Water and Its Relation to Soils and Crops

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PREFACE

This review, which first appeared in Volume 11 of *Advances in Agronomy*, was written as part of the work of the Committee on Soil-Crop-Water Relationships, appointed early in 1957 by the Agricultural Board of the National Academy of Science-National Research Council.

Serving as editor of *Advances in Agronomy* has been a rewarding experience on several grounds. In the past decade the editor has learned a good deal about agronomy and the ways of agronomists. Above all, however, he has had impressed on him a realization of the vigor of agronomic research, and of its accelerated pace. Investigators are abandoning empiricism and tackling head-on many of the tougher problems of soil science and crop science, frequently using the knowledge and skills developed in more basic sciences, or adapting them ingeniously to their needs. Many examples of this are to be found in this treatment of the complexities of water in relation to the growth of plants in soils. In preparing this contribution, under the leadership of M. B. Russell, the committee sought to prepare a definitive and critical statement of the knowledge in the field, so that investigators in contiguous areas of agronomic science would be informed as to the present understanding of the many problems of water in relation to plant growth and crop productivity.

*Ann Arbor, Michigan*  

A. G. Norman
Preface

This review has been written as part of the work of the Committee on Soil-Crop-Water Relationships, appointed early in 1957 by the Agricultural Board of the National Academy of Science—National Research Council. In its consideration of present knowledge and research
needs in the broad field described in its name, the Committee has recog­
nized that much work has been done on many facets of the total
subject. Since several disciplinary fields are involved, it is difficult to
obtain an integrated picture of the many interrelations that exist in the
soil-plant-water system. This review is an attempt to develop such an
over-all picture. The focus of discussion is on the part of the hydrologic
cycle that begins when the raindrop strikes the soil surface and ends when
the water molecule returns to the atmosphere or moves out of the range
of plant roots.

In determining the relevance of material, many subjective decisions
were necessary. Not all possible topics are included, nor are those pre­
sentcd all discussed in equal detail. Such variations reflect both the
authors' evaluation of the need for detail and the degree to which the
subject seems to diverge from the central theme of the review. Even in the
more abridged discussions, however, an attempt has been made to call
attention to existing reviews or references through which the reader can
obtain more detailed treatments.

Several members of the Committee actively participated in the prep­
aration of the review. Others not on the Committee also assisted in the
writing of certain sections. The authorship of each section is indicated in
the Table of Contents and in the text. The membership of the Soil-Crop-
Water Relationships Committee is: G. W. Burton, A. S. Crafts, R. M.
Hagan, L. W. Hurlbut, P. J. Kramer, Dan Wiersma, and M. B. Russell,
Chairman.

I. Introduction

Water, the earth's most abundant compound, is a vital constituent in
all living matter. Because of its unique properties and ubiquitous nature,
water affects in innumerable ways all aspects of human activity. It con­
tinues to reshape the landscape, is a dominant factor governing all aspects
of the environment on the earth's surface, and since the beginning has
been intimately involved in the rise and fall of civilizations. The use and
control of water is therefore of vital concern to every human being and
to every nation.

High mobility is one of the distinguishing characteristics of water.
Since it is the only compound that exists naturally in substantial quantities
in the three physical states—solid, liquid, and gas—and since substantial
quantities of heat are involved in transformations between ice, liquid
water, and water vapor, this compound also plays a major role in the
thermal economy of the earth and its atmosphere. The high mobility and
thermal behavior of water are well illustrated in the series of inter-
connected dynamic events that are collectively called the hydrologic cycle. This review is concerned with biologic phenomena representing only a small sector of the hydrologic cycle: those involving water's interrelations with soils and crops.

Water may be considered as a renewable natural resource. From the geologic point of view it is indestructible, though for man's purposes it can be used up through important changes that modify its suitability for other uses. Such incompatibility of alternative uses is a fundamental factor affecting man's attempt to achieve maximum benefits from water use. The fact that water use itself undergoes continuous changes as a consequence of population changes and technologic advances further complicates the problem of achieving maximum benefits. History records that man has long recognized a need for developing procedures that will reconcile the conflicting demands for water. Recent reports by Ackerman and Löff (1959), The President's Water Resources Policy Commission (1950), and The Presidential Advisory Committee on Water Resources Policy (1955) emphasize that a need still exists for improved water policies in the United States. No attempt will be made in this article to discuss the broad problem of resource development or the political and economic aspects of alternative use of water, although it is recognized that, in the final analysis, the use of water in the production of crops is inextricably linked with the broader economic, social, and political aspects of total water resource development.

Although many aspects of the relation of water to soils and to crops have been discussed in recent comprehensive reviews, the authors of this article feel that insufficient attention has been given the interrelations between the properties and processes that characterize the soil-plant-water system. Therefore the main purpose of this review is to focus attention on the nature and importance of such interrelations and on the dynamic and interconnected nature of water in the soil-plant-atmosphere system. Although the review places major emphasis on conditions and problems encountered in the United States, it is believed that the principles discussed have wider applications and can serve as a basis for analyzing similar phenomena under different soil, crop, and climatic conditions in other countries.

The discussion opens with a brief review of the physical nature of water, since its behavior in soils and plants is a direct consequence of the unique properties of the water molecule. This is followed by a discussion of the several components of the agricultural water supply and of the principal factors affecting water use by plants. The broad effects of water on soil properties and a brief discussion of the intake and storage of water lead to a more detailed consideration of soil factors affecting
the development of roots. Attention then turns to the physiologic role of water in plants and to the response of crops to excessive water and to drought. Interactions of the total soil-plant-water system are then considered, together with certain management practices that affect it. The review concludes with a brief summary and a statement concerning broad areas of research that merit increased attention.

II. Water and the Hydrologic Cycle

To understand the role of water in crop production it is first necessary to examine the properties of the compound itself and to appreciate the over-all physical aspects of the hydrologic cycle of which agricultural water usage is a component part. Such are the objectives of this section.

A. The Physical Nature of Water

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The water molecule is one of the simplest known, but its properties and characteristics are unique, which explains why this compound occupies such a vital role in all biological and most of the physical and chemical phenomena known to man (Hutchinson, 1957; Dorsey, 1940; Hendricks, 1955; Crafts et al., 1949). The two small hydrogen atoms and the much larger oxygen atom are held together by chemical bonds formed by pairs of electrons. Each pair consists of the orbital electron of the hydrogen atom and one of the outer orbital electrons of the oxygen atom. The remaining four outer orbital electrons of the oxygen atom also tend to form two pairs, which, as a consequence of mutual repulsion, tend to arrange themselves as far apart as possible from each other and from the two pairs formed with the hydrogen atoms. Thus the water molecule can be considered as an oxygen atom around which, and attracted to it, are four pairs of electrons forming the points of a tetrahedron. Since the hydrogen atoms are located at two corners of the tetrahedral arrangement of electron pairs, there results an asymmetric distribution of charge in the water molecule, which is reflected in its highly dipolar character. Another important consequence of the structure of the water molecule arises from the asymmetric distribution of electrons around the hydrogen nucleus. This gives rise to an attraction, called hydrogen bonding, between the hydrogen of the water molecule and unsatisfied electron pairs of other molecules. Since two such unsatisfied pairs are present in the water molecule itself, this type of bonding, although much weaker than
the O—H chemical bond, is a factor of prime importance in determining the physical properties of water.

The high heat of vaporization, a property of water that is of great significance in relation to the hydrologic cycle, is a manifestation of the high degree of hydrogen bonding of water. Such bonds, which have to be broken in transforming water from the liquid to vapor state, also account for the fact that this transformation takes place at a temperature 260° C. above that of another simple molecule, methane, which has nearly the same molecular weight but is free of hydrogen bonding between its molecules.

Hydrogen bonding and the tetrahedral distribution of electron pairs around the oxygen atom also serve to explain the unusual increase in volume that occurs when water freezes. The open nature of the spatial arrangement of the water molecules arising from the bonding between the water molecules gives ice a lower specific gravity than water. The ice structure, upon melting, partially collapses, with water molecules occupying the “open spaces” in the ice structure. The facts that ice is less dense than water and that water has maximum density at a temperature slightly above the freezing point are both properties of great significance in the role of water in the thermal and hydrologic phenomena of the earth and its atmosphere.

Hydrogen bonding is also responsible for the viscous nature of water and for the rapid decrease in this property as temperature increases. The intermolecular hydrogen bonds are disrupted by heat. Other important consequences of hydrogen bonding are the properties of adhesion, cohesion, and surface tension, properties that largely determine the retention and movement of water through porous media, such as soil and plant tissues.

A final illustration of the unique properties arising from water’s molecular structure is the solvent action that is so intimately related to the role of water in biological systems. Water acts as a solvent for organic and some inorganic compounds by the mechanism of hydrogen bonding. In the case of saltlike compounds, water acts as a solvent by means of charge interaction as a consequence of the separation of charge between the hydrogen and oxygen atoms in the water molecule.

In addition to the physical phenomena discussed above, stemming largely from the unique ability of the water molecules to associate through hydrogen bonding, the molecular structure of water has profound effects on its chemical properties. These properties depend on breaking the strong hydrogen-to-oxygen bond, resulting in the formation of the positive hydrogen ion and negatively charged hydroxyl ion. Through this mechanism, water becomes an active participant in chemical reactions and, as
such, is involved in most of the important chemical processes occurring in nature.

Throughout the remaining sections of this article, water is considered in terms of its more macroscopic and familiar properties and in its behavior in soils and plants. The reader is asked to remember, however, that the observed behavior of this truly unique compound is, in the final analysis, traceable back to the structure and electronic configuration of the water molecule itself.

B. The Agricultural Water Supply

M. B. Russell and L. W. Hurlbut

Water may be considered as the lifeblood of the earth. Its mobility, energy transformations, and physical and chemical behavior impinge on every facet of organic life. We live in and are part of the unending flux of water known as the hydrologic cycle. This complex series of interconnected flows and phase changes is shown in part in the schematic diagram in Fig. 1.

The water that is agriculturally useful during any one year is an extremely small part of the world's total water supply. Including ground water to a depth of 12,500 feet, total supply is estimated to be about 165 trillion acre-feet. Roughly 93 per cent of this amount is found in the oceans and seas, and 7 per cent in fresh-water forms. The latter consists primarily of ground water (about 5 per cent), and polar ice and glaciers (about 2 per cent). The total amount of water in lakes, rivers, and soil moisture is about 1 per cent of the total fresh-water supply, or only about 0.08 per cent of the world's total water supply. A summary of estimated quantities of water in the several parts of the earth's hydrosphere is shown in Table I. Interchange of water is continuous, at varying speeds, among the several parts of the hydrosphere. In some instances the transit time is of the order of thousands of years, as in the case of deep ground-water movement or the cyclic movement of water through the polar ice caps and glaciers. Short-term cycles of only a few hours are also common, as in the case of the return of water to the atmosphere by evaporation from the wet soil surface immediately following a rain. The part of the hydrologic cycle of greatest general agricultural concern is the annual precipitation cycle. Each year about 89 billion acre-feet of water fall on the land surfaces of the world. This amount to 78 times the moisture content of the earth's atmosphere, and 135 times the estimated amount of water stored in the soil. Roughly four-fifths of annual precipitation returns directly to
TABLE I

<table>
<thead>
<tr>
<th>Estimated and Relative Quantities of Water in the Earth's Hydrosphere*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acre-feet</td>
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<tr>
<td>Total water</td>
</tr>
<tr>
<td>Total fresh water</td>
</tr>
<tr>
<td>Ground water to 12,500-ft. depth</td>
</tr>
<tr>
<td>Lakes and streams</td>
</tr>
<tr>
<td>Atmosphere</td>
</tr>
<tr>
<td>Soil moisture</td>
</tr>
<tr>
<td>Plants and animals</td>
</tr>
<tr>
<td>Annual precipitation</td>
</tr>
<tr>
<td>Annual runoff</td>
</tr>
</tbody>
</table>

* Adapted from Ackerman and Lof (1959).

The atmosphere, as evapotranspiration, with the remaining one-fifth accounted for in stream flow. Except for the relatively small amounts of water used from the ground-water reserves, whose cycle of depletion and recharge is much longer, practically all agricultural water use is identified with the annual precipitation cycle and involves the use of relatively short-term, low-capacity storage media.

The water resources of continental United States are tabulated in summary in Table II. These data indicate that average annual precipitation is about 30 inches and average annual runoff is about 8 inches. Usable ground-water reserves are estimated to be equal to ten years of precipitation, and the total storage in lakes is 3\% times the yearly precipitation. The average amount of available water stored in the soil for the area of the United States, however, is only about 3\% inches of water.

If the water supplies discussed in the preceding paragraphs were uniformly distributed over the United States, and if seasonal distribution

TABLE II

<table>
<thead>
<tr>
<th>Water Resources of Continental United States*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Annual precipitation</td>
</tr>
<tr>
<td>Annual runoff</td>
</tr>
<tr>
<td>Estimated total usable ground water</td>
</tr>
<tr>
<td>Soil moisture</td>
</tr>
<tr>
<td>Lake storage</td>
</tr>
<tr>
<td>Average annual precipitation</td>
</tr>
<tr>
<td>Average annual runoff</td>
</tr>
<tr>
<td>Average soil moisture storage</td>
</tr>
</tbody>
</table>

* Adapted from Ackerman and Lof (1959).
of the precipitation were matched to crop needs, there would be few areas of agricultural water shortage in this country. Neither of the two foregoing conditions exist, however, with the result that many areas are characterized by a marked imbalance between available water and agricultural needs. Geographic distribution of precipitation and runoff is shown in Figs. 2 and 3. Figure 4 shows the manner in which agricultural water use, as measured by potential evaporation, varies throughout the United States. The preceding figures indicated that, on the average, the eastern part of the United States and parts of the Pacific Northwest are regions of water surplus. The area west of the 95th meridian is, except for some of the mountain areas, a region of moisture deficiency if potential evaporation is taken as an index of agricultural water need. Even in the regions of average annual water surplus, water deficiencies are common in specific localities, because of (1) failure of seasonal distribution of rainfall to match seasonal water needs, (2) deviations of annual rainfall from average values, (3) excessive runoff resulting from high intensity of precipitation, steep topography, or low infiltration rate, as with frozen soil, and (4) low soil-moisture storage capacity for supplying crop needs between rains.

Current rainfall and soil moisture constitute the "working water supply" for crop production. Because of its agricultural significance, water storage by the soil is of great importance, even though it averages only about 12 per cent of annual rainfall and 0.01 per cent of the world's fresh-water supply. Even so, the soil plays an important role in the hydrologic cycle. As a water storage medium it reduces runoff peaks, supplies moisture for growing plants, and retains a significant portion of precipitation in a manner permitting its early evaporation back to the atmosphere.

The water storage capacity of soil is a function of its depth and physical composition. The volume fraction of voids multiplied by the soil depth is a measure of the gross water storage capacity of a unit area of soil. In many soils the volume fraction of voids varies with depth, making necessary an integration over each of the soil horizons to obtain the total profile storage capacity.

In well-drained soils, and in dry regions where the subsoil is perennially dry, not all of the soil pores remain filled with water. Therefore the effective storage capacity of a soil is determined by the volume fraction of pores that remain water-filled after water essentially ceases to move downward. The volume fraction of water retained under such conditions is affected by soil texture, ranging from 0.08, for sands, to 0.30, for clays. For soils of intermediate textures such as loams and silt loams, 0.25 is a good approximation of the gross field water storage capacity. Using this figure, we find that 3 feet of a silt loam soil will store 9 inches
Fig. 2. Average annual precipitation for United States (Ewans and Leuna, 1907).
Fig. 3. Average annual runoff for United States (Langbein and Wells, 1950).
Fig. 4. Average annual potential evapotranspiration for United States (Thornthwaite, 1948).
of water. However, not all of this water is available to plants. The volume fraction unavailable to plants is also a function of soil texture, increasing from about 0.04, for sands, to 0.18, for clays, with 0.10 being a good approximation for soils of medium texture. As shown in Fig. 5, about 60 per cent of the effective storage capacity of well-drained soils may be considered available to plants. Factors affecting the retention of water by soils, the laws governing its movement, and its availability to plants are discussed in later sections of this review.

In localities where rainfall and soil-moisture storage are inadequate to meet crop needs, other components of the hydrologic cycle must be drawn on to correct the deficiency. Surface water from streams and lakes and ground water are the sources that can be used. It can be seen from Tables I and II that each of these sources of water is much larger than the annual rainfall, and each has an order of magnitude larger than the soil moisture supply. However, as with annual precipitation surface and ground-water supplies, as shown in Figs. 3 and 6, are not uniformly distributed and, in fact, are largely concentrated in those areas where current rainfall and soil storage are most adequate. Thus, in the humid region east of the 95th meridian, all streams of any size are permanent, and annual runoff exceeds 10 inches in most areas. Even there, surplus stream flow undergoes a pronounced seasonal variation. Except in Florida and the southeastern coastal plains, half or more of the annual runoff occurs in three months of the year. Since the period of peak stream flow
Fig. 6. Ground-water areas in the United States (Thomas, 1933).
is in the late winter or early spring, it does not coincide with the period of maximum agricultural need. Therefore, to achieve maximum use, runoff must be impounded for periods of about six months.

Average annual runoff is much less in the Great Plains region than in the more humid Eastern States, and seasonal concentration is more pronounced—50 to 70 per cent in a three-month period over most of the region. Flow in major streams in this region is stabilized to some degree by runoff from the bordering mountains to the west.

Runoff patterns in the western third of the United States reflect the mountainous nature of much of this area. Rainfall and soil storage are generally insufficient for intensive agricultural production. Irrigation, based on impounded mountain streams and on ground-water supplies, is widely practiced throughout this region. Runoff from the lowland areas is slight except in the Puget Sound area.

As might be expected, the ground-water supplies depicted in Fig. 6 reflect in a general way the precipitation and evapotranspiration patterns and the geologic structures of the country. Three major types of ground-water areas are shown in Fig. 6: (1) the channels and associated alluvial deposits along water courses, (2) loose sands and gravels in glacial drift and outwash, and (3) such consolidated rocks as limestones, basalt, and sandstones. In 1950, ground-water withdrawals accounted for about 20 per cent of all the water withdrawn for municipal, rural, industrial, and irrigation use. The last accounts for more than 60 per cent of all ground water used in the United States. Nearly all of rural use, 25 per cent of municipal use, 7 per cent of industrial use, and 25 per cent of irrigation use are supplied from ground-water sources. The usefulness of a ground-water source is determined by capacity, depth and recharge rate of the aquifer, and, in some instances, the chemical quality of the water. Large quantities of ground water are held in clays and fine-textured materials of such low permeability that the discharge rate from wells is too low for practical utilization. It is estimated that 80 per cent of all water obtained from wells in the United States comes from unconsolidated sand and gravels, 5 per cent from limestone, 5 per cent from sandstone, and 2 per cent from basalt. For ground-water aquifers to serve as a continuing source of water, recharge rate must equal withdrawal rate. In some areas in the southwestern United States the underground water reserves are being steadily depleted (Fig. 7) and remedial measures are being employed to increase the recharge rate (Mitchelson and Muckel, 1937; Muckel and Schiff, 1955).

The chemical nature, or quality, of surface and ground-water supplies has an important bearing on their agricultural usefulness. Water quality for irrigation is determined by total concentration of soluble salts, con-
centation of sodium and proportion of sodium to divalent ions, concentration of bicarbonate, and the content of toxic qualities of certain minor elements (Richards, 1954; Thorne and Peterson, 1949). In humid regions, the water quality of streams is not a factor affecting their use for irrigation unless industrial pollution is heavy at the point of water withdrawal. In subhumid and arid regions, however, variations in water quality are great among different streams and different parts of a given stream (Fireman and Hayward, 1955). Ground water also varies widely in quality, reflecting both the nature of the source of recharge and the chemical properties of the aquifer. Salt water may invade fresh-water aquifers if excessive pumping shifts the interface between fresh water and salt water.

The concentration of soluble salts in the soil solution is increased by the loss of water from the soil by evaporation and transpiration. To prevent a continued build-up of salt concentration, the net downward flow of water through the soil must be great enough to carry the soluble salts out of the plant root zone. Thus the salt balance of the soil is determined by the amount and quality of irrigation water applied and the effectiveness of the leaching and drainage processes. The relation of water
quality to soil behavior and to plant growth and irrigation practice is discussed in later sections of this review.

As mentioned above, roughly three-fourths of the precipitation reaching the soil surface returns to the atmosphere by evaporation and transpiration. Since stream flow and the recharge of surface and underground supplies depend on the residual one-fourth of the precipitation, it is apparent that factors affecting evapotranspiration have a major influence on the yield of watersheds and river basins. Evaporative loss from lakes, ponds, and water-storage reservoirs becomes a major factor when the surface-to-volume ratio of the water body is large, as in shallow farm ponds, where seasonal evaporation loss will frequently be 25 per cent or more of the storage capacity of the pond. Surface-applied monomolecular organic films substantially reduce such losses and may offer a practical solution to this problem (Mansfield, 1955; Moran and Garstka, 1957).

Water intercepted by plants or absorbed by the upper 2 inches of the soil is readily available for evaporation. It normally returns to the atmosphere within a few hours of the end of rain. For this reason, small showers (less than 0.10 inch) are of limited effectiveness, except as they change transpiration losses by shifting the energy balance and water-vapor pressure of the leaf environment, thereby reducing plant use of soil moisture. Interception losses are affected by the nature of the vegetation and the type of precipitation, but are estimated to amount to 5 to 15 per cent of annual precipitation.

Water that has penetrated more deeply into the soil is less susceptible to quick return to the atmosphere by evaporation, but may be returned through plant transpiration. Such return by nonbeneficial vegetation is a major factor affecting ground-water supplies in certain arid regions. In the seventeen Western States, an estimated 20 to 25 million acre-feet of water are wasted annually by nonbeneficial plant use (Robinson, 1952). This is equivalent to about two-thirds of the storage capacity of Lake Mead. The effects of use and management practices on consumptive use of water and yield of watersheds are discussed further in later sections of this review.

In summary, it can be said that the agricultural water supply of the United States is generally good. The rapid growth of use for municipal, industrial, and irrigation purposes is shown in Table III. Since the economic return per unit of water used is lower for crop production than for use by industries or municipalities, the long-range situation indicates a need for greatly increasing agricultural water-use efficiency. Figure 8 illustrates the major causes of the present low efficiency of water currently used for irrigation. East of the 95th meridian, where annual precipitation equals or exceeds potential evaporation, soil moisture and surface
TABLE III

Present and Estimated Water Use for the United States

<table>
<thead>
<tr>
<th>Use</th>
<th>Estimated use, 1950 Billion gal./day Per cent</th>
<th>Estimated need, 1975 Billion gal./day Per cent</th>
<th>Increase (per cent) 1950-75</th>
</tr>
</thead>
<tbody>
<tr>
<td>Municipal and rural</td>
<td>17</td>
<td>9</td>
<td>25</td>
</tr>
<tr>
<td>Direct industrial</td>
<td>80</td>
<td>43</td>
<td>215</td>
</tr>
<tr>
<td>Irrigation</td>
<td>88</td>
<td>48</td>
<td>119</td>
</tr>
<tr>
<td></td>
<td>185</td>
<td>100</td>
<td>350</td>
</tr>
</tbody>
</table>

The Presidential Advisory Committee on Water Resources Policy (1955).

and ground-water supplies of high-quality water are available to meet crop needs during periods of moisture deficiency, which are normally short. In the Great Plains area, moisture deficits occur regularly. These may be alleviated by more complete development and use of surface and ground-water supplies and by management practices that reduce the short-term recycling of moisture back to the atmosphere. Agricultural water needs in the Mountain and Pacific Coast States can be met by transporting water from higher-elevation, nonagricultural areas to the productive valleys. Improved technology in storage, transport, and utilization of irrigation water will permit further development of ir-

![Diagram of water conveyance](image)

**VALUES IN FEET-DEPTH OF WATER**

Fig. 8. A schematic summary of water conveyance (U. S. Dept. Agr. Yearbook Agr. 1955, p. 120).
rigated agriculture in this region coincident with the expansion of indus­
trial and municipal water use. Long-term increases in the total fresh­
water supply for the United States may come from techniques for weather 
modification, economical recovery of sea water, and the development of 
techniques for sustained use of low-yield aquifers.

C. AGRICULTURAL WATER USE

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Having considered various aspects of the agricultural water supply, par­
ticularly in the United States, attention now turns to the physical 
aspects of water use by crops. This is primarily an energy-controlled 
process, but it is modified by plant, soil, and atmospheric factors that 
govern the absorption and distribution of energy at evaporating surfaces, 
and by the flux of liquid water to, and water vapor from, such surfaces. 
Biologic processes that affect water use are discussed in later sections 
of the review. For further discussion of the topics presented here, the 
reader is referred to several recent publications (Deacon et al., 1958; 
Leettu and Davidson, 1957; Kramer, 1959; McIvoy, 1957; Penman, 1948a, 
1956).

