation of the data applies only to the conditions under which the experiments were made, and no prediction can be made as to the behavior of the parent or hybrid material when grown under other conditions." This statement refers to the known susceptibility of Dawson to some populations of fly in eastern United States. Cartwright and Wiebe also state that "the data furnish no idea as to the fundamental nature of resistance. The answer to that problem might be of some help in the breeding program, but it is not necessary for such a program." This point of view is paramount in any project for the breeding of resistance to insect attack.

In a later paper Noble and Suneson (1943) confirmed the presence of two genetic factors in Dawson by isolating and recombining these factors. The F₁ of crosses involving both factors which were called, respectively, H₁ and H₂ showed a range from 5 to 25 per cent infestation, with most of the families falling below the mid-class value of 17.5 per cent. The F₁ families which involved either single factor for resistance had infestation ranging from 25 to 42 per cent. The susceptible parent Poso had an infestation of 83 per cent and the resistant parent Dawson had no infestation. Tests indicated that the genes H₁ and H₂ were about equal in their ability to impart resistance but definitely inferior to Dawson or to lines possessing both factors. The range in infestation for Dawson was 0 to 2 per cent and for lines carrying single factors 0 to 10 per cent.

In California the Bureau of Entomology and Plant Quarantine and Bureau of Plant Industry, Soils and Agricultural Engineering have cooperated in a back-crossing program to incorporate the two fly resistant genes from Dawson into commercial wheats (Briggs
1938; Suneson 1947). The wheat variety Poso 42, C.I.12237 (Dawson x Poso) is a composite of 45 F1 lines resulting after the sixth back-cross to Poso and was released to farmers in 1942 (Annand 1943). The variety Big Club 43, C.I. 12244, is a composite of 144 F2 lines that were resistant to hessian fly, bunt, and stem rust. It is the result of three independent back-cross breeding programs in which resistance to fly was derived from Dawson, resistance to bunt from Martin, and resistance to stem rust from Hope; it was released to farmers in California in 1944. Performance of these fly-resistant varieties has been equal to susceptible varieties in the absence of hessian fly (Suneson 1947) and should surpass such varieties when fly is a factor in yield. Suneson and Noble (1950) reported that the resistant varieties Poso 42 and Big Club 43 had replaced susceptible varieties in the hessian fly infested areas of California to such an extent that resistance studies in that area had been abandoned because of the low fly population. In a later quarterly report, which is quoted here by their permission (letter from Mr. C. M. Packard, Bureau of Entomology and Plant Quarantine, Jan. 11, 1950), Mr. W. B. Noble stated that “as the acreage of resistant varieties Big Club 43 and Poso 42 has increased, the fly population has decreased until it is now difficult to find enough fly-forms for seasonal history observations. . . . Less than 1 per cent average infestation occurred in the fly-infested counties of Butte and Solano (in 1949).”

Information in inheritance of resistance to hessian fly in winter wheat at the Kansas Station. At the Kansas Station considerable information has been accumulated concerning the inheritance of resistance to hessian fly of the hard-wheat belt in crosses between the varieties of winter wheat. The purpose of the study of hybrids has been primarily the production of strains of wheat as good or better in agronomic characters as those then grown and in addition resistant to the hessian fly. These practical considerations have always been given precedence, and space limitations have prevented the detailed study of the large number of hybrids required to place fly resistance of the various crosses studied on a factorial basis. There have been other disturbing variables. The impurity of resistant parental varieties were not recognized earlier in the work and methods of study of hybrids were developed gradually. All of the winter wheats so far studied have been largely susceptible to the fly of the soft-wheat belt and
populations of hard-wheat-belt fly brought in for use at Manhattan have always contained a variable percentage of individuals able to infest those winter wheats which were resistant to the bulk of the population. While the presence of biotypes of fly does not prevent a rough classification of the relative resistance of varieties, it does interfere with the correct classification of a segregating population, because a small number of the resistant segregates is infested. In contrast to this difficulty involving resistant plants there has always been a small number of escapes among the susceptible strains of wheat owing to the destruction of eggs or the fact that no eggs were laid on some plants. During the first fifteen years in which the hybrids were studied there was a conspicuous lack of continuity of comparable data involving the same degree or intensity of infestation. On several occasions the years in which plantings were made for genetic analyses have coincided with those in which infestation was too light for this purpose, although progress could be made in selecting from the more resistant families of plants.

Throughout all of these years, however, there has been abundant evidence of the fact that resistance to hessian fly was inherited (Painter, Salmon, and Parker 1931). With the discovery of resistance in certain spring wheats that gave protection against the larger part of the fly population, the detailed study of the type of resistance from winter wheats, which was usable against only a part of the fly population, was curtailed. The nature and extent of the evidence concerning inheritance of fly resistance in winter wheats and some tentative conclusions regarding genetic factors involved are discussed below.

There are several groups of facts which point toward a complex genetic situation in the inheritance of fly resistance and in factors affecting fly resistance when all of the different resistant varieties are taken into consideration. There is reason to believe that the different kinds of resistance discussed in a preceding paragraph each involve a different genetic complex. The high first-stage larval mortality which is found in a number of winter wheats also appears to have different genetic bases in the several varieties. The two genes $H_1$ and $H_2$ found in Dawson, singly and in combination, may be present in these other winter wheats and may account for many of the differences found. How many of these different groups of factors may be involved
is not known. The low oviposition found on some durum wheats has so far been located rarely among the winter wheats. However, it appears to have a genetic basis (Painter 1936). The different tolerance reactions, such as the ability to produce grain in spite of presence of the fly (Suneson and Kiesselbach 1934), differential tillering ability (Painter, Salmon, and Parker 1931), and stiffness of straw may each be expected to involve different genetic combinations. The presence of biological strains allows us to differentiate further between winter wheats of approximately equal resistance to fly in the hard-wheat belt. For instance, Dawson, Illini Chief, and some other varieties have been uniformly and highly susceptible in the soft-wheat belt, while Kawvale, Blackhull, and Fulhard have been only partially susceptible in some of the same tests; hence we may expect these two groups of varieties to possess different factorial bases for resistance. Some of the spring wheats which possess and transmit high resistance to the soft-wheat-belt type of fly will be discussed later.

There is also genetic evidence of the factorial distinctness in the different resistant varieties. In 1930, for instance, among eight F₃ lines of the cross Kawvale (resistant) x Fulhard (resistant) tested in the greenhouse, one proved susceptible. The F₃ progeny from these plants were susceptible in the field in 1931. Since that time several other susceptible segregates as well as resistant ones have been found in this cross. This would indicate that at least one factor for resistance was different in the two varieties. In other crosses between resistant varieties susceptible segregates have been found.

In the fall of 1933 a number of crosses involving ten resistant and six susceptible parents was planted in the fly nursery (Table 4). Although the infestation was light, it appeared possible to group these various F₂ hybrids into several different classifications on the basis of the infestation of both parents and hybrids. This would indicate that at least two and perhaps three different sets of genetic factors were involved among the varieties studied.

A program for the breeding of hessian fly resistant wheat began in 1918 with hybrids made by John H. Parker, involving crosses between the resistant wheat, Illini Chief and susceptible wheats Marquis and Kanred. The first reports concerning the evidence of the inheritance of fly resistance are given by McColloch (Farrell 1924). The subsequent history of these hybrids is given...
Table 4  INFESTATION OF VARIOUS \( F_2 \) HYBRIDS AND PARENTS AT MANHATTAN, KANSAS, FALL 1933
(Data grouped on basis of infestations in each variety and cross)

<table>
<thead>
<tr>
<th>PARENTS</th>
<th>Number of Plants</th>
<th>Per cent infested</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Average infestation of susceptible parents</td>
<td>315</td>
</tr>
<tr>
<td></td>
<td>Average infestation of resistant parents</td>
<td>381</td>
</tr>
<tr>
<td></td>
<td>Average infestation of low resistant parents</td>
<td>106</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>( F_2 ) HYBRIDS</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Crosses of resistant x resistant</td>
<td>153</td>
<td>1.3</td>
</tr>
<tr>
<td>Crosses of resistant(^2) x susceptible (1st group)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Resistant Variety</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kawvale</td>
<td>75</td>
<td>2.7</td>
</tr>
<tr>
<td>Michigan Wonder</td>
<td>313</td>
<td>3.8</td>
</tr>
<tr>
<td>Malakov</td>
<td>367</td>
<td>5.1</td>
</tr>
<tr>
<td>Valprize</td>
<td>71</td>
<td>4.2</td>
</tr>
<tr>
<td>Total</td>
<td>826</td>
<td>4.4</td>
</tr>
<tr>
<td>Crosses of low resistant x susceptible (2nd group)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oakley</td>
<td>188</td>
<td>14.7</td>
</tr>
<tr>
<td>Cornell sel.</td>
<td>63</td>
<td>12.7</td>
</tr>
<tr>
<td>Total</td>
<td>251</td>
<td>13.9</td>
</tr>
<tr>
<td>Crosses of low resistant x susceptible (3rd group)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Valley x St. Louis</td>
<td>72</td>
<td>29.2</td>
</tr>
<tr>
<td>Grand Prize</td>
<td>72</td>
<td>29.2</td>
</tr>
</tbody>
</table>

\(^1\) Minturki, (Kanred x Hard Federation sel.), Tenmarq, Quivira, Cheyenne, Oto.  
\(^2\) Fulhard, Michigan Wonder, Red Rock, Malakov, Kawvale, (Kanred x Hard Federation sel.).  
\(^3\) Oakley, Cornell sel., (Valley x St. Louis Grand Prize).  

by Painter et al. (1931). These authors stated that "the most important fact brought out by these data is that resistance is an inherited character which may be combined with other desirable ones and that fly resistance is not closely linked with any observed agronomic character such as awn type and kernel texture." None of these hybrids have been found promising enough to be developed for distribution to farmers.  
In a cross between Illini Chief and Tenmarq involving a small number of plants tested in \( F_1 \), resistance appeared to be recessive.
In the former generation a total of 44 strains not previously studied for fly but selected at random gave 13 resistant samples, 16 intermediate, and 15 having an infestation equal or greater than the Tenmarq parent. Some of these hybrids have been tested in later generations and have retained their resistance to fly but none have been outstanding agronomically, though they appeared to be better than the earlier hybrids involving this resistant parent.

Following 1928 a number of hybrids involving Kawvale as the resistant parent were studied at the Kansas Station, since at that time Kawvale was the most promising fly-resistant wheat known for the area. The most emphasis has been placed on the cross Kawvale x Tenmarq and its reciprocal. The F₁ and F₂ were not studied for fly resistance. The third and fourth generations of the cross were studied by Hollingsworth (1933). The infestation secured was too low for a satisfactory factorial analysis but subsequent studies have shown that it was high enough to permit the selection of the more resistant segregates. In other words, although the infestation was not high enough for a genetic study, it was high enough to permit satisfactory plant-breeding progress. There appeared to be evidence that several interrelated genes may be involved. Hollingsworth (1933), in a study of agronomic characters such as purple straw, grain texture, kernel shape and rust resistance of the hybrids, found no close relationships with resistance to the hessian fly.

In the F₅ generation an opportunity occurred for a measurement of the effectiveness of the selection for hessian fly resistance, which had been made in spite of low infestation in F₁ and F₂. Twenty-six of the F₅ families had been previously selected for fly resistance. Of these, 81 per cent had resistance comparable to Kawvale, the resistant parent. Alongside of these 26 rows there were 70 different strains, also Kawvale x Tenmarq, which had been grown in the agronomy and botany nurseries and selected for characters other than fly resistance. Only 47 per cent of these F₅ families showed a resistance equal to the Kawvale parent. In examining this same group of 70 rows from the standpoint of susceptibility, 6 rows, or 9 per cent of the total, had an infestation equal to or greater than Tenmarq. In this same nursery there were 44 unselected F₅ rows of the cross Illini Chief x Tenmarq
in which 15 rows, or 34 per cent of the total, had an infestation equal to or greater than Tenmarq. This would appear to indicate that genetic relationships for resistance to hessian fly were more complex in the case of Kawvale x Tenmarq than in Illini Chief x Tenmarq and to indicate the dominance of resistance in the case of Kawvale x Tenmarq.

In the Kawvale x Tenmarq hybrids and in crosses involving some of these hybrids, resistance has tended to be dominant. In some other crosses between Kawvale and other susceptible winter wheats, resistance has tended to be intermediate or recessive, suggesting the presence of modifying factors in the susceptible parents. The presence in the test plots of a varying population with respect to the proportion of biotypes of fly has made it difficult to assess the genetic factorial basis under Kansas conditions.

In the F6 generation the Kawvale x Tenmarq hybrids were harvested in bulk and for several years tested for resistance to hessian fly and for agronomic characters, especially for ability to yield. Such yields were often much higher than the commercial varieties with which they were compared.

At the time selections of the hybrid Kawvale x Tenmarq were being studied at Manhattan, seed of a number of third-generation plants were sent to Lincoln, Nebraska, and there a strain, Nebraska No. 1086, later named Pawnee, was selected from the progeny of an F3 plant in 1932. During the time of selection there was present in the Nebraska Agronomy Nursery a heavy natural infestation of the hessian fly (Kiesselbach et al. 1933; Suneson and Kiesselbach 1934). The fly resistance of Pawnee at that time was partly responsible for bringing this strain to the attention of the agronomists. Since the choosing of the strain there has been little subsequent selection in it. Comparative tests were carried out on this and other strains from the same cross originally selected at the Nebraska and the Kansas experiment stations. Pawnee (Nebr. No. 1086, C.I. 11669) appeared to be the best of these on the basis of all the various characters studied, although probably other selections had higher fly resistance. It was released to farmers in Nebraska in 1942 and in Kansas and Oklahoma in 1943.

The agronomic characteristics of Pawnee that were reported by Reitz and Laude (1943), Quisenberry (1944), and others, and reviewed by Painter and Jones (1945) show that this variety
has a unique combination of commercially desirable characters. In 42 tests in 13 Kansas experiment stations and fields during six years, Pawnee has yielded from 17 to 42 per cent more than other varieties grown commercially in the area before its release (Reitz and Laude 1943). Similar high yields have been reported in neighboring states. “In addition to its innate yielding ability, Pawnee ordinarily has a higher test weight than its parents and many other hard red winter wheats grown commercially. It is short, stiff-strawed, winter-hardy, and matures early. As reported by Reitz and Laude (1943), Pawnee is practically immune to loose smut, resistant to some common forms of leaf and stem rust, and moderately resistant to stinking smut, or bunt. Pawnee is reported to have milling and baking qualities similar to those of Turkey wheat. Among the disadvantages of this variety may be mentioned its susceptibility to speckled leaf blotch (Septoria) and possibly greater susceptibility to greenbug and chinch bug injury than that of Turkey wheat and some other common varieties. Thus, aside from its resistance to the hessian fly, Pawnee is a highly desirable wheat, with good inherent yielding capacity and possessing the best combination of wheat-pest resistance and other characteristics now available in a commercial winter wheat.” (Painter and Jones 1945.)

Behavior of Pawnee under nursery conditions and in farmers' fields. The information which follows is drawn from reports on experimental tests of Pawnee before its release to farmers (Painter and Jones 1945) and during the years of increasing acreage on farms (Painter and Jones 1948). The earlier study showed that “the value of Pawnee is a result of both tolerance and resistance to the fly in central Kansas and is shown by (1) a 50 per cent lower infestation than the susceptible variety Tenmarq, as measured by percentage of plants infested; (2) approximately a 75 per cent lower tiller infestation, as compared with the susceptible variety Tenmarq; (3) a decrease in the size of puparia and a decreased rate of development, and perhaps other biological differences; (4) comparatively low fly injury to infested plants, especially in the fall, and to individually infested tillers in both fall and spring; and (5) an excess in yield in comparison with Tenmarq, up to more than twice as much as the latter variety under heavy fly infestation. In evaluating the hessian fly resistance of Pawnee, it is necessary to consider all these factors.”
Like its resistant parent Kawvale, Pawnee has shown less resistance to fly in the eastern quarter of Kansas than in central and western Kansas (See Fig. 24).

Much of this geographical variation in the resistance of Pawnee appears to be the result of known differences in the population of fly in this area (Painter et al. 1931). Pawnee was slightly but significantly inferior to Kawvale in fly resistance in a long series of tests in central Kansas.

Pawnee was recommended primarily as an additional means of combating the hessian fly, but under any circumstances should give a certain amount of automatic control. Judging from variety tests under severe fly conditions and because of the effectiveness of the tolerance factors, it appears that complete crop failures caused by fly infestation are not likely to occur where Pawnee is planted. Such complete crop failures from fly injury have occurred repeatedly in central Kansas on individual farms where the non-resistant hard red winter wheats had been planted (Figs. 25, 26).

In the early years of the distribution of Pawnee to farmers, especially in 1945-46, there were outbreaks of hessian fly in various
areas of central Kansas with severe killing of plants in fields of susceptible varieties. Such fields gave low yields of grain and sometimes were plowed up in the spring, while nearby fields of Pawnee gave normal or above normal yields for the community. These contrasts, similar to those seen in nursery and plot tests, were

plainly evident to farmers and were important reasons for the wide-spread planting and rapid increase in use of the variety.

In central Kansas, in the summer of 1947, the average tiller infestation of 58 fields was 8 per cent and for 62 neighboring fields of susceptible wheat 25 per cent. Pawnee had a lower infestation in all of 27 paired comparisons where this variety was growing with a susceptible one in the same farmer's field. These are
indications that the fly resistance of Pawnee under farm conditions appears to be equal to or better than that demonstrated under experimental tests. The years 1944–47 were highly favorable ones for the development of both wheat and hessian fly. Yet, despite this, there was a decrease in the population of fly following 1946 in central Kansas, where the acreage of Pawnee is greatest and where it is resistant to fly. Table 5 has been adapted from Painter and Jones (1948) with the addition of data for 1947–48 from the same sources as that of the preceding year.

By the fall of 1946, three years after its release, Pawnee occupied 24.7 per cent of the wheat acreage of Kansas and was the leading variety in acreage (Collins 1947). The following crop year it was estimated to occupy 35.2 per cent of the total seeded acreage, or over five million acres and more than twice that of the second-ranking variety (Collins and Schlicht 1948). In 24 of the 105 counties in the state in 1947–48 it occupied 80 per cent or more of the acreage of wheat in the county. Pawnee was reported as grown on about one million acres in eastern Nebraska in 1946 (Quisenberry et al. 1947). It was reported that in these fields of Pawnee fly infestation was low or absent (Muma and Bare 1947). Later (Hixon 1948) it was reported that "no county in that area (the southeastern quarter of Nebraska) had enough hessian fly to constitute a serious problem, and it was noted that the almost universal sowing of fly-resistant Pawnee wheat had...
practically eliminated hessian fly in many counties." Additional information on the relationship between hessian fly infestation yield and dates of planting have been given by Kieselbach and Lyness (1945, 1948). At Lincoln, Nebraska, the safe seeding date to escape hessian fly in 1943-44 was September 26. In a date-of-planting-variety test that crop year the susceptible variety Nebred carried 74 per cent of the plants infested and yielded 8.6 bushels while Pawnee had 13 per cent infestation and yielded 32.7 bushels when planted September 15, 1943. The same year neither Nebred nor Pawnee planted October 1 had fall-fly infestation and Nebred from this plot yielded 24.7 bushels; Pawnee, 28.1 bushels. The use of this resistant variety has not only reduced the level of the hessian fly population but permitted more latitude in dates of planting.

The production of Pawnee has not been the result of the work of one or two persons. It has been the cooperative work of the Departments of Agronomy, Botany, and Entomology of the Kansas Agricultural Experiment Station, the Department of Agronomy, Nebraska Agricultural Experiment Station, and the Bureau of Entomology and Bureau of Plant Industry of the U.S. Department of Agriculture, aided by the Agricultural Experiment Stations of other states. From the standpoint of the hessian fly it is considered only a partial solution, usable until more resistant strains now under test are available.

Hessian fly resistance in spring wheats, foreign introductions, and in species other than *Triticum aestivum* (*vulgare*). Most of the data so far reviewed have dealt with the hessian fly infestation primarily in winter wheats and in the one species, *Triticum aestivum*. The early reports from California (Wickson 1886, Woodworth 1891, and Kellner 1892) as well as scattered information in other reports indicated a high resistance among the durum spring wheats (*Triticum durum*). Data presented by McColloch and Salmon (1918) gave evidence that a part of this resistance is the result of low oviposition on at least some of these wheats. In 1928 A. A. Sapehin and L. A. Sapehin showed that fly resistance of a variety of *Triticum durum* could be transferred to a spring-wheat hybrid between *T. durum* and *T. aestivum*. When the occasion has permitted, spring wheats and species of *Triticum* other than *T. aestivum* were exposed to infestation by hessian fly near Manhattan, Hays, Leavenworth, and Oskaloosa,
Kansas. The two latter tests were in the area in which Dawson, Illini Chief, and many other winter wheats are not resistant to the fly as a result of the presence of different biological strains. The results of these tests have been given briefly in the Biennial Reports of the Director of the Kansas Experiment Station for 1930–32 (Painter et al. 1932) and 1932–34 (Painter and Parker 1934), and at the North Central States Entomologists’ Conference in 1933 (Painter 1933). Table 6 is adapted from the proceedings of the conference and is an example of the type of data secured.

Table 6 Infestation of Species and Varieties of Wheat by Hessian Fly at Manhattan, Kansas, Spring, 1932

<table>
<thead>
<tr>
<th>Species and Variety</th>
<th>% Tillers Infested</th>
<th>Fly on 30 Plants</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>EINKORN</strong> (Triticum monococcum)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Einkorn</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Double Einkorn</td>
<td>1.3</td>
<td>8</td>
</tr>
<tr>
<td><strong>EMMER</strong> (Triticum dicoccum)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vernal Emmer 1524-1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Yaraslav Emmer</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Vernal Emmer 3686</td>
<td>32.3</td>
<td>240</td>
</tr>
<tr>
<td>Khapli Emmer</td>
<td>34.4</td>
<td>212</td>
</tr>
<tr>
<td><strong>POLISH</strong> (Triticum polonicum)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>4.1</td>
<td>6</td>
</tr>
<tr>
<td><strong>DURUM</strong> (Triticum durum)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Madona</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Iumillo-4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Kubanka 2094-2</td>
<td>1.1</td>
<td>2</td>
</tr>
<tr>
<td>Peniad</td>
<td>15.0</td>
<td>44</td>
</tr>
<tr>
<td>Spelmar</td>
<td>36.6</td>
<td>196</td>
</tr>
<tr>
<td>Kubanka (Ag.N.4346)</td>
<td>37.7</td>
<td>302</td>
</tr>
<tr>
<td>Arnauta</td>
<td>56.0</td>
<td>555</td>
</tr>
<tr>
<td><strong>COMMON SPRING</strong> (Triticum aestivum)</td>
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</tr>
<tr>
<td>Pusa</td>
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<td>56</td>
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<tr>
<td>Marquis</td>
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</tr>
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<td>Ceres</td>
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<tr>
<td><strong>SPECIES HYBRIDS</strong></td>
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</tr>
<tr>
<td>Marquillo</td>
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</tr>
<tr>
<td>Hope</td>
<td>76.7</td>
<td>1176</td>
</tr>
<tr>
<td><strong>WINTER WHEAT</strong> (Spring planted)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tenmarq</td>
<td>91.0</td>
<td>2090</td>
</tr>
</tbody>
</table>

Many spring-wheat varieties other than those on this list have been under infestation tests, and the majority have proved susceptible. This was particularly true of a large number of the common spring
wheats. In the test in the spring of 1932, most of these susceptible varieties had 100 per cent of the plants infested.

In general, the results of these studies on different species of *Triticum* have indicated that wherever a fairly large number of varieties was studied, a wide range in difference in hessian fly infestation could be found. Only two varieties of Einkorn (*T. monococcum*) have been under infestation and both proved to be resistant. The spring Emmers show a considerable variation in susceptibility and it is interesting to note that a strain of Black Winter Emmer (McColloch and Salmon 1918) was susceptible when grown along with winter-wheat varieties in the nursery. Some strains of spring Emmer were highly resistant, others fairly susceptible. Among the former was Yaraslov, which is one parent of the varieties Hope and H44. A single variety of Polish was fairly resistant. A number of durum wheats was under observation, and the range in susceptibility and resistance was great even among different strains carrying the same name. This is illustrated by the difference in infestation of two strains of Kubanka. Most of the common spring and club wheats have been susceptible. Pusa 4 escaped infestation because of early maturity.

Of particular interest was the hessian fly reaction of some of the interspecific hybrids produced by plant breeders in a successful effort to transfer the high stem-rust resistance of other wheat species to *Triticum aestivum*. The infestations of two of these hybrids, Marquillo and Hope, are recorded in Table 6. Marquillo is the result of a cross of Jumillo durum, which is resistant to fly and rust, and Marquis spring wheat, which is susceptible. This hybrid was bred at the Minnesota station and for a time was grown on farms in that state (Wilson and Arny 1930). At least a part of the resistance to hessian fly present in Jumillo was found to have been accidentally transferred to Marquillo. Hope wheat is the result of an interspecific cross made by McFadden while working in South Dakota. It is derived from a cross between Yaraslav Emmer, which is resistant to the fly, and Marquis spring wheat. The fly resistance of the Emmer parent unfortunately has not been carried over to the common spring segregate. A number of other interspecific common spring wheat segregates from the above hybrids as well as others were tested, but none were found to be particularly resistant.

At the Indiana Agricultural Experiment Station, Packard and
Noble, working in cooperation with federal and state agronomists and plant pathologists, in 1935 discovered the high resistance to hessian fly of Illinois No. 1 W38, C.112061, and subsequently of other common bread wheats (Caldwell and Compton 1939). Tests by federal and state entomologists in California and Kansas confirmed and extended these findings (Painter and Parker 1936). Another strain discovered about the same time in Indiana and since then proved valuable in plant breeding was an unnamed durum, the foreign plant introduction F.P.I.94587. This durum variety has remained practically free from fly wherever it has been tested so far and under conditions of high temperature that result in higher than usual infestation of most other resistant wheats (Cartwright, Caldwell, and Compton 1946). For the next several years an effort was made to test all available varieties and species of wheat under the highest possible infestations in the field and in the greenhouse (Jones 1945). After examining about 3,000 domestic and foreign varieties for infestation by fly a list of the more resistant strains was published (Cartwright and Shands 1944). A list compiled in the same way by E. T. Jones (1945), following tests conducted in Kansas and Missouri, includes most of the same varieties. The list given by Cartwright and Shands records also the stem- and leaf-rust resistance of the strains studied and indicates that resistance to these diseases and hessian fly sometimes occurs in the same strains.

About 6 per cent of the varieties tested showed enough resistance to be given in the list. These included 3 club wheats, 1 Emmer, 1 poulard, 21 durums and 92 common wheats (Cartwright and Shands 1944). The durums as a group had a higher level of resistance and the list included only those that have had a consistently higher resistance than the common wheats. These may approach the resistance of F.P.I.94587. A number of the foreign plant introductions were mixed for resistance and susceptibility, or sometimes for other characters, and selections on the list are represented by dash numbers attached to the original record number. Several of the resistant common spring wheats from the United States are related by selection or hybridization to Java, one of the oldest spring-wheat varieties still grown there. A small group of introductions from Turkey had high resistance and winter habit and are the only varieties of non-hybrid origin known to have this combination.
The number of hessian fly resistant strains which originated in Portugal is far larger than would be expected on the basis of chance. This is especially true if we add to this group those resistant strains of Latin American origin which probably trace back eventually to somewhere on the Iberian peninsula. Of all the resistant spring wheats of all species on the list, not including reselections, 25 are from Portugal, 2 from Spain, 19 from Latin America and 26 from the rest of the world.

In Russia, Chesnokov (1939a, 1939b) reported on a similar study, involving about 400 varieties in the field and 250 in cages. Infestation in the varieties of 7 species studied ranged from 100 to 0 per cent of plants infested. Varieties with no infestation were found in *T. monococcum*, *T. durum*, and *T. aestivum*. Among varieties found to be resistant in Russia were San Martin and "Triumph" from Argentina and Marquillo from the United States. The widest range in infestation was shown by the durums and the common wheats, which were represented by 71 and 230 varieties, respectively.

Trials for a study of varietal resistance to hessian fly have been begun in New Zealand (Anon. 1945, 1946). The crosses Tuscan x Tainui and 7 x Tainui were reported to show resistance to this insect.

In North Dakota the spring-wheat variety Mida has been reported as having the lowest infestation by hessian fly of any varieties grown commercially (Butcher 1946; Smith 1946). As an average in tests for two years the infestation was 26 per cent for Mida, compared with 64 per cent for Ceres.

**Breeding for higher fly resistance from the spring wheats.** Marquillo was the first common wheat found that has been resistant to hessian fly in the field, thus far, wherever it has been tried. The importance of its use in breeding for resistance is evident. Crosses were first made between Marquillo and certain winter wheats at the Kansas Station in the spring of 1932. At that time successful crosses were made between Marquillo and Tenmarq, Minturki, Oro, Kawvale, and Kanred x Hard Federation. Since that time additional hybrids have been made with Illini Chief sel. 223415 and Michigan Wonder. Crosses were also made with six other winter wheats (Fulhard, Clarkan, Fultz, Honor, Chief-kan, and Shepherd), but the F1 plants died after reaching the three- or four-leaf stage, indicating the presence of some kind of
a lethal factor or combination (Heyne et al. 1943). The early results of hybridization involving Marquillo have been recorded (Painter et al. 1940; Reitz et al. 1943).

Back-crosses and compound-crosses were made between fly-resistant F₁ Marquillo hybrids and winter wheats. The F₁ plants of these compound crosses have been nearly as heavily infested as the susceptible parents, indicating that susceptibility to hessian fly tends to be inherited as a dominant character when these plants are tested in the greenhouse. Tests of F₁ hybrids between Marquillo and winter wheats gave similar results as have a number of subsequent F₂ plants involving resistant hybrids carrying Marquillo genes. It is not known whether this susceptibility of the F₁ plants concerns both high oviposition and high larval survival or only the latter character (Fig. 27).

Infestation counts were made on the F₁ Marquillo hybrids with winter wheats at Manhattan in the fall of 1933, and on the F₁ plants of the compound-crosses and back-crosses at Manhattan in the fall of 1936 and at Springfield, Missouri, in the fall of 1936.
as well as in the spring of 1937. All four were similar in that the
F1 population had an infestation about one-third as heavy as the
susceptible parent. This type of reversal of dominance when the
infestation of the F1 plants and F2 populations from these F1 plants
are compared, may indicate a fairly complex genetic combination
of characters for resistance or a delicate physiological balance in
the heterozygote.

In the F1 and succeeding generations the more susceptible
plants and strains were discarded as were lines which lacked de­sirable agronomic characters. During these generations natural
selection for winter hardiness also occurred. No evidence was
secured of the factorial basis of fly resistance. By F2, however,
following continued selection for fly resistance, the infestations of
more than 70 per cent of the hybrids at one of the nurseries were
within the range of the Marquillo parental rows while there were
only one or two of the 326 hybrids grown which approached the
susceptibility of the winter parents. All of these hybrid segregates
had the winter habit of growth and some approached the winter
hardiness of their parents.

In the F2 generation at Springfield, Missouri, an infestation
occurred in which up to as many as 270 larvae were removed
from a plant consisting of a single tiller (Fig. 29). Under these
conditions the winter parents had a complete infestation and in
most cases were entirely killed. The winter wheat with the best
survival was a row of Kawvale, in which 21 per cent of the plants
survived the infestation. Under these conditions and with an
average of 44 per cent of the plants infested for Marquillo, some
of the hybrids had as low as 32 per cent of the plants infested and
85 per cent of the rows had a higher survival after the fly infesta­
tion than did any row of a winter parent. In many cases there
was no close relationship between the per cent of plants infested by
fly and the per cent of plants surviving the infestation. This fact
as well as other data seem to indicate that the genetic factors
for low larval survival (antibiosis) and for ability to survive fly
infestation (tolerance) were not the same and perhaps not even
genetically linked. In a fully susceptible variety it generally has
been assumed that the number of plants killed by fly would be
proportional to the intensity of the infestation. In this population
of Marquillo hybrids which were undergoing some segregation
for resistance to the hessian fly there were some segregates which
Fig. 28. These 217 larvae were removed from a Tenmarq plant of a single tiller from Springfield, Mo. fly nursery, natural infestation, fall of 1935. Seventy-four per cent of the larvae showed evidence of feeding and growth. (Painter et al. 1940.)

Fig. 29. These 270 larvae were removed from a Marquillo x Oro plant of a single tiller from Springfield, Mo. fly nursery, natural infestation, fall of 1935. Only 11 per cent of the larvae showed some evidence of feeding and growth. (Painter et al. 1940.)
had both a high fly infestation and a high ability to withstand injury by the fly. There are other segregates in which a low fly infestation was not accompanied by a high ability to withstand injury. In a number of the segregates, however, factors for low infestation and for ability to survive the infestation appeared in the same strain. In part this was the result of the normal association between intensity of infestation and amount of killing by fly, those not having this association being killed by fly or discarded. In part it appeared to be merely chance association of more or less independent genetic factors. The fact that Marquillo and apparently some of its hybrids carried genetic factors for low oviposition rate further complicated this relationship between plant survival and infestation. In other words, it appeared that three characteristics were responsible for the difference between winter wheats and the winter-type Marquillo hybrids under fly infestation. These were low oviposition rate, low larval survival, and high ability of the plants to survive infestation. There was evidence that these three characters were governed by different genetic complexes but, on the other hand, were inter-related in their effects so far as final infestation and survival of infested plants were concerned.

There has been evidence among these Marquillo hybrids that some lines which had been saved because of possession of desirable agronomic characters were still segregating at a low level of resistance. Practically all the lines which were selected have passed through the disease nursery and carry more resistance to stem rust than do the ordinary winter wheats. Many of them carried resistance to leaf rust equal to that of the better winter wheats and some of the crosses between Marquillo and Oro or Minturki carried resistance to bunt. Both hard and soft kernels were represented among some of the hybrids.

These first Marquillo hybrids were extensively tested in yield nurseries in Kansas (Reitz et al. 1943) and elsewhere (Johnston et al. 1948) as well as in fly nurseries. Evidence was frequent that the fly resistance of these hybrids as well as their disease resistance was high enough to be of great benefit when such hazards were present. Some of these hybrids were grown in ¼-acre yield-test plots. Yielding ability appeared equal to the better commercial wheats being grown, but all strains were somewhat deficient in winter hardiness. Various fly-resistant Marquillo hybrids in Fa
and F₁ as well as later-generation hybrids were crossed to different winter-wheat varieties and hybrids to provide additional winter hardiness.

A number of these compound Marquillo hybrids were tested in yield nurseries and in fly nurseries for resistance to hessian fly. One of the best of these strains, Kawvale-Marquillo x Kawvale-

**FIG. 30.** Comparison of infestation and injury to plants of wheat varieties by hessian fly, Manhattan, Kansas, Nov. 1946. Each small stake marks an infested plant. Row 551 Pawnee, 65% plants infested. Row 552, Tenmarq, 95% plants infested. Row 553, Kawvale-Marquillo x Kawvale-Tenmarq, C.I.12128 (Ponca, 1951), 11% plants infested.

Tenmarq C.I.12128, had the highest two-year average yield in regional tests 1944-46; it also was under test on branch stations and farmers' fields in 1946-48. It appears equal, or nearly equal, to Pawnee in most desirable characters and superior in fly resistance, leaf-rust resistance, and bread-making quality. In 40 tests during the years 1942–1947, C.I.12128 had an average of 2.8 per cent plants infested compared to an average of 80 per cent for Tenmarq and 6 per cent for one of the best original Marquillo hybrids in the same tests (Fig. 30). Its pedigree and relationship to Kawvale and Pawnee are indicated on the chart in Fig. 31.
In Minnesota 1914
Lumillo Durum x Marquis bread wheat
28 chromosomes

Marquillo
42 chromosomes

1932
Marquillo x Kawvale

1935
Sel. 32 FN 762-2 x Sel. 32 FN 185

Kawvale-Marquillo x Kawvale Tenmarq
C.I. 12128
(Ponca, 1951)

Indiana Swamp 1919

Kawvale
To Kansas Farmers 1931

1928
Kawvale x Tenmarq

Pawnee
C.I. 11669
To Kansas Farmers 1943
Leading variety 1946-1947
35% acreage 1947-1948

Marquillo resistance
Kawvale resistance

Fig. 31. Origins of some of the hessian fly-resistant wheats being used in the Kansas wheat improvement program. The dates given are the years in which crosses or selections were made.

Ill. No. 1 W38 has been used in crosses in Kansas, but so far has not given satisfactory hybrid selections. Better types of wheat have been bred from crosses involving a wheat from Uruguay, IV Cl - # (C.I.12034), which has given resistance equal to that from Ill. No. 1. The durum wheat F.P.I.94587 was crossed to
Pawnee in 1939 and common wheat segregates carrying the near immunity of the durum were in yield tests in 1948. Nothing is known concerning their bread-making qualities.

The higher level of resistance to fly has been sought from a number of sources for transfer to winter wheats (Jones 1945; Painter 1945). The following strains have been used in this program: Marquillo C.I. 6887, Ill. No. 1 W38, Centenario, Marvel C.I. 8876, Kearney C.I. 6585, Triunfo, Renacimiento sel., IV CI- 16 + C.I. 12034, IV y gelou C.I. 12001, and the foreign plant introductions 119344-7, 26206-8, 56244-4, and 94587. From the standpoint of practical wheat breeding the usefulness of the different hybrids originating from these parents has varied greatly.

**Breeding for fly resistance from the spring wheats for use in soft red winter wheat.** The attempts to breed a fly-resistant soft wheat received new impetus with the discovery in 1935 of the high degree of fly resistance of Ill. No. 1 W38 and a few other spring-wheat varieties (Skinner 1936; Caldwell and Compton 1939; Cartwright and Benton 1939; Packard 1941). These findings came about when C. M. Packard and associates studied a heavy natural hessian fly infestation in the disease-resistance wheat-breeding nursery at Purdue University Agricultural Experiment Station at Lafayette, Indiana. Under cooperative arrangements between the Bureau of Entomology and Plant Quarantine, Bureau of Plant Industry, U.S. Department of Agriculture, and the Indiana, and later other, State Experiment Stations, crosses between fly-resistant spring wheats and commercial soft-winter wheats were made and studied. In the early crosses, in addition to Ill. No. 1 W38, the following strains were used as sources of resistance: Kawvale-Marquillo selection from the Kansas Station, Ill. No. 1 x (Norka-Carina), and the Durum P.I. 94587. By 1940 homozygous winter-wheat-type F2 and F3 generation hybrids, carrying the fly-resistant factors of Marquillo and Ill. No. 1 W38 and also resistant to leaf rust, were ready for the agronomic test. By this time also the high resistance of the durum P.I. 94587 had been transferred to winter-type F2 generation lines of common bread-wheat type. These hybrids as well as hybrids involving Ill. No. 1 W38 resistance had been crossed back to winter wheats for additional winter hardness and grain quality (Cartwright and Benton 1939). In tests to determine the fly resistance of these segregating wheat populations often over
50,000 plants were tested annually by exposing them to fly infestation in the field or greenhouse.

Within a few years (Annand 1947) five lines from some of these crosses appeared better than the others and were being increased in 1948 for possible distribution to farmers (Salter 1948). Two of these, carrying the cereal investigation numbers 12456 and 12530, are highly resistant to leaf rust. Both are selections from the cross Trumbull x (W38 x Fultz-Hungarian 128).

In addition to the breeding of fly-resistant wheats for practical use, several outstanding contributions to the knowledge of insect resistance have come from Cartwright and his associates. The location of many new sources of hessian fly resistance (Cartwright and Shands 1944) has already been mentioned as has the study of the presence of biotypes of fly (Cartwright and Noble 1947). The latter report and also the demonstration of a variation in the expression of genes for resistance as a result of differences in temperature (Cartwright, Caldwell, and Compton 1946) have aided in understanding differences in the results of various tests. The fly reaction of the durum P.L. 94587 and certain hybrids deriving the fly resistance from it have not been affected so far by environmental conditions, including both biotypes of fly and high temperature.

The inheritance of resistance derived from spring wheats. The inheritance of resistance to hessian fly was demonstrated many times early in the study of fly resistance, but the number of genetic factors involved is still being studied although much progress has been made (Noble, Cartwright, and Suneson 1940; Caldwell, Cartwright, and Compton 1946; Cartwright and Shands 1946). The genetic relationships of Dawson and Ill. No. 1 W38 are discussed in the first two papers. In California the resistance of Dawson had been shown to result from two genetic factors, H1 and H2 (Cartwright and Wiebe 1936). In California Dawson was more resistant than Ill. No. 1. In Indiana Dawson behaves as a susceptible wheat and Ill. No. 1 as a resistant one. A study of populations of the hybrids between these two wheats in early generations clearly indicated a one-factor difference between them. The factor was called Hs. In crosses with susceptible wheats in Indiana it tended to be dominant under field conditions and recessive when tested in the greenhouse. In Kansas, F1 hybrids involving Ill. No. 1 have been uninfested in the field, indicating the dominance of resistance.
well et al. (1946) state that "resistance derived from W38 and its hybrid progenies is shown to have two expressions in resistant genotypes, viz., (a) the capacity, under favorable conditions, to suppress the development of hessian fly larvae with resultant normal plant growth; and (b) the capacity to grow nearly normally and not to show stunting under conditions that prevent the full development of resistance and thus permit infestation to occur. The second capacity was invariably associated with the first and may be used as a criterion of the presence of the Hs factor pair under greenhouse or high-temperature conditions." They have evidence that the same gene in W38 governs resistance to both the Indiana and the California populations of fly, although the resistance is at different levels, being greater in Indiana than in California.

The early crosses between the durum P.I. 94587 (28 chromosomes) and common bread wheats (42 chromosomes) did not permit conclusions regarding the exact factorial basis of resistance because of meiotic disturbances present here as in most interspecific crosses. True breeding segregates possessing moderate resistance modifiable under high temperatures is reported (Caldwell et al. 1946), and the writers suggest that the difference between the durum and susceptible wheats results from at least two gene pairs.

Among the numerous strains of fly-resistant spring wheats derived from various sources there is a question concerning the possible number of genetic factors for resistance. A partial answer has been given by Cartwright and Shands (1946) by experiments in which they crossed each of eleven different strains of common spring wheats that were resistant to hessian fly with Ill. No. 1 W38 and studied the infestation of approximately 100 F1 lines of each cross. Five of these resistant x resistant crosses of spring wheat gave fully susceptible segregates in proportions suggesting 15 to 1 ratios. This indicates that these five strains of resistant wheats carry at least one genetic factor by which they differ from the Hs factor carried by Ill. No. 1. These five wheats were Beirao P.I. 56202-5, Barbella-Santa-Martha P.I. 56222-13, Portuguez P.I. 56204-7, unnamed P.I. 94349-5, and unnamed P.I. 94571-14. In addition, the last three varieties are resistant to the laboratory strain of fly able to infest Ill. No. 1 W38. The spring wheats that possess at least one genetic factor, Hs, in common with Ill. No. 1 W38 were Beirao P.I. 56202-2, Lobeiro-Barbella P.I. 56225-1, Triunfo P.I. 104138-3, unnamed P.I. 94379-3, unnamed P.I. 111245-10, and unnamed
P.I. 125390-8. It will be noticed that two strains selected out of the same plant introduction, Beirao, differ in their genetic composition. Suneson and Noble (1950), studying inheritance of resistance to fly in California, found that resistance in Java was recessive and suggested the symbol \( h \) for this gene. Resistance in Marquillo was also recessive and probably different from that in Java. Resistance in Dixon and Kawvale tended to be partially dominant and dominant, respectively, and were shown to be independent of the factors \( H_1 \) and \( H_2 \) derived from Dawson. From all the evidence presented there appear to be six or probably more different pairs of genetic factors concerned with resistance in the group of hessian fly resistant wheats that have been studied. These different genetic factors provide a means for combating the presence of biotypes of fly by combining the factors in the same wheat variety. The possibility of the use of these factors as well as the use of the durum factors resistant to all known strains of fly are being explored in both Kansas and Indiana.

Uniform hessian fly test nurseries were established in the years 1935–36 under the leadership of C. M. Packard and have contributed to our knowledge of fly resistance. Strains of wheat contributed by the cooperators were assembled at one locality, packaged, and sent for planting to various places where fly nurseries were maintained or heavy infestations were likely. Counts of infestation were made where possible and the resulting information sent to the cooperating agencies.

The basis and value of fly resistance. Very little information concerning the basis of resistance is available beyond that given by earlier writers. The most potent feature of the higher levels of hessian fly resistance has been the antibiotic action of the resistant plants. The larvae reach the normal feeding position in such plants, but most or all of them do not grow. Jones (1940) has followed the life history of larvae on resistant and susceptible plants under various conditions and found also a slowing up of development of those larvae that do mature on certain resistant plant varieties. He made the suggestion that growth of tissues of resistant plants crushed the larvae after these reached the feeding position. It has been difficult, however, to determine whether these larvae were already dead or moribund at the time the crushing action began. Jones would associate both cell turgor and greater amount of crude fiber with the action of resistant varieties.
Tolerance to injury by fly is of considerable economic importance in Pawnee (Painter and Jones 1945) and in Marquillo hybrids (Painter et al. 1940). Such tolerance also occurs in otherwise susceptible wheats, but appears to be totally lacking in Turkey and many other hard red winter wheats (Fig. 15, 25, 30).

It should be noted that 25 years after the first crosses were made between fly-resistant and fly-susceptible wheats, new varieties carrying these resistant characters were being distributed to farmers. Thirty years after the first crosses were made, these fly-resistant wheats, Poco 42 and Big Club 43 in California and Pawnee in Kansas and neighboring states, were being grown on several millions of acres. Prospects were good for the distribution to farmers of varieties possessing higher resistance and better quality in other respects. It should be emphasized that these goals have been reached without exact knowledge of the mechanism of resistance and, in the early stages, without exact information about the genetic factors involved.

RESISTANCE TO THE WHEAT STEM SAWFLY (CEPHUS CINCTUS NORT.) AND RELATED SPECIES

Biology of the wheat sawflies. The genus Cephus, to which the wheat stem sawfly belongs, contains a large number of species, only one of which (cinctus) is native to North America. Two other species, the European wheat stem sawfly, Cephus pygmaeus (L.), and the black grain stem sawfly, Cephus tabidus (F.), have been introduced into the United States and occur in the northeastern states, particularly New York, Pennsylvania, Maryland, Ohio, and Virginia (Udine 1941). All three species have similar life histories and do similar damage to wheat and other grasses.

Cephus cinctus has been a major limiting factor in the production of wheat, spreading through the Canadian provinces of Alberta and Saskatchewan and into the states of North Dakota and Montana and neighboring areas. Its original host plants appear to have been the native grasses, particularly Agropyron, and the injury to wheat in Canada has steadily increased since C. cinctus was first collected in 1895. The ecology and life history of this species has been studied by Ainslie (1929) and Seamans (1945). In Canada the adults begin to emerge about the middle of June, the females ovipositing in the young hollow stems of grasses and wheat. The
eggs hatch in about eight days and the larvae mature about the
time the culms mature. Only one larva per stem matures, since
the surviving larva destroys the other eggs or larvae present. The
stems preferred for oviposition appear to be those in which the
wheat or grass head is just ready to emerge from the upper leaf
sheath, but earlier or later culms may be infested. When mature,
the larva moves to the lower part of the stem and cuts a V-shaped
groove entirely around the inside of the stem and about an inch
above the surface of the ground. The weakened stem often breaks
off at this point. The stub of the stem is plugged with a mass of
frass and debris, and the larva forms a cell within the stem beneath
this plug, in which it passes the winter. Pupation occurs the fol­
lowing May or June. Seamans (1945) has shown that dry or wet
conditions at certain seasons of the year affect the insect adversely.

In addition to wheat and Agropyron, Ainslie (1929) reported
the following as food plants: one or more species of Elymus, Hor­
deam, Bromus, Phleum, Deschampsia, Calamagrostis, Festuca, bar­
ley, rye, and spelt. Farstad (1944) has recorded considerable in­
festation in flax, but in no case were the insects able to complete the
life cycle on this plant. Farstad and Platt (1946) have also
recorded the differences in infestation and damage to barley varie­
ties by Cephus cinctus. The infestation was less than on the
susceptible wheat varieties Apex and Thatcher and the amount of
cutting of stems much smaller. The cutting varied on the average
from 2.1 per cent for Trebi to 21.7 for Hannchen. Parasitization
of the larvae by Microbracon cephi was high on barley and survival
of the sawflies apparently low.

While the sex ratio of these wasp-like insects is normal in most
areas, Farstad (1938) has reported that in southern Alberta a popu­
lation normally consisting entirely of females may have been re­
sponsible for the marked increase in the number of insects present.

The principal damage done by the stem sawflies is the result of
the breaking over of the culm so that the wheat head is harvested
with difficulty or not at all. Particularly with regard to the wheat
stem sawfly, a reduction in yield occurs even though the head is
recovered (Munro 1945). In Canada this has been estimated to
amount to about 10 per cent reduction in yield and a reduction of
one step or grade in the quality of grain.

Sources of resistance to wheat stem sawfly, and basis and in­
heritance of resistance. In Russia early reports indicated that
varieties of wheat with solid straw were resistant to *C. pygmaeus* and *C. (Trachelus) tabidus* (Shchegolev 1926, 1927). The former was reported to attack mostly winter wheat, the latter spring wheat, with the intensity of attack varying with the maturity of the different wheat varieties.

In the spring-wheat area of Canada the earliest attempts to locate sawfly-resistant wheats were begun by Kemp in 1929 and experiments extending through 1933 were reported (Kemp 1934). The first year it was found that the solid-straw Golden Ball durum wheat and the semisolid white-straw Tuscan were not as seriously affected as other wheats and the lack of infestation was confirmed in cage tests in later years. In 1933 a test was conducted of 38 strains of solid-strawed wheats obtained from New Zealand, but originally coming from New Zealand, Spain, Portugal, and Morocco. When subjected to natural infestation the percentage of infested culms ranged from 0.8 to 39.2 on these wheats and the percentage of culms severed ranged from 0 to 6.8 per cent. Marquis and other hollow stem wheats were considerably damaged. Kemp found that the larvae were often dead in the solid or partly solid stems and were often stopped at the nodes from boring down the stem to the normal place of hibernation.

Farstad (1940), in his doctor's thesis, has made a thorough study of the development of the wheat stem sawflies in various host plants, including the resistant varieties S-615, S-633, and Golden Ball, which were originally studied by Kemp. Although hindered by the low degree of development of solidness of stem under cage and greenhouse conditions, he confirmed the relationship between this character of the stem and resistance to *Cephus cinctus*. He reported that "there is a direct relationship between the amount and consistency of the pith tissue present and the degree of effect upon the developing *C. cinctus*. It therefore appears as though the resistance is of a mechanical nature rather than a nutritional one. Platt and Farstad (1941), quoting apparently from the thesis itself, reported that "the exact physiological nature of resistance is not known, but there are certain observations which may be of value in its interpretation. Whenever pith tissue completely fills the lumen of a stem, there appears to be a mechanical impediment to the movement of the larva. Larvae which hatch from eggs completely surrounded by pith do not survive. It therefore appears as though the pith itself lacks certain nutritional factors."
essential to growth. All larval feeding takes place in a tissue layer adjoining the fibro-vascular bundles. Thus, if the pithy tissue is firm and compact, it appears as though the larvae might have difficulty in moving with sufficient ease to obtain an adequate food supply.” Farstad found that in the case of *Agropyron elongatum*, which is highly resistant and largely with solid stems, the hollow stems produced appear to have a deleterious effect on larval growth.

In view of the evident importance of the solid-straw characteristic in sawfly resistance and its variability, a detailed study of the influence of environmental factors was made by Platt (1941). The study involved the solid-straw Golden Ball durum, and the solid-stemmed common wheat varieties S-615 and S-633 that had been studied by Kemp and by Farstad. The two common wheat varieties were grown at from 12 to 17 stations in Canada for three years. The latter had been purified by plant-row selection for several years before being used in the experiments. In the study each stem was classified in one of six groups from 0 (completely hollow) to 5 (completely solid), the intermediate steps representing different degrees of solidification. A solid stem was one in which the stem cavity was completely filled with pith.

In field experiments the S-615 and S-633 varied in degree of solidness from year to year and from locality to locality, its over-all range being from 0.5 to 4.9. The variety Golden Ball, on the other hand, was essentially solid-stemmed at all points where it was grown. A study was made of possible causes of the variation in solidness of the common wheats. Apparently soil differences were not a major factor. The results indicated that the expression of the solid-stem character was favored by long hours of sunshine and high temperature in June at times when the rainfall was low through the growing season.

In greenhouse experiments it was found that S-615 and S-633 were essentially hollow regardless of other conditions. In spacing experiments the index of solidness increased as the distance between plants increased, when the rows were 14 inches apart. An experiment in which plants were lightly shaded during the early morning and late afternoon provided plants of S-615 that were completely hollow and full shade had a slight effect on the solidness of stem of Golden Ball. The results of the whole group of experiments suggest that light is the most important character limiting the expression of the solid character. In the field the expression of solidness of
stem was therefore favored by the long hours of sunshine during the
time that the stem was elongating.

A study of the inheritance of solid stern in crosses between S-615
and S-633, and Renown and Thatcher showed that the difference
between hollow and solid stem depended on three gene pairs, with
the hollow condition dominant and with any four or more genes,
if present, giving the hollow condition. The number of genes in­
olved in this character and in other desirable characters, such as
rust resistance, yield, and quality, were such that it would be neces­
sary to grow large populations of hybrids in order to secure the
desired combinations (Platt, Darroch, and Kemp 1941).