1. Crop Characteristics

The main effect that type of crop has on consumptive use of water 
is the number of months the crop is in leaf. In designing or operating 
an irrigation system one is interested not only in the peak rate of water use 
but also in total seasonal use. A perennial crop, such as alfalfa, may have 
a low transpiration rate during the winter, but its use of water will in­
crease and continue fairly high right through the spring, summer, and 
fall. On the other hand, with a crop such as sugar beets, which is not 
planted until spring and does not completely cover the ground for some 
time, the rate of water use will be low until complete ground cover is 
achieved; further, water use ceases when the crop is harvested. Thus, total 
water use is appreciably lower in sugar beets than in alfalfa.

Percentage of ground cover also has an important effect on water use. 
A wet, bare soil surface will evaporate initially at quite a high rate, but 
evaporation is considerably reduced as soon as a thin layer of the surface 
soil dries out. If a crop in its young stages consists of small plants covering, 
say, 25 per cent of the soil surface, virtually no water will be lost from the 
bare soil in between the plants, provided, of course, that the soil surface 
is not rewetted by rain or irrigation. It might be expected, therefore, that
the use of water per acre by a crop would be more once the plants have grown sufficiently to cover the ground surface completely.

Figure 9, a plot of the accumulated evapotranspiration against the various months of the year for a number of crops, shows that, though the curves start at different times of the year, they have essentially equal slopes during the summer months. This suggests that, given adequate moisture and complete plant cover, evapotranspiration is independent of crop type. Thornthwaite, the first to separate the climatic factors from the crop and soil factors, introduced the concept of potential evapotranspiration (Thornthwaite, 1954). This maximum evaporation that can occur from crops under given climatic conditions was defined more pre-

![Figure 9. The seasonal distribution of water use by three crops.](image)

cisely, by Penman, as "the amount of water transpired in unit time by a short, green crop completely shading the ground, of uniform height and never short of water." Starting with this definition, Penman made the following two generalizations: First, for complete crop covers of different plants having about the same color, i.e., the same reflectivity, the potential evapotranspiration rate is the same, irrespective of plant or soil type. Second, this potential evapotranspiration rate is determined by the prevailing weather.

The curves already referred to support such a concept. Since potential evapotranspiration is extremely difficult to measure, experimental data (Lemon et al., 1957; Mather, 1954; Rider, 1957; Penman, 1949; Makkink and van Heemst, 1956; Mendel, 1945) put forward in support of the concept, or otherwise, is of doubtful value. In some experiments there is evidence that soil and plant factors cannot be neglected, but in others there have been poor experimental techniques or inadvertent oversight of complicating factors. Nevertheless, it has not been demonstrated by
reliable experiments that there is any marked difference in the potential evapotranspiration rates of various crops. Penman (1956) and Neumann (1953) have attempted to show on theoretical grounds that the concept is valid, but the assumptions in their approaches do not permit an accuracy of better than about ±10%. The reasons why different crops cannot be expected to have exactly the same evapotranspiration will be apparent in the following discussion of the physics of evaporation.

2. Physics of Evaporation

Evaporation from natural surfaces, such as open water, bare soil, or vegetative cover, is a diffusive process, by which water in the form of vapor is transferred from the underlying surface to the atmosphere. Because the atmosphere is in a continuous state of turbulence, the process is overwhelmingly turbulent rather than molecular.

There are two necessary physical requirements in the evaporation process. First, a source of heat is needed, to cause the liquid water to vaporize. This source may be in solar energy, in the air blowing over the surface, or in the underlying surface itself. Second, diffusion of matter can proceed only in the presence of a gradient of concentration of the substance in question. Thus, evaporation can occur only when the vapor concentration at the evaporating surface exceeds that in the overlying air.

The first of these considerations provides the basis of the energy-balance approach to the study of evaporation. To use it, it is not necessary to know the details of the process, but simply to be able to measure or to estimate all the other factors contributing to the thermal balance at the evaporating surface. Solar energy arrives at the upper limit of the earth's atmosphere at the rate of about 2 calories per square centimeter per minute. A considerable fraction of this is reflected or scattered by the atmosphere back into space, and does not affect the energy balance at the earth's surface. A schematic picture of the energy balances obtaining at the earth's surface at midday and at night is shown in Fig. 10. The thermal balance can be written in the following equation form:

\[ R_e - R_r - R_{lw} = H_s + H_t + H_e \]

where \( R_e \) is the incoming solar radiation, \( R_r \) the reflected solar radiation, \( R_{lw} \) the net outgoing longwave radiation, \( H_s \) the sensible heat flow into the air, \( H_t \) the heat flow into the soil, and \( H_e \) the evaporation heat, or latent heat flow into the air.

Since the main source of energy for evaporation or transpiration is solar radiation, it is obvious that evapotranspiration must be less in regions where this intensity is low. The effect of the radiation is to in-
crease the temperature of objects that absorb it. During the day, therefore, plant foliage would always be warmer than the adjacent air if other factors did not enter in. As the leaf temperature is increased, however, so is the vapor pressure of the air in the substomatal cavity, since the saturation vapor pressure of air in contact with a wet surface is a function of the surface temperature. The vapor pressure gradient from the leaf outward into the adjacent air, which causes the water loss from the leaves, is also increased. The evaporation of liquid water requires energy in the form of latent heat; transpiration therefore has a cooling effect on leaves. In direct sunlight, leaves probably will still be at a higher temperature than will the nearby air, because of the large quantities of solar energy absorbed, but leaves in the shade may well be at a lower temperature than air because of the cooling effect of transpiration.

If the air around the leaves is perfectly still, the flow of vapor will gradually increase the vapor pressure there, reducing the vapor-pressure gradient and thus reducing the transpiration rate. In the presence of wind, however, the moistened air is moved away from the leaves and replaced by drier air from some distance away. The vapor-pressure gradient con-
times to be maintained, and, within limits, an increase in wind speed will cause an increase in transpiration rate. Again, if the humidity of the air in the region is low, the transpiration rate will be higher than if humidity is high.

The effect of increasing the air temperature is not quite so obvious. If the amount of water held in the air remains constant, increasing the temperature will of course decrease the relative humidity, but the actual pressure of water vapor will remain the same. However, increased air temperature will result in an increased leaf temperature of the plants, which in turn will result in an increased saturation vapor pressure at the leaf surface. Again, the net effect is to increase the vapor-pressure gradient from the leaf to the air, thus increasing the transpiration rate.

Since the solar energy absorbed by a leaf is used, not only in evaporating water but also in heating the air and the plant, it might be expected that there would be an upper limit, given by the solar energy available, to the rate of evaporation or transpiration. This is not always true (Halstead and Covey, 1957). For example, consider an isolated plant in dry surroundings; none of the radiation absorbed by the surroundings goes into evaporating water, so that the temperature of the surroundings is increased over the temperature of the plant. When this heated air blows over the cooler plant, some of the extra heat of the air is given up to the plant and can be used to increase the transpiration rate. Under such conditions of advective heating, plant transpiration can exceed the maximum rate possible if radiation were the only source of energy.

The thermal-balance equation gives the conditions that need to be met if potential evapotranspiration is to be independent of the crop and not exceed evaporation from a free water surface. Considering the first factor, the incoming solar radiation will, of course, be independent of crop type, but the amount of reflected shortwave radiation may not be (Geiger, 1950). This will depend on crop reflectivity. The loss of heat by longwave radiation will depend on the temperature, but, as a first approximation, can probably be considered independent of crop type. Thus, the energy available for evaporation will be the same only for crops of similar color.

The amount of heat flowing into the soil will depend on the insulating properties of the crop above the soil surface. These may well differ between a short turf lawn and alfalfa 2 feet high. The sensible and latent heat flowing into the air will depend on the turbulence of the overlying air layers, and this will differ with the crops. A crop such as sugar beets, which has considerable variations in the height of the upper layer of vegetation, will cause greater turbulence in the overlying air than will a short-grass surface. A crop such as wheat, which bends in the
wind, also will have a different effect on the energy transferred by
turbulence. These all suggest that the concept of potential evapotrans-
piration is only an approximate one, with certain crops using either more
or less water than the average.

In comparing a crop to a water surface, the interval over which the
evaporation is considered is of considerable importance. Vegetation
virtually ceases to transpire at night, but a water surface continues to
evaporate. In fact, the considerable quantity of heat absorbed by a water
body during the day becomes a source of heat at night. Thus, over a
period of, say, a month, evaporation from water will probably exceed
transpiration from a crop. Over a few hours during the day, however, a
crop may evaporate more than a water surface.

3. Methods of Determining Evapotranspiration

a. Water-balance methods. All these methods make use of some form
of the hydrologic equation

\[ P = E + O + D + W \]

where \( P \) is precipitation, \( E \) is evaporation, \( O \) is surface runoff, \( D \) is sub-
surface drainage, and \( W \) is the change in water content of the block of
soil being considered. By measuring or eliminating all but one of these
variables, the remaining one can be found.

A well-known application of this principle on a large scale is the
catchment area balance sheet, where, over long periods or from one state
of wetness or dryness to the next similar one, \( W \) can be neglected, \( P \) and
\( O \) are generally comparatively easy to measure, and \( D \) is small enough to
require only an estimate. Where lakes and reservoirs are known to be
free from seepage, \( D \) can be neglected, stream gaging will give \( O \), and \( W \)
can be obtained volumetrically.

On a smaller scale, enclosing a block of soil eliminates \( O \) and \( D \), and
\( W \) can be obtained by periodically weighing soil and container. This is
the principle of lysimeters (Harrold and Dreibelbis, 1951, 1953; King
et al., 1956; Kohne et al., 1940). A lysimeter is a soil mass, including
vegetation, isolated from its surroundings. By use of precise weighing
mechanisms, evapotranspiration over short periods can be determined
with a high degree of precision. Difficulties in isolating a soil block and
yet maintaining its representative nature have the consequence that no
single standard type of lysimeter suits all problems and soil types.

To ensure representative behavior, a number of precautions must be
taken. In particular, containers should be large enough to reduce the
importance of boundary effects and to avoid restricting root development.
To ensure proper drainage, the bottom of an isolated soil column will
often require artificial application of a moisture suction equivalent to that present at the same depth in the natural soil. Finally, because of possible advection effects, the influence of the surroundings must be reduced. To do this, each lysimeter should have around it a guard area maintained under the same crop and moisture conditions. For the same reason the container wall and the surrounding retaining wall should be as thin as possible, though not made of metal, which will increase heat flow to the deeper layers of the soil.

Because of the very high cost of adequate lysimeter installations, a somewhat simpler device has been developed by Thornthwaite and others (Garnier, 1952; Gilbert and van Bavel, 1954; Mather, 1950, 1951). These potential evapotranspirometers, as they are called, are really a specialized form of lysimeter, limited in use to soils kept permanently moist. Instrumentally, they can be very simple. The basic requirements are a simple container, such as a large oil drum, with provision for irrigation and collecting and measuring percolation. In operation, a measured amount of water, always sufficient to bring about some drainage, is applied at regular intervals. With the soil never far from field capacity, \( W \) in the hydrologic equation can generally be neglected by comparison with \( D \), particularly over long periods. The water consumption is then obtained as the difference between the amount of water supplied and that collected as percolate.

The least expensive, but often also the least accurate, method of arriving at \( W \) is by sampling changes in soil moisture content throughout the volume of soil considered. Evapotranspiration from soil areas of any size can be determined in this way if there is no water table and if deep percolation is absent or measurable. Various means are available for measuring the soil moisture content, but the most precise yield evapotranspiration values accurate to only about \( \pm 5 \) per cent in uniform soil thoroughly permeated by roots, and then only when the period of measurement is relatively long, e.g., a week or more. The recent development of a neutron-scattering method promises greater accuracy over shorter intervals.

Apart from the poor resolution of the sampling method, there are two further sources of error. In humid regions an unknown percentage of measured rainfall may be lost by runoff or deep percolation instead of increasing soil moisture storage in the sampling zone. Further, any additions of moisture from dew are not included. In some regions an appreciable percentage of total annual precipitation may come in this form. Soil moisture sampling would indicate lower evapotranspiration from a crop under these conditions than under a similar climate with no dew.

b. Standard devices. Because of their ease of operation, standardized
tanks of water have become the most widely adopted evaporation instruments throughout the world. Considerable effort has been devoted to empirical studies using pans of arbitrary dimensions, construction, and exposure (Kohler, 1952; Kohler et al., 1955; Bonython, 1950; Pruitt, 1959; Ramdas, 1957; Eichner, 1931, 1934; Young, 1947, 1948). What is sought, ideally, is a single conversion factor applicable at any time under all conditions. In actual fact there are large variations in the conversion factors, depending in part on the size and type of pans used, the local environment, and the season. Most of this work has been applied directly to large water surfaces, and the assumption made that transpiration from an irrigated area will be similar to evaporation from such a water area.

Not all of this variation in coefficients is due to the pans themselves. The evaporation rate from a large water surface is itself affected by such local characteristics as the depth and turbidity of the water and its rate of mixing. These determine the vertical extent of the water that shares in the incoming energy supply during the day or summer and supplies energy to the surface at night or in winter. In other words, they determine the effective heat-storage capacity of the lake and, hence, the degree of “lagging” of its daily and annual cycle of temperature and vapor pressure.

Thus, the peak temperature and vapor pressure of a lake of sufficient depth will occur appreciably later than that of the surrounding countryside or a nearby pan. Its peak rate of evaporation will do likewise. An extreme example is afforded by the contrast between Lake Superior and a smaller, neighboring lake. The peak evaporation of the former occurs in winter, six months after that of the latter. The reason is that the large heat capacity of Lake Superior causes its surface vapor pressure to exceed the vapor pressure of the cold, overlying air in winter, whereas in summer it will not warm sufficiently for the surface vapor pressure to exceed that of the overlying air, moistened by strong evaporation over the land.

Such phase differences, combined with appreciable amplitude differences, put out of question a universal pan coefficient. They also make it dangerous to apply existing empirical coefficients outside the ranges for which they have been determined. Although tank readings may have some use for indicating rates of evapotranspiration from thoroughly moist soil and vegetation, they again become inapplicable when water stress occurs Under arid conditions, natural evapotranspiration may be virtually zero while pan evaporation, because of advection of heat from the surroundings, might increase rather than decrease.

Other simple devices are being used in various parts of the world. One is a very shallow, black-metal evaporation pan. Virtually no solar radiation is reflected, and the half-inch layer of water contained in the pan has a very small heat capacity. Rate of evaporation and rate of transpiration
might be more closely related with this type of pan than from the normal depth of water used in standard tanks.

The Piche evaporimeter (Prescott and Stirk, 1951; de Vries and Venema, 1954) consists of a piece of blotting paper clamped across the mouth of a water-filled glass tube. It is supposed to simulate the behavior of transpiring plants. However, it gives little more than an indication of the water demand on a single leaf having the same exposure as the paper disk. When compared with the demands of vegetation as a whole, this device overestimates the effect of wind and underestimates that of radiation.

Yet another device is the porous porcelain atmometer (Livingston, 1935). Strictly speaking, an atmometer is defined as any instrument of whatever form for measuring evaporation rates. However, the term is now more commonly applied to these porcelain spheres. Various workers have shown that such atmometers are sensitive to solar radiation, air movement, and the dryness of the surrounding air. Livingston originally used only white atmometers, but, realizing that plants absorbed more energy than these, he used darkened atmometers to make his measurements more representative of plant transpiration. Later, black and white atmometers were paired and the difference in their evaporation rates was found to be very well correlated with crop use of water (Halkias et al., 1955; Robertson and Holmes, 1956).

Other workers have found a high degree of correlation between the difference in black and white atmometer evaporation and the intensity of solar radiation (O'Connor, 1955). However, using a difference in evaporation rates between two atmometers involves certain difficulties. Since a fairly small difference between two large quantities is involved, a small error in either quantity gives a very large percentage error in their difference. Further, dust and other types of soiling under field conditions make it difficult to maintain the reflectivity of either atmometer within a few per cent of its nominal value. Thus, the difference between evaporation rates can vary up to 25 per cent or more.

c. Empirical equations. Because the meteorological factors on which evaporation depends are hard to measure over a large area with sufficient accuracy, several workers have combined more easily measured climatic elements into simple empirical formulas to give the water loss.

The first empirical formula to be discussed is that of Blaney and Criddle (1950). This formula is based on the mean monthly temperature and the percentage of total annual daytime hours that occur in that month. The formula \( U = KF \) is used, where \( U \) is the consumptive use over the period, \( K \) is a coefficient depending on the crop, and \( F \) is the sum of the monthly consumptive use factors for the period considered. The monthly
The consumptive use factor is equal to the mean monthly temperature in degrees Fahrenheit multiplied by the monthly percentage of daytime hours occurring in the year divided by 100. One disadvantage is that the coefficient $K$ must be determined empirically for each different crop in the area in which it is desired to use the formula. Although this formula provides a reasonably good estimate of evapotranspiration in some moist regions, it fails badly in dry regions or in areas, such as that of Hawaii, where temperature variations are small.

It is at first difficult to see why this formula should fit experimental data at all, since evapotranspiration does not depend on monthly temperature, and only indirectly on the number of daytime hours in the month. A consideration of the physical bases of evapotranspiration, however, shows that the underlying physics suffice for this to be a reasonable approximation. As mentioned previously, evapotranspiration depends in part on the vapor-pressure gradient from the evaporating surface to the air. The surface vapor pressure is a function of the surface temperature, whereas the vapor pressure in the air is relatively constant during the day. A simplifying approximation is thus to relate evaporation to surface temperature. A further approximation is to replace surface temperature with air temperature, which reveals the basis for the Blaney-Criddle formula. The term involving the daylight hours takes into account the fact that transpiration is predominantly a daytime process.

Another formula has been developed by Prescott (1952), who uses the quantity “saturation deficit” raised to a power that is empirically determined. Saturation deficit is an estimate of the drying power of the air, on which evaporation is supposed to depend. It is equal to saturation vapor pressure at air temperature minus actual vapor pressure at the same temperature. Actually, evaporation does not depend on the saturation deficit, but the difference between the saturation vapor pressure at the surface temperature and the actual vapor pressure in the overlying air can be approximated by the saturation deficit.

A third formula, which is well known, was developed by Thornthwaite (1948). His formula is based on latitude and mean monthly temperature. The actual formula and method of working are somewhat complicated, but their basis can be justified in the same way as the Blaney-Criddle formula. Thornthwaite’s formula gives reasonably good estimates in climates similar to the humid climate in which it was developed, but the values it gives are considerably too low for semiarid climates. Also, it gives values which are out of phase with solar radiation (van Wijk and de Vries, 1954; van Wijk et al., 1953).

Since the various empirical formulas show greater or smaller errors in different climatic regions, it is worth considering which climatic ele-
ments are the most appropriate to use. This depends in part on the type of problem for which the formula is required. In considering the requirements of proposed irrigation systems in new areas, it must be kept in mind that introducing irrigation will change the local climate. Any formula based on existing climatic elements will therefore not hold when the climate is changed. In such cases the formulas should be mainly in terms of the more conservative weather elements. Precipitation and incoming solar radiation are among the most conservative elements; net radiation, temperature, and wind speed are less so; and atmospheric humidity least. For this reason, Thornthwaite takes the somewhat extreme view that humidity factors should be excluded, but this obviously leads to difficulties between humid and arid climates. Since evapotranspiration is predominantly a daytime process, the factors in any empirical formula should be weighted heavily toward daytime values. Thus, mean maximum air temperatures or the saturation deficit at the time of maximum temperature might be expected to give greater reliability than the mean values employed at present.

From the foregoing it is seen how simple empirical formulas can be useful over limited climatic ranges, but will require more factors for extended use. In view of the drastic simplifications involved, accuracy should not be expected for such formulas. If used, they should be developed for specific purposes and not expected to apply over a great range of latitudes or climates.

Two other formulas should be mentioned at this time. They might be called semiempirical and have been developed independently by Penman (1948a, b, c, 1952) and Ferguson (1952). Both of these workers derived approximate solutions to evaporation formulas based on physical considerations. The more readily measured meteorological quantities are then used in these approximate solutions. Both formulas apply strictly to water surfaces. Penman's formula, which includes net radiation, saturation deficit, and wind speed, appears to fit both humid and semiarid conditions reasonably well (Pearl, 1954; Penman, 1953). Its main drawback is in the tedious computations that are often required, but this is likely to apply to any formula that includes radiation.

d. Vapor-flow methods. There are several approaches to finding the upward flow of water vapor into the atmosphere. The scientific study of evaporation began with Dalton, who designed experiments to investigate the factors controlling it and showed his results to be consistent with the formula that now bears his name, although there is no evidence that he expressed his results in this form. The rate of evaporation is given by the product of the vapor-pressure gradient from the evaporating surface into the overlying air and a function of the wind speed.
Many important evaporation studies have been undertaken, usually confined to evaporation from small water surfaces, and the constants in the Dalton equation determined (Kennedy, 1933; Marciano and Harbeck, 1952; Pasquill, 1949). Part of the variation of the experimental values of the constants is due to the different types and sizes of tank employed. Some is due to the arbitrary measuring heights used for both wind speed and atmospheric vapor pressure. The remainder arises from omission of other important factors in the Dalton formula. As previously discussed, it is the turbulent conductivity of the air, rather than actual wind speed, that conducts water vapor along the vapor-pressure gradient. Determination of this turbulent eddy conductivity under various meteorological conditions provides one of the most challenging problems in agricultural meteorology today.

The second vapor-flow method involves direct determination of the eddy flow of water vapor in the atmosphere. At any point in the atmosphere, turbulent air movement will normally be present, giving rise to a fluctuating vertical component of wind speed. In the presence of a vertical moisture gradient these fluctuations will be associated with simultaneous fluctuations in the moisture content of the air. On the average, rising air will tend to be moister than descending air when the vapor-pressure gradient is directed away from the surface. This will give rise to a net transfer of water vapor.

The mean rate of this transfer per unit of time and area is known as the vertical eddy flux of water vapor. Up to several meters above the surface, storage and side-flow effects in the intervening air layers are negligible, so that the eddy flux anywhere within this layer is virtually equal to evapotranspiration at the surface. The tremendous instrumental difficulties involved in measuring turbulent fluctuations of vertical wind speed and the moisture content of the air at a point have been surmounted by a group in Australia, and appropriate equipment has been in use there for some years (McIlroy, 1955; Swinbank, 1951, 1955). Recently additional instrumentation has enabled automatic averaging, multiplication, and integration of the quantities involved as the eddy fluctuations are detected, so that evapotranspiration over an interval is given as a reading on a counter (Taylor, 1958; Taylor and Dyer, 1958).

This method is completely independent of the nature of the underlying surface, and in no way disturbs it. It is, therefore, the best method currently available for measuring evapotranspiration from natural surfaces. The only limitation is in the height of the sensing elements. The closer they are to the surface, the more nearly does the eddy flux become a measure of surface evapotranspiration, though the greater is the influence of inhomogeneities in the underlying surface. As the height of the
measurements increases, the readings become more representative of an extensive area.

The final method to be discussed is that known as the aerodynamic approach. Like the Dalton equation, this method makes use of the general flow law, which states that the rate of flow of any quantity is equal to the product of the concentration gradient and the conductivity, but it is based on a better physical understanding of the principles involved. It considers the turbulent transfer of water vapor at a small distance above the ground, rather than the over-all process of ground-to-air transfer. In its basic form the empirical wind coefficient is replaced by the eddy conductivity. The moisture gradient can be measured directly between two heights, so the problem becomes one of finding a suitable expression for eddy conductivity in terms of other measurable quantities.

Under most conditions near the ground, the eddy conductivity of water vapor can be assumed to be equal to that for momentum. The latter is in principle determinable from measurements of changes in wind speed with height. Considerable precision in the measurements is necessary when this approach is used, since even small errors in individual measurements can alter the final result considerably. However, the physics underlying the method, together with the limitations and precautions that must be observed in its use, are now fairly well understood (Halstead, 1951; Osborn, 1951; Pasquill, 1949a, b, 1950; Rider and Robinson, 1951; Rider, 1954a, b; Thornthwaite and Holzman, 1942). It has been shown to be workable with water surfaces, pastures, and short crops, but is not likely to be practical with tall crops, such as orchards, or with flexible crops, such as wheat, which bend to varying degrees with changes in wind speed.

e. Surface-energy balance. The basic equation used above in discussing the physics of evaporation was an energy equation. It is possible to measure a sufficient number of terms in this equation to calculate the evaporation (Cummings, 1940; Penman, 1951; Smoker, 1947; Anderson, 1952; Holzman, 1941; Suomi and Tanner, 1958). The over-all radiation balance can be found from separate measurements of the incoming and outgoing components of both shortwave and longwave radiation. However, it is far better to obtain net radiation directly, using one of several designs of net radiometers now available.

Heat flow into the soil is more difficult to determine, but, except over short periods, it is only a small component of the balance, and is often neglected. It can be measured directly with heat-flow meters buried in the ground, or can be found from changes in the temperature profile of the soil, combined with measurements or estimates of its heat capacity. The partition of the remaining energy between evaporation and heating of the
air has to be approached indirectly, since the heating of the air cannot be measured any more easily than evaporation itself.

This partition is usually carried out by means of the Bowen ratio. Bowen derived an expression for the ratio of sensible heat flow to latent heat flow as being proportional to the ratio of the temperature difference between two heights and the vapor-pressure difference between the same heights (Bowen, 1926). Strictly speaking, this holds only under neutral conditions, i.e., when the rate of temperature fall with increasing height from the earth's surface is small. Whenever this temperature fall becomes large, as in the middle of the day, buoyancy effects begin to play a part, and there is some evidence that, under these conditions, sensible heat is transferred from the surface more readily than water vapor. However, by working close enough to the ground, such effects can be reduced, and it becomes reasonable to assume equal eddy conductivities for heat and water vapor. As in the aerodynamic method, accurate measurement of humidity is a problem. Nevertheless, this method appears attractive.

f. Advantages and disadvantages of the above methods. Of the water-balance methods, application of the hydrologic equation to large areas is useful only over long periods and can tell us nothing about the process of evaporation. Similarly, the measurement of changes in soil moisture content will never be accurate enough for short periods. Large weighing lysimeters with adequate moisture control and guard-ring areas are capable of high accuracy over short intervals. The main disadvantages here are immobility and the high cost of installation. Where only moist conditions are being considered, the simple form of potential evapotranspirometer is worthy of consideration.

Where great accuracy is not required, evapotranspiration from crops can be correlated with evaporation from standard devices. For certain purposes, evaporation pans can still be useful, and, for reasons of continuity and comparability of records, these devices cannot yet be abandoned.

Empirical formulas, although of some help where only scanty data are obtainable, should not be expected to apply outside the range of conditions for which they were derived. Since such formulas have relatively poor physical bases for giving reasonably good approximations to actual evapotranspiration, one suspects that this phenomenon is fairly insensitive to appreciable changes in many of the factors on which it depends. There is, therefore, some reason to hope for the development of simpler formulas, such as the Dalton equation, that will have sufficient accuracy and yet require only simple meteorological observations. Of all the formulas adequately tested so far, Dalton's formula and Penman's formula are the only ones that appear to have sufficient reliability.
Of the other vapor-flow methods, the eddy-flux determination should, with further development, have considerable use. The mobility of the equipment is an advantage, as is the considerable range of natural and crop surfaces that can be investigated without disturbance. The aerodynamic method has been shown to be workable with some crops, but computation of the results is laborious. It is likely to be more useful and practical in short-period studies than in protracted investigations.

The energy-balance method has the advantage of requiring only relatively simple instrumentation and is capable of fair accuracy when temperature and humidity observations are made at low levels. A disadvantage is the considerable labor involved in analyzing the records, as in the aerodynamic method.

4. Amount and Importance of Dew

Many conflicting opinions have been expressed about the importance of dew for vegetation, but very few of them have been substantiated by sufficiently accurate experimental measurements. The atmospheric processes involved in the deposition of dew are just the reverse of those in evaporation and can be studied through the application of the same principles (Neuman, 1956; Yamamoto, 1937). Basically, over an extensive area, there is some upper limit to the energy that can be released from the latent heat of dew condensation. Second, dew formation requires a vapor-pressure gradient directed from the atmosphere to the condensing surface. These gradients are smaller than those of the opposite sign, observed during the day, and the vertical-eddy conductivities are at least a magnitude smaller. The quantities involved in dew fall are, therefore, correspondingly less than in evaporation.

For a large area the net outgoing radiation per unit area of projected horizontal surface is controlled by temperature and humidity. The latent heat of the total dew released will, in general, fall for short of this radiated heat, since heat is also brought to the surface by eddy conduction. This leads to the assignment of an upper limit of about 1 mm. per night for the depth of the film of dew released (Monteith, 1957). Even in quite moist air this would be the total amount of vapor held in the lowest several hundred feet of air over the surface. It is therefore clear that a much deeper layer contributes to dew fall, since this layer of air does not dry out appreciably during the night. It also follows that there can be no general law of proportionality between dew deposition and plant leaf area, as has sometimes been assumed. This assumption has, in fact, led on occasions to estimates in excess of the physical limits mentioned above.

These principles must be modified before being applied to isolated
plants, because the pattern of radiation and moisture flow may then be
distorted from the previous one-dimensional form. A single tall plant
surrounded by bare soil, or a shorter crop, will radiate more than in
proportion to its projected area (Angus, 1958). The leafier plants, with
poorer thermal diffusivity, will cool more than others, thus attracting
dew toward them. The process of dew attraction brought about in this
way, however, is one in which some parts gain at the expense of others,
and the limitations on the average deposit over a large area are in no
way affected. There may thus be an optimum spacing at which the high­
est possible fraction of the dew is attracted to the plants rather than to
the intervening barer areas, and it may well be that the natural habit
of some desert species to grow in clumps separated by clear spaces rep­
resents to some extent a natural regression toward this optimum.

When the thermal diffusivity of the surface is lowered—for example,
by tillage, mulching, or crop growth—the surface temperature will be
lowered. When such a surface is of considerable extent, the application
of energy conservation indicates that the rate of dew fall is unlikely to
be affected, i.e., the dew on a large area of tall grass will be no greater
than on a large area of short grass, but if such areas occur in patches,
random advection from warmer and moister areas will enhance the rate
of dew formation. In the same way, dew will normally condense on the
top of the plant cover, which is the coldest part, and the lower parts
may be entirely dew free. These factors depend entirely on the nature
of the crop, and studies purporting to deal with variations of dew with
height above ground are almost meaningless as such.

Since the vapor-pressure gradient is small, the difficulties inherent in
making reliable measurements of dew can be seen from the foregOing
discussion. Small variations in the temperature, and hence the saturation
vapor pressure, of the condensing surface will have a large effect on the
gradient, and hence a large effect on the rate of condensation. It is there­
fore virtually impossible to obtain on a standard, artificial surface, meas­
urements of dew that are generally representative of natural vegetation.

If the condensed moisture is absorbed in some way—for example, by
filter papers—and then weighed, the moisture will probably have come
not only from the atmosphere but also from the soil. Any moisture from
the soil will, of course, be of no additional benefit to plants in arid re­
gions. The only reliable way of determining condensation from atmos­
pheric sources is to weigh an isolated representative portion of the natu­
ral surface (Craddock, 1951; Jennings and Monteith, 1954), although an
optical method has been attempted (Duvdevani, 1947). Lysimeters of
sufficient sensitivity could be used, but the dead mass of soil that must
be included usually makes sensitivity insufficient to detect the small amount of dew condensation.

Since the maximum amount of dew condensation on a uniform extensive area may be only 10 per cent of the water normally transpired during the following day, and even for isolated plants is unlikely to exceed 50 per cent of daytime transpiration, it is difficult to find any physical explanation for the importance that is attached to dew in many arid regions (Ashbel, 1936). It appears that, for dew to have any appreciable benefit, a plant must be able to exercise some physiological control in reducing rate of transpiration appreciably.

There are two possible roles that dew may play. The passive role is to remain on the surface (Drummond, 1945) and delay the rise in temperature and the onset of transpiration stress the following day. There is good evidence that the evaporation of liquid water from plant foliage conserves the same amount of water in the soil that would otherwise have been removed by the plant. The possible active role of dew is to be taken up by the plant and enter into the liquid cycle within (Stone et al., 1950; Stone and Shachori, 1954). However, the physiological details of such a role are still matters of controversy, requiring more research.

III. Interactions of Water and Soil

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As already mentioned, the soil plays an important stabilizing role in the part of the hydrologic cycle that is of agricultural significance. Water, in turn, plays a major part in determining the properties of the soil. These interactions are briefly discussed in this section.

A. Water as a Factor Affecting Soil Properties

Water plays a major role in determining the nature of soils and the properties and processes that govern their agricultural usefulness. In the geologic processes leading to soil formation, water has participated in the two major processes of weathering and erosion. The nature and extent of weathering is a major factor governing the inorganic nutrient status of a soil. Such weathering, as well as the biological processes that determine the nitrogen supply in the soil, are both determined primarily by temperature and the moisture supply. However, this article is limited to other ways in which water affects soils and crop production.
Water, either in liquid or solid form, has been the major vehicle for the movement, segregation, and deposition of soil parent materials. When soil detachment and movement are accelerated by water movement resulting from man-induced changes in land use, a soil-management problem is created. Major problems have resulted in many agricultural areas. No discussion of the many important agricultural, social, and economic aspects of erosion control will be attempted here, although it must be recognized that such phenomena are an important facet of the over-all hydrologic cycle and have many far-reaching effects on crop production.

Within the more restricted framework of current crop production practices, water has important effects on the amount and kinds of nutrients found in the soil and on their availability to plants. In the permeable soils of humid regions where there is an annual flux of water through the solum, planning a fertility program involves consideration of the loss of soluble soil constituents by leaching. The supply of soluble ions such as nitrate must be matched to uptake by roots if excessive losses are to be avoided. On soil having an appreciable base exchange capacity, leaching of other nutrients is less critical; but, in very sandy soils, these also must be applied at relatively frequent intervals in small amounts matched to crop needs if efficient fertilizer use is to be obtained.

In subhumid and arid regions the soluble salts are not leached from the soil but tend to be concentrated at the soil surface as the result of movement of water to the surface and its loss by evaporation. The concentrations of total soluble salts or of sodium are sufficient in some soils to prevent their use in agriculture. In subhumid and arid soils the possibility that toxic salt concentrations will develop in the surface soil must always be considered when irrigation water is supplied. In all irrigation systems in such soils, water applied as rainfall or irrigation must be sufficient to provide a net downward flux of water through the soil profile.

Waterlogging, caused by excessive water and inadequate drainage,

<table>
<thead>
<tr>
<th>Element</th>
<th>Normal form in well-oxidized soils</th>
<th>Reduced form in waterlogged soils</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carbon</td>
<td>$\text{CO}_2$</td>
<td>$\text{CH}_4$</td>
</tr>
<tr>
<td>Carbon</td>
<td>$-$</td>
<td>Complex aldehydes, etc.</td>
</tr>
<tr>
<td>Nitrogen</td>
<td>$\text{NO}_3^-$</td>
<td>$\text{N}_2$ and $\text{NH}_3$</td>
</tr>
<tr>
<td>Sulfur</td>
<td>$\text{SO}_4^{2-}$</td>
<td>$\text{H}_2\text{S}$</td>
</tr>
<tr>
<td>Iron</td>
<td>$\text{Fe}^{3+}$ (ferric)</td>
<td>$\text{Fe}^{2+}$ (ferrous)</td>
</tr>
<tr>
<td>Manganese</td>
<td>$\text{Mn}^{3+}$ (manganic)</td>
<td>$\text{Mn}^{2+}$ (manganous)</td>
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</table>

* Russell (1952).
results in significant changes in the level of oxidation and solubility of several important nutrient ions and soil constituents (Robinson, 1930). A summary of such changes is given in Table IV. Because of the altered solubilities and ionic forms associated with anaerobic soil conditions, plants subjected to waterlogged conditions may show either toxicity or deficiency symptoms. A more detailed discussion of plant responses to excessive water will be found in a later section of this article.

On the purely physical side, water modifies the thermal properties of the soil largely through an increase in heat capacity accompanying the increase in volume fraction of water in the soil. For this reason, both the magnitude and rate of diurnal and seasonal changes in temperature are smaller in wet soils than in dry soils. The movement of air into and out of the soil also is highly dependent on the amount of water present in the soil voids.

Finally the effects of water on mechanical behavior should be mentioned. Dry soils are able to support heavy loads, because of the rigidity of the individual soil particles and the high internal friction of the soil mass. But added water reduces internal friction, making the soil susceptible to plastic deformation and consolidation. As water is further increased, the soil takes on the properties of a fluid and loses its load-bearing properties entirely. This extreme change in the rheologic properties is of agricultural importance particularly as it affects the susceptibility of soils to compaction when subjected to traffic, as in tillage operations. The effects of moisture content and organic matter on the compaction that will result from a given amount of impact are shown in Fig. 11.

![Fig. 11. The effect of moisture content on soil compaction. Soils A and B contain 2.8 and 4.1 per cent organic matter, respectively (Free et al., 1947).](image)
B. The Intake and Storage of Water by Soil

Water arriving at the soil surface moves laterally over the surface, infiltrates the soil, or is impounded on the surface until it returns to the atmosphere by evaporation. The division of incident water into these three portions is determined by the amount and intensity of the precipitation and by the slope and water-intake characteristics of the soil surface. Water impounded in small irregularities on the soil surface evaporates rather quickly, contributing little to crop production, and can be considered as a loss of water from the agriculturally important part of the hydrologic cycle. Standing surface water may contribute to the incidence and spread of crop diseases, and, if present for extended periods, will cause serious crop damage by restricting the movement of oxygen into, and carbon dioxide out of, the soil.

Water that moves over the soil surface concentrates in drainage ways and reaches stream channels. Such water, accounting for about one-fourth of total precipitation of the United States, is a major source of water for irrigation. Erosion, one of the important consequences of runoff, reduces the productive capacity of agricultural lands and the capacity of water-storage structures. Although both of these phenomena are of great significance as factors affecting crop production, they are outside the scope of this article, and are not discussed herein.

The entry of water into soil and its retention in the rooting zone for use by crop plants are processes of paramount agricultural importance in the hydrologic cycle. The capacity of a soil to store water is described above as a function, primarily, of its depth and porosity. The amount of water that actually enters the soil also depends on porosity, as well as on previous moisture content and the intensity and duration of precipitation. Infiltration tends to be higher in warm months than in cool months, and is greatly affected by the type of vegetative cover on the soil. It is correlated positively with organic matter content, the percentage of large pores, and state of aggregation of the surface soil. The rate of water intake decreases with time during a given infiltration period, partly because of the plugging of larger pores in the soil surface that accompanies destruction of the surface aggregates. A protective cover of living or dead vegetation dissipates the kinetic energy of the falling raindrops, greatly reducing such aggregate destruction and slowing the rate of decrease of infiltration. The effects of soil texture and type of crop on the rate of water infiltration are shown in Fig. 12.

Water that enters the soil is held by capillary and surface forces. The affinity with which it is held is a reciprocal function of moisture content. Thus, at high moisture contents, water will move out of the soil by
WATER AND ITS RELATION TO SOILS AND CROPS

Fig. 12. The effects of texture and vegetative cover on infiltration (Musgrave, 1955).

Gravity, whereas at lower moisture it is retained even against extracting forces several thousand times that of gravity. Moisture desorption curves representing the functional relation between moisture content and the security with which the water is held by the soil have proved to be a very useful way of describing soil-water relations. Figure 13 shows typical desorption curves for three soils of widely differing textures. The curves illustrate the fact that soils of similar gross moisture-storage ca-

Fig. 13. Idealized moisture-retention curves for three soils.
The energy of retention of soil moisture is expressed in terms of an equivalent negative pressure, called soil moisture tension. This important moisture parameter can be measured in situ by soil moisture tensiometers. Such measurements are useful in analyzing soil moisture movement and water usage by plants. Although tensiometers are limited to tensions of 1 atmosphere or less, this covers the range in which most moisture-flow occurs and in which 50 per cent or more of the water use by plants is found. Soluble salts in the soil also affect water uptake by plants. The effects of such salts on the energy status of soil water is described by the osmotic pressure of the soil solution. Therefore, in soils containing significant quantities of soluble salts, soil moisture tension and osmotic pressure are summed to describe soil moisture-plant relations. This sum is called the soil moisture stress.

When water enters the surface of a dry soil, it moves downward, under the influence of attractive forces and gravity, in the form of a more or less well-defined wetting front. If the amount of water added is insufficient to cause the wetting front to reach the lower end of the soil mass or to contact a zone of moisture saturation, the downward movement will stop within a few hours after water entry at the surface is discontinued. The moisture content of the wetted portion of the soil column, in quasi-equilibrium with drier soil below, is known as field capacity (FC). This parameter represents, for most practical purposes in well-drained soils, the upper limit of soil moisture used by plants. For many soils of medium texture it is approximately equal to the water retained by a soil at a soil moisture tension of ½ atmosphere.

The lower limit of plant-available soil moisture is known as the permanent-wilting percentage (PWP). This biologically determined parameter is measured by growing dwarf sunflowers in a standardized quantity of soil. When the plants have attained a given size, no further water is added to the soil and the plants are allowed to wilt. When the wilt reaches a predetermined severity, the plants are removed and the moisture content of the soil is determined. The moisture percentage so obtained is called the PWP and represents for most practical purposes the lower limit of plant-available water in a soil. For many soils it is closely approximated by the moisture content held at a soil moisture tension of 15 atmospheres (FAP).

The movement of water into and through soil is the result of a potential gradient. In saturated soils the soil moisture tension is at or near zero throughout the entire soil mass. Under such conditions the driving force causing flow is the gradient of the gravitational potential, and
Water and its relation to soils and crops

Water thus flowing is commonly known as gravitational water. This is the water that flows downward through the soil into the drainage channels. Water flow in saturated soils is described by Darcy’s Law, \( v = k_i \), which states that the velocity of flow, \( v \), is proportional to the hydraulic gradient, \( i \). Hydraulic conductivity, \( k \), a parameter dependent on the properties of the fluid and the porosity of the soil, is widely used to characterize drainage and water-transmitting behavior of soils.

The flow of water in unsaturated soils is more difficult to analyze. In such situations, flow occurs as a consequence of gradients in soil moisture tensions and/or the gravitational potential. The vector sum of these two gradients is termed the net driving force, and may result in flow in any direction. The proportionality between the velocity of flow and the net driving force is a function of the properties of the liquid and of the volume and configuration of the liquid-filled pores. This proportionality is expressed as hydraulic conductivity and is highly dependent on the volume fraction of water in the soil. The effects on moisture-transmitting ability of changes in degree of saturation of soils of different texture are shown schematically in Fig. 14. It is seen that the relative water transmissibilities of coarse and fine-grained soils undergo a reversal at relatively low degrees of unsaturation. In view of recent investigations emphasizing the importance of moisture transmission as a factor affecting water uptake by plant roots, the curves in Fig. 14 give added significance to the effects of soil texture on soil-water-plant relationships.

Water also moves through unsaturated soils by vapor transfer. Such movement is a consequence of gradients in the aqueous vapor pressure in the soil atmosphere. Since the vapor pressure of water is strongly

Fig. 14. Curves summarizing the effects of texture and moisture content on the water-transmitting ability of soils.
temperature dependent and insensitive to soil moisture changes in the plant-available moisture range, the flow of water vapor in soil is largely the result of temperature differences, with vapor moving toward areas of lower temperature. Because vapor transport occurs through the air-filled voids, its importance as a moisture-moving process increases as the degree of unsaturation of the soil increases. Vapor transport is probably responsible for much of the seasonal changes in the profile distribution of water in soils in which the moisture content is well below field capacity.

Although the gross water-storage capacity of a given soil is essentially constant, the amount of water present usually undergoes rather wide seasonal variations. In humid regions of the United States, the soil profile is normally recharged to capacity at the beginning of the growing season. Depletion of subsoil water reserves occurs during the summer months, when evapotranspiration exceeds precipitation. During the fall, winter, and early spring, precipitation normally exceeds evapotranspiration, and the subsoil is recharged. In regions where total annual precipitation is less than potential evapotranspiration, the subsoil is seldom recharged to capacity, and efficient water management becomes the prime consideration in land use.

The annual depletion and recharge cycle that characterizes soil moisture storage emphasizes the importance of the process of water entry into the soil. For rainfall to be fully effective in using the soil storage capacity, its rate of fall must not exceed the rate at which water can infiltrate the soil.

Where topography is uneven and annual precipitation is less than annual potential evaporation, or only slightly greater, major attention should be placed on maintaining the highest possible infiltration rate for efficient use of water. This can be accomplished by providing a protective canopy of living or dead vegetation over the soil surface as much of the time as possible, and by developing a stable well-aggregated surface soil. On sloping land, water-retention practices that increase the time available for water infiltration are also effective in increasing profile recharge.

In summary, it may be said that the soil acts as an important water-storage device that smooths out month-to-month fluctuations in water supply available for plant use. The capacity of the soil for storage of available water is determined by its texture and porosity and the rooting volume of the crop. The rates of movement of water into and through the soil are important in determining the effectiveness of a soil as a storage medium of water for plants.
IV. The Soil Environment and Root Development

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The amount of soil water that is available to a plant is determined by the moisture characteristics of the soil, the depth to which the plant roots extend, and the proliferation or density of the roots.

The moisture characteristics, such as field capacity and wilting percentage (commonly used as limits of plant-available water) are peculiar to a soil, and are a function of texture, structure, and organic matter. Little can be done to alter these limits; greater possibilities lie in changing the characteristics of the plant, enabling it to extend its rooting system deeper into the soil, thereby enlarging its reservoir of water.

The density of root proliferation in the soil is also an important consideration. Water in unsaturated soil moves very slowly, and only a distance of a few centimeters. It is necessary for the plant to have roots that completely ramify in its rooting zone in order to utilize all water available within the reservoir.

Plants vary genetically in their rooting characteristics. Some, such as onions and potatoes, have a sparse rooting system and are unable to use all the soil water within the root zone; others, such as the forage grasses and sorghums, have very fibrous, dense roots. Lettuce has a single tap root, whereas corn extends out a distance from its base. Alfalfa has a deep root; that of Ladino clover is very shallow. Whether a plant is an annual or perennial is another factor affecting its water relations. An annual plant must extend its roots down into the soil to make available all the water it can potentially use. A perennial rooting system is already established as to depth, and needs only to extend its small roots and root hairs to be able to utilize the entire amount of soil water. Rooting characteristics of plants are difficult to observe. However, techniques have been developed for studying root distribution and activity (Weaver, 1926; Bloodworth et al., 1958; Lipps et al., 1957).

Plants may be limited in their rooting by other factors than genetics. Any factor that will affect the vigor or condition of a plant may be expected to influence its extraction of moisture from the soil. Physical conditions of the soil, such as moisture, aeration, compaction (bulk density), and temperature can limit or enhance the growth of roots. Chemically, the pH, fertility, and salinity of the soil have been shown to influence the rooting of plants. Crop-management practices, such as cutting the
top growth at different physiological stages, and the cultivation and cutting of surface roots alter rooting habits and the ultimate water economy of the crop. The presence or absence of beneficial or harmful soil organisms and diseases and insects, as brought about by any of these physical or chemical soil conditions, may limit root growth and the ability to absorb soil moisture.

A number of recent reviews (Hagan, 1952; Richards and Wadleigh, 1952; Lutz, 1952; Russell, 1952) consider over-all plant growth as affected by soil conditions. Root development is discussed as part of the presentation. The intent here is not to repeat the reports of those reviewers, but to use them as a basis for discussing additional, recently acquired knowledge of the effects of soil environment and root development.

Soil moisture below the wilting point or at saturation is detrimental to root development. Roots of some plants have been observed to extend into a dry soil layer if a portion of the root is in a moist area, but they were unable to absorb radioactive phosphorus from the dry soil (Hunter and Kelley, 1946b). The absorption of nutrients from a dry soil may be of importance in humid regions where the major portion of the fertility lies in the surface soil. If roots can obtain moisture from deeper, infertile soil, but are not able to utilize the essential plant nutrients in the dry surface layer, it may be necessary to keep the entire soil profile moist in order to maintain a proper moisture-fertility balance. In the main, this would not be as serious a problem in arid sections where soil is younger and less differentiated. This may account for some of the differences in thinking on the importance of irrigation frequency to maximum yields.

It is generally agreed that plants are able to extract very little, if any, moisture from soil, the major portion of which is below the wilting point. The importance of root extension into dry soil layers could be threefold: (1) roots penetrating from a moist surface soil through a dry layer down into a moist subsoil region would have an additional water supply; (2) roots in a dry area would be available for water absorption at a subsequent rain or irrigation; or (3) roots may be able to take up plant nutrients from soil deficient in water.

Cell elongation in roots and hypocotyls have different demands on the water supply to maintain growth (Ronnike, 1957). Studies of lupine seedlings grown in sphagnum media of various water contents have shown that hypocotyl elongation is totally inhibited at diffusion pressure deficits (DPD) of 8 to 10 atmospheres, while root growth continued at DPD values far beyond 15 atmospheres.

Winter wheat grown in Nebraska has been found to penetrate into soil that is below the 15-atmosphere percentage (Knock et al., 1957).
Eight weeks after planting on plots preirrigated to depths 0, 2, 4, and 6 feet, roots attained a depth in excess of 3 feet in the deeper wetted plots, whereas they grew 2½ feet with wetting depths of 0 and 2 feet. Roots from plots with no supplemental moisture formed a dense network, with long branches, even though soil moisture was below the wilting percentage.

An inverse relationship exists between soil moisture content and aeration (Baney, 1949; Taylor, 1949). Oxygen is essential for root growth and aerobic respiration. There is no general agreement as to whether the limiting factor for optimum root function is insufficient oxygen or excess carbon dioxide. The rate of gaseous diffusion to and from the root surface may be of greater physiologic importance than the actual concentration of oxygen or carbon dioxide in the soil voids since it is necessary that the soil atmosphere be continually replaced and renewed, largely by diffusion, which is linearly related to the volume of air-filled pores in the soil. It is clear that variations in moisture content will greatly affect soil aeration.

A marked interaction between soil moisture tension and aeration has been observed on the growth of corn seedlings (Gingrich and Russell, 1956). When oxygen was not limiting, radicle elongation became progressively less as soil moisture tension increased from 1 through 12 atmospheres, being most sensitive to tension in the range of 1 to 3 atmospheres. There was an interdependence of oxygen and moisture tension on radicle elongation, and at low soil moisture tensions, an oxygen concentration of 10.5 per cent or higher was needed for maximum growth.