An attempt was made to transfer the solid-stern character from
Golden Ball durum (28 chromosomes) to common bread wheat
(42 chromosomes) but without success (Platt and Larson 1944).
This transfer was attempted because of the greater stability of the
solid straw in the durum wheat and hence the greater resistance to
the sawfly under varying environmental conditions. The crosses
involved two different varieties of common wheat, Renown and
Rust Laboratory selection 1097, and were studied in detail princi­
pally in F2, with general observations of selected lines in F3 and
later generations. In the two crosses a total of about 25,000 F2
plants were studied. The solid-straw character was combined with
some characteristics typical of the common bread wheats, but all
plants or lines having these combinations were sterile or, if fertile,
had only 28 chromosomes characteristic of the durum parent. It
was concluded that it was "not practical to attempt to transfer the
solid-stem character from T. durum to T. vulgare by hybridization."

Platt and Farstad (1946) reported on the sawfly damage to a
number of wheat varieties studied in 24 different nurseries during
the period 1941–1945. This was part of a cooperative experiment
between the Dominion Experiment Station, Swift Current, Sas­
katchewan, and the Dominion Entomological Laboratory, Leth­
bridge, Canada. Special nurseries were planted early each year
under conditions favorable for the establishment of heavy infesta­
tions by sawflies. The figures used for damage to the varieties were
the averages of percentages of stems cut, resulting from two in­
dependent estimates on each of several replicates. Detailed studies
made during one of the years indicated that none of the varieties
studied had any particular resistance to oviposition. Statistical
analyses and notes on techniques were given. Differences were
found to exist in the amount of damage done to hollow-stemmed common-wheat varieties and between the two solid-stemmed common wheats S-615 and S-633. Often these differences were significant. The solid-stem durum, Golden Ball, was the most resistant. The hollow-stemmed durums were much more resistant than the hollow-stemmed common wheats. On the average, Mindum was slightly more susceptible than S-615 and slightly less so than S-633. Data given regarding some of these varieties are reproduced in Table 7. The data studied demonstrated that factors other than stem solidness are involved in sawfly resistance. Since no solid-stemmed variety studied was completely susceptible, however, the association between the solid-stem character and resistance has been useful in a plant-breeding program.

**Table 7** PERCENTAGE OF WHEAT STEMS CUT BY SAWFLIES AVERAGE OF ALL STATIONS, 1941-1945

(From Platt and Farstad, 1946)

<table>
<thead>
<tr>
<th>Variety</th>
<th>Kind of wheat</th>
<th>Character of stem</th>
<th>Av. % cutting</th>
</tr>
</thead>
<tbody>
<tr>
<td>Golden Ball</td>
<td>durum</td>
<td>solid</td>
<td>6.8</td>
</tr>
<tr>
<td>Sivouska No. 3</td>
<td>durum</td>
<td>hollow</td>
<td>12.2</td>
</tr>
<tr>
<td>S-615</td>
<td>common</td>
<td>solid</td>
<td>13.6</td>
</tr>
<tr>
<td>Mindum</td>
<td>durum</td>
<td>hollow</td>
<td>18.4</td>
</tr>
<tr>
<td>Icumillo</td>
<td>durum</td>
<td>hollow</td>
<td>19.8</td>
</tr>
<tr>
<td>S-633</td>
<td>common</td>
<td>solid</td>
<td>26.7</td>
</tr>
<tr>
<td>Red Bobs</td>
<td>common</td>
<td>hollow</td>
<td>56.5</td>
</tr>
<tr>
<td>Regent</td>
<td>common</td>
<td>hollow</td>
<td>57.2</td>
</tr>
<tr>
<td>Thatcher</td>
<td>common</td>
<td>hollow</td>
<td>60.7</td>
</tr>
<tr>
<td>Marquis</td>
<td>common</td>
<td>hollow</td>
<td>61.8</td>
</tr>
<tr>
<td>Apex</td>
<td>common</td>
<td>hollow</td>
<td>68.3</td>
</tr>
</tbody>
</table>

Production and characteristics of the wheat variety Rescue. The breeding program, begun about 1937 and directed toward the production of a commercially acceptable sawfly-resistant wheat, reached its first goal with the general distribution of Rescue wheat to farmers in Canada in 1947. This variety of beardless hard red spring wheat was selected in 1942 from a hybrid line of the cross between Apex and S-615. It was tested in nursery trials at five locations in Canada in 1943-47 and grown for increase on a field scale in 1946.

Observations on the behavior of Rescue and of its parents and Thatcher with respect to sawfly in Alberta and Saskatchewan,
Canada, and Montana were reported by Platt, Farstad, and Callenbach (1948). In nurseries designed to give high infestations of sawflies the average per cent cutting in 22 tests during 1943-47 was as follows:

<table>
<thead>
<tr>
<th>Variety</th>
<th>Per Cent Cutting</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rescue</td>
<td>9.3</td>
</tr>
<tr>
<td>S-615</td>
<td>12.7</td>
</tr>
<tr>
<td>Thatcher</td>
<td>61.9</td>
</tr>
<tr>
<td>Apex</td>
<td>71.4</td>
</tr>
</tbody>
</table>

These averages include tests for four years at Regina, where for some reason the average infestation for Rescue was 36.3 compared to 90.3 for Apex and thus considerably less resistant than elsewhere. Rescue tended to be more resistant than its resistant parent S-615 at all stations for all years. In standard yield tests in southwestern Saskatchewan Rescue was damaged 2.4 per cent and Thatcher in the same tests 35.5 per cent. In farmers' fields in 1946 and 1947 Rescue was highly resistant and no reports of serious damage were received from growers. In nursery trials in Montana, Rescue showed satisfactory resistance in all except a few tests, especially in 1947. Even in areas where nurseries showed Rescue to be less resistant, the performance of the variety on a field scale appeared to be satisfactory. The differences in the damage to resistant wheats in different areas are probably related to environmental differences, but what these are has not always been easily apparent. According to information in the press (Trower 1948) Rescue was seeded on about 1½ million acres in 1948.

In agronomic and milling qualities Rescue is hardly equal to the varieties now in use. It carries some resistance to stem rust, but is susceptible to leaf rust and bunt. In North Dakota (Stoa 1947), in the absence or near absence of sawfly damage, Rescue often yielded appreciably less than Thatcher and other commonly grown susceptible varieties. It is deficient in certain milling characteristics so that it cannot be graded higher than No. 3 market grade in Canada. According to Stoa the yield in Canada has been from 10 to 15 per cent below the more commonly grown varieties. As indicated by its name, Rescue is intended to be used in areas where severe sawfly damage may occur and only until better quality-resistant varieties are available. Hybridization directed toward the production of such varieties is under way in both Canada and the United States. In Pennsylvania crosses have been made with the
intention of incorporating the solid-straw character into winter wheats for possible use against the two species of sawflies present in that area (Jones 1943).

RESISTANCE OF WHEAT TO VARIOUS INSECTS

Observations of varietal differences in wheat to a number of additional insects have been reported (Packard 1941; Jones 1943). Many of these observations were incidental to other studies and often denote a presence or absence of synchronization between insect and plant life histories, or some other type of pseudoresistance. Only abstracts of some of the literature have been available to the author and there are indications that additional information and bibliographic references may be available in the original papers.

In several papers in North America there are recorded cases of differential feeding of grasshoppers on wheat varieties mostly during the grasshopper outbreaks of 1933 to 1940, and additional unpublished observations are known to exist. The species involved was usually the lesser migratory grasshopper *Melanoplus mexicanus mexicanus* Sauss., but other species may occasionally have been present. Injury to wheat may be to the foliage of the seedling or leaves of the mature plant, but injuries to the glumes and developing seed may also occur. There is, however, another common but peculiar type of damage. In the ripening wheat plant one of the last parts to lose its green color (and presumably its moisture and food value) to the grasshopper is that part of the stem immediately below the head. If grasshoppers move into ripening wheat, heads are frequently cut off just at this point by the insect. The insects may be in search of food, or moisture, or both. Grasshoppers are sensitive to their environment, including previous foods (Wilbur et al. 1942). Their feeding habits are known to be conditioned by moisture and temperature, so that apparent preferences must be interpreted with care. Yet in spite of these possible sources of error, the same varieties have been mentioned as resistant or susceptible on several occasions. All records appear to be concerned with preference but antibiotic differences are not excluded.

Clark (1936) reported that the common red spring-wheat variety Ceres was resistant to grasshoppers. Smith (1939) reported from North Dakota a highly significant correlation between the percentage of wheat heads cut off by *M. mexicanus* and the per-
The selections studied included many unnamed hybrids. Among the named varieties listed, Hard Federation with 75 per cent stem rust and 15 per cent of heads cut off was an exception to the trend. Among the remaining named varieties there were two groups. Those with rust readings of 2 to 15 per cent had grasshopper injuries of 20 to 35 per cent, while the group with rust readings of 60 to 75 had grasshopper injury of 58 to 95 per cent. Reward was the most susceptible variety, and the reading for Ceres was 73 per cent for stem rust and 72 per cent for grasshopper injury. The possible reasons suggested for the correlation between rust infection and grasshopper damage was (1) greater sugar content of rusted stems; (2) high protein content of rust spores; (3) soft and juicy stems of some varieties; and (4) wheat stems injured by rust pustules are more easily broken over and chewed off than normal stems. No clear association between maturity and grasshopper injury was noted among the wheats studied (Table 8).

Table 8  THE RESISTANCE OF WHEAT TO TWO DIFFERENT SPECIES OF GRASSHOPPERS IN RELATION TO STEM RUST INFECTION AND TO EARLINESS

<table>
<thead>
<tr>
<th>Spring wheat variety</th>
<th>Melanoplus mexicanus North Dakota</th>
<th>Melanoplus bistatatus South Dakota</th>
<th>Relative maturity of plants</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>% Heads cut off</td>
<td>% Stem rust</td>
<td>% Heads clipped</td>
</tr>
<tr>
<td>Clarendon</td>
<td>---</td>
<td>---</td>
<td>36.3</td>
</tr>
<tr>
<td>Triunfo</td>
<td>---</td>
<td>---</td>
<td>37.0</td>
</tr>
<tr>
<td>Pilot</td>
<td>20</td>
<td>2</td>
<td>43</td>
</tr>
<tr>
<td>Ceres</td>
<td>72</td>
<td>73</td>
<td>43.3</td>
</tr>
<tr>
<td>Hope</td>
<td>20</td>
<td>2</td>
<td>48</td>
</tr>
<tr>
<td>Thatcher</td>
<td>31</td>
<td>6</td>
<td>70.7</td>
</tr>
<tr>
<td>Reward</td>
<td>95</td>
<td>75</td>
<td>83.0</td>
</tr>
<tr>
<td>Marquis</td>
<td>80</td>
<td>75</td>
<td>90.7</td>
</tr>
<tr>
<td>Hard Federation</td>
<td>15</td>
<td>75</td>
<td>---</td>
</tr>
</tbody>
</table>

1 Smith, 1939.
2 Hehn and Grafius, 1949.
3 E = relatively early maturing; L = relatively late maturing varieties.

Swenson (1940) reported Ceres as having the least damage by grasshoppers at Highmore, South Dakota, in 1938, while Marquis,
Reward, and Quality had about twice as much injury as Ceres. A hybrid, Hope x Ceres had almost as low injury as did Ceres. The same writer, Swenson (1941), reported that the Argentine variety Triunfo (Triumpho) exhibited considerable resistance to grasshoppers, as did the variety Clarendon. Both of these have been used in a breeding program in South Dakota.

Jacobson and Farstad (1941) reported on the percentage of heads cut off by grasshoppers (M. mexicanus) in two plots of 41 wheat varieties at two localities in Alberta, Canada. Ceres with 1.7 per cent was again among the least injured varieties. Black Persian with an average of 42.8 per cent was the most injured followed by Renown with 28.5 and Mindum with 19.6 per cent. The variety Reward had 17.2 per cent injury. Jones (1943) reported that four replications of Lumillo durum and the hessian fly resistant durum, P.I. 94587, were completely stripped by a heavy infestation of grasshoppers whereas 100 rows of other spring and winter wheats in the same test were uninjured.

Hehn and Grafius (1949) have reported on the injury done to 11 spring-wheat varieties by Melanoplus bivittatus (Say) in the course of one field and two greenhouse tests. It was reported that among wheat varieties in South Dakota “growers of hard red spring wheat have frequently observed that Ceres, Pilot, and Rival suffer less damage from grasshopper attack than Reward and Thatcher.” Results obtained in the experiments agreed with these observations previously made on a field scale. In addition two other varieties, Clarendon, C.I. 8462, and Triunfo F.P.I. 104138, were also resistant, the former variety having the least damage in all three tests. The type of damage studied was the tendency of the grasshoppers to cut the wheat heads by feeding on the culm below the head. The percentage of heads clipped in this manner varied from 36.3 for Clarendon and 37.3 for Triunfo to 83.0 for Reward and 90.7 for Marquis in the field test. Under greenhouse conditions an average of 19.5 per cent of the heads of Clarendon were clipped and 92 per cent of the heads of Reward and Thatcher. In the field test negative correlation ($r = -0.91$) was found between the clipping of the heads and the microns of peripheral mechanical tissue in a 720-micron sector of the culm taken 1 centimeter below the peduncle. A positive correlation ($r = +0.91$) was found between similar measurements of chlorenchyma tissue and the percentage of clipping. Similar sig-
significant correlations were found between these three characteristics in the greenhouse tests.

In these tests in South Dakota no relationship was found between the date of heading of the varieties and the injury. Likewise, no relationship was found between the stem-rust infection and grasshopper damage since both Triunfo and Reward near the two extremes of damage both had 80 per cent stem-rust infection in the field test. This is contrary to the situation found by Smith (1939) in North Dakota. Hehn and Grafius (1949) suggested that in the South Dakota tests the rust did not occur early enough to influence the quantity or quality of the mechanical tissue in the culm. The lower level of rust infection on such varieties as Ceres in the South Dakota test and particularly the fact that different species of grasshoppers were involved may also be adequate explanations of the differences found (Table 8).

Jones (1937) studied the reaction of many varieties and hybrids of winter wheat to chinch bugs, *Blissus leucopterus*, under conditions that gave extreme differences between resistance and susceptibility. During a mild winter numerous adult chinch bugs hibernated in the fall-planted wheat nursery instead of in bunch grass as is usually done. Late in the fall

![Figure 32. Susceptible wheat plants stunted by chinch bugs, *Blissus leucopterus* (Say), together with single, unstunted resistant plant from the same row, Manhattan, Kansas, 1935. (From E. T. Jones, Bur. Ent. and Fl. Quar.) (Jones 1937.)](image)
and early in the spring they fed on the wheat of these nursery rows. Inheritance of resistance was clearly evident. The variety Fulhard was resistant, the variety Oro susceptible, while some of the fixed hybrids involving these two varieties were resistant, others susceptible. The susceptible strains were reduced to about half the height of the resistant ones, although they were sometimes in adjoining rows. The same type of differences in wheat varieties to chinch bugs has been observed on other occasions at Manhattan, Kansas, but the differences involved fewer numbers of strains and were less uniform (Figs. 32, 33).

The green grain bug, *Chlorochroa uhleri* Stal., and several related species have been reported as damaging the milling and baking quality of wheat grain. The insects doing similar damage include *Chlorochroa sayi* Stal. in other parts of the United States, and species of *Aelia* and *Eurygaster* in Russia (Kretovich et. al. 1943). The insects feed on the immature kernels and, by doing so, reducing the yield, cause shrunken kernels, and affect the milling
In North Dakota differences in injury by C. uldrn to 13 varieties of spring wheat have been reported (Harris et al. 1941). Renown and Thatcher were the least injured with 16.8 and 18.0 per cent of kernels damaged, while Rival had 52 per cent. Samples of grain of Thatcher and Rival were each separated into plump, intermediate, and shrunken kernels and each type of each variety was milled and baked separately. The shrunken and intermediate grain of Rival made much poorer bread than corresponding kernels of Thatcher, indicating a degree of tolerance in the latter variety.

The greenbug, Toxoptera graminum (Rond.), is an aphid that sometimes causes spectacular destruction of wheat and other small grains over large areas. The insect occurs sometimes in outbreak numbers in localities where small grains are grown in Europe, North and South America, and parts of Asia. It does much more damage in proportion to its numbers than any other aphid on wheat. Wadley (1931) has recorded that the greenbug was more difficult to rear on Minum durum than on the few common, winter-wheat varieties studied, and that on Vernal Emmer less than 10 per cent of the aphids matured and no second generation developed. During a heavy outbreak in Texas and Oklahoma in 1942, Atkins and Dahms (1945) made extensive observations on the difference in injury to varieties of oats, barley, and wheat. Differences between the 14 varieties of oats studied were not extensive, but wide differences were found between the considerable number of varieties of barley examined. Smooth Awn 86, Hankow, Omugi, Mignon, and several others were highly resistant. The winter-wheat varieties studied were intermediate in range of resistance between the oats and the barley varieties. Highest resistance among the wheat varieties was shown by Marquillo x Oro strains, Denton, Hope x Turkey, C.I. 11964, and wheats belonging to the Blackhull group of varieties. The Marquillo hybrids are known to be resistant also to hessian fly; the other strains are susceptible. Among the most susceptible strains were selections of Kawvale x Tenmarq, including Pawnee. There was little evidence of any relationship between maturity and resistance in the early spring, but there was some evidence of segregation among some of the wheat crosses. In connection with a project at the Oklahoma Experiment Station on breeding for resistance to Toxoptera, Dahms (1943) reported possible
differences in strains of this insect in respect to the interaction between insects and plants. In Uruguay, Silveira and Conde (1945) reported some differences in susceptibility among varieties of wheat and rye in laboratory tests.

Strickland (1931) studied the behavior of four common spring-wheat varieties in the presence of the northern grain wireworm, *Ludius aen'pennis* Kby. His experiments showed that the beetle larvae had considerably less preference for the germinating seed and young seedlings of Garnet than for those of Marquis or Ruby, but compared to Marquis and Reward the older seedlings of Garnet recovered very poorly from attack. As a result, the yield of Garnet on soil infested with this wireworm was sometimes observed to be less than the yield of other varieties under the same conditions.

The larvae of the two gall midges attacking the young kernels of wheat usually have been studied together and sometimes confused. The reports are therefore not always trustworthy. Barnes (1928) gives characters for distinguishing the two species in all stages. The insects generally do more damage in areas that are cool and moist at the time the wheat is in head. Muhlow (1935) gave a detailed report on the two species *Contarinia tritici* (Kirby) and *Sitodiplosis mosellana* (Geh.) as they occur in Sweden, where *C. tritici* causes at least 90 per cent of the damage done by both species to the kernels and glumes of the wheat. The percentage of injury to kernels of both spring- and winter-wheat varieties is given in a series of tables. There was a high correlation between early maturity and severe injury, although several varieties do not agree with the trend. Rademacher and Klee (1936) have also studied varietal differences in infestation by these two insects. Recher (1945) has given an account of the life history of the wheat midge (*S. mosellana*) in the northwestern part of the United States. He finds no differences in infestation in three spring-wheat varieties but reported that an infestation had been observed in which barley varieties ranged in infestation from 0 to 49.9 per cent.

Some evidence of the presence in wheat varieties of resistance to injury from the wheat-stem maggot (*Meromyza americana* Fitch) has been presented by Gilbertson (1925) and Dunham (1934) and less detailed information in some earlier publications. Dunham found that the spring-wheat varieties Hope, Ceres, and Supreme were significantly more resistant to the wheat-stem maggot than the varieties Reward and Thatcher. An analysis of the fac-
tors entering into the differential infestations of varieties by the spring generation has been given by Allen and Painter (1937). The difference in infestation has been shown to depend not only upon the variety involved, but upon the relationship between the peak number of second-generation adults present and laying eggs, and a particular stage of maturity in which the plants are more attractive to the female or more palatable to the larvae. The analysis was made by a study of the relation between the date of first heading and average varietal infestation, and the relation to data collected in date-of-planting-variety plots. Minturki was apparently the most resistant variety studied when compared to other varieties. Bigger (1938) reported on the infestation by the insect in ten spring-wheat varieties which varied in percentage of tillers infested from 0.05 per cent for Comet and Komar to 11 per cent for Klein C 390% from Argentina.

Several other species of Chloropidae infest wheat and other small grains. The relationship between insect life history and susceptible stage of plant growth appears to present a similar problem to that found in the case of Meromyza americana. Varietal differences in infestation of wheat by Chlorops pumilionis Bjerk, the gout fly, have been reported by several writers. Chrzanowski (1926) as well as later writers found that earlier maturing plants were less attacked than others. Watzl (1931) reported on an examination of infestation by the insect in 30 varieties of wheat grown in Czechoslovakia. Generally, the later maturing varieties were more heavily infested but there were exceptions to this correlation. Susceptible varieties were thought to have thicker stems and broader leaves. Fleishmann (1931) in Hungary found a range in infestation in different varieties from 1.6 to 23.7 per cent. In many areas in Europe the gout fly is more particularly a pest of barley, and OzoJo (1929) reports that the percentage of attack on barley varieties varied from 9.2 to 55.5. In general, again, the early varieties were the least injured. Jasnowski (1938) has studied the inheritance of resistance of wheat to this insect.

The frit fly, Osectinella frit (L.), is known particularly as a pest of oats, and much work has been done in England on resistance to the insect in that crop. There are some reports from Russia concerned with resistance to the insect in wheat (Rubtsov 1935; Kirichenko 1935; Belyaev and Kharzhenko 1936; Kovalevskii 1946). Chesnokov (1936, 1937, 1939, 1940) has made the most extensive study.
During the course of three years 450 forms, mostly spring wheats, were tested in two areas. Some varieties did not behave in the same fashion in both areas. Varieties of the species *T. monococcum*, *persicum*, and *timopheevi* showed the least injury while varieties of durum wheat had a range of 5.1 to 85.6 in injury and common wheats from 3.6 to 90.0.

A few reports are available concerning the resistance of wheat to the fly *Hylemya (Phorbia) genitalis* Schn. (Sakharov 1923, 1933; Barulina 1933; Rubtzov 1935; Venturi 1944). In several of these papers resistance is correlated with a coarse, tough ligule or susceptibility with the lack of a ligule.

Varieties and hybrids of wheat are reported to differ in tolerance to the jointworm, *Harmolita tritici* (Fitch) (Painter et al. 1940) although no detailed data are presented. The differences observed during the period covered by the report and since that time have been differences in the number of galls formed and in the amount of lodging and breaking at the point where the galls form.

Painter and Bryson (1934) have reported that Einkorn is resistant to the wheat straw-worm, *Harmolita grandis* (Riley). An amphidiploid wheat x rye has also been found to be resistant in tests at the Kansas Experiment Station, where attempts have been underway to transfer this resistance to common wheat. In the wheat x rye hybrid some of the larvae hatch but do not mature. In a hybrid between wheat x rye (susceptible to fly but resistant to wheat straw-worm), and IV Cl x Comanche (resistant to hessian fly, but susceptible to straw-worm) the three F1 plants grown in the field showed no straw-worm infestation in the spring and no fly infestation either in fall or in spring. Infestation by both insects in susceptible wheats was medium to high. In later generations segregation occurred for both types of resistance but the desired combination has not yet been secured.

On a few occasions resistance to more than one insect has been found in the same strain of wheat. In no case has there been any evidence that the basis of resistance to the insects was the same. The Marquillo x Oro strains that were resistant to greenbug were in addition resistant to hessian fly. While some of the Marquillo x Oro lines were also tolerant to jointworm, data are lacking for the particular strains that were resistant to greenbugs. The variety Triunfo of South American origin is resistant to both hessian fly and grasshoppers. It should be possible to get combinations of any
desired resistance to insects in wheat where genes for such resistance exist in the species \textit{T. aestivum} or perhaps even elsewhere in the genus \textit{Triticum}.

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RESISTANCE TO INSECTS IN WHEAT


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WATZL, O. On the susceptibility of the various varieties of wheat to attack


CHAPTER V

RESISTANCE TO INSECTS IN CORN

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Indian corn or maize,\(^1\) *Zea mays* L., has several distinctions of importance in a study of insect resistance. Aside from its high economic value where it is grown in the United States, Argentina, Southern Europe, South Africa, and elsewhere, it is probably the best known plant from a genetic standpoint. More than 300 genes are known (Emerson, Beadle, and Frazer 1935) and many have been assigned positions in the 10 linkage groups. These include genes for disease resistance (*loc. cit.*) and for insect resistance (Horovitz and Marchioni 1941).

\(^1\) The term *corn* will be used generally in this discussion since this term, rather than maize, predominates in the literature dealing with resistance to insects in this crop.
The genus *Zea* is monotypic and evidence generally points to South or Central America as the place of origin of the single included species. Wild forms of corn are unknown and the origin of cultivated corn is still being studied. Mangelsdorf and Reeves (1939) have presented on this subject a tripartite hypothesis (1) that cultivated maize originated from a wild form of pod corn which was once and perhaps still is indigenous to the lowlands of South America; (2) that teosinte, the closest relative of maize, is a recent product of the natural hybridization of *Zea* and *Tripsacum*, which occurred after cultivated maize had been introduced by man to Central America; (3) that new types of maize, originating directly or indirectly from this cross and exhibiting admixtures with *Tripsacum*, comprise the majority of Central and North American varieties (Mangelsdorf 1947). Thus hybridization with *Tripsacum* may have furnished genes for insect resistance that entered corn germ plasma by way of teosinte (*Euchlaena*). Mangelsdorf (1947) reports that teosinte is intermediate between *Zea* and *Tripsacum* in resistance in the greenhouse to *Perigrinus maidis* (Ashm.), the corn leafhopper. And Gernert (1917) reported that teosinte x corn hybrids carried resistance to the corn aphids. Teosinte also shows some resistance to grasshoppers (*Melanoplus* spp.) in Kansas.

The usual classification of corn as dent, flint, flour, pod, pop, or sweet corn has long been known to be artificial. Using the methods of modern taxonomy and the accumulated information on genetics and cytology, a new classification has been proposed (Anderson and Cutler 1942) that may be a better guide to possible sources of resistance. One of the primitive types of corn found, "maiz reventador," has been mentioned as "having the hard-surfaced leaves and stems . . . resistant to insect attack" and "tight tough husks which protect the ear." (Anderson 1944.) Both the primary center of cultivation in South America and the secondary one in Central America may furnish genes for insect resistance not known in North America now.

Corn varieties as in farmers' fields are almost completely open-pollinated, every plant being different genetically from every other plant. Self-pollination must be accomplished by the experimenter by covering with bags both the tassel and silks of a plant. The pollen is transferred to the silks or stigmas of the same plant from which foreign pollen previously had been excluded. This inbreed-
ing leads rapidly to genetic homozygosity and to deterioration in size and vigor of the inbred line. But the vigor is restored when two unrelated inbred lines are crossed. The term “hybrid,” as used for commercial seed corn, refers to a first-generation (F₁) hybrid of this type. In practice, however, four different inbred lines are involved. Inbred A is crossed with inbred B in one isolated field, and inbred C and D in another to form two single crosses. The next year the single-cross hybrid A x B is crossed on the hybrid C x D to give the “four-way cross” or “double cross” which the farmer plants for the commercial crop. The mechanics of selecting inbreds and testing crosses have been constantly improved (Sprague 1946) and numerous techniques devised for handling the problems involved.

The use of hybrid corn, in contrast to open-pollinated varieties, has increased from far less than 1 per cent of the acreage in 1933 until by 1948 nearly 100 per cent of the acreage of several states was planted with hybrid corn. Along with the increase in yield this use of hybrid corn has brought some hazards. Only relatively few inbreds are known to have constituted the bulk of the commercial hybrid corn (Anderson 1944). Thus proportionately little of the total available germ plasm is now represented. Steps are being taken to preserve the better corn-belt varieties and also to survey more of the germ plasm available in Central and South America. Early studies of insect resistance in corn were concerned with varieties, later and more exact studies were possible with inbred lines.

In the study of the insect resistance of corn inbred lines and hybrids the reaction of the two should be clearly distinguished. If resistance is completely recessive, an inbred may be highly resistant to an insect, but most of the hybrids (F₁) involving it as one parent may be susceptible. When resistance is dominant the inbred and hybrid will both be resistant and the inbred more readily usable. The insect resistance of corn is reported where possible either in terms of the reaction of the inbred itself or in terms of the reaction of the inbred in hybrid combination.

The literature on corn is already voluminous. There has been excellent cooperation between corn breeders who have exchanged breeding material and mimeographed unpublished data. In the uniform nursery tests conducted by the Federal Bureau of Plant Industry with the help of the various state experiment stations.
corn plants have sometimes been infested or injured by various insects. The reports on these tests therefore often contain information on resistance or susceptibility of the several inbreds or hybrids to insects. In 1942 a committee of the North Central States Entomologists compiled a report recording the resistance of many experimental inbreds to six different insects and circulated this report among entomologists and corn breeders. A few years later committees were appointed from the corn-improvement conferences of the southern, northeastern, and north-central regions to recommend uniform methods of taking notes on resistance to corn insects (Jenkins 1947, 1948a, 1948b). Records from the corn-performance tests conducted by the several states to compare standard open-pollinated varieties with commercial and experimental hybrid corns often contain references to differential injury by various insects. In the discussion that follows these latter will not be referred to unless they contain material of unusual interest.

Most injurious North American corn insects feed on a number of plants and were originally members of the grassland community of the area. These insects took over this new grass as a host plant when farmers’ corn fields replaced prairies and meadows. Only a few species may be confined largely to corn; the corn root worm, *Diabrotica longicornis*, and corn root aphid, *Anuraphis maidis-radiicis*, are two of these; the southwestern corn borer, *Diatraea grandi-tella*, may be a third. A few corn insects have moved to this new host from some of the dicotyledonous weeds; the European corn borer, may be a representative of this group. These corn insects, then, differ from many others for which plant resistance has been found, in that they are mostly feeders with a wide host-plant range. There are six insect species or groups of species for which there is considerable information concerning resistance and several more for which a little information is available. Some general summaries on the resistance of corn to insects have been given by Bigger (1941, 1943). Most of the species of insects studied in respect to resistance are as follows:

Acridiidae (Grasshoppers and locusts)
*Melanoplus* spp.
*Schistocerca paranensis* Burm.
*Dichroplus arrogant Stal.*
*Scyllina variablis* Burm.

Lygaeidae
*Blaus leucopeterus* (Say) (Chinch bug)
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Aphididae
*Aphididae*
*Aphis maidis* Fitch (Corn leaf aphid)
*Anuraphis maidi-radicis* (Forbes) (Corn root aphid)

Noctuidae
*Heliothis armigera* (Hbn.) *(obsoleta F.)* (Corn earworm)

Pyralididae
*Pyrausta nubilalis* (Hubner) (European corn borer)
*Diatraea grandisella* Dyar (Southwestern corn borer)

Chrysomelidae
*Diabrotica undecimpunctata* (F.) (Southern corn rootworm)
*Diabrotica longicornis* (Say) (Corn rootworm)
*Diabrotica virgifera* Lec. (Colorado corn rootworm)

Scarabaeidae
*Phyllophaga* spp. (White grub)
*Popillia japonica* Newman (Japanese beetle)

Stored-grain insects including especially
*Sitotroga cerealella* (Oliv.) (Angoumois grain moth)
*Sitophilus oryza* (L.) (Rice weevil)

Differences in strains of corn have been shown or are known to exist in injury or infestation by *Chaetocnema pulicaria* Melsh., the corn flea beetle (Elliott 1942), *Euxesta stigmatias* Loew (Barber 1939), *Oscinella frit* (L.), the frit fly (Cunliffe 1946), the fall army worm, *Laphygma frugiperda* (A. and S.) (Ditman and Cory 1936), wireworms (*Melhus et al. 1949*) and a few other insects.

RESISTANCE TO GRASSHOPPERS AND LOCUSTS IN CORN

In the dryer parts of the areas where corn is grown and, less often, elsewhere, grasshoppers or locusts or both have been a recurring menace. Entomologists and others have been prone to consider these insects as eating "anything green." Detailed studies, however, have usually shown that these insects have distinct food preferences (Isely 1938, 1944). In some cases it has been shown that kinds of plants differ widely in their value as food for grasshoppers (*Hodge 1933*; *Taubet et al. 1945*). *Riley, Packard, and Thomas (1878)* reported on the great difference in susceptibility to grasshoppers between corn and sorghums as crops grown by farmers. This difference has been seen many times during each grasshopper outbreak in areas in North America where these crops are grown.

(Brunson and Painter 1938) and holds for all species of grasshoppers that have been observed in outbreak numbers.

Hume (1931, 1933) reported that injury to dent corn was much greater than to flint corn (Rainbow variety). The species of grasshopper involved was not mentioned. Brunson and Painter (1938) reported on differential feeding of grasshoppers (mostly *Melanoplus differentialis* (Thomas) and *Melanoplus bicinctatus* (Say)) on varieties, top crosses, and hybrids in the Manhattan, Kansas, corn nursery in 1936. The amount of defoliation on each plot was independently estimated by three observers. There were five replications and often the variation between replications was not significant, indicating a surprisingly even distribution of the grasshoppers. The extreme range of variation for the average of five plots of each strain was from 3 to 73 per cent. In various experiments differences between strains of 12 per cent or less were significant. Among nine open-pollinated varieties tested, five strains of Reid Yellow Dent with 24.0 to 31.4 per cent defoliation were the most injured. Cassel, a white-seeded variety, and Hays Golden, a yellow-seeded variety, with 7.6 and 7.8 per cent, respectively, were the least injured. Some of the better known inbreds recorded in top crosses had the following amounts of injury:

<table>
<thead>
<tr>
<th>Inbred record no.</th>
<th>Ave. % defoliation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kans. Y531 (K151)</td>
<td>4.6</td>
</tr>
<tr>
<td>Kans. P555 (K55)</td>
<td>7.0</td>
</tr>
<tr>
<td>Kans. Y555 (K155)</td>
<td>9.2</td>
</tr>
<tr>
<td>Ill. Tr.</td>
<td>12.6</td>
</tr>
<tr>
<td>Ill. R4</td>
<td>15.0</td>
</tr>
<tr>
<td>Ill. WF9</td>
<td>22.0</td>
</tr>
<tr>
<td>Iowa L317C</td>
<td>25.4</td>
</tr>
<tr>
<td>Ill. Hy.</td>
<td>31.0</td>
</tr>
</tbody>
</table>

Among the hybrids in the tests, those made up of inbreds derived from Kansas varieties had strikingly less injury than hybrids from states in the central or eastern part of the corn belt. There appeared to be no relationship between degree of injury and maturity of the strains under observation. Two types of injury were observed: the grasshoppers either ate the blades of the leaves, except for the midribs, or they chewed off the leaves where the latter were attached to the stalk. A third type of damage has sometimes been observed in which grasshoppers eat the silks and tips of ears so that pollination is more or less prevented. "The
Kansas inbred lines involved in the top crosses and hybrids reported on, have come from varieties adapted to a grasshopper-infested environment where occasional severe outbreaks have been experienced. Under these conditions and with the variability in corn . . . , it would seem reasonable to assume that natural selection has operated to eliminate the variants most susceptible to grasshopper injury and to favor the propagation of local varieties from the most grasshopper-resistant individuals" (Brunson and Painter 1938). Later observations in Kansas, when only parts of a nursery planting had been injured, have confirmed some of the observations reported.

Some data collected in the field in 1941 and in the greenhouse in 1942 and 1946 were reported by Neuschwander (1946) in an unpublished master's thesis. In 1941 mixed populations of *Melanoplus differentialis* and *M. bivittatus* infested several corn variety tests rather uniformly. Among the double-cross hybrids and open-pollinated varieties reported in one 1941 test, Pride of Saline and the Kansas hybrids K1501, K2234, K2182, K2222, and K1585 were estimated as having less than 21 per cent of the leaf surface removed while U.S. 13 and U.S. 35 had from 71 to 80 per cent removed. Two of these hybrids, differing greatly in resistance, are shown side by side in Fig. 1. In this test, there was a significant correlation with the date of pollen shedding, but this correlation was thought to be fortuitous because most of the Kansas hybrids were later than those from eastern states. In another experiment, yellow-seeded inbreds in hybrid combinations showed the following average injury: Oh. 07, 21.2 per cent; U.S. 540, 22.5 per cent; WF9, 25.6 per cent; Ind. 38-11, 27.8 per cent; Iowa L317, 32.2 per cent; and Ill. Hy., 43.3 per cent. The inbred Oh. 07 is a selection from a cross of U.S. 540 and Ill. L., and probably carries the same resistance as U.S. 540; this resistance tended to be dominant to the susceptibility of Hy. In a third experiment white-seeded inbreds in hybrid combinations showed the following average injury: Ky. 27, 15.6 per cent; K64, 23.3 per cent; K55, 28.8 per cent; and Ind. 33-16, 34.4 per cent. The susceptibility of the Ind. 33-16 tended to be recessive to the resistance of Ky. 27.

Neuschwander (1946) grew corn plants in pots in the greenhouse in 1942 and 1946 until the seedlings were 15 to 20 inches tall and tested their resistance to the feeding of half-grown nymphs of *Melanoplus bivittatus*. The hybrid K1585, (K155 x K201) x
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(K4 x Ind. 38-11), was resistant in both field and greenhouse (seedling) tests and was more resistant in the greenhouse than K2234, (K41 x K55) x (K63 x K64), while the latter was more resistant in the field. Both these hybrids that carry some resistance to the two common pest grasshoppers of Eastern Kansas have been released to farmers. Comparative greenhouse tests with a "Maiz Amargo" variety from Argentina in four replications showed the amargo with 46 per cent of the leaf surface removed, Kansas 1585 with 51 per cent, and U.S. 35 with 83 per cent. The greenhouse tests gave results that corresponded fairly well with those secured in the field and gave indications that several genes for both resistance and susceptibility might be involved.

In a study of the performance of hybrids in the grasshopper outbreak of 1936, workers in Illinois (Dungan et al. 1938a) found evidence that inbreds Iowa L317, Ind. 38-11, and Iowa Pr may carry factors contributing to unattractiveness to grasshoppers. Bigger (1943) reported that different lines of corn had a definite effect upon the development of Melanoplus differentialis when reared on them in the greenhouse. In the 1940 annual report of the Bureau of Plant Industry it is reported that grasshoppers reared on Kansas K4 and Illinois N-11 were smaller and took a longer time to reach maturity than those reared on susceptible inbred lines. Thus apparently antibiosis as well as preference is concerned in the resistance of corn to grasshoppers. Little has been done in the United States to determine whether strains resistant to one species of grasshopper are also resistant to others. Differences are known to exist in the food habits and grass preferences of the economic species, but it is impossible to forecast what the final results will be. It has not been the thought of investigators of this subject that resistance to grasshoppers will replace other control measures, but rather that it will decrease the frequency of need for such measures, particularly when the insects are not in widespread outbreaks.

In areas in northern Argentina the "langosta" or migratory locust, Schistocerca paranensis, often moves into crops causing severe devastation. A group of native strains of corn, called "bitter corn" or "Maiz amargo," have long been known to possess considerable resistance to the attacks of this insect (Dawson 1917). The origin of these corn varieties is apparently not recorded. Early in the 1930's Horovitz (1937) selected corn of the amargo type
from that grown in Argentine provinces of Entre Ríos, Santa Fe, and Chaco. After inbreeding for one year the progeny were tested for resistance in regions subject to locusts and reselected. At the end of three years the strains appeared uniform for resistance. In field tests the amount of damage was graded from 0 to 4. The common varieties were graded from 3.5 to 4; the amargo selections, from 0.5 to 2.5 in various tests. The correlation was high between

The resistant quality appeared to be inherited and of considerable importance. The degree of resistance varied from strain to strain.

Marchioni (1940) described cage tests for the study of resistance of corn to grasshoppers. In some tests seedling plants about 15 centimeters high were exposed to locusts (Schistocerca paranensis). Maíz amargo, “Maíz amargo precoz,” a hybrid Amargo x Curenton, and a susceptible variety Piamonte, were used in the cages. Tests with seedlings made possible a rough classification.

Fig. 34. The method of testing for resistance to locusts in corn as first used by Marchioni. In the center are four leaves of the variety Piamonte (susceptible); on each side are the eight leaves from each of two hybrids deriving their resistance from Maíz Amargo. (Photo from Horovitz and Marchioni 1942.)
useful for selection. A second kind of test was devised, using sections 10 to 12 centimeters long of leaves from older plants set upright in trays of moist sand. In these tests in cages the locusts ate all except the midribs of the leaves of susceptible varieties but scarcely touched the leaves of Maiz amargo (Fig. 34). Some of the hybrid strains were in each category; some of the amargo strains were less resistant than others. Bredemann and Radloff (1938) and Boerger, CaneI, and Burdenski (1939), in investigations of Maiz amargo, thought that resistance was associated with hairiness of the plants.

Horovitz and Marchioni (1942) demonstrated in an excellent series of experiments that the amargo characteristic resulting in grasshopper resistance in one inbred line was the result of a single recessive character carried on chromosome I. Resistance was tested by the method worked out by the second author. Known susceptible and resistant check leaves were included in the tests and records of test leaves were taken when the susceptible leaves were completely eaten and the control amargo hardly touched. Each cage contained 40 locusts (S. paranensis) for 24 to 48 hours. Tests using the grasshoppers *Dichroplus arrogant* Stal. and *Scyllina variabilis* Burm. classified the corn in the same way as did the locusts. A single strain of Maiz amargo was crossed with the "genetic tester" strains of corn, each of which carried mutant genes known to be located on a single chromosome. Some of the genes on the first chromosome showed typical linkage relationships, and a consideration of the several crosses indicated that only a single gene "ag" was responsible for resistance to locusts in the line studied.

It was stated that the various lines of amargo show different degrees of resistance and that these may result from (1) multiple alleles of the gene "ag," (2) a single principal gene "ag" and secondary modifiers which would establish different levels of resistance in the lines and (3) different resistant corns governed by non-homologous genes. Tests were planned to find out the true relationships.

Horovitz and Marchioni gave some consideration to the possible cause of resistance but were unable to associate it with anthocyanin pigment, yellow endosperm, or chemical composition governed by the sweet or waxy genes. Leaf hairiness was definitely not related to resistance since the susceptible Piamontes variety was more hairy than the resistant amargo used in these studies.
CHINCH BUG RESISTANCE IN CORN

In the western and central part of the area of North America where corn is grown, chinch bugs, Blissus leucopterus (Say), occur in more or less abundance every year and at rather frequent intervals in destructive numbers. Most studies on chinch bug resistance in corn have been limited to those years in which the insects were present in outbreak proportions; no projects carried on over a period of several years have been reported. Many elements of the biology of chinch bugs are discussed in connection with the resistance to chinch bugs in sorghums, a crop about which more detailed information is available. In corn the information regarding chinch bugs deals primarily with the injury by the second-generation bugs in Illinois and with the last instars and adults of the first- as well as the second-generation bugs in Kansas and Oklahoma. Over most parts of the corn belt the first-generation chinch bugs migrate on foot in hordes to corn or sorghum from adjacent small grain fields and the young corn plants are frequently killed quickly. In parts of Oklahoma this first-generation migration often takes place by flight and a third generation occurs. In all areas there is a redistribution of the adults of the first generation to corn fields where the second generation hatches out and matures. The second-generation injury results in stunted and weak plants that often fall over, and in decreased yield consisting of poor grain.

Flint (1921), Burlison and Flint (1923), Flint and Hackleman (1923), and Flint and Larrimer (1933) have reported observations and experiments on chinch bug resistance in corn. Summarizing these studies Flint et al. (1934) stated that "some varieties of corn can withstand the feeding of the second brood of chinch bugs and still produce a reasonably good crop of grain. There is no variety, however, that can withstand the on-slaught of a horde of hungry first-brood bugs traveling on foot from adjoining fields of small grains." Experimental work carried on over a period of six years in Illinois has shown that several varieties of corn were resistant. Black Hawk, Champion White Pearl, Golden Beauty, and Mohawk have been found the most promising of the several varieties included in these experiments. Under conditions of heavy chinch bug infestation, these varieties have made a fair yield, whereas other varieties grown in the same field were so badly damaged as to produce very little grain. None of these varieties were safe against...
chinch bugs, however, and they appeared to depend for their resistance upon certain vegetative characters. Practically as many bugs occurred on the resistant as on the non-resistant varieties of corn.

Holbert et al. (1934; 1935) have obtained results which suggested that some inbred lines of corn carry dominant factors for chinch bug resistance while other inbred lines carry dominant factors for chinch bug susceptibility. The results suggested also that strains of corn may be developed which will combine chinch bug resistance in a significant degree with other important characteristics concerned with satisfactory yields of high-quality grain.

Painter, Snelling, and Brunson (1935) reported their studies of hybrid vigor and other factors in relation to chinch bug resistance in corn. Field trials of selfed lines and F₁ crosses at Manhattan, Kansas, and Lawton, Oklahoma, showed that vigorous F₁ crosses are better able to survive chinch bug attacks than the much less vigorous selfed lines, though there were clear-cut differences among the selfed lines tested. Wide differences among open-pollinated varieties were also reported. Of these varieties, Harmon White, Pride of Saline, and Midland had the lowest average percentage of dead plants for the two-year test at Lawton, Oklahoma, while eight of the ten F₁ hybrids tested at Manhattan and all the hybrids at Lawton were superior to the open-pollinated variety, Pride of Saline, which was used as a check. Generally there was no agreement between the behavior of the same inbred, hybrid, or variety at Lawton and Manhattan, correlations being non-significant in all three cases. Interannual correlations between 1933 and 1934, however, were highly significant for percentage of corn plants killed by bugs at Lawton. There are at least three factors that may have caused the discrepancy in the results at the two stations: (1) a difference in the size and age of the plants at the two stations (age resistance), (2) a difference in the type and duration of attack—sudden and short at Manhattan (Fig. 35), less sudden and long at Lawton, (3) some strains of corn were better adapted to one locality than to the other. Probably all three factors were concerned in the differences reported.

Holbert, Flint, Bigger, and Dungan (1935) have shown that chinch bug resistant corn varieties on the average gave over 50 per cent better yield than the average of local varieties and that some hybrids were particularly outstanding. Difference in chinch bug resistance was measured on the basis of percentage of plants
Fig. 55. A comparison of injury to strains of corn by chinch bugs that walked into the plot from the wheat stubble in the foreground. Staked rows, left to right, are: Krug open pollinated variety; inbred Iowa L317; F₁ hybrid L317 x Bl 349A; inbred Bl 349A; and inbred L24, Manhattan, Kansas, 1934.
standing after chinch bug infestation and as the ratio of total yield to yield of sound corn. They state that "these results to date suggest the possibility of producing hybrids that are not only outstanding in yield and quality of grain in years when chinch bugs are not present, but also possess a high degree of resistance to damage from second-brood chinch bug attack, thus making such strains of very great value in years of heavy chinch bug outbreaks."

Some of the varieties reported as resistant to chinch bugs have been Champion White Pearl, Waddell Golden Beauty, Pride of Saline, Midland, Mohawk, Black Hawk, and Hays Golden. Most of these varieties have been grown in chinch bug territory for long periods of years and some trace back directly to cultivation in those localities by the Indians. Possibly they have undergone a certain amount of natural selection.

Some of the inbreds reported (Dungan et al. 1938a, Bryan and Jugenheimer 1937) as transmitting chinch bug resistance are: Hy (Ill.), 205 (Iowa), K4 (Kans.), R4 (Ill.), 90 (Ill.), 5120 (Ill.), WF9 (Ind.) and 38-11 (Ind.).

Little is known regarding the mechanism of resistance except that resistant strains are tolerant and thus able to survive and produce a satisfactory crop in the presence of a large chinch bug population that would damage a susceptible strain severely. Flint and Hackleman (1923) stated that "field observations have shown no marked difference in the number of bugs present on the different varieties of corn when growing together." This agrees with observations of other investigators so far as reported. It is apparent from studies in Illinois, Kansas, and Oklahoma that the relative adaptation of a variety to conditions of the test other than chinch bugs has an important relationship not only to yield but also to the percentage of plants killed by the bugs. Results in the three states are not entirely in agreement with respect to different strains. Adaptation of the variety is perhaps a part of the reason for these differences; preference may be involved also (Holbert 1946).

Corn, like sorghum, contains varieties and strains that are resistant but not immune. Under severest attacks, the most resistant sorts will be destroyed. But the differences known at present are clearly of economic importance. Further study of a wider range of types of corn and selection under more severe infestations may increase the known range of resistance.
RESISTANCE TO CORN LEAF APHID IN CORN

The corn leaf aphid, *Aphis maidis* Fitch, is present every year in the North American corn belt; in some years it does extensive damage. It occurs in many parts of the world in both temperate

and tropical areas. Besides attacking corn it is a serious pest of sorghums and transmits a mosaic disease to sugar cane. It occurs on a number of wild grasses and is reported to overwinter on barley and perhaps other plants in the warmer parts of its range. Several generations occur each year, the number depending on temperature and other conditions. Usually the insect appears in the corn fields about midsummer and continues to be present until frost. It is often a nuisance in greenhouses where corn is being raised for

![Image of corn plant with aphids]
breeding purposes. In the field the use of resistant strains of corn appears to be the only practical means of control (Fig. 36).

The damage done by the corn leaf aphid to corn is less evident than that done by many other insects that actually may be of less importance. The aphids are first noticeable in the whorl and upper leaves, but when the tassel appears they breed abundantly on it. The feeding, if severe, may cause death of parts of leaves or even the entire plant. Less severe and more common infestations result in a reduction or even prevention of pollen shedding on a part or all of the tassel. In this manner, if aphids are common enough, grain production is reduced through partial prevention of pollination. Walter and Brunson (1940) reported that when the tassel was infested, the leaves also were invariably infested. Snelling, Blanchard, and Bigger (1940) reported that 48 per cent of the aphid-infested plants in a corn-performance test were barren, while only 1 or 2 per cent of the uninfested plants failed to bear an ear. This indicates a serious physiological effect on the plant, caused by feeding by the aphids, with one of the results commonly being the retardation or prevention of the development of the ear shoot.

Gernert (1917) reported that four rows of F1 plants of Euchelarna mexicana (teosinte) x Yellow Dent corn as well as the teosinte parent remained free from aphids, both A. maidis and Anuraphis maidi-radicis, while the corn nearby was infested by both species. These plants were growing in the greenhouse but similar conditions were observed in the field. This is apparently the only reference to resistance to the corn root aphid. The ants which regularly accompany the root aphids appeared on teosinte and the hybrid, but no aphids developed on these plants. At Manhattan, Kansas, in 1949, when a severe corn leaf aphid infestation developed on corn, small colonies of the aphids could be found in the whorl of teosinte (a Florida strain) late in the season.

McColloch (1921) reported on the corn leaf aphid infestation on 30 corn varieties for two years on four different plots and found considerable difference in infestation. In general, the later maturing varieties were more severely damaged, but there were some exceptions to this relationship. White Democrat, Commercial White, and Midland Yellow Dent showed the highest infestation, while Colby Bloody Butcher, Pink Bloody Butcher, Silver King, and Minnesota No. 13 showed the lowest infestation.
In 1938 and 1939 there was a widespread outbreak of the corn leaf aphid in the central and northern part of the corn belt. This was in part the result of favorable weather conditions and low numbers of parasites and predators, but the widespread use of inbreds and hybrids susceptible to the aphid was certainly also a favorable factor. The outbreak made possible numerous observations in corn-breeding nurseries, some of which have been reported from Illinois, Indiana, and Ohio, respectively, in varying detail (Snelling, Blanchard, and Bigger 1940; Walter and Brunson 1940; Huber and Stringfield 1940, 1942). The papers dealt with different groups of inbreds and hybrids but agreed in regard to the fact that resistance to aphids is inherited.

Both in Illinois (Snelling et al. 1940) and in Ohio (Huber and Stringfield 1940) inbred WF9 was regarded as being highly susceptible to aphids when in hybrid combination. In Illinois it was not so heavily infested as an inbred. The susceptibility appeared to be dominant. Inbred 38-11 was reported to be highly susceptible as an inbred both in Indiana (Walter and Brunson 1940) and in Illinois (Snelling et al. 1940). In both these localities its reaction in hybrid combination tended to follow the reaction of the inbred with which it was crossed. In other words, the susceptibility of 38-11 tended to be recessive. In both Indiana and Illinois inbred U.S. 540 behaved like 38-11, except that infestations were not as heavy as on the latter inbred and hybrids derived from it. In Ohio inbred 38-11 was reported as moderately resistant and 540 as susceptible. Among other inbreds reported as being susceptible, either as an inbred, or in hybrid combination, or both, were M1, Ind. Tr., Oh. 02, Oh. 84, and U.S. 4–8. The inbred R4 was reported by Walter and Brunson to be very resistant, no aphids developing on any plant. The inbred was able to transmit resistance to a high degree, only a few aphids developing on a very few hybrid plants. In Illinois the inbred had less than 4 per cent of plants infested as an average of three tests. There it was resistant in all hybrid combinations except those with WF9. In Ohio it rated as moderately resistant. The inbred L317 was regarded as highly resistant in Ohio but as moderately resistant in Illinois. The inbred Ill. A was resistant in Illinois and Indiana but moderately susceptible in Ohio. The following inbreds were resistant at one or more localities: Ohio 51, YS79 (Kans. 179), and Hy31.

The inbreds recorded above all have yellow endosperm. Snell-
ling and his associates gave a table of the aphid reactions of inbreds with white kernels. The inbreds Ky. 2075 and U.S. 24 were resistant as inbreds, while Kentucky inbreds 122, 56, and 89 were susceptible.

The genetics of resistance does not appear to be simple. Snelling, Blanchard, and Bigger stated that "there are indications that the response of the hybrids may in some cases be explained best on the assumption of complementary factors contributed by the two parents." Walter and Brunson suggested that individual inbreds differed greatly in their prepotency in transmitting susceptibility or resistance to their hybrids. Neither group found any plant character or group of characters that could be consistently correlated with aphid susceptibility. The peculiar tassel type exemplified by the aphid-resistant R4, in which the leaves closely enclose the tassel until pollen shedding, was cited as an example that might have been thought to be correlated with susceptibility but was not.