Plants vary in their ability to withstand saturated or poorly aerated conditions. Rice, on the one hand, grows in standing water, apparently possessing some mechanism whereby oxygen is supplied to the roots. Other plants, such as tobacco, are highly sensitive to lack of good aeration (Harris and van Bavel, 1957). Studies of the oxygen:carbon dioxide ratio of the tobacco root atmosphere have shown a decrease in root weights as oxygen percentage decreased from 21 to 0 per cent, but the decline was not drastic until carbon dioxide concentration was greater than oxygen concentration.

A water table definitely limits the volume in which good soil aeration exists. Plants can use the moisture from the water table if it is near enough to the surface for the roots to reach the capillary fringe. However, a water table too close to the surface can be detrimental, because of the restriction it places on the rooting volume. A fluctuating water table is especially deleterious to plants. As the water table rises, roots are killed; then, as it recedes, the plant is left with insufficient root surface to absorb enough water or nutrients to meet its needs. Such fluc-
tation may occur with a tile drainage system that removes excess water too slowly to prevent loss of a large portion of the lower roots, but which eventually lowers the water table below the still-active root zone. The effects of a fluctuating water table have been observed most frequently in orchards, especially citrus (Jamison, 1956; Ford, 1954). Growth of apple-tree roots has been observed to be limited by a water table fluctuating between depths a few feet below the surface. When water table depths were lowered and stabilized between depths of 30 and 70 inches, the size of the trees increased, and the quantity of feeder roots doubled in four years (Greenham, 1956).

Grasses vary in their ability to withstand a high water table. In a study of forty-two species grown in pots with water levels maintained at 36 cm. below the surface, three main types of root development, related to difference in susceptibility to carbon dioxide, were observed: (1) vigorous growth down to layers of high moisture saturation (Lolium-type); (2) some roots penetrating moisture-saturated layers (Poa-type), and (3) roots dying at high moisture contents (Dactylis-type) (Baumann and Klauss, 1955).

Soil aeration is also related to structure or aggregation. Generally, the larger the aggregates, the more rapid the exchange of atmospheric oxygen and soil carbon dioxide. Where synthetic conditioners have aggregated the soil, improved root development has followed (Hely et al., 1954). After 2 weeks of growth in coarse, medium, and fine aggregated soils, the rooting of carnation cuttings had progressed farthest in coarse aggregated soil and least in the medium. The fine aggregated soil showed intermediate results, probably because cracks formed at the insertion of cuttings, improving aeration. It was concluded that rooting was correlated with oxygen diffusion (Monselise and Hagin, 1955).

Tillage operations with large, heavy machinery tend to compact soils. Compacted soil shows reduced oxygen diffusion and provides a mechanical impedance to the growth of roots. Root penetration studies with sunflowers and grapes showed no penetration of sands having bulk densities greater than 1.75 g./cc. The critical values for clays ranged from 1.46 to 1.63 g./cc. (Veihmeyer and Hendrickson, 1948). Failure of roots to penetrate soils of higher bulk density was attributed to the small pore size rather than the lack of oxygen. The rigidity of the pore structure also affects root penetration (Wiersum, 1957). Other work has shown a pronounced interaction of mechanical impedance and aeration on the root growth of seedlings (Gill and Miller, 1956). As reported by other investigators, they noted that in the absence of mechanical impedance, a 50 per cent reduction of normal oxygen supply did not impair seedling elongation, and growth did not cease at concentrations as low as 1 per
cent oxygen. As soon as mechanical restraint was applied, however, growth reductions occurred at a relatively modest decrease in oxygen content, and the rate of growth fell to zero at small levels of impedance when oxygen contents were low.

Horizons within some soil types possess high bulk densities naturally. Corn roots in four soil types derived from Wisconsin Glacial Till, under similar fertility, pH, and weather conditions, have shown root penetration of about 3 feet in the Elliott and Clarence soils, with subsoil bulk densities of 1.70 g./cc. The lower bulk densities of Ringbrook and Saybrook subsoils permitted deeper rooting (Fehrenbacher and Rust, 1956). Low aeration associated with the high bulk density was thought to limit root development.

Even though a soil has good structure and aeration, it does not necessarily follow that roots will penetrate deeply if fertility is inadequate (Fehrenbacher and Snider, 1954). Corn roots have been observed to penetrate to a depth of 6 feet in a fertile permeable Muscatine silt loam, but to be limited to 3 feet by a compact layer in Elliott silt loam, and to 3 feet in Cisne silt loam—not because of structure but because of low pH and poor fertility. At the A₁ and A₂ horizons of the Cisne, the fertility level was so low that corn roots did not develop vigorously enough to penetrate into the more compact soil of the B horizon. On limed and fertilized plots, corn roots were able to grow into the more dense subsoil and obtain additional moisture from it. Soil moisture at the Band D horizons averaged 5 per cent lower in fertilized plots than in untreated plots.

To some extent, plants may be able to overcome compact layers if there is adequate fertility in the subsoil. Phosphorus and calcium appear to be of major importance for root development. Grass roots were compared in two Crete soils in Nebraska, one deficient in soluble phosphorus at the B horizon, the other with a relatively high level. In the deficient soil, roots were restricted to the surface horizon, while development in the latter was good in the subsoil. The limited root development in the surface layer of the Butler soil has been associated with a low content of nitrogen and exchangeable calcium. The Judson soil, with a good supply of plant nutrients in all depths of its profile, supports deeply rooted bluegrass, whereas the same grass had a shallow root system in Carrington, which is deficient in available phosphorus in the subsoil (Fox et al., 1953). A favorable chemical environment has also been shown to be more essential than a favorable physical environment for deep, fibrous, and well-nodulated rooting of alfalfa (Fox and Lippes, 1955b).

It is generally observed that increasing the nitrogen content of the soil will decrease the root:top ratio. With high nitrogen, more of the
carbohydrates are used for the synthesis of top tissue, and less translocated to the roots. Studies of wheat grown in nutrient solutions of varying nitrogen content have shown that, with a nitrogen deficiency, the roots were longer and more slender, owing to an increase in cell length (Bosemark, 1954). On examination it was noted that inhibition from a high nitrogen supply was the result of the combined action of reduced cell multiplication and cell elongation, and perhaps of some relation between nitrogen supply and the natural auxins that affect root growth.

The placement and composition of the fertilizer band have been shown to affect the rooting habit of corn (Duncan and Ohlrogge, 1958). A 1:5 ratio of nitrogen and phosphorus seems to favor the most profuse root system. The total weight of corn roots is practically the same, whether the fertilizer is placed in a band or is mixed in equal amount throughout the plow layer. With band placement, a mass of fine, well-branched roots is located in the fertilized area, whereas with broadcast application the roots are more evenly distributed through the soil. Although band fertilization may stimulate growth earlier, it would seem that the corn plant would have a larger reservoir of water available in the case of the broadcast application.

Nitrogen does not always depress root development, as evidenced by work with winter wheat grown at four moisture levels and three nitrogen fertilizer rates (Kmock et al., 1957). Added nitrogen increased root weights at all moisture levels and at nearly all soil depths and permitted more complete utilization of subsoil moisture. When ample nitrogen was supplied, moisture was depleted to a depth of 8 feet. Similar results have been reported for nitrogen in increasing the rate of root penetration of several species of grasses (Burton et al., 1954; Haas, 1958).

Minor elements, though they have not received much attention, may also play a part in root growth. A zinc deficiency has been shown to reduce the meristematic activity of the tip tissue and cambium of the tomato root (Carlton, 1954). In the absence of zinc, small tumors were observed, similar to those formed on roots exposed to low concentrations of certain growth-regulating substances. This suggests an interrelationship between plant hormones and zinc.

A number of workers have tried subsoiling and deep placement of fertilizer as a means of improving root development. Younts and York (1956) reported that deeper root penetration of corn and crimson clover was stimulated in the early season by concentrating fertilizer in the surface 12 inches. Toward the end of the season, deep placement stimulated greater root activity in the 24–26-inch layer. Nitrogen depressed root activity at all depths throughout the entire growing season.

Corn roots were found not to penetrate deeply into a compacted silty
clay loam soil with a bulk density of 1.5 g/cc., mainly because of lack of oxygen. Subsoiling alone encouraged better root development in such soil, but fertilization of the subsoil promoted even greater growth (Bertrand and Kohnke, 1957; Kohnke and Bertrand, 1956). In Plainfield fine sand, corn roots penetrated to 6 feet in fertilized subsoil, and to 4 feet in check plots, with intermediate penetration in a subsoiled plot. Improved root development on Leon fine sand, Osa fine sand, and Norfolk loamy fine sand has been reported from deep placement of fertilizer (Robertson et al., 1957).

Salinity and alkalinity are major problems of crop production in some areas of the world. A high salt content not only increases osmotic tension enough to alter plant metabolism, but also affects the amount of roots developed for water and nutrient absorption. From earlier work (Breazeale and McGeorge, 1932), the low content of carbon dioxide found in alkaline-calcareous soils is believed to lower the availability of phosphorus. Since this element is effective in stimulating root growth, this may be a partial explanation of reduced root development in alkaline soils. Studies with radish seedlings grown in soil systems of various calcium:sodium ratios showed maximum elongation in the soil that was 10 per cent saturated with sodium. Elongation rate decreased as the sodium:calcium ratio increased (Schreiber et al., 1957). Root length of peas decreased as the sodium:calcium ratio increased, and root growth was greatly reduced at 60 per cent sodium saturation (Elgabaly and Ghan, 1958).

Work reported from Russia (Strogonov, 1956) shows that cotton roots will continue vertically downward in weakly saline soils, but, in highly saline conditions, growth is decreased and root tip may be killed. Saline layers stimulated lateral root growth. Studies of red kidney beans, corn, cotton, and alfalfa grown in layered soils with concentrations of NaCl ranging from 0.00 to 0.25 per cent showed that few bean roots penetrated layers containing 0.1 per cent salt, whereas corn was not seriously limited until the 0.2 per cent concentration was encountered. Alfalfa roots penetrated all the layers of saline soil, as did cotton roots (Wadleigh et al., 1947). Others have reported that alfalfa roots penetrated a horizon at which there was a high sodium content, though fibrousness and abundance were reduced (Fox and Lipps, 1955a). Excessive sodium accumulation by roots may affect root functions, particularly water absorption (Bernstein and Pearson, 1956). With the fertilizer band placed near the corn row, the primary roots died and shriveled up as soon as they came in contact with the high salt content of the fertilizer band. However, a dense mass of active secondary roots developed in this highly osmotic area (Duncan and Ohlrogge, 1958).
Diseases and insects hosting on plant roots are subject to the same physical limitation as the root itself (Hagan, 1952). Frequently, moisture and oxygen supply have an influence on their virulence, growth, and multiplication. Heavy irrigation has been shown to increase the amount of nematode infection on tomatoes (Oteifa and El-Gindi, 1957). This effect is attributed to the fact that the organism, dormant under dry soil conditions, is stimulated as soon as moisture is added. Also, films of irrigation water tend to carry nematode larvae from one plant to the other. In addition to moisture content, large pore size and adequate aeration seem to affect the infection and rate of emergence of the nematode larvae (Wallace, 1956).

Verticillium wilt infection takes place mainly from the soil through the root system, and in the case of cotton is restricted to highly alkaline soils. Conflicting views on the influence of soil conditions on the Verticillium organism are discussed in a review (Issac, 1956). It is generally agreed that increasing soil nitrogen increases the incidence of the disease. The incidence in pot cultures was decreased by adding sulfate of potash or ammonium sulfate, or by decreasing the soil moisture. The frequency of irrigation of cotton, especially in early season, increased both prevalence of the disease and the severity of lygus bug infestation (Stockton and Doneen, 1957).

Certain crop-management practices also can influence root development; this is especially true with grass and forage crops, where grazing and clipping occur during the summer months. Using moisture extraction as a measure of root activity, with pasture mixtures clipped at intervals of 2, 3, 4, and 5 weeks, it was found that, if the botanical composition remained unchanged, the distribution of root absorption for Ladino clover-grass and broadleaf trefoil-grass mixtures remained unchanged by clipping frequency (Hagan and Peterson, 1953). Other studies have shown that the roots of some grass species are affected by frequent clipping (Weaver and Zink, 1946). Bromus inermis lost 15 per cent of its roots during a growing season if clipped at 10-day intervals, and Agropyron cristatum lost 73 per cent.

Another management practice influencing the roots is cultivation. Serious root damage in orchards has resulted from two or three summer cultivations, especially if the depths were allowed to vary (Coker, 1955). Surface moisture and nutrients thus become unavailable to the plant, and light precipitations are lost by evaporation. Also, the surface layer has the greatest concentration of available nutrients.

Much of the research reported to date on root development and the physical and chemical conditions of the soil has been of a qualitative nature and was frequently based on observations incidental to an experi-
ment directed toward another objective. Work of Weaver and others, who have made extensive studies on the rooting habits of many cultivated and native plants, has been of real value in understanding variations between species. In view of the heterogeneous nature of soils and the many other plant and climatic factors that affect crop growth and root development, the need for fundamental studies becomes apparent. The use of highly controlled experimental conditions involving a limited number of variables would seem to be a fruitful approach. More extensive research on the physiology and morphology of roots grown under known physical and chemical conditions would assist in giving a better understanding of plant root behavior.

V. Plant-Water Relations

Following examination of the water-soil and soil-root systems, attention is now turned to the remaining two-component combination: the functions of water in the plant and the responses of crops to excessive water and to drought. Admittedly, these responses are conditioned by the soil and the atmospheric environment, but the following discussion centers on the binary system of plant and water.

A. The Role of Water in the Physiology of Plants

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Duke University, Durham, North Carolina

Everyone knows that plant growth and crop yields are often reduced by water deficits, but too little is known about the mechanism of such reductions. Insufficient attention has been given to the role of water in the physiology of plants. Much is known about the factors affecting the availability of soil water and its absorption by plants, and about the factors affecting the rate of loss of water by transpiration. There has been little attempt, however, to correlate the numerous studies of soil, atmospheric, and plant-water relations and to use them in explaining plant growth behavior. This is unfortunate, because concentration on any single phase of water relations, such as soil moisture or evapotranspiration, cannot fully explain the variations in the quantity and quality of plant growth that are caused by variations in water supply.

The most important aspect of plant-water relations is the internal water balance, because internal water balance and turgidity are closely related to the rates of various physiological processes that control the quantity and quality of plant growth. The internal water balance is not
an independent condition, but is controlled by the relative rates of water absorption and water loss. It seems clear that we not only need more information about plant-water relations, but that we also need better correlation of data already available.

The physiological significance of water deficits is herein discussed under three general headings: (1) How internal water deficits affect plant growth. (2) Why internal water deficits develop. (3) Methods of measuring internal water deficits.

I. Water in Relation to Growth

It is a basic biological principle that the quantity and quality of growth made by a plant is controlled by its hereditary potentialities and its environment, acting through its internal physiological and biochemical processes and conditions. The only way in which environmental factors such as water, temperature, or mineral nutrients can affect growth is by affecting internal processes and conditions. Thus, the effects of water deficits on physiological and biochemical processes must be studied to understand why they reduce plant yields.

a. Functions of water in plants. Consideration will first be given to the role of water in plants, where it serves the following four general functions: (1) Water is an important constituent of protoplasm. It makes up 85 to 90 per cent of the fresh weight of actively growing plant parts, and even trees are more than half water. As water content decreases, physiological activity usually decreases, and extreme dehydration kills most plants. The relation of water content to physiological processes is shown very strikingly in seeds, where respiration and other physiological activity increase manyfold as water content increases. (2) In photosynthesis, water is as essential a reagent as carbon dioxide. It is also an essential reagent in hydrolytic processes such as digestion of starch to sugar. (3) Water is the solvent in which salts and gases enter plants and in which solutes move from cell to cell and tissue to tissue within the plant. (4) Water is essential to maintain sufficient turgidity for growth of cells and maintenance of the form and position of leaves, new shoots, and other slightly lignified structures. Turgidity also is important in connection with the opening of stomata and the movement of flower parts and leaves. Lack of turgidity results in immediate reduction or cessation of growth.

The total quantity of water required for these essential functions is relatively small, usually less than 5 per cent of all the water absorbed. Most of the water entering a plant is lost in transpiration, directly contributing little or nothing to its growth.

The data for corn in Table V show that in this instance, only 1
WATER AND ITS RELATION TO SOILS AND CROPS

TABLE V
An Estimated Water Budget for a Corn Plant

<table>
<thead>
<tr>
<th>Description</th>
<th>Amount</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water occurring as constituent, solvent, and in maintenance of turgidity</td>
<td>1,872 grams</td>
</tr>
<tr>
<td>Water used as a reactant</td>
<td>250 grams</td>
</tr>
<tr>
<td>Water lost in transpiration</td>
<td>202,106 grams</td>
</tr>
<tr>
<td></td>
<td>204,228 grams or 54 gallons</td>
</tr>
</tbody>
</table>

*Miller (1938).

per cent of the water passing through the plants was used in them. However, failure to replace water lost by transpiration results in loss of turgidity, cessation of growth, and eventual death from dehydration.

b. Effects of water deficits on certain physiological processes. It is probable that every process in plants is more or less affected by water deficit. The effects of water deficits on only a few processes have been studied in sufficient detail to deserve special mention, and the relation of water supply to physiological processes has been concisely reviewed by Richards and Wadleigh (1952). Unfortunately, in most of these studies, physiological processes and conditions were merely correlated with soil moisture content; no attempt was made to measure soil moisture tension or the internal water deficit of the plants. It seems probable that, in studying the effects of water deficits on plant processes, internal water balance ought to be determined in order to have some quantitative measure of the extent of the water deficit existing in the plants.

Stomatal opening seems to be one of the most sensitive plant processes with respect to internal water deficits. A slight decrease in turgidity sometimes is accompanied by increased opening of stomata (Stahl, 1955), but further reduction is nearly always accompanied by a decrease in stomatal aperture. According to Magness and associates (1935), stomata of apple trees begin to close prematurely long before soil water falls to the permanent-wilting percentage. Decreasing soil moisture also causes premature closure in citrus (Oppenheimer, 1953; Oppenheimer and Elze, 1941). Stomata usually close earlier each day as soil water becomes less available, until finally they may remain open for only a short time each morning (Aldrich and Work, 1934, in pear; Jones, 1931, in peach; Maximov and Zernova, 1936, in wheat). Figure 15 shows the effects of water deficit on stomatal closure.

Premature closure of stomata is undesirable because, in at least some species, it cuts off the supply of carbon dioxide for photosynthesis (Nutman, 1937), although, in others, considerable carbon dioxide appears
to enter through the epidermis (Dugger, 1952; Freeland, 1948; Mitchell, 1936).

One effect of stomatal closure is to reduce transpiration, because by far the larger fraction of water loss occurs through the stomata. This reduction would be desirable in itself, for there is little doubt that very responsive stomata that close early in the development of an internal water deficit must materially increase drought resistance and survival (Pisek, 1956; Stocker, 1956); but, unfortunately, they also reduce photosynthesis by reducing the supply of carbon dioxide. For this reason it is doubtful if very responsive stomata are desirable in crop plants, except, possibly, in plants such as tomato, which seems to manufacture most of its food before noon. The relation of stomatal behavior to control of water loss and photosynthesis of crop plants deserves further study.

When the stomata are closed, water loss is controlled by the characteristics of the cuticle or by the waxy layer covering the leaf epidermis. This suggests the possibility of reducing cuticular transpiration by applying some sort of waterproof film to the leaves, and coatings of wax and latex have proved moderately successful in protecting nursery stock and other plants after transplanting (Allen, 1955; Comar and Barr, 1944). Various practical difficulties limit their usefulness at present, but they show promise for some purposes where water conservation is more important than reduction in photosynthesis.

There has been much argument as to the time when transpiration begins to decrease in plants in drying soil. Veihmeyer and Hendrickson

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**Fig. 15.** Effects of moisture deficit on daily closure of stomata of pear. From Kramer (1949), after Aldrich and Work (1934).
(1950) long contended that transpiration does not decrease materially until soil moisture falls almost to the permanent-wilting percentage, but it now seems clear that transpiration and other physiological processes are usually affected considerably earlier (Gates, 1955; Richards and Wadleigh, 1952; Slatyer, 1955, 1957). Figure 16 shows the changes in transpiration, relative turgidity, and growth of tomato and cotton plants subjected to increasing soil moisture stress.

Most of the controversy on this subject could have been avoided had it been realized more clearly that plant processes are controlled directly by the water content of the plant, and only indirectly by the water content of the soil. If the diffusion pressure deficit or the relative turgidity of the leaves had been measured, it would have been possible to correlate physiological processes with the water condition inside the plant. If, in addition, the moisture tension of the soil at various stages of drying had been known, it would have been possible to correlate soil and plant water conditions with the course of transpiration and other processes.

It seems that, in all studies of the effects of water on plant growth,
we need an accurate characterization of plant water conditions as well as of soil water conditions. This is essential to indicate when water actually becomes a limiting factor within the plant.

Plant scientists have long been interested in differences in the efficiency with which plants of different species use water. This is usually expressed in terms of pounds of water used per pound of dry matter produced, and is often termed the "water requirement." This is an unfortunate term, because there is no specific water requirement, but only a highly variable ratio of water used to dry matter produced. Since this ratio is largely controlled by transpiration, it might more accurately be termed the transpiration ratio. Miller (1938) summarized much of the early work on transpiration ratio. In measurements at Akron, Colorado, extending over several years and involving plants of about 150 species, the transpiration ratio varied from 216, for Kursk millet, to 1131, for Franseria, a native weed. Polster (1950) estimated that the amount of water required to produce a gram of dry matter in a German forest ranged from 170 g. for beech and Douglas fir, to 317 g. for birch, and 344 g. for oak.

Although it was obvious that wide variations exist among species in the transpiration ratio, interest in this aspect of water relations has lagged. Probably this is chiefly because the concept of evapotranspiration advanced by Penman and others indicated that the type of plant cover would make little difference in total water loss from an area of land.

Recently, interest has again developed in possible differences in efficiency of water use and their relation to crop yields when subjected to drought. An example is a recent German paper by Koch (1957), in which he describes daily changes in the ratio of photosynthesis to transpiration and discusses the possibility of modifying this relationship. Other examples of renewed interest in efficiency of water use are a study of water use by cotton, peanuts, and sorghum, by Slatyer (1955) in Australia, and one on grasses, by Burton and associates (1957) in Georgia.

It has been known for many years that fertilization and other cultural practices that increase yields usually increase the efficiency of water use by crops. This is supported by extensive investigations by Arland and colleagues at Leipzig (Arland, 1955; Zwicker, 1954), whose work on the physiology of crop plants should be better known. Burton, Prine, and Jackson's experiments summarized in Table VI also show that, in four of five grasses tested, increasing the nitrogen supply greatly increased the amount of dry matter produced per unit of water used. Another result was that Coastal and Suwanee Bermudagrasses, the most drought-resistant of the five grasses studied, produced more dry matter per unit of water under drought conditions than when well watered,
TABLE VI

Effect of Rainfall and Nitrogen Supply on the Water Use of Five Grasses

<table>
<thead>
<tr>
<th>Grass</th>
<th>Nitrogen added (lb./A.)</th>
<th>1953</th>
<th></th>
<th>1954</th>
<th></th>
<th>1955</th>
<th></th>
<th>1956</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>50</td>
<td>100</td>
<td>200</td>
<td>50</td>
<td>100</td>
<td>200</td>
<td>50</td>
<td>100</td>
</tr>
<tr>
<td>Coastal Bermudagrass</td>
<td>2478</td>
<td>1431</td>
<td>803</td>
<td>1547</td>
<td>982</td>
<td>504</td>
<td>41</td>
<td>641</td>
<td></td>
</tr>
<tr>
<td>Suwanee Bermudagrass</td>
<td>1923</td>
<td>1105</td>
<td>692</td>
<td>1107</td>
<td>725</td>
<td>452</td>
<td>55</td>
<td>452</td>
<td></td>
</tr>
<tr>
<td>Common Bermudagrass</td>
<td>6812</td>
<td>2896</td>
<td>1540</td>
<td>9738</td>
<td>5028</td>
<td>4336</td>
<td>33</td>
<td>4336</td>
<td></td>
</tr>
<tr>
<td>Pensacola Bahiagrass</td>
<td>2200</td>
<td>1321</td>
<td>870</td>
<td>1945</td>
<td>1239</td>
<td></td>
<td>1239</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pangolagrass</td>
<td>2249</td>
<td>1385</td>
<td>2240</td>
<td>2843</td>
<td>2513</td>
<td></td>
<td>3016</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Burton et al. (1957).

Rainfall April 1 through October 31 was 39.66 inches in 1953 and 13.08 inches in 1954.

whereas the reverse was true for the less drought-resistant species. When the physiological causes for these differences are learned, we will be on our way toward a physiological explanation of drought resistance.

Ballard (1933) claimed that increasing nitrogen supply reduced transpiration ratio, by changing the pattern of growth rather than by decreasing transpiration per unit of leaf surface. Williams (1935) found that increasing the supply of phosphorus decreased the transpiration ratio of oats (i.e., increased the amount of dry matter produced per unit of water used) by decreasing transpiration rate per unit of leaf surface. More studies of this type are needed to add to our understanding of the various factors that affect the efficiency of water use by plants.