There is some lack of agreement regarding the reaction of particular inbred lines. This is, in part, an expression of the known high sensitivity of aphids to environmental conditions and, in part, the effect of differences in the manner of reporting results. The single figure given by Huber and Stringfield includes readings on both inbreds and inbreds in hybrid combination, while these are reported separately by the other workers. Both at Illinois and at Indiana (Walter and Brunson 1946) there were clear indications that some of the inbred lines were not uniform in their resistance or susceptibility. This could lead to discrepancies in the results at different stations. Examples of the reactions of some commonly used inbred lines are given in Table 9.

Huber and Stringfield also present evidence regarding a relationship between European corn borer infestation or damage as measured by different criteria and the aphid infestation on the same plants. The correlation coefficients ranged from 0.29 to 0.50 for relationships of the actual infestations or damage of these two insects in the same plots. All correlations are significant. The authors state: "It would seem that at least preliminary classifications of breeding material in respect to susceptibility to the corn borer might be made on the basis of aphid populations." They also were able to predict with a high degree of probability the aphid infestation rating of hybrids on the basis of the performance of inbreds.
Table 9  
APHID INFESTATION RATINGS OF VARIOUS CORN INBREDS 1  
in several localities

<table>
<thead>
<tr>
<th>Inbred line</th>
<th>State or origin</th>
<th>Illinois 2 percentage of plants infested</th>
<th>Indiana 3 index no. of % and intensity</th>
<th>Ohio 4 rating as inbreds and hybrids</th>
<th>Pennsylvania 5 grade</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>as inbreds</td>
<td>as inbreds</td>
<td>as hybrids</td>
<td>as hybrids</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2 sta. avr.</td>
<td>in hybrid combination</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>51</td>
<td>Ohio</td>
<td>0</td>
<td>4</td>
<td>9</td>
<td>1</td>
</tr>
<tr>
<td>R4</td>
<td>Ill.</td>
<td>3.7</td>
<td>0</td>
<td>1.2</td>
<td>50</td>
</tr>
<tr>
<td>A</td>
<td>Ill.</td>
<td>4.9</td>
<td>4</td>
<td>3.3</td>
<td>85</td>
</tr>
<tr>
<td>WF9</td>
<td>Ind.</td>
<td>12.0</td>
<td>40.1</td>
<td>100</td>
<td>4</td>
</tr>
<tr>
<td>L317</td>
<td>Iowa</td>
<td>35.4</td>
<td>10.3</td>
<td>18</td>
<td>3</td>
</tr>
<tr>
<td>Hy</td>
<td>Ill.</td>
<td>25.9</td>
<td>14.8</td>
<td>68</td>
<td>2</td>
</tr>
<tr>
<td>Tr</td>
<td>Ind.</td>
<td>47.1</td>
<td></td>
<td>108</td>
<td>4</td>
</tr>
<tr>
<td>38-11</td>
<td>Ind.</td>
<td>53.1</td>
<td>14.1</td>
<td>49</td>
<td>3</td>
</tr>
<tr>
<td>540</td>
<td>U.S.</td>
<td>59.9</td>
<td>17.4</td>
<td>105</td>
<td></td>
</tr>
<tr>
<td>02</td>
<td>Ohio sus.</td>
<td>0</td>
<td>103</td>
<td>15.0</td>
<td>105</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>201</td>
</tr>
</tbody>
</table>

1 Low numbers indicate resistance, high numbers susceptibility.  
2 Snelling, Blanchard, and Bigger 1940.  
3 Walter and Brunson 1940.  
4 Huber and Stringfield 1942.  
5 Huber, Seem, Coon, and Wernham 1948.

Haber and Gaessler (1942) studied the chemical constituents of tassels of sweet-corn inbreds, some of which were susceptible and some resistant to aphids. Differences were shown in the percentage of total sugars present, but no relationship could be demonstrated between susceptibility to aphids and sugar content or any other of the constituents measured. Inbred No. 7 was resistant to aphids, inbreds 45 and C7 susceptible, all three are sweet-corn strains. Emerson and Cushing (1945, 1946) reported that a study was being made of the inheritance of aphid resistance in corn.

Coon (1948) reported on the relation between the type of tassel and the aphid infestation of both inbreds and hybrids. The inbreds in which the tassel was exposed quickly and completely from the leaves tended to have the lowest aphid populations.
cant, exceptions were noted in both directions in all categories. The tassels that are enclosed the longest time provide a favorable habitat for the aphids. In all possible hybrid combinations of ten inbreds the most resistant inbreds were Wis. 22 and Pa. 55 and the most susceptible Ind. WF9 and Iowa L289.

Coon, Miller, and Aurand (1948) present evidence of a correlation between the carotene content of corn grain and the degree of aphid infestation on the same 44 hybrids \( (r = 0.5697) \). The ten inbreds involved were rated on their performance in all possible hybrid combinations. The inbreds Wis. 22 and Ohio 51A had the highest resistance; inbreds Ill. M14 and Ind. WF9 were the most susceptible. The hybrids studied were those with yellow endosperm. If carotene is actually connected with aphid resistance, the corn with white grain should be resistant; yet a wide range of resistance and susceptibility to aphids exists also among white hybrids and inbreds.

In all these studies there is a fair degree of agreement in regard to which inbreds transmit susceptibility but less agreement in respect to resistance. What is needed is a satisfactory technique of maintaining aphids and testing inbreds and hybrids under more controlled conditions. The inheritance of resistance could then be worked out and reasons for differences in results better understood.

RESISTANCE TO CORN EARWORM IN CORN

Throughout its world-wide distribution perhaps no plant-feeding insect can equal the corn earworm, *Heliothis armigera* (Hbn.) \((= H. obsoleta)\), in its total destructiveness each year, especially when one considers its many hosts. Until the problem was partially solved by use of resistant varieties, this insect was the major factor (Collins and Kempton 1917), in preventing the profitable growing of sweet corn in the southern United States. From one to seven generations a year have been reported in different places; in Kansas there are three and a partial fourth. Isely (1935) has reported a 30-day minimum life cycle under most favorable conditions. Eggs are laid singly and a single female may lay more than 2,500. Early generations of the larvae feed in the whorl or curl of young corn plants and do a characteristic type of injury sometimes known as "ragworm" or "bud worm" injury. Eggs of some of the later generations are laid on corn silks predominantly and the larvae feed on the silk and developing grain of the ear. The number of eggs received by each ear is influenced both by the number of moths
laying eggs and by the number of ears in the area that have recently come into the silking stage. When silks are available, the moths show a decided preference for them (McColloch 1920; Phillips and Barber 1933). Some of the later eggs are laid and larvae develop on a wide range of host plants, which also support a varying population throughout the growing season. Of the plants of economic importance cotton, tomato, beans, soybeans, alfalfa, and sorghum (heads) are among those most often reported as injured. Isely (1935) has shown, however, that these different plants and even parts of the same plant are not of equal value as food when measured by size, length of life, or fecundity. To complicate matters further, food habits do not appear to be the same in all localities. In South Africa (Parsons et al. 1938) the fecundity of H. armigera was greater when reared on cotton than when reared on com. This is the reverse of the situation found in North America (Isely 1935). We are dealing here either with different biotypes, or with some peculiar factor in the environment, or perhaps with the use of different plant varieties.

It has long been known that corn earworm larvae have strong cannibalistic tendencies, but more recently Barber (1935) has studied this habit thoroughly. The data presented in this publication indicated that individuals may be reared from egg to adult entirely on maimed earworm larvae but, under such conditions, require more time for their life history than usual. The relationship between this habit and resistance lies in the effect of long tight husks in confining larvae of varying instars within a small space, where the larger apparently seek out and kill the smaller ones and feed on them. Evidence was presented that "the average numbers of larvae found in these ears (with varying husk length) decreased as the length of the husk increased, suggesting a proportional increase in the degree of cannibalism." In a series of papers Phillips, Barber, and Dicke, either as associates or separately, have studied thoroughly many phases of earworm activity in relation to the corn plant (Barber 1936, 1938, 1941, 1943, 1944; Barber and Dicke 1939; Dicke 1939; Phillips and Barber 1933, 1936, 1940). Many of the phases examined are of importance in studies of resistance

1 Heliothis virescens (F.) and several other species of "bollworm" occur on cotton and on some occasions may have been mistaken for H. armigera. The fall armyworm Laphygma frugiperda (A. and S.) sometimes injures corn in ways that are similar to H. armigera. These facts again emphasize the difficulty and the importance of accurate identification of immature insects.
of corn to this insect. A series of papers by Ditman and his asso­ciates on the metabolism of the corn earworm also have a bearing on resistance (Ditman 1938; Ditman and Weiland 1938; Ditman et al. 1940).

Smith (1919) has discussed nine ways in which the feeding of corn earworm may result in injury to corn. Since all of these must be considered in a study of resistance to this insect, they may be listed briefly as follows: (1) feeding on bud and young leaves; (2) feeding on developing tassel; (3) cutting of silk and prevention of fertilization of some grains, leading sometimes to production of nubbins; (4) feeding on young kernels; (5) damage especially to sweet corn as a result of earworm excrement; (6) feeding permits the development of many different species of molds and bacteria, some of which are toxic to domestic animals; (7) feeding on the hardened kernels by burrowing through the lower part of the kernel and eating the germ; (8) the holes made by corn earworm permit the entrance of a number of other insects; and (9) earworm larvae sometimes bore into the stalk and shank of the ear.

The prospect for a study of host resistance would not appear encouraging in an insect with such omnivorous food habits. But a rapidly growing body of evidence indicates that there is a small but constant and economically important difference in resistance among the different sorts of corn. A study of these differences has been forced on plant breeders and entomologists by the failure to find other practicable methods of control on a field scale.

Resistance to corn earworm among corn varieties. In reviewing the literature on the resistance of corn to corn earworm, no particular distinction has been made between sweet corn and field corn since, so far as earworms are concerned, the only difference is that greater improvement has been possible in the case of resistance in sweet corn. The principles of inheritance and mechanisms of resistance are probably the same in both cases and the two types are interrelated through the cross-breeding programs.

The first study of resistance to corn earworm and one of the first attempts to use plant hybridization in insect control was carried out by Collins and Kempton (1917). Their paper, “Breeding sweet corn resistant to corn earworm” is a most extensive and thorough study. They had four possible protective characters in mind at the beginning of the experiment: “(1) The distance which the husks extend beyond the tip of the ear. . . . (2) The thickness
of the husks' covering. . . .

(3) The texture of the husks. . . .

(4) Number and size of husk leaves. . . . Their experiments were begun in 1912 by crossing three varieties of sweet corn—Stowell's Evergreen, Early Evergreen, and Early Cory—with two varieties of field corn—Brownsville and Marrainto—both of which had long thick harsh husks. Ear-to-row breeding was carried on for several years, selecting for sweet kernels and for characters thought to denote earworm resistance. Selections were planted in southern California in 1915 and in Maryland in 1916 and measure-

Table 10 INTERPROGENY CORRELATIONS BETWEEN DIFFERENT MEASURES OF EARWORM INFESTATION AND VARIOUS PLANT CHARACTERS

(Adapted from Collins and Kempton, 1917, p. 560)

<table>
<thead>
<tr>
<th></th>
<th>Damage</th>
<th>Number of larvae</th>
<th>Damage per larva</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prolongations</td>
<td>-0.71†</td>
<td>-0.60†</td>
<td>-0.75†</td>
</tr>
<tr>
<td>Length of husks</td>
<td>-0.68†</td>
<td>-0.56†</td>
<td>-0.78†</td>
</tr>
<tr>
<td>Number of layers</td>
<td>-0.52†</td>
<td>-0.51†</td>
<td>-0.45*</td>
</tr>
<tr>
<td>Days to silking</td>
<td>-0.36*</td>
<td>-0.56†</td>
<td>-0.12</td>
</tr>
<tr>
<td>Maturity</td>
<td>-0.32</td>
<td>-0.49†</td>
<td>-0.04</td>
</tr>
<tr>
<td>Husk leaves</td>
<td>+0.31</td>
<td>+0.52†</td>
<td>+0.12</td>
</tr>
<tr>
<td>Days silking to harvest</td>
<td>-0.03</td>
<td>-0.23</td>
<td>-0.12</td>
</tr>
<tr>
<td>Number of husks</td>
<td>-0.08</td>
<td>-0.15</td>
<td>-0.01</td>
</tr>
<tr>
<td>Length of ear</td>
<td>+0.01</td>
<td>+0.03</td>
<td>+0.06</td>
</tr>
<tr>
<td>Number of rows</td>
<td>+0.05</td>
<td>-0.16</td>
<td>-0.16</td>
</tr>
</tbody>
</table>

N = 31.

* r = 0.355 or greater, significant.
† r = 0.456 or greater, highly significant.

ments were taken on 13 characters of agronomic importance, including the ones mentioned above together with number of larvae, and damage per larva. Probable errors are given for all characters and correlations indicated between the 13 characters (Table 10), between progenies and parents, as well as interannular correlations.

Three measures of earworm infestation are used: (1) amount of damage, (2) number of larvae, and (3) damage per larva. In interprogeny correlations all three of these showed significant negative correlation with (1) prolongation of husk beyond ear, (2) length of husks, and (3) number of husk layers. Days from plant-
ing to silking showed significant correlations with damage and number of larvae but not with damage per larva. The reason for this is not evident. The number of larvae showed significant negative correlation with maturity and positive correlation with number of husk leaves. None of these three measures of earworm infestation gave significant correlations with days from silking to harvest, number of husks, length of ear, or number of rows of grain. In other words, an increase in length of husk beyond the ear, and an increase in number of husk layers tends to result in a decrease in earworm infestation and damage. "Thus an average increase of 4.8 centimeters in prolongation was accompanied by an average reduction of 5 per cent in damage." "A closer study, however, indicates that the relatively close correlation between prolongation and damage is probably not to be completely explained on the basis of a simple physical protection. The chief reason for doubting the apparent direct relation between prolongation and damage is that prolongation appears to have nearly as much effect on the number of larvae as on the amount of damage, the correlation being 0.60 ± 0.08. Since all the larvae found inside the husks were counted, whether they had gained access to the ear or not, prolongation can hardly be held to have reduced the number of larvae in any such manner as it might be expected to reduce the damage" (Collins and Kempton 1917, p. 561). One of the missing factors which may explain the relation between prolongation of husk beyond the ear and number of larvae lies in the cannibalistic habits of the earworms which result in a reduction in their numbers when the larvae are confined to a small space (Barber 1936). Another possible explanation is that genetic factors resulting in reduction of larvae through unfavorable food conditions, etc., may be linked with some of the factors for long husks. Selections for these factors may have been made in parallel with those for long husks either intentionally or unintentionally. It is important to note that the correlation between prolongation of husk beyond ear and length of ear is negative but not quite significant. This would indicate a tendency that in selecting for long husk, there is danger of selecting for a short ear, which is an undesirable character.

Collins and Kempton state further: "The writers therefore conclude that if the relatively close interprogeny correlation between prolongation and damage is due to the association of prolongation with other protective characters, these characters were not included
in the notes. The differences between intra- and interprogeny regression remain unexplained, and in the light of this disparity it should be kept in mind, no assurance can be given that an increase in the prolongation in other stocks will be followed by the same rapid increase in immunity found in the course of these experiments.” The correctness of this point of view is born out by work in Arkansas (McClelland 1929) and in California (Poole 1937) and by work at the Kansas Agricultural Experiment Station, where little relationship could be found in some strains between length of husk and earworm resistance both in sweet corn and in field corn.

The authors suggest that the significant positive correlation between number of husk leaves and number of larvae \((r = +0.52)\) may be due to these leaves providing additional places for the moth to deposit eggs near the tip of the ear. It is stated that “a large number of layers (of husks) appears to be a protective character second only to prolongation in importance. . . . It is difficult to explain the correlation between numbers of layers and damage as a result of any direct protection.” And the authors again suggest that “number of layers is positively correlated with some protective character not considered in these experiments.”

The speed with which the grains harden had been suggested as a possible difference between sweet and field corn that is related to resistance. However, it was found that this rapidity of maturing could not have been an important factor causing differences in damage in these experiments.

There are two indications pointed out in the paper that the moths exercise a choice in depositing their eggs. One of these is the difference in the numbers of larvae found in the different ears of various progenies. Another is the high correlation between extent of damage on the first and second ears of the same rows. This correlation is higher than that between prolongation and damage, indicating that the similar damage is not entirely due to similar prolongation. An interesting fact brought out is that “on the average the more larvae there are in an ear, the greater is the damage done by the individual larva.” Perhaps this indicates the greater suitability of the media on which more eggs are deposited or that larvae leave ears that are distasteful to them. On the other hand, there was no observable relationship between sweetness of grains and high earworm damage, though no detailed analyses were undertaken.
Some of the facts or probable relationships brought out by this important paper are:

1. Resistance to corn earworm may be transmitted from field corn to sweet corn.

2. Low damage was found to be significantly correlated with a number of morphological characters which are mostly interrelated. The greatest correlation occurred with prolongation of husk, followed by large number of layers of husk and few husk leaves.

3. Resistant progenies were low both in number of larvae and damage per larva, possibly indicating that plants avoided by moths were also less acceptable to the larvae and that "at least a part of the immunity is the result of chemical differences, perhaps the presence of some volatile substance distasteful alike to the moth and the larva."

4. No difficulty was experienced in securing by hybridization and selection the desired plant characters in combination with the seed characters of sweet corn.

The value of shucks in preventing damage by various insects apparently was first presented by Hinds (1914). Kyle (1918), in connection with a study of the protection which shucks give against various insects, presents data on 213 ears regarding the value of shucks in preventing earworm damage to field corn. He states "that the longer shuck extension afforded 7 per cent more protection than the shorter shuck extension." He also suggests "the possibility of breeding a shuck extension long enough to be entirely effective against corn earworms." The latter statement is perhaps too optimistic.

McColloch (1920, 1922, 1924), in a series of three papers dealing with various phases of corn earworm life history and control, has brought out several important facts of interest in connection with earworm resistance. A detailed study was made of four varieties: Boone County White, Kansas Sunflower, Commercial White, and Hildreth. In 32 plots grown over a period of six years the ranking in respect to the percentage of plots with lowest number of eggs has been in the order given above. Boone County White had 43.7 per cent of the plots with the lowest number of eggs, and Hildreth had 12.5 per cent. The four varieties ranked in the same order in respect to total number of eggs, with Boone County White having 1,089 eggs and Hildreth 2,354. These differences are partly, if not wholly, accounted for on the basis of the relationship between time of silking or maturity and the number of
eggs. Three morphological characters have a bearing on oviposition. More eggs were deposited on plants having rough and hairy leaves. The number of leaves or the leaf area of a plant would have a bearing on the number of eggs deposited, as would the number of ears and the total time in which those ears would be attractive to the earworm. McColloch also found that it was possible to attract moths and cause oviposition on threads soaked with juice from crushed corn silk and also on threads soaked with maizenic acid (Farrell 1921), one of the constituents of corn silk. In recommendations made on use of time of planting for corn earworm control it was pointed out that the date of planting would differ with different varieties as well as with localities. It was found that certain hybrids homozygous for the character of having a few male florets on the ears were remarkably free from earworm injury (Farrell 1924; Call 1927).

Cartwright (1930), in a three-year study of the relation of various insects to shuck length in corn, gives some data regarding corn earworm injury on three classes of shuck extension—0 to 1, 1½ to 2½, and 3 to 6 inches, respectively. In one of the years ears with the longest shuck extension had approximately 4 per cent more ears damaged than the group with the shortest extension. In the other two years the longest shuck extension group had approximately 15 per cent and 11 per cent fewer ears damaged. A separate study of 22 varieties was made and it was concluded that "varietal resistance to corn earworm . . . is negligible in the varieties studied."

Many details of the value of husk protection provided by length and tightness have been studied by Phillips and Barber (1931). The investigation occupied five years and concerned 51,717 ears, on which measurements were taken. The ears of 13 varieties studied for a varying number of years were classified on the character of the husks into five classes from long tight husks to short loose ones. They showed that oviposition was approximately equal on silks of ears of these different husk types. "In no one variety was the proportion of the various husk-type classes the same in any two years or in any two plots." Hence this character was subject to environmental influences as was the intensity of infestation. Considering all years, and all varieties and plots the ears with short loose husks had an average of 39.14 kernels injured per ear and the long tight husks an average of 18.79, a
difference of 20.35 kernels per ear in favor of the latter class. The average of the other classes was strictly intermediate. In general, varieties with an larger percentage of long tight husks had less damage than those with the larger percentage of short loose ones, Silver King being the only exception to this general trend. By several methods of measurement it is shown that injury extends farther down the ear in the classes with looser and shorter husks. It is concluded that the most effective protection was offered by a husk which extends for at least five inches beyond the tip of the cob and was tightly wrapped throughout its entire length. This type of husk will, for the most part, limit the activity of the earworm to the long narrow silk channel beyond the ear. This paper appears to give adequate proof that on the average for the varieties studied and under Virginia conditions the difference in type of husk is of importance in reducing earworm damage and in accounting for some of the differences in earworm damage between different varieties.

However, the authors do not discuss the still greater intervarietal differences in damage shown in their data (Phillips and Barber 1931) (Table 11). The differences in average number of kernels injured per ear within varieties, because of the difference between long tight and short loose husks, ranges from 19.06 for Wisconsin No. 27 to 0.68 for Yellow Creole. Thus, varieties differ in the amount of protection afforded by the same difference in type of husk (Table 11). In the short loose type of husks, which is shown to carry little protection from corn earworm, there is a maximum difference of 34.95 kernels per ear between the variety with the greatest damage and the variety with the least. A similar average maximum difference between varieties for all husk classes represented in 28.84 kernels per ear. These figures for maximum differences between varieties are approximately three times the average maximum difference (9.06) between all ears of all varieties having the extreme types of husks, long tight and short loose. Hence it appears that differences between varieties may be of more importance than differences in husk type, and that the “Plant Ind. husk-type breeding” strain carries factors for resistance in addition to length of husk.

Popov (1934), in Bulgaria, reported that varieties of corn with long thick close-fitting husks were less severely damaged by the earworm.
### Table 11

VARIATION IN CORN EARWORM DAMAGE WITHIN DIFFERENT VARIETIES RESULTING FROM HUSK TYPE, COMPARED WITH THE DIFFERENCE BETWEEN VARIETIES

(Adapted from Phillips and Barber, 1931, Table 3)

<table>
<thead>
<tr>
<th>Variety</th>
<th>Long tight husks</th>
<th>Short loose husks</th>
<th>Differences within varieties due to husk type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Boone County White</td>
<td>24.78</td>
<td>41.76</td>
<td>17.02</td>
</tr>
<tr>
<td>Reid's Yellow Dent</td>
<td>27.83</td>
<td>37.62</td>
<td>9.79</td>
</tr>
<tr>
<td>Phillips' White</td>
<td>14.81</td>
<td>19.74</td>
<td>4.93</td>
</tr>
<tr>
<td>Silver King</td>
<td>15.50</td>
<td>29.39</td>
<td>13.89</td>
</tr>
<tr>
<td>Hickory King</td>
<td>7.92</td>
<td>20.78</td>
<td>12.86</td>
</tr>
<tr>
<td>Florida Flint</td>
<td>15.76</td>
<td>26.29</td>
<td>10.53</td>
</tr>
<tr>
<td>Wisconsin No. 37</td>
<td>26.09</td>
<td>45.15</td>
<td>19.06</td>
</tr>
<tr>
<td>Yellow Creole</td>
<td>12.70</td>
<td>13.38</td>
<td>.68</td>
</tr>
<tr>
<td>Cuban Yellow</td>
<td>5.47</td>
<td>11.50</td>
<td>6.03</td>
</tr>
<tr>
<td>Willett's Prolific</td>
<td>10.57</td>
<td>14.26</td>
<td>3.69</td>
</tr>
<tr>
<td>Garrick's Prolific</td>
<td>10.88</td>
<td>18.33</td>
<td>7.45</td>
</tr>
<tr>
<td>Lippard's Prolific</td>
<td>17.95</td>
<td>27.11</td>
<td>9.16</td>
</tr>
<tr>
<td>&quot;Plant Ind. husk-type breeding&quot;</td>
<td>7.61</td>
<td>10.20</td>
<td>2.59</td>
</tr>
</tbody>
</table>

Average difference within varieties due to husk type

<table>
<thead>
<tr>
<th>Variety</th>
<th>Long tight husks</th>
<th>Short loose husks</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average</td>
<td>20.62</td>
<td>34.95</td>
</tr>
</tbody>
</table>

Maximum average difference between varieties listed above in each husk type

<table>
<thead>
<tr>
<th>Class of husk type</th>
<th>Maximum average difference between varieties listed above in each husk type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Long tight</td>
<td>20.62</td>
</tr>
<tr>
<td>Medium tight</td>
<td>26.22</td>
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<tr>
<td>Short tight</td>
<td>27.36</td>
</tr>
<tr>
<td>Long loose</td>
<td>33.47</td>
</tr>
<tr>
<td>Medium loose</td>
<td>30.45</td>
</tr>
<tr>
<td>Short loose</td>
<td>34.95</td>
</tr>
<tr>
<td>Average (weighted)</td>
<td>28.84</td>
</tr>
</tbody>
</table>

In a study of 13,151 ears of sweet corn, Ditman and Cory (1936) also found both length and tightness of husk either alone or in combination to be of importance in reducing earworm injury. They also state “that in working over a large number of varieties and strains, there at times appeared to be some unknown factor or factors which seemed to cause some degree of immunity to ear-
worm injury," Country Gentleman and its types were found usually to be among the ones most resistant to injury.

Hawthorn and Fletcher (1933) and Mangelsdorf (1934), working with sweet corn in Texas, found that while most varieties were so badly damaged by corn earworm that they furnished few marketable ears, two varieties bred at College Station, Texas, by P. C. Mangelsdorf were relatively highly resistant. Honey June had 84.8 per cent of the ears marketable and Sure Cropper Sugar 73.3 per cent. Oregon Evergreen with 48.8 per cent was the commercial variety with the best rating. Eighty-six to 100 per cent of the ears were infested in the various sorts but in those named a large amount of the infestations was confined to the extreme tip of the ear. Honey June is from the cross Country Gentleman sweet corn x Mexican June field corn and Sure Cropper Sugar from the cross Sure Cropper field corn x Country Gentleman. Similar results with these varieties were found at several stations in Texas. The authors consider the resistance to be primarily, if not entirely, the result of the presence of long tight husks in these sweet corn varieties.

Records of further tests at Winter Haven, Texas, are given by Hawthorn (1936, 1937). In the first paper Georgia No. 439, Georgia 428, Papago, and several selections of Honey June, Texas Evergreen, and Sure Cropper Sugar are listed as among the more resistant sweet corns with 74 and 89 per cent of the ears marketable, although practically all strains had all ears infested. In the 1936 tests, reported in 1937, two strains from the Florida Experiment Station were reported as highly resistant with 97.2 and 83.3 per cent marketable ears, and several yellow-kerneled strains from the Iowa Experiment Station were reported to show "sufficient resistance to the earworm to merit further attention." Some of the latter had more than 60 per cent of the ears marketable as compared to Stowell's Evergreen with 11.2 per cent. No evidence is given that these newer varieties have particularly long or tight husks.

Ditman and Cory (1936), working in Maryland, found a considerable difference in resistance to corn earworm injury in sweet corn varieties. Hopeland, Narrow Grain, two selections of Country Gentleman, and Country Gentleman hybrid were among the lowest 12 varieties in damage each of the three years they were tested. Honey June and Sure Cropper Sugar both showed considerably less injury than other varieties in one test. It is interesting to note that
although resistant to earworms the former variety was badly dam­
aged by fall armyworm, which ate through the husks near the
base of the ear.

Burk, Cross, and Hixson (1936) found at Stillwater, Oklahoma,
the five corn varieties with the highest percentage of marketable
ears to be Trucker's Favorite, Texas Honey June, Norfolk Market,
Stowell's Evergreen, and Black Mexican. A classification of 3,150
ears into three classes with tight, medium, and loose husks shows
a 17.4 increase in percentage of marketable ears as a result of tight­
ness of husk. They found no evidence that the length of husk had
any influence on the amount of corn earworm injury in the test.

Poole (1935, 1936) reported on the resistance of corn to corn
earworm in California. With reference to corn earworm damage,
ears were classified in five classes from (1) ears damaged beyond
marketability, to (5) ears free from attack; and varieties are also
rated on the basis of percentage of marketable ears. By both rat­
ings, Oregon Evergreen, Papago, Florida 191, Sure Cropper Sugar,
and Honey June were among the more resistant sweet corn varieties
with from 73.2 to 82 per cent of the ears marketable, while other
strains of sweet corn ranged as low as 9.4 per cent of the ears
marketable. The field corns ranged from 40 to 100 per cent mar­
ketable ears while half of the sweet corns tested had proportionately
fewer marketable ears than any variety of field corn. Among the
total ears of all varieties, no significant correlation was found be­
tween length of husk and earworm injury. When the varieties were
studied individually, both positive and negative correlations between
these characters were found but in only 6 out of 36 varieties studied
did resistance give a significant correlation with greater length of
husk. The author says: "Evidently then such genetic factors
as are responsible for the observed freedom from injury are
only casually associated with husk projection; the real factors
con­ferring resistance are as yet undetermined, but are very likely some
chemical compound, or the tightness and number of husks." In a
carefully designed experiment involving five varieties it was found
that "variance between varieties is apparently of the same order of
difference whether all varieties silked concurrently or at different
times," and that "the different degrees of resistance to earworm
injury shown by these varieties are not caused by differences in
time when silks are exposed." Inheritance was studied by means
of back-crossing F1 plants to resistant and to susceptible parents,
respectively, and recording the injury to the progeny by corn earworm. It was found that resistance was inherited and that possibly in three cases the new hybrid populations may have been superior to either parent. The evidence presented “may be interpreted to mean that in these crosses the number of pairs of factors for earworm resistance was relatively small and that different dominant factors for resistance in some cases at least were contributed from each parent. 

Evidence for transgressive variation caused by different dominant factors coming from each parent is shown by the Oregon Evergreen x Honey June cross. In this case, the range in degree of resistance disclosed from the reciprocal back crosses was the smallest observed; yet in each back cross population the injury index and percentage of ears marketable was greater than in the best replicate of its recurrent parent.”

In a short note Barber (1937) called attention to the preference of the corn earworm moth for oviposition on sweet corn. During a three-year study eggs were found to be 15, 10, and 8 times as plentiful on sweet corn than on field corn. The same relationship occurred in both fall and spring. No data are given regarding the exact varieties studied.

Walker and Anderson (1938) have reported on a series of tests in Virginia (1934 to 1937) of sweet corn varieties and hybrids, in which the ears produced were graded in four classes of injury by earworm and the percentage of marketable ears also given for each variety each year. The early maturing varieties tested were all so badly injured that it was doubtful if they could be grown on a commercial scale. Of the later maturing varieties the following produced from 69 to 98 per cent marketable ears: Honey June, Sure Cropper Sugar, Money Maker, Aunt Mary's, Redgreen Hybrid, Oregon Evergreen, Stowell's Evergreen, and Golden Cross Bantam. In the tests it was reported that “the length of husk projection beyond the tip of the ear was not necessarily an important factor in the protection from earworm injury, as Spanish Gold, one of the most severely injured varieties, had a husk projection nearly twice as long as that of Honey June, one of the most resistant varieties.”

In a series of short papers Poole (1937, 1938, 1941) furnished progress reports on the work done at the Regional Vegetable Breeding Laboratory, Charleston, S.C., in breeding for earworm resistance in sweet corn. Cuban Yellow Flint, Sure Cropper Sugar, Tuxpan, and Davis Prolific have given the highest degree of resistance. The
latter two varieties, together with Papago, Mexican June, and Oregon Evergreen, have been outstanding parents in transmitting earworm resistance. Aunt Mary's Sweet and Purdue 51 were also mentioned as being resistant. In a study of the relation of six characters to resistance, an obligate relationship was not found with any. In addition to resistance the characters studied were: extension of husk, elapsed time to tassel, plant height, ear weight, ear length, and number of husks. It appeared that the highest type of resistance was associated with southern dent corns that have become adapted in regions where the earworm is a constant feature of the environment.

A tropical sweet corn, USDA-34, has been developed (Harper 1946) for use particularly in Puerto Rico. One of its important characteristics has been resistance to earworm. Several other experiment stations in the southern states, notably Mississippi, Georgia, and Florida, have published reports regarding differences in earworm injury to sweet corn varieties and hybrids (Eckhardt et al. 1944; Bowers 1945; Bowers et al. 1947). These tests indicated that varieties previously reported as resistant elsewhere and also some of the hybrid sweet corn were resistant under the condition under which they were tested.

Magoon et al. (1945) in a further report on the Regional Vegetable Breeding Laboratory has stated that "eggs of the moth carefully placed on ears of resistant strains and held under favorable conditions fail to hatch and eventually perish." Four open-pollinated varieties, Kiawah, Edisto, Wappoo, and Carowa, were released to growers in 1944, largely on account of their high resistance to earworm. Other characteristics of these varieties are given in the publication.

Resistance to corn earworm among corn inbreds and hybrids.

With the increased interest in the possibility of commercial utilization of hybrid corn, studies were begun on insect resistance with this type of material in several localities. At the Kansas Agricultural Experiment Station studies on this insect were begun about 1919. Reports on some varietal material and on hybrids are given by Painter and Brunson (1940). The study was carried on during the years 1929 to 1937, inclusive, and concerned over 73,000 ears, of which more than 96 per cent had been naturally infested by this insect. In the early part of the study resistance was measured on the basis of percentage of ears infested. When it was evident that
differences existed also in the degree of infestation, a scheme was used in classifying the ears into six classes—class 1 including those ears with no evident infestation and class 6 those with the greatest damage (Painter, Brunson, and Parker 1932). A photograph showing characteristic ears in each class was used to help standardize the procedure of classification. The plant material used was chiefly that grown in the breeding and yield-testing experiments of the Department of Agronomy, supplemented by a few special experiments. The hybrid and inbred material used was therefore more or less a random sample of the corn germ plasm being used for corn improvement at the Kansas Station. The information gained was used by the plant breeder as one of the criteria upon which the continuance or discarding of the strains depended. It is believed that a selection beginning with open-pollinated varieties would have made possible the discovery of higher degrees of resistance (Figs. 37, 38).

During the early years of study, open-pollinated varieties were examined and a few of these were included each year. In those years when a considerable number were studied, there was a high correlation between class of injury and date of flowering, the later varieties being the more severely injured. It appeared that there was no varietal difference in earworm injury of practical importance that was independent of the date of flowering.

Most of the studies of inbred lines were made in the terms of the average performance of the inbred in hybrid combination. Where statistical methods were used, a minimum difference between hybrids of from 0.6 to 1.0 class of injury has been found to be significant in various tests. For all these strains information was available on the date of flowering. In general, little relationship was found between the class of injury of hybrids and this variable. In some experiments the correlation between amount of injury and date of flowering was positive and significant, in others it was negative and significant but, in most cases, the relationship was either non-significant or barely significant. There was evidence that resistant strains were not as greatly influenced by the date of silking as were susceptible ones. The reason for the significant relation in the case of the varieties appears to be that the number of susceptible plants in such varieties far exceeds the number of resistant ones and that it is these susceptible plants which are responsible for the general relationship.
FIG. 37. Corn earworm damage to all ears harvested from four plots of the moderately resistant inbred Kansas K4, Manhattan, Kansas, October, 1939. Inbred K4 is moderately susceptible in Kansas as an average of most hybrid combinations.

FIG. 38. Corn earworm damage to all ears harvested from four plots of the highly susceptible inbred U.S. 187-2. Some ears were completely eaten by the larvae. Compare with Fig. 37. The plants from which these ears (Fig. 38) were taken were grown in the same experiment and exposed to the same conditions as those shown in Fig. 37. Manhattan, Kansas, October, 1939.
A study was made in 1931 of the relation of class of injury to the length of husk extension. In the two groups of hybrids studied there appeared to be some relationship. In one group of hybrids, the correlation between average class of injury and average husk extension was negative and highly significant statistically \( r = -0.29 \). However, a study of those hybrids having the least and those having the most injury showed that it was easily possible to find hybrids with a very small amount of earworm injury and with only slight husk extension. Again, therefore, the relation between class of injury and husk extension was not an obligate one. Late damage by the earworm to the hard flinty kernels was so frequent that no consideration was given to this character as one possibly related to resistance.

Each year the corn earworm does some damage in Kansas to the upper leaves of the young corn plants. This type of injury to the curl has been known as "budworm" or "ragworm" injury. On three occasions this damage was severe enough to make possible a study of resistance to it, and the relation of budworm injury to ear injury. In 1934 there was a highly significant correlation between the curl injury to parental inbreds and to F₁ hybrids involving these inbreds, indicating the inheritance of resistance to budworm injury. There was also a highly significant correlation between the percentage of infested plants in identical hybrids in successive years. There was, however, no close relationship between the percentage of plants showing budworm injury and the average class of injury to the ear. This would indicate that the resistance to the two types of damage is governed by different genetic factors. An inbred which confers on its hybrids a high degree of resistance to budworm injury would be desirable since such a character might help to limit the increase of earworm in the field.

The various inbred lines in single-cross combinations were studied over a period of several years. There was under study a group of white-kernel inbreds derived from the variety Pride of Saline. A considerable number of these inbred lines were better than the average of the variety for resistance to the earworm. White-seeded inbreds PS₄, PS₅, PS₁₁, and PS₁₄ were outstanding in their resistance to the earworm. Among the inbreds with yellow endosperm color that had a high degree of resistance to earworm, Kansas inbreds K₁₂₆, K₁₅₁, K₁₅₅, K₁₇₉, and K₂₃₀ have been outstanding in recent studies. Inbreds Iowa L₃₁₇, Kans. K₄ and
U.S.D.A. CI.187-2 were moderately susceptible to highly susceptible. The relative ranks of the different inbreds and hybrids from year to year under highly variable conditions have been quite constant (Fig. 39).

At the end of this period of study there was an opportunity to measure the results of this testing program. In 1939, when the first corn-performance test was conducted in Kansas, all of the 40 Kansas Experiment Station double-cross hybrids in the test had less earworm injury than any single out-of-state hybrid or commercial hybrid. In the Kansas corn-performance test in 1940 four of the seven Kansas Experiment Station hybrids were significantly less injured than the open-pollinated variety Pride of Saline. In
this same test only 1 out of 18 commercial hybrids was less injured than the Pride of Saline. In the 1941 Kansas corn-performance test 8 of the 16 Kansas Experiment Station hybrids were better than the average of the open-pollinated varieties while only 7 out of the 55 commercial hybrids were less severely damaged than the open-pollinated varieties. It appeared that the differences found were worth utilizing in commercial hybrids but that it may be possible to get a higher degree of resistance by a more intensive breeding program.

During the time that these studies were in progress at the Kansas Station, similar studies were being made at the Illinois Experiment Station. Some of these have been reported in various papers (Dungan et al. 1938; Blanchard, Bigger, and Snelling 1941; Jenkins 1942). In the study published in 1941 one or more records are given on 69 inbred lines and on the performance of a number of these inbred lines as single-cross hybrids. The ears were given an artificial infestation as well as the natural infestation. Damage was measured in five classes with class 1 representing the least damage. The various strains were measured also in terms of percentage of ears damaged more than class 2 (or damaged for not more than ¼ inch from the tip). The individual inbred lines differed greatly in the amount of damage and in their ability to transmit resistance. In some cases the resistance appeared to be dominant, in other cases, recessive. In part the reaction of the hybrids depended on the susceptible parent involved. Usually crosses between two susceptible lines gave susceptible hybrids. The one exception to this was the cross Ind. 38-11 x Kans. KYS, in which the F₁ hybrid was resistant. Resistance to earworm was clearly inherited and the resistance was stable through several localities in which the tests were made. There were data taken on early and on late damage to the ear by the earworm, but the correlation between these two types of damage was very low. The early damage occurred soon after pollination and the late damage, done by the following generation of the earworm, occurred after the kernels had hardened.

The following white-seed inbreds were resistant as inbreds: Kans. PS4, Ky. 27, and Ind. 33-16. Inbred Ky. 27 transmitted resistance in hybrid combinations. The inbred Mo. B103 had high injury by the earworm both as an inbred line and in hybrid combinations. The following yellow inbreds were resistant as inbreds: Iowa 701,
RESISTANCE TO INSECTS IN CORN

U.S. 540, Ill. R4, Ind. WF9; and the following hybrids usually showed resistance in hybrid combinations: U.S. 540, Ill. R4, Ind. WF9, and Ill. 90. The inbred Ind. 38-11 was susceptible as an inbred and usually very susceptible in hybrid combinations. Inbred U.S. 187-2 and Ind. P8 were susceptible as inbreds, and Oh. 02 susceptible in hybrid combinations. In general, the ears of the single crosses were damaged less than the ears of the inbreds.

In a report to the North Central Corn Improvement Conference (Jenkins 1942) Snelling stated that a cooperative program of breeding for insect resistance in corn had been set up at the Illinois Agricultural Experiment Station in 1937. He further reported that in three years of uniform regional tests in 1939 to 1941 the reaction of the particular corn strains to earworm had been relatively stable over a region involving 11 states.

Blanchard and his associates (1942) reported on methods of determining differential earworm damage and of securing young larvae in abundance for these tests. Five to seven larvae which were placed on ears twice at intervals of three to six days gave the most severe damage to susceptible varieties. When the ears were hand-pollinated, they were also infested two or three days after pollination. Ears that were artificially pollinated and covered by a paper sack were somewhat more injured than artificially infested ears that were naturally pollinated. A higher rate of larval survival occurred on some strains than on others. Selections from corn varieties had been made which showed promise of being highly resistant to earworm. The method described permits the simultaneous inbreeding and selection of such strains of corn.

Dicke and Jenkins (1945) have reported on the difference in susceptibility to damage by corn earworm of certain strains of field corn when in hybrid combinations. The experiments were conducted at Arlington, Virginia, in the neighborhood of Washington, D.C., on strains being tested primarily for other qualities. The writers believed that long tight husks extending at least an inch beyond the tip of the ear and the presence of flinty grain of hard texture near the tip of the ear offered the best protection against damage from heavy earworm populations. Due attention was paid to the relationship of egg deposition and to the time of silking of the various strains. Data were presented that were derived from records of many ears, from top crosses, double crosses and single...
crosses, with emphasis particularly on the latter. The inbred lines, possessing outstanding ability to contribute resistance in hybrids, were the following:

<table>
<thead>
<tr>
<th>Yellow</th>
<th>White</th>
</tr>
</thead>
<tbody>
<tr>
<td>CI.2</td>
<td>K55</td>
</tr>
<tr>
<td>23R7</td>
<td>CI.43</td>
</tr>
<tr>
<td>CI.6</td>
<td>T18C</td>
</tr>
<tr>
<td>CI.7</td>
<td>Cl.61</td>
</tr>
<tr>
<td>K3n</td>
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</tr>
<tr>
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<td>Cl.23</td>
</tr>
<tr>
<td>317Lh</td>
<td>Ky27</td>
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<tr>
<td></td>
<td>LanLhw</td>
</tr>
<tr>
<td></td>
<td>Ky30A</td>
</tr>
<tr>
<td></td>
<td>38Lhw</td>
</tr>
</tbody>
</table>

Included among the single crosses and double crosses studied were some long-husked strains produced by crossing certain Corn Belt lines with an inbred line normally having about 6 inches of husk extension. The first generations were back-crossed to the Corn Belt parent and then selfed during a period of selection for long husks. These long-husked inbreds contributed some additional protection when crossed onto other ordinary Corn Belt lines. The long-husked lines involving 317Lh were outstanding for resistance. In general, the white hybrids studied did not appear as a group to be superior to the yellow ones. The resistance contributed by resistant inbreds was such that hybrids involving them had two or three times as many ears, grading class 1 or better than did hybrids involving the most susceptible inbred lines. Among four-way or double crosses at least three inbreds, resistant to the earworm, were required in order to give effective protection from the insects. In such hybrids there was evidence of segregation for resistance among individual plants. Among the yellow lines contributing a high degree of susceptibility in crosses were L317, P8, K4, R94, CI.1, and CI.3.

Richey (1944) reported on budworm damage at Tennessee Experiment Station to several inbred lines when in hybrid combinations. Inbreds T13 and T61 contributed susceptibility and T18 resistance. The hybrid T13 x T61 had 71 per cent of the plants damaged by this early generation of the earworm. The differential injury was not associated with differences in plant height or maturity. Similar differences have been reported at the North Carolina Experiment Station (Sixty-seventh Annual Report, North Carolina Agricultural Station: 19–22, 1944).

In a study of the relation of husk characters to corn earworm damage Douglas (1947) found that, in Mississippi, a 2- or 3-inch husk extension, which is normal for most varieties, furnished as
much protection from earworm as a 5- or 6-inch extension. In varietal material there was a disadvantageous negative correlation between husk length, and length and weight of ears. The hybrid La. 1030 had low earworm injury that did not depend on extreme length and tightness of husk.

Walter (1948) has reported on the earworm reaction of a large number of sweet corn inbreds. The majority of these were experimental lines but some were released and are being used in commercial hybrids. The reaction was observed under heavy natural infestation at Weslaco, Texas, and under natural infestation supplemented by the artificial addition of six young larvae per ear at Lafayette, Indiana, and Urbana, Illinois. Most of the strains gave a very similar reaction under the different conditions, the most notable exception being P51, which was resistant to natural infestation but susceptible when the larvae were placed on ears under the selfing bags. Egg counts indicated that the moths showed no preference for or against this inbred. Records of classes of injury were taken on the basis of the number of kernels destroyed approximately as follows: class 1—less than 1; class 2—10; class 3—20; class 4—30; and class 5—40 kernels. Lines were rated as resistant, intermediate, or susceptible according to whether they occurred in the upper, middle, or lower third of the respective tests. Among some of the more resistant sweet corn lines as inbreds were: Ill. 107a, Ind. 662, Iowa H5, Ohio E13, Ill. 5j, Ill. 27a, Ind. FR34, Ind. 8344, Iowa 4011, Iowa 4024A, and Ill. 14n. The following Evergreen inbreds from the U.S. Regional Vegetable Breeding Laboratory were very resistant: 2d-2d-Od(Sel) and 81-1-3-5-2-11. Records are also given on the rating of a number of experimental and commercial hybrids and a few varieties.

In these and other papers there have been reported the following as the chief mechanisms affecting the resistance of corn to the earworm:

1. Number of husk leaves.
2. Number of husk layers.
3. Synchronization of time of silking and peak of oviposition.
4. Length of silking period; number of ears.
5. Total of leaf area available for oviposition.
6. Hairiness of plant.
7. Male florets at tip of ear.
8. Length of husk, cannibalism of larvae.
(9) Tightness of husks.
(10) Hardness of the kernels.
(11) Attractiveness for oviposition.
(12) Value as food for larvae.

All except the last four—or perhaps just the last two—can be regarded as of minor significance or, in part, as features of the environment. There has been evidence that several of these factors, especially those relating to flowering and husk characters have been more apparent in the case of otherwise susceptible strains. It has been shown that moisture has a strong positive effect on the length of husk (Barber 1944) and this may explain for instance why Kans. PS55 was rated as the most resistant white inbred near the east coast and the most susceptible one in Kansas. Differences in results of various experiments in regard to length of husk may also relate to the particular strains involved in a test. Almost certainly the basic difference in resistance to the earworm is one of differential survival of the larvae (Holbert 1946), supplemented in some cases by differential oviposition. Published evidence of details concerning these points is not available as yet.

RESISTANCE TO THE EUROPEAN CORN BORER IN CORN

Since the European corn borer (Pyrausta nubilalis (Hbn.)) was discovered in the United States in 1917, it perhaps has been studied as thoroughly as any other single insect of high economic importance. It now occupies much of the northeastern quarter, or more, of the United States and adjacent parts of Canada, infesting corn throughout the corn belt states in which this crop is of the greatest importance. In Europe and Asia, where it is a native insect, it infests corn but is also a pest of millet, hops, hemp, and similar crops. A few other species of Pyrausta, which are of little economic importance, occur in North America but other more distantly related species in the same family include many destructive pests.

There were two or three separate introductions of the corn borer, one near Boston, Mass., the others near Lake Erie and in New York. The borer population in New England was made up of a multiple-generation strain which normally has two generations there, but has three generations where it has migrated south along the Atlantic Coast. In the Great Lakes area the population has consisted mostly of single-generation individuals, but a small part of the population
with a tendency toward the multivoltine habit has been noted repeatedly since the earliest studies in Ontario (Wishart 1947). As this part of the population of the European corn borer has spread south and west, especially since 1936, the proportion of insects showing the multiple-generation habit has increased, partly as a result apparently of natural selection that favored this type. Arbutnot (1944) has studied the relations between these two populations. The multivoltine characteristic was found to be a dominant genetic character and appeared to be sex-linked. The New England borers were found to represent a homozygous multiple-generation strain; the material from Toledo, Ohio, was found to be heterozygous, with a complex of multiple- and single-generation strains occurring together. It was possible to isolate a single-generation stock with a different growth rate and with a different diapause relationship from that of the multivoltine stock. This single-generation strain required a period of cold for several months before pupation occurred; the multivoltine strain continued to go through its life history without diapause. The moths showed a decided preference for mating with others from the same area; in crosses between New England females and Toledo males, only 23.8 per cent of the eggs were fertile compared with 71 to 96 per cent in the reciprocal cross and in parent stocks. In the next generation, in both cross and reciprocal, there was low survival of the larvae.

There is clear indication of a host-plant relationship associated with the two populations present in the United States. Most entomologists would relate the host-plant differences to the numbers of the various hosts available at the time of oviposition. Although this feature of the environment is of utmost importance, a hereditary difference between strains of borers in host preference and in ability to utilize different host plants must not be overlooked. In the multiple-generation area, in New England, borers have been found in over 200 plants. Eggs and borers occur on weeds and crop plants at a distance from corn (Hodgson 1928). In the Lake Erie area, at the beginning of the borer invasion, the insect was found largely on corn or in weeds in corn fields (Neiswander and Huber 1927; Huber et al. 1928; Dicke 1932). Borers present in weeds were largely migrants from corn. With the increase in the multiple-generation strain in the western area, there has been some increase in infestation of other plants especially potatoes. Data presented by
Arbuthnot (1944) show differences in survival rate of the New England and the Ohio strain larvae when reared on green beans. There is also some indication of host-plant-related strains of *Pyrausta nubilalis* in Europe (Thompson and Parker 1928). These host-plant relationships need more thorough study, for they may have an important bearing on the problem of breeding plants resistant to the European corn borer.

Bottger (1940, 1942) has studied the nutritive requirements of the European corn borer and developed a synthetic food medium on which he was able to grow the insect from egg to adult. The females reared, however, laid infertile eggs. This was the first time that a phytophagous insect had been so reared. There was considerable variation in the amount of pupation on the different foods and synthetic media, but it was reported that the variations were not due solely to differences in nutrition. In the earlier paper a report was given of the enzymes found in the digestive tracts of hibernating larvae. These tests indicated the presence of both "sucrose- and protein-splitting enzymes" and an absence of enzymes capable of hydrolizing starch. Differences were found in the survival and weight of larvae reared on internodes or leaves of different kinds of corn. On both tissues hybrid A x Tr gave higher survival and greater weight of larvae than did hybrid Hy x R4. Beck and his associates (1949) have made further significant contributions toward the development of a synthetic food medium for rearing corn borer larvae and thus analyzing their nutritional needs.

The total injury done by the borer appears as a reduction in yield. This has been the result of an increase in the number of barren plants, an increase in the number of unmarketable ears, and a decrease in the size of ears (Patch et al. 1941). Another type of injury is the breakage of plants because of the tunneling of the borer. If it occurs below the ear, harvesting is interfered with and the loss of corn from fungi and rodents increased. Neiswander and Herr (1930) showed that up to a level of six borers per plant the reduction in yield per borer per plant was 5.4 per cent for Golden Bantam sweet corn, 3.25 per cent for Smoky Dent, and 1.8 per cent for Burr Learning field corn. There was an inverse correlation between the percentage reduction in yield and length of the period between planting and silking, and the same relation with size of stalk. A breakage of stalks was found to increase at the rate of 6.09 per cent per borer per stalk. Patch and his associates (1941) made
a three-year study of the effect on yield and stalk breakage of hybrids and open-pollinated varieties for populations of borers ranging up to nearly 20 per stalk. They found that the marketable yield of open-pollinated varieties was reduced on the average 3.64 per cent per borer per plant and the yield of hybrids reduced 2.99 per cent per borer per plant. The advantage of the hybrids as a group was an important one and originated primarily from the smaller increase in the number of barren plants and unmarketable ears. Up to a population of seven borers per plant both hybrids and varieties showed an increase in breakage below the ear at the rate of about 1.47 per cent per borer per plant. These figures for losses involved primarily the single-generation strain.

In addition to reduction in yield and increase in stalk breakage the European corn borer does several other types of damage: feeding on and making holes in leaves; feeding on anthers and other parts of tassel, frequently causing breakage of its branches; tunneling and causing breakage in the midrib and near the point of junction of leaf and leaf sheath; tunneling in the stalk; tunneling in the shank and in the ear itself. These different types of damage are related to the stage of development and survival of the larvae as well as to the stage of development of the plant. These features have been studied by Huber et al. (1928), Beard and Turner (1942), Beard (1943), Patch (1943), Turner (1945), Batchelder (1946) and others. The eggs are laid on the leaves and the young larvae, especially of the first and second instars, feed in the young tissue of the leaves where they are rolled in the whorl. Often the second and third instars feed in the young tassel, which structure is most favorable for larval survival. The developing ear is also a favorable place for the development of the young larvae. Rarely, if ever, do the larvae bore into the plant before the fourth instar and some do not do so until they are in the fifth instar. Since there are five or six instars, only about a third of the larval feeding period of the European corn borer is spent as a borer. The heaviest mortality occurs in the first instar and often amounts to 70 per cent or more (Huber 1936). It has also been shown (Neiswander and Huber 1931) that "other things being equal there is an inverse relationship between the number of eggs deposited and the rate of larval survival." According to the data presented this decrease in larval survival begins at a point somewhere between 100 and 250 eggs per plant, but up to about 100 eggs per plant there is an in-
crease in the survival with each increase in the number of eggs. This factor of competition has not been studied in relation to resistant and susceptible strains of corn but the results suggest that a level of infestation may be reached in which no more increase is possible on susceptible strains while resistant ones may still give an increase in survival. The level at which this occurs appears to be found rarely in natural infestations but may have occurred in some artificially infested corn. The survival of larvae would also be influenced by size of plants and other factors.

The ovipositing moths show a general preference for corn in the flowering stages and those stages just preceding and following flowering. Beard (1943) reports that in Connecticut the first and second generations of the corn borer show distinct differences in the pattern of oviposition relative to growth stages of the sweet corn plant. There is also an increasing gradient in the percentage of survival of young larvae that are beginning to feed as the plant approaches and passes the flowering stage. This increase appears to be related not only to the presence of the tassel and the higher survival of the larvae that feed on it, but also to changes in the rest of the plant that accompany the appearance of the tassel and ear shoot. The synchronization between stages of plant development and the peak of oviposition is different for the single- and multiple-generation forms and varies also from place to place and from year to year.

The moths show a general preference for taller over shorter corn. This has been studied by a number of investigators (Huber et al. 1928; Neiswander and Huber 1929; Patch 1942) and is apparent especially in open-pollinated corn. The preference for taller corn is for plots of corn rather than single plants. The height of plants as well as stage of maturity at time of moth flight are influenced by variety, fertilizer treatments, time of planting (Ficht 1931, Kelshemer and Polvka 1931; Schlesberg and Mathes 1937), and other conditions of the environment. There have been noted, however, some cases in which shorter inbreds or hybrids were preferred for oviposition to neighboring taller ones (Patch and Dey 1948).

There appears to be every opportunity for this insect to carry into the plant spores and other stages of bacteria and fungi. These possibilities exist less in the case of resistant strains of corn but in general introduction of these pathogenes increases the damage done by the insect.
Early studies of resistance to European corn borer. A group of varieties and hybrids were studied in Ohio in 1927 (Huber et al. 1928). An important relationship found was the greater infestation of early maturing strains in comparison with late ones, considerable variation being found in the population of borers on different varieties planted on the same date and on the same varieties planted on different dates. Independent of these relationships there appeared evidence of difference in attractiveness as well as in survival of larvae between such varieties as Golden Bantam and Clarage. On the basis of these early tests it was planned to study strains to determine "(1) the degree to which they become infested, (2) the degree to which they are damaged by approximately equal infestation, and (3) whether strains may be found or developed that can be planted later than usual and will produce a profitable yield of sound corn." The general problems and possibilities thus were recognized rather early in the study of the resistance to the European corn borer in the United States.

Shortly after the introduction of the European corn borer into North America some studies were made of the infestation of several varieties of corn by this insect under European conditions (Eltinger and Chorine 1930, 1931; Haas 1929; Roubaud 1927, 1928a, 1928b, 1929, 1930; Vouk 1930; Vukasovic 1932). Generally the American varieties appeared to be more susceptible; Dent de Chevalier or Pierdezahn and Hatif d'Auxonne were cited as resistant in some tests but only tolerant in others. There appeared to be some question concerning the identity of the varieties carrying the same name in the several tests. Roubaud attempted to demonstrate the inheritance of acquired resistance to the borer.

Beginning in 1926, in Michigan, Marston (1929, 1930, 1931) and Marston and Dibble (1930) sought for sources of resistance to the borer but with little success, except in the case of the South American corn, Maiz Amargo. Crosses were made with adapted Michigan varieties in 1926 following some indication of borer resistance in Maiz Amargo. The following year moths were caged on the separate parent varieties. About 150 eggs were laid on Maiz Amargo and only one larva found after the corn reached maturity. Michigan corn varieties under similar conditions were heavily infested with eggs and completely destroyed by larvae. The Maiz Amargo was used as the male parent and Duncan, Golden Glow, and Red Cob Ensilage as female parents. Later crosses were made.
with the sweet corn Golden Bantam and with other sweet corn varieties. Most of the F1 plants from Dent parentage were grown under cages but the few left unprotected were infested. The next year the Duncan Yellow Dent parent had 68 per cent plants infested, Maiz Amargo 5 per cent and the two F2 populations 18 and 8 per cent, respectively. The F2 plants were hand-pollinated and the following year grown in ear rows. Out of 935 such rows, 227 were not infested, a ratio of 3.1 to 1. The uninfested rows varied considerably in height and earliness. The infestation of the examples of F2 rows given (Marston 1930) varied from 0 to 41 per cent. It is stated that resistance to borer derived from Maiz Amargo is a "simple Mendelian character, recessive to that characteristic of standard Michigan corn varieties which makes them subject to heavy attack and severe damage." Since the infestation resulted only from natural oviposition of moths free to choose between the segregates it is suggested here that the segregating character may be one for nonpreference rather than antibiosis. The behavior of the moths caged on Maiz Amargo suggests the same interpretation. In a later paper (Marston 1931) evidence is present that resistance derived from Maiz Amargo was not due to late maturity. In 1936 Michigan hybrid No. 561 was distributed to farmers in that state as a borer-resistant Dent corn. It was a top cross between an inbred line and S-10, a synthetic variety made by blending 91 inbred lines. In crosses between Maiz Amargo and Golden Bantam (Marston and Mahoney 1932), 21 of the 65 F1 inbred progenies were resistant and had sweet corn of the type of Golden Bantam, but were of later maturity. There appeared to be no correlation between Amargo type of plant and corn borer resistance.

Studies of the resistance to European corn borer in inbreds and hybrids. From almost the first work on resistance to the European corn borer some studies have been made of differences in infestation of hybrids and, to a smaller extent, of inbreds. It was realized quite early that the small differences between lines and the relationship to maturity as well as other sources of variability made replication and statistical analysis especially necessary. The methods used are given in most of the papers (see especially Meyers et al. 1937; Patch et al. 1942; Patch and Everly 1945, 1948) but it was fortunate that several of the workers were especially competent in this field.
There have been, in general, two types of work on resistance to the European corn borer. In Canada (Caesar 1936; Thompson 1938, 1939, 1940, 1941, 1942) and at several of the state experiment stations (for example, Ficht 1936, 1939; Huber 1939, 1944; Jones et al. 1939; Pepper and Garrison 1941; Flint et al. 1942; Dungan et al. 1946) information was gathered on the corn borer infestation of, or damage to, hybrids and open-pollinated varieties adapted to the locality where the tests were being conducted.

Sometimes these studies were made in especially designed tests; at other times they were made in corn-performance tests, where both commercial and experimental hybrids were being compared for yield and other agronomic characters. After the borers were full-grown, usually ten or more stalks of each strain of corn were dis-

![Comparable parts of younger leaves from strains of corn resistant (left) and susceptible (right) to the attack of the first and second instar larvae of the European corn borer, *Pyrausta nubilalis* (Hbn.). The feeding was done when the leaves were low in the whorl. This difference in damage corresponds to high and low mortality of the larvae which fed on these strains. Similar differences in damage by insects with chewing mouth parts have been observed in other plants showing resistance to insects.](image-url)
sected and the numbers of borers recorded. In more recent tests other methods of measuring differences in resistance were used (Fig. 40). In all cases small but fairly consistent differences were found in the resistance to borers as represented by differential survival, or in tolerance as measured by stalk breakage, or both. Generally, also many hybrids were superior to the open-pollinated varieties in yield under borer infestation and in the lower amount of stalk breakage.

In contrast to these studies, which were often principally of local interest, experiments of more general applicability have been carried on by several state experiment stations, especially Ohio, and by the U.S. Department of Agriculture in cooperation with various states in experiments near Toledo, Ohio, and at LaFayette, Indiana. Because of the small size of the differences found between strains of corn, some of the earlier studies were directed toward determining whether these differences were real and independent of such plant characteristics as height and the synchronization of moth flight and date of flowering.

Meyers and his associates (Meyers et al. 1937) reported on a study of the natural infestation in corn hybrids in northern Ohio for the period 1926–32. As high as 800 strains were under observation during some of the years. The infestation on inbred lines was too low to be of significant value; hence the study was based primarily on hybrids and open-pollinated varieties which received a rather heavy natural infestation. The relationship between height, maturity, and corn borer infestation was confirmed but by a use of multiple regression it was possible to make adjustments for these variables and show that there were additional differences which represented true resistance. This resistance was measured in terms of the difference between the predicted and the observed number of borers in the several strains. In general, the open-pollinated varieties tended to approximate the expected infestation. Among the hybrids, however, there were some with considerably more borers than expected and others with considerably less. The resistant hybrids had about 20 per cent fewer borers than did the open-pollinated varieties in the same test. Since in the experiments considerably less than 100 per cent of the stalks were infested in any season, it was believed that the resistance would become of greater economic importance as the infestation became higher. It was found that the variation in total eggs per plot was rather slight but
that variations in the final population of borers were almost as much of a hereditary character as were differences in yield.

Patch (1937) reported on a study of differences between a borer-susceptible hybrid, A x Tr, and a resistant one, R4 x Hy. These two hybrids were planted on several different dates and in order to assure infestation, one to four egg masses were added to each plant. It was shown that these two hybrids were very much alike in leaf area, in maturity, and in height. Differences were found, however, between the two hybrids in each of the stages of maturity studied. The number of borers reaching maturity in the ten plantings of hybrid R4 x Hy was equal to 46.6 per cent of the number reaching maturity in strain A x Ty. Thus, under heavy artificial infestation differences in resistance in field corn were evident at all the stages of plant maturity studied.

Schlosberg and Baker (1939) made a similar study of differences in larval survival on two inbred strains of sweet corn. Each strain was artificially infested at 22 stages of plant development with an average rate of 90 eggs per plant. One of these inbreds, M1828, was somewhat more attractive to the moths for oviposition and matured a little earlier. It should therefore have had a higher borer survival than the other strain, C2. However, M1828 had a lower borer survival at all stages of maturity except one, and the differences were statistically significant when the infestation occurred from 25 to 5 days prior to silk appearance. In both of these last papers mentioned a lower larval population was always associated with earlier stages of plant development. These studies were concerned with the single-generation strain of the borer and, in conjunction with other similar studies, they clearly indicate the presence of resistance.

Along with increased information on resistance to the European corn borer have come improved methods of study. The first records on resistance involved the percentage of plants infested as a result of natural infestation. Ficht (1936) calculated resistance on the basis of percentage of full-grown larvae resulting from an estimated number of eggs per 100 plants. With the use of methods of causing an artificial infestation (Patch and Pierce 1933; Patch 1947), which usually provided an infestation of all plants, records were taken of the number of borers per plant or per groups of plants, sometimes ten or twenty in a group. Along with records of borers it usually was necessary also to record the time of flowering.
and the height at time of infestation. The relationship to a number of other variables concerned with the plant or the insects were also studied (Meyers et al. 1937). Several papers have dealt with methods of allowing for variability resulting from characters other than resistance (Meyers et al. 1937; Patch, Holbert, and Everly 1942; Patch and Everly 1945, 1948). In the last mentioned papers resistance and susceptibility were reported in terms of the deviation from the predicted population of European corn borer or the percentage of deviation from the predicted population. Huber (1937) and Huber and Stringfield (1942) made use of the number, or the number and size of feeding punctures made by the young larvae feeding in the whorl of the young corn plant. On resistant strains of corn these feeding punctures were fewer in number and smaller in size than they were on susceptible strains. When both size and number were considered, the kinds of corn were graded by inspection from grade 1, where the holes were few and small, to grade 5, where they were many and large. Such estimates could be made quickly and permit the preliminary classification of a large number of strains. In a report to the corn-improvement conference of the North Central Region a committee recommended the evaluation of European corn borer resistance in strains of corn on two bases (Neiswander, Snelling, and Dicke 1949). Strain resistance, primarily to borer establishment and survival, was to be ranked from 1 to 5 and recorded not later than early roasting-ear stage on the basis of amount of injury to leaves, leaf sheaths, and number of burrows in the stalk. The differences in strain tolerance, or the relative ability of a strain to withstand injury in spite of larval feeding, were to be ranked from 1 to 5 just prior to harvest on the basis of broken stalks, broken tassels, broken ear shanks, and broken leaves.

The various experimental and commercial inbreds and hybrids from many of the states have been investigated as possible sources of resistance. The Maiz Amargo and hybrids derived from this variety in the work at Michigan Agricultural Experiment Station (Marston 1930, 1933) have been studied under heavier infestations than were available earlier. Thompson (1938) found that Michigan hybrid No. 561 was somewhat better for resistance than the open-pollinated varieties tested but little, if any, better than other hybrids. According to Patch and Bottger (1935) Michigan synthetic variety No. 10 and several other hybrids derived from Maiz
Amargo were not particularly resistant. Patch, Bottger, and App (1938) reported on a detailed study of Michigan hybrid No. 561 in comparison with the known susceptible single cross A x Tr. The plants received additional egg masses as well as the natural infestation. Michigan hybrid No. 561 as well as Michigan inbred No. 1450 and the synthetic variety S-10, from which the hybrid was derived, all showed very little evidence of resistance derived from lack of borer survival. The Michigan hybrid showed a greater number of egg masses naturally deposited on it. This was perhaps due to its greater height. The hybrid also failed to show any greater yield under borer infestation than would normally be expected of it.
Patch and Bottger (1937) gave one of the first lists of resistant inbreds tested under artificial infestation. The six inbreds, Mich. 77, Mich. 2774, Ill. R4, Mich. 106, Iowa L317B2, and Iowa 1205, had significantly fewer borers surviving than were expected on the basis of their time of flowering. The results were based on two-year tests in northern Ohio. The resistance of four of these—Mich. 77, Mich. 106, Iowa L317, and Ill. R4—was confirmed (Patch, Holbert, and Everly 1942), and inbred Wis. CC5 was added to the list as resistant in tests as inbreds and was also classified as transmitting borer resistance to hybrids. The five inbreds listed above had 32 per cent less than the predicted number of borers on the basis of tests in hybrid combination. Inbreds Ill. A, Ill. 90, Ind. WF9, and U.S. 187-2 were classified as susceptible since they
RESISTANCE TO INSECTS IN CORN

averaged 33 per cent more than the predicted number of borers. In an extension circular (Flint et al. 1942) the use of resistant hybrids was recommended and the following inbreds were listed as resistant: Ill. R4, Ill. Hy, Iowa L317, Ohio 40B, Ohio 56 and Wis. CC5. Patch and Everly (1945) reported the following inbreds to be resistant in hybrid combination: Ind. P6, Kans. K230, Iowa L304A, and Mich. 285. Inbreds Kans. K230, Kans. K226, Mich. 285, and Ill. 408 were resistant as inbreds. These strains were in addition to those previously reported and are all lines involving field corn (Figs. 41, 42, and 43).

From tests of 977 inbred lines and strains of sweet corn, Schlossberg and Baker (1948) reported that 44 different inbreds showed some resistance, having from 42 to 2 per cent fewer borers than were predicted for them in tests extending over a period of three or more years. Thirteen of these lines were already in commercial use for hybrid sweet corn. Two of them, Mich. 3116 and Mich. 1826, may have derived their resistance from Maiz Amargo. The inbred lines studied were from the open-pollinated varieties Bantam, Country Gentleman, and Evergreen. Among the resistant inbreds already in commercial use were Minn. 77, Iowa 45, Pur. 14, Iowa 1627, Iowa 1445, Ill. 8, Pur. FR22, Md. H84, Ill. 55, Ill. 13, and Ill. 11. Among the highly resistant inbred lines in experimental use only at the time the tests were run were Pur. W675-1, Iowa 461, Iowa 1434, Wis. 360, Iowa S5316-5, and Iowa S5348-1.

The information referred to above and much other published and unpublished information has been used by corn breeders in the state experiment stations and also by the commercial seed corn companies. Some results of the information on resistant inbred lines have begun to be evident. Stringfield and Pfaff (1947) reported the corn borer leaf injury on 30 different double-cross hybrids grown in Franklin County, Ohio, in 1947. On the basis of scoring from 0 (no injury) to 5 (heavy), the five more resistant hybrids all had a score of less than 1 and all were Ohio Experiment Station hybrids. Some of the reduction in borer population following the first introduction into the states of Ohio, Indiana, and Illinois, in contrast to the more recently and heavily infested areas in Iowa and Missouri, may be the result of the increasing use of a greater number of borer-resistant hybrids.

Some study has been given to sources of tolerance to borer attack. Patch and Bottger (1935) reported that hybrid A x Tr
possessed a degree of tolerance to the borer. Comparative records have been taken on many corn-performance tests on the amount of damage done by borer infestation. In 1945 (Dungan et al. 1946) 71 different entries in an Illinois performance test ranged from 25 to 72 per cent of the plants broken below the ear because of damage by the borer (Figs. 44, 45). Brunson (1948) reported that under heavy populations of the European corn borer, combinations involving the inbred Ind. P8 were noticeably low in stalk breakage. Indiana hybrid 816A, (WF9 x P8), (Hy x L317), (Brunson and Miles 1948) was approved by the Indiana Agricultural Experiment Station for distribution or recommendation to the Indiana farmers in part because of its tolerance to corn borer infestation.

Fig. 44. (Left) Injury of European corn borer to mature corn plants of the hybrid S.D. 101 x (A x M14), Toledo, Ohio, 1946. Note broken leaves and stalks. Compare with lack of injury to the hybrid, Mich. 5191 x (A x M14), Fig. 45. (Courtesy U.S. Dept. Agr., Bur. Ent. and Pl. Quar.)

Fig. 45. (Right) Resistance to European corn borer in mature plants of hybrid Mich. 5191 x (A x M14), Toledo, Ohio, 1946. Compare with severe injury to S.D. 101 x (A x M14), Fig. 44, which was grown in a neighboring row and had a comparable hand infestation. (Courtesy U.S. Dept. Agr., Bur. Ent. and Pl. Quar.)
Many of the commercial and experimental hybrids in current use in the more important corn-growing states have been tested for resistance to the European corn borer. Studies are now being directed toward the addition of resistant genes to otherwise desirable inbreds, the selection for resistance under heavy borer populations in open-pollinated varieties, and from exotic strains of corn (Snelling 1945). A synthetic variety was produced (Wiidakas 1945) by permitting a number of inbred lines carrying resistance to the corn borer to interpollinate. The synthetic variety so produced may be used as a variety or as a source from which new borer-resistant lines may be selected.

Along with the search for sources of resistance to the European corn borer, studies have been made of various characters which might be associated with resistance. A number of these studies have already been discussed in this review. One of the first hybrids which was found to carry considerable resistance was the hybrid Hy x R4. A striking characteristic of this hybrid was the tendency for the upper leaves of the plant to enclose the tassel tightly until it is nearly ready to shed its pollen. This character was thought of as being one which reduced the survival rate of young borers by preventing their easy access to the tassel. It was discussed by Patch and Botter (1935). Pictures are shown contrasting this character with the normal condition of this plant. Rather early, however, (Patch and Botter 1937) other equally resistant strains were found which did not have this character, and doubt was expressed as to whether it was a character necessary for resistance (Huber 1937). More detailed studies of this and related problems by Patch (1943) showed evidence that while the resistant inbreds had definite borer resistance above that contributed by tassel eclosion, its delayed appearance in the case of Hy x R4 seemed to result in the presence of fewer borers in the tassel of that hybrid and, hence, made some contribution to its resistance.

The detailed study of survival, weight, and location of European corn borers feeding on resistant and susceptible field corn by Patch (1943), comparing the hybrids Hy x R4 and A x Tr, showed very definitely that the differentiation in the survival of borers took place during the first four days after hatching and occurred in the whorl of leaves at the top of the plant. There was very little difference between the resistant and susceptible hybrids in the survival of borers at any other time or place. It was pointed out that this
difference in survival was related to the pin-point feeding areas on young leaves of Hy x R4, as compared with the larger feeding areas on the young leaves of the susceptible hybrid A x Tr. These findings agreed with those of Huber (1938), who reported briefly a similar comparison of several susceptible and resistant strains. Both investigators found that borers gained weight more slowly on resistant than on susceptible strains of corn, especially during their early life as larvae. Patch stated that young borers found in the tassel weighed much more than borers of the same age found elsewhere on the plant, evidently indicating that the tassels were more nutritious than other parts of the plant. All evidence so far presented points to the fact that differences between hybrids are established during the early days of larval life and occur in the wet basal area of the partly unfurled leaves. It has also been established “that the presence of pollen in the tassel buds, the axis of the leaves, and similar places after shedding is associated with high rates of larval survival” (Annand 1945). This relationship with respect to pollen appears to be associated with the higher survival of second-generation larvae of the multivoltine strain, which larve hatch nearer the time of pollen shedding. They are thus able to avoid feeding on the leaves which has so far been associated with the difference between resistant and susceptible corn. This difference in survival on resistant and susceptible hybrids at later stages of maturity has been studied in detail by Patch and Deay (1948).

Huber and Stringfield (1940, 1942) have shown a correlation between the resistance of corn leaf aphids (Aphis maidis Fitch) and resistance to European corn borer. While the correlation is not perfect, it does furnish a possible method of classifying breeding material for resistance to both insects when it is grown in the presence of either.

Pepper and Garrison (1941) showed that New Jersey hybrid No. 2 for a three-year period had a low survival of larvae and relatively small injury in comparison with several other hybrids. This hybrid received fewer eggs and also had a lower final borer population when it was hand-infested. New Jersey hybrid No. 2 was superior in this respect to the better known resistant hybrid Hy x R4. A study was made of the hardness of the stem wall of the top internode of plants of several strains of corn. It was found that somewhat higher pressure was required to puncture the stem of hybrid No. 2 than was true in the case of any of six other strains studied.
No evidence was presented, however, that the older larvae which might enter the stems at this point showed lower survival on hybrid No. 2.

The increase in the multiple-generation strain in the central states has brought a change in the biotic environment of the corn borer, oviposition by the second-generation European corn borer occurring near or after the emergence of tassels. This places the young larvae on the plant at a time when the resistance mechanism in the whorl, effective against the single-generation strain, is largely
inoperative (Patch and Deay 1948). Many of the inbreds, re­
sistant to the single-generation strain, therefore appear to be
susceptible to the second generation of the multivoltine stock in
respect to survival of borers. Differential attractiveness of strains
and differences in tolerance still appear to be effective against both
biotypes of the borer. Future studies of resistance to the multi­
voltine strain must involve the search for antibiotic resistance in
parts of the corn plant in addition to the whorl and the combination
of such resistance with non-preference and tolerance. That sources
of such resistance exist is suggested by the results in the area of the
multivoltine stock in New Jersey (Pepper and Garrison 1941) and
elsewhere (Fig. 46). So far only a minute portion of the total corn
germ plasm of the world has been tested for the presence of genes
for resistance to the European corn borer.

RESISTANCE TO THE SOUTHWESTERN
CORN BORER IN CORN

The southwestern corn borer (*Diatraea grandiosella* Dyar),
which moved into the United States from northern Mexico about
1913, was by 1948 distributed through southern Arizona, western
Texas, and most of New Mexico, Oklahoma, and Kansas. This
insect belongs in the same genus as the destructive sugar cane moth
borer (*D. saccharalis* (Fab.)) and is distantly related to the Euro­
pean corn borer. Heavy infestations often result in stunting of
plants or death of the central buds and production of lateral
branches. The characteristic injury is done by the second, or
hibernating, generation of borers. After forming a pupal chamber
at the lower end of the stalk below soil level the larvae often return
and cut a V-shaped notch around the inside of the stalk about
6 inches above the ground level. This results in the lodging of
many stalks, which will occur even if only a single borer is present
per stalk.

Some study has been made by the Oklahoma (Walton and
Bieberdorf 1948) and the Kansas Agricultural Experiment Sta­
tions (Wilbur *et al.* 1950) of the resistance of corn to the south­
western corn borer, but little detailed information is available yet.
Resistance has been measured in terms of percentage of plants in­
fested, percentage of infested stalks with live larvae, percentage of
infested stalks lodged because of the borer, and average number of
borer holes per infested stalk. In the experiments at the Kansas
Station the hybrid K228 x K230 has generally had lower infestation and a higher percentage of infested plants lodged than other strains in the same test. As in the case of the European corn borer earlier maturing strains tend to have somewhat lower infestation by the southwestern corn borer.

RESISTANCE TO CORN ROOTWORMS IN CORN

The species of beetles grouped as corn rootworms *Diabrotica* spp. are considered together here because of the similarity of their injury to corn rather than because strains of corn resistant to one are necessarily resistant to the others. Information on the latter point is scarce. Both the corn rootworm or northern corn rootworm (*D. longicornis* (Say)) and the Colorado corn rootworm (*D. virgifera* Lec.) pass the winter as eggs that have been placed by the female in the soil about the base of corn stalks. They are not known to feed on any other plant except corn and occur in numbers only in fields that have been planted with corn for two or more years. The Colorado corn rootworm occurs in central and western Kansas and in Nebraska, Colorado, and New Mexico. Tate and Bare (1946) reported some difference between hybrids resulting from the differences in ability to replace quickly and adequately the destroyed roots. Details as to hybrids represented were not given. Lonnquist and Kiesselbach (1948), following a study of the Colorado corn rootworm at Lexington, Nebraska, reported that there were two types of heritable resistance: "(1) a tendency to grow new roots in replacement of those that have been injured, and (2) the occurrence of a substance within the plant tissue that is repulsive to the rootworms" (Figs. 47, 48).

*Diabrotica longicornis* appears most abundantly in the northern part of the Mississippi valley. The damage done by this species is similar to that done by the southern corn rootworm (*D. duodecimpunctata* (F.)). The larvae of the two species can be separated with certainty only by microscopic characters, although the adults are very different in appearance. The two species may occur together as larvae in fields where corn has been grown without an intervening crop. However, since corn tests are usually planted on land on which a different crop had been planted the preceding year, most records of rootworm differences among strains of corn refer to damage by *D. duodecimpunctata*. Records definitely connected with *D. longicornis* are not available.
The southern corn rootworm adults pass the winter in the southern part of the United States (Arant 1929). Adults of the next generation migrate northward, appearing in May in the more northern corn-growing states, where one or two generations occur each year. The beetles feed on the corn leaves to some extent but their favorite food consists of parts of flowers of a number of species of plants. If adults are sufficiently abundant, their feeding on the silks of susceptible strains of corn may prevent part of the pollination. The larvae feed on the roots of a number of plants, mostly species of grass and cucurbits. Isely (1929) recorded that, on the plants tested, the larvae grew best on corn, but slower and with a higher mortality rate on cucurbits than on any of the grasses tried. In addition to pruning of the roots, the larvae may drill through the seedling stem, killing the bud and eventually reducing the stand. The larvae of the second generation trim off, or feed on,
the roots and allow the entrance of disease organisms. Lodging near tasseling time follows the loss of the roots. If lodging occurs before flowering, there is a reduction of yield because of faulty pollination. Damage is often more severe on the more fertile soils (Bigger et al. 1938).

Resistance has been measured on the basis of the percentage of plants showing leaf injury and the percentage of plants lodged 30 degrees or more. Differences of the latter kind have been reported between hybrids in the corn performance or other tests of several experiment stations, especially Illinois (Bigger et al. 1938; Copper et al. 1941; Dungan et al. 1934, 1938b, 1939, 1943, 1944, 1945; Huber 1938; Huber et al. 1940).

Bigger, Snelling, and Blanchard (1941) have published detailed records of the differential injury to inbreds and hybrids by the southern corn rootworm. A study was made of injury by the adults at two localities in 1937 and of injury by the larvae during three years at a total of five localities. In the case of the inbreds there appeared to be little correlation between injury by the adults and by the larvae to the strains involved. For example, Iowa 701 had low root and high leaf injury, inbred Ill. 2675 had high root and low leaf injury, Iowa L317 was severely injured in both ways, but inbreds Kans. Kys. and Ill. 5679 were lightly injured by both larvae and adults. Inbred Ind. 38-11 had only 5 per cent of the plants lodged because of rootworm injury compared to 48 per cent for Ill. R4 and Ill. 2675 as an average of 5 tests. However, Ill. R4 and Ind. 38-11 were intermediate in regard to leaf injury. Inbred 38-11 also transmitted to hybrids the ability to prevent lodging as a result of attack by the southern corn rootworm. Less extensive data are presented regarding the differences in resistance to southern corn rootworms among inbreds and hybrids with white grain.

Fennell (1946) reported that varieties resistant to rootworms (Diabrotica spp.) had been obtained from the mountainous region of Chirripo, Costa Rica. One of these, Chirripo 1 showed an especially high level of resistance.

Both tolerance and antibiosis enter into the differences in resistance to rootworm among strains of corn. Bigger (1942) and Bigger and March (1943) reported that larvae of the southern corn rootworm could not be reared to the adult stage on some lines, especially on inbred Ind. 38-11, but were easily reared to maturity on others. The various hybrids and inbreds normally differ greatly
in the size and strength of the root systems. Corn breeders have discarded many strains because of weakness in this respect. Hence the tests reported generally did not involve many strains with small or weak root systems. The differences that did occur in branching and size of root system entered to some extent into the differences in lodging following attack by the rootworms. The tolerance of some strains was shown by their ability to develop new roots above the point of pruning almost as fast as the larvae ate off the roots (Bigger et al. 1938, 1941). This appeared to be the principal factor in the differences found. Some of the resistant strains also resisted rotting of the roots which, in other strains, followed attack of the rootworms.

RESISTANCE TO WHITE GRUBS AND OTHER SCARABAEIDAE IN CORN

The larvae (white grubs) of insects of the family Scarabaeidae, principally those of the genus *Phyllophaga*, are notorious in their destruction of the roots of plants, especially the grasses. The adults feed on the foliage of plants, some using a number of species, others are highly restricted in their diet. Most of the larvae are distinguishable to species only on the basis of microscopic structures, which are often internal. The various species differ also in their life histories and habits. Bigger, Flint, and Shropshire (1939) reported wide differences in lodging caused by white grubs feeding on the roots of corn in a plot of hybrid corn. The hybrid Tr x L317 had an average of about 80 per cent of the stalks lodged while the most resistant hybrid 90 x 4211 had less than 6 per cent of the stalks that were lodged. Other hybrids were intermediate in this respect.

Hoegemeyer (1941), at the Kansas Agricultural Experiment Station, made a study of the differential injury to strains of corn by white grubs (*Phyllophaga* spp., including *P. submucida* (Lec.)). The material used was a replicated experiment designed to study agronomic characters among six inbred lines, their 15 possible single crosses, and 29 of the 45 possible double-cross combinations between them. The lines were derived from Pride of Saline, a white-kerned open-pollinated variety. They had been inbred more than six generations but had not been studied previously for resistance to white grubs. The insect infestation was fairly uniform through-
out the test area, six to eight grubs being found under each stalk of corn.

None of the six inbred lines was significantly different from the rest in injury by the white grubs. Both the single crosses and double crosses showed significant differences in injury. The least injured single cross, K41 x K54, had 20 per cent of the plants lodged; the most severely injured single cross had 87 per cent of the plants lodged. "The single crosses having the least root injury, when combined, gave those double-cross combinations which were least injured, whereas the more severely damaged single crosses in combination gave double crosses which were more severely damaged by white grubs." An examination of the roots of the various strains showed that the difference in the lodging was the result of a difference in the amount of injury done to the brace roots and the feeding roots in the different hybrids. The roots of the inbreds were not visibly damaged by the white grubs.

The Japanese beetle, Popillia japonica Newman, which occurs in the northeastern United States, belongs to the same family of insects as the white grubs and the larvae are quite similar in appearance and habits. These larvae feed to some extent on the roots of corn, but differences between strains of corn in this regard have not been recorded. The adults, however, often feed in numbers on the newly emerged silks of corn. When the silks are cut off before or within six or seven hours after pollination, fertilization is prevented for the most part and a poor set of seed occurs (Coon 1945, Huber et al. 1948). Differences between strains of corn have been reported in connection with variety-time-of-planting plots in New Jersey (Langford et al. 1944). Data on a total of 19 varieties and hybrids are reported for two years but only three open-pollinated varieties are in both tests, all the other strains being different. Wide differences in damage were recorded between planting dates, the earlier dates having the greatest damage by Japanese beetle, but later plantings may be damaged by frost. However, the over-all difference between varieties in percentage of grain lost in 1938 was 25.2 per cent and in 1941, 19.1 per cent. Differences in grain losses up to 9.4 bushels were recorded between varieties differing in mid-silking dates by one day or less. In view of the small number of strains studied such differences deserve study on a wider basis rather than to be dismissed with the statement: "Varietal resistance has not been proved." The further statement
made by the authors that “in the absence of preferred varieties and other preferred food serious damage may result to a variety showing resistance when planted in a mixed series” is totally unsupported by any data presented in this case and has not been true of any other adequately studied case of insect resistance.

RESISTANCE TO CERTAIN STORED-GRAIN INSECTS IN CORN

Among the insects that damage grain in storage several species can begin their destructive feeding before the grain is harvested. Of those damaging corn the rice weevil, *Sitophilus oryza* (L.), and the Angoumois grain moth, *Sitotroga cerealella* (Oliv.), cause especially heavy damage in the southern United States. In that area and in similar climates the rice weevil, either as a larva or as an adult, may pass the winter outside, often in grain in cribs. The adult female chews a small hole in the grain and deposits eggs in the cavity produced. The larvae live within the grain. Infestation may take place in the fall while the ears are still on the stalks or after the grain is harvested. Under favorable conditions the life cycle may be completed in from four to seven weeks. There may be four or more generations a year. Varietal differences in infestation by the rice weevil have been observed for some time and recently have been investigated more systematically.

Hinds (1914), in discussing weevil resistance in corn varieties, reported that infestation depended primarily upon length and tightness of the husk covering on the maturing ear. He noted that the earlier corn got the most weevils where they had an opportunity to reproduce and multiply for a longer period before corn was stored. Among the more promising varieties from the standpoint of weevil resistance in Alabama were Experiment Station Yellow, Whatley’s Prolific, Moyer’s Prolific, Randell’s Brand, and USDA 181. Kyle (1918) studied infestation of rice weevil on 1,949 ears. “Of these 48 per cent were in poor shucks, 28 per cent in good shucks with worm holes, and 25 per cent in good shucks without worm holes.” The “worm holes” had been made by the earworm during their emergence from the ear for pupation. Among the ears without the holes 9 per cent had weevil infestation, and such ears stored in the shucks showed little increase in infestation during storage for ten months. Laboratory study confirmed the fact that the beetles
do not ordinarily cut through the husk to reach the kernels. However, the insect is able to eat the hardest corn, including popcorn.

Kempton (1917) has called attention to a variety of corn from Bolivia, in which the mottled kernels had considerably lower infestation by the Angoumois grain moth than kernels which were of the same color throughout.

Cartwright (1930) in South Carolina studied the relation of husk length to infestation by the rice weevil and associated insects among 22 different varieties for three years. About a third of the ears were infested by rice weevil. Damage by earworm was frequently followed by damage by rice weevil. Ears uninsected by earworm had 13.72 per cent of the ears infested by weevils while earworm-infested ears showed 36.52 per cent with weevil infestation. There was also, in general, an inverse correlation between weevil injury and length of husk. There appeared to be, however, important differences in infestation of varieties that could not be accounted for on the basis of length of husk. Coker's Ellis showed the least number of damaged grains per infested ear in each of the three years it was tested and had the lowest percentage of ears infested for two years and the third lowest the last year of test. It is suggested that this low infestation may be the result of unattractiveness or resistance to the rice weevil. Considerably smaller differences in infestation of different varieties were shown by the pink cornworm, Pyroderces rileyi Wals., and the Angoumois grain moth.

During additional tests in 1935 and 1936 counts of weevil-infested ears in corn varieties were recorded (Cartwright 1936, 1937). In the tests reported for the two years Coker's Ellis and Pee Dee No. 5 were among the lower varieties in percentage of ears infested and Hasting's Prolific and Mosby's Prolific were the most heavily infested by the rice weevil. The infestation by Angoumois grain moth was light, and the ranking of varieties according to infestation by this insect did not parallel the ranking in infestation by the rice weevil.

In the cooperative regional tests of resistance of corn to insects (Blanchard and Snelling 1942) differences between inbred lines in hybrid combinations were recorded. In several of the southern states differences in the percentage of weevil ears have been reported in connection with corn-performance tests. For example, during four years (Hull et al. 1941) data were taken in Florida in
order to record the percentage of weevily ears in the varieties and hybrids tested. Ears infested with weevils were scattered in some of the plots to provide a heavier and more uniform infestation. The maximum weevil resistance, together with somewhat lower yields, occurred in the Cuban Flint varieties. Eckhardt, Douglas, and Hammer (1946) reported on the percentage of weevily ears among varieties and hybrids in most of the corn-performance tests in Mississippi in 1945. The average number of infested ears among 17 strains in all tests ranged from 15 per cent for hybrid La. 502, 16 per cent for hybrid La. 1030 and 22 per cent for Miss. 5111 (= Dixie 11) to 51 per cent for N.C. 1028. The hybrids included those most resistant and most susceptible to weevils; the varieties for the most part were intermediate. There was a slight relationship with length of husk but this character would not explain all the differences for there was only an average difference of 0.1 inch in length between La. 1030, the second on the list, and N.C. 1028, the most susceptible. The hybrid La. 1030 also had a good record for yield and erect stalks at harvest. In a bulletin from North Carolina (Cooke and Moore 1947) the strains of corn recommended for growing by farmers were graded in regard to their performance for various characters, including weevil resistance. In the latter respect the hybrids N.C. 27 (yellow) and Wood S315 (white) had good records. In Georgia (Lebedeff and Brooks 1948) differences in infestation by weevils in varieties and hybrids were reported either on the basis of percentage of ears infested or in three grades. The Georgia hybrids Ga. 7154 and Ga. 7151 and the Florida hybrid Fla. W-1 had good records for resistance to weevils.

A committee from the Southern Corn Improvement Conference recommended (Jenkins 1947) that the following methods should be used for taking data on rice weevil infestation in southern uniform corn tests:

"(1) First determine and record the number of infested and non-infested ears in each plot.

"(2) Next, examine infested ears and grade them on a bulk basis as follows:

"Light (grade 1)—5% or less of the kernels showing weevil emergence holes."
"Medium grade (grade 2)—5% through 25% of the kernels showing emergence holes.  
"Heavy (grade 3)—more than 25% of the kernels showing emergence holes."

There is little published information in regard to the relative importance of factors concerned in resistance to the rice weevil, nor is there any information available regarding infestation of inbred lines. Husk protection certainly is responsible for part of the differences in infestation, especially between open-pollinated varieties. Differences in maturity of the corn also may be reflected in the differences in infestation. There may be additional factors for resistance, consisting either of preference, or antibiosis, or both, which are independent of husk length and maturity. The study of infestation in grain would require careful attention to moisture content of the grain and other environmental factors, for stored-grain insects breed slowly or not at all when the moisture content of their food falls below about 10 per cent. It should be noted that two strains of the rice weevil have been described (Birch 1944; Richards 1945) which differ in preferred host (wheat and corn), ecological relations, size and life history.

Corn has been unique in respect to the number of insects for which considerable information is available regarding differential infestation and damage to varieties, inbreds, and hybrids. Yet it also offers far larger opportunities. Compared with the study of hessian fly resistance in wheat only a small fraction of the available corn germ plasm has been surveyed for genes for insect resistance. There are difficulties in the way of doing this but they are not insurmountable. There have also been no extensive searches for insect resistance by selection within open-pollinated varieties of corn. Studies of both kinds should give more and better genes for resistance than are now known. When that is done, the studies should involve tests on each kind of corn studied, with the major corn pests in nurseries or in laboratory tests designed for the purpose. Genes for resistance, when found, can be incorporated into commercial inbreds by means of genetic techniques, which are better known in corn than in any other field crop. It is particularly fortunate also that more corn breeders are acquainted with insect resistance and its possibilities than are other groups of plant breeders.
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CHAPTER VI
RESISTANCE TO INSECTS IN COTTON

I. Introduction and information about the crop and insects to which resistance has been reported.
   A. Biology and feeding habits of Empoasca spp.
   B. Resistance to Empoasca fascialis (Jac.) (Africa).
   C. Resistance to Empoasca deviata Dst. (India).
   D. Resistance to Empoasca terra-reginae Pauli (Queensland).
   E. Resistance to other species of Empoasca in cotton.
   F. Possible mechanisms of resistance to Empoasca.

II. Resistance to other insects in cotton.
   A. Resistance to thrips (Thysanoptera) in cotton.
   B. Resistance to various species of Hemiptera in cotton.
   C. Resistance to cotton aphid, Aphis gossypii Glov.
   D. Resistance to black scale and white fly.
   E. Resistance to bollworm and other species of Lepidoptera.
   F. Resistance to the boll weevil, Anthonomus grandis Boh.
   G. Resistance to other species of Coleoptera.

IV. Bibliography.

The genus Gossypium, to which cotton belongs, is made up of a number of wild species and four species that have been cultivated by man. The cultivated species and one wild one, G. tomentosum Nutt., differ from the others in having the seeds covered with partly thickened, convoluted lint that can be spun and made into cloth. In the other wild species the seeds may be nearly naked or covered with fully thickened, unconvoluted hairs that cannot be spun. Species in the genus are present mostly in tropical, subtropical, or warm temperate climates in Asia, Africa, Australia, North and South America, and Hawaii and neighboring islands. The cultivated species of the old world, G. herbaceum L. and G. arboreum L., and the wild species of the old world have 13 large chromosomes.
as the number of chromosomes in their gametes, while the wild American cottons have 13 small chromosomes. The American cultivated species, *G. hirsutum* L., and *G. barbadense* L., and the wild species *G. tomentosum*, which have a total of 26 chromosomes (13 small and 13 large), appear to be hybrids between old-world species and wild new-world species. It is considered that *G. arboreum* and *G. raimondii* Ulbrich are the species most nearly related to the progenitor of the cultivated new-world cottons (Hutchinson et al. 1947; Stephens 1947).

The cultivated varieties include both annual and perennial shrub or tree types, but nearly all of the cotton of commerce comes from varieties cultivated as annuals and most of it from the new-world species. The Upland varieties belong to the species *hirsutum*, the Sea Island and Egyptian varieties to the species *barbadense*. Crosses between these two species give vigorous *F₁* plants but many plants in later generations have low viability. The colchicine technique has made possible a more extensive study of the behavior of species crosses (Stephens 1947) and perhaps the utilization of genes from wild species in commercial cottons. The genetics of cotton has been reviewed by Harland (1932) and descriptions and history of American varieties have been studied by Ware (1936).

Cotton in the farmer's field is partly self-pollinated and partly cross-pollinated. Hence improved varieties grown together in one area have been difficult to keep pure of mixture with other types. In some localities provision is made for growing only one variety. In addition to propagation by seed, cotton may be budded, grafted, or grown from cuttings (Harland 1927).

The principal insects injuring cotton have been those that feed on the leaf or on the squares (flower buds) or bolls. In connection with the latter structures studies have been made which show a relationship between the stages of development and susceptibility to various insects (Martin et al. 1923; Dunnam 1926; Rainey 1948). Rainey's paper deals with the changes in the principal chemical constituents of the developing boll and the relation of these changes to varying susceptibility to cotton stainers and several species of bollworms at different periods in the growth of the plant. Observations concerning resistance have been made in connection with a considerable number of cotton insects. The breeding of cotton varieties for resistance to leafhoppers has been carried on successfully in Africa, India, and Australia by selection and hybrid-
zation. No extended attempts have been made to breed for resistance to other insects in cotton, although the observations made often have indicated the possibility of success. Reports of resistance in these cases have concerned varieties. Progeny tests of individual plants apparently resistant to these other insects have rarely been attempted, although this method of selection has been successful in other crops and in cotton for other characteristics. In the United States, little attention has been paid to breeding of insect-resistant cotton varieties.

The insects for which observations on resistance have been made are as follows:

**Thysanoptera** ('Thrips')
- Frankliniella fusca (Hinds) (Tobacco thrips)
- Frankliniella tritici (Fitch) (Flower thrips)
- Frankliniella runneri Morg.
- Sericosthrips variabilis Beach

**Hemiptera**
- Psyllus seriatus (Reut.) (Cotton fleahopper)
- Lygus simoni Reut.
- Dydderaeus spp. (Cotton stainers)

**Hemiptera**
- Empoasca spp. (Leafhoppers or jassids)
- Aphis gossypii Glov. (Cotton aphid)
- Bemisia gossypierda Misra and Lamba (Cotton white fly)
- Saissetia nigra (Nietn.) (Black scale)

**Lepidoptera**
- Pectinophora (or Platyedra) gossypiella (Saund.) (Pink bollworm)
- Solenia derogata (Fab.) (cotton leafroller)
- Holothrix armigera (Hbn.) (or Chloridea obsOLEcta Fab.) (Cotton bollworm (or corn earworm))
- Diparopsis castanea Hmps. (Red or Sudan bollworm)
- Earias insulana Boield. (and other species) (Egyptian or spiny bollworm)

Dahms (1943) has reviewed some of the more important literature on insect resistance in cotton.

**RESISTANCE TO LEAFHOPPERS, OR "JASSIDS"** *(EMPOASCA SPP.), IN COTTON*

The genus *Empoasca*, species of which occur on all continents, includes many insects that are injurious to crops. Some of the general features of the biology and feeding habits of species of this
INSECT RESISTANCE IN CROP PLANTS

genus, especially *E. fabae* Harris, are discussed in connection with the resistance of potatoes to leafhoppers. From the information given there a few points merit special emphasis. The different species of *Empoasca* often are distinguishable only on the basis of the internal male genitalia. Species differentiated in that manner sometimes differ in biology, in host plants, in feeding habits, and in the character of the injury done to their host. The red and yellow coloration of leaves and some other characteristic injuries of *E. fabae* result from changes in the photosynthetic following interruption or stoppages of the vascular tissue, which result from insect feeding. Resistance to *Empoasca fabae* in *Solanum* results from preference, antibiosis, and tolerance, the exact combination of the three factors depending on the plant variety or species concerned. Hairiness is not of concern in the resistance of potatoes to *E. fabae*, but appears to be a part of the resistance of soybeans and of some other legumes to this insect (Johnson and Hollowell 1935). The use of DDT on potatoes and on legumes for the control of leafhoppers has shown that *Empoasca fabae* did far more damage to these crops than previously supposed. The resistance to leafhoppers present in the potato variety Sequoia has given nearly as much protection from the insect as has the use of insecticides. On cotton, *E. fabae* causes only slight injury, even when abundant. It was necessary to cage a considerable number of individuals for some time on cotton before leaf malformation developed (Watts 1935).

The information Husain and Lal (1940) have supplied concerning the species of *Empoasca* reported to infest the cotton plant is reproduced in the accompanying table (Table 12). Abbas and Afzal (1944) have added one additional species, *E. minor* Pruthi, which was collected in numbers on cotton in the Punjab. Wells (1943) has reported *E. maculata* as damaging cotton in Queensland. The differing economic status of what are reported to be the same species in various localities may have occurred because of the difficulty of exact identification, especially before the discovery of the importance of the internal male genitalia. The three species that have caused the most trouble on cotton and for which resistance has been reported are *E. fascialis* (Jac.) in Africa, *E. devastans* Dist. in the subcontinent of India, and *E. terra-reginae* Paoli in Australia. Breeding for leafhopper resistance has been successful on all three continents. In these areas careful population studies involving examination of the male genitalia of *Empoasca* have been
<table>
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<tr>
<th>Species</th>
<th>Locality</th>
<th>Economic status</th>
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<td>Italian Somaliland</td>
<td>injurious</td>
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<td><em>E. formosana</em> Paoli</td>
<td>Madras</td>
<td>not injurious</td>
</tr>
<tr>
<td><em>E. devastans</em> Dist.</td>
<td>Punjab</td>
<td>very injurious</td>
</tr>
<tr>
<td></td>
<td>N.W.F.P.</td>
<td>not injurious</td>
</tr>
<tr>
<td></td>
<td>Sind</td>
<td>very injurious</td>
</tr>
<tr>
<td></td>
<td>Bombay</td>
<td>not injurious</td>
</tr>
<tr>
<td></td>
<td>Madras</td>
<td>very injurious</td>
</tr>
<tr>
<td></td>
<td>Mysore</td>
<td>not injurious</td>
</tr>
<tr>
<td></td>
<td>Hyderabad-Deccan</td>
<td>not injurious</td>
</tr>
<tr>
<td></td>
<td>Central Provinces</td>
<td>not injurious</td>
</tr>
<tr>
<td></td>
<td>United Provinces</td>
<td>not injurious</td>
</tr>
<tr>
<td></td>
<td>Bihar</td>
<td>not injurious</td>
</tr>
<tr>
<td></td>
<td>Delhi</td>
<td>not injurious</td>
</tr>
<tr>
<td></td>
<td>Punjab</td>
<td>not injurious</td>
</tr>
<tr>
<td><em>E. punjabensis</em> Pruthi</td>
<td>Sind</td>
<td>not injurious</td>
</tr>
<tr>
<td><em>E. kerri</em> var. <em>moti</em> Pruthi</td>
<td>Fiji</td>
<td>injurious</td>
</tr>
<tr>
<td><em>Empoasca</em> sp.</td>
<td>Papua</td>
<td>injurious</td>
</tr>
</tbody>
</table>
reported only for the Punjab (Abbas and Afzal 1945). Har­
greaves (1936) reported that in 1934 in Uganda three species of
Empoasca were present on cotton and that E. benedottoi Paoli was
the most abundant. An average of more than 17 nymphs per 10
leaves caused little damage.

**Resistance to Empoasca fascialis (Jac.) in Africa.** The breeding
of cotton varieties resistant to leafhoppers (jassids) has been suc­
cessful particularly in South Africa, where since early in the project
the work has been under the direction of F. R. Parnell. The first
widespread severe outbreak of Empoasca fascialis occurred in the
Union of South Africa in 1922–23. In the years which immediately
followed, the yield of cotton in most parts of the eastern Transvaal
low veld was reduced at least by 25 per cent (Worrall 1923, 1925).
The breeding of suitable resistant types was so successful that this
leafhopper is no longer considered a pest of importance to the com­
cmercial crop. It is reported that the “present strain grown com­
mercially, U.4/5143, does not go through the season entirely
free from all damage to the leaf, but the crop is never affected to
an appreciable extent.” (Parnell et al. 1949.) In recent years
the problem has been to retain and increase the leafhopper resistance
of cotton varieties being improved for other characters.

Empoasca fascialis is an active greenish leafhopper about 4
millimeters in length that normally lives on the lower surface of the
cotton leaves about the base of the principal veins. Several food
plants as well as cotton have been reported as affected, including
castor-oil plant, okra (Hibiscus esculentus), and Bombax ceiba
(Vuillet 1924). Parnell (1927) reports that E. fascialis, toge­
ther with one other species, in each case were collected on groundnuts
and on Tepary beans near Barberton, South Africa. The time
required for life from egg to adult is usually from 20 to 30 days,
depending on the location and time of year (Vuillet 1924; Parnell
1927). Eggs are laid in the thick veins of the leaf and in the petiole
and soft parts of the stem (Moerdyk 1927). Sometimes the
damage done by the leafhopper has been thought to be the result
of a disease organism but studies by a number of investigators have
shown that it is probably caused by the toxic action of the saliva
(Parnell 1927; Moerdyk 1927; Peat 1928; Russo 1931). The
feeding of relatively few of the leafhoppers, especially the nymphs,
causes the edges of the leaves to turn yellow, then red; later the
whole of the leaf turns red; finally it dries up but is shed only slowly.
Parnell reported that by the time the general reddening is clearly evident, up to seven or eight nymphs per leaf may be found on susceptible cotton. Nymphs were caged in glass rings ¾ inch in diameter on leaves of cotton. He reported that “six nymphs in one or two days produced a very definite yellow circle on the leaf, the time taken varying with the temperature, which presumably affected the feeding, and with the variety of cotton.” Moerdyk found extreme stunting following leafhopper attack, and most reports indicated a considerable reduction in yield following leafhopper injury. Gaddum (1942) in Kenya, working with a leafhopper identified as *E. fascialis*, did not secure a reduction in yield following infestation in cage tests. The injury was normally most severe as the cotton neared maturity. Any factor such as drought or water-logged soil that decreased the vigor of the plant increased susceptibility to the leafhopper (Parnell 1927). Detailed information is not available on the exact method of feeding of the insect. Peat (1928), however, has studied histologically the effects of the feeding on plant tissue. He found discoloration along the course of the minor vascular bundles and also in sections through the bigger bundles in the area on which insects had been confined. The injury did not spread far from the site of the feeding. The first reports concerning differences among varieties in regard to injury by *Empoasca fascialis* were given by Worrall (1923). The Sea Island varieties and Pima, an Egyptian variety (*G. barbadense*), were the most severely and also the first to be injured. The American Upland cotton varieties (*G. hirsutum*) were less injured but varied considerably in injury both between varieties and among individual plants in a variety. These individual resistant plants were the basis of most of the early breeding for jassid-resistant cotton. Of the upland varieties, all plants of Watt’s Long Staple and Meade were susceptible, the latter variety being slightly less so. Improved Bancroft, a commonly grown South African variety, included a considerable number of resistant plants, but Zululand hybrid had more resistant types than any variety under observation in 1923. Without exception the resistant types were more hairy than the susceptible ones. Worrall (1925) reported the receipt of Selection No. 295 of the Cambadia variety (*G. hirsutum*) from Mr. Hilson, cotton specialist, Coimbatore, India. In his tests this selection appeared practically immune and Worrall’s photographs show plants of the variety large and flourishing among stunted
INSECT RESISTANCE IN CROP PLANTS

plants of other varieties. The selection was extremely hairy and free from immature leafhoppers. Parnell (1927) reported that it was possible to find nymphs on Cambodia only occasionally.