As Burton has pointed out, it is difficult to breed plants for drought resistance and efficient use of water until we know what plant factors are responsible for these desired characteristics. It seems, as Parker (1956) suggests, that drought resistance may depend on various characteristics occurring throughout plants. These may range from depth of rooting, thickness of cutin, and responsiveness of stomata, to permeability, structure of protoplasm, and reaction of enzyme systems to dehydration.

Rate of photosynthesis is rarely limited by lack of water as a reagent, but is often limited because dehydration of protoplasm reduces its photosynthetic capacity (Brilliant, 1924; Dastur, 1925; Ensgraber, 1954), and
because stomatal closure reduces the supply of carbon dioxide. Many investigators have reported large decreases in photosynthesis in wilting leaves (Ashton, 1956; Brilliant, 1924; Dastur, 1925; Schneider and Childers, 1941; Thomas and Hill, 1949; Upchurch et al., 1955; Verduin and Loomis, 1944; and others).

There has been much discussion as to whether photosynthesis is materially reduced before soil water approaches the permanent-wilting percentage. Schneider and Childers (1941) reported that photosynthesis of apple leaves was reduced 50 per cent before wilting was visible, and in wilted leaves fell to only 15 per cent of the expected rate. The original rate was regained rather slowly after rewatering. Similar results were reported for several forest trees (Bourdeau, 1954; Kozlowski, 1949). On the other hand, no reduction in photosynthesis was observed in Ladino clover until the readily available soil moisture was almost entirely depleted, although the rate fell rapidly when wilting occurred (Upchurch et al., 1955), and similar results were observed for apple, by Allmendinger et al. (1943), and for pecan, by Loustalot (1945).

Unfortunately, neither the soil moisture tension nor the water deficit in the leaves was reported in any of these studies. Hence, it is impossible to determine what relation existed between leaf turgor or leaf water deficit and photosynthesis before wilting was visible. For really conclusive studies of the relation of water supply to photosynthesis, measurement should be made of changes in leaf water conditions at the time that photosynthesis is measured.

There is some evidence that rate of photosynthesis is maximum in some leaves at slightly less than maximum leaf turgor (Brilliant, 1924; Schneider and Childers, 1941); this has been attributed to the wider stomatal apertures at slightly less than maximum turgidity (Stålfelt, 1955). But, opposed to this view is the claim that, in at least some plants, the stomata exercise less control over photosynthesis than over water loss (Heinicke and Childers, 1936; Mitchell, 1936; Schneider and Childers, 1941). Verduin and Loomis (1944) reported that the porosity of corn leaves to gases was greatly reduced by wilting, but lack of a high correlation between porosity (measured with a porometer) and photosynthesis indicated that factors in addition to stomatal closure are responsible for the reduction in photosynthesis.

As shown in Fig. 17 midday reduction in photosynthesis occurs in plants of many species on sunny days. This reduction is usually attributed to midday closure of stomata (Nutman, 1937; Polster, 1950). It does not occur on cloudy days. Stocker and associates (1954) regard midday sprinkling of crops in hot weather as very beneficial by keeping leaves turgid and stomata open, preventing a midday decrease in photosynthesis.
The cooling effects of sprinkling might also reduce respiration, thereby increasing net photosynthesis. Bloodworth et al. (1956) concluded that showers too light to increase soil moisture materially may be quite beneficial in decreasing internal water deficits. Irrigation by sprinkling during periods of high evapotranspiration might produce unexpectedly good results in proportion to the amount of water applied if wetting the leaves increases photosynthesis and, by its cooling effect, decreases respiration. Dew and atmospheric moisture may also increase growth far beyond the same amount of water added to the soil, because it produces direct rehydration of tissues. The importance of dew may be much greater than is generally believed, and it certainly deserves more study (Gessner, 1956; Slatyer, 1956, 1957; Stone et al., 1956; Stone, 1957).

Fig. 17. The diurnal variations of photosynthesis and transpiration for birch, beech, and oak (Polster, 1956).
Ordinarily, a decrease in water content is accompanied by a decrease in respiration, but respiration occasionally increases during dehydration. Schneider and Childers (1941) found that respiration was increasing in apple trees in drying soil while photosynthesis was decreasing, and Upchurch et al. (1955) found small increases in respiration of wilting Ladino clover. Increased respiration, combined with a decreased photosynthesis, can seriously reduce the amount of food available for other processes. The effects of water supply on respiration are particularly noticeable in dry seeds, where a small increase in water content above a certain critical content results in a very marked increase in respiration (Bakke and Noecker, 1933; Appleman and Brown, 1946).

The nature and course of various biochemical reactions are often changed by water deficits, resulting in changes in chemical composition. Best known is the decrease in proportion of starch to sugar in plants subjected to water deficits, because of increased hydrolysis of starch. This has been observed in many plants, including apple (Magness et al., 1933), beans (Wadleigh and Ayers, 1945), cotton (Eaton and Ergle, 1948), and beans and tomato (Woodhams and Kozlowski, 1954). In most instances, total carbohydrate reserves are decreased.

In general, water deficits seem to increase nitrogen content, but this probably depends on the stage of growth at which the deficit develops and on the organ sampled. It is said that water stress during maturation increases the protein content of wheat (Miller, 1938), and Table VII shows that the concentration of total nitrogen and nicotine is significantly increased in tobacco plants subjected to drought, but the sugar content and burning quality are decreased (Darkis et al., 1937; van Bavel, 1953). Water deficits are said to reduce the concentration of quinine sulfate and other alkaloids in cinchona (Loustalot et al., 1947). Gates (1955, 1957) concluded that even small reductions in water content have marked effects on metabolism. During moderate wilting, uptake of nitrogen and

<table>
<thead>
<tr>
<th>Average soil moisture stress (cm. H2O)</th>
<th>Yield (lbs/A)</th>
<th>Value (dollars/100 lbs.)</th>
<th>Nicotine (%)</th>
<th>Total N (%)</th>
<th>Sugars (%)</th>
<th>Burn test</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>1640</td>
<td>23.74</td>
<td>1.76</td>
<td>1.65</td>
<td>21.18</td>
<td>1.47</td>
</tr>
<tr>
<td>242</td>
<td>1622</td>
<td>22.81</td>
<td>2.10</td>
<td>1.67</td>
<td>22.56</td>
<td>1.40</td>
</tr>
<tr>
<td>1470</td>
<td>1334</td>
<td>18.35</td>
<td>4.02</td>
<td>2.40</td>
<td>14.85</td>
<td>1.25</td>
</tr>
</tbody>
</table>

* van Bavel (1953).
phosphorus by tomato plants was reduced, and both elements tended to move out of leaves into stems. Even moderate wilting caused leaf changes resembling senescence, but during recovery they tended to return to a more juvenile condition. Wilting is known to disturb the normal pattern of translocation in plants and probably also affects composition by affecting enzyme activity. Some information on enzyme activity was recently summarized by Mothes (1956).

Sometimes a moderate water deficit produces desirable changes in composition. For example, the rubber content of guayule plants is increased by a moderate water deficit (Wadleigh et al., 1946), and the quality of apples (Overley et al., 1932) and of pears (Ilyall and Aldrich, 1944) is improved by moderate moisture stress during the latter part of the season. Clark and Levitt (1956) found an increase in lipids in soybean leaves subjected to wilting, which was accompanied by decreased transpiration and increased resistance to dehydration. Tobacco subjected to a moderate water deficit produces leaves with more body and aroma than does tobacco not so treated (Garner, 1946).

Protoplasmic properties such as permeability and viscosity are modified by water deficits (Levitt, 1951, 1956), but there is no general agreement as to the nature or causes of these changes. We are almost entirely ignorant of the protoplasmic factors that give some plants greater resistance to dehydration than others. Some of these differences are related to cell size and shape (Iljin, 1953), but there are also basic differences in protoplasmic characteristics that have not yet been adequately explained. There is obviously a great need for more investigation of the effects of dehydration on the properties of protoplasm itself, as well as on the processes of entire plants.

The effect of water deficits on growth as expressed in terms of yield is dealt with elsewhere, but is discussed here in terms of cell processes. In terms of cells, growth consists of cell division, enlargement, differentiation, and maturation. Although the relations between turgor and growth are not fully understood, all of these processes are affected by water deficits and dehydration of the protoplasm. Cell division is reduced, but cell enlargement is reduced even more, because some degree of turgor is essential to the expansion of cells (Broyer, 1950; Burström, 1956; Cleland and Bonner, 1956; Heyn, 1940). One of the first effects of water deficit is a decrease in or cessation of elongation of stems and enlargement of leaves and fruits, because these processes are dependent on a turgid condition of the cells.

Loomis (1934) and Thut and Loomis (1944) concluded that the supply of water to the growing point is the most important factor affecting the rate of growth of corn. Their work indicated that water supply is
limited and growth reduced by (1) bright light, (2) deficient soil moisture, and (3) low humidity, important in the order named. Thus, atmospheric factors were even more important than soil moisture in reducing the growth of corn. As a result, in hot, dry weather, when transpiration is rapid, corn and other plants often grow more at night than during the day. Nightingale and Mitchell (1934) found that tomatoes grown in moist soil at a constant temperature were much smaller and more woody if kept at a relative humidity of 35 per cent than when grown at a relative humidity of 70 per cent. This demonstrates the importance of atmospheric conditions on the internal water balance of plants, even when growing in moist soil.

A decrease in leaf size from lack of turgidity is especially serious because it decreases the photosynthetic surface and production of food. According to Watson (1947, 1956), yield of crops is more closely related to leaf area than to variations in photosynthetic efficiency per unit of leaf area. Hence, the first requirement for high yields is a large leaf area. The effect of increased humidity on the leaf size of tobacco grown under artificial shades is well known. Wadleigh and Gauch (1948) found that enlargement of cotton leaves ceased by the time the soil moisture stress reached 15 atmospheres, and Slatyer also has data showing a decrease in stem elongation and a slowing of increase in dry weight with increasing soil moisture stress.

The effects of water deficit and dehydration on differentiation are equally important (Meyer and Anderson, 1952; Richards and Wadleigh, 1952). In general, water deficit hastens maturation of cells and tissues, increases the thickness of cell walls, and decreases succulence. This not only decreases the size of plants and their yield, but may also decrease quality, especially in the case of pasture and hay crops (Willoughby, 1944). On the other hand, the increased amount of dry matter and supporting tissue produced in plants subjected to a moderate water deficit may be beneficial by increasing stem strength or resistance of fruit to injury by bruising. The increased thickness of cutin often found on plant organs matured in dry air is beneficial because it reduces cuticular transpiration.

The Australians are making particularly valuable studies on the effect of water deficits on growth. Gates (1955) found that even moderate wilting affects plant growth and claimed that it is erroneous to suppose that plant growth is affected only after permanent wilting is reached. He found, relative to tomato plant weight, that leaf weight increase was slowed down while stem weight increase was increased, and that, after recovery from wilting, growth rates of moderately to slightly wilted plants soon increased above the growth rate of controls. Perhaps this was be-
cause growth was checked more than photosynthesis by moderate wilting. Plants wilted more severely probably would not have recovered so rapidly (Ashby and May, 1941). Williams and Shapter (1955) studied the effects of moderate wilting on the distribution of dry matter in barley and rye. They found that the effects varied with the stage of growth at which the plants were allowed to wilt, and suggested that failure to consider the possibility of differences in behavior at different stages of growth has resulted in much confusion regarding the effects of water deficits on growth. The plant parts growing most actively at the time a water deficit occurs are most affected, and this causes many of the differential effects of wilting that have been reported for various organs. Williams and Shapter found that, in addition to reduction in growth, the rate of photosynthesis per unit of leaf area was reduced, the uptake of phosphorus was reduced and nitrogen content of leaves was decreased, whereas that of stems increased.

As Gates (1955) said, the value of these studies would be greatly increased if the water content, or preferably the diffusion pressure deficit, of the plant tissues were known. Only from careful studies of changes in composition of various organs and in rates of processes can we hope to learn how water deficits affect plant growth.

In studies of the effects of water on growth it must be remembered that the full effects of water supply on growth will be expressed only if the plants are well supplied with nutrients, especially nitrogen. This was pointed out long ago by Crowther (1934), and shows up nicely in a recent paper by Burton and associates (1957). Nitrogen deficiency sometimes checks growth as much as lack of water if the surface soil containing most of the nitrogen becomes so dry that salt as well as water absorption is hindered.

2. Why Water Deficits Develop in Plants

In view of the importance of internal water deficits it is desirable to discuss their causes. As mentioned previously, plant-water relations consist of a group of interrelated and interdependent processes. Thus the internal water balance or degree of turgidity of a plant depends on the relative rates of water absorption and water loss, and is affected by the complex of atmospheric, soil, and plant factors that modify the rates of absorption and transpiration.

The transpiration rate of well-watered plants is controlled by such plant factors as leaf area, internal leaf structure, thickness of cutin, and extent of stomatal opening, and by such environmental factors as solar radiation, humidity, temperature, and wind. The rate of water absorption depends on the rate of water loss, the extent and efficiency of root systems,
and the availability of soil moisture. The rate of water absorption is affected by aeration, concentration of the soil solution, and soil temperature, as well as by the soil moisture tension.

It is not surprising that two processes controlled by quite different sets of factors do not always keep in step. As shown in Fig. 18 the rate of absorption even in moist soil tends to lag behind the rate of transpiration, chiefly because of resistance to the movement of water into roots.

![Diurnal variations in transpiration and water absorption during a bright, hot summer day](image)

Fig. 18. Diurnal variations in transpiration and water absorption during a bright, hot summer day (Kramer, 1949).

(Kramer, 1949). On hot, sunny days the rate of transpiration so far exceeds absorption that severe midday water deficits often develop, even in plants growing in moist soil. Such deficits usually are eliminated by absorption during the night, but, as soil moisture is depleted, absorption becomes slower and slower, and the midday deficit persists later and later, until permanent wilting finally occurs and growth ceases.

Thus, plant water deficits can be caused either by excessive loss of
water, by slow absorption of water, or by a combination of the two. Deficits caused by excessive transpiration are usually shorter and less severe than those caused by inadequate absorption, but periods of hot, dry, windy weather can cause severe damage, even to plants in moist soil, by causing excessive transpiration. Conversely, during foggy, showery, humid weather, even plants in dry soil may be subjected to relatively small water deficits. Thus, the effects of soil-moisture supply may be greatly modified by atmospheric conditions that affect the rate of transpiration, as noted by Hagan (1955) and Letey and Peters (1957).

This situation explains why the behavior of plants cannot be explained satisfactorily in terms of either soil or atmospheric conditions alone (Hagan, 1955). Plant growth is affected by the turgor, or internal water balance, which depends on the relative rates of absorption and transpiration, which are affected by both atmospheric and soil conditions.

The internal water balance, or turgidity, of the plant represents the integration of all the factors affecting plant water relations. Thus, we need to give more attention to the internal water balance as a measure of whether or not plants are adequately supplied with water. This approach seems to have been applied with considerable success to sugar cane in Hawaii (Clements and Kubota, 1942) and to various crops in Israel (Oppenheimer, 1953).

In this connection it seems possible that more attention ought to be given to plant factors that reduce water loss, such as thickness of cutin and responsiveness of stomata. Emphasis on the idea that evapotranspiration should be potentially equal from all types of vegetation cover has led to neglect of the probability that differences in rate of water loss may exist between different kinds of plants. It seems very probable that, under identical environmental conditions, plants with thick layers of cutin and stomata that close promptly as soon as a water deficit begins to develop are likely to survive drought better than those with less responsive stomata (Pisek, 1956; Stocker, 1956). Rider (1957) recently warned that there is reason to doubt if evapotranspiration is the same from all types of plant cover. It seems probable that more attention should be given to the importance of anatomical and physiological factors in controlling water loss.

3. Measurement of Water Deficits

There has been considerable uncertainty concerning the best method of measuring or characterizing the condition of plants and plant tissues with respect to water. Ecologists have concerned themselves with this problem for many years, but have not settled on a single method.

a. Water content. The oldest method is to express the water content
as percentage of fresh or dry weight. The water content of plant tissue varies with species, organs, tissues, and age. It also varies with the time of day, and in perennial plants with the season of the year.

In general, young tissue has a high water content, but as cells mature the walls thicken and the proportion of dry matter increases, causing a decrease in percentage of water. For example, Ackley (1954) found that the water content of pear leaves decreased from 73 to 59 per cent of their fresh weight from May to August, although water content per leaf increased somewhat. Practically all herbaceous species tend to become more woody and lower in water content as they mature, and this trend is particularly notable in seeds (Shirk, 1942). A noticeable decrease in water content at about the time of flower bud initiation is said to occur in some annual plants (Loehwing, 1942; Burns, 1951; Dennison, 1945; Hall, 1949).

In addition to the seasonal changes caused by maturation, there are also well-defined seasonal changes in trees caused by seasonal differences in the balance between absorption and transpiration. In general, maximum water content of tree trunks seems to be attained in the spring, just before the leaves open, and decreases to a minimum in late summer, shortly before leaf fall (Clark and Gibbs, 1957; Gibbs, 1939). The tissues of most transpiring plants show diurnal variations in water content, with the maximum at night and the minimum near midday (Wilson et al., 1953). These midday deficits are important physiologically because they often cause stomatal closure and reduction in photosynthesis, as well as less obvious disturbances of other physiological processes.

One important effect of reduction in water content is the increase in osmotic pressure of cell sap that often accompanies it. Also, there is often an undesirable increase in diffusion pressure deficit.

It is obvious that percentage water content is too variable to be very useful as an indicator for evaluating water conditions in plants or plant tissues, because it is affected by age and kind of tissue as well as by environmental factors. One refinement is to make moisture content measurements on leaves or other parts of the same age, as is done on growing leaf sheaths of sugar cane in Hawaii (Clements and Kubota, 1942). This seems to have proved to be a satisfactory indicator for irrigation of sugar cane, and might be adapted to some other plants.

**Relative turgidity.** Many years ago, Stocker (1929) suggested that a good measure of internal water balance is the amount of water taken up by leaves or twigs that are allowed to absorb water until saturated. The saturation deficit is calculated as follows:

\[
\text{Saturated fresh weight} - \text{field fresh weight} \times 100 = \text{saturation deficit}
\]

\[
\text{Saturated fresh weight} - \text{oven-dry weight}
\]
This procedure has been used in Europe, but considerable time is required for a twig or large leaf to attain equilibrium.

A variation of this method was introduced by Weatherley (1950) for measuring the "relative turgidity" of plant tissue. Disks of leaf tissue about 1 cm. in diameter are cut out of leaves, weighed, floated on water until they attain equilibrium, and their fresh weight and oven-dry weight obtained. The relative turgidity is then calculated as follows:

\[
\frac{\text{Field fresh weight} - \text{oven-dry weight}}{\text{Saturated fresh weight} - \text{oven-dry weight}} \times 100 = \text{relative turgidity}
\]

This method requires smaller samples of tissue and less time than the Stocker method, and the method of calculation is more satisfactory because the smaller the uptake of water, the larger the number representing relative turgidity.

This method has been used extensively by Slatyer (1955, 1957), who decided that it gave a good measure of internal water balance in plants of several species. Werner (1954) also used it to measure changes in water balance in several varieties of potatoes, and Oppenheimer (1954) reported favorably on its use. It seems that relative turgidity may be a useful measure of water balance in plants, and might even be used as an indicator for irrigation. Its use is based on the assumption that the fully turgid condition is normal and desirable, but this assumption perhaps needs more study. The time of day when plants are sampled will make considerable difference in the relative turgidity observed, and early-morning sampling seems best for most purposes. Unfortunately, the effect of a given relative turgidity is not the same in all species; hence, the critical level probably must be determined for each species, and perhaps even for each variety (Slatyer, 1957).

c. Osmotic pressure. At one time, osmotic pressure of sap expressed from leaves or other plant organs was used extensively as an indicator of the water conditions in plants, and this is still favored by Walter (1955). Much of the work in this field is summarized by Miller (1938), and methods and results are discussed by Crafts and associates (1949). In general, dehydration is accompanied by increase in osmotic pressure, and increase in water content by decrease in osmotic pressure, but osmotic pressure is not sufficiently sensitive to be used as an indicator of small changes in water balance.

d. Diffusion pressure deficit. In recent years attention has tended to shift from measurements of osmotic pressure to measurements of diffusion pressure deficit, because the latter is a more sensitive indicator of the degree of turgidity. The diffusion pressure deficit (Meyer, 1945; Crafts, et al., 1949; Meyer and Anderson, 1952) is a measure of the pressure with
which water tends to move into cells and tissues, and is comparable to the total soil-moisture stress (moisture tension plus osmotic pressure) of a soil. Fully turgid tissue has a zero diffusion pressure deficit, and the diffusion pressure deficit increases as the water deficit increases until it equals the osmotic pressure, except that, when, as shown in Fig. 19, negative wall pressure or tension develops, it may even exceed the osmotic pressure (Slatyer, 1957). This value is particularly useful because it is expressed in atmospheres and can therefore be compared with soil moisture tension and osmotic pressure of the soil solution.

The chief obstacle to extensive use of the diffusion pressure deficit is the difficulty of measuring it. One method is to determine the concentration of sucrose or mannitol in which no change in length occurs in strips of tissue, but this is applicable only to thin tissues containing little supportive tissue. Another method is to determine the concentration of solutions in which no change in weight of pieces of tissue occurs, but this is applicable only to tissue, such as beet or potato, from which a number of uniform pieces of tissue can be cut. Lemée and Laisné (1951) immersed pieces of leaf tissue in sugar solutions of various concentrations and determined the changes in concentration of the solution by measuring the change in refractive index with a refractometer. This method was described by Ashby and Wolf (1947). Slatyer (1957) determined the diffusion pressure deficit of leaf tissue by placing disks over solutions of various vapor pressures to find at what solution diffusion pressure deficit no gain or loss of water occurred. This method requires careful control of temperature. Weatherley and Slatyer (1957) suggest that if the rela-

![Fig. 19. Effect of soil moisture stress on diffusion pressure deficit, osmotic pressure, and relative turgidity (Slatyer, 1957).](image-url)
tion of the diffusion pressure deficit to the relative turgidity were es- 
established for a species, the relative turgidity might be used to estimate the 
diffusion pressure deficit.

e. Stomatal opening. As mentioned earlier, in many plants premature 
closure of stomata is one of the most sensitive indicators of water deficit. 
More or less successful attempts have been made, especially in Israel (see 
Oppenheimer, 1953; Oppenheimer and Elze, 1941), to use the closure of 
stomata as an indicator of developing water deficit before visible wilting 
occurs. For this purpose the extent of infiltration by a series of liquids of 
different surface tensions has been used to estimate the degree of stomatal 
opening. If stomata are wide open, even a substance of relatively high 
surface tension, such as kerosene, penetrates readily; if nearly closed, 
only one of low surface tension will enter. Alvim and Havis (1954) found 
that a graded series of Nujol and n-dodecane gave a good range of surface 
tensions. In Israel, kerosene seems to have been used most often, and this 
method is described by Oppenheimer and Elze (1941), Oppenheimer 
(1953), and others. It is, of course, only an indirect indicator of water 
deficit, not a quantitative measure.

f. Other possibilities. One of the most useful tools would be some kind 
of instrument that indicates changes in the water balance of tissues of 
growing plants. One possibility being investigated is measurement of 
changes in electrical resistance by inserting electrodes into the plant 
tissue. Another possibility might be to measure changes in electrical 
capacitance. The difficulties of calibrating such methods seem quite 
formidable, but this field deserves more study.

Bloodworth and associates (1956) used the rate of flow of the trans- 
spiration stream as an indicator of transpiration rate and internal water 
conditions. Although this permitted an analysis of the effects of irrigation 
practices and defoliants on transpiration, it provides no direct evidence 
concerning internal water balance.

4. Summary

1. Plant growth is affected by internal water deficits because they 
affect numerous internal processes and conditions, such as turgidity, dif- 
fusion pressure deficit, photosynthesis, respiration, and cell enlargement. 
Changes in these processes and conditions modify both the quantity and 
quality of plant growth. We therefore need more information concerning 
the relationship between internal water balance and plant processes.

2. Water deficits occur in plants because the rate of water loss often 
exceeds the rate of absorption. Although the two processes are partly 
interdependent, absorption is controlled chiefly by soil factors, and water 
loss chiefly by atmospheric factors, and they often occur at different rates.
Water deficits can occur because of rapid water loss or slow absorption, or a combination of the two. Thus, it is impossible to explain plant growth solely in terms of either water supply or the rate of evapotranspiration.

3. The most important factor in plant-water relations is internal water balance, because this is the result of the interaction of all plant and environmental factors as integrated by the plant itself. Furthermore, it is internal water content that affects the processes controlling growth. A reliable method is therefore needed to evaluate internal water balance. Water content has been used for sugar cane, and relative turgidity appears promising enough to deserve further investigation, but neither measures the energy status of the water. Osmotic pressure is not sufficiently sensitive, nor does it measure the free energy. Diffusion pressure deficit seems to be the best measure in theory, because it is a measure of the free-energy status and is expressed in the same units as soil moisture stress, but it is difficult to measure.

4. Some simple method is needed to measure the water balance of crop plants in the field in order to detect internal water deficits before wilting occurs.

B. Drought Tolerance of Plants

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Even in humid regions, crop plants may develop water deficits severe enough to be described as drought conditions. Such deficits may arise from augmented transpiration caused by the high desiccating capacity of the aerial environment, or by a reduction in the absorption of water from the soil. The term drought resistance as used here refers to the overall suitability of plants for cultivation under dry conditions. As will be apparent from the following discussion, such resistance may arise from many sources, one of which is the capacity of the plant tissue to survive desiccation. Drought hardness is the term used to describe the latter phenomenon.

Drought resistance was first reviewed in a comprehensive manner by Maximov (1935). More recent reviews (Levitt, 1951, 1956; Ilijin, 1957; Kursanov, 1956; Richards and Wadleigh, 1952) have been used to prepare this discussion. The above reviews contain extensive bibliographies, to which the reader is referred for a more detailed discussion of the various aspects of drought resistance. Since this subject has apparently received continuing research attention in the U.S.S.R., it is hoped that translations of the numerous articles cited by Kursanov will become available soon.
The complexity of drought tolerance is illustrated by the following schematic summary of the processes and properties that contribute to it (Newton and Martin, 1930).

Drought Resistance

A. Absorption
1. Soil factors
   a. Available moisture
   b. Concentration of soil solution
   c. Toxic substances in solution
   d. Temperature
   e. Aeration
2. Root development
   a. Spread and depth of penetration
   b. Intensiveness of branching
   c. Number and persistence of root hairs
3. Physiological adaptations
   a. Osmotic pressure of cell sap of root hairs
   b. Imbibition pressure of hydrophilic colloids in cells
   c. Mucoelastic secretions in region of root hairs

B. Transpiration
1. Atmospheric factors
   a. Temperature
   b. Humidity
   c. Air movements
   d. Light intensity
   e. Atmospheric pressure
2. Structural features
   a. Ratio of root to leaf
   b. Conducting tissue
   c. Reduction of leaf surface
   d. Rolling, folding, or thickening of leaves
   e. Deciduous leaves
   f. Epidermal coverings
   g. Diminution of intercellular spaces
   h. Stomata stomata
   i. Size and number of stomata
   j. Stomatal regulation
   k. Surface hairs
3. Physiological adaptations
   a. Osmotic pressure of cell sap
   b. Imbibition pressure of hydrophilic colloids in cells

C. Wilt endurance

From the foregoing summary it is seen that plants exhibit drought tolerance either because of factors affecting their intake or loss of water or because the plants are able to survive tissue desiccation. Since the physical and physiological processes involved in the movement of water into, through, and out of the plant have been discussed in previous sec-
tions of this article; they are not repeated here; attention will be restricted
to the more specific question of drought hardiness. Appropriate literature
citations will be found in Levitt (1956), Iljin (1957), or Kursanov (1956)
for each of the statements made in the remainder of this section.

Reproductive bodies, such as seed and spores, are noted for their
ability to remain viable under rather severe desiccation. To a certain de­
gree, seedlings in their earliest stages also show drought hardness con­
siderably above that which they possess at later stages of growth. This is
in agreement with the fact that, within a given plant, the younger tissues
are the most hardy. Such hardiness is due, in part at least, to the greater
ease with which water can move to the younger tissues.

Drought injury is believed to result both from metabolic and mechani­
cal effects that accompany tissue dehydration and overheating. Since the
effects of moisture deficiency on plant metabolism have been discussed in
the preceding section, it will suffice here to recall that net photosynthesis
may be reduced as much as 90 per cent when leaves are badly wilted. Also,
cellular water depletion may result in irreversible reduction of the pro­
tein-synthesizing capacity of the chloroplasts and in a loss of the ability
of protoplasmic structures to bind certain enzymes.

Structural changes in the protoplasm, resulting from mechanical stress
induced by the loss of water from the cells, are believed to be a major
cause of drought injury. Cell size and the speed of water removal are
both positively correlated with the severity of the protoplasmic disruption.
Increased resistance to such injury is effected by pretreatments that
produce plasmolysis in the cells. The severity of the protoplasmic injury
is reduced if subsequent rehydration of the tissues is slow.

Drought-hardy plants usually have smaller cells than those living in
moist habitats. When desiccated, small cells undergo a much smaller
proportionate reduction in volume than do large cells and therefore do
not suffer as large disturbances as the latter. Although there are variations
between species, it is generally accepted that increased osmotic values
are characteristic of plants having superior drought hardiness. Cellular
water deficit often is accompanied by an increase in the hydrolysis of
starch to sugars. The higher osmotic values not only increase the ability
of the cells to retain water, but also may have an additional effect by
increasing the resistance of the protoplasm to dehydration.

In a general way, drought hardness varies inversely with the natural
water content of the tissues; there are, however, many exceptions to this
rule. For many years it has been believed that resistance to tissue desic­
cation was related to the bound water content of the protoplasm. How­
ever, widespread unequivocal demonstration of such a relation has been
hampered by the considerable difficulties encountered in measuring the
amount of protoplasmic-bound water independent of water adsorbed by non-protoplasmic plant constituents and of the water in the cellular solution itself.

Significant increases in permeability to polar substances and in viscosity of the protoplasm have been observed in plants subjected to drought conditions. Such changes in the physical properties of the protoplasm are considered to result from concurrent changes in solute concentration and from the protoplasm dehydration that result from drought conditions. Some evidence has been published of the importance of the calcium:potassium ratio to observed changes in protoplasmic permeability and viscosity. However, the analyses were based on the total foliar content of the ions, which is not considered to indicate the ionic constitution of the protoplasm itself; therefore, no definite statement on the role of ionic ratios to the physical properties of the protoplasm seems justified at this time. The hypothesis also has been advanced that hydration of the colloids in wheat leaves (and, presumably, their drought hardness) depends on the hydrophilic nature of the adsorbed cations. The effects of anions in such reactions were found to be more complex and to depend on the age of the plant. If this hypothesis can be substantiated, it raises the possibility of influencing drought hardness by nutritional means.

Of all of the theories advanced to explain drought injury, the completely mechanical explanation advanced by Iljin seems to be the most adequate. Further detailed biochemical and biophysical studies at the cellular and subcellular levels may lead to a more complete understanding of plant response to drought conditions, but the phenomenon may presently be described as follows, based on Iljin’s theory (Levitt, 1956):

“. . . it is not the water loss itself that kills, but the mechanical injuries that accompany drying and remoistening. When a plant part dies, the cells collapse. The protoplasm is pulled inward by the shrinking vacuole, outward by the resisting wall to which it adheres. If the cell wall is sufficiently rigid it opposes the collapse and thereby subjects the protoplasm to a strong tension that may lead to destruction. If the wall is thin and soft, it is pulled together with the vacuole and forms folds and wrinkles. Before regaining their normal size and shape, cells that survive drying are subjected to new mechanical stresses and remoistening, which may lead to death.”
The effects of excess water on soil properties, discussed in Section III, A, explain in part the reductions in crop growth associated with poor drainage. In addition, such conditions also directly affect the normal processes of the plants themselves, largely because of the deficient soil aeration that is a corollary of inadequate drainage. Since the effects of soil aeration on plant growth and physiologic processes have been the subject of recent reviews (Russell, 1952; Wesseling et al., 1957), only the general nature of the phenomena rather than a detailed discussion of specific research findings is presented here.

Aquatic plants and those indigenous to poorly drained soils frequently adapt themselves by a superficial rooting system or by morphological root modifications that serve to supply oxygen for the normal aerobic respiration of the submerged tissues. When roots grown in well-aerated soil are deprived of oxygen by soil flooding, the roots die, except that certain species develop an adventitious root system that enables the plant to continue growth. Roots of some plants develop large intercellular spaces when grown in poorly aerated media. The differences exhibited by plants in their tendency to develop adventitious roots or intercellular spaces are believed to explain in part the differences between crops in tolerance to submergence.

Poor aeration arising from inadequate soil drainage affects both the growth and functioning of roots. The uptake of water is influenced in two ways. Of minor importance is the effect of insufficient oxygen on the respiration-dependent or "active" water absorption. The effects of low oxygen or high carbon dioxide on root permeability are responsible for the great reduction in water intake that follows root submergence.

Aeration is a major factor affecting the uptake and accumulation of nutrient ions by roots. The role of aerobic metabolism, both as a source of energy and as a factor governing root permeability, is well established. Since this process is oxygen-dependent, it is apparent why restricted aeration is usually followed by the appearance of serious nutrient-deficiency symptoms in plants. Toxicity symptoms also may accompany poor soil aeration, because of its effects on the solubility and level of oxidation of both inorganic and organic compounds found in soils.

Lack of aeration is a major factor causing damage to flooded plants,
but some available evidence indicates that deleterious effects are also produced by microbiological activity in an anaerobic environment.

The extent of damage caused by the flooding of standing crops depends on the plant species, the duration of the flooding, the prevalent temperatures at the time of flooding, and the organs in the process of being formed. Most plants are quite tolerant to flooding during the dormant period. During the growing season, some plants show moderate tolerance and others die soon after the onset of the flooding. Cereals are severely damaged when flooded at the time of flowering and initial ear formation, but are quite tolerant when the grain matures. The manner in which some plants, notably pear trees, certain forest trees, and grasses, can withstand long periods of submersion of their root system during the growing period is not understood.

Injury to crops is particularly severe when they are flooded on hot days. The damage thus done is generally referred to as scalding. Although the physiological reasons for this behavior are uncertain, certain measures can be taken to reduce scalding damage in irrigated crops.

Silt deposits are often left behind by irrigation or flood waters. They may have a beneficial effect because of their nutrient content or by helping to improve the texture of a coarse soil. Silt deposits are harmful when they reduce the infiltration rate of fine-textured soils or when they coat plant surfaces, thereby making the plants more sensitive to injury by heat.

The contribution made by the water supply from a relatively shallow water table is often largely overlooked, but practical experience and field observations have shown that crop production can be substantially increased by careful management of this source of water. Even a relatively deep water table may serve as a primary source of water in alfalfa, meadow, and forest tree production under certain conditions.

A high water table can be either harmful or beneficial to crop production. An optimum level of water table seems to exist for each particular crop under given conditions, but attainment of this optimum level under field conditions is not easily achieved. A crop may be damaged by submersion of the deeper roots or by a lack of aeration in the overlying soil resulting from a high water table. Roots forced near the surface of the soil may suffer from nitrogen or other nutritional deficiency. If the water table falls rapidly in the spring, roots may remain near the surface, with the result that the plants become more susceptible to drought injury during periods of lower rainfall.

Under field conditions, the optimum level for the water table may frequently be exceeded because of rains during the growing season. The permeability of the soil and the water-table-control mechanisms em-
employed determine the ease with which the water table can be controlled at any predetermined level under given conditions. Opportunity for effective control is greatest in highly permeable sandy soils, and least in clays.

The difficulty encountered in maintaining an optimum level of water table also arises out of the variable rate of consumptive water use by the crop, so that, theoretically, different levels of water table should be maintained at different times during the growing season. However, raising the water table at times of high consumptive water use may kill the deeper roots, induce weed infestation and diseases, and make land operation difficult. In certain cases, high bulk yields obtained at a high water table may be offset by a low protein content of the crop.

The success of subirrigation will depend on whether the moisture removed by the roots is replenished by capillary rise with sufficient rapidity. The magnitude of the rate of rise is such that, under most growing conditions, the two factors can be matched in sandy soils and in peat. The rate of capillary rise in a clay soil is often too slow to make up for moisture removal in the root zone; therefore, this soil tends to dry out, even where a water table is close to the surface, unless the crop uses moisture at a low rate or recurrent rain assists moisture supply. However, even under conditions of high consumptive use and in the absence of rain, crops can still benefit from a relatively high water table level in a clay soil, if it is stable and if the roots can penetrate into the capillary fringe, just above the water table.

The effects of water table elevation on the yield of several crops have been studied at a few locations and summarized by Wesseling et al. (1957). The yield responses were found to vary widely from year to year, largely because of differences in the amount and seasonal distribution of rainfall. Major differences in response were found between crops and between locations, indicating the importance of the rooting habits of the crop and the physical characteristics of the soil. Because of the complex nature of soil-crop-weather interactions, the limited data now available do not permit any generalizations on optimum water table depths for specific crops. Similar difficulties are encountered in summarizing the results of many experiments in which yields are compared on drained and undrained land.

The small amount of information available on the optimum depth of the water table during the off-growing season indicates that a high water table during that period may lower crop production in the subsequent season, perhaps because of deterioration of soil structure under water-logged conditions. For a more extended discussion of crop re-
VI. Soil-Plant-Water Interrelations

In preceding sections the hydrologic cycle and the three possible binary combinations of soil, plant, and water have been discussed. Most of the phenomena encountered in the field, however, represent the interaction of all three components. Therefore the remainder of this review considers the behavior of plants as affected simultaneously by soils and water, the effects on water of the combined action of soils and plants, and the joint influence of water and plants on soil behavior. The role of certain management practices in modifying such responses is also considered.

A. INTERPRETATION OF PLANT RESPONSES TO SOIL MOISTURE REGIMES

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The response of crops to various soil moisture regimes is a matter of great agricultural importance, but little general agreement. One school of thought maintains that soil moisture is available for plant growth equally over the range from FC (field capacity) to PWP (permanent-wilting percentage). Much experimental evidence supporting this view has been cited by Veihmeyer and his colleagues, in their own papers and in reviews citing the work of many others. Another group of investigators maintains that plant growth shows differential response as soil moisture varies between FC and PWP. Several review articles and many research papers have presented experimental evidence supporting this view. The two views are presented schematically in Fig. 20.

The voluminous literature (Stanhill, 1957) on the opposing positions is not recapitulated here; rather, the experimental results presented by both sides are examined to discover areas of general agreement and to pinpoint the crucial conflicts. The hope is to lay bare the reasons for the difference and perhaps to suggest what kinds of information are needed to resolve the conflict.

Overgeneralization appears to have been a major factor in creating and maintaining the controversy. Many soil, plant, and environmental factors are known to affect the dynamic processes of water in the soil-plant-atmosphere continuum, perhaps in unknown ways. In many ex-
periments the observed plant response is the integrated effect of all such growth factors, and many of these factors may have varied considerably during the course of the experiment. Thus the response of a mature prune tree growing on a deep, permeable soil in the Sacramento Valley cannot be predicted from the response of a corn plant in Iowa. Neither is it possible to predict the behavior of the Iowa corn plant from studies on the amount of root elongation occurring in 24 hours in a highly controlled root-culture experiment. Experience has shown that altering certain environmental factors within known limits has little effect on plant responses to differences in soil moisture. However, until the nature of the response curve of all such factors and their interactions are more completely studied, it is very doubtful if generalizations can be made about plant responses to various soil moisture conditions in the field.

1. Factors Involved in Interpreting Experimental Data

Let us examine the difficulties encountered in arriving at a general relationship between soil moisture availability and plant growth, and some of the factors that complicate the interpretation of available experimental data. This discussion is by no means complete. The examples chosen simply illustrate some of the problems involved.

a. Soil moisture movement in unsaturated soils. It is obvious that plant growth may be slowed by lack of water. However, there is no reason to expect any symptoms of damage as long as water uptake does not lag appreciably behind water loss from the leaves. In essence, the theory of equal availability of soil moisture between FC and PWP im-
plies that the rate of moisture uptake is not limiting in that range. The opposing theory—that plant growth shows differential response as soil moisture is varied from FC to PWP—assumes that increasing moisture stresses decrease water uptake to a harmful degree. Both theories have received thermodynamic justifications (Veihmeyer, 1956; Wadleigh, 1946). Interest in the kinetic aspects of moisture movement to roots has developed recently, and several papers (Taylor and Hadlock, 1956; Bigger, 1956; Gingrich and Russell, 1957; Phillip, 1957; Peters, 1957) have stressed the necessity of giving the dynamic aspects of soil moisture much more emphasis than in the past.

Peters (1957) devised an experiment that illustrates the difference in effect on plant growth of soil moisture stress and soil moisture content. Germinated corn seeds in controlled-growth chambers were covered with soils (soil and sand mixed in various proportions) that had been brought to definite soil-moisture-tension values. The results are presented in Figs. 21 and 22. The number on each curve in Fig. 21 indicates the per cent of soil in the mixture. At the same tension, plants grew better in fine soil than in coarse soil. Thus, soil moisture tension...
was not the only factor affecting water availability; moisture content was also important, probably because of the greater unsaturated hydraulic conductivity in fine soil. Another experiment seems to point the same way. Gingrich and Russell (1957) used a series of soil samples and mannitol solutions of corresponding stresses. The results, presented in Figs. 23 and 24, show that corn seedlings grew better in osmotic solutions than in soil samples having the same stress. The fresh weight and elongation of the seedlings decreased with increasing stresses, both in soil and in osmotic solutions. Dry weight, however, decreased only in the soil, remaining relatively unaffected in osmotic solutions. The greatest stress tested was 12 atmospheres. The authors concluded that the water-transmission characteristics of the unsaturated soil, a factor not involved in osmotic solutions, were responsible for the differences. The effect is most pronounced at stresses of 1 to 3 atmospheres. Because young seedlings were used, one should be cautious in drawing conclusions about well-established plants. The results nevertheless illustrate the importance of considering rate of moisture movement to the roots in addition to moisture stress values.

b. Fertility considerations. The relation of fertility to water availability is very complex. A recent review (Hawthorne, 1956) listed nine papers reporting that P uptake is unaffected by soil moisture within the
WATER AND ITS RELATION TO SOILS AND CROPS

Fig. 23. The effect of soil moisture tension and osmotic stress on corn radicle elongation (Gingrich and Russell, 1957).

Fig. 24. Effect of soil moisture tension and osmotic stress on the dry weight of corn seedlings (Gingrich and Russell, 1957).
available range, twelve papers reporting that P uptake is decreased by increased soil moisture stress, and some papers reporting that P uptake is increased by decreased soil moisture content. Such conflict is only to be expected, for the lack of agreement on water availability should lead to inconsistent results in a more complex relationship that depends at least partially on moisture movement.

From an experiment with corn seedlings growing both in osmotic solutions and in soil samples, Danielson and Russell (1957) concluded that the accumulation rate of $\text{NH}_4^+$ is reduced by increasing soil moisture tension, but not directly affected by increasing osmotic concentrations in solution. They proposed that the results might reflect slower water movement in the soil, and hence slower water uptake by the plant. Other evidence confirms these conclusions for various cations and anions (Dean and Gledhill, 1956; Wadleigh and Richards, 1951). Over the growing season, plant growth may be influenced as much by nutrient uptake as by water uptake. Since nutrient and water uptakes may be closely linked, fertility considerations are of great importance in analyzing the results of irrigation experiments.

Where some essential element is confined to the upper soil, a drying-out of the root zone in that layer may seriously retard plant growth even when the plant has adequate water. F. J. Hills and co-workers (unpublished data, University of California, Davis) showed that sugar beets in a phosphate-fertilized soil suffered phosphorus deficiency whenever
the surface soil dried out, even though deeper roots were obtaining sufficient water to maintain plant turgor. This sort of situation may occur often in studies of the relations between soil moisture availability and plant growth. Then increased yield from increased irrigation is not entirely—if at all—attributable to a correction of inadequate moisture.

In Fig. 25 a series of curves shows the interaction between soil moisture and the level of nitrogen fertilization. The figure is idealized, but can be plotted from data obtained in many experiments. Isoyield contour lines are plotted for various irrigation and fertilization levels. Nitrogen status is clearly a limiting factor, for yield increases greatly with fertilizer applications. Such data support both views on soil moisture availability: at low nitrogen levels, water is equally available between FC and PWP for plant growth; at higher nitrogen levels, yield is materially reduced by drier irrigation treatments within the available range.

The importance of the relation of fertility to irrigation practice is again illustrated in Fig. 26. Plants were irrigated every 2 weeks, with group C receiving enough water to wet the complete root zone, group B receiving twice as much, and group A three times as much. At each level of fertilization yield decreased with increased water. Nitrogen was evidently
leached from the soil by heavy water applications. These results indicate
the importance of regulating irrigation water carefully.

c. Stage of growth. Some data (Hagan et al., 1957; Petinov, 1954;
Shardakov, 1957) have indicated that optimal soil moisture for plant
growth may vary with a plant’s stage of growth: germination, vegetative
growth, flower, or maturity, for example. If we assume the various
stages of growth to be a function of their respective moisture supplies,
we obtain the following:

\[ G_1 = f_1 \text{ (soil moisture)} \] germination
\[ G_2 = f_2 \text{ (soil moisture)} \] emergence
\[ G_3 = f_3 \text{ (soil moisture)} \] vegetative growth
\[ G_4 = f_4 \text{ (soil moisture)} \] flower and bud initiation
\[ G_5 = f_5 \text{ (soil moisture)} \] fruit development

To continue this idea further, functional relationships within each of
these stages are not independent of the previous stages. The relationships
become:

\[ G_{\text{germination}} = f (G_{\text{seed}}, \text{soil moisture}) \]
\[ G_{\text{emergence}} = f (G_2, G_3, \text{soil moisture}) \]
\[ G_{\text{flowering}} = f (G_5, G_4, G_3, \text{soil moisture}) \]

If these growing periods become infinitesimally small, and, hence, in
finite in number, we can (given sufficient mathematical knowledge and

*Fig. 27. A schematic representation of the idea that the cumulative growth curves
of crops may differ owing to variations of soil moisture stress at various stages of
growth. Curve A illustrates the growth curve under one series of soil moisture values.
Curve B illustrates the relation for another.*
data) calculate growth curves such as those in Fig. 27. The total growth of a crop is a summation of the growth at each growth stage as affected by the particular relationships to the prevailing moisture regime for a given set of conditions described by known values for other soil factors, plant factors, and climatic factors.

An irreversible influence of soil moisture on the growth rate at any particular stage may affect subsequent growth and total yield at maturity. This consideration is of great importance. Some data indicate that moisture availability or other factors are so critical at certain stages that growth can be restricted at later stages, whether or not growing conditions are then optimal. An established example is the importance of irrigating corn just before tasseling (Robins and Domingo, 1953). A deficiency in soil moisture then will permanently restrict growth, regardless of later irrigation.

The preceding discussion illustrates two points: (1) many variables are involved, and (2) the changing relations between growth stage and soil moisture availability make extremely difficult the formulation of a widely applicable general relationship between plant growth and soil moisture.

d. Growth and yield. What is meant by plant growth is often insufficiently specified, thereby complicating the interpretation of results in irrigation experiments. We easily recognize several different manifestations of growth: elongation of plant organs, increase in fresh or dry

![Figure 28](image-url)  
**Fig. 28.** Difference in effects of moisture depletion on dry weight yield of shrub and on yield of rubber per acre (adapted from Hunter and Kelley, 1948a).
weight, development of reproductive rather than vegetative organs, etc. They result from intricate combinations of many physiological processes; probably not all are equally affected by changes in the internal water balance of cells and tissues when soil moisture stress is increased. Many examples support this idea, though the results sometimes contradict each other. Following are some of the findings reported, including some conflicting results:

In guayule the dry-weight yield of vegetative parts was decreased with increasing soil moisture stress, but the yield of rubber increased (Hunter and Kelley, 1946a). This is shown in Fig. 28. The per cent of

![Graph](image)

**Fig. 29. Effect of irrigation treatment on clover green forage and seed yield (Hagan et al., 1957).**

sugar in cane and beets was raised by increasing the moisture stress (Rabie, 1948; Wiersma, 1955). As shown in Table VII increasing soil moisture stress is reported to decrease sugar content and increase nicotine and nitrogen in tobacco (van Bavel, 1953). Tests on beans and tomatoes indicate that soil moisture stress depleted the reduced starch and sugars in the roots, stems, and leaves before the soil reached the wilting percentage (Woodhams and Kozlowski, 1954). Moisture deficiency in the soil was reported to increase oxidase and catalase activity and reduce ascorbic acid content in tobacco leaves (Tombesi, 1951).

The fact that various measurable aspects of growth do not respond
in the same manner to moisture stress must be recognized in analyzing plant-soil-water relations and proposing efficient irrigation practices. Furthermore, from a practical standpoint, harvestable yield is more important than potential yield or "growth." Increase in vegetative growth does not necessarily indicate an increase in potential yield, and an increase in potential yield does not always mean an increase in harvestable yield. In addition, considerations of market quality and nutrient content may be involved. Therefore the irrigation practice to be applied to one crop may not be adequate for another depending on the type of organ harvested. A study of the influence of soil moisture stress on various aspects of growth in Ladino clover (Hagan et al., 1957) has shown that increasing soil moisture stress decreases forage production and potential seed production, but increases the yield of harvestable seed; it holds preharvest germination of newly produced seed to a minimum by keeping dry the atmosphere around the plants. This is shown in Figs. 29 and 30.