Parnell (1925) reported on the beginning of the breeding for resistance to this insect in South Africa. In the first test, seed from a few plant selections made earlier were included along with commonly grown varieties and importations from India and from the United States. Parnell has given the classification of plants of seven varieties in the several degrees of damage done by jassids. These are recorded in Table 13. The selection Z.1 from a single plant, picked out the preceding year from Zululand hybrid, gave the most resistant progeny of any available at the time. Parnell (1925) reported that "all resistant plants are distinctly hairy, though all hairy plants are not necessarily highly resistant." He decided to concentrate entirely on single-plant selections and that year (1925) made the single-plant selection that became the basis for the jassid-resistant varieties grown in South Africa since 1929 (Parnell 1925, 1926, 1935). This plant, called U.4, was grown in a progeny row of 230 plants in 1926, a special bulk on one acre in 1928, and small plots on a few farms in 1928. In 1929 over 200 tons of seed were raised in large plots on many farms and in the following years U.4 replaced all other varieties in the low veld and was distributed in other areas. The photographs reproduced in Parnell's report (1928) contrast vividly the difference at harvest time between plots

Table 13  THE PROPORTION OF PLANTS OF 7 VARIETIES OF COTTON CLASSIFIED IN FIVE DEGREES OF INJURY

<table>
<thead>
<tr>
<th>Variety</th>
<th>Percentage of plants showing degree of injury indicated</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cambodia</td>
<td>nil slight moderate rather bad bad</td>
</tr>
<tr>
<td>Z.1</td>
<td>100  —  —  —  —</td>
</tr>
<tr>
<td>Uganda</td>
<td>4  60  36  —  —</td>
</tr>
<tr>
<td>Improved Bancroft</td>
<td>3  8  27  32  40</td>
</tr>
<tr>
<td>Zululand Hybrid</td>
<td>—  2  14  38  46</td>
</tr>
<tr>
<td>Griffin</td>
<td>—  —  2  27  71</td>
</tr>
<tr>
<td>Watt's Long Staple</td>
<td>—  —  —  —  100</td>
</tr>
</tbody>
</table>

(After Parnell 1925)
Fig. 49. One of the early plots of U4 cotton grown in the presence of the leafhopper, *Empoasca fascialis* (Jac.), South Africa, 1926-27. The cotton shows normal development. (Parnell 1928, plate 4.) (Courtesy Empire Cotton Growing Corporation.)

Fig. 50. Plot of a commercial cotton variety, susceptible to and severely injured by *Empoasca fascialis* (Jac.), South Africa, 1926-27. The plot was grown near that of U4 illustrated in Fig. 49. (Parnell 1928, plate 8.) (Courtesy Empire Cotton Growing Corporation.)
of U.4 and other currently grown commercial varieties (Figs. 49, 50).

The selection U.4 was picked out of a variety, Uganda (G. hirsutum), which probably came originally from a place of that name but as grown in South Africa was badly mixed. Parnell (1935) gave a table, which is copied here and shows the yield in comparison with local varieties (Table 14).

Table 14 THE TWO-YEAR MEAN (1927-29) YIELD OF U.4 COMPARED WITH LOCAL ADAPTED SOUTH AFRICAN COTTON VARIETIES

<table>
<thead>
<tr>
<th>Locality</th>
<th>Pounds of seed cotton per acre</th>
<th>Local variety in same test</th>
<th>Name of local variety</th>
</tr>
</thead>
<tbody>
<tr>
<td>Barberton, East Transvaal</td>
<td>921</td>
<td>319</td>
<td>Improved Bancroft</td>
</tr>
<tr>
<td>Bremerdorp, Swaziland</td>
<td>1,741</td>
<td>506</td>
<td>Uganda</td>
</tr>
<tr>
<td>Margut, Zululand</td>
<td>842</td>
<td>526</td>
<td>Zululand Hybrid</td>
</tr>
</tbody>
</table>

The early record of U.4 was so outstanding that it was necessary to explain to South African farmers that in the early stages of distribution small lots of seed were issued to only 60 farmers in order to spread the risk of loss and get the maximum yield (Cameron 1928). Evidently many farmers had written in, asking for seed. Two years later Peat (1930) reported that in Southern Rhodesia jassids had become less numerous, perhaps owing to the planting of resistant varieties.

While U.4 made possible at that time the growing of cotton profitably where, because of the leafhoppers, it would rarely have been profitable earlier, the length of staple of the selection was shorter than desirable. Selections and crosses were made for the purpose of increasing the level of resistance and improving the quality of the cotton. Brief reports of the cotton breeding and additional information are recorded in the annual progress reports of the Experiment Stations of the Empire Cotton Growing Corporation, London, England.

Considerable improvement was secured by selection within the original U.4 bulk. These improved selections were distributed to
farmers after such selections had demonstrated their value in variety tests. In such a test in 1939–1940 it was reported that the selection U.4/4/052 yielded 18 per cent more pounds of lint per acre than the original U.4 bulk. This selection had been put into general cultivation in 1935–36 (MacDonald, Fielding, and Ruston 1941). The reselection U.4/052/5143, which in the same test yielded 46 per cent more than U.4, was put into general cultivation in 1939–40.

These U.4 selections appear to have considerable tolerance as well as generally lower populations of leafhoppers. In a location and a season when the population was particularly heavy the number of nymphs by March "reached the unprecedented figure of 8 nymphs per leaf (compared with the previous heaviest infestation recorded on U.4 strains of around 3 nymphs per leaf in 1932 and 1930)." Under these conditions some injury and fairly heavy leaf shedding took place but the yield was about 300 pounds of seed cotton per acre compared with about 4 pounds per acre from Bancroft, a susceptible variety (McKinstry and Prentice 1937).

In the hybridization program to increase the hairiness, or the lint quality, or both, various crosses were made, including those between strains of U.4 and Cambodia, Sea Island, and M.U.8. The last was an extremely hairy strain of upland type from India. A cross between Cambodia (resistant) and Watt's Long Staple (susceptible) was made in the 1924–25 season. The F1 grown the following season was only slightly less resistant and less hairy than the Cambodia parent. One of the first available pictures showing inheritance of resistance to an insect is given in this report (Parnell 1927) (Fig. 51). These hybrids were grown under heavy infestation by Empoasca and selections made on the basis of injury, hairiness, and to some extent nymphal populations. In the F2 of one cross between U.4 and Sea Island cottons it was reported (Parnell and MacDonald 1943) that two-thirds of the plants were classified as rather badly damaged or worse and less than 10 per cent as showing slight or no damage. In some crosses difficulty was experienced in combining high-quality lint with a high degree of hairiness but in others the combination was successfully made. The cross with Cambodia produced some desirable types, one of which, A 2106, from the cross U.4/5143 x Cambodia, was increased for further tests and distribution to farmers. This strain was highly resistant, being decidedly more hairy than the U.4 strains, and also had high yields for several years (Parnell et al. 1945; MacDonald et al. 1946,
1947). The hybrids selected at the Barberton, South Africa, station were tested at other experiment stations under direction of the Empire Cotton Growing Corporation and their performance reported in various annual reports. At some of these stations and elsewhere (Miller 1945) selection and hybridization were carried on in breeding for resistance to leafhoppers as well as to other insects.

In the Anglo-Egyptian Sudan, an attempt was made to transfer hairiness to the Egyptian varieties (G. barbadense) from G. hirsutum, tomentosum, anomalum, and arboreum by a program of interspecific hybridization and backcrossing (Knight 1946).

Resistance to Empoasca devastans Dist. (India). The leafhopper Empoasca devastans is rather widely distributed in the cotton-growing regions of the Indian Union and Pakistan. According to Hussain and Lai (1940) different degrees of injury are caused by this insect in different areas. According to these authors, as many as eleven generations occur each year, with considerable overlap.
ping. Each generation lasts from 15 to 46 days, depending on the time of year. Eggs are laid in the leaf veins and hatch in from 4 to 11 days. The average number of eggs laid by caged females is 15 and mated females live from 5 to 7 weeks. The nymphs feed near the bases of the leaves at first, but older ones feed over the whole of the lower leaf surface. A number of alternate hosts are used at different times of the year. These include, at Lyallpur, hollyhock (*Althaea rosea*), castor bean (*Ricinus communis*), eggplant (*Solanum melongena*), potato (*Solanum tuberosum*), okra (*Hibiscus esculentus*), *Hibiscus vitifolius*, and, at Delhi, *Hibiscus cannabinus* and various cucurbits (Husain and Lal 1940). Abbas and Afzal (1945) found that only a few adults were produced by nymphs of *E. devastans* when reared on guara (*Cyamopsis psoralioides*) and no nymphs hatched from adults caged on this plant. On the other hand, normal development and hatching of nymphs occurred on cotton. Adults of *Emoasca kerri* produced many nymphs when caged on guara and few when caged on cotton. However, first-instar nymphs of *E. kerri* produced about as many adults when reared on cotton as on guara. Both species of *Emoasca* were collected on cotton.

The effect of the feeding of *E. devastans* on cotton appears to be very similar to the injury described as caused by *E. fascialis*. The nymphal population of *devastans* increased on plants up to an age of 30 to 45 days, depending on the variety, and then the number of nymphs decreased (Ghani, Afzal, and Nanda 1945). This was true also of the populations on plants as measured in several ways (Verma and Afzal 1940). In this respect *devastans* appears to differ from *fascialis*. Parnell et al. (1949) called attention to a difference in the behavior of the nymphs of the two species in respect to the ease with which they might be counted. Afzal, Rajaraman, and Abbas (1943) maintained populations of from 200 to 300 nymphs per cage on plants of susceptible and resistant varieties of cotton. Under these cage conditions there were significant reductions in plant growth, number of flowers, number of bolls, and weight of seed cotton in the susceptible variety (38 F) compared with the uninfested controls of the same variety. The various qualities of the lint were also affected adversely and, significantly, in the susceptible variety. In the resistant variety 289 F/43 yield was not affected and quality was even slightly higher in the cotton from the plants caged with the leafhoppers. Thus this Indian
variety shows definite tolerance to attack. Cotton planted early was generally less injured and carried a lower leafhopper population than cotton planted later (Husain and Lal 1940; Afzal 1941). Yield also decreased with later sowing. The population increased with the increase in the amount of water applied to the crop. The population per plant tends to be higher in more widely spaced plots (Afzal and Ghani 1949).

The injury caused by leafhoppers to cotton was mentioned by entomologists rather early (Lefroy 1906; Roberts 1915). The first selection of cotton for resistance was made beginning about 1913 against “red leaf blight,” which was thought to be a disease but apparently was the injury caused by Empoasca (Kottur 1922). It was noted that hairy plants in the Dharwar-American cotton were resistant. Selections were made and the strain maintained by mass selection. The Dharwar-American cotton came from seed imported into that part of India from New Orleans and from Georgia in 1819. It was well adapted to a definite area but when selection began, the cotton grown was found to be badly mixed for leaf hairiness, lint quality, and ginning percentage. The selected strain was known as Gadag I and for six years, 1915–20, had a yield of 159 pounds of lint per acre and a ginning percentage of 36 per cent, compared with 121 pounds and 29.3 per cent for Dharwar-American. A considerable premium was paid by merchants and mill owners for the cotton produced from Gadag I. Later Kottur and Maralihalli (1931) mentioned that “red leaf blight” was associated with leafhoppers and that Gadag I continued to be resistant. Such hairy types of cotton, however, were attacked by thrips.

Apparently some selection and breeding for resistance to leafhoppers was done at various other places and times in India, but about 1937 the Indian Central Cotton Committee began a more coordinated project on this subject with the breeding for resistant varieties to be done particularly at Lyallpur. The native “Desi” cottons (G. arboreum) are immune or highly resistant to the jassids and the upland varieties differ in their susceptibility, the less susceptible ones being those commonly grown in the Punjab. Detailed records of relative populations of several of these varieties are given by Verma and Afzal (1940) and typical data are reproduced in the accompanying table (Table 15). Records taken by counting the number of nymphs on a comparable number of plants or by fumigating the plants and counting the total numbers of nymphs
Table 15 RELATION OF LEAFHOPPERS TO COTTON VARIETIES IN THE PUNJAB

(Adapted from Verma and Afzal 1940)

<table>
<thead>
<tr>
<th>Varieties</th>
<th>Number of leafhopper adults collected by sweeping</th>
<th>Average number of eggs laid per female</th>
<th>Percentage of nymphs reaching adult stage</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1937</td>
<td>1938</td>
<td>1937</td>
</tr>
<tr>
<td>Gossypium arboreum</td>
<td></td>
<td></td>
<td>1.4</td>
</tr>
<tr>
<td>39 Mollisoni</td>
<td>10.60 ± 2.60</td>
<td>1.7</td>
<td>1.2</td>
</tr>
<tr>
<td>Jubilee Cotton</td>
<td></td>
<td></td>
<td>6.6</td>
</tr>
<tr>
<td>Gossypium hirsutum</td>
<td></td>
<td></td>
<td>6.6</td>
</tr>
<tr>
<td>L.S.S.</td>
<td>247.6 ± 69.5</td>
<td>15.25 ± 3.14</td>
<td>7.05</td>
</tr>
<tr>
<td>4 F</td>
<td>288.4 ± 80.0</td>
<td>20.80 ± 4.44</td>
<td>6.6</td>
</tr>
<tr>
<td>289 F/43</td>
<td>307.7 ± 80.2</td>
<td>21.85 ± 4.40</td>
<td>—</td>
</tr>
<tr>
<td>100 F</td>
<td>341.9 ± 87.5</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>38 F</td>
<td>557.1 ± 144.0</td>
<td>104.90 ± 18.27</td>
<td>—</td>
</tr>
<tr>
<td>289 F/K25</td>
<td></td>
<td></td>
<td>6.6</td>
</tr>
</tbody>
</table>

and adults gave strikingly similar results. These authors also report on the nymphal development and oviposition on the several varieties as indicated in the table. Verma and Afzal (1940) and Husain and Lal (1940) report very little difference in the percentage of nymphs reaching the adult stage, although records given by the latter authors show that development required slightly longer on resistant varieties. Both groups of workers found that fewer eggs were laid and correspondingly fewer nymphs removed from resistant than from susceptible varieties.

It is reported (Husain and Lal 1940, Afzal 1941) that several introductions of U.4, the variety which was resistant to *E. fascialis* in South Africa, were susceptible to *E. devastans* in the Punjab and Madras although the plants were "profusely hairy." Cambodia cotton from Madras was highly resistant in the Punjab but apparently less resistant than it had been in Madras and in South Africa.

A number of crosses has been made for the improvement of the quality of the lint and degree of resistance in adapted varieties of cotton. Information on these crosses are given in some of the an-
nual reports of the Indian Central Cotton Committee. Some of these have been crosses between adapted strains of upland. In the cross 920 Cambodia (resistant) x 58 F (susceptible) resistance was dominant in F₁ and the F₂ plants were classified as 43 resistant and 17 susceptible, which appears to show that resistance to *E. devastans* in this cross was governed by a single genetic factor (Afzal 1941). The analysis of the F₂ was made during a year of heavy jassid infestation. In the same year analyses of a series of crosses involving resistance from several sources showed that while most hairy plants were resistant, some of the hairy segregates were susceptible and an appreciable number of the sparsely hairy plants were resistant to *Empoasca devastans* in the Punjab. Among 877 plants studied, 110 were classified as sparsely hairy and resistant and 25 as hairy but susceptible. Both these groups represent combinations different from the parental varieties and contrary to the usual situation in South Africa in respect to leafhopper resistance and hairiness in cotton. This confirms earlier reports by Lal (1937) and Husain and Lal (1940). In a study of 45 segregates from another group of crosses one was found that was susceptible to leafhoppers despite having a mean of more than 140 hairs per centimeter on the leaves. It should be recorded that “in the Punjab 4 F₁, S.S., and 289 F₂/43 are markedly resistant varieties and cover extensive areas in localities where jassids are a serious menace.” (Afzal and Abbas 1944.) The crosses are being made for increasing the leafhopper resistance and improving the quality of these cottons.

**Resistance to *Empoasca terra-reginae* Paoli (Queensland).** There appears to be more than one species of *Empoasca* on cotton in Queensland although *E. terra-reginae* is the described species according to Sloan (1938). Another species mentioned as causing damage to cotton was *E. maculata* (Wells 1943). The damage appears similar to that described as done by *E. fascialis* and *E. devastans*. Details on the life history and distribution of the species of *Empoasca* involved do not appear to be available.

At the Empire Cotton Growing Corporation Experiment Station in Queensland breeding for leafhopper resistance began about 1937 (Peters 1940). Cottons had been imported from South Africa and elsewhere in a search for resistant types. The variety Miller (*G. hirsutum*) was the least susceptible of the adapted varieties grown in the area but its resistance was “only about 30 per
The variety Ferguson from Trinidad was reported to be immune (Wells 1943). Individual plants in the variety Miller that appeared to be resistant were selected in 1938–39 (Peters 1940). Some of these were carried in mass selection as Miller 41 J, which strain showed about 20 per cent increase in resistance over that of the parent variety (Marriott 1943). This strain, Miller 41 J, was released to farmers in about 1943 and the progeny of an individual plant selection, Miller III-26, increased for distribution (Wells 1944a). This selection was higher yielding and more uniform in quality than the original variety from which it was bred.

Meanwhile crosses were made between high quality-strains of upland cotton and leafhopper-resistant varieties, such as U.4 and Ferguson. The F1 plants of the cross Miller x U.4 were practically as resistant as the U.4 parent (Peters 1940; Marriott 1943). Backcrosses to Miller were used to combine desirable characters from that adapted variety with leafhopper resistance from the non-recurrent parent. It was reported that while resistant plants were generally hairy “not all hairy plants were resistant” (Marriott 1943). However, when populations of leafhoppers were low the characters of hairiness was used in selecting resistant plants. It was reported that the length and density of hairs were adversely affected by dry conditions (Wells 1948). Selections of considerable commercial promise have been secured and tested under various soil and climatic conditions. Short reports on the progress of this program for breeding leafhopper-resistant cotton varieties for Australia are given in the annual reports of the Department of Agriculture and Stock of Queensland as well as in other progress reports from the Experiment Stations of the Empire Cotton Growing Corporation there.

**Resistance to other species of *Empoasca* in cotton.** Scattered reports of injury and of resistance to leafhoppers have been noted in various publications. In Fiji some selections of New Guinea Kidney cottons appeared to be fairly jassid-resistant (Anson 1928). The species of leafhopper was undetermined. In connection with a study of the biology of *Empoasca bigutulla* Mats. in Formosa mention is made that varieties with hairy leaves were less injured than others (Anon. 1938). There are at least two reports from Java (Dekker 1938; Franssen and Muller 1938) connecting resistance
to *Empoasca* spp. with the hairiness of leaf of Cambodia and other types of cotton. In Thailand it is reported that leafhoppers did more damage to American varieties than to Cambodian varieties (Jotisalkara 1938).

**Possible mechanisms of resistance to *Empoasca* in cotton.** Repeatedly and from the very first literature on the subject, resistance to leafhoppers in cotton has been found to be correlated with hairiness of the plant and particularly of the leaves. There has also been rather frequent evidence that not all hairy plants were resistant. This has been true in an early report from Africa (Parnell 1925), in Queensland (Marriott 1943) and particularly in India (Lal 1937; Husain and Lal 1940; Afzal 1941; Afzal and Abbas 1944; Lal and Husain 1945). Parnell et al. (1944) presented a scatter diagram showing the relationship between hair length, hair density per square millimeter, and the number of nymphs per 10 leaves for 72 plants from the F_2 generation of crosses between U.4 (*G. hirsutum*) and Sea Island and Egyptian cottons (*G. barbadense*). One plant with hair length of about 0.7 millimeter falls in the class having 54 to 95 nymphs. There were only 4 plants with longer hairs, all having 0 to 5 nymphs. One of the plants with a density of about 26 hairs per square millimeter had over 150 nymphs and another with about 25 hairs per square millimeter was in the class of plants having 96 to 149 nymphs. There were only two plants with greater density and these both were in the class having 24 to 53 nymphs. These individual plants at the two extremes appear to indicate that there was no causal relation between either hair length or density and number of nymphs. Both length and density were considered in the selection for resistance by means of the hairiness character.

As has been recorded above, U.4 is resistant to *E. fascialis* in Africa but susceptible to *E. devastans* in the Punjab, while retaining a measure of hairiness in both places. In common with cases of resistance in other crops and insects it is not surprising to find a plant variety resistant to one species of insect but susceptible to another closely related one. This difference in insect species involved probably is responsible for most of the differences in results in regard to hairiness and resistance in the two areas. Another possible source of some of the differences in the results is the complex genetic bases which hairiness and probably also resistance have. Hairiness is also complex morphologically, involving not only length...
# HAIRS AND JASSIDS

## HIRSUTUM STRAIN TRIAL

<table>
<thead>
<tr>
<th>Strain</th>
<th>Jassids per 1,000 Leaves</th>
</tr>
</thead>
<tbody>
<tr>
<td>M.U. 8</td>
<td>3</td>
</tr>
<tr>
<td>A. 2106</td>
<td>32</td>
</tr>
<tr>
<td>U. 4</td>
<td>137</td>
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<tr>
<td>5143</td>
<td>462</td>
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<tr>
<td>B.P. 52 L.H.</td>
<td>1,409</td>
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<tr>
<td>MEADE</td>
<td>2,586</td>
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<tr>
<td>COKER WILDS</td>
<td></td>
</tr>
</tbody>
</table>

![Scale](image)

**Fig. 52.** Six typical strips from leaf blades of different varieties of cotton showing character of hairiness. *Right,* typical numbers of leafhopper nymphs, *Empoasca fascialis* (Jac.). *Below,* a nymph photographed to the same scale. (After Parnell et al. 1945.) (Courtesy Empire Cotton Growing Corporation.)

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and density but also the groupings and the angles which the hairs make with the surface of the leaf. Methods of recording the hairs have differed.

In South Africa the association of resistance and hairiness has been studied in detail in respect to varieties and single plants of *G. hirsutum* and *G. barbadense*, and plants from interspecific crosses between these species (Parnell et al. 1944; 1945; 1949; MacDonald et al. 1946, 1947). A method was devised of cutting and photographing sections of a leaf so that hair length and density could be determined accurately (Fig. 52). Resistance was determined on the basis of injury and numbers of nymphs. Injury, when near the maximum, was recorded for each plot in ten grades from “0” for “no visible symptoms” to “9” for “very bad damage—plant leafless.” In the 1943-44 season varieties scored in this way ranged from 0 for M.U.8. to 7.50 for Tidewater. The number of nymphs was counted at eight weekly intervals on four or five leaves per plant and five plants per plot. The geometric means of the totals of the plot counts of each variety were used and calculated to a basis of the number of nymphs per 1,000 leaves. On such a basis the number of nymphs per 1,000 leaves in 1943-44 ranged from 3 for M.U.8. to 3,838 for Acala and in 1944-45 from 0 to 6,942 for the same two varieties. The correlations calculated between the numbers of nymphs and the numbers of hairs exceeding 0.3 millimeter in height were \( r = -0.926 \) for 1943-44 and \( r = -0.987 \) for 1944-45. Parnell and his associates have brought together a considerable amount of data, all of which showed a high correlation between hairiness and resistance to *E. fascalis* at Barberton, South Africa. They consider that “the evidence points emphatically to a simple relationship of direct cause and effect and not to a genetic linkage between hairiness and some other factor conferring resistance.” Four lines of evidence were given in support of this conclusion: (1) There was a consistent negative correlation through diverse plant material between average hairiness and resistance. (2) Although a considerable number of genes is known to be involved in the inheritance of hairiness, the association between hairiness and resistance occurred irrespective of the origin or genetic diversity of the plant material; that is, the relationship is with hairs of a certain length and number and not with particular genes for hairiness. (3) The non-hairy foliage of resistant seedlings was susceptible to leafhoppers until hairiness developed. (4) In
more mature plants both resistance and hairiness decreased with the expanding leaf, especially in moderately resistant strains.

Both length and density of hairs are required for resistance. For moderate resistance a density of 60 hairs 0.5 millimeter long is required and for high resistance over 150 hairs 0.5 millimeter long are needed. Evidence is presented that it is necessary to take midrib hairiness into consideration in certain cases but that relative hairiness of the petiole and stem may be ignored.

While the association between hairiness and resistance to *Empoasca fasciata* appears well established in cotton, little evidence is available concerning the way in which hairiness affects the leafhopper so vitally. The association involved appears to be one of preference of the adult for glabrous leaves or lack of preference for hairy ones. It may be a non-preference requiring contact of the adult with the hairs. Peat (1928) reported that nymphs placed on the hairy Cambodia leaves "showed signs of discomfort, and were not so active as on the leaves of less hairy plants." Apparently, no studies of the behavior of adults have been made, although it is reported that eggs have been laid on both resistant and susceptible strains. The females appear to be attracted from a distance, which if true, may indicate differences in attraction by differences in reflection of light from the hairy and less hairy leaves as a possible mechanism of preference.

Parnell (1927) reports field observations indicating differences in the tolerance of strains to attack of the leafhopper. By placing a few nymphs in small cages on comparable leaves of different varieties and noting the discoloration caused, it was found that the amount of injury differed between the strains. Cambodia appeared to show considerable tolerance in such tests. Some of the genes for tolerance, therefore, may be independent of those related to the resistance that is associated with hairiness. The available information does not rule out the possible presence of genes for antibiosis in the resistant cottons.

In Queensland, a strong association between hairiness and resistance to *Empoasca terra-reginae* has also been reported. This association, however, does not appear to be complete but has been used in breeding for jassid resistance. Sloan (1938) and Wells (1943) both mention that certain varieties appear more tolerant than others to the same population level of leafhoppers. Since U4 is resistant both in South Africa and Queensland, it appears
likely that at least some of the same genetic factors in the plant and
the same behavior patterns in the insects are involved.

In the Punjab resistance to *Empoasca devastans* appears to be
on a partially different basis than in the two other species. Since
U.4 is susceptible there, this leafhopper must react to a different
level of hairiness compared to the other two species discussed or is
associated with hairiness through one of the genetic possibilities
discussed in Chapter II. The presence of resistant but sparsely
hairy segregates in crosses has been reported (Afzal 1941). It is
useful to have such segregates since susceptibility to thrips (Kottur
and Maralihalli 1931) and to aphids (Peat 1928; Dunnham and
Clark 1939) has been associated with hairy cottons, and hairy leaves
sometimes make ginning operations more difficult.

Verma and Afzal (1940) have shown that *E. devastans* lays
fewer eggs on resistant than on susceptible cotton. The fecundity
of adult females was not affected by rearing the nymphs on re­
sistant plants (Hussain and Lal 1940), but since the adult lays eggs
over a period of several weeks the fecundity may be affected by
their food while the eggs are developing. Thus it is possible that
antibiotic factors are involved in resistance of cotton to this insect.

There appears to be clear evidence that tolerance is involved in
resistance to *E. devastans* (Afzal, Rajaraman, and Abbas 1943)
and is independent of preference. Several other characters possibly
related to resistance have been studied. Susceptible varieties are
reported to have higher moisture content, but there was no associa­
tion of resistance either with the thickness of the cuticle or the pH
of the cell sap (Afzal and Abbas 1944). In the case of Victory
(susceptible) and 4 F (resistant) varieties of cotton the latter had
tougher veins (Afzal and Ghani 1949). In this same paper evi­
dence was presented that hairiness increased with closer spacing and
that, in the event of later plantings, it decreased with the hairy
variety and increased with the less hairy one. The interactions of
hairiness, moisture content of veins, toughness of veins, and leaf­
hopper populations are also discussed.

Afzal and Ghani (1948) have reported on a study of resistance
to *E. devastans* as related to toughness and hairiness in two hybrid
F, progenies of crosses involving Cambodia and three Punjab­
American cottons. Counts of populations were based on counts of
all nymphs that hatched out on leaves of each plant during the
period of severe infestation. Hairiness was measured by counting
the number of hairs on one centimeter length of each of the prominent leaf-veins. The toughness of the leaf-veins was measured by means of a special apparatus. The correlations between hairiness and toughness and between hairiness and leafhopper populations were all significant. The correlation between toughness and leafhopper population was highly significant in one progeny but not in the other. A study by means of partial regression showed that toughness alone played a very insignificant part in determining the jassid population on a plant. In general as the hairiness increased, the jassid population also decreased. There were, however, at least two clear-cut exceptions to this general trend in these F1 progenies.

In the same paper the authors reported that they shaved the hairs from the leaf-veins of alternate leaves of four plants of 199 F, a hairy and resistant cotton variety, and counted the number of nymphs emerging from eggs laid on these leaves. In experiments during two years there were practically the same number of nymphs emerging from the shaved as from the unshaved leaves. These data appear to demonstrate that the resistance of cotton to *Empoasca devastans* is not the result of the physical presence of hairs on the leaf-veins but, on the other hand, the association between the two characters is close enough to make the use of that association of importance in cotton breeding for leafhopper resistance.

The association of hairiness and resistance to leafhoppers or other insects frequently has been reported in the literature. Sometimes later studies have shown this association to be merely fortuitous. Such an association should never be considered a prime prerequisite of resistance until adequate evidence is available for each insect species and group of crop varieties concerned. Varieties of beans and other plants with hooked hairs on which insects are caught and die (Poos and Smith 1931; Trouvelot and Thenard 1931; Gandara 1931; McKinney 1938) present a different relationship compared to the plants having simple hairs that has been considered here (Fig. 53).

**RESISTANCE TO OTHER INSECTS IN COTTON**

**Resistance to thrips in cotton.** Thrips are minute insects, usually not more than 3 millimeters long, that do a characteristic type of damage to leaves. Wardle and Simpson (1927) have presented one of the best analyses available of the method of feeding and kind of injury done by thrips. The species used, *Thrips tabaci*
Tangential view of simple hairs on petiole of Michigan red clover. 50 x.

Tangential view of hooked hairs on petiole of stringless greenpod bean. 50 x.

Tangential view of hooked hairs on petiole of stringless greenpod bean. 100 x.

Fig. 53. Different types of hair which are related to degree of infestation by small insects because some get caught on the hooked hairs. The upper two photographs are made at the same magnification. (Photos by F. W. Poos; Poos and Smith 1931.)
Lind., normally feeds on onion and tobacco but less commonly on cotton (Watts 1936a). The experiments were conducted in the greenhouse in England on five varieties of cotton. Detailed data were not given but it was said that the hairy Indian and American cottons were attacked more than the smooth-leafed Egyptian cotton. It was suggested further that difference in resistance might result from differences in thickness of epidermis. The latter suggestion apparently is based on measurements of the mouth-parts and plant cells.

The lower part of the head and mouth-parts formed a hollow cone that is applied to the leaf surface. The mouth-parts consisted of four styles, at least three of which could be protruded from the cone into the leaf. The single heavily sclerotized mandible came out of the cone for about 11 micra, the two more slender maxillae about 27 micra. A typical cotton leaf in cross section measured 143 micra, the upper epidermis 17 micra, the palisade tissue 54 micra, the mesophyll layer 61 micra, and the lower epidermis 11 micra (Fig. 54). A slit was made in a single epidermal cell by means of the mandible which, however, could not pierce the opposite wall. This latter is done by the longer and more slender maxillae, which also could reach and pierce a few of the mesophyll cells immediately beneath. Material from these cells was sucked up into the insect by action of a pharyngeal pump, and air partly filled the space left. The characteristic small round spots were produced in this way.

Wardle and Simpson (1927) reported that the injury by *Thrips tabaci* on cotton was similar to that produced by *Heliothrips indicus* Bagn., which injures cotton in the Sudan. Watts (1936a) has reported on the biology of the flower thrips *Frankliniella tritici* (Fitch) on cotton. Eleven different species of thrips were recorded as present on cotton in South Carolina, *F. tritici* being the most common at the time of the study. This insect,
in common with other species occurring in the southern states, injures cotton only when the plant is in the seedling stage with from two to six leaves. Significant injury may be done by an average of as few as one adult thrip to every five, week-old seedlings. The thrips feed in the bud and on the undersurface of the young leaves. The plants are stunted, the leaves distorted, and the terminal bud may be destroyed. The setback that the plants receive delays their flowering and hence makes them more severely infested by boll weevils. *F. tritici* is also found in the flowers but no injury has been reported to the floral parts. This species is widely distributed through the United States and is known to feed on a large number of different plants.

Thirty-two different varieties of cotton were studied by Watts (1935) but it was reported that none showed definite resistance. No detailed data are given. *F. tritici* was the most abundant species but *Frankliniella fusca* (Hinds), the tobacco thrips, was more abundant than in previous years. The following year (Watts 1936b) records were taken on 36 varieties but another species of thrip *Sericothrips variabilis* (Beach) constituted 75 per cent of all thrips on young cotton while three other species were present. The percentage of stalks injured ranged from 5.26 per cent for D.P.L. No. 11 to 19.12 per cent for Woolsey Cleveland. Four strains of Humco Carolina Foster were second, third, fourth, and sixth from the lowest in injury. The next year (Watts 1937) the ratios of the three species were *S. variabilis*, 1.6; *F. tritici*, 1; and *F. fusca*, 82.7. In each of 46 varieties 800 stalks were examined. The injury ranged from 3.62 per cent of the plants damaged in Humco Carolina Foster 14-52-6 to 22 per cent in Marett's 100-1. In general, about twice as many blossoms opened on the uninjured plants as on the injured ones. These observations were all made in experimental fields in South Carolina.

The same year, near Stoneville, Mississippi, Dunnam and Clark (1937) took records on thrips injury to 40 varieties. Four species, *Frankliniella runneri* Morgan, *F. tritici*, *F. fusca* and *S. variabilis*, contributed to the damage but the proportion of the different species present is not given. The infestation was less when the cotton averaged 2.79 stalks per hill and was also less when chopping was done early rather than late. Evidently the thrips population built up on the weeds and, when the latter were cut out, migrated to the cotton plants. There were usually losses in number of bolls,
seed cotton, and staple length in the damaged plants in comparison with the undamaged ones. It is stated that "since it is shown that the number of stalks per hill influenced the amount of damage, it is not logical to attribute any variation in damage to varietal resistance." However, two varieties produced about the same number of bolls on both injured and normal plants but in an equal number of bolls on both types of plants less seed cotton was produced by the damaged plants. Twelve of the 40 varieties showed a greater number of bolls on the damaged plants and six of these showed a slight gain in seed cotton. Evidently some of the varieties may have possessed a greater tolerance to thrips attack.

Fletcher (1940) reported that counts of thrips injury to cotton varieties were made for three years. The last year 36 varieties of cotton were examined and, while a number of the varieties had practically all the terminal buds severely injured, several had somewhat more than 50 per cent uninjured. Detailed data were not published nor the species concerned mentioned.

Research workers at the Georgia Experiment Station have reported (Stuckey 1944, 1945) that the Empire cotton variety had the strongest resistance to thrips of any variety tested. The species of thrips concerned is not mentioned. As an average of results at two stations in 1943 Empire had 11 per cent of the plants damaged, while other varieties in the same tests ranged in injury from 16 to 51 per cent. In 1944 at one location Empire had 19.4 per cent of the plants with aborted terminal buds while the other 11 varieties in the test ranged from 22.0 to 50.0 per cent. This variety was reported not only to be low in percentage of plants damaged, but also showed less injury to the affected plants. Empire was also reported to have good yields and quality of lint in tests performed in Georgia and other southern states.

The information so far available indicates that a degree of tolerance and other forms of resistance to thrips is present in varieties of cotton. It also suggests that plants may be resistant to one species of thrips but not to another. If one may judge by other insects and crops, comparative studies of the biology and feeding habits of the four or five species involved and careful variety tests with each are necessary before one can assume that a variety of cotton resistant to one species of thrips will also be resistant to the others. Progeny tests of seed from uninjured plants surviving heavy thrip infestations may also show that strains selected out of
the more resistant varieties are better than the bulk seed of the variety.

Resistance to various species of Hemiptera in cotton. Several species in the order Hemiptera, or true bugs, feed in the developing flower buds or squares and on the bolls and foliage of cotton. In the United States, particularly in Texas and Oklahoma, *Psallus seriatus* Reut., the cotton fleahopper, a mirid, sometimes has caused heavy losses because of the shedding of the squares when these are scarcely a sixteenth of an inch in size. Various lesions and other peculiarities in the appearance of infested plants develop (Painter 1930). Several other less common species on cotton, including *Lygus oblineatus* (Say), the tarnished plant bug, cause a similar type of damage. There are important ecological conditions, including alternate host plants that are related to damage by the cotton fleahopper and which must be considered in a study of resistance (Thomas and Owen 1937). Workers at the Texas Station have conducted a series of tests for resistance to this insect, involving up to 20 varieties and extending over a period of years (Thomas et al. 1933, 1934; Thomas and Bibby 1935; Thomas et al. 1938; Gaines et al. 1939, 1940; Gaines and Owen 1941). Difficulty was experienced in securing a satisfactory infestation during several years. Under light infestations some of the varieties lost few of the minute square under the same conditions that others lost a large proportion of the squares (Thomas et al. 1933). In one year the varieties ranged from 10 to 30 per cent of the squares blasted by the insect (Thomas and Bibby 1935). In some of the later tests half of each variety plot was dusted with sulphur to control the cotton fleahopper. Those varieties that gave the least increase in yield as a result of insecticidal application were considered most resistant. Generally the early varieties had the highest population of the insects and also the highest yield. Dunlavy et al. (1942) studied *Psallus* infestation in eight cotton varieties in Oklahoma, where the number of insects per 100 plants ranged from 84 to 107. From a comparison of 15 varieties in areas where plants were infested and uninfested by the insects, they concluded that Acala 8 appeared to be the most susceptible variety. Strong (1940) reported that in a study of four varieties in two localities in Texas the average seasonal infestation at both locations was more than twice as high in the most susceptible as in the most resistant varieties. There was evidence that insecticides were more effective against the cotton
fleahopper on some varieties than on others. In connection with other studies (Painter 1930) it seemed to me that individual plants growing side by side showed wide differences in injury by the cotton fleahopper. There appears to have been no attempt to find out whether the progeny of such plants would behave the same way.

*Lygus simonyi* Reut. is another species of mirid that injures cotton in Africa, particularly in Uganda. The insect causes holes and distortion of the leaves and shedding of the small squares and terminal buds. Taylor (1945) has given an excellent report on the biology of the insect and the damaged caused. Gwynn (1938, 1939), after three years of study, reported that there were consistent differences in the susceptibility of different varieties of cotton. He reported also that similar differences in varietal susceptibility could be demonstrated in case of the injury of another mirid *Helopeltis bergrothi* Reut. Stephenson (1940) provides more detailed information regarding the degree of injury by *Lygus* to cotton varieties. Jameson (1940, 1944) reported that the cotton varieties S.P.102, S.P.89, and B.P.50 suffered consistently less damage than other varieties tested at the same time. Later (Weatherley 1946), under severe *Lygus* infestation, B.P.50 gave highest yields although leaf damage counts showed no varietal differences. The hairy cotton M.U.8A was reported (Jameson and Weatherley 1945) to have been attacked by *Lygus* to a lesser extent than any other in the trials of 1943–44, and also to have yielded better than the others. The paper by Taylor (1945) presented somewhat of a summary of studies of resistance to this insect. He pointed out that glabrous plants were less susceptible in the field than moderately hairy ones. Various species and hybrids of *Gossypium* tested against *Lygus* in the laboratory all showed much damage. Taylor recommended work on *G. hirsutum*, in which individual plants have been shown to differ in injury. Such differences were reported to be inherited.

The cotton stainers *Dysdercus* spp. (family Pyrrhocoridae) are found generally in warmer parts of the cotton-growing areas on all the continents. They are considered destructive particularly because of the various boll rots which they transmit to cotton. Pearson (1934, 1947) found that the stage of maturity of the cotton at the time when the cotton stainers move into the field is a determining factor in the amount of disease which develops. Creighton (1938) reported that females of *D. suturellus* Schaef. probably required fresh bolls for food before eggs matured satisfactorily.
Mumford (1926) has brought together the available information regarding the possibility of inducing resistance to cotton stainers by soil treatments. He believed that water balance was of crucial importance. The paper contains a good bibliography and a list of species reported together with their food plants. He reported that indigenous cottons are more resistant than cultivated ones.

Rainey (1948) has discussed the changes in the chemical constituents of the cotton boll at different stages of growth as it affects the susceptibility to Dysdercus and the diseases that may be carried. Mason and Jones (1924) reported that in Nigeria native cottons were less susceptible to cotton stainers than varieties from America. In Peru (Boza 1945; Boza et al. 1945) promising results were obtained in breeding for resistance to D. ruficollis L. in cotton. Part of the work has been directed toward the selection of individual plants that were resistant to several pathogens carried by these insects.

Resistance to cotton aphid, *Aphit gossypii* Glov. Among the several species of aphids that occur on cotton, *Aphit gossypii* is usually the most common and destructive. However, Yakhontov (1930), working in the U.S.S.R. on susceptibility of the cotton varieties to aphids, reported that *A. gossypii* was the least injurious of four species present. Association with hairiness has been reported on several occasions. Working with Cawnpore American Cotton in India Burt and Haider (1921), according to Harland (1932), found that susceptibility to aphids was associated with smooth leaves. In other reports the contrary has been true. Peat (1928) in South Africa found that hairy cottons such as Cambodia suffered more than glabrous ones from aphid attack. The species concerned in these reports is not given but presumably is *A. gossypii*.

Reinhard (1927), in a study of wing production in this species, reared progeny from individual females on 59 single cotton plants. The progeny produced ranged from 7 to 81. It is possible that these progeny differences may result from dissimilarities in the plants as food for this aphid. About 1938 the U.S. Bureau of Entomology began to give attention to developing aphid-resistant varieties of cotton (Strong 1940). This was apparently the result of studies made at Stoneville, Mississippi, in 1932 and reported by Dunnam and Clark (1938). It was found that in a group of varieties showing different levels of pilosity "the aphid population
increased in direct proportion to the number of hairs on the lower leaf surfaces. . . . No correlation was found between the numbers of parasitized aphids and the pilosity of leaves, although the percentage of parasitism was greater on the glabrous types of cotton with the smaller aphid populations." Annand (1943) reported that some of the strains of cotton developed at Stoneville, Mississippi, are now about 25 per cent resistant to aphids. In further studies (Annand 1946) it was found that strains with the greatest number of hairs on the veinlets are more susceptible to aphids. About 3,500 plants were involved in this study. As recorded in Chapter II, a high level of resistance to *A. gossypii* has been found in varieties of cantaloupe.

**Resistance to black scale and white fly.** Two of the early studies of the inheritance of pest resistance in cotton were those regarding the leaf blister mite, *Eriophyes gossypii* Banks (Harland 1916, 1919), and the black scale, *Saissetia nigra* Nietn. (Harland 1917). Since the former is an Arachnid and not an insect, it is not discussed here. The black scale is a widely distributed pest of cotton and several other tropical and subtropical plants. Among the strains of Seredo cotton introduced from Brazil into the West Indies in 1914, Harland found two types that were immune to black scale at St. Vincent. When these strains were crossed with local varieties the F₁ showed almost complete immunity. No F₂ cultures were grown (Harland 1932). In reciprocal grafts between resistant and susceptible cottons only the susceptible branches were attacked.

The cotton white fly, *Bemisia tabaci* Gennadius (= *B. gossypiperda* Misra and Lamba, family Aleurodidae), injures cotton in India and in various parts of Africa. It has also been reported to transmit virus diseases of cotton and others of its various host plants. The eggs are laid on tender leaves on which the nymphs later feed, causing the stunting of plants and decreasing yield. It has been reported by Husain *et al.* (1936) that this insect infests the indigenous cottons (*G. arboreum*) of the Punjab early in the season and the upland varieties later. These authors correlated this behavior with changes in the acidity of the sap, which differed in pH in the varieties from season to season and from year to year. The insect appeared to be partial toward plants in which sap showed higher pH values. Afral (1947) also reported that breeding for resistance to this insect was being carried on in the Punjab.
Resistance to bollworms and other species of Lepidoptera in cotton. The larvae of a considerable group of species of moths, mostly belonging in the family Noctuidae, feed in the bolls, seeds, and squares of cotton. Frequently they are treated together in the entomological literature and for that reason are so grouped here. This must not be taken to mean that cotton varieties resistant to one species of bollworm will be necessarily resistant to the others, for the species differ in habits, time of attack, and probably also in food requirements. As indicated earlier in this chapter, several studies have been made of the development of fruiting structures of cotton in an effort to relate these to various insect problems. These studies should be taken into consideration by those working on bollworm resistance.

Perhaps the most destructive and widespread species of this group is Heliothis armigera (Hbn.), the bollworm or the American bollworm, as it is known in other parts of the world. The biology of the species is considered in the chapter on corn. The considerable research recorded there has shown that it is possible to select strains of this host plant showing resistance to Heliothis that is of economic importance. The species is recorded from all continents, but it exhibits some difference in biology in the different areas (Isely 1935; Parsons et al. 1938; Rainey 1940). These papers record the striking differences that the species of host, or part of the host used, exerts on the development of the bollworm. Considerable study has been made of the environmental factors influencing the distribution of the bollworm in cotton fields as well as between cotton fields (Fletcher 1929, 1937, 1941; Thomas and Dunnam 1931; Gaines 1933; Marshall 1936). Such variations must be considered in any study of resistance. Parnell (1938) warns that in a field where plants are variable the bollworm tends to oviposit on the better developed plants, sometimes leaving the lightly fruiting types undamaged. Varietal differences in amount of oviposition done by the bollworm have been reported by several workers (Peat 1935; Parsons and Marshall 1940; Rainey 1941) but few details have been given. In view of the success with corn, resistance to Heliothis in cotton should repay further study.

The pink bollworm, Pectinophora (or Platyedra) gossypiella (Saund.) is one of the most destructive of the pests of cotton. Its original home has been variously stated as India, Africa, or Australia. In addition to these areas it has been introduced into Brazil,
Mexico, parts of the United States, Hawaiian Islands, various islands of the West Indies, and a few other places. Eggs are laid on the green boll or adjacent parts of the plant, and the larvae spend most of their life in the seeds of the cotton. The insect can mature on few, if any, species of plants other than those of the genus *Gossypium*. There are several early reports that indicated that the indigenous cottons of India were less infested by the pink bollworm than the imported upland varieties (Fletcher 1914, 1919; Marlatt 1918). This has been confirmed by the later detailed experiments of Husain and his associates (1940) in the studies of fields and variety plots, and under cage conditions. Examples of their field results are given in the accompanying table (Table 16).

**Table 16** PINK BOLLWORM INFESTATION IN COTTON VARIETY TEST
LYALLPUR, PUNJAB, 1933
(After Husain, Atta and Kahn 1940)

<table>
<thead>
<tr>
<th>Variety</th>
<th>% Green bolls attacked</th>
<th>Number of larvae per 100 bolls</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Sept. 9</td>
<td>Sept. 29</td>
</tr>
<tr>
<td><em>G. arborum</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>sanguineum</em></td>
<td>9</td>
<td>24</td>
</tr>
<tr>
<td>Mollisoni</td>
<td>17</td>
<td>25</td>
</tr>
<tr>
<td><em>G. hirsutum</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>43 F</td>
<td>44</td>
<td>39</td>
</tr>
<tr>
<td>4 F</td>
<td>44</td>
<td>44</td>
</tr>
<tr>
<td>289 F</td>
<td>30</td>
<td>50</td>
</tr>
</tbody>
</table>

The results in cages were quite similar. Squire (1939) has reported on the resistance of *Gossypium trifolium*, an American species of wild cotton, to the pink bollworm. About half of the larvae that were placed on the bolls of this species failed to penetrate them and none became established or fed on the seeds. However, some of the first-instar larvae that were placed on seeds removed from the capsules were able to feed. MacDonald *et al.* (1940) reported that three back-crosses, (*G. trifolium* x Sea Island) x Sea Island, which had been resistant to bollworm (pink bollworm?) in Trinidad were susceptible to the species of bollworms present in South Africa. This is not surprising since different species of insects apparently were involved.
The native Haitian cotton, *G. hirsutum* var. *punctatum*, has been reported to show considerable resistance to the pink bollworm (Wolcott 1927, 1928). In the latter paper it is reported that a maximum infestation of 51 per cent of the bolls was obtained when the insect was forced onto these cottons by the maturing of the Sea Island and upland types. Thereafter the infestation declined on the Haitian cotton. Earlier in the season when Haitian cotton had 17 per cent infestation, the percentage for the introduced varieties ranged from 70 to 84 per cent. Still earlier in the season the range in infestation was from 19 per cent on Mebane to 52 per cent on Pima. In the absence of other types of cotton the pink bollworm can barely maintain itself on the Haitian cotton. Audant and Occenad (1937) reported that commercial damage by this insect continued to be negligible although the Haitian cottons were fully susceptible to the boll weevil (Audant 1938). Deger (1936) reported from Guatemala the existence of a hybrid between perennial and upland cottons that was resistant to the pink bollworm as well as to the boll weevil. Its lint and yield quality appeared to be satisfactory.

Fenton (1928) reported that the pink bollworm infested less than 4 per cent of the bolls of *Coccygium thurberi* (*Thurberia thespesoides*), the Arizona wild cotton, while cultivated cotton nearby had about 100 per cent infestation. Reports from studies in Texas (Chapman 1937, 1938, 1941) indicated no resistance in the commercial varieties studied, although early varieties escaped to some extent and some differences were found in the extent to which the grade of lint was lowered by comparable infestations. According to Knight (1944), Harland has reported that *G. thurberi* was not attacked by the pink bollworm either in Trinidad or in Brazil. This wild cotton showed a complete absence of this insect also in the Anglo-Egyptian Sudan although the neighboring commercial cotton had a 97 per cent attack. At this Shambat Substation of the Empire Cotton Growing Corporation, both *G. thurberi* and *G. armourianum* were crossed with the commercial variety Sakel (*G. barbadense*) in an attempt to transfer resistance to the bollworm, possessed by the wild species, to commercial cotton (Anson et al. 1945; Knight 1946, 1947). At first these attempts were unsuccessful but later, with the aid of colchicine, fertile hexaploid plants were secured and backcrossed to the commercial parent. The hybrid *thurberi x barbadense* was called "thurbadense" and...
the hybrid *armourianum* x *barbadense* called "armadense." Both these interspecific hybrids showed resistance to the pink bollworm. A back-cross program is now being carried on with them (Anson et al. 1948). In this same article it was reported that *G. somalense* showed marked resistance to the pink bollworm and that *G. anomalum* appeared resistant to the pink bollworm but susceptible to the Egyptian bollworm, *Earias insulana*. For *G. raimondii* the reverse appeared to be the case.

In some of the brief annual reports of the experiment stations of the Empire Cotton Growing Corporation it has not been clear always which bollworms were under observation in the resistance studies that were recorded. Smith (1933) has reported that no cotton variety was immune to the red bollworm, *Diparopsis castanea* Hampson, in South Africa, where most of the studies of this insect have been made (Rainey 1941). The four wild species, *G. thurberi*, *G. armourianum*, *G. somalense*, and *G. raimondii* were reported (Anson et al. 1948) to be resistant to the Egyptian bollworm, *Earias insulana* Boisd. Breeding for resistance to this insect, using some of these species, was under way in the Anglo-Egyptian Sudan.

Cheo (1943), in studying a cotton leafroller, *Sylepta derogata* Fab., found that cotton varieties with divided leaves had about 9 per cent of the plants with one-half or more of the leaves rolled by this insect, while varieties with undivided leaves had 95 per cent of the plants with one-half or more of the leaves rolled. Further observations on *S. derogata* have been reported by Ma (1945).

**Resistance to the boll weevil, Anthonomus grandis** Boh. Few plant-feeding insects anywhere have caused such widespread permanent changes in agriculture as did the boll weevil when it moved into the United States from Mexico (Ware 1936). Most aspects of the biology of the boll weevil have been as thoroughly studied as those of any other plant-feeding insect. During the early years of the boll weevil invasion use was made of the principle of host evasion by replacing the old late-maturing varieties with early maturing ones (Cook 1912, 1924; Lewis and McLendon 1920; Hunter 1907, 1912, 1917; Hunter and Coad 1922; Ballard and Simpson 1925; Isely 1934). Cook (1911) stated that the ideal form of earliness consisted of the production of the crop rapidly, as soon as fruiting begins. The boll weevil injures the cotton both through the feeding of the adults on squares and young bolls and through
oviposition and the feeding of larvae on these same parts of the plant. Under exceptional circumstances seedling plants may be stunted or killed by the feeding of the weevils that have just emerged from hibernation. A little feeding may be done on leaves. The adults feed particularly on the anthers and developing pollen of the flower buds, or squares (Fig. 55), often causing such squares and also bolls to drop to the ground after the feeding or oviposition has occurred. There have been marked differences in the length of life of weevils which had been fed on young bolls, leaves, and squares. Hunter and Pierce (1912) reported that the average duration of life on the foregoing plant parts was 20.3, 24.5 and 62.7 days respectively. Fenton and Dunnam (1929) reported that the average fecundity of weevils reared on squares was about three times as high as when reared on young bolls. Isely (1928a) reported a wider difference in the fecundity of weevils so reared.

The five boll weevils reared on althea (Hibiscus syriacus) (Coad 1914; Gaines 1933) are the only ones known to have been reared on any plants other than those of the genus Gossypium. In that genus this insect has been reared on varieties of G. hirsutum and G. barbadense. Gossypium klotzschianum var. davidsonii, a wild cotton on the coast of the Gulf of California, has also been reported as a food plant (Smith 1921). There are several reports of Anthonomus grandis feeding on G. thurberi (Thurberia thespesioides), the wild cotton of Arizona (Smith 1921; Loftin 1946), but it is not clear whether or not those records refer only to A. grandis thurberiae, the subspecies that normally breeds on this plant. This latter subspecies can maintain itself with some difficulty on cotton and hybridizes.
under cage conditions with the typical subspecies of boll weevil (Coad 1915). There appears to be no information on infestation of other species of *Gossypium* by the boll weevil. The wild cotton of Arizona (*G. thurberi*) was not infested naturally by the boll weevil, *A. grandis grandis*, in southern Texas even when growing near heavily infested cotton fields (Coad 1915).

During the early years of the boll weevil invasion of the United States several expeditions were sent to Mexico and Central America to look for weevil-resistant cottons. Emphasis, however, was placed on host evasion and on characteristics of the cotton plant that were thought to be distasteful or destructive to the weevil (Ware 1936; Cook 1904, 1906, 1911). Such characters were small or deeply lobed leaves, hairy stems and leaves, earliness, extra floral nectaries to attract predaceous insects, etc. The development of ability to proliferate cells and crush the young weevil larvac or eggs was also stressed and was studied in detail by Hinds (1906) and Smith (1936) (Fig. 56). Hinds' studies showed that the mortality caused by proliferation amounted to 13.5 per cent in squares and 6.3 per cent in bolls. Smith's records showed less than 1 per cent mortality due to this cause. Little difference was found in the amount of proliferation among the varieties studied but progenies of plants that might have this characteristic well developed were not examined. Irregularity of fruiting also has been stressed as an undesirable characteristic affecting susceptibility to the weevil (Calhoun 1933). Various small differences in susceptibility have been reported in varieties. In general, the Sea Island varieties, *G. barbadense*, have been more susceptible than the upland varie-
tis, *G. hirsutum* (Hunter and Pierce 1912; Smith 1921; Cook and Doyle 1927). According to Smith there was little difference in the longevity or fecundity of weevils fed on the two species of cotton but 49.4 per cent emerged from the Sea Island squares compared with 36.9 per cent from the same number of upland squares. In contrast, 1,500 upland bolls produced 100 weevils while the same number of Sea Island bolls produced 650 weevils. Cook and Doyle believed that this latter result was on account of the thinner walls of the bolls of Sea Island cottons. Dunnam (1926) studied the rate of growth of bolls of three varieties of cotton in relation to various aspects of boll weevil biology and damage. A male and a female insect were placed in cages over bolls for 24 hours and the bolls protected from further attack. The loss, calculated as the percentage of the total number of locks or divisions of the bolls damaged by weevils caged on them when the bolls were 1 to 5 days old, was 79 per cent for Dixie Triumph, 93 per cent for Webber 49, and 100 per cent for Humco Cleveland. Similar figures for bolls 26 to 30 days old were 17, 8, and 2 per cent, respectively, for these varieties. There were no losses of bolls 40 days old or older. Fenton and Dunnam (1929) also reported a small difference in the susceptibility to the weevil in three varieties of cotton in respect to damage to bolls. Hison (1939) found in a study of 8 varieties for 2 seasons that the normally higher yielding ones showed a tendency both to be more heavily infested and to yield more even in the presence of this infestation than the others. Gaines and Dean (1947) showed that different cotton varieties were infested with boll weevil and bollworm to a different extent after receiving similar treatment with insecticides. Strong (1938) reported that investigators in the Bureau of Entomology, working with 44 varieties, had concluded that those plants having bolls with walls of medium thickness were more resistant to boll weevil than those with either thick or thin walls.

Deger (1936), working in Guatemala, reported that a hybrid between perennial and upland cottons with good lint quality showed promise of resistance to the boll weevil and to the pink bollworm. It is perennial in habit.

The preference aspects of resistance to the boll weevil in cotton have received some attention but probably deserve further study. The scarcity of weevils on other plants in the neighborhood of cotton indicates the highly obligate relationship of the insect to the
host plant and the possibility of resistance through a lack in some feature of the attractiveness. One such factor is leaf color. Hunter and Pierce (1912) reported on series of experiments in which adult weevils were allowed to go to light transmitted through tubes of different color. The relative attractiveness of green and red in these tests was 6.0 and 3.8. Isely (1928b) designed experiments to test the relationship of leaf size and leaf color on boll weevil infestation. Varieties differing in leaf size showed no significant differences in infestation. All plots of the red-leaved variety Winesap showed lower infestation in 1925 than adjacent green-leaved varieties during about the first month of infestation. Later in the season uninfested squares were rare on any variety. Experiments in 1926 furnished the data for results recorded in Table 17. It seems probable that the lower infestation of Winesap

<table>
<thead>
<tr>
<th>Variety</th>
<th>Leaf color</th>
<th>Aug. 17</th>
<th>Aug. 24</th>
<th>Aug. 31</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winesap</td>
<td>red</td>
<td>14.25</td>
<td>16.12</td>
<td>32.25</td>
</tr>
<tr>
<td>Okra leaf (Texas)</td>
<td>green</td>
<td>29.75</td>
<td>41.12</td>
<td>66.00</td>
</tr>
<tr>
<td>Lone Star</td>
<td>green</td>
<td>32.75</td>
<td>57.75</td>
<td>70.00</td>
</tr>
</tbody>
</table>

is the result of the red leaf color. However, it may be associated with some other character. None of the red-leaved varieties known at the time when Isely worked on this project were good enough to be recommended for planting. The red leaf color is the result of a single genetic factor (Harland 1932) and if it proves to be definitely related to lack of preference by the weevil, the character can be transferred to more desirable varieties.

Considerable study has been given to the chemical senses of the boll weevil (McIndoo 1926), but there appears to have been only one attempt to study odors affecting the attractiveness of different cotton varieties to the boll weevil. Folsom (1931) studied the reaction of this insect under laboratory conditions to four varieties of cotton, using about 24 beetles in each test. The results have
been copied in Table 18. While the differences were small, so were the number of varieties studied. It has been shown also that two substances, ammonium hydroxide and trimethylamine, are attractive to the weevil at certain concentrations. These substances are found in the plant and in dew (probably mostly water of guttation) collected from the cotton plants. Whether such attractive substances differ in concentration in different varieties and plants or are absent in others apparently has not been studied.

Table 18  **REACTIONS OF BOLL WEEVIL ADULTS TO FRESH LEAVES OF FOUR VARIETIES OF COTTON**  
(After Folsom 1931)

<table>
<thead>
<tr>
<th>Variety</th>
<th>Number of tests</th>
<th>Percentage of weevils reacting</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>positive</td>
</tr>
<tr>
<td>Wannamaker Big Boll</td>
<td>5</td>
<td>61.0</td>
</tr>
<tr>
<td>Mexican Tree Cotton</td>
<td>3</td>
<td>60.0</td>
</tr>
<tr>
<td>Sea Island Cotton</td>
<td>3</td>
<td>68.1</td>
</tr>
<tr>
<td>Pima Cotton</td>
<td>3</td>
<td>75.0</td>
</tr>
</tbody>
</table>

In the studies related to resistance of the boll weevil to cotton enough has been done to give some promising leads, particularly if such studies involve individual plants and some of the other species of *Gossypium*. Loftin (1946), in discussing insecticidal control of the boll weevil, pointed out that it is not necessary to get 100 per cent control of the weevil. Likewise, it is not necessary to have a cotton that is immune to the weevil as has sometimes been sought. The cotton plants normally set more squares than the plant can support as bolls, and apparently many are shed normally. It is necessary therefore to have a variety that is sufficiently boll weevil resistant to maintain a favorable balance between the production of squares and their shedding so that a normal crop can be produced.

**Resistance to other species of Coleoptera in cotton.** The cotton stem weevil, *Pemphredes affinis* Est., bores into the stems of cotton, damaging particularly the young plants in Madras and in other areas of India. Ballard (1923) gave information that some strains of Cambodia are less liable to attack when they are young than are other strains. *Gossypium arboreum indicum* was reported to
be less injured than *G. herbaceum*. Dharmajarajulu et al. (1934) reported that selection and isolation of resistant and tolerant strains were being done. Dharmajarajulu (1936), presenting the results of a study of the mechanism of resistance, showed that gall formation and production of callus took place first. A part of the callus tissue then broke down and formed a gum which flooded the burrows of the larvae and killed them.

Knight (1942) reported that the Tanguis variety from Peru and the F₁ of a cross between Tanguis and Sakel strains of cotton both showed fair resistance to flea beetles. The species involved is not recorded.

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INSECT RESISTANCE IN CROP PLANTS


CHAPTER VII

RESISTANCE TO INSECTS IN SORGHUMS

I. Introduction.
A. The crop and varieties.
B. Insect species injurious to sorghums and those for which resistance has been reported.

II. Chinch bug resistance in sorghums.
A. Biology of the chinch bug, *Blissus leucopterus* (Say).
   (1) Resistance to chinch bugs in grasses and other crops.
B. Biology and resistance studies in other species of *Blissus*.
C. Early observations on varietal reactions to chinch bugs in sorghum.
D. Later observations on varietal reactions.
E. Inheritance of resistance to chinch bug injury.
F. Studies on the basis of chinch bug resistance.

III. Resistance to other insects in sorghums.
A. Resistance to Orthoptera and Hemiptera other than *Blissus*.
C. Resistance to species of Lepidoptera.
D. Resistance to the sorghum midge, *Contarinia sorghicola* (Coq.).

IV. Bibliography.

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The sorghums, *Sorghum vulgare* Pers., include a diverse group of varieties of crop plants that are usually grown as annuals and utilized in many ways. In Africa and Asia, where cultivation of the species may have originated, the grain is used for human food. This is much less true of other areas, such as in the United States, Australia, South America, and Europe, where the grain, stalk, and leaves are used as food for livestock. Certain varieties with sweet stalks, the sorgo varieties, are used in the production of sirup; the panicles of others, e.g., the broomcorns, are made into brooms. Other industrial uses have been developed.

The related species, Johnson grass (*S. halopense* (L.)) is peren...
nial and has twice the number of chromosomes found in the sorghums. Hybrids between the two species have often been produced. There is about 5 per cent cross-pollination when two different varieties of sorghum are grown in adjacent rows. Ten pairs of chromosomes are present in the sorghums and several linkage groups are known. Crosses between plants of different varieties often exhibit considerable hybrid vigor. In the United States the chief sorghum-growing area extends from North Dakota to Texas, just west of the corn-producing region. Sorghums are also planted in the southern states and in irrigated regions in the western states (Vinal, Stephens, and Martin 1936; Karper and Quinby 1937, 1947). Artschwager (1948) has made a detailed study of the morphology of sorghums, which may be of interest in connection with studies of insect resistance.

Under certain environmental conditions the sorghums develop a high content of hydrocyanic acid, which differs in amount in different varieties (Franzke et al. 1939). The presence of this poison has suggested the possibility that it may be related to the cause of resistance to certain insects in sorghums. No clear evidence supporting this idea has been reported, however.

The insects that attack the sorghums in the United States have been chiefly those with general feeding habits, such as the corn earworm, or insects that feed on grasses, such as the chinch bugs. The one exception appears to be the sorghum midge, Contarinia sorghicola (Coq.), which damages sorghums in Africa, North America, and elsewhere, and appears to be confined to the sorghums and related species.

The resistance of sorghums to chinch bugs, Blitius leucopterus (Say), has been about as thoroughly analyzed as that to any insect species and crop. Little study has been made of resistance to other insects. Varietal differences have been reported against the attack of the following species.

Orthoptera
   Acrididae
   Melanoplus spp. (Grasshoppers)
Hemiptera
   Lygaeidae
   Blittiis leucopterus (Say) (Chinch bug)
   Pentatomidae
   Soluba pungens (F.) (Rice stink bug)
Homoptera

Aphididae

*Aphis maidis* Fitch (Corn leaf aphid)

Lepidoptera

Noctuidae

*Heliothis armigera* (Hbn.) (Cotton boll worm or corn earworm)

Pyralidoidea

*Pyrausta nubilalis* (Hbn.) (European corn borer)

"*Diatraea diatraea*" (Stem borer)

Diptera

*Contarinia sorghicola* (Coq.) (Sorghum midge)

Dahms (1943) has reviewed the literature on the resistance to insects in sorghums.

**CHINCH BUG RESISTANCE IN SORGHUMS**

The chinch bug, *Blissus leucopterus* (Say), is an insect that is widely distributed in the northern Mississippi valley and adjacent areas in North America and at intervals occurs in destructive numbers on small grains, corn, and sorghums. Over much of this territory there are two generations a year and the insect hibernates as an adult in the bunch grass or under various types of debris. In southwestern Oklahoma and perhaps other places there are three generations a year and hibernation occurs around Johnson grass and in sorghum stubble fields. Upon emergence in the spring the adults fly to small grain fields, where eggs are laid about the food plants. These plants mature over much of the area before the chinch bug reaches the adult stage and the nymphs migrate sometimes in vast numbers to adjoining corn and sorghum fields, where they complete their development and pass the next generation before flying back to hibernation quarters. A certain amount of redistribution occurs by the flight of adults in midsummer. Against this redistribution no effective control is known except the use of resistant varieties. In southwestern Oklahoma the spring migration from the small grains is also by flight so that in this case the use of resistant varieties for control is necessary (Snelling 1936).

Chinch bugs feed normally on various species belonging to the grass family. A fairly complete list of known host plants is given by Horton and Satterthwait (1922). Bugs may be collected on dicotyledenous plants on which they occasionally feed but which they have never damaged. In Kansas and Oklahoma the usual
order of food preference among small grains is barley, wheat, and oats. In Illinois all spring small grains and winter wheat were attacked, but oats were the least attractive (Benton and Flint 1938).

The history of the chinch bug in the United States has been one of recurring outbreaks at intervals of from 5 to 10 years. During such periods, which usually coincide with times of drought, these insects are present in small grains, corn, and sorghums in astounding abundance. In wet years the adults tend to seek the drier and sunnier parts of the field where plants are spaced farther apart.

A study of the feeding methods of the chinch bugs (Painter 1928) has shown that the objective of the stylets is usually the phloem tissue of the vascular bundles where a number of branches of the stylet sheaths usually extend to the various tubes. Besides the phloem, the xylem, epidermis, mesophyll, sclerenchyma, protoxylem, and bundle parenchyma tissue are pierced. Sometimes the stylets pass through the heaviest part of the sclerenchyma. The stylets pass intracellularly but there is little other evidence of injury even to the cells directly concerned. The food of the chinch bug comes primarily from the phloem tissue (Figs. 9, 12, 57).

Thomas (1879) suggested the early planting of spring grains, the growing of crops on which the chinch bugs do not feed, and separating such crops as methods of control. Osborn (1888) recommended the manipulation of dates of planting in order to minimize injury by this insect. He mentioned the necessity of planting immune crops, such as clover, buckwheat, flax. These food habits of the chinch bug are the basis for the recommendations for fighting the chinch bug with crops in the following publications: Burlison and Flint (1919, 1923), Flint and Burlison (1920), Flint et al. (1934), and Henson and Drake (1934).

Hayes and Johnston (1925) made observations on an invasion of chinch bugs among nearly one hundred species of native and introduced grasses at Manhattan, Kansas, and found that “the different species showed different degrees of resistance to injury, and later some of them exhibited marked ability to recover.” There appeared to be no relationship between the degree of injury and the tribal classification to which a grass species belonged. When three or more species in any genus were studied, marked differences in injury were recorded. In the genus Bromus, represented by 23 species, Festuca, by 7, and Brachystio, by 4, the differences in injury to various species ranged from “slight” to “killed.” Where chinch
Fig. 57. Chinch bugs feeding on sorghum plants, Manhattan, Kansas, 1933, illustrating the gregarious habits of feeding and the size of the insects in relation to that of the plants. Injury to the plants is not clearly evident unless the insects are much more numerous or the plants much smaller than those shown.

bugs hibernated in bunch grass, definite preferences for certain grass species were shown, Andropogon scoparius, the little bluestem, and Sorghastrum nutans, the Indian grass, being specially favored. Wide differences in numbers of bugs present in adjacent plants of these grasses would suggest that this preference may extend to individual plants or strains of bunch grass. Burke (1934) reared chinch bugs.
on a number of grasses but found no significant difference in the length of time required for development from egg to adult. None could be reared on dicotyledenous plants.

**Biology and resistance studies in other species of **Blissus.** There are about a dozen described species of Blissus in North America, but relatively little is known about the biology of most of them. MacLeod and Maxwell (1937) in a study of a related species, the hairy chinch bug (Blissus hirtus Montd.), on different varieties of lawn and grass for golf greens, found a wide range in number of bugs per square foot and in degree of damage. Eight different varieties of grass had from 1.7 to 27.9 chinch bugs per square foot and a slight degree of damage. Seven other varieties ranging from 47.8 to 136.7 chinch bugs per square foot had moderate to severe injury. The degree of damage was approximately proportional to the chinch bug population. Prendergast (1943) reported that another related species, Blissus mixtus Barber, occurred in large numbers on particular plants of its host grass, Ammophila arenarius, but appeared entirely absent from certain other plants of the same species.

The resistance of corn to chinch bugs and of wheat to the same insect has been discussed in the sections dealing with these crops.

General observations on the reaction of sorghum varieties to chinch bugs have been reported by several earlier investigators, but only in more recent years have systematic or quantitative studies of resistance been made.

**Early observations on varietal reactions to chinch bugs in sorghum.** At the beginning of the century Cottrell et al. (1900) reported that "kafir corn is not proof against chinch bugs and chinch bugs when very thick will kill it, but an ordinary attack such as will seriously injure corn does not seem to hurt kafir corn much. When only a few inches high, kafir corn is readily destroyed by this pest." Ball and Leidigh (1908), Churchill and Wright (1914), Cunningham and Kenney (1918), Vinall and Getty (1920), Getty (1921, 1934), Vinall, Getty and Cron (1924), and several other agronomists have mentioned the high susceptibility of milo to chinch bugs, and several of these mentioned the intermediate reaction of feterita and the relative resistance of the kafirs and sweet sorghums.

Conner (1911) reported that Planter sorgo lodged badly if attacked by chinch bugs. Ball (1913) reported that "the Kaoliang
seem to be slightly less susceptible to chinch bug injury than the milos, though more so than the kafirs.” Borman (1914) stated that “there are no sorghums known to be proof against chinch bugs. All are affected more or less according to the varying juiciness of the stalk at the time of the attack. However all sorghums have greater resisting and greater recuperative powers than corn at corresponding stages of growth. An attack of chinch bugs that would totally destroy a crop of corn might not destroy a crop of kafir, milo, feterita or sorgo.” Vinall (1920) stated that the chinch bug often did considerable damage to Sudan grass.

Hayes (1922) observed that young milo plants were more seriously injured by chinch bugs than any of the other sorghums. He also observed that milo crosses exhibiting hybrid vigor were not injured by the chinch bugs. Hayes and Parker (1922) collected data on the resistance of sorghum varieties and hybrids to chinch bug injury. Some of these data on the inheritance of chinch bug resistance in the F3 generation of the cross Kansas Orange x Dwarf Yellow milo are included in a later bulletin (Snelling, Painter, Parker, and Osborn 1937). Whitehead (1924) made some preliminary studies on the cause of resistance and also obtained data on the inheritance of chinch bug resistance and susceptibility in the F3 generation of the cross Kansas Orange x Dwarf Yellow milo.

Daane and Klages (1928) reported that complete failures resulting from chinch bug damage have been the rule with milo and milo hybrids tested at Stillwater, Oklahoma. “Straightneck maize” is able to endure chinch bug invasions somewhat better than white and yellow milo or Desert maize, but even with it, complete failures have been frequent. Parker (1931) described the reaction of certain sorghum varieties and hybrids to chinch bugs, as observed at Manhattan, Kansas, and showed that chinch bug resistance is a heritable character. Kiltz et al. (1933) stated that because of chinch bug injuries, the growing of milos and, to a lesser extent, of feteritas was not to be recommended for the chinch bug infested area of Oklahoma, while all true kafirs, Darno, and Schrock were fairly dependable. Although most of the sweet sorghums were fairly resistant, Honey sorgo was quite susceptible. Fargo or Straightneck milo was not as susceptible to chinch bug injury as were most milos.

Martin (1933) stated that there were wide differences in the susceptibility of grain-sorghum varieties to chinch bug injury. The
millos were particularly susceptible, Feterita and Hegari somewhat susceptible, while the kafirs showed considerable resistance. Many hybrid sorghums have been tested for resistance to chinch bug injury, and a few strains that possess a resistance greater than that of either parent have been found.

Aicher (1933) stated that “Wheatland, like Dwarf Yellow milo, is subject to serious chinch bug injury, and that in the eastern section of Kansas, the use of Wheatland will be limited by chinch bugs.” Stewart, Gross, Kiesselbach, and Anderson (1934) in a report of the cooperative sorghum trials in Nebraska, stated that in a test in Webster County, chinch bugs were present in numbers and injured the millos considerably. Kalo, although reported as susceptible to chinch bugs, showed much less injury than the milos. Atlas, Sumac, and Black Amber sorgos as well as the kafirs were apparently most resistant to chinch bug injury. Wheatland, Sooner, and Day milos belonged to the group that was susceptible. Swanson and Laude (1934) stated that the kafirs, in general, were fairly resistant to chinch bug injury, while milo and many of the varieties derived from milo were highly susceptible. Some of these more recent papers had taken into consideration results obtained at Manhattan, Kansas, and Lawton, Oklahoma, which were then unpublished.

Several reports of the director of the Kansas Agricultural Experiment Station have given short accounts of the development of the study of the chinch bug resistance in sorghum but these have been summarized in the technical bulletin “The resistance of sorghums to the chinch bugs, Blissus leucopterus (Say)” by Snelling, Painter, Parker, and Osborn (1937) from which the account which follows has been taken. The bulletin “Resistant varieties of sorghum and corn in relation to chinch bug control in Oklahoma” by Snelling and Dahms (1937) reviewed some of the information on varieties recorded in the publication mentioned above.

Later observations on varietal reactions. The data presented in the bulletin by Snelling et al. (1937) were gathered at Manhattan, Kansas, at intervals during a period of more than fifteen years and in five consecutive years at Lawton, Oklahoma, in cooperation between the Kansas Agricultural Experiment Station and the Bureau of Plant Industry.

Injury by the chinch bug was primarily the result of mass attack, which in many cases caused the death of the plants. In others the growth was stunted and the yield of grain or fodder reduced.
rate of killing was highly variable in different tests; the most resistant plants would be killed if they were small enough and if there were enough chinch bugs. In all attacks, however, there was a wide variation among the different varieties in respect to speed with which death occurred and to the relative number of plants killed. The killing and the reduction in yield was often complicated by the date of planting, the earliness, drought resistance, and adaptation of the different varieties. Under conditions at Manhattan, where the chinch bugs moved in on foot at one end of the row, the plants near that end were frequently reduced in size. The amount of this reduction in size also varied with different varieties. In all of the characters by means of which resistance of sorghums to chinch bugs had been measured, the results have always been relative and influenced largely by the intensity of infestation. In all varieties there appeared to be an age resistance, the older plants of all varieties being more difficult to kill than younger ones. This has been shown by means of different dates of planting. When the plants were large because of earlier dates of planting, and the number of bugs small even the susceptible varieties survived. When the plants were small and the bugs numerous because of later dates of planting, most of the resistant plants were killed. Yet in spite of these differences in intensity of infestation and in age resistance the rank of the different varieties in each test was approximately the same. Most cases of discrepancy were evidently explainable on the basis of earliness, lateness, specific adaptation, or previous selection for resistance. The measurements reported for different varieties were based on the percentage of plants killed or the percentage of plants injured in a given test.

Some of the more important or better known of the various sorghum varieties tested were roughly divided into four groups as shown at the top of page 335.

The varieties of sorghums studied covered a wide range of morphological and economic types. The different groups of sorghums may be discussed together. Among the sorgos tested were nine or ten varieties and a number of advanced hybrids. Most of these were relatively resistant to the chinch bugs, many of them highly so; Leoti Red, the Sumac and Amber varieties showing the least resistance. Tests performed since the completion of the bulletin have shown that some varieties of sorgo were as susceptible as the milo varieties. Atlas sorgo, which was one of the most resistant
<table>
<thead>
<tr>
<th>Resistant varieties</th>
<th>Susceptible varieties</th>
</tr>
</thead>
<tbody>
<tr>
<td>Atlas sorgo</td>
<td>Dwarf Yellow milo</td>
</tr>
<tr>
<td>Sunrise sorgo</td>
<td>Dwarf White milo</td>
</tr>
<tr>
<td>Kansas Orange sorgo</td>
<td>Sooner milo</td>
</tr>
<tr>
<td>Dawn kafir</td>
<td>Finney milo</td>
</tr>
<tr>
<td>Blackhull kafir</td>
<td>Beaver milo</td>
</tr>
<tr>
<td>Western Blackhull kafir</td>
<td>Wheatland milo</td>
</tr>
<tr>
<td>Pink kafir</td>
<td></td>
</tr>
<tr>
<td>Club</td>
<td></td>
</tr>
<tr>
<td>Darso</td>
<td></td>
</tr>
<tr>
<td>Intermediate varieties</td>
<td>Varieties sometimes escaping</td>
</tr>
<tr>
<td></td>
<td>injury because of earliness or other</td>
</tr>
<tr>
<td></td>
<td>causes</td>
</tr>
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<td></td>
<td></td>
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<td></td>
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</tbody>
</table>

of any of the varieties of sorghum tested, was distributed about 1928 and, according to the 1936 Yearbook of Agriculture, became the most popular sorgo in eastern Kansas, Missouri, and eastern Nebraska. It is notable for its white palatable seeds and its resistance to lodging. A part of its popularity in this area is a result of its high resistance to chinch bugs.

Most of the 15 or 16 kafir varieties studied were resistant, though they varied in ranking. Only Meade Red kafir was classified as intermediate in respect to resistance and the unusual variety, Double Dwarf Red, as susceptible. The latter is a weak type which does not develop well even in the absence of chinch bugs. Dawn kafir was perhaps the most resistant in this group.

The feterita varieties were susceptible or intermediate in their reaction but frequently escaped to some extent as a result of earliness or other causes.

As a group, the milo varieties were the most susceptible. Except in cases where some of them escape because of earliness, they were the first varieties to be killed in any test or, in cases where most of the plants in a test lived through the experiment, the milos were always the most severely injured.

The derivatives and hybrids involving feterita, kafir, and milo behave, as should be expected, in a variety of ways. In general, such varieties as Wheatland, which are suitable for harvesting with a combine and which were bred under non-chinch bug conditions,
have been highly susceptible. On the other hand, a Kansas Orange
sorgo x Dwarf Yellow milo hybrid bred at the Kansas Station for
resistance to chinch bugs was one of the most resistant strains
studied.

On several occasions and with a number of varieties it has been
shown that there has been a close relationship between the resistance
to chinch bugs and the grain yield. While this might be expected
in the case of severely injured varieties, it appeared to hold also for
the relatively resistant or less injured ones as well. Thus, even
when chinch bugs failed to injure visibly the more resistant varieties,
they were actually taking a toll in the yield of grain and perhaps
also in forage yield or quality. The value of resistant varieties
would exist even in years of light chinch bug infestation.

"Varieties of a sorghum apparently homozygous for agronomic
characters but which have never been subjected to chinch bug
injury have been shown to be heterozygous for the genetic factors
governing resistance or susceptibility when grown in the presence
of chinch bugs" (Snelling et al. 1937). This heterozygous con-
dition for resistance or susceptibility to chinch bugs has been demon-
strated in the case of three sorts of sorghum. In two cases the
strains involved were of known and recent hybrid origin. In the
case of Chiltex, a variety resulting from a kafir x feterita cross, the
two-year average per cent of dead plants was 76.5 for the un-
selected variety and 47.3 for the strain which had been selected
under heavy chinch bug infestation. A kafir-milo hybrid, Kansas
no. 27-317, was completely destroyed in both of the years 1933 and
1934 while a selection from this hybrid derived from a single plant
that had survived a heavy chinch bug infestation, had only 46.6 per
cent of the plants killed during the same period.

A similar resistant selection was obtained from Darso, a variety
which has been in cultivation for a long time. During the two-year
period the average per cent of killing was 58.5 for the ordinary
variety, Darso, and 28.4 for the selection which had originated
the preceding year from a single surviving plant.

In the case of Chiltex and Darso the resistant selections were
indistinguishable from the parent varieties except on the basis of
chinch bug reaction. The resistant selection of kafir x milo, Kans.
27-317, was not quite identical with its parental type. Those re-
sistant selections originating by a kind of natural selection illustrated
one method of securing resistant varieties, limited of course by the
agronomic characters of the parental type. Such an origin will not explain the wide range of resistant and susceptible types found among the sorghums when they were first introduced into this country.

Swenk and Tate (1940) recommended the use of resistant sorghums where possible for the control of chinch bugs and gave the following classification of the varieties then commonly grown in Nebraska:

<table>
<thead>
<tr>
<th>Resistant</th>
<th>Intermediate</th>
<th>Susceptible</th>
</tr>
</thead>
<tbody>
<tr>
<td>Western Blackhull</td>
<td>Kalo</td>
<td>Sooner milo</td>
</tr>
<tr>
<td>Club</td>
<td>Early Kalo</td>
<td>Day milo</td>
</tr>
<tr>
<td>Pink kafir</td>
<td>Hegari</td>
<td>Colby milo</td>
</tr>
<tr>
<td>Cheyenne</td>
<td>Leoti</td>
<td>Wheatland</td>
</tr>
<tr>
<td>Atlas</td>
<td>Black Amber</td>
<td>Feterita</td>
</tr>
</tbody>
</table>

Reports (Quinby 1941; Karper, Quinby, Stevens, and Jones 1941) from the Texas Agricultural Experiment Station indicated that the Club x Day hybrids bred at the Lawton (Oklahoma) Experiment Station were promising and highly resistant to chinch bugs. Two new varieties, Caprock and Plainsman, which were distributed to farmers in 1941 were reported to be able to withstand chinch bug infestations better than milo. These two varieties are selections from milo x kafir hybrids. McDowell (1944) reported that a new variety, Sweet Sudan grass (Leoti sorgo x Sudan 2), was more chinch bug resistant than ordinary Sudan grass.

At the Oklahoma Experiment Station studies have been continued on resistance of sorghums to chinch bugs (Sieglinger 1946) in cooperation with the federal Department of Agriculture. Three new varieties have been released (Salter 1948; Blizzard 1948) that are resistant to chinch bugs. These include Combine Winter kafir 44-14, which is reported to be more resistant than Martin or Wheatland milo, and Kaferita 811, a white-seeded variety that appeared to be the most resistant of any variety so far tested at Stillwater, Oklahoma. The third variety was a chinch bug resistant strain of Honey sorgo, which in addition to being insect resistant, produced a good grade of sirup and forage.

The white-seeded kafir 44-14 is a selection from the cross Sharon kafir x Dwarf feterita-kaoliang and is short enough to be harvested with a combine. It has given good yields in Kansas, where it was also approved for distribution to farmers in 1950.
There have been a series of years at Lincoln, Nebraska, in which severe chinch bug injury has occurred in the sorghum-improvement nurseries of the Agricultural Experiment Station. Some of the results have been reported. Webster and Kieselbach (1945) reported that the varieties Martin, Westland, and Day should not be grown in areas infested by chinch bugs because of the high susceptibility of these varieties. In such areas in southeast Nebraska, Western Blackhull, Pink kafir, Club, Early Kalo, and Kalo gave satisfactory yields. Webster (1947), studying the sorghum varieties under conditions during which the chinch bugs completely killed the plants in many plots of the milos and milo hybrids, found that a Kansas selection no. 433 was the most promising of all Sudan grass strains tested in 1946 from the standpoint of vigor, yield, forage quality, lodging resistance, and chinch bug resistance but that it had a prussic acid content even higher than that of Texas Sweet.

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Fig. 58. Reaction to chinch bugs of F1 sorghum plants and their parents, Lawton, Oklahoma, 1932. Left, Dwarf yellow milo; center, F1 Dwarf yellow milo x Dwarf Freed; right, Dwarf Freed. The F1 hybrid showed no hybrid vigor and was intermediate in reaction to chinch bugs. (From Snelling, Painter, Parker, and Osborn 1937.)
Inheritance of resistance to chinch bug injury. Three types of chinch bug reaction have been found among F1 plants resulting from crosses of different varieties of sorghums (Snelling et al. 1937). In certain crosses, such as Feterita x Dawn kafir, the F1 plants exhibited marked vigor and reached maturity without any apparent injury by the chinch bug. In the cross Dwarf Freed x Dwarf Yellow milo the F1 hybrids did not exhibit hybrid vigor and were eventually all killed by chinch bugs. However, the F1 plants were approximately intermediate in their chinch bug reaction between the two unequally susceptible parents. The third type of chinch bug reaction is represented by the Feterita x Dwarf Yellow milo F1 hybrid, which showed marked hybrid vigor and survived a heavy infestation that early in the season had destroyed all the parental plants of both varieties. Hybrid vigor, which in sorghums is expressed by luxuriant growth, large stalk, and abundant root system was apparently responsible for much of the chinch bug resistance.
of this hybrid. Because of the size of the stalk with more vascular bundles beyond the reach of the chinch bugs and because of abundant root system, larger than that of the parental plants, the F1 plants showed a type of tolerance that may be different from that exhibited by normally resistant varieties. In addition, it is possible that a part of the resistance of these vigorous F1 plants was the result of recombination of genetic factors for resistance, carried but not shown, by the susceptible parents (Figs. 56, 59).

Highly resistant field hybrids have been a striking feature of many plots of susceptible sorghums when these plants were left with little apparent injury after the destruction of the ordinary parental variety. A number of these plants which had survived in susceptible varieties have been studied during later generations. These F2 plants, as well as those in which both parents were known, have shown that hybrid vigor persisted in a considerable degree after the first generation hybrid. Hybrid vigor hence tended to increase the average resistance of the F2 population, thus obscuring genetic results (Fig. 60).

One hundred F1 lines of a cross Sharon kafr x Dwarf Yellow milo were studied at Lawton, Oklahoma, in 1934. Since the injury to both F1 plants and parents was progressive, becoming more severe as the season advanced, genetic results if based on percentage of dead plants would depend in part on the time in the season at which the data were recorded. When the percentages of F1 plants killed were recorded at the time of maximum difference in the injury to the two parents, the data suggested that resistance was dominant in this cross. This apparent dominance of resistance was perhaps the result, in part, of a persistence of the hybrid vigor which had been more evident in the two preceding generations. At about this time each F1 line in this cross was classified as resistant, intermediate or segregating, or susceptible. Grouped in this way and at this stage of injury the observed figures gave a very close fit to the ratio of three resistant or intermediate to one susceptible, and "might be taken to indicate that one main factor pair governs chinch bug resistance in this cross." Among the facts which indicated that this might not be the correct genetic interpretation was the occurrence of several lines apparently homozygous for the intermediate reaction to chinch bugs. In addition to this, nine F2 lines at the end of the season of exposure to chinch bugs had more nearly normal plant development than the resistant Sharon kafr parent.
"The superiority of some of the F₃ lines was due to their earliness and ability to head under adverse environmental conditions imposed by both drought and chinch bugs." (Snelling et al. 1937.)

A considerable number of hybrids of generations beyond F₃ have been studied both at Manhattan and at Lawton. In several cases there has been abundant evidence of transgressive segregation for resistance. In fact, the two strains with the best chinch bug records were hybrids. One was Kansas Orange x Dwarf Yellow milo (Kans. no. 24-136), the other, Red Amber x Feterita (Kans. Botany no. 2513). Both of these hybrids were more resistant than either parent but neither was of sufficient agronomic value to be recommended for distribution. They did, however, indicate the possibility of the development of strains more resistant to chinch bugs than any so far available. On the other hand, some of the advanced hybrids which had been produced without reference to
INSECT RESISTANCE IN CROP PLANTS

their chinch bug resistance were more susceptible than either parent. Thus, while chinch bug resistance could not be placed on a definite genetic basis, there was abundant evidence of its inheritance. Some important facts on the inheritance of the antibiotic form of resistance are discussed following the next few paragraphs.

Studies on the basis of chinch bug resistance. Since the injury to sorghums was the result of the feeding of chinch bugs, it was to be expected that resistance to their attack would likewise be concerned somehow with the act of taking food. In contrast to the individuals of some species of Hemiptera, which have caused injury to plants far out of proportion to the size of the insect, the damage done by chinch bugs has been the result of a mass attack by a large number of insects. With the young plants it seemed evident that death was the result of the withdrawal of liquids from the plant more rapidly than they could be replaced. Among larger plants various reactions were to be found depending upon variety, condition of growth, or intensity of infestation. Severe stunting with red or yellow coloration of the leaves has been a frequent result of chinch bug attack.

"Experiments and observations indicate that injury may result from a combination of one or more of at least four factors:

"(1) The direct withdrawal of plant fluids from cells and especially from the xylem and phloem tubes by the chinch bugs.

"(2) The exudation of plant fluids from punctures left open after the feeding of the insects, with possible attendant interference with root pressure and translocation.

"(3) A clogging of the plant conductive tissue with stylet sheath material deposited by the bugs.

"(4) Openings in the plant tissues are provided through which fungi and bacteria can enter. Wound response involving deposition of pigments frequently takes place in the region of chinch bug punctures." (Snelling et al. 1937.)

On several occasions the plant characters of varieties and hybrids have been studied in an attempt to find some relationship between one or more visible characters and chinch bug resistance. Some association has been found between chinch bug resistance and color of stigma, sweetness of stalk, height of plant, tightness of the leaf sheath, and perhaps a few other characters. In no case, however, has there been a close enough association to aid in the selection of resistant plants, and it is possible that the relations which have
been found were merely present because of the particular group of varieties studied.

Varietal preference, as it may apply to resistance, has been partially explored in two ways: (1) by a study of the olfactory responses of the chinch bugs, and (2) by counts and observations of the number of bugs on varieties of contrasting reaction. Among different varieties of sorghums the distribution of the chinch bugs in experimental plots presented many irregularities. The insects themselves were difficult to count in the field. On some occasions at Manhattan the bugs appeared to show a preference for certain varieties, especially when only a few of the insects were present. On the other hand, where the bugs were present in large numbers it was difficult to observe any consistent difference in the number of bugs on the various varieties. Two sets of counts have been made on the numbers of bugs present on adjacent plants of Dwarf Yellow milo (susceptible) and Kansas Orange sorgo (resistant), one count at Manhattan, the other at Lawton. In both cases the total number of bugs found was greater on the resistant variety than on the susceptible one. Studies with a field olfactometer indicated that under the duress of starvation chinch bugs showed only a weak olfactory response. On the other hand, laboratory tests by Dahms, Snelling, and Fenton (1936b) showed that adult chinch bugs had a preference for Dwarf Yellow milo, feterita and Blackhull kafir over Atlas sorgo. In these laboratory tests, however, the bugs had an opportunity for feeding as well as being attracted by the odor of the plants.

Studies of the location and character of the feeding punctures of the chinch bugs on resistant and susceptible sorghums have given some information, principally of a negative character, on the mechanism of resistance. The stylet sheath, which consists of material largely or wholly of insect origin and which forms about the stylets of the insect in the plant tissue, was not found to differ materially in composition or persistence in different varieties. The stylets of the chinch bugs apparently pierced with ease the lignified tissue on their way to the phloem bundles.

The location and number of punctures was studied on Dwarf Yellow milo and Kansas Orange. Averages of 444 ± 39 punctures on Dwarf Yellow milo and 387 ± 35 for Kansas Orange were recorded. The difference between the two varieties was not significant. However there appeared to be a significant difference in
the location of the punctures of the chinch bugs on the two varieties. On the resistant Kansas Orange the punctures were fairly equally distributed on the leaf blades and leaf sheaths; on the plants of milo there were about three times as many punctures on the leaf sheaths as on the blades. This difference could perhaps be explained on the basis of the morphology of the two plant varieties. Since the leaf sheaths of milo fit more loosely about the stem, the chinch bugs were permitted to congregate behind the leaf sheath, thus being protected and puncturing the sheaths from both sides. Injury to the milo plants through disruption of the transport system by the feeding of the bugs hence would be greater than in the case of Kansas Orange. This was especially true since the vascular bundles are fewer in number on the leaf sheath than on the blade in all varieties. This relation between the location of the punctures and morphology of the plant appeared to be one of the factors in the difference in injury between these two varieties. This type of difference was not to be found, however, between certain other pairs of resistant and susceptible varieties; loosely fitting sheaths being present principally among the milo varieties and their derivatives.

Table 19 EFFECT OF SORGHUM VARIETIES ON EGG DEPOSITION, LONGEVITY, AND DEVELOPMENT OF CHINCH BUGS AT LAWTON, OKLAHOMA, 1936 AND 1937

(From Dahms 1948)

<table>
<thead>
<tr>
<th>Variety of sorghum</th>
<th>Average number of eggs laid per female on seedling plants</th>
<th>Average length of life of female in days on seedling plants</th>
<th>Days required for development from hatching to adult on seedling plants</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dwarf Yellow milo</td>
<td>99.4</td>
<td>56.8</td>
<td>31.50</td>
</tr>
<tr>
<td>Wheatland</td>
<td>93.0</td>
<td>65.9</td>
<td>31.83</td>
</tr>
<tr>
<td>Honey sorgo</td>
<td>46.0</td>
<td>54.3</td>
<td>33.27</td>
</tr>
<tr>
<td>Blackhull kafir</td>
<td>21.2</td>
<td>48.2</td>
<td>33.90</td>
</tr>
<tr>
<td>Sharon kafir</td>
<td>16.3</td>
<td>40.9</td>
<td>37.90</td>
</tr>
<tr>
<td>Kansas Orange x</td>
<td>7.3</td>
<td>32.5</td>
<td>36.73</td>
</tr>
<tr>
<td>Dwarf Yellow milo</td>
<td>3.9</td>
<td>25.9</td>
<td>37.87</td>
</tr>
<tr>
<td>Atlas sorgo</td>
<td>1.7</td>
<td>27.3</td>
<td>41.40</td>
</tr>
<tr>
<td>Feterita</td>
<td>0.3</td>
<td>21.4</td>
<td>37.05</td>
</tr>
</tbody>
</table>
RESISTANCE TO INSECTS IN SORGHUMS

Probably the most striking difference between susceptible and resistant varieties was that reported by Dahms, Snelling, and Fenton (1936 a,b; Dahms 1948). This difference lay in the effect of the chinch bug resistant varieties on various phases of the biology of the insect. On resistant varieties, when compared with susceptible ones, the longevity of adults was reduced, the speed of nymphal development as well as the size of the resulting adults decreased, and the number of eggs deposited greatly curtailed. There was also a very much higher mortality on resistant varieties than on some of the susceptible ones. Characteristic results, as recorded in a later publication (Dahms 1948), are given in Table 19. It will be noted that in the case of feterita the average number of eggs laid per female and the average length of life resembled the resistant varieties rather than the susceptible ones. In the field feterita behaves as a susceptible variety. Its behavior however in this respect has not been uniform and these data in regard to the biology of the insects may perhaps explain part of the erratic behavior of this variety.

The effect of varieties used as food on the biology of the chinch bug was studied for four different ages of the plant (Dahms 1948). Generally the difference in effect tended to decrease as the age of the plant increased. The difference between varieties was almost always greater when seedling plants were used. This is illustrated by Table 20. Only the differences in number of eggs and in time required for development were significant statistically in the rearings on the older plants, although in general the differences found agreed with those found earlier when bugs were reared on seedlings of the same varieties. The one exception was feterita, which behaved like a resistant plant in the seedling stage but like a susceptible when tested as an older plant. This difference in the reaction of bugs reared on feterita helps to explain the possibility of transgressive segregation for resistance when this variety is used as one parent of a hybrid.

Dahms and Fenton (1940) have shown by field and laboratory experiments that the tolerance of both the resistant Atlas sorgo and the susceptible Dwarf Yellow milo and Finney milo was decreased by the addition of sodium nitrate to the soil in which the plants were growing. The addition of superphosphate generally increased the tolerance of both resistant and susceptible varieties. In the field the differences within a variety as induced by fertilizer treat-
ment was far less than the difference between resistant and susceptible varieties. In a laboratory study of oviposition and longevity of chinch bugs fed on Atlas sorgo and Finney milo plants that were grown in various nutrient solutions, Dahms (1947) found that the females laid more eggs on plants growing in solutions high in nitrogen or low in phosphorus than on plants growing in solutions low in nitrogen or high in phosphorus. The longevity of female chinch bugs feeding on Atlas did not appear to be influenced much by the contents of the nutrient solutions used. In general, the bugs lived longer on those Finney milo plants on which the rate of oviposition was low. In the case of both longevity and oviposition the differences induced by the nutrient solutions in either variety were less than the differences between the resistant and susceptible varieties used.

Dahms and Martin (1940) reported on a study of the oviposition of chinch bugs on plants of 11 F₁ hybrids and their parents. They found that the ability to cause a decrease in the number of eggs laid was inherited usually as a dominant character. Neither the number of eggs laid nor the longevity of the females appeared

Table 20  A COMPARISON OF STATISTICAL SIGNIFICANCE OF DIFFERENCE IN FIVE FEATURES OF THE BIOLOGY OF CHINCH BUGS WHEN FED ON YOUNG AND OLD PLANTS OF SUSCEPTIBLE AND RESISTANT VARIETIES OF SORGHUM
(From Dahms 1948)

<table>
<thead>
<tr>
<th>Differences in</th>
<th>When chinch bugs fed on</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>seedling plants</td>
</tr>
<tr>
<td>Numbers of eggs laid</td>
<td>highly significant</td>
</tr>
<tr>
<td>(more eggs laid on susceptible varieties)</td>
<td>significant</td>
</tr>
<tr>
<td>Length of life of adult female</td>
<td>highly significant</td>
</tr>
<tr>
<td>(longer on susceptible varieties)</td>
<td></td>
</tr>
<tr>
<td>Length of body of adults</td>
<td></td>
</tr>
<tr>
<td>(longer on susceptible varieties)</td>
<td></td>
</tr>
<tr>
<td>Days required for development from hatching to adult</td>
<td>extremely different</td>
</tr>
<tr>
<td>(shorter on susceptible varieties)</td>
<td>significant</td>
</tr>
<tr>
<td>Percentage of mortality</td>
<td>highly significant</td>
</tr>
<tr>
<td>(lower on susceptible varieties)</td>
<td></td>
</tr>
</tbody>
</table>
to be affected by the extent of hybrid vigor of the F₁ plants as measured by height of plant, diameter of stalk, and number of tillers.

Extensive chemical analyses of different sorghum varieties at various stages of growth have been made (Webster and Mitchell 1940; Webster and Heller 1942; Webster and Wall 1942; Webster, Sieglinger, and Davies 1948) in an effort to associate some chemical characteristic with resistance to chinch bugs in sorghums. However, Webster et al. (1948) stated that "no positive relationship between chemical composition and chinch bug injury has been found." This is perhaps not surprising since the entire plant was analyzed and the chemical basis for resistance to chinch bugs may be an attribute of specific cells or tissues. Differences between these and other tissues may obscure important characteristics when mixtures of both are analyzed.

The following factors have been shown to have a definite bearing on some cases of the difference in resistance between resistant and susceptible sorghums. They are listed somewhat in the order of their importance. Their relationship is indicated in the accompanying diagram (Fig. 61).

1. Resistant varieties have the ability to withstand and perhaps repair injury done by the chinch bugs, so that such varieties grow and reproduce in spite of the chinch bug infestation. As suggested by a study of the F₁ hybrids, a part of this tolerance may be the result of a better developed root system, a better utilization of food, and greater general vigor.

2. The difference in the food value for the chinch bugs of the various varieties is very marked. Certain resistant varieties under lab-
oratory tests almost inhibit reproduction and greatly increase the mortality of the insect when plants are in the seedling stage and make less marked changes when the plants used as food are older.

(3) At least under certain conditions chinch bugs exhibit a preference for certain susceptible varieties.

(4) Some morphological characters of the plants of some varieties, such as loosely fitting sheaths, may increase the possibility of damage done by chinch bugs.

(5) Some varieties evade chinch bug injury through their carliness or through their adaptation to certain particular environmental conditions, especially drought.

(6) Various environmental factors, such as certain fertilizers, condition the expression of resistance or susceptibility to some extent.

Since some individual varieties show several of these different mechanisms, the result must be cumulative, thus increasing the resistance over that due to a single mechanism. Almost certainly these several mechanisms of resistance are not governed by the same genetic factors. Analyses of some of the mechanisms of resistance of sorghums to chinch bugs have been fairly thorough but progress can still be made in improving the level of resistance, particularly among the dwarf sorghums that may be harvested with a combine.

RESISTANCE TO OTHER INSECTS IN SORGHUMS

Reports of resistance to insects other than the chinch bug among the varieties of sorghums have been widely scattered and have been studied to only a slight extent.

Resistance to Orthoptera and to other Hemiptera. The striking difference in the susceptibility of corn and sorghums to grasshoppers has been mentioned in the section dealing with the resistance of corn to grasshoppers. In the United States this greater resistance of sorghum has been shown against all species that have been observed in outbreak numbers, but chiefly in respect to Melanoplus differentialis (Thomas), M. biivittatus (Say), and M. mexicanus (Sauss.). However, Uvarov (1928) records an Asiatic species of grasshoppers (Colemania spharioidei I. Bd.) that feeds chiefly on sorghums. In the central United States during the grasshopper outbreaks of the early 1930's, the difference in injury between corn and sorghum by grasshoppers was so great that there was a considerable increase in the acreage of the sorghum crop. Hume and Franzke (1934) reported that the acreage of sorghums increased
in South Dakota from 69,000 acres in 1930 to 166,000 acres in 1933. This was because of the greater resistance of sorghums to adverse conditions, especially grasshoppers and drought.

Under heavy grasshopper attack certain varieties of sorghum are injured more than others. Hayes (1922) wrote that Sudan grass and the milos were more susceptible to grasshopper attack than were kafir, feterita, or the sweet sorghums. Brunson and Painter (1938) reported that “in general, injury to the sorgos and the kafirs was less than to milo and to some of the newer varieties originating from hybrids involving milo.” These observations were made in the various varietal nurseries and the grasshopper species usually most abundant were *M. diferentialis* and *M. bivittatus*.

Dahms (1943) studied the injury to heads of sorghums caused by the feeding of the rice stinkbug *Soluba pugnax* (F.), which had not been reported previously as injuring this crop. Twenty-five bugs or more caged on a head of Sumac sorgo prevented the production of normal seeds. The bugs fed on the immature ovaries. Plots of different varieties on different dates of planting were available for study. In general, plants that matured later for reasons of date of planting or varietal characteristics were more severely injured. There were, however, differences in the injury to varieties having the same maturity. This was true, for example, of three strains of White Darso. The selection Kans. 33-378 was much less injured and gave a higher yield than the other two in the same test.

**Resistance to the corn leaf aphid, *Aphis maidis* Fitch.** The corn leaf aphid has been discussed in connection with the resistance of corn to that insect. The aphid is, however, perhaps more common on sorghums than on corn. It is a pest in North and South America, Japan, South Africa, and Hawaii. McColloch (1921) reported that infestation in heads of kafir resulted in a loss of 33 per cent of the weight and 50 per cent of the volume of the seeds. Hayes (1922) showed by experiments a reduction of about 4 per cent occurred in the germination of injured compared with uninjured seeds of Blackhull kafir. Injury by the insect is also associated with discoloration of the plant and decay of stalks and of heads that emerge poorly from the upper leaf sheath.

Davis (1909) reported that this insect preferred broomcorn to other sorghums or corn. On the broomcorn crop the discoloration which often follows feeding of the insect on the parts that are made
350 INSECT RESISTANCE IN CROP PLANTS

into brooms is undesirable. McColloch (1921) reported on the percentage of plants injured among 17 varieties of sorghum. These data have been reproduced in Table 21. In observations in Kansas

<table>
<thead>
<tr>
<th>Variety</th>
<th>Per cent of plants injured</th>
<th>Variety</th>
<th>Per cent of plants injured</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sudan</td>
<td>3</td>
<td>Yellow milo</td>
<td>78</td>
</tr>
<tr>
<td>Dwarf Sumac</td>
<td>21</td>
<td>Blackhull kafir</td>
<td>78</td>
</tr>
<tr>
<td>Kansas Orange</td>
<td>26</td>
<td>Freed</td>
<td>79</td>
</tr>
<tr>
<td>Dawn kafir</td>
<td>46</td>
<td>Red kafir</td>
<td>85</td>
</tr>
<tr>
<td>Sumac</td>
<td>46</td>
<td>Red Amber</td>
<td>86</td>
</tr>
<tr>
<td>Dwarf Blackhull kafir</td>
<td>65</td>
<td>Shrock</td>
<td>92</td>
</tr>
<tr>
<td>Sunset kafir</td>
<td>67</td>
<td>Darso</td>
<td>96</td>
</tr>
<tr>
<td>Hegari</td>
<td>67</td>
<td>Feterita</td>
<td>97</td>
</tr>
<tr>
<td>Pink kafir</td>
<td>75</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

in 1949 the resistance of Sudan varieties was again evident and the variety Norghum showed considerable resistance.

Venkatraman and Thomas (1932), in a study of intergeneric hybrids between sugar cane (*Saccharum, P.O.J. 2725*) and *Sorghum* (variety Periamanjal or Durra) reported that the sorghum was infested by colonies of aphids. The sugar cane was not infested and only a few of the hybrids supported aphids. According to Plant Breeding Abstracts (Anonymous 1946) an attempt is being made in Swaziland, South Africa, to improve the quality of a local dwarf aphid-resistant kafir by crossing it with other strains.

**Resistance to species of Lepidoptera.** The corn earworm *Heliothis armigera* (Hbn.) is often destructive to sorghums in the United States by feeding on the developing seeds and, to a lesser extent, in the curl. The biology of this species has been discussed in the section on resistance to it in corn and in cotton. Often six to eight larvae can be removed from one sorghum head. It has been observed that presence of larvae and damage were more prevalent in heads that were compact and dense rather than in those in which the panicle was loose. An experiment by Quinby and Gaines (1942) gives a possible explanation. Nearly 200 heads of Sumac...
sorgo were covered with paper bags for two weeks and the yield compared with neighboring unbagged heads. The bagged heads had up to six earworm larvae in each and yielded 0.002 pound per head. The unbagged heads had fewer larvae and yielded 0.074 pound per head. The experimenters believed that this difference was the result of the activities of predators and parasites living on the caterpillars in the unbagged heads but not on those in the bagged ones. Larvae in loose heads would be similarly unprotected.