![Graph showing the influence of date of harvest on observed relation between soil moisture depletion and harvestable yield of Ladino clover seed. Midseason harvest made on July 23, final harvest August 17. Reduced yield at time of final harvest on E treatment (wet) was caused by germination of seeds from heads produced earlier in the season (Hagan et al., 1957).](image-url)
e. Importance of the root system. The nature of the root system is important in determining the relation between measurable soil moisture stress and plant growth. Different interpretations of root development and moisture conditions within root-penetrated soil contribute to contradictory views on plant-soil-water relations. When soil and growing conditions are favorable, many perennial crops develop well-branched root systems that thoroughly permeate the soil to depths characteristic of the plants. Below these depths the density of the root systems diminishes until moisture extraction cannot be detected. It is desirable to distinguish what may be called the “complete extraction” zone from the “partial extraction,” or “transition,” zone. The complete extraction zone may be defined as the volume—or, with closely spaced plants, the depth—from which the plant can remove all available water. In this zone the soil is thoroughly permeated with fine roots. The transition zone contains a varying concentration of roots, usually decreasing with depth. The existence of this transition zone often seriously complicates the interpretation of soil moisture experiments.

With the expanding root systems of annual crops, analysis of moisture conditions is even more complicated. In the seedling stage, only a tap root or a few branched roots penetrate the soil. Later some annuals rapidly develop well-branched root systems that continually permeate ever-greater soil volumes. At the same time some roots grow out ahead into a correspondingly enlarging transition zone. Thus, if the soil has been wet to field capacity to a considerable depth, these growing roots continuously come into contact with additional supplies of available water at low tensions. If the roots are well branched and grow rapidly enough, they may contact new supplies of readily available water fast enough to meet the needs of transpiration. On a pre-irrigated deep alluvial soil at Davis, California, a crop with a rapidly extending root system, such as watermelon, does not respond to later irrigations, although a relatively high soil moisture stress may develop within an ever-increasing soil volume. Other annuals send out but a few widely spaced roots, leaving large volumes of unexplored soil between roots, particularly in the early stages of growth. In such cases, soil moisture samples, or even moisture-indicating devices, may give quite a false picture of moisture conditions at the root surface. Even when the measured soil moisture stress may be quite low, crops with sparse roots will respond to irrigations. As shown in Fig. 3, the sparser the roots, the greater the likelihood that growth will be retarded if irrigation is delayed.

Were it possible to sample only the soil adjacent to absorbing roots, one might find that actual moisture stress conditions are considerably higher than is indicated by present methods. Until methods are devel-
oped to measure the moisture stress experienced by sparsely rooted crops, it apparently will be necessary to establish for them some rather arbitrary moisture depletion limits. Such limits will depend on other soil factors, stage of growth, and climatic conditions.

It is not uncommon to find reports that yields decline unless crops are irrigated at some given soil moisture stress. But the depth at which the stress was measured is often not stated, and its relation to rooting depth and spatial density is seldom indicated. Where spatial density diminishes rapidly with depth, plant response at conventionally measured moisture stresses will vary markedly over a short depth interval.

![Diagram showing the effects of spatial density of roots on the relation of growth to the apparent depletion of available moisture.](image)

**Fig. 31.** Schematic representation of the effects of spatial density of roots on the relation of growth to the apparent depletion of available moisture (Hagan, 1955).

The suggestion has been made (Wadleigh, 1946) that roots in the sparsely developed part of the root zone, presumably absorbing water against low soil moisture stresses, may mask the effects of relatively high soil moisture stresses developed in denser parts of the root system. Thus, it may be argued that, whenever widely spaced roots extend through a considerable volume of soil, depletion of most of the available moisture from the dense portion of the root zone may have relatively little influence on growth. This idea is represented in Fig. 32. Whether or not the crop will respond to increasing stress within the complete extraction zone will depend on whether the roots in the transition zone can supply water fast enough to maintain the optimum water balance in the plant.
Evaluation of effective soil moisture is complicated particularly in annual crops by the unknown fraction of roots in the transition zone and their continued extension into moist soil.

Data on grain sorghum presented in Table VIII are interesting in this connection. There was no significant difference in yield between a rather wet irrigation treatment (treatment E) and a single irrigation applied early in the season (treatment D) although other treatments, such as later irrigation (treatments B and C), receiving as much water or

**TABLE VIII**

Effects of Irrigation Treatment on Yield of Grain Sorghum

<table>
<thead>
<tr>
<th>Irrigation treatment</th>
<th>Yield (lb./A.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. No irrigation</td>
<td>3805</td>
</tr>
<tr>
<td>B. One irrigation at early boot stage</td>
<td>4744</td>
</tr>
<tr>
<td>C. Two irrigations; one at first stress symptoms; one at second boot stage</td>
<td>5537</td>
</tr>
<tr>
<td>D. One irrigation when plants 6 inches high</td>
<td>5747</td>
</tr>
<tr>
<td>E. One irrigation when plants 6 inches high; six additional irrigations at 11-day intervals</td>
<td>5725</td>
</tr>
</tbody>
</table>

* Unpublished data, D. W. Henderson, University of California.
more, decreased yield significantly. This may indicate that considerable available moisture near the soil surface is essential for rapid adequate root growth early in the season; otherwise, yield may be depressed.

f. Plant diseases. Plant diseases, nematodes, and insects may also complicate the interpretation of soil moisture studies. By reducing root surface, soil-borne plant diseases and nematodes may cause crops to respond favorably to irrigation at very low moisture stress levels. Because plant diseases and insects often do well in moist environments, their development (and resulting damage) may be increased under wet irrigation regimes. Disease and insect infestations favored by frequent irrigation may reduce yields more than moisture deficiencies involved in drier irrigation regimes that are unfavorable to such infestations. The data in Table IX illustrate the effect of irrigation frequency on the severity of wilt infection on cotton. The early June irrigations were probably responsible for the greater infestation and smaller yield of treatment A.

g. Climatic considerations. The aerial environment influences the relation between soil moisture availability and growth or potential yield. As a first example, let us take rate of photosynthesis in a controlled environment. Figure 33 illustrates the relation between soil moisture and rate of photosynthesis of Ladino clover under constant temperature, humidity, and continuous light (Upchurch et al., 1955). These results agree well with the theory of equal soil moisture availability. However, several investigators (Richards and Waidleigh, 1952) have pointed out that the rate of photosynthesis depends on leaf turgidity rather than soil moisture per se. This suggests that the relation for Ladino clover may depend on atmospheric environmental conditions. One might predict that, at lower humidity and higher light intensity, the relation would fit the second viewpoint on moisture availability. Japanese investigators (Nagisi and Satoo, 1954) who worked on pine and Cryptomeria, reported

<table>
<thead>
<tr>
<th>Treatment</th>
<th>A</th>
<th>B</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of irrigations</td>
<td>7</td>
<td>5</td>
</tr>
<tr>
<td>Date of first irrigation</td>
<td>6/15</td>
<td>7/9</td>
</tr>
<tr>
<td>Yield (bales/acre)</td>
<td>1.74</td>
<td>2.16</td>
</tr>
<tr>
<td>Per cent plants infected</td>
<td>71</td>
<td>38</td>
</tr>
</tbody>
</table>

* Stockton and Doneen (1957).
that "the higher the level of light intensity, the more effect of decreasing of soil moisture could be observed." Thus Fig. 34 indicates that, under conditions favoring greater water losses from the leaf surface, the rate of photosynthesis diminishes as soil moisture diminishes. Figure 35 illustrates sugar beet yield as a function of irrigation treat-
ment—in Logan, Utah (Kelley and Haddock, 1954) and in Davis, California (Doneen, 1942; Marcum et al., 1942). Although the irrigation treatments were not identical in the two locations, they were similar enough to warrant comparison. The widely divergent results lead to opposing conclusions. Both dry treatments closely approached the wilting point, but yield was unaffected at Davis and markedly decreased at Logan. At Logan, yield was highest with the wettest treatment; at Davis, yield was not significantly affected by the various moisture treatments.

It is probable that the differences between these two experiments primarily reflect differences in root development and climate. The date of planting sugar beets is February or early March in California, and May in Utah. Sugar beets in Davis have about four months to develop a deep and well-branched root system before the hot dry weather and high-evaporation conditions of summer. This is not the case in Utah. Measurements of soil moisture stress, which were used as indicators of the various irrigation treatments, do not approximate the situation near the root surface under these conditions. The indicated stress is much smaller than that actually experienced by the roots. As shown in Fig. 35 effects
on sugar percentages were also diametrically opposed. The divergence may have resulted from differences in fertility levels and differences in moisture stress that developed within the plant after the last irrigation.

2. Present Status and Future Outlook

It is generally agreed that the growth and physiologic well-being of living plants is partly determined by the water status of the plant tissues. A full expression of the effects of varying the water status cannot be obtained if factors other than water are simultaneously limiting the plant processes being studied.

The movement of water into, through, and out of a plant is in response to an over-all free-energy difference exceeding by several orders of magnitude that in soils in the range from FC to PWP. Much of the over-all free-energy difference is in the laminar air layers immediately adjacent to the leaf surface, and in the substomatal cavities. Thus the free energy of water in the root cells has the same order of magnitude as the free energy of soil water in the FC to PWP range. If measured during a drying cycle, the energy of retention of water by soils is a continuous single-valued function of the moisture content, with functional dependence being determined by the nature and extent of the hydrated surface and, at high moisture contents, by the size distribution of the soil voids. The energy-moisture content relation of soils exhibits marked hysteresis, hence no fixed relation exists between the two variables even if the antecedent moisture variations are identical. The full significance of such hysteresis effects in relations to soil moisture-plant growth responses remains to be established. On a macroscopic, or field-scale, basis, most water use by plants occurs at continuously decreasing soil moisture percentages, interrupted by sudden returns to field capacity or above. On that basis it appears that hysteresis effects might be ignored in interpreting soil moisture-plant behavior experiments. However, at the root-soil interface and on the basis of the diurnal variations of water intake rate, it is apparent that the soil immediately adjacent to the absorbing root probably undergoes cyclic wetting and drying, and would therefore exhibit hysteresis with respect to the energy-moisture content relationship.

The free energy of soil water is determined not only by the energy of retention by the soil but also by its concentration of solutes. In fertilizer bands and in many soils of arid regions the soluble-salt, or osmotic, effects on the free energy of soil water may be of the same order as those due to interfacial forces found in the moisture range from FC to PWP. Here too, the short-term changes occurring immediately adjacent to the absorbing root are not established.
The impossibility of uniformly rewetting a given volume of soil to moisture contents lower than the field capacity without resorting to mechanical mixing is generally recognized, as is the corollary impossibility of maintaining in the presence of living roots a constant soil moisture at values below field capacity. Therefore, two principal types of experiments are used to study plant response over the soil moisture range from FC to PWP.

In one type, plant behavior is studied as soil moisture is reduced by root withdrawals or by evaporation over a predetermined portion of the FC to PWP range. When the desired degree of depletion is achieved, sufficient water is added to bring the entire soil volume up to FC. Plant observations may then be repeated over another cycle of depletion. Thus the plant is subjected to one or more cycles of soil moisture depletion and recharge. Such cycles may have predetermined amplitudes, ranging essentially from zero to 100 per cent of the FC to PWP moisture range. When differential plant responses are observed in such experiments, attempts are usually made to relate the responses to a depth- and/or a time-averaged mean moisture content characteristic of each moisture regime. There is little a priori basis for such an averaging process, since it implicitly assumes that a linear soil moisture-plant response function exists. If the averaging extends over several cycles, it further assumes that the plant responses are independent of previous treatment history. There is no justification, therefore, for attempting to relate the observed plant response to such an artificial mean moisture content. Plant responses can with validity be related only to the different soil moisture regimes under which they were produced, unless it can be demonstrated that the assumptions implicit in the averaging process are justified.

The second principal kind of experiment used to study soil moisture-plant relations is the short-term, constant-moisture type. In such studies different soil moistures, either within or extending beyond the FC to PWP range, are prepared by distributing water mechanically through the experimental soil. Plant roots are then brought into contact with the soil and allowed to grow for a period short enough that the soil moisture changes resulting from the withdrawal of water by roots are too small to alter initial soil moisture content materially. Observed plant responses may be thus related to a particular soil moisture condition. But such studies warrant no conclusions as to the effects to be expected from continued exposure of roots to such conditions, since it is recognized that plants are capable of making gradual physiologic adjustments to slowly changing root environmental conditions. A modification of the constant-moisture type of study has also been used, in which small plants are transplanted into rather large volumes of soil of known moisture content.
It is assumed that the roots will then grow through the soil fast enough to keep in contact with essentially constant soil moisture. This assumption may be open to serious question, but the procedure does permit longer periods of study and may enable the plant to make physiologic adjustments. Therefore, more valid conclusions can be drawn concerning the nature of the soil moisture-plant growth relation.

Most investigators agree that differences exist among plants and among the several physiologic processes, both in the nature and extent of response to changes in soil moisture in the FC to PWP range. In general, vegetative growth and cell enlargement are more commonly involved than are reproductive growth and cell division. Perhaps because of differences in seasons when vegetative growth occurs, the nature and extent of their root systems, and storage within the plants, perennial crops as a class are less responsive to soil moisture changes than annuals.

It is generally agreed that extended exposure of a major portion of a plant's root system to moisture contents at or below the PWP results in injury from which the plant may recover only slowly and only partially when the soil moisture content is raised. No general quantitative statement can at present be made concerning the portion of roots that can be so affected or the length of the exposure or the recovery time. Such quantities undoubtedly will vary with the crop, its stage of growth, intensity of the transpiration demand, the leaf:root surface ratio, and the moisture-transmitting characteristics of the soil.

In view of the great complexity of the response of plants to differential moisture conditions, it appears that two major lines of experimentation should be further developed.

One type would be field study of the response to controlled soil moisture regimes of individual crops on specific soils. The scientific usefulness of such experiments will be greatly enhanced if detailed supplementary data concerning the soil, the plant, and the aerial environment are also collected during the full course of the study. A lack of relevant supplementary data on an experiment frequently makes it impossible to rationalize treatment responses that, viewed by themselves, appear contradictory.

The second type of investigation needed involves highly controlled studies in which, to the extent possible, all environmental factors other than the one under study are held constant at known levels. By systematically studying the effects of each factor separately, the range of plant tolerance and the shape of the response curve can be established for each independent variable. The interactions arising from simultaneous variation of two or more variables can then be examined. In this
WATER AND ITS RELATION TO SOILS AND CROPS

way it will be gradually possible to increase the complexity of experimental treatments, in a known and controlled fashion, to a level approaching that encountered in the field.

The two main avenues of attack on the problem of plant response to soil moisture obviously apply equally well to other growth factors. The results obtained from the two kinds of experiments will in time tend to converge, and will, perhaps, lead to valid generalizations of wide applicability. It is doubtful if either of the two lines by itself would ever yield such generalizations.

It is true that any studies of the response of plants to environmental variations may make a contribution to a more complete understanding of crop responses to different soil moisture conditions, but it is believed that the most rapid advance of knowledge in this important field will come from added information on the following specific topics:

1. The development of techniques for measuring, without plant injury, the energy status and dynamic behavior of water in living plants and plant parts. To date, most studies of plant response to moisture environment have used treatments defined in terms of moisture conditions external to the plant. In view of the highly dynamic nature of water in the soil-plant-atmosphere continuum, it is very doubtful that equivalence of external moisture conditions can be construed to result in equivalence of the moisture conditions within a particular plant part or organ. Consequently, differences in plant response, which frequently occur even though the externally measured moisture conditions are identical, may be fully explainable in terms of the moisture conditions obtaining in the plant at the site of the observed response.

2. A detailed study of the energy, vapor, and gaseous fluxes occurring at leaf surfaces. Large amounts of radiant energy reach the leaf surface. The manner in which this energy is dissipated is a major factor affecting the water economy of the plant. The energy status undergoes tremendous changes within a very short distance at the leaf-atmosphere interface. The changes arising in that critical region from the effects of environmental variations are only qualitatively understood, but may hold the key to the dynamics of water in plants. Associated studies of gaseous exchange also should be made, because of the importance of such exchange in photosynthesis.

3. More detailed information on root growth and on the root area that is operative in water intake. The lack of more quantitative information on the root area through which water is absorbed, the longevity of such absorptive areas, and the rate of root advance through soils are serious barriers to a more quantitative analysis of water movement from the soil.
into the root. An extensive study of the effects of various treatments on these root parameters would logically follow the development of reliable techniques for the measurement of such parameters.

(4) Greater attention to the short-term fluctuations in moisture within the plant. Although diurnal variations in transpiration, translocation, and metabolism are generally recognized, their significance to over-all plant behavior merits greater attention. Thus it may well be found that the amplitude of such diurnal fluctuations may be of much greater physiologic significance than the mean value obtained by averaging over one or more days. In fact, fluctuations at frequencies less than 24 hours may be of even greater significance.

(5) An examination of the physiologic adjustments of plants to moisture stress. The detailed biochemical study of physiologic processes has developed to the point where investigations of the effects of moisture stress on such processes may be feasible. Until such studies can be made, it is doubtful if anything other than an empirical approach can be made to the study of the effects of moisture condition on plant composition and quality.

B. FACTORS AFFECTING IRRIGATION PRACTICE AND WATER-USE EFFICIENCY

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Irrigation practices must be adapted to many social, economic, climatic, and topographic conditions as well as to characteristics of crops, soils, and water supply. Since integration of all these factors into a workable system of irrigation management on an irrigated farm is largely the responsibility of the farmer, actual practices are frequently determined by the knowledge, skill, and temperament of the individual. Water-use efficiency is best considered in terms of the factors that influence irrigation management rather than in terms of the practices themselves. This approach not only points out the reasons for certain practices, but also is less complex. It permits some generalization in terms of more or less typical reaction to factors determining irrigation practices and water-use efficiency. These factors are segregated for discussion, but it should be remembered that they are interrelated, and that water-use efficiency in any given situation is determined by several interdependent factors.

1. Concepts of Water-Use Efficiency

The meaning of water-use efficiency depends on the viewpoint. In the broad sense, high water-use efficiency might involve maximum utiliza-
tion of all the water falling on areas of collection and use and would require allocation of water supplies to conflicting uses for greater public benefit. To the agriculturist, high water-use efficiency means that the maximum possible percentage of precipitation be used by plants of economic or esthetic value. The agriculturist's viewpoint might even be based on maximizing monetary returns or food or feed value per unit volume of water available. Short-term and long-term points of view may differ, particularly in arid areas where it is essential to "waste" some water to maintain a favorable salt balance for sustained productivity of the land.

Water supplies are subject to loss throughout the processes of precipitation, collection, storage, conveyance, and use, just as power is lost in each component part of a compound machine. The efficiency of the entire process or of any part may be calculated. However, interpretation of water-use efficiencies depends on a clear understanding of the bases of calculation. Water-application efficiency on the farm is the subject of most of the following discussion. Water-application efficiency is specifically defined as the ratio of the volume of water stored in the root zone of the crop to the volume of water delivered to the farm. Nevertheless, certain precautions must be observed in interpretation. It is possible to apply a shallow depth of water with poor uniformity, so that the water is all retained in the root zone. The calculated water-application efficiency would be high, but if subsequent irrigations were applied in the same manner, crop yields would be drastically reduced or evaporation and percolation losses would be excessive, depending on the frequency of irrigation. It should also be noted that low water-application efficiency arising from deep percolation is not necessarily serious from the standpoint of over-all water supply utilization, because of the possibility of re-use. The principal factors then become costs of storing and distributing "wasted" water, costs of reclamation, damage caused by any water out of control, and deterioration of water quality. In some areas, re-use of runoff water on individual farms or fields is an accepted practice.

2. Economic and Organizational Factors

Many general considerations influence irrigation practice and water-application efficiency, principally economic and social. Some are quite indirect, consisting of pressures from the general public, in the form of conflicting demands for water supplies or resistance to nuisances caused by uncontrolled water.

a. Water costs. High water-application efficiency is markedly encouraged by high water costs. Where there is only sufficient water to meet crop requirements, waste is discouraged even though the unit cost of
water is low. The basis for levying charges for water is also important. Many farmers pay essentially an annual charge per acre, which is independent of the actual volume of water, because such a procedure is convenient for the agency delivering the water or because it is the only legal means of collecting money under the laws authorizing the agency. Water-application efficiency is higher if the farmer pays for the actual volume delivered, and is further encouraged by limiting the amount he may receive per irrigated acre. In some areas, strict limits are replaced by increasing unit cost as the quantity of water delivered per acre increases.

b. Crop value. One might assume that production of crops of high monetary returns would encourage high water-application efficiency because of the high potential return per unit volume of water used. However, the opposite is true in general. Acreages of high-value crops are frequently limited, and there is a marked tendency to apply excessive depths to eliminate water as a limiting factor in yield or quality. This has proved true even where water costs are high, because of the possibility of added profits far in excess of additional water costs. In the other extreme, low-value crops are frequently neglected or given inadequate irrigation for maximum yields. While water per se is not wasted, potential production per unit volume of water may be lost.

c. Water delivery schedules. High water-application efficiency is discouraged by delivery schedules that do not match crop requirements and water-storage capacities of soils, or that result in unmanageable stream sizes. Deliveries beginning or ending at inconvenient times often lead to neglect, and deliveries extending through night hours are difficult to avoid, but have obvious disadvantages.

Continuous delivery usually involves allotment of an irrigation stream to each farmer, based on his irrigated acreage. This stream is delivered to him continuously throughout the irrigation season. There is no adjustment of the stream to conform to lower rates of water use by crops (and smaller acreages requiring irrigation) in spring and fall as compared to requirements in midsummer. If the stream size is adequate for midseason, earlier and later deliveries are excessive. Stream sizes are small, and may be inadequate for efficient application, especially for certain methods. Adjustment of stream size to conform more closely to changing requirements would increase efficiency if still smaller stream sizes in spring and fall were not a serious factor.

From the standpoint of the agency delivering water, continuous delivery has advantages. Canal capacities required are low, and delivery, measurement, and record-keeping operations are much simplified by constant flows throughout the system.
In rotation delivery, the streams that might be allotted to a group of farmers under continuous delivery are combined and delivered to each farmer in turn for a period based on his irrigated acreage or water right. The principal advantages are larger streams and elimination of irrigation as a constant operation. Adapting rotation schedules to crop requirements and water-storage capacities of soils is often difficult, however, especially where cropping patterns are variable and soils heterogeneous. In extreme cases, depths of water application exceed the storage capacity of the soil, yet the crop suffers from drought before the succeeding irrigation.

Rotation delivery is still relatively simple for the agency delivering water. Flows in main canals are constant, and required capacities are minimized, since rotation is accomplished mainly on the laterals. Fixed schedules simplify routing of water and keeping records. However, there are many different schedules of varying degrees of complexity.

For the irrigator, the best delivery system is demand delivery. He may receive water at his request at any time at the desired flow rate for the period he wishes, provided he gives reasonable advance notice. In some instances, limitations may be imposed by the capacity of the delivery and control system or by the total seasonal water supply.

Over-all operation of the demand delivery system is complex. Canal capacities must be high to meet peak demands. Routing, control, and records are complicated by shifts in flows and delivery points that are difficult to predict much in advance. Usually more water is spilled into waste ways near the ends of the canals than in other types of delivery systems, to assure steady flows and good service to farmers.

Except in rare cases where water is delivered through pipes with adequate and strategically placed storage facilities, night deliveries cannot be avoided. Reservoirs on the farm capable of storing overnight deliveries not only eliminate this problem but afford greater flexibility and may further increase water-application efficiency by allowing the use of larger streams. The principal objection to reservoirs is cost, especially if they must be lined to prevent seepage losses.

d. Water rights. One of the major reasons for adopting a continuous delivery schedule is that the farmer receives water in exactly the manner prescribed by his water right, since the right may state that he is entitled to a given flow of water for a stipulated period. The beneficiary of such a right has no incentive to save water for use elsewhere, and he very likely interprets any move to do so as an infringement of his right.

The laws of the Western States limit exercise of water rights to reasonable beneficial use. However, the courts usually interpret losses
incurred in storage, delivery, and application in the system currently in operation as reasonable, provided there is no obvious negligence.

The exercise of water rights may be controlled either by individual water users or by the agency operating the system, depending in part on the type of organization. Control of water rights by the agency rather than by individuals tends to encourage conservation of water, since surplus supplies may be used to irrigate additional land within the geographical boundaries, or they may be sold to an outside agency.