Hsu (1935, 1936) has studied the infestation by borers in more than a thousand strains of sorghum in north China in 1933 and 1934. Several species were involved, of which *Pyrausta nubilalis* (Hbn.), the European corn borer, and "*Diatraea diatrea*" were the most important. The varieties were not classified in regard to infestation by the several species of borer. Apparently it was assumed that strains of sorghum resistant to one species would also be resistant to the others. Reasons for questioning the validity of such assumptions have been discussed in one of the general chapters. Hsu showed however that the difference in infestation between strains was statistically significant. Twenty-three strains out of 981 in a replicated test had less than 4 per cent infestation and 29 had more than 25 per cent. Under controlled infestation in a cage and by hand infestation with larvae, it was shown that the difference between strains was probably one of preference for oviposition. The lack of borers appeared to be associated with the presence of white grain and high infestation with tall plants. Correlation between the results of tests in 1933 and 1934 was significant and indicated the probability that resistance was inherited.

The southwestern corn borer *Diatraea grandiosella* Dyar will develop in sorghums in Kansas but the larvae average only about half the size of those found in corn (Wilbur, Bryson, and Painter 1950). It is doubtful whether these borers in sorghum survive to form moths the following spring. In a comparison between corn and sorghums some form of preference on the part of the borer must be present for the insect is always more plentiful in sorghums planted next to corn. No information on differential infestation of sorghum varieties is available.

**Resistance to the sorghum midge, *Contarinia sorghicola* (Coq.).**

This minute fly, which belongs with the gall-making Diptera and is distantly related to the hessian fly, appears to have been introduced into the United States from southern Asia where the same or a re-
lated species occurs. The insect also has been reported in North Africa and South America. In North America the sorghum midge occurs in the southeastern states and west to central Kansas and western Texas. In addition to sorghum it occurs on Johnson grass and has been reared from two grasses, *Triodia flava* (L.) and *Setaria lutescens* Weigel. The eggs are usually laid when the plants are in bloom and are deposited inside the glumes. The larvae feed on the developing ovary of the flower and pupation occurs inside the spikelet. A cocoon sometimes is formed there and normally the insect passes the winter in the sorghum head. The larvae may remain dormant in the cocoon for more than a year.

Ball and Hastings (1912) reported that Sumac sorgo appeared to be resistant. The short glumes of this variety were suggested as a possible reason for its resistance. Karper *et al.* (1932) reported that Darno and Schrock may be resistant since they yielded better under midge infestation. Cowland (1936) in the Anglo-Egyptian Sudan stated that some varieties of Sudan appeared more resistant than others. Walter (1941) studied infestation among 47 varieties of sorghum, including such diverse types as broomcorn, several koaliangs, White Durra, Sudan grass, and the more widely grown kafirs, milos, feteritas, and sorgos. He reported that no varietal resistance was found in the varieties studied. No attempt has been recorded to study the possibility of selecting for resistance within varieties.

The outlook for breeding for insect resistance in sorghums is well stated by Dahms (1943) as follows: “The use of resistant varieties to lessen injury from insects that attack sorghums would appear to deserve more attention, because the control of insects on a crop of low value per acre precludes the use of insecticides. Furthermore, there is a possibility that the growing of resistant varieties would reduce the insect population; this certainly would appear to be true in growing chinch bug-resistant sorghums, since the resistant varieties have been shown to have an adverse effect on the chinch bug.”

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CHAPTER VIII

RESISTANCE TO INSECTS IN POTATO

I. Introduction.
   A. Varieties and species of Solanum.
   B. Insects for which resistance has been reported.
II. Resistance of potatoes to leafhoppers, Empoasca fabae (Harr.).
    A. Taxonomy and biology of Empoasca spp.
    B. Resistance to Empoasca fabae in potato varieties and hybrids.
III. Resistance to Colorado potato beetle in potato and in other species of Solanum.
    A. Biology of the beetle.
    B. Differences in injury to varieties of Solanum tuberosum.
    C. Resistance to Colorado potato beetle in Solanum spp. and in interspecific hybrids.
IV. Resistance to flea beetles in potato.
V. Resistance to aphids in potato.
VI. Resistance to the potato psyllid.
VII. Resistance to other insects in potato.
    A. Resistance to wireworms.
    B. Resistance to the potato tuberworm.
    C. Resistance to the Rutherglen bug.
VIII. Bibliography.

The "Irish" potato (Solanum tuberosum L.) is one of the half-dozen leading food plants of the world. It is grown most extensively in Europe and America and to a less extent in the cooler parts of other continents. The original home is in the Andean region of South America, where varieties of S. tuberosum L. and S. andigenum Juz. and Buk. and a few other species are grown for food by the natives.

Varieties and species of Solanum. A number of species of Solanum occur especially in the highlands of South and Central America and some are tuber-bearing. Collections of these species have been
made by plant breeders from the U.S.S.R., Great Britain, the U.S. Department of Agriculture and others. At Cambridge, England, some fifteen hundred lines are maintained (Hawkes 1947). The species of Solanum form a polyploid series with 12 as the basic chromosome number (Table 22). Those varieties of S. tuberosum cultivated in the northern hemisphere that have been studied have 48 chromosomes as the somatic number, but varieties of this species are known with 24, 36, and 60 chromosomes (Hawkes 1947). Certain wild species are being used in programs for breeding frost, disease, and insect resistance. Many of the wild species have 24 as the somatic number (Stevenson and Clark 1937) but polyploid strains are known in some cases (Hawkes 1947). Apparently there is a multiformity of types in the mountain valleys of South America, so that a diversity of reaction to insects and other conditions as well as crossability would not be surprising.

Various types of sterility are common in commercial varieties grown in the United States. Some varieties have not been known to set seed but, in general, more seed is produced in northern climates or at higher elevations. Partially offsetting this barrier of frequent sterility is the ease of vegetative production, which permits the rapid multiplication of clones bearing the desired characters. In areas where potatoes are grown commercially, workers have difficulty in producing seed, and thus cooperation with breeders in other regions is often required. In the United States a national breeding program was set up which since 1934 has included a project concerned with insect resistance. In Europe an international program for control of the Colorado potato beetle included work on breeding for resistance to this insect. In the U.S.S.R. interspecific hybridization has been done in part for breeding for insect resistance (Bukasov 1940). In reporting some of the varieties recently distributed in the United States the reaction to some insects have been given (Gardner, Schmidt, and Stevenson 1945; Jehle and Stevenson 1945; Hardenburg and Stevenson 1943; and Bushnell, Sikesman, and Stevenson 1945). Recently several varieties carrying genes from Solanum demissum have been released (Reddick and Peterson 1947). In view of the known resistance to insects in the wild-species parent it will be of interest to see whether any of this resistance has been accidentally carried over into these varieties.

The insects injurious to the potato belong generally to two
### Table 22

**SOME SPECIES OF Solanum REPORTED TO HAVE SOME RESISTANCE TO INSECTS**

<table>
<thead>
<tr>
<th>Name</th>
<th>Chromosome number</th>
<th>Colorado potato beetle, <em>Leptinotarsa decemlineata</em></th>
<th>Potato leafhopper, <em>Empoasca fabae</em></th>
<th>Potato flea beetle, <em>Epitrix cumanensis</em></th>
<th>Hybrids with <em>luteum</em> reported by</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>barbatus</em></td>
<td>24</td>
<td>resistant (Brues.)</td>
<td>moderately susceptible 28</td>
<td>resistant 3</td>
<td>Hawks 1947</td>
</tr>
<tr>
<td><em>bulbocastanum</em></td>
<td>24</td>
<td>resistant, poisonous (?)</td>
<td>near immune 0</td>
<td>moderately susceptible 48</td>
<td>Livermore and Johnstone 1940</td>
</tr>
<tr>
<td><em>Caldavii</em></td>
<td>24</td>
<td>resistant to moderately susceptible</td>
<td>highly resistant 0.2</td>
<td>moderately susceptible 44</td>
<td>Marchal et al. 1935</td>
</tr>
<tr>
<td><em>chacoense</em></td>
<td>24</td>
<td>resistant, poisonous (?)</td>
<td>resistant 1.4</td>
<td>moderately resistant 42</td>
<td>Trouvelot 1938</td>
</tr>
<tr>
<td><em>Commerciumii</em></td>
<td>36</td>
<td>resistant, poisonous (?)</td>
<td>resistant 6</td>
<td>moderately resistant 11, 18</td>
<td>Reddick 1947</td>
</tr>
<tr>
<td><em>demissum</em></td>
<td>24, 60, 72</td>
<td>resistant</td>
<td>highly resistant 0.2</td>
<td>moderately resistant 10</td>
<td>Reddick et al. 1947</td>
</tr>
<tr>
<td><em>ferrugieri</em></td>
<td>48</td>
<td>resistant</td>
<td>resistant 1.4</td>
<td>moderately resistant 18</td>
<td></td>
</tr>
<tr>
<td><em>Henrii</em></td>
<td>24</td>
<td>resistant</td>
<td>highly resistant 0.2</td>
<td>highly resistant 0.2</td>
<td></td>
</tr>
<tr>
<td><em>Jamei</em></td>
<td>24</td>
<td>resistant</td>
<td>susceptible 50 to moderately</td>
<td>susceptible 97 to moderately resistant</td>
<td></td>
</tr>
<tr>
<td><em>polyanthum</em></td>
<td>48, also</td>
<td>susceptible</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>tuberosum</em></td>
<td>24, 36, 60</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1. Sleeman (1940); the figures indicate approximate intensity of infestation or injury.
2. Trouvelot; Brues et al.
groups: those that are confined largely to the Solanaceae, like the Colorado potato beetle (*Leptinotarsa decemlineata* (Say)), and those that have a wider range of food plants, like the potato leafhopper (*Empoasca fabae* (Harr.)). A very important phase of the relation of insects to potato is concerned with the transmission of the several virus diseases. Various strains of potato have sometimes been reported as showing more or less "field immunity" to some of these diseases without indication of the possible resistance to the vectors.

Varieties of potato or species of *Solanum* have been reported as showing resistance to at least 14 species or groups of species of insects. These are as follows:

**Hemiptera**
- Lygaeidae
  - *Nysius vinitor* Berg. (Rutherglen bug)

**Homoptera**
- Cicadellidae
  - *Empoasca fabae* (Harr.) (Potato leafhopper)
  - *Empoasca punjabensis* Pruthi
- Psyllidae
  - *Paratriozona cockerelli* (Sulc.) (Potato psyllid)
- Aphididae
  - *Macrosiphum solani* (Asm.) (= *gei* auct.) (Potato aphid)
  - *Myias persicae* (Sulz.) (Green peach aphid)

**Lepidoptera**
- Gelechiidae
  - *Gnorimoschema operculella* (Zell.) (Potato tuberworm)
-Coleoptera
- Elateridae
  - *Agrionodes obscurus* (L.) (Wireworm)
  - *Ludius arietinis destructor* Brown (Wireworm)
  - *Limonius agonus* (Say) (Eastern field wire worm)
- Chrysomelidae
  - *Leptinotarsa decemlineata* (Say) (Colorado potato beetle)
  - *Epitrix cucumeris* (Harr.) (Potato flea beetle)
  - *Epitrix tuberi* Gentry (Tuber flea beetle)
  - *Epitrix subcrinita* (Lee.) (Western potato flea beetle)

**RESISTANCE OF POTATOES TO LEAFHOPPERS**

The destructive leafhoppers on potato belong for the most part to the genus *Empoasca*, which occurs in both North and South America, Europe, Asia, Australia, and Africa. There are about 200 Nearctic species known, of which at least 15 are of economic
importance in their relation to potatoes or other crops. An equal number of species outside the Nearctic region are reported to be destructive to crops. In 1931, DeLong showed that it was impossible to separate many of the species except by examination of the internal male genitalia, while Smith and Poos (1931) and Poos and Wheeler (1943) have shown that these species were distinct in many aspects of their biology. Much of the information recorded here regarding these insects is taken from these papers and those on the biology of *Empoasca fabae* by DeLong (1938) and by Slesman (1937a). At least four species outside the United States are recorded as injurious to potato. These are *E. benedettoi* Paoli in Palestine, *decipiens* Paoli in Italy, *flavescens* (Fabr.) in Europe and North Africa, and *punjabensis* Pruthi in India. Resistance of certain varieties of potato to the last named species has been reported (Vivai 1942).

**Taxonomy and biology of *Empoasca* spp.** In the United States the following seven species have been reared on potato by Poos (1943) and others: *abrupta* DeLong, *bifurcata* DeLong, *delongi* Poos, *fabae* (Harr.), *filamenta* DeLong, *recurvata* DeLong, and *solana* DeLong. Most of the species of *Empoasca* that have been studied feed primarily on mesophyll tissue and produce a stippling or mottling of the leaves. Three species, *fabae*, *recurvata*, and *solana*, appear to be primarily phloem-feeding species and produce more severe symptoms. Of the species named, *fabae* is by far the most abundant and injurious in the area where it occurs. On potato the injury is called "hopperbum" and was first described and defined by Ball (1918). It consists of a wrinkling of the leaves, which later roll upward, dry, and burn, beginning at the tip of the leaf. This sometimes causes the death of the leaf and finally the defoliation of the plant. Some of the other food plants show similar symptoms. The potato leafhopper *fabae* has been recorded as reared from more than 100 different species of plants but, as shown by Poos and Smith (1931), the insect does not thrive equally well on all. These workers list the order of preference for oviposition, as measured by the number of nymphs hatched, with potato first, followed in order by Whippoorwill cowpea, dahlia, non-pubescent soybean (P.I. 55069), alfalfa, Stringless Greenpod bean, Dixie soybean, and red clover (Fig. 62).

The host plants also differed in value as food for the developing nymphs. The percentages of nymphs that reached the last nymphal
instar or the adult stage on these hosts were Hairy Peruvian alfalfa 91, potato 82, Whippoorwill cowpea 81, Kansas Common alfalfa 77, non-pubescent soybean (P.I. 55069) 72, Russian red clover 66, Tennessee red clover 58, white clover selection 57, Dixie soybean 57, Herman soybean 51, Michigan red clover 50, Stringless Green-pod 37, and Zigzag clover (*Trifolium medium*) 18 per cent. The

![Image](image_url)

**Fig. 62.** Degrees of pubescence shown by *left*, Hairy Peruvian alfalfa; *right*, Kansas Common alfalfa; and *below*, *Empoasca fabae* (Harris). Although pubescence is frequently mentioned in connection with the resistance of some legumes to this insect, it does not appear to be a factor in the resistance of alfalfa or potatoes. (Photo by F. W. Poos; Poos and Smith 1931.)

disease-like injury resulting from the feeding of *fabae* differs on the various host plants and is known by various names. In addition to the hopperburn of potato, a similar condition on peanuts is known as “peanut pouts” and the stunting and discoloration of alfalfa as “alfalfa yellows.” The factors responsible for the damage by *Empoasca* spp. has been the subject of several investigations which have been reviewed by Carter (1939), Putman (1941), and Medler (1941), but the usefulness of resistant varieties in such a study has
not been sufficiently exploited. *Empoasca solana* has been shown to inject diastase and probably invertase into the feeding medium (Herford 1935). It is not certain what other substances may be injected that may prove toxic. Materials injected into the plant, including the sheath substance that forms about the stylets, result in the disruption of the conducting system of the plant. The feeding of *E. fabae*, according to Johnson (1934), leads to an accumulation of food materials, especially sugar and starch, in localized regions beyond the feeding area and eventually in the orange and red coloration characteristic of injury on alfalfa and other legumes.

The feeding of *E. fabae* on apple (Marshall *et al.* 1942) resulted in a more detrimental effect on leaf metabolism (photosynthesis and transpiration) than did the feeding of an equal number of individuals of either of two other species of leafhoppers. In common with other Homoptera, leafhoppers pump out of the plant large quantities of plant sap and excrete large quantities of liquid. This contributes to the wilting of the susceptible plants and the apparently greater drought hardiness of leafhopper-resistant varieties. The possible reduction in yield of potatoes caused by *Empoasca fabae* has been estimated at up to 50 per cent (Sleesman and Stevenson 1941) but the recent use of more efficient insecticides indicates that such an estimate was far too low (Wilson and Sleesman 1947; Wolfenbarger and Heuberger 1946; Linn *et al.* 1948) even for light infestations by the insect.

*Empoasca fabae* occurs widely throughout the eastern half of the United States up to about 2,000 feet elevation. It has not been shown to hibernate in the northern states but migrates from the south each year. Eggs are laid in the leaf veins and petioles. At Columbus, Ohio, there are usually two complete and often another incomplete generation each year. The average length for each brood varies from 21 to 36 days, with the temperature and the season as well as with the kind of host and probably the condition and age of the host. Several methods of measuring resistance of potato varieties and species to leafhoppers have been used. The rapidly moving adults are difficult to catch in a net or to count in the field. Since nymphs are less active they may be counted on the individual leaves (Sleesman and Bushnell 1937). Such a count reflects both the amount of adult preference for oviposition and the usability of the variety as food for the young insects. Two methods of estimating injury have been used. Allen and Riemann (1939)
have carefully divided and weighed the portions of leaves of varieties and calculated the percentage of the total leaf tissue showing hopperburn. Sleesman and his co-workers have recorded hopperburn in three, four, or six classes of injury (Sleesman and Stevenson 1941). In some cases diseases, particularly late blight, if present, may interfere with estimates of injury. Sleesman (1940b) has compared various species of *Solanum* by placing newly hatched nymphs on plants and recording survival after ten days.

**Resistance to *Empoasca fabae* in potato varieties and hybrids.** Ball (1919), in connection with the first detailed evidence of the relation of *Empoasca* to hopperburn, noted considerable difference in varietal susceptibility to attack. Listed in order, Triumph was the most susceptible followed by Irish Cobbler, Early Ohio, Green Mountain, and Rural. Ball reported that the difference appeared to be related to the amount of foliage available for egg deposition by the spring brood of leafhoppers. Dudley and Wilson (1921) also reported some difference in injury among the varieties observed.

Later investigators have confirmed the relationship of injury to maturity and the general rating of the varieties as found by Ball. Sleesman and Bushnell (1937) found a highly significant correlation \( r = -0.67 \) between leafhopper populations and maturity among 15 varieties studied. Bliss Triumph carried a higher population than would be expected. Similar results were reported by the senior author in other papers (Sleesman 1937, 1938). By careful measurements of the percentage of hopperburned leaf tissue obtained from 17 varieties, Allen and Rieman (1939), in Wisconsin, showed that Pioneer Rural, Houma, Katahdin, and Russet Rural had low proportions of necrotic tissue and Triumph, Warba, and White Blossom Cobbler were highly susceptible. Of particular interest in that paper was the report that selections of individual hills from segregating populations of potatoes that were resistant or susceptible to leafhoppers in one year retained their respective ratings the following year. Five of these selections had less than 2 per cent of injured leaf tissue in plots where leaves of the Irish Cobbler check ranged from 48 to 85 per cent necrotic tissue. A large proportion of the selections had less injury than the most resistant commercial variety tested. Likewise some of the selections made for susceptibility developed more hopperburn than did the most susceptible variety tested. At the same time other selections
were made from miscellaneous strains, including some of South American origin.

A later report from Wisconsin (Allen et al. 1940) dealt particularly with the relation of maturity to resistance. By means of planting-date experiments these authors found that the percentage of hopperburn was reduced on all varieties by deferring the planting date and that stage of maturity was not a prime factor in resistance. Nymphal populations were correlated with the percentage of hopperburn under these varying dates of planting.

A new variety, Sequoia, was released to farmers in 1939 (Gardner et al. 1945) after having attracted attention by its resistance to leafhoppers during tests in North Carolina in 1930 and 1932, and was found to possess other desirable qualities. It has been reported resistant to leafhoppers also in Indiana, Illinois, and Ohio (Stevenson 1947). In the Ohio tests in 1940 it showed a fair degree of tolerance in spite of carrying a considerable population of nymphs (Sleesman and Stevenson 1941), where both the number of nymphs and the degree of hopperburn were somewhat lower than usual.

The relative rating of various commercial varieties as reported in the papers mentioned above is given in Table 23.

A longer account by Sleesman and Stevenson (1941) gave interesting details regarding sources of resistance to leafhoppers and the behavior of populations of potato plants which were segregating for resistance. These were studied during the period 1934 to 1940 in Ohio and Maryland. Seedlings from self-pollinated plants of the variety Katahdin showed large enough differences in hopperburn injury to suggest that the variety was heterozygous or mixed in genes for leafhopper resistance. Plants of the crosses President x Katahdin, Ackersegen x Katahdin, and Ackersegen x Earlaine showed evidences of segregation in 1934 to 1936, the populations of the first two crosses being significantly more resistant than the Green Mountain checks. Both these involved only the moderate degree of resistance available at the time the crosses were made. All these populations appeared to give segregates that could have had higher resistance to hopperburn than was available in Green Mountain.

Five selfed lines from the cross President x Katahdin tested in 1936 and 1937 likewise showed a segregation for resistance and susceptibility and each family was significantly more resistant than Green Mountain. Other crosses tested during those years similarly showed segregation for resistance with the cross 3897-90 (a selection
### Table 23: Leafhopper Populations on and Injury to Potato Varieties

<table>
<thead>
<tr>
<th>Variety</th>
<th>Relative maturity</th>
<th>Nymphal populations</th>
<th>% Total hoppers born, Allen and Reiman 1940</th>
<th>Class of hoppers born (All 1940)</th>
<th>% of foliage damaged 8/27-8/6p</th>
<th>Planted at Urbana, Ill., Apr. 13</th>
<th>Mean per acre untreated with EDT</th>
<th>Mean number of hoppers per leaf</th>
<th>Planted at Des Plaines, Ill., May 25</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blue Triumph</td>
<td>early</td>
<td>155</td>
<td>3.0</td>
<td>100</td>
<td>46.0</td>
<td>severe</td>
<td>158</td>
<td>46.4</td>
<td>moderate</td>
</tr>
<tr>
<td>Irish Cobbler</td>
<td>early</td>
<td>103</td>
<td>3.0</td>
<td>97</td>
<td>33.7</td>
<td>severe</td>
<td>218</td>
<td>46.0</td>
<td>severe</td>
</tr>
<tr>
<td>Wapato</td>
<td>early</td>
<td>76</td>
<td>3.0</td>
<td>100</td>
<td>46.0</td>
<td>severe</td>
<td>158</td>
<td>46.0</td>
<td>moderate</td>
</tr>
<tr>
<td>Earline</td>
<td>early</td>
<td>69</td>
<td>3.0</td>
<td>97</td>
<td>22.3</td>
<td>moderate</td>
<td>149</td>
<td>46.0</td>
<td>severe</td>
</tr>
<tr>
<td>Chipewa</td>
<td>medium</td>
<td>71</td>
<td>2.0</td>
<td>43</td>
<td>22.3</td>
<td>moderate</td>
<td>149</td>
<td>46.0</td>
<td>moderate</td>
</tr>
<tr>
<td>Powhatan</td>
<td>late</td>
<td>55</td>
<td>3.0</td>
<td>80</td>
<td>22.3</td>
<td>moderate</td>
<td>149</td>
<td>46.0</td>
<td>moderate</td>
</tr>
<tr>
<td>Sebago</td>
<td>late</td>
<td>55</td>
<td>3.0</td>
<td>80</td>
<td>22.3</td>
<td>moderate</td>
<td>149</td>
<td>46.0</td>
<td>moderate</td>
</tr>
<tr>
<td>Kasslick</td>
<td>late</td>
<td>33</td>
<td>1.7</td>
<td>70</td>
<td>22.3</td>
<td>moderate</td>
<td>149</td>
<td>46.0</td>
<td>moderate</td>
</tr>
<tr>
<td>Romaini Rustler</td>
<td>late</td>
<td>20</td>
<td>2.0</td>
<td>80</td>
<td>22.3</td>
<td>moderate</td>
<td>149</td>
<td>46.0</td>
<td>moderate</td>
</tr>
<tr>
<td>Rustic New Yorker</td>
<td>late</td>
<td>17</td>
<td>1.7</td>
<td>70</td>
<td>22.3</td>
<td>moderate</td>
<td>149</td>
<td>46.0</td>
<td>moderate</td>
</tr>
<tr>
<td>Green Mountain</td>
<td>late</td>
<td>20</td>
<td>1.7</td>
<td>70</td>
<td>22.3</td>
<td>moderate</td>
<td>149</td>
<td>46.0</td>
<td>moderate</td>
</tr>
<tr>
<td>Housa</td>
<td>late</td>
<td>15</td>
<td>2.0</td>
<td>80</td>
<td>22.3</td>
<td>moderate</td>
<td>149</td>
<td>46.0</td>
<td>moderate</td>
</tr>
<tr>
<td>Septoria</td>
<td>late</td>
<td>35</td>
<td>1.7</td>
<td>70</td>
<td>22.3</td>
<td>moderate</td>
<td>149</td>
<td>46.0</td>
<td>moderate</td>
</tr>
</tbody>
</table>

- *Allen and Reiman 1940.
- *Allen, Rieser, and McFarlane 1940.
- *Liin, Apple, and Arnold 1940 (difference for significance in leafhopper populations at 5 per cent level for April 13 planting, 3.7; for May 23 planting, 5.2).
from German seed) x (President x Katahdin (sel. 336-18)) giving the highest degree of resistance to hopperburn (Fig. 63).

A study was made of the relationship between resistance to leafhoppers and resistance to late blight in several of these crosses. The correlations were not significant or only barely so. Hence the genetic characters governing these conditions do not appear to be linked. This necessitates the separate testing for these two desirable characters but presents no apparent barrier to finding strains carrying both.

The results indicated above are concerned only with resistance to injury by the leafhopper, but there are also differences in populations of leafhoppers to be found on various plants.

Thirty-two seedlings that in 1937 had shown nymphal populations greater than 10 per leaf and 62 seedlings that had shown less than 3 per leaf were re-examined in 1938. This second year the level of leafhopper population was generally higher, the average number of nymphs for the susceptible group being 12.6 ± 0.79, and for the low group 6.5 ± 0.45. The seedlings with few exceptions belonged in comparable classes both years.
The seedlings from five crosses and two selfed lines were tested for nymphal populations in 1938 and 1939, and for hopperburn as well the last year. In this experiment the correlations between years were all non-significant for comparisons of leafhopper populations on the segregating hybrids. The correlations were barely significant in one case and non-significant in the other between the nymph counts and hopperburn on the same plants. The authors recommended that for definite conclusions regarding leafhopper populations it was necessary to make counts over a period of years. They also rightly concluded that "the differences in seedling reaction to hopperburn are not all caused by the differences in leafhopper populations." This conclusion would be strengthened by noting that the leafhopper populations depended both on the attraction of the female for oviposition and on the usability of the plant as food by the young leafhopper. The amount of hopperburn depended not only on tolerance of the various plants and size of the insect population but on environmental factors affecting both. These factors were evidently different during the two years. Experience with populations of plants segregating for resistance to various insects has shown that such segregating plant populations are more sensitive to environmental conditions than are plants more homozygous for resistance or susceptibility. These potato populations then may have been segregating for at least three different genetic factors or groups of factors.

In the same paper Sleesman and Stevenson reported a study of varieties and unnamed seedlings in 1940, in which there was further evidence that tolerance to hopperburn was independent of the nymphal population on the strains studied. Irish cobbler with an average population of 45 nymphs per 5 leaves was severely injured but the variety Nonesuch with only 13.3 nymphs had equal injury. The varieties Sequoia and Blue Salad showed only slight hopperburn in spite of nymphal populations of 40 to 48, respectively.

In a progress report Sleesman and Bushnell (1945a) classified Sequoia as the most resistant and also as a high-yielding variety: Ackersegen as resistant but not high-yielding; Potomac, Mohawk, Green Mountain, Menominee, and Norkota as intermediate; Bliss Triumph, Irish Cobbler, Warba, and Earlaine as early and susceptible; and Pontiac, Sebago, and Katahdin as late and susceptible.

In connection with spraying experiments involving 10 varieties with leafhopper populations ranging from 68 for Bliss Triumph
to 0 on Sequoia, yields were reported on sprayed and unsprayed varietal plants (Wilson and Sleesman 1947). Leafhoppers, flea beetles, and late blight were the objects of the spray program. The three varieties with the highest leafhopper population showed the greatest percentage of increase from spraying. The average number of leafhoppers on the three most severely infested varieties was 44 per 10 leaves and the yield increase 134 per cent, whereas the three varieties with the lowest population (less than 1 per 10 leaves) had a yield increase of 97 per cent. This indicates the importance of leafhopper control but also the possibility of further improvement of the leafhopper-resistant varieties by adding more genes for yield.

Linn, Apple, and Arnold (1948) reported a comparison of leafhopper populations, hopperburn, and yield for 17 varieties, both in the presence and absence of treatment with DDT. Two dates of planting and two localities were involved. In both dates of planting the variety Sequoia showed moderate leafhopper populations and only mild hopperburn. Of particular interest is the fact that Sequoia gave approximately twice the average yield of other varieties when exposed to leafhopper damage. Furthermore, at the earlier date of planting Sequoia gave only 11 per cent increase in yield when treated with DDT for leafhopper control. The later planting of Sequoia gave an increase of 74 per cent in the plot treated with DDT over the untreated plot. This increase, however, was the least of any of the 11 varieties in this particular test. Statements similar to that concerning the yield can be made concerning pounds of starch per acre. This would indicate that breeding for resistance approaches in value as a control measure the treatment by insecticides. For some reason the control of leafhoppers, both by resistant varieties and by insecticides, was not as good on the second date of planting as on the first. Examples of the data presented are given in the general table of leafhopper populations on and injury to potato varieties (Table 23).

Some new varieties, notably Erie, Ontario, Menominee, Mesaba, and Pawnee, showed low levels of population or moderate to mild hopperburn, or both. An investigation of varietal resistance to leafhoppers has also been carried on in Nebraska (Burr 1944; Hill 1945).

Sleesman (1940b) recorded the leafhopper population of 12 wild species of Solanum in comparison with S. tuberosum in 1938 and of S. polyadenium and S. tuberosum in 1936 and 1937. The
most susceptible wild species, *S. bulbocastanum*, had slightly more than half as many leafhopper nymphs as *S. tuberosum*. The other species had less than half as many as the cultivated potato and most of the species had very low populations. It is notable that the two varieties of *neantipoviczii* and *demissum* differed somewhat in the number of leafhoppers present. The relative populations of several species is recorded in Table 22, which gives other information about these species of *Solanum*.

In an experiment to determine the ability of the leafhoppers to live on some of these species, 20 young nymphs were placed on each of five plants of four different species of *Solanum*. After ten days the mortality recorded was *S. tuberosum* (Irish Cobbler) 3 per cent, *S. demissum* 63 per cent, *S. caldasii* 88 per cent, and *S. polyadenium* 100 per cent. Some of these wild *Solanum* species may furnish excellent sources of resistance to leafhoppers, for they apparently have genes for antibiotic factors not possessed by *S. tuberosum*.

**RESISTANCE TO COLORADO POTATO BEETLE IN POTATO AND OTHER SPECIES OF SOLANUM**

The Colorado potato beetle, *Leptinotarsa decemlineata* (Say), is a native American insect that spread across the eastern half of the United States in the middle of the 19th century when cultivation of potato reached its native habitat near the foothills of the Rocky Mountains. The buffalo bur, *Solanum rostratum* Dunal., is the original host and still a favorite food plant of this beetle. In 1922 the Colorado potato beetle was discovered in a large area in France after being eradicated several times from various places in Europe during the preceding decades. It has since spread into Belgium, Holland, Germany, and other countries of western Europe.

Except for this single form the forty or more *Leptinotarsa* species known are to be found only in North and South America as far south as Peru. Several species have been reported as feeding on different members of *Solanaceae*.

**Biology of the beetle.** Some of the most recent accounts of the life history of the Colorado potato beetle are by Gibson and others (1925) and Trouvelot (1934-35). The beetle hibernates underground as an adult and may occasionally live over a second winter. In the early spring the adults fly to their food plants, feed, mate, and
Fig. 64. The Colorado potato beetle, *Leptinotarsa decemlineata* (Say), an American species also occurring in Europe. A, various stages of the beetle on a potato plant; B and C, pupae; D, adult; and E, mature larva. (After Eusig. By permission of the Macmillan Company.)

The female places the masses of orange-yellow eggs on the underside of the leaves and each may lay a thousand or more eggs. A definite preference is shown for the large terminal leaflets as a site for oviposition. The larvae hatch in a few days, feed
on the egg shells, and then strip off the lower part of the leaf blade, leaving the upper epidermis intact. Shortly afterward the young larvae migrate to the top of the plant and feed on the younger leaves. At first the midribs of the leaves are left but the older larvae may eat even the stems of the plants. It is estimated (Gibson 1925) that ten larvae consumed approximately 43 square inches, or about 8 grams, of leaf tissue and that a single insect during its lifetime as adult and larvae consumed at least 22.8 square inches, or 4.23 grams. Pupation occurs in the soil. Ordinarily one and sometimes a partial second generation occurs but under controlled conditions, four or five generations have been reared in one season. The amount of foliage consumed by both larvae and adults and the high fecundity are important elements in the destructiveness of this insect which, if not controlled, can quickly defoliate a potato field (Fig. 64).

McIndoo (1926, 1935) has studied the relative attractiveness of some of the food plants of the Colorado potato beetle by experimental methods and furnished evidence that odor is an important element in the attractiveness of the various plant species to the adult. Among the cultivated crops beside potato the insect has been reported as injuring tomato (Lycopersicum esculentum Mill.) and egg-plant (Solanum melongena L.). Sometimes it has been impossible to rear the beetle on tomato (Gibson et al. 1925), but Kozlovsky (1936), Alford (1943), and Boczkowska (1946d) have reported that varieties differ widely in their usability as food by the larvae, although all were inferior to potato in this respect.1

Differences in injury to varieties of Solanum tuberosum. In the early literature concerning this insect in North America, the difference in injury to some varieties (Saunders and Reed 1871) is occasionally referred to, but the ease of control of the beetle with arsenicals led to a neglect of biological studies of the insect and no extensive tests have ever been reported in North America.

In Europe the question of the susceptibility of varieties of potato, Solanum tuberosum, has recently been studied more intensively. Trouvelot and his associates (1936, 1937) found little difference in

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1A report by Chin (1950), received after this manuscript was completed, has given a report on a thorough and detailed study of the physiological and behavioral relations between larvae of Leptinotarsa decemlineata and various food plants. The findings of other investigators as reported in this book were amplified, in a few cases corrected, and new facts brought to light.
attractiveness among the commonly cultivated varieties except that which could be attributed to time of development of foliage and size of plant. Elsewhere the varieties Pepo and Wohltman have been reported to show less injury than other varieties (Feytaud et al. 1935). Schaper (1938c) found six cultivated varieties of potatoes that might be worth further investigation. The differences appeared to be differences in level of susceptibility or low resistance. Boczkowska (1945a) compared ten Polish varieties of potato in regard to various effects on the life history of the Colorado potato beetle. Most varieties showed varying levels of susceptibility. The variety Odyniec, however, reduced the relative fecundity of adult females that fed upon it, and larvae that feed on the variety Marszalek gave a low percentage of adults and showed a high first-instar mortality. It was also shown (Boczkowska 1946b) that this partial resistance was sometimes caused by the lower preference of the adults for certain varieties (varieties Marszalek, Wohltman) and sometimes by the more vigorous development of the variety, even though it was preferred by the beetle (varieties Sobieszynske, Rosafolia). In other papers (Boczkowska 1945b, 1946a) the varieties Bintje and Eerstelingen were reported to have had 30 and 44 percent fewer eggs laid on them in fields than did the variety Institute de Beauvais. In the cages the percentages were 25 and 36, respectively, compared to Institute de Beauvais at 100. The behavior of the insect differed on two varieties, Ackesegeen and Institute de Beauvais, although these were both fairly susceptible. Fewer eggs were deposited on the second variety but the larvae developed better on the first one. There was a difference in the recovery of these two varieties after defoliation but this reaction may be different in other localities.

Resistance to Colorado potato beetle in *Solanum* spp. and interspecific hybrids. In 1940 Brues reported on the food preferences of the Colorado potato beetle for different wild and cultivated species of *Solanum*. Several of these species did not support a population of beetles and on some of them the insects that had fed were unable to survive hibernation. Among the more resistant species in his tests were *S. marginatum* and *S. barbisetum*. The most extensive studies on species of *Solanum* and on interspecific hybrids have been made by Trouvelot and his co-workers in France, and by Schwartz, Muller-Bohme, Schaper, and Sellke in Germany. The reports of this work occur in a number of papers.
and often with few or no bibliographic references, making it difficult to collate the information. This research is, however, one of the more extensive studies of its kind that has been made to date. The studies on *Solanum* spp. were begun in France soon after 1930 (Marchal 1933; Marchal et al. 1935), and with the spread of the Colorado potato beetle into other European countries an international conference on the subject was called in Brussels by the Belgian government in 1936. An international committee for the study of the control of the insect was formed and several reports have been issued (Feytaud et al. 1938). This work was interrupted in 1939 by the war but a report on the status of the German experiments has been given by Black and Driver (1946).

The exact classification of the different species of *Solanum* in regard to resistance to *L. decemlineata* is difficult on account of the great range of behavior patterns and effects shown by the insect when exposed to, or when feeding on, the various species. A number of species appear to be more susceptible than the cultivated potato, *S. tuberosum*. Trouvelot and his co-workers (1933a) group the species approximately as follows:

1. The young larvae least restless and made best growth on *S. marginatum* and *S. stramonifolium*.
2. Almost as good growth on *S. cornutum*, *dulcamara*, *gilo*, *andigenum*, and *rostratum*.
3. Larvae more restless and made less rapid growth on *S. tuberosum* (potato), *laciniatum* and *etuberosum*.
4. Length of larval development great on *S. pyracanthum*, *balbisii*, *heterodoxum*.
5. Development short but many young larvae died on *S. aropurpureum*.
6. Larvae restless and fed feebly on *S. ciliatum*, and *caldasii*.
7. Only partial development permitted on *S. mammosum*, *demissum* var. *klotzkii*.
8. Larvae fed some days but died before reaching one-half normal size on *S. commersonii*, *bonariense*, *cerveantesii*, *robustum*, *guineense*, *auriculatum*, and *aviculare*.
9. Only feeble feeding and only slight growth on *S. hendersonii*, *capsicastrum*, *memphiticum*, *nodiflorum*, and *robertiella*.
10. Very feeble feeding and no growth on *S. insulae-paschali*, *radicans*, *pseudocapsicum*, *nigrum*.
11. Abandoned without tasting *S. aculeatissimum* and *rantonetti*. 
Schaper (1938b) gave the following classification of the species of Solanum tested through 1937.

<table>
<thead>
<tr>
<th>Group I</th>
<th>Strongly susceptible</th>
</tr>
</thead>
<tbody>
<tr>
<td>marginatum</td>
<td>stramonifolium</td>
</tr>
<tr>
<td>cornutum</td>
<td>dulcamara</td>
</tr>
<tr>
<td>gilo</td>
<td>andigenum</td>
</tr>
<tr>
<td>rostratum</td>
<td></td>
</tr>
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</table>

<table>
<thead>
<tr>
<th>Group II</th>
<th>Moderately susceptible</th>
</tr>
</thead>
<tbody>
<tr>
<td>tuberosum</td>
<td>etuberosum</td>
</tr>
<tr>
<td>lacinatum</td>
<td>acaule</td>
</tr>
<tr>
<td>chacoense</td>
<td>ajuscoense</td>
</tr>
<tr>
<td>antipovicii</td>
<td>vallis mexici</td>
</tr>
<tr>
<td>neanepovicii</td>
<td>candelarium</td>
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<td>reddickii</td>
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</table>

<table>
<thead>
<tr>
<th>Group III</th>
<th>Moderately resistant</th>
</tr>
</thead>
<tbody>
<tr>
<td>pyracanthum</td>
<td>baldisi</td>
</tr>
<tr>
<td>heterodoxum</td>
<td>atropurpureum</td>
</tr>
<tr>
<td>caldasii</td>
<td>commersonii</td>
</tr>
<tr>
<td>verrucosum</td>
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</table>

<table>
<thead>
<tr>
<th>Group IV</th>
<th>Resistant</th>
</tr>
</thead>
<tbody>
<tr>
<td>mammosum</td>
<td>demissum var. kloekii</td>
</tr>
<tr>
<td>commersonii</td>
<td>bonariense</td>
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<td>guineense</td>
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<td>aviculare</td>
</tr>
<tr>
<td>hendersonii</td>
<td>capiscastrum</td>
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<tr>
<td>memphitium</td>
<td>nodiflorum</td>
</tr>
<tr>
<td>roberti-eliae</td>
<td>polyadenium</td>
</tr>
<tr>
<td>henryi</td>
<td>demissum</td>
</tr>
<tr>
<td>jamesii</td>
<td>milanii</td>
</tr>
</tbody>
</table>

Additional information presented in a later paper (Trouvelot et al. 1933b) indicated that only rarely were mechanical obstacles, such as long and dense plant hairs, present in some species of Solanum, of importance in the biology of the insects. Often there was no relationship between the attractiveness of the species for oviposition and the usability as food for the larvae. In some species the plants were neglected by the adult but favorable for larval development. In others eggs were laid on species that would not support larval development. Other species reported as
resistant by other workers were polyadenium, henryi, jamesii, and millianii. Schaper (1939) has reported that caldesii and commersonii were definitely poisonous to the insect and, according to the same writer, different plants of demissum and chacoense varied in their resistance to this insect. Some of these wild species are tuber-bearing and have desirable characters not found in the cultivated potatoes with which some of the wild species have been crossed. The hybrids have varying degrees of fertility. The general level of resistance and other characters of some of these species are given in Table 22.

Trouvelot and Grison (1935) have studied the attractiveness of six species of Solanum to the Colorado potato beetle. The species edinense was highly attractive, followed by tuberosum, utile demissum, caldesii, jamesii, and commersonii, ranking in that order of attractiveness. On the last species no eggs were laid. These species were compared in the same cages.

A detailed biological study of the behavior and physiology of Leptinotarsa decemlineata (Say) on the cultivated potato, S. tuberosum, on S. demissum, and on hybrids between these two species has been made. Demissum was only slightly less attractive for the beetles than was tuberosum and eggs were readily laid upon it. The first instar larvae, however, quickly showed the effects of feeding. The larvae feed very little, taking up about half a square millimeter of surface, after which many abandoned the plant. According to Bushel and Chevalier (1938) this abandonment was as high as 99 per cent. The larvae that did not leave the plant fed and grew very slowly, and the few that reached maturity required about twice as long and weighed less than half as much as did larvae reared on tuberosum. When second instar larvae were transferred to demissum the length of life in this instar was doubled and the final weight reduced by about 60 per cent in comparison with those that had fed on potato. One of the hybrids reported in this paper was similar to demissum but the effects on the insect were not quite so severe. The coloration of the larvae feeding on demissum was abnormal resulting from lack of secretion of subcutaneous glands and from lack of formation of fat reserve as well as perhaps other changes in the pigment. Besides their restlessness and tendency to abandon feeding the larvae showed other abnormal behavior. Some of them vomited or secreted drops of saliva and reacted differently to vibrations. There were alterations in the excreta and a re-
duction in the rate of heart beat when the insect fed on _demissum_ (Trouvelot and Busnel 1937).

The effects on the fourth-instar larvae were studied by Trouvelot and Brejoux (1939). Insects of this age were found to eat only about 12 per cent as much foliage of _demissum_ as did larvae feeding on potato. These larvae on _demissum_ had relatively long periods of immobility while larvae artificially underfed on potato moved about continually but immediately began feeding when they had the opportunity. Immobile larvae transferred from _demissum_ to _tuberosum_ usually did not begin to eat until after a period of 45 minutes to 2½ hours. The intensity of these reactions varied with different larvae and with different varieties of _demissum_.

Busnel (1938) compared the amount of reserve food accumulated as a result of the feeding of this insect on the two species and found that lipoids and glucosides were reduced one-third to one-fourth among the insects that fed on _demissum_ in contrast to those feeding on _tuberosum_. This indicated that such insects went into hibernation poorly prepared for the winter. Trouvelot (1938a) considered that the establishment of a permanent colony of the potato beetle on this plant species would be impossible.

Roucourt and Trouvelot (1936) and Chauvin (1945) studied the chemical characteristics of the material that attracted the insects to potato. In detailed experiments on 250 varieties or species of plants there appeared to be no orientation of the larvae from a distance. The insects are retained on certain plants only after tasting their leaves. The active principle which caused the larvae to feed was extracted with hot alcohol and some of its chemical and physical characters studied. This active principle was identified at various stages of the study by soaking disks of elder pith in the liquid containing the test substances. Under such tests the larvae fed as readily on the disks saturated with the extracted material as on disks treated with the pressed juice of potato leaves. The various other extracted liquids used in these experiments were studied by similar means. These workers do not believe that this active material is solanin and this observation has been confirmed by Hagenuth (1941). Extracts from various species of _Solanum_ differed in their attractiveness to the beetles. The extract from _edinense_ was more attractive to the beetles than the extract from _tuberosum_. The extract from _commersonii_ was about as attractive as that from _tuberosum_, that from _antipoviczii_ and _caldasii_ less
than half as attractive, and the extracts from aculeatissimum and cestrum parkii were not attractive at all. It is believed that the peculiarities of behavior of adults and larvae on the species demissum and tuberosum can be explained by the presence of an attractive principle in both the species named and a repellent or actually toxic principle present in the leaves of demissum. The toxicity of demissum, however, has been questioned by Sellke (1941) and Muller and Sellke (1941). The foliage of demissum apparently might be sufficiently nutritive for normal growth of the larvae if they could or would eat enough of it. They are prevented from doing this either by substances that are poisonous or which repel them. According to Trouvelot (1939a, 1939b) some attributes of the deleterious materials are known. They exist only in plants living in sunny situations and occur little, if at all, in the flower petals. They are attenuated by etiolation. Spectrographic examination of some of the hybrids has indicated that certain of them carry a good part of the resistance present in the parent demissum.

Resistance to the Colorado potato beetle in hybrids was first reported by Marchal and others (1935) in crosses involving demissum and commersonii, and cultivated potatoes. Various attributes of these and other interspecific hybrids have been reported in papers by Trouvelot and his associates, by Schwartz (1939), Scaper (1939), Sellke (1939, 1940), Muller and Sellke (1941), and Crepin (1942). Hybrids involving demissum x tuberosum generally showed an intermediate degree of resistance in the first generations but clones differed in this character, and later generations or back-crosses were often more susceptible. Progenies from the cross S. polyadenium x jamessi were highly resistant as were some of the triple hybrids S. acuale x demissum x tuberosum. The various clones of S. chacoense differed in resistance in the same way as reported for different clones of S. demissum (Muller and Sellke 1941; Torka 1943). Stelzner (1943) reported that crosses between S. tuberosum and chacoense usually give triploids (2n = 36) in the first generation with occasional tetraploids (2n = 48) which were fertile. The cross between demissum (2n = 72) and chacoence (2n = 24) produced a tetraploid which was reported to be fertile and resistant to Leptinotarsa. Colchicine treatment of chacoense also produced tetraploids, some of which would cross with tuberosum. The resistance in hybrids involving chacoense behaved as a recessive character (Black and Driver 1946). Some-
what over 1500 different clones of these hybrids were studied before 1940.

Some of the hybrids were reported to have had yields of tubers that approached those of cultivated potatoes and to have possessed other desirable characters not found in *tuberosum*. It is evident that larger populations and perhaps other parental combinations may be necessary before the high resistance to the Colorado potato beetle is transferred to commercial varieties of potatoes. The fact that genes for disease resistance from *demissum* have been successfully transferred to several commercial varieties in North America (Reddick and Peterson 1947) suggests that similar success may be possible for resistance to insects, although Josse (1948) is inclined to question this possibility.

**RESISTANCE OF POTATOES TO FLEA BEETLES**

Most of the flea beetles that attack potato belong to the genus *Epitrix*, which occurs in Europe, and North and South America, the various species feeding especially on plants of the families Solanaceae and Cucurbitaceae. At least six species of these flea beetles have been reported as injuring potatoes in various localities in North America, the species that is most abundant being different in different areas. Resistance has been reported principally to two black species which, according to Gentner (1944), have been confused or carried under one name, *Epitrix cucumeris* (Harr.). This name apparently should be carried by a species distributed from Canada to Florida and westward into North Dakota, South Dakota, Nebraska, and Kansas. It is known as the potato flea beetle and injures primarily the foliage of the plant. No serious tuber damage has been reported except in North Carolina (Kulash 1947), where the tobacco flea beetle, *E. hirtipennis* (Harr.), also was present and may have been responsible for the damage. *Epitrix tuberis* Gent. occurs in Oregon, Washington, Colorado, and western Nebraska, where the adults do some damage to the foliage but where the larvae do serious damage to the tubers by burrowing into the flesh. These burrows are only about a fourth of an inch deep but become filled with corky material, forming “pimples” or long serpentine tunnels just beneath the surface of the tuber. Both these species, *cucumeris* and *tuberis*, have been collected on numerous hosts. Landis and Hill (1946) showed that the food plants do not all serve equally well in supporting the flea beetle population.
Hanson (1933) reported differences in varietal injury to tubers that most certainly were caused largely by *E. tuberis*. Gold Coin had the least, an average of 12.70 injuries per tuber, while Beauty Hebron had the most, 48.95. Netted Gem had an average of 17.25 injuries per tuber. A recent paper (Davis, Landis, and Randall 1948) presents evidence that a potato variety, Doe Bay Red, was resistant to the potato-feeding activities of *E. tuberis* in the state of Washington. This variety originated locally. Tests were made in 1946 of this variety and Netted Gem, Chippewa, Burbank, and White Rose, in which the numbers of flea beetles emerging from various hills of potato were collected and the damage done to foliage and tubers reported. The foliage of all varieties showed some injury with the variety Chippewa showing somewhat less than the others. Of the two adult flea beetles emerging from hills of different varieties of potatoes, *E. tuberis* was about ten times as numerous as *E. subcrinata*, the western potato flea beetle. Significantly, more adult flea beetles emerged from nine hills of Doe Bay Red (a total of 1629 specimens) than came from a similar number of hills of any other variety. Somewhat fewer adults of *subcrinata* emerged from these same hills than came from other varieties. The number of larval tunnels, however, were significantly less on Doe Bay Red than on other varieties. On this variety there were twenty tunnels per tuber compared with 61 and 84 on the other varieties. The yield of Doe Bay Red was somewhat below the other varieties. The authors showed that “this resistance to injury could not be attributed to such differences as tuber set, tuber size, or tuber yield.”

Against populations of *E. cucumeris* Sleesman (1937b) reported differences in the number of flea beetle punctures per leaf on 19 varieties in Ohio in 1936. These ranged from 9 on Russet Rural to 26 on Chippewa. No relationship was indicated between plant maturity and flea beetle injury. Wilson and Sleesman (1947) gave a report of differences in injury to ten varieties. This information is reported in Table 24. In the same table there are recorded the counts, made by Maughan (1937), of the number of flea beetles per plant and flea beetle holes per leaflet on potatoes in Orange County, N.Y., in 1935–36. No particular species of flea beetle is mentioned but presumably *cucumeris* was the one involved. Of particular importance in this paper, however, is the suggestion that the same number of beetles per plant may do different amounts of damage on the several varieties.
<table>
<thead>
<tr>
<th>Varieties</th>
<th>Relative number of flea beetle punctures per leaf 1936</th>
<th>Orange Co., N.Y. 1935</th>
<th>Flea beetles</th>
<th>Orange Co., N.Y. 1936</th>
<th>Flea beetles per plant</th>
<th>Wooster, Ohio July 15, 1946</th>
<th>Flea beetles per 1.5-centimeter disk</th>
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<tbody>
<tr>
<td>Sequoia</td>
<td>9 3</td>
<td>77</td>
<td>0.9</td>
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<td>11</td>
<td>10</td>
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<tr>
<td>Rustic Rural</td>
<td>10 2</td>
<td>52</td>
<td>2.6</td>
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<td>11</td>
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<tr>
<td>Biara Triumph</td>
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<tr>
<td>Katahdin</td>
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<td>17</td>
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<tr>
<td>Cobblor</td>
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</tr>
</tbody>
</table>

1 Slesman (1937b).
2 Maughan (1937).
3 Wilson and Slesman (1947).
Hill (1945) reported records of the numbers of feeding holes of potato flea beetles, probably *E. cucumeris*, on leaves of different varieties of potato. These ranged from 166 to 2,386, with Irish Cobbler having the least. The resistance of the variety Sequoia has been mentioned in a number of publications, especially as grown in North Carolina, Indiana, Ohio (Stevenson 1947), and Virginia (Anderson and Walker 1940).

The injury by *E. cucumeris* to 11 species of *Solanum* has been reported by Sleesman (1940b). The reaction of some of these species is given in Table 22. *Solanum polyadenium* was reported to be highly resistant in tests extending over two years. Tests in the laboratory in 1939 indicated that the odor, possessed by this plant species and produced by an oil or ester, had something to do with the lower injury on this variety. Most of the small amount of feeding reported in the field was on the mature lower leaves where the odor was less pronounced. In the laboratory adult feeding on the leaf disks 1.25 centimeters in diameter showed 28.9 punctures on immature leaves of *polyadenium*, 100.9 punctures on mature leaves and 132.8 on immature leaves that had been washed with soap and water. Comparable areas of the leaf surface on *S. tuberosum* (Irish Cobbler) showed 456.4 punctures. Other species of *Solanum*, especially *bulbocastanum*, *fendleri*, *demiscum* and *neosativicizii*, showed moderate resistance but apparently much more than that shown by ordinary varieties of *tuberosum*.

RESISTANCE OF POTATOES TO APHIDS

A considerable number of species of aphids have been reported as feeding on potatoes. Simpson and Shands (1946) have reported on the biology of four species that may reach large populations individually or collectively on potato in Maine. The two species most commonly reported, however, are the green peach aphid, *Myzus persicae* (Sulz.), and the potato aphid, * Macrosiphum solanifolii* (Ash.) (= *gei* auct.). Both are widely distributed throughout the world and both are factors in the transmission of virus diseases of plants. Both spend the winter in the egg stage, the peach aphid on various stone fruits and the potato aphid on wild roses. A number of generations occur each year. These two insects differ in the character of their injury. Young and Morris (1930) reported that in Montana "*Macrosiphum solanifolii* causes brown dots and general browning of veins when many non-viruliferous individuals feed
RESISTANCE TO INSECTS IN POTATO

... upon normal Bliss Triumph potatoes in the greenhouse. Some similar injury occurred in the field on Green Mountain potatoes. In heavy infestations of *M. persicae* in the greenhouse the leaflets were severely dwarfed and curled and the tops dwarfed and spindling as symptoms of the injury caused by the aphids. Houser, Guyton, and Lowery (1917) reported that in Ohio injury by *M. solanifoli* to potato caused curling of leaves and sometimes eventual death of the plant. On tomatoes only occasionally did the leaves curl as a result of the feeding of this insect but the flowers of both tomato and eggplant dropped as a result of the injury. Roberts (1940) reported differences in both the rate and manner of feeding of these two species on various host plants, particularly potato and tobacco. Bald, Norris, and Helson (1946) in Australia reported that *M. persicae* fed primarily on the phloem tissue of mature leaves while *M. solanifoli* fed either on phloem or mesophyll tissue close behind the growing point. It is evident, therefore, that resistance to these two species may be governed by different genetic factors and should be considered separately.

An early report by Whitehead, Currie, and Davies (1932) was that Kerr’s Pink was less susceptible to injury than some other varieties under conditions of light infestation of both *M. solanifoli* and *M. persicae*. Maughan (1937) reported aphid populations on eleven varieties of potatoes, ranging from 539 to 3,323, but did not state the species involved. Burnham and MacLeod (1942) in New Brunswick reported that Katahdin was susceptible and killed by *M. persicae* while Green Mountain, Up-to-date, and President were more resistant. Cockerham (1943) reported that *Solanum polyadenium* appeared to be distasteful to aphids, while in the Annual Report of the John Innes’ Horticultural Institution for 1945, a tetraploid form of this species was recorded as showing resistance to aphid attack. Bald, Norris, and Helson (1946), working in Australia, on eight varieties did not find any difference in populations of aphids apart from the physiological age of the host plant. The two species, *M. persicae* and *M. solanifoli*, were studied separately over a period of two years. The authors found no evidence of preference for any varieties by the aphids. Among the varieties studied were Brownell, Carmen, Up-to-date, Delaware, Bismark, Katahdin, President, and Snowflake. Folson and Stevenson (1946) in reporting on cooperative work on disease and aphid resistance conducted in Maine and New Brunswick, indicated that...
resistance to virus causing leaf roll was transmitted independently of resistance to *M. persicae*. Hovey and Simpson (1944) gave further details of this work and recorded counts of aphids on 26 varieties.

Adams (1946) has given in detail tests conducted over the period from 1939 to 1944 and involving from 4 to 80 varieties of potatoes and species of *Solanum*. In tests in the greenhouse *Myzus persicae* from a single greenhouse stock culture was used to infest equally, plants of the potato varieties being studied. At weekly intervals thereafter notes were taken on the size of the population and the nature and degree of injury. In the field plants were grown under cloth cages and in various experiments infested with 10, 50, or 100 aphids. The potato varieties studied came from various sources and included a part of the British Empire potato collection and material which came as a result of a cooperative program with the Maine Experiment Station in 1943 and the following years. Counts or estimates of the aphid population were made at intervals in the field. Five classes of injury were used and the characteristics of each class were described in the paper. Some of the very susceptible varieties such as Katahdin were rather quickly killed by the aphids. Tolerant varieties were those which supported high populations with little injury and few winged forms. “Resistant plants are those which are associated with the production of very limited populations or no aphids, and which show no physical injury when small populations do occur.” “Very resistant plants approach immunity both as regards aphid populations and injury.”

*Solanum polyadenium* was classified as immune to foliage infestation and Adams reported after a number of tests that, “Finally a turnip top from the aphid stock chamber, very heavily infested with *Myzus persicae*, totalling thousands, was introduced into one cage of *Solanum polyadenium* in an attempt to force the aphids to feed upon this host. The cage was examined 48 hours later. Numerous aphids were crawling over the *polyadenium*, ground surface, and cage sides. Three days later there were no living aphids noted in the cage.” In the laboratory it was possible to establish aphids in a limited number and for a limited time only on the stolons of *polyadenium* which appeared to be free from the oil characteristic of the leaves. Stringer (1946) also obtained data suggesting that this immunity to aphid attack appeared to be due to the repellent
action of the oil which accumulated around the tarsi. The effect in preventing feeding was considered to be mechanical.

The different varieties studied were mostly susceptible and some such as Katahdin extremely so (Adams 1946). The various species of Solanum as a group were more resistant than the varieties of S. tuberosum with S. demissum as the most susceptible of these wild varieties of potato. A seedling potato selected at Fredericton, New Brunswick, (no. 996-1-4) from the cross ((S. demissum x Katahdin) x Katahdin) x Katahdin, was highly resistant to the peach aphid and apparently indicated that the resistance from this

Rating of some of the more important varieties and species of Solanum for aphid (Mycus persicae) resistance

<table>
<thead>
<tr>
<th>Very susceptible</th>
<th>Tolerant</th>
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<tbody>
<tr>
<td>Katahdin</td>
<td>Arran Victory</td>
</tr>
<tr>
<td>Garnet Chili</td>
<td>Early Rose</td>
</tr>
<tr>
<td>Seedling no. 41958</td>
<td>Early Ohio</td>
</tr>
<tr>
<td></td>
<td>Green Mountain</td>
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<tr>
<td>Susceptible</td>
<td></td>
</tr>
<tr>
<td>Arran Banner</td>
<td>President</td>
</tr>
<tr>
<td>Bliss Triumph</td>
<td>Red Warba</td>
</tr>
<tr>
<td>Burbank</td>
<td>S. jemensis</td>
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<tr>
<td>Chippewa</td>
<td>Triumph</td>
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<tr>
<td>Earlane</td>
<td>Warba</td>
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<tr>
<td>Erie</td>
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<tr>
<td>Golden</td>
<td></td>
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<tr>
<td>Idaho Russet</td>
<td>Ackersen (?)</td>
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<tr>
<td>Irish Cobbler</td>
<td>British Queen</td>
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<tr>
<td>Kerrs Pink</td>
<td>De Sota</td>
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<tr>
<td>Menaqua</td>
<td>Early Pinkeye</td>
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<tr>
<td>Mohawk</td>
<td>Houma</td>
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<tr>
<td>Norkota</td>
<td>Irish Daisy</td>
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<tr>
<td>Pawnee</td>
<td>LaSalle</td>
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<tr>
<td>Pontiac</td>
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<tr>
<td>Red McClure</td>
<td>S. caldariai-glabrescens</td>
</tr>
<tr>
<td>Rural New Yorker</td>
<td>S. neoantipouiczii</td>
</tr>
<tr>
<td>Russet Rural</td>
<td>S. ajoucoense</td>
</tr>
<tr>
<td>Sequoia</td>
<td>S. commersonii</td>
</tr>
<tr>
<td>Snowflaker</td>
<td>S. acaule</td>
</tr>
<tr>
<td>S. demissum</td>
<td>S. antipouiczii</td>
</tr>
<tr>
<td>Spalding Rose</td>
<td>Seedling no. 996</td>
</tr>
<tr>
<td>Sébago</td>
<td>Up-to-date</td>
</tr>
</tbody>
</table>

Immune
S. polyadenium
wild species may have been transmitted to S. tuberosum. Most of
the species and varieties were consistent in their behavior to the
aphid. Adams reported, however, that Sequoia was resistant in
tests but that a field of potatoes of this variety near Kentville, Nova
Scotia, had been seen which was severely injured by an abundant
population of M. persicae.

Some of the more important varieties and species are classified
as shown on page 385 (Adams 1946).

RESISTANCE TO THE POTATO PSYLLID

The potato, Paratrioz a cockerelli (Sulc), psyllid has been
known as a pest of tomatoes since 1894 (Daniels 1937) but in 1927
was first connected with the disease-like condition now known in
potatoes as psyllid yellows. Our knowledge of this condition has
been summarized by Carter (1939). Psyllid yellows is a systemic
condition of the plant which may be caused by the nymphs, but not
the adults, and results in a yellow or purplish color of the younger
leaves with some subsequent degeneration and rosette formation.
The most destructive result of the psyllid infestation is the formation
of numerous small potatoes that are not salable.

According to Daniels (1937) the life cycle from egg to adult
required a little more than three weeks and there were eight to ten
generations per year. The insect hibernated as an adult coming out
in the early spring to feed, and often passed a generation on native
wild hosts that belong mostly to the family Solanaceae. According
to Wallis (1946) hibernation does not occur in Nebraska and
Wyoming. The disease-like condition resulting from the psyllids
has been reported from the many places in the western half of the
United States and Canada wherever potatoes are grown. Pletsch
(1947) gave extensive life history data on the psyllid and lists of
plants on which it had been collected but did not deal with possible
differences in biology on different potato varieties. He showed,
however, that there were differences in the biology of the insect on
its several species of cultivated host plants.

Knowlton and Thomas (1934) listed forty different species of
plants on which the insect can complete its life cycle. Several
writers have indicated that differences existed in the reaction of
varieties of potato to the feeding of the insect. Daniels (1937) re-
ported in Colorado that the varieties that were most susceptible
were "Early Gobblers, Triumphs, Peach Blows (McClures), and
Russet Burbanks." Hartman (1937) studied a group of varieties for two years in which he compared the yield from comparable plots infested by psyllids and those which were sprayed with lime sulphur for the control of this insect. He reported that the varieties Pearl, Late Ohio, and Cobbler appeared to be partially resistant to the effects of the psyllid.

A more extended study, 1936 through 1939, has been made by Babb and his associates (Babb and Kraus 1937a; Babb, Kraus, and Star 1944) and is concerned with 86 varieties and seedling selections, including some from South America. Their conclusions were that although there was little evidence of resistance, several of the varieties, including particularly Cobbler and Bliss Triumph, showed a measurable degree of tolerance as measured by a comparison between sprayed and unsprayed plots. Evidence presented showed that low yields occurred where tuber injury was severe but that high tuber injury was not always associated with severe injury to the tops of the plants. The stage of plant maturity at the onset of the insect infestation as well as tolerance to the attack was concerned. The authors explained these relationships as follows:

"The inter-relationship of these factors provides an insight into the manner by which the psyllid yellows disease produced its effects on potatoes. Psyllid infestation takes place with great rapidity and thus the psyllid yellows disease attacks varieties of the early, mid-season, and late-maturing varieties of potatoes at different stages of physiological maturity. When the disease attacks them after tuber formation is well advanced its effects on yields are not so serious as they are when it attacks them before tuber formation has been initiated or during the early stages of tuber formation. In the latter case tubers that have set show severe symptoms of the disease; or, if they have not started to set, normal tuber formation is inhibited. With respect to the vines, the apparent effects of the disease are more pronounced on the early maturing varieties than on the late varieties because at the time of attack they are physiologically more mature and declining in vegetative vigor. Under such conditions the effects of the psyllid attack appear more pronounced than they would if the plants were younger and more vegetative.

"Despite the high significance of the correlation between earliness of maturity and yields, it is evident that there are exceptions to the general rule that the earlier maturing varieties produced higher
yields than those maturing later. Of particularly interest in this study are those varieties which, though later maturing than the checks, nevertheless produced equal or higher yields."

The results given above were secured in 1937. In 1938 none of the unsprayed plots produced marketable tubers indicating that the measure of tolerance possessed by some of the varieties is not sufficient for a year of severe injury. In 1939 experiments involving a combination of variety and date of planting showed that Cobbler and Bliss Triumph carry a degree of tolerance independent of the factors for earliness. In normal years with low or average psyllid populations these two varieties as well as a few others which are listed in the last paper may be expected to produce fair yields without spray protection. Some of the late-maturing varieties which gave fair yields may possess genes for resistance in addition to those carried by Bliss Triumph and Cobbler. There is no evidence in any of the papers that preference or antibiosis is involved in resistance of potatoes to the psyllids. Cooperative studies concerning resistance to potato psyllids between the Colorado Experiment Station and the Greeley, Colorado, potato station have been considered briefly in several annual reports (Henney 1944, 1947). Strains selected in the greenhouses have shown resistance in the field but have not had satisfactory yields.

RESISTANCE TO OTHER INSECTS IN POTATO

Three papers have been concerned with the resistance to wireworms found injuring the tubers of potato varieties. These larvae of beetles belonging to the family Elateridae are known to burrow through the ground feeding on roots and other underground parts of the plants. It has sometimes been questioned whether the larvae actually feed on potato tubers or merely burrow through them when these objects are in their path. In recent papers (Crombie and Darrah 1947; Thorpe et al. 1947; and Lee 1948) evidence is given that certain plant products exert a definite attraction for these larvae. Miles and Cohen (1939), in a study of four early, four medium, and four main crop varieties of potatoes in England, demonstrated the existence of varietal differences in injury within each group. In these experiments 98 per cent of the larvae reared were Agriotes obscurus (L.). Telford (1942), working for two years with Ludius antipennis destructor Brown in North Dakota, found that under field conditions Early Ohio was most susceptible
to wireworm attack. Bliss Triumph least susceptible, and Cobbler intermediate; Warba and Sebago were also less susceptible. Telford indicated that great wireworm injury may occur in the potato varieties which have fewer tubers per hill and which have these growing in closer proximity to each other. Rawlins (1943) gave tables showing the difference in injury to potato varieties by the larvae of the species Limonius agonus (Say). The varieties differed not only in the percentage of tubers injured but also in the severity of injury. In his experiments Irish Cobbler and Bliss Triumph were susceptible, Russet Rural and Warba resistant. Although the injury done by one species of wireworm is superficially similar to that done by every other one, there is no reason to expect that these species belonging in different genera should react in the same way to the varieties of potato studied.

The potato tuber worm, Gnorimoschema opérculella (Zell.), is a cosmopolitan insect which feeds on the tubers of potato in storage and also on the potato plants in the field as well as on other solanaceous plants. Bald and Helson (1944), in a study in Australia of the feeding of this insect on foliage of five potato varieties, found no evidence of varietal preference by this insect but did find a difference between the varieties associated with replacement of tissue destroyed by this insect. In this respect Early Carmen (= Green Mountain) was most severely damaged and the variety Snowflake least damaged. Considerable differences in susceptibility of tubers to injury by this insect have been found in Australia in tests of 33 varieties of potatoes (17th Rpt. Council Sci. and Industr. Res. Australia 1942-43, pp. 15-20, 1944).

Differences in the injury done to 58 potato varieties by the Rutherglen bug (Nysius vinitor Berg.) have been reported in Australia by Graves and Rochford (1946). This insect feeds on a number of plants and the damage done was apparently primarily caused by the adults which fly into the potato fields. The feeding of the insect causes the withering of the tip of the branches, sometimes ending in the death of susceptible plants. Warba and Mesaba were susceptible and President, Rural New Yorker, Scotia, Up-to-date, Snowflake, Iverness Favorite, Dunbar Standard, and Early Rose were reported as resistant. There was evidence of wide variation in amount of injury within some varieties but others were injured uniformly. The relative susceptibility of some varieties was different in different localities but the varieties Snowflake and Facto
(Up-to-date) were resistant in both localities where studies were carried on.

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CHAPTER IX

METHODS AND PROBLEMS IN BREEDING FOR RESISTANCE TO INSECTS IN CROP PLANTS

I. Introduction.
   A. An intimate knowledge of biology and feeding habits of insect involved is basic in resistance studies.
   B. Where possible ability to recognize each stage of the insect and kind of damage done is also important.

II. The maintenance of insect populations.
   A. The most useful population is one which gives the maximum difference between resistant and susceptible types.
   B. Utilizing populations in the field.
      (1) Taking advantage of insect outbreaks.
      (2) Taking test varieties to infested areas.
      (3) Bringing in insects to test varieties in an experimental field.
      (4) Value of permanent nursery plots and continuity of experiments.
   C. Cage and laboratory methods.
      (1) Augmenting natural field populations.
      (2) Greenhouse and cage testing.
         (a) Validity must be checked by field tests.
         (b) Method used important—some will duplicate field results, others will not.

III. Varietal survey methods.
   A. Extensive vs. intensive study; the use of each.
   B. Value of uniform nurseries.
   C. Independent checking of work by other research men is not unnecessary duplication.

IV. Sources of resistant types.
   A. Within crop species.
      (1) Varieties from original home of insect.
      (2) Areas where greatest morphological diversity of a crop exists are those where greatest physiological diversity is likely to be found.
   B. Within species related to crop plants.
      (1) Often valuable if they can be used.
      (2) Because of problems involved these sources have often been the last resort.

V. The measurement of resistance.
   A. Relative measurements using a susceptible or a well-known variety as a standard.
      (1) Measurements based on insect populations.
      (2) Measurements based on insect damage.
   B. In the absence of a susceptible variety some independent measure of an insect population must be found.
The study of insect resistance in crop plants presents some problems and requires some methods of study that are common to other projects in entomology and in plant breeding. In these respects the usual textbooks and other references on the subjects are useful. This is particularly true of the book on plant breeding by Hayes and Immer (1942) and the compendium on insectary methods by Peterson (1947). There are, however, some special problems and methods that bear discussion here. In a large cooperative project on insect resistance the entomologist and plant breeder will handle their respective problems, but it is desirable that each should be aware of the difficulties and the possibilities of the other's field. In small projects and at the beginning of others a single person may have to carry both fields. The information contained in this chapter may be of help on these occasions.

The entomological work connected with breeding plants for resistance to insects differs from other work with insect control in several ways. A population of insects must be built up and maintained in the field or laboratory rather than be destroyed. This involves a different point of view and sometimes unexpected difficulties. The results that can be secured in some aspects of resistance studies usually are proportional to the number of plants and strains that can be analyzed. Methods must be designed to examine large numbers of plants for insect infestation or damage, frequently in a very short period of time. In certain phases of the study quantity may be more important than a high degree of accuracy. The entomologist must be aware of the conditions of the plants which are the hosts of the insects he is studying. A change in them may
affect his results. Beyond this, the study of insect resistance requires that the entomologist have a genetic viewpoint as well as the ecological one which is required by most entomological work. The exceptional plants, or varieties that are different from their neighbors in respect to insect infestation, may be an undesirable source of annoyance in ecological studies or insecticidal tests. These exceptional plants are the basis of resistance studies. Whether the apparently resistant plant is actually resistant can be discovered only by the progeny test, an experimental procedure not often used in other entomological work. The production of varieties resistant to insects usually requires a minimum of six to ten years and often much longer. Continuity of experiments over such a period of time is a prerequisite to success.

Most plant breeders ordinarily would wish to avoid insect infestation because of the differences in yields and interpretations which are introduced. If there is cooperation in a project on insect resistance, these opportunities to take additional data on resistance will be welcome, even if they occur in plots designed for other purposes. Resistance studies will often involve replicated plantings at unusual dates and places in order to secure the necessary insect infestation. Sometimes it will also be necessary to use as a source of resistance those varieties which the average plant breeder would have discarded long ago. The source of the highest level of hessian fly resistance in use at the Kansas Station is a wheat variety (P.I. 94587) so poorly adapted that a seed supply can only be maintained with difficulty in Kansas. By hybridization well-adapted strains carrying the resistance have been obtained.

An intimate knowledge of the biology and feeding habits of the insect involved is basic in any resistance studies. Such knowledge would include information often considered of less importance in other insect-control work. Information on details of the life history are necessary in order to plan for maintenance of the continuity of insect populations that will be needed in testing and breeding programs. Studies of biology and behavior are needed to distinguish true genetic resistance from pseudoresistance and to separate the different types of resistance when present. Studies of feeding habits may contribute to an understanding of the mechanisms of resistance. Studies of injury are required because separate genes for resistance may be found to each of the different kinds that may be present.
Associated with a recognition of different types of injury is the need for ability to recognize each stage of the insect and to separate these from related species that may occur. The importance of accurate identification of the insect concerned has already been emphasized in Chapter III.

THE MAINTENANCE OF INSECT POPULATIONS

The most useful insect population is one which gives the maximum difference between resistant and susceptible types. If breeding for insect resistance is to be done, a prime necessity is that a desirable level of infestation of the particular insect must be present each year. If in some years infestations are too light to permit separation of resistant and susceptible strains, selection of plants in segregating generations cannot be done and much susceptible material is accumulated. On the other hand, the production of too severe an infestation has sometimes been recommended. The infestation cannot be too heavy if one is dealing with immunity, which, however, has been rare in insect resistance. In the early years of the study of resistance of sorghums to chinch bugs a segregating population of the cross Kansas Orange (resistant) x Dwarf Yellow milo (susceptible) was exposed to a chinch bug population that destroyed all except one plant. This plant gave rise to a strain which over a period of years had the highest resistance among the sorghums tested but is of poor agronomic quality. Quite probably the heavy chinch bug infestation destroyed strains more valuable from an agronomic standpoint that were only slightly less resistant. This emphasizes the need for regulating insect populations so that they give the maximum difference between resistant and susceptible types and provide for some choice among the more resistant segregates from a cross.

Utilizing populations in the field. Many insects occur normally in outbreak numbers at intervals of several years. Considerable data have been accumulated as a result of taking advantage of these outbreaks when they occur in a varietal nursery. Several of the first hessian fly resistant strains of wheat were discovered in this way. Most of the information gathered in the United States on resistance of strains of corn to grasshoppers and to chinch bugs has been secured in a similar manner. In Kansas the outbreak of pea aphids on alfalfa in 1934 made it possible to select in farmers' fields individual alfalfa plants showing varying degrees of resistance to this insect (Painter and Grandfield 1935). The progenies of these
plants were studied later under controlled conditions. The studies depending on outbreaks of insects have the disadvantage that they lack the continuity necessary for a breeding program and that the level of infestation may be unsatisfactory. Their advantage lies in the fact that much material can be studied with little cost or effort. Unexpected infestations in varietal nurseries in the past have furnished evidence that has led to a study of insect resistance. The first resistant strains of some crops have been obtained in that way. Additional contributions may be expected from the same source in the future (Figs. 1, 14).

In parts of the area occupied by most injurious insects there nearly always have been localities where infestation and damage have been more severe or more frequent than elsewhere. The area of heavy infestation by some other insects changes from year to year but may be predicted on the basis of insect surveys. Workers in insect resistance can arrange to take the plant strains to be tested to these temporary or more permanent regions of higher infestation. This has been done with several insects. In the southern and southwestern parts of the corn-growing area of the United States the corn earworm usually infests 100 per cent of the ears of corn grown. Infestations approaching this level occur only at rare intervals in the main corn-growing areas. Workers in the U.S. Department of Agriculture have taken advantage of this situation not only to get more satisfactory infestations of earworm in corn inbreds and hybrids but also to grow and study two crops a year (Walter 1948). One crop was grown in southern Texas under natural infestation, the other in Indiana or Illinois, artificially infested. The frequent abundance of chinch bugs in some localities in Oklahoma has made that state a desirable one in which to conduct tests of the resistance of sorghums to that insect. When test varieties are placed at a distance from the base experiment station, it has sometimes been impossible to study satisfactorily characters other than resistance. This has been the situation in work with the southwestern corn borer in Kansas. There records were taken in the infested area on selections during one year and the more resistant ones were replanted for agronomic study and selection from remnant seed the next year. This alternation of selections with and without the presence of the insect has some advantages but it is generally less efficient than repeated selection under satisfactory infestations.
It has sometimes been possible to bring the insects to experimental field plots near the laboratory where the test varieties may be studied in greater detail. This has been satisfactory in the study of the resistance of wheat to hessian fly, since this insect can be collected in the infested stubble and stored over the summer for use in plots in the following fall. With some insects the population can be kept up to a satisfactory level by placing the test plot in a larger area of susceptible host plants or by interplanting rows of known susceptible varieties among those being tested. Parnell et al. (1949) wrote of this as "bombardment effect" and used this method in the study of resistance of cotton to leafhoppers. Insecticides sometimes may be used to regulate the level of population in the border rows so that it will be of a satisfactory intensity. Since DDT encourages the increase of some aphids and some other species of insects, its use may be advisable in breeding for resistance to insects affected in such a manner. Where insects have alternate hosts, as is true of chinch bugs, proper use may be made of them to provide a satisfactory population (Figs. 35, 65).

In the breeding of insect-resistant plants a provision for having available an insect population of approximately the same level year after year is a necessity. The provision of permanent or semi-permanent testing areas sometimes aids in the solution of this problem. Platt and Farstad (1946) have described such areas, which are being used in a study of the resistance of wheat to the wheat stem sawfly and where adequate populations can be maintained for research purposes. In these areas provision is made for rotation with fallow and for alternate hosts of the insect. With most field methods planting dates usually can be changed to affect the infestation in the desired direction.

Cage and laboratory methods. With many insects, natural populations in the field are not entirely satisfactory for testing plant varieties and selections for resistance. The best work on resistance can perhaps be done by augmenting the natural field populations so that a uniform infestation is obtained. This method has been used in breeding for resistance to the European corn borer (Patch and Peirce 1933). The methods used there have undergone gradual improvement. At present corn stalks containing hibernating larvae are collected in the fall and placed in a large screen cage for protection from rodents, etc. When the moths emerge in the spring, they are collected into cages where they oviposit on sheets
Fig. 65. The 1946-47 bessian fly nursery, Manhattan, Kansas, designed for testing resistance of individual plants and strains of wheat to this insect. Stubble from heavily infested fields of the previous crop has been planted in alleys and about nursery as a source of infestation. The long rows on the right contain plants of a susceptible variety planted earlier than the test varieties in the short rows on the left. The susceptible plants also serve as a source of infestation.
of waxed paper. Pieces of paper carrying the eggs are placed on the corn plant just before the eggs are ready to hatch. A somewhat similar method has been worked out for rearing corn earworm (Blanchard et al. 1942), except that in this case the larvae are placed on the silks after hatching.

These methods of enhancing the normal numbers of insects not only give a more uniform population but also permit many modifications, including variable dates of infestation and differences in numbers of larvae. These more concise controls of infestation may be desirable not only in the testing of varieties from all available sources for resistance and in studies in the inheritance of resistance but also in investigations regarding the mechanisms of resistance.

The small space in greenhouses and cages ordinarily necessitates the limiting of studies involving such equipment to special problems. Where the separations of resistant and susceptible plants can be made in the seedling stage, large enough numbers of plants often can be handled for varietal and genetic experiments. This has been true of some of the studies on resistance of wheat to 'hessian fly (Painter et al. 1931; Cartwright and LaHue 1944).

Ivanoff (1945) found the seedling method in the greenhouse satisfactory for testing resistance of cantaloupe varieties to the melon aphid. Apple-tree seedlings have been tested for resistance to woolly apple aphid (Crane et al. 1936) in greenhouse and insectary.

The validity of tests in the greenhouse and in cages must be checked repeatedly under field conditions. Either plants, or insects, or both, may behave differently under cages than they do outdoors. The cage test is ordinarily more severe than a field test for the resistant varieties because the level of infestation is usually higher. Nevertheless the results from cage tests usually check fairly well with field results. There have been some occasions when this was not true. Breider (1939), after studying the grape phylloxera on species and varieties of Vitis in field and greenhouse, found morphological plant characters of some kinds that were affected by growth in a greenhouse but not outside, and corresponding differences in susceptibility to the phylloxera. Other strains of grapes were not affected in this manner. Breider stresses the importance of using both greenhouse and field conditions in practical plant-breeding studies of the phylloxera problem. Platt and Farstad (1946) found that resistance to the wheat stem sawfly in common bread wheat could not be studied in cages because varieties that
were resistant just outside the cage were heavily infested inside it. Yet the resistance involved has persisted under most field conditions and has proved to be of high commercial value. In early studies of insect resistance in a crop, greenhouse and cage tests may make conditions so severe that valuable sources of resistance, particularly that resulting from non-preference, may be discarded.

Cage and greenhouse studies may be necessary in determining which of the three types of resistance are carried by the varieties found to have lower infestation or damage. These experiments will involve counts of eggs, studies of behavior of adults, amount of injury or yield reduction under attack from varying numbers of insects, and the study of the divers results of antibiosis. The particular methods to be used will have to be designed to fit the insect under study and the level of resistance involved.

**VARIETAL SURVEY METHODS**

**Extensive vs. intensive study; the use of each.** In the early stages of search for resistance in a crop it is necessary to test many different samples, varieties, or strains. The chance of finding resistant strains usually is related to the number that can be studied. During this period it may be necessary to sacrifice accuracy if numbers cannot otherwise be handled. Since the bulk of the material is likely to be susceptible, there should be little disadvantage in doing this. However, the investigator should be on the alert for the few unusual resistant plants that may and often have occurred in otherwise susceptible material. Lots of seeds often have not been uniform for reaction to insects studied and a moderately susceptible strain sometimes has contained a few highly resistant plants.

In contrast, after sources of apparent resistance have been found, intensive studies with careful experimental design may be necessary to distinguish between true resistance and pseudoresistance. Such careful intensive tests will also be needed to evaluate different sources of resistance, especially when multiple factors are responsible for the resistance.

Since resistance acts as a hidden character that becomes apparent in an otherwise homogeneous strain when it is grown in the presence of an insect, mass selection may sometimes be used to advantage in conserving and concentrating the genes for resistance. The use of bulks made early in the selection program for leafhopper resistance in cotton in South Africa (Parnell 1935) and in Quee-
land (Wells 1944) gave the farmers some protection from the insect while better strains of resistant cotton were being developed in part from these bulks or related strains.

**Value of uniform nurseries.** Records of the use of uniform nurseries for study of insect resistance are available in the case of insects attacking corn and the hessian fly and the wheat stem sawfly on wheat. In uniform nurseries strains gathered from a number of sources are packaged and numbered at one place but seed or plants from the same source are planted in a uniform manner in several localities. All of these have served to establish the validity of various kinds of insect resistance in these crops under widely different environmental conditions. Uniform nurseries are useful not only as demonstrations but also to test for the presence of biological strains of insects. Frequently such nurseries permit the study of the resistance of the same strains under widely differing levels of infestation and have speeded up the collection of information on the more promising material under study.

The uniform nurseries often furnish an additional benefit when the records derived from them are taken by different people. This provides an independent checking of results that may be advantageous to all the research men concerned.

The U.S. Department of Agriculture, in cooperation with the various state experiment stations, maintains uniform nurseries for evaluating promising strains of a number of crops, such as wheat, corn, sorghum, alfalfa, barley, and oats. While these nurseries usually are primarily for the purpose of comparing the yields of the strains included, notes are often taken on the degree of infection by various diseases that occur naturally in the nursery. Less often data on insect infestations or damage have been recorded. Sometimes this insect information has led to a new appreciation of the possibilities of insect resistance.

**Sources of resistant types of plants**

There are two general sources of genes for resistance: those provided by the variability within the crop species, and those in plant species closely enough related to the crop species to cross with it. Research on resistance should begin in the former but the latter should not be neglected. There appear to be been, in general, two conditions under which genes for resistance have occurred in plants. Strains which have been exposed to infestations of a par-
ticular insect over long periods of time have sometimes been found to carry genes for resistance less common elsewhere in the crop. Brunson and Painter (1938) in a study of grasshopper resistance found that "as a rule the varieties and inbred lines of corn showing the greatest resistance originated in areas where grasshoppers are a natural element of the environment." It was suggested that natural selection had tended to eliminate the more susceptible elements in the corn population of those areas. In contrast, as far as records are available, the sorghum varieties that were brought to the United States from Africa and Asia already differed in respect to chinch bug resistance before they came in contact with chinch bugs. No insects comparable to chinch bugs have been reported as injuring sorghums in their country of origin; hence natural selection, as we ordinarily think of it, cannot have been responsible for development of resistance. This chinch bug situation may be an example of the known tendency for genetic differences to accumulate when small populations of living things are isolated, as might be the situation when strains of sorghums were grown near some of the native villages or tribes in their countries of origin. Hence one should remember that the presence of the insect resisted is not essential to the development of resistance.

Varieties and selections of crop plants for testing for resistance to insects may be obtained from a number of sources. Individual research men in different localities have been liberal in exchanging plant materials. Governmental expeditions have sometimes been sent out to seek plants having particular characteristics. On several occasions disease-resistant plants have been sought and found. Apparently the single case where insect resistance—of cotton to the boll weevil—was sought, was unsuccessful. Governments of some countries have regular departments concerned with the introduction of useful plants. In the U.S. Department of Agriculture there is a Division of Plant Exploration and Introduction in the Bureau of Plant Industry, Soils and Agricultural Engineering, which issues occasional lists of foreign plant introductions. Of these, Plant Inventory No. 157, issued November 1949, gave information concerning nearly a thousand such introductions. One of the sections of the Food and Agriculture Organization of the United Nations is concerned with the exchange of information and the facilitation of the introduction of new and useful plants into the member countries (Hudson 1949).
Sources within the crop species. The first potential source of resistance to be examined will be the commonly grown and adapted varieties in the area where the experiments are being conducted. If resistance can be found among such varieties, the problems of breeding a satisfactory variety are greatly simplified. Attention should be given to the possibility of isolating resistant strains out of varieties that are homozygous for visible characters. This type of selection has been performed in the breeding for resistance to hessian fly in wheat (Painter et al. 1931) and in resistance of sorghums to chinch bugs (Snelling et al. 1937). Selection of perennial plants made from old or abandoned orchards or fields where a few individual plants have persisted in spite of hazards including insects, may also furnish a source of resistance.

The importation and testing of varieties that have been cultivated for a long time in the original home of the insect may be a potential source of resistance, particularly of the tolerance mechanisms. It has been difficult to determine the original source of some insects, for example, the earworm or bollworm (*Heliothis armigera* (Hbn.)), when these insects now have nearly worldwide distribution. For such insects this method may not be applicable. Grape vines resistant to the grape phylloxera were successfully sought in the original home of the insects in one of the first uses of resistant plants for insect control. In one or more instances genes for resistance, for reasons not evident, have been found more abundantly in a particular geographic area. As described in the section on wheat insects, more hessian fly resistant wheat varieties and probably more different genes for resistance to that insect have come from the Iberian peninsula than from any other wheat-growing area. This has not been considered to be the area of origin of this insect. Ingram et al. (1943) reported that most of the sugar-cane varieties from Turkestan transmitted resistance to *Diatraea saccharalis* (F.), the sugar cane borer, while most varieties from other locations were susceptible.

It is well known that the plants show much greater morphological diversity in certain areas near the centers of origin of each crop than in other areas. Insect resistance, however, is more frequently dependent on physiological than morphological characters. Anderson (1947) suggests that areas of high morphological diversity are likely to show a similar range in physiological characters. Hence varieties taken from regions of morphological multifor...
may include among their physiological variation characters for insect resistance. As such they are of particular interest to the plant breeder.

**Sources within species related to crop plants.** The search for genes for resistance often need not be confined to the crop species. The newer techniques in plant breeding make it possible to cross plant species that have been difficult or impossible to cross until recently. The accomplishment is still not easy and often brings a train of new problems. For this reason interspecific crosses are generally a resort to be used if resistance cannot be found in the crop species or when much higher degrees of resistance have been found in related species. Interspecific crosses have been successfully used or are being used in breeding for resistance to insects in wheat, grapes, potatoes, cotton, and a few other crops. A number of successful undertakings using interspecific hybridization have been recorded in breeding for disease resistance.

**THE MEASUREMENTS OF RESISTANCE**

A knowledge of the biology of the insect being studied is often of utmost importance in the measurement of resistance. Insects are rarely distributed at random over a field, and sometimes no reasonable amount of randomization or replication can take the place of sound judgment regarding biological factors involved in the placing of plots. Most of the short-horned grasshoppers lay eggs in the soil, but the different species show distinct preferences in respect to type of soil and neighboring vegetation. Many hibernating or migrating species of insects, such as boll weevils or chinch bugs, tend to infest crops nearest to their alternate host or hibernating place, and plots for comparison should be placed at right angles to such areas. When proper allowance has been made for the biological sources of lack of randomness, some of the usual statistical tools can be used. For a general discussion of this subject the usual textbooks should be consulted. There are, however, some papers dealing with the statistical treatment of records of insect populations or studies of insect resistance that might be useful (Baten and Hutson 1943; Beal 1939; Bliss 1941; Finney 1941; Greenslade and Pearce 1940; Harrington et al. 1945; Huber 1938; Platt and Farstad 1946; Parnell et al. 1949; Walker 1942, Williams 1937). Some
specific problems have been considered earlier in connection with
the review of the studies of resistance to specific insects in corn,
wheat, cotton, etc. Examples of various ways of measuring resis­
tance may be found in reports of some of the corn-improvement
conferences (Neiswander et al. 1949) and as recorded in the chap­
ter on resistance to insects in corn. The recommended methods
often involve the estimating and scoring of insect populations in
three or more (usually five) categories and are more quickly done
than counts or measures.

Relative measurements using a susceptible or a well-known variety
as a standard. The difficulty of an absolute measurement of re­
sistance has already been stressed. The resistant variety ordinarily
suffers more or less injury but always less than the susceptible ones
do under the same conditions. Resistance is ordinarily measured in
terms that reflect a comparison with one variety, or the average of
a group, of susceptible varieties.

There usually are two ways of measuring resistance: some form
of count of insect populations and some kind of estimate of the
amount of damage. The first measures differences in preference
and antibiosis, separately or combined, when such differences exist
between the plants or plant varieties. The estimates of damage
measure the combined effects of preference, antibiosis, and tolerance
or, if the estimates are given in terms of damage per insect, are
measures of tolerance alone.

Measurements based on insect populations may be made at any
period in the life history but are usually easiest to make during the
most sedentary stages in the insect’s life cycle. Sometimes counts
made at a series of intervals during the life history provide additional
information. Counts of eggs may suggest whether preference is a
part of the resistance phenomenon. Sometimes special means may
be used to make the eggs visible (Curtis 1942). An alternative
method used with Empoasca spp., the leafhoppers on cotton, has
been to count the newly hatched young. Comparisons of counts
of eggs with counts of partially or fully grown insects may suggest
whether antibiosis is involved in the particular kind of resistance
under study.

Direct measures of insect populations consist of counts of in­
dividual insects or colonies of insects. When the insects are too ac­
tive or too numerous for exact counts, estimates by weight or volume
Insect resistance in crop plants sometimes can be made. The use of a sweep net for measuring insect populations sometimes has been severely criticized, and rightly so in some cases (DeLong 1932; Gray and Treloar 1933; Carpenter 1936; Carpenter and Ford 1936; Romney 1945). The method has definite limitations, which are discussed in the papers listed, especially the last. In addition to the personal element, collections will vary because of density or distribution of plant populations, the kind of insect, temperature, and wind velocity. Verma and Afzal (1940) found the method satisfactory for records of leafhoppers on cotton varieties when the spacing was the same between plants. Records of differences in pea aphid populations on varieties of alfalfa have been taken with a sweep net (Painter and Grandfield 1935) and the volume of aphids present has been measured in a graduated cylinder. Aphids in a representative volume were counted. There were wide differences between varieties and similar results in different replications. The net used for some studies at the Kansas Station has been a 1-foot square net. One side is kept parallel to the ground in taking the sweeps. Another method of making population records has been to kill all the insects on a plant with cyanide and count only an aliquot part of those collected.

There are also various indirect methods by which an insect population may be estimated. One of these in the case of aphids has been the number of shed skins which may be left even after the insects themselves have disappeared. The number of predators present is often a close index of the number of aphids and often more easily estimated. Jones (1938) has made use of parasite exit holes as evidence of a concealed but heavily parasitized hessian fly population. Excreta of insects are often identifiable to species or groups of species but sometimes vary in correspondence with different food plants. This material when collected in cloths under trees has been used for estimating insect abundance (Nolts 1939). Such indirect methods must be used with caution and require correction by checking with actual populations.

Estimates of damage may be related either to insect populations or tolerance of the plants or both. Damage done by an insect is sometimes a better species characteristic than the insect's morphological character. Yet in other situations it is often easy to confuse the damage done by two or more species. Sometimes insect injury has been confused with disease conditions, especially in the case of insects with sucking mouth-parts. If estimates of damage
are to be used, the injury should be so diagnostic that there is small chance of making mistakes.

Bald and Nelson (1944), after a study of the potato tuberworm, *Gnorimoschema opercul ella* (Zell.), have discussed methods of estimating foliage damage that may have applicability to other similar problems. Frequently it is necessary to estimate the area of foliage eaten by an insect. Baten (1942) gives directions for using a nomogram in finding the areas of bean leaves. In studies of food preferences of grasshoppers Isely (1946) has used photographic records of the results of the tests. Photographs of different degrees of injury may be used to standardize estimates of damage. They have been used in separating corn earworm injury into five classes by comparing each ear with pictures of the standards. Wadley (1949) has suggested further refining the methods of weighting the various classes in accordance with the numbers of grains destroyed. Such weighted estimates were more reliable in separating the resistant strains. Hartzell (1946) has given detailed consideration to the methods for estimating the injury to grape leaves by leafhoppers. The methods he uses may have wider applicability to other insects.

In the absence of a susceptible variety some independent measure of an insect population must be found. The widespread planting of a highly insect-resistant crop variety may be a catastrophic event for an insect. The insect-population size may decrease abruptly. Since other conditions affect insect populations, records of the insect resisted and these conditions should be taken during the increase in the planting of the resistant variety. Only by such means can the value of the resistant variety be assessed properly. When no susceptible variety is available for use as a standard, the damage can be compared with that done in other years by the same level of insect population as measured by the number of ovipositing females or insects coming out of hibernation, etc. This problem will require study in each individual case.

Special methods of measurement required in a study of the inheritance of resistance. A knowledge of the method of inheritance of insect resistance is of great practical importance in planning the system of breeding to be used, in distinguishing the number of genes available from different sources, and their relation to different types of resistance.
If first-generation hybrids can be grown for comparison with the parents under insect infestation, some information can be gained regarding dominance and perhaps numbers of the factors.

Usually the analyses of F₁ populations are not very reliable because of the presence of individual plants that escape infestation or of individual resistant plants that are too heavily infested. Under some conditions the F₁ may give important information when infested, but usually it is preferable to grow this generation where it will be affected by the insects only slightly or not at all. The progeny from each self-fertilized F₁ plant grown under infestation can then be used the following season with greater accuracy as a means of classifying that segregating generation (Fig. 66). This procedure is necessary because resistance usually is relative and individual plants in segregating populations are often difficult to classify. Plants heterozygous for resistance may be affected more easily by environmental characters than are homozygous ones. This possibility must be considered in comparing results of different years or in different localities.

When resistance is available from several sources, there is a possibility of combining different genes to give a higher level of resistance than that existing in a single parental stock. Special tests may have to be designed in handling studies of this kind. Where the several genes involve different types of resistance, such as preference and tolerance, these tests may be less difficult than if different genes bring about the same final result. In the resistance of wheat to hessian fly the presence of any of several different genes in homozygous condition in the plant results in the death of the hessian fly larvae. The presence of these genes may be detected by genetic tests, by differences in the level of resistance under different environmental conditions, and by the use of different biotypes of fly.

**THE ROLE OF ENTOMOLOGIST AND PLANT BREEDER, AGRONOMIST OR HORTICULTURIST IN BREEDING INSECT-RESISTANT PLANTS**

The importance of cooperation between the investigators working on the insect and those working on the plant already has been discussed, but some suggestions regarding the parts of the study to be handled by each may be worthwhile. The detailed division of work will depend not only on character of the project but also on the respective training, experience, and abilities of each investigator.
After plants were selected for individual study next year the remaining plants were bulked.

FIG. 66. The methods used in handling Marquillo hybrids in a study of resistance to Hessian fly, illustrate the use of the progeny of a single plant of the preceding generation as a test of the inheritance of insect resistance or susceptibility carried by that plant. (Painter et al. 1940.)
and the facilities for work. Suggested outlines of this division may be about as follows:

I. **Studies requiring cooperative work:**
   A. The broad planning of the program, frequent joint examination of material being studied, consideration of the data, and sharing responsibility for writing up the results.
   B. A study of factors other than genetic resistance that cause differences between varieties in infestation or damage by insects.
   C. Determination of the number of genetic factors, or groups of factors, governing resistance in different varieties and the manner of expression of such resistance.
   D. The planning of crosses to be made.
   E. Selection of plants of segregating generations studied under insect infestation so that desirable characters in addition to insect resistance may be secured.

II. **The entomologist should be primarily responsible for the following:**
   A. Production and management of insect infestation in field or laboratory in order to secure the maximum differences between resistant and susceptible varieties.
   B. The identification of the insect involved, including a study of biological races or related species as a part of the problem.
   C. General surveys to determine insect infestation in fields and varietal nurseries.
   D. Testing of new plant strains for insect resistance.
   E. The principal responsibility for growing these and the segregating populations of plants when under insect infestation.
   F. The testing of individual plants which are to be used as parents.
   G. The determination of degree of infestation or damage to plants under test.
   H. Following the behavior of a resistant variety and insect population in the fields after release of the variety to growers.

III. **The plant breeder should take primary responsibility for the following:**
   A. A knowledge of the crop and of selections and hybrids made, in the various aspects as related to yield, quality, and adaptability.
   B. The assembling of plant material representing the "genic store" of the crop and, if necessary and possible, species related to it. This means more than just the varieties locally available.
   C. Securing new strains of crop plants for testing.
D. The study of yield, adaptation, and quality characteristics of strains found to be insect-resistant, particularly through segregating generations.
E. Arranging for tests of industrial and other qualities by other agencies where necessary.
F. Through other agencies secure tests over a wider range of territory.
G. Increase, testing, and distribution of insect-resistant varieties.

A PROGRAM FOR BREEDING FOR INSECT RESISTANCE

Relation to and comparison with other crop improvement problems. It should be emphasized again that the study of insect re-

![Diagram showing the cooperative wheat improvement program at the Kansas Agricultural Experiment Station.](image)

Fig. 67. The cooperative wheat improvement program at the Kansas Agricultural Experiment Station, of which the breeding for hessian fly resistance is a part, illustrates the relation of an insect resistance project to other parts of the program and the length of time required in a breeding and testing program. The arrows indicate the origin of seed of strains being tested.

...stistance must be organized as a part of the crop-improvement program. An insect-resistant plant that is of poor quality probably will not be approved by the agronomists or horticulturists and, what is more important, will not be grown by the farmers. It may be necessary for the entomologist to accept temporarily a resistant variety...
that is of somewhat lower degree of resistance than he might wish in order to have one that can be grown on farms (Fig. 67).

Plant breeders, in general, are probably more familiar with the process and possibilities of breeding for disease resistance, which has become an accepted part of crop improvement programs. Perhaps more of such breeding has been done because both pathogene and host were plants and the training of the breeder was in the field of botany, but other reasons may have entered into the situation as well. The chief differences in problems encountered in breeding for disease resistance and insect resistance may be summarized as in Table 25.

Table 25 DIFFERENCES BETWEEN INSECT RESISTANCE AND DISEASE RESISTANCE

<table>
<thead>
<tr>
<th>Disease resistance</th>
<th>Insect resistance</th>
</tr>
</thead>
<tbody>
<tr>
<td>The organism resisted has fairly simple organization.</td>
<td>The organism has complex organization.</td>
</tr>
<tr>
<td>Finding mechanisms chance, except at very close range.</td>
<td>In addition to chance, finding mechanisms (i.e., senses) are important. Insect can move about more or less freely.</td>
</tr>
<tr>
<td>Host specificity more marked.</td>
<td>Subsistence foods important. The insect can survive for a while on less acceptable foods.</td>
</tr>
<tr>
<td>Cases of biological strains and numbers of strains of more common occurrence.</td>
<td>Biological strains less common or less known and involving fewer strains.</td>
</tr>
<tr>
<td>Less complex reactions.</td>
<td>Conditioned reactions, instincts, and taxes present. Some learning possible.</td>
</tr>
<tr>
<td>Less complex digestion.</td>
<td>Digestive fluids more complex in each individual.</td>
</tr>
</tbody>
</table>

STEPS IN A PROGRAM OF BREEDING FOR INSECT RESISTANCE

The way in which a program for insect resistance can develop will depend in part on the character of the crop and of the insect involved as well as the information available at the beginning. The order of development of such a program may be somewhat as follows:

2. A search for new germ plasm that may carry resistance.
   a. In new selections out of older varieties.
During the course of the study various clues may develop regarding the mechanisms of resistance and these may be studied as time permits. A knowledge of the ultimate cause of resistance, important as it may be from a biological point of view, is not essential to the practical breeding of insect-resistant crops. There have been only a few occasions when a knowledge of the cause of resistance has aided in plant breeding and at least as many where overemphasis on the search for it has delayed the practical development of insect-resistant varieties. These statements do not apply to experiments to distinguish between true resistance and pseudoresistance, nor to the classification into the three types.

Many possibilities still remain in the use of insect-resistant plants. Little has been done in the field of forest insects or insects affecting ornamental plants where the major emphasis in cultural control has been along the lines of induced resistance. This has been so because some important pests of these crops tend to attack only moribund or severely injured plants. With a few notable exceptions there has been little research on insect resistance in horticultural crops. Among more than 500 varieties in a register of fruit and nut plants for which characteristics are given, insect resistance is mentioned only twice (Brooks and Olmo 1944, 1946, 1947). In some of these crops there exist definite possibilities of reducing the cost of production and perhaps improving the quality of the product by means of insect-resistant varieties.

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INSECT RESISTANCE IN CROP PLANTS


CHAPTER X
SELECTED SUPPLEMENTARY BIBLIOGRAPHY

I. Introduction.
A. The function of the selected bibliography.
B. References to abstracts.

II. Classification used for crops and insects.

III. Selected bibliography.

The preceding chapters, particularly the general ones, contain references to papers on resistance that are not concerned with the five field crops which are discussed in detail. This selected bibliography of additional references is given in order to make the information contained in this volume more nearly complete. The bibliographies and general papers published by earlier writers, which are listed following Chapter I, should also be consulted since they contain some general information; the same applies to a few papers on specific crops omitted from this bibliography. The papers that have been omitted have been those that merely recommended the study of resistance in specific cases or contained information repeated in later publications. Some shorter and perhaps less important papers have been included here when references were not available in the earlier bibliographies. The amount of information presented in the different articles varied widely. A few references on resistance to mites have been included but no effort has been made to include all such papers. References to publications that appeared after the chapters on specific crops had been completed have been inserted in this supplementary bibliography.

The work done with three crops and insects perhaps deserve thorough study by anyone interested in insect resistance. These are
oats and frit fly (*Oscinella frit* (L.)), apple and woolly apple aphid (*Eriosoma lanigerum* (Hausm.)), and grapes and phylloxera (*Phylloxera vitifoliae* (Fitch)). The lists of references concerned with the first two are believed to be fairly complete. The European publications on grape phylloxera have not always been available to me and some important references may have been missed.

Notes and references to abstracts are given following some of the references. The letters B.A. refer to Biological Abstracts; H.A. to Herbage Abstracts; P.B.A. to Plant Breeding Abstracts; and R.A.E. to the Review of Applied Entomology series A. In the last case the numbers which follow refer to volumes and pages. In the other abstracts they refer to volumes and abstract numbers or, less commonly, to volumes and pages. Where references are given to two abstracts, both should be consulted since they may be written from two points of view.

The classification of crops and insects used in this supplementary bibliography follows. Where papers on an individual insect or crop are listed under a subheading, additional references concerned with the several insects or several crops may be found under the general sections.

Cereals in general
- Wheat (see Chapter IV)
- Corn (see Chapter V)
- Sorghum (see Chapter VII)
- Oats
- Barley
- Rice
- Sunflower and other oil plants

Forage and other grasses
- Miscellaneous field crops and resistance to general seed-feeding insects
- Legumes in general
  - Alfalfa and clovers
  - Beans, including soy beans, and peas
  - Garden and truck crops in general
- Onions resistant to onion thrips (*Thrips tabaci* Lind.)
- Potato (see Chapter VIII)
- Roots and tubers other than potato
- Cotton (see Chapter VI)
- Fiber crops other than cotton
- Sugar cane resistant to various insects
- Sugar cane resistant to moth borer (*Diatraea saccharalis* (F.))
- Stimulants, tea, coffee, tobacco, cocoa, etc.
SELECTED SUPPLEMENTARY BIBLIOGRAPHY

Fruits and nuts, general
- Apples resistant to codling moth (*Carpocapsa pomonella* (L.))
- Apples resistant to woolly apple aphid (*Eriosoma lanigerum* (Hausm.))
- Apples resistant to other insects
- Citrus and other tropical and subtropical fruits
- Strawberries
- Grapes resistant to phylloxera (*Phylloxera vitifoliae* (Fitch))
- Ornamental plants
- Resistance to cutworms, grasshoppers, and other general feeders
- Forest trees
- Resistance of wood to termites

CEREALS IN GENERAL


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WHEAT

(See Chapter IV)


CORN

(See Chapter V)


SELECTED SUPPLEMENTARY BIBLIOGRAPHY

Corn, sorghum, oats


SORGHUM

(See Chapter VII)


Oats


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Oats


Oats


Barley

Barley


BARLEY


BARLEY


BARLEY


BARLEY


BARLEY


BARLEY


BARLEY


BARLEY


BARLEY


BARLEY


BARLEY


BARLEY


BARLEY


BARLEY


BARLEY


BARLEY


BARLEY

RICE


Sunflower and other oil plants, forage and other grasses

SUNFLOWER AND OTHER OIL PLANTS


FORAGE AND OTHER GRASSES


Forage and other grasses, miscellaneous


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MISCELLANEOUS FIELD CROPS AND RESISTANCE TO GENERAL SEED FEEDING INSECTS

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LEGUMES IN GENERAL


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ALF ALF AND CLOVERS


Alfalfa and clovers


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Garden and truck crops


Garden and truck crops, onions


ONIONS RESISTANT TO ONION THRIPS


Onions, potatoes, roots and tubers other than potatoes


POTATO

(See Chapter VIII)


SELECTED SUPPLEMENTARY BIBLIOGRAPHY

Roots and tubers, cotton, other fiber crops, sugarcane


COTTON

(See Chapter VI)


FIBER CROPS OTHER THAN COTTON


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SUGARCANE RESISTANT TO MOTH BORER
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Sugarcane


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Sugarcane


Sugarcane, tea, coffee, tobacco, cacao, etc.

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