3. Engineering Factors

The planning and engineering of farm irrigation systems are complicated by the number of variables involved and by difficulty in evaluating them quantitatively. This is especially apparent when one considers the choice of several types of systems and the need for flexibility in operation. The principal need is to adapt the system to existing site conditions so that the irrigator has the means of applying an adequate depth of water, uniformly and efficiently, at proper intervals, under all cropping conditions anticipated. If the range of operating conditions is great enough, temporary or portable components of the system may be desirable. Furthermore, the irrigation system must be integrated into an over-all plan that provides for surface drainage and other forms of water control on the farm.

a. Distribution systems. The means of conveyance and control of water must meet several requirements to allow efficient irrigation in normal operation. There must be adequate capacity to deliver the required flow to any point on the farm. The system must minimize seepage losses, allow complete control of the water, and be convenient to operate and maintain. In practice, operational convenience and ease of maintenance frequently determine the degree of control actually exercised, and therefore affect water-application efficiency.

b. Irrigation layout. With certain methods of water application, especially flooding and sprinkling, the area to be irrigated at one time is more or less fixed by the layout of the system. Since efficient irrigation requires careful adjustment of the area irrigated to the stream size, the water-intake rate of the soil, the slope of the land surface, and the depth of water to be applied, system dimensions must be carefully chosen. This consideration includes the area of basins, length and width of border strips, length and spacing of furrows, and length and spacing of sprinkler laterals. Here again, the need for flexibility may be met by making these dimensions as small as is practical for other considerations. For example, if border strips are so large that the entire irrigation stream is required for one strip for ordinary depths of water applied, it is virtually impossible
to apply a shallow depth, since a larger stream would be necessary but
would not be available. On the other hand, if dimensions are such that
two or more strips are ordinarily irrigated at one time, the irrigator
would also have the option of using the entire stream on one strip should
it prove desirable.

c. Land grading. Until recently, land grading was practiced only to the
extent of removing high spots inaccessible to water or filling low spots in
which water ponded. Now the trend is not only toward continuity of
slope, but uniformity as well. In deep uniform soils, it is likewise fairly
common practice to change the magnitude of the slope to a more desirable
one for surface irrigation. Along with the greater land-grading precision
that is possible with modern equipment and techniques, these trends have
contributed greatly to more efficient irrigation. Grading also eliminates
odd-shaped fields, thus facilitating irrigation and other operations. Slope
requirements vary for different conditions and methods of irrigation. It
is unfortunate that some land is being graded that should be irrigated by
a method that does not require extensive grading. The result is exposure
of subsoil with undesirable physical or chemical properties and loss of
production.

d. Collection and return systems. Where water intake rates of soils are
slow, prolonged irrigation is necessary for adequate penetration of water.
With ordinary precision of land grading, runoff is unavoidable if good
coverage is attained. Unless runoff water is reclaimed and re-used, low
efficiency of water application results. One essential feature of a system
that collects runoff water is a small storage sump or reservoir, which
eliminates the need for the irrigator to handle highly variable flows. The
water may be pumped from the sump with a float-operated pump, either
directly onto a lower field or, more commonly, through a pipe back into
the distribution system. The collection and return system also has the
advantage of providing for surface drainage of irrigation water.

4. Operational Factors

There is a tendency for many farmers to spend large sums on land
grading and other features of the irrigation system, only to defeat the
purpose of these investments by improper operation. The reason is not
known, but possibly the feeling is that a well-engineered system should
operate more or less automatically. However, in most systems, flexibility
and automation are not compatible. The scarcity and cost of skilled irriga­
tion labor is another factor, and, especially in certain surface irrigation
methods, a skilled irrigator who understands irrigation requirements and
the behavior of water on the surface and in the soil is absolutely essential
for efficient irrigation.
Irrigation should be both adequate and efficient. The majority of irrigators meet the first requirement, but often do so by excessive irrigation. The tendency is to consider irrigation as an operation similar to plowing, for example, without any attempt to put it on a quantitative basis, both in regard to timing and depth of water application.

a. Control of timing. Efficient irrigation must begin with proper timing and a reasonable estimate of the average depth of water required. The irrigator's task then becomes one of applying the water uniformly without excessive runoff. Even though they are vital, the timing and depth of water to be applied are difficult to determine with facilities available to most farmers. Fortunately, however, water can be applied more frequently than is necessary, and high efficiencies will still be attained if the depth applied is not excessive. The difficulty lies in the fact that most farmers tend to put on the same depth when irrigating frequently as when irrigation intervals are longer. In many cases, this is due to limitations of the method of irrigation or the irrigation layout. With most surface irrigation systems it is more difficult to apply a shallow depth uniformly than a greater depth unless the water intake rate is very slow, and the result is low efficiency for shallow irrigation. Thus, any factor that affects depth of irrigation tends to influence surface irrigation efficiency—including water-storage capacity of the soil, depth of rooting, intensity of rooting (whether resulting from genetic factors, soil physical characteristics, root diseases, or nematodes), and soil salinity. The depth of water should be considered in relation to the water-intake rate of the soil, and perhaps the best criterion for difficulty in attaining uniform application with surface irrigation is the duration of irrigation or the depth applied divided by the intake rate. If the duration is very short, irrigation is likely to be nonuniform; if it is long, runoff losses become excessive.

b. Attendance. Except in extreme cases of poor design, most of the disadvantages of irrigation systems can be offset by frequent adjustment and increased attendance, particularly by a skilled irrigator. There is a limit to the amount of labor that can be profitably expended, however, because labor costs may exceed the value of the water saved. Then the only possible incentive to conservation of water is avoidance of injury to crops or soils by surplus water.

C. Crop Management for Improved Water-Use Efficiency

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At the 6th International Grassland Congress, Schofield (1952) stated that the consumptive use, or maximum "evaporation," of water by plants
depends on the weather, particularly on the amount of incident solar radiation. He expressed the opinion that it was influenced scarcely at all by the nature of the vegetation so long as it was green. Van Bavel and Wilson (1952) found evidence in North Carolina for concluding that "a closed vegetation cover under equal meteorological conditions disposes of the soil water supply with equal rapidity, regardless of the botanical composition." The work of Blaney and Morin (1942), Penman (1948c, 1951), and Thornthwaite and Mather (1951), although not completely confirmed by experimental data, points to solar radiation and its effects on weather as being largely responsible for consumptive use rates. If this generally accepted, broad relationship holds, then plant breeders and agronomists, as they have increased the yields of crops in a given region, have automatically and often unconsciously improved the efficiency of water use. Hundreds of examples exist to prove that crops specialists, through breeding and management, can make a substantial contribution to solving the world problem of dwindling water resources.

1. Selection of Crop

Species vary greatly in the amount of water they require to produce a pound of dry matter. Even varieties within a species may show great differences in water-use efficiency. As shown in Table VI Burton and associates observed the respective water uses of common Bermuda, Coastal Bermuda, and Pensacola Bahia to be 1546, 803, and 570 in a wet year, and 4336, 641, and 1239 in a dry year. They observed striking differences in the rate of growth, depth, distribution and P32 absorptive powers of the roots of these grasses, with a tendency toward correlation with their efficiencies in water use. Increasing the depth, ramification, and growth rate of plant roots through breeding should result in increased water-use efficiency. Hagan (1957) reported that, because of rapid root growth, watermelons on a deep alluvial soil may not respond to irrigation even though a relatively high soil moisture stress may develop within an ever-increasing soil volume. Thus, proper choice of species or variety may materially improve the efficiency with which dwindling water resources may be used.

Drought is unquestionably the most important environmental factor influencing the growth of plants in the semiarid regions of the world. Nevertheless comparatively little specific breeding for drought resistance has been carried on, probably because of the complex and poorly understood nature of plant reactions to severe moisture stress. Ashton (1948), reviewing more than a hundred papers dealing with techniques of breeding for drought resistance, concluded: "in general, physical characters such as water requirements and transpiration rate, and anatomical and morphologi-
cal characters have not been found to provide a simple and practical index of drought resistance in selection work. In the case of physico-chemical characters, there is less general agreement as to their significance in breeding investigations. Thus, most investigators have used the direct method of testing for drought resistance in field or pot experiments and in drought chambers. Wilting tests and techniques that permit rating varieties on their resistance to artificial drought and heat have been promising. Of particular interest to breeders who must screen large populations have been methods that involve the testing of seedlings or germinating seeds. A lack of agreement concerning the value of these techniques, however, is proof that a standard method of screening all plant populations for drought resistance has not been established. The complexity of the problem and Ashton’s observation that “in all the crops investigated, the capacity to endure drought varies according to the stage of growth” indicate that one standardized method may never test drought resistance in all plants. It is believed, however, that original research in this area can lead to the development of methods that will greatly facilitate the breeding of drought-resistant varieties.

Although there has been comparatively little specific breeding for drought resistance, much progress has resulted as breeders have sought to improve the adaptation of species to arid environments. Not only have improved varieties from such programs been more drought resistant, but they have often shown greater salt tolerance as well. California Marisout barley, for example, bred for the dry sections of California, is much better adapted to high-salt soils than other varieties of this species (Suneson, 1957).

Since consumptive use of water is geared largely to solar radiation, moving a crop to a cooler region or a cooler part of the growing season may, within limits, increase the quantity of plant product per unit of water used. Increasing the hardiness of winter wheats allowed this principle to operate as wheat production moved northward. Breeding corn capable of germinating at lower temperatures increased its efficiency of water use as it permitted its growth in the northern United States. Investigators in California have increased the water-use efficiency of wheat by breeding the Ramona variety, which matures 30 days earlier than old varieties (Suneson, 1957). Obviously, much of the increased efficiency derived from shortening the growing season of a crop may be lost if rainfall during the remainder of the year cannot be conserved. Controlling weeds and manipulating the soil to permit recharging the soil profile with water are generally recommended. These practices, highly desirable in some regions, may lead to both water and nutrient losses in regions of high rainfall.
Growing crops during periods when rainfall is most apt to be available generally makes for most efficient water use. This is nature's way. Desert plants bloom after the rain, exhaust the moisture that fell, and die. Storing water in soil or reservoirs may be costly, and involves water, and often soil, loss as well. By breeding varieties capable of growing during the rainy periods, the geneticist can often automatically increase the efficiency of water use. In India and Africa, very short-season millets (Pennisetum glaucum) have been developed for dry years when the sorghums fail. Planted after a rain, these varieties with rapidly developing root systems are able to make a small yield of grain, largely on the moisture in the soil.

Extending the maturity date may result in greater efficiency of water use. In the southeastern United States the soil profile is almost always overcharged during the winter. Thus, it is impossible to carry over water from one summer to the next. To attempt to do so will merely result in accentuated leaching losses of the already limited soil-nutrient supply. Here, short-season varieties like common Pearl millet (Pennisetum glaucum) are as efficient during their short season as the full-season STAR variety. However, they produce less forage during the frost-free period than do the full-season varieties, and hence are less efficient in using the water that must be used or lost.

Heterosis, which seems to increase the efficiency of most plant processes and increases yields, may be expected to increase water-use efficiency any time the plant breeder can incorporate it into the varieties that he is creating. Deeper root systems with greater ramification will probably be one of the desirable changes associated with heterosis, as shown for corn by Kieselbach and Weising (1935).

Some species and varieties, such as sorghum and Coastal Bermuda, are able to remain green during periods of high moisture stress, whereas others turn brown and die. There is need for much fundamental research designed to discover the characteristics that are responsible for the drought tolerance of such plants. Armed with this information, the plant breeder should be more efficient and successful in increasing the drought tolerance of other species.

An analysis of the cause of crop loss during drought may assist plant breeders by pinpointing changes that must be made. During the summer of 1954, much corn in the Southeast failed to produce grain because of pollen failure during a severe drought at the time of pollination. Varieties capable of producing pollen during such periods of moisture stress could have produced some grain.

Although plant breeders have made, and will continue to make, progress in breeding for drought resistance and increased efficiency in
water use, advances can be greatly accelerated once the responsible plant characteristics are understood. The urgent need for fundamental research in this field is apparent.

2. Cultural Practices

A study of successful dryland farming reveals that a wise choice of cultural practices can do much to improve the efficiency of water use. Leaving cultivated crop residues on the soil during the winter in the snow belt often conserves water in the form of snow that might otherwise be blown from the field. Such residues have been shown to reduce runoff and increase infiltration of the torrential rains that characterize the area. The mulching effect of these dead residues, by reducing evaporation losses, has made for more efficient water use. This has been one of the benefits claimed from stubble-mulch farming, which endeavors to keep substantial portions of the dead plant refuse at the soil surface throughout the cropping season.

Planting cultivated crops in rows on the contour has increased the infiltration of summer rainfall. Cloddy tillage in areas where summer fallowing is practiced has increased infiltration rates and reduced water and soil losses. Thorough weed control in fallowing operations has facilitated water storage by eliminating transpiration losses.

Research conducted at the many dryland experiment stations has demonstrated the tremendous influence of seeding date and rate upon the establishment and production of crop plants. Generally, the earliest safe planting date is best, because it enables the plants to utilize accumulated winter moisture and experience lower evapotranspiration rates. Plant populations must be large enough to permit full use of the available moisture (accumulated and expected) if maximum water-use efficiency is to result. Excessive seeding rates, however, can drastically reduce grain yields. To hedge against loss from excessive plant population during droughts, most farmers usually plant somewhat less than the optimum stand where rainfall is an undependable entity.

Cultural practices must take into consideration the very important root system of the plant. Soil treatments—physical, chemical, or both—that will increase the rooting volume of the soil will make for better crop yields and more efficient water use. Deep cultivation that prunes roots, particularly as maturity approaches, can materially reduce the yields of corn and similar crops. Thus, for maximum water-use efficiency, cultivation must be designed to control weeds without pruning roots. The use of pre- and postemergent herbicides may become increasingly important in achieving this end.
Obviously, pasture and range management that will minimize runoff and maximize infiltration of water will increase efficiency in the use of available precipitation. Part of the reduction in yield experienced on overgrazed ranges may be due to a lack of sufficient vegetation to hold the rain and snow that fall.

Overgrazing also reduces water-use efficiency by restricting the depth and ramification of the grass roots. Crider (1954) has shown that cutting off half or more of the top growth of several grasses, including smooth brome, causes the roots to stop growing for as long as 6 to 18 days. Obviously, such roots are unable to move into areas of available water. Interestingly enough, orchardgrass roots did not stop growing when the plant was defoliated. Removing only 40 per cent of the foliage did not restrict root growth of any of the grasses studied.

Management that will increase the production of total digestible nutrients (TDN) will increase the efficiency of water use by pasture and forage plants. Prine and Burton (1956) showed that extending the period between clippings in Coastal Bermuda from 1 to 6 weeks more than doubled the annual production of dry matter. Since digestibility of the grass decreased with age, the increase in TDN was not as great as the increase in dry matter. Generally, because of digestibility differences, the TDN per acre per year was lower when the grass was cut at 8-week intervals than when it was cut at 6-week intervals, even though the yields were often higher.

The water-use efficiency of plants can be increased in a number of ways without altering the growing season or changing their climatic environment. One of the most obvious of these is to control all features of the environment so that water is the limiting factor for growth. Actually, agronomists have been doing this for years, usually without fully realizing the significance of their results as far as water use was concerned. As early as 1912, Montgomery and Kiesselbach (1912) reported that applying manure to corn growing on an infertile soil reduced from 550 g. to 350 g. the water required to produce a gram of dry matter. More recently, Stansberry et al. (1955) showed that increasing from 100 to 500 pounds per acre the P₂O₅ applied to irrigated alfalfa decreased from 14.2 to 8.4 the acre-inches of water required to produce a ton of hay. Burton et al. (1957) found that the pounds of water required to produce 1 pound of dry Coastal Bermuda hay decreased from 2478 to 803 as the nitrogen application was increased from 50 to 200 pounds per acre. If consumptive use of water is reasonably constant, regardless of crop yield, then any improvement in the environment, such as disease and insect control, adequate nutrition, proper cultivation, etc., that results in increased yields will also result in increased efficiency of water use.
Moisture is the primary factor limiting crop production in the Great Plains. This region, extending roughly from the 95th meridian to the Continental Divide, has an annual rainfall that varies from 40 inches in the southeast, to 12 inches in central Montana. Even so, the area suffers an average water deficit ranging from zero, along its eastern boundary, to nearly 40 per cent, at its western edges. Other areas, notably the Columbia basin and portions of the Intermountain region, have similar rainfall deficiencies. Of equal significance to the average annual deficit are the rather wide annual and seasonal variations in precipitation that characterize the subhumid areas. Such variation is illustrated in Fig. 36, which shows annual precipitation values ranging between 50 and 200 per cent of normal. Moisture conservation and its efficient use by crops are therefore the first considerations in managing soils and crops in these areas (Hobbs, 1957).
Storage of moisture in the soil to meet peak crop demands is the major practice used to overcome moisture deficits. Numerous long-time studies have shown a close relation between crop yields and the amount of available soil moisture in the root zone. Results from fifteen field stations have shown that the average yield of spring wheat increased from 6.9 to 12.6 to 19.9 bushels per acre when the soil at planting time was wetted to depths of 1, 2, and 3 feet, respectively. Under continuous wheat, such depths of wetting were observed in about 30, 44, and 26 per cent of the years, respectively. In the Great Plains a minimum of 8 inches of precipitation is required for wheat to produce grain, and each additional inch on the average increases wheat yields 2.2 bushels per acre. In southern Canada, 5 or 6 inches of stored moisture plus crop-season rainfall was found to be required to produce a minimum spring wheat yield of 1 or 2 bushels per acre. Each inch of water above the 5-inch minimum gave an average increase of 3.4 bushels per acre (Narum et al., 1957).

Summer fallowing is the most widespread practice used to overcome the moisture shortage in dry-farming areas. This essentially consists of using for one crop the moisture received in two years. As presently practiced, however, it is very inefficient. Even in the cooler parts of the region, the efficiency of moisture storage by summer fallow seldom exceeds 30 per cent, and at Fort Hays, Kansas, the 40-year average efficiency was only 15 per cent (Evans and Lemon, 1957). Low efficiency is caused by evaporation of moisture from the soil surface and its loss through runoff or transpiration by weeds. Storage efficiency is highest in the fall, winter, and spring, except where runoff is excessive from frozen soil. Low storage efficiency in the Great Plains arises in part from the high concentration of rainfall in the summer months, when evaporative losses are high. In Utah, a 15-year study gave an average storage efficiency of 31 per cent on a yearly basis, but a 69 per cent efficiency during the winter, when undisturbed stubble effectively held the snow. The summer period following spring plowing showed a net loss of 6 per cent, even though 4.7 inches of rain fell during that period. An efficiency of 36 per cent was recorded during the winter, following the seeding of winter wheat.

Failure to control weeds or volunteer crop plants further reduces the efficiency of summer fallowing. Although some weed growth occurs in grain stubble following harvest, the moisture losses induced thereby are more than offset by the increased moisture stored by the snow-trapping action of the stubble. Therefore, unless weed growth is very heavy, cultivation is usually deferred until the spring or summer following harvest. Such control should begin as early as possible to prevent losses of stored moisture by transpiration. Figure 37 summarizes a three-year
study in Saskatchewan on the effect of date at which cultivation was started.

Subsoiling or deep plowing have been widely studied as means of improving soil moisture storage. In general, such practices have not proved effective in increasing water entry or penetration; however, in special situations, reductions in runoff and increased subsoil moisture storage have been reported. Because of the increased power required, deep tillage is more expensive than conventional methods, and should be limited to those special soil situations where definite yield increases can be obtained.

Contour cultivation is another moisture-conserving practice that is widely used on sloping land in both humid and subhumid regions. By reducing the velocity of water movement over the soil, this practice gives a longer time for water entry into the soil. A summary of results from thirty-seven locations in twelve states indicated an increase of 11 per cent in corn yields attributable to contouring. A similar comparison showed a 20 per cent yield increase for wheat. Although the amount of water saved by contouring is usually small in terms of increasing the supply in the root zone, the small increments frequently come at critical stages in the growth period, thereby giving substantial yield increases.

Mechanical barriers or terraces are useful in moisture conservation. In low-rainfall areas on permeable soils of moderate slopes, level terraces without outlets are used to catch runoff water and permit it to enter the soil. The effects of terracing and contouring on soil moisture supply and cotton yields are shown in Table X.

The redistribution of runoff water from adjacent sloping areas onto a smaller cropped area is another water conservation practice used in subhumid areas. In a nine-year study, increases in moisture of about 15 per cent of average annual rainfall were obtained by spreading the runoff
## Table X

Summary of Experiments Comparing Runoff and Soil Losses under Different Cropping Systems

<table>
<thead>
<tr>
<th>Location</th>
<th>Annual precipitation (inches)</th>
<th>Slope (%)</th>
<th>Continuous row crops</th>
<th>Rotation</th>
<th>Meadow</th>
<th>Bare</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clarinda, Iowa</td>
<td>28.3</td>
<td>9</td>
<td>18.7</td>
<td>38.3</td>
<td>8.8</td>
<td>2.2</td>
<td>0.03</td>
</tr>
<tr>
<td>LaCrosse, Wis.</td>
<td>32.6</td>
<td>16</td>
<td>29.2</td>
<td>111.7</td>
<td>17.0</td>
<td>17.0</td>
<td>0.4</td>
</tr>
<tr>
<td>Zanesville, Ohio</td>
<td>38.0</td>
<td>12</td>
<td>40.3</td>
<td>59.3</td>
<td>19.8</td>
<td>13.4</td>
<td>4.4</td>
</tr>
<tr>
<td>Pullman, Wash.</td>
<td>18.9</td>
<td>30</td>
<td>0.3</td>
<td>0.03</td>
<td>0.8</td>
<td>0.5</td>
<td>0.2</td>
</tr>
<tr>
<td>Temple, Texas</td>
<td>33.8</td>
<td>2</td>
<td>10.8</td>
<td>7.8</td>
<td>10.8</td>
<td>7.0</td>
<td>1.2</td>
</tr>
<tr>
<td>Temple, Texas</td>
<td>32.7</td>
<td>4</td>
<td>13.0</td>
<td>20.2</td>
<td>5.7</td>
<td>8.6</td>
<td>0.05</td>
</tr>
<tr>
<td>Bethany, Mo.</td>
<td>29.5</td>
<td>8</td>
<td>27.1</td>
<td>50.9</td>
<td>16.2</td>
<td>9.1</td>
<td>8.1</td>
</tr>
<tr>
<td>Statesville, N. C.</td>
<td>47.8</td>
<td>10</td>
<td>12.4</td>
<td>31.2</td>
<td>10.0</td>
<td>14.4</td>
<td>1.9</td>
</tr>
<tr>
<td>Guthrie, Okla.</td>
<td>30.2</td>
<td>7.7</td>
<td>12.5</td>
<td>18.9</td>
<td>10.2</td>
<td>4.2</td>
<td>1.0</td>
</tr>
<tr>
<td>Tyler, Texas</td>
<td>40.7</td>
<td>8.8</td>
<td>17.8</td>
<td>22.4</td>
<td>17.3</td>
<td>17.2</td>
<td>1.0</td>
</tr>
<tr>
<td>Watkinsville, Ga.</td>
<td>40.7</td>
<td>7</td>
<td>23.6</td>
<td>26.9</td>
<td>10.5</td>
<td>3.2</td>
<td></td>
</tr>
</tbody>
</table>

* (1) Average annual runoff as percentage of precipitation; (2) average annual soil loss in tons per acre.
* Continuous spring wheat, no continuous row crop reported.
* Data from the cotton plots of the rotation only.
Residue management is important in moisture conservation in the Great Plains. The role of stubble in holding snow has been reported repeatedly. Runoff is reduced and soil moisture storage is increased by tillage practices that leave crop residues on the surface rather than incorporating them into the soil. Residue mulches reduce somewhat the rate of evaporative loss from the soil, but the total loss by evaporation is unaffected. Since surface mulches may increase the amount of intercepted water that is quickly lost by evaporation, it is apparent that they are of little value in reducing evaporative losses of moisture from the soil.

The selection of crops and their management are other ways in which increased efficiency of moisture can be achieved in subhumid regions. The most obvious example is that of such crops as winter wheat, which make their growth during the cool season, when the transpiration demand is relatively low. The sequence in which crops are grown also is determined in part by their relative moisture demands. Thus, the yield of grain in the first year after a crop such as alfalfa is grown, is usually depressed because of a deep exhaustion of subsoil moisture by the deep-rooted perennial predecessor. Row crops, such as corn, usually do not utilize available soil moisture as completely as do grains; crops that follow, therefore, are favored by the greater amount of residual soil moisture. Deep-rooted crops, such as alfalfa, and crops that can resume growth after a drought interruption, such as cotton and sorghum, are more tolerant of periods of moisture deficit.

In all crops, however, adequate fertilization and proper planting rates are important factors affecting water-use efficiency. Numerous experiments have been reported in which proper fertilization has given substantial increases in yield with little or no change in the amount of water used. As pointed out in an earlier section of this article, adequate fertilization is essential for extensive and vigorous root development, which is necessary for effective exploitation of subsoil moisture.

Large areas of the subhumid regions of the United States are used for grazing. Conservation and efficient use of water are the prime problems on rangeland, and their practical solution depends largely on reducing runoff losses and increasing infiltration. The rate of water intake is greatly affected by soil characteristics, vegetation, and the intensity of grazing. Soils of intermediate texture show the greatest improvement in infiltration in response to good management. Making pits in short-grass range has been shown to increase water intake, increasing grazing capacity 33 per cent. Vegetative barriers of unpalatable plants to increase snow trapping,
and water spreading to replenish ground water, give promise as means of improving the supply of moisture in some range lands.

In summary it can be said that the central problem of moisture conservation in subhumid regions is that of increasing subsoil water storage. Water that penetrates below the surface soil layer is safe from evaporative loss, and, given suitable soil and crop management practices, can be used for crop production. The fact that 70 to 80 per cent of the rainfall is lost during a summer-fallow year, and perhaps as much as 90 per cent is lost by evaporation during a crop year, indicates the tremendous potential that still exists for increasing the efficiency of agricultural water use in subhumid areas.

E. MANAGEMENT PRACTICES AFFECTING RUNOFF AND WATER YIELD

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As mentioned in an earlier section of this review, roughly one-fifth of total annual precipitation in the United States appears as stream flow. Since surface runoff is the major path taken by water in moving from the intercepting surface to the channels of concentration, study of the factors affecting the process is of considerable hydrologic importance. The amount and intensity distribution of the precipitation, the storage-capacity and water-intake characteristics of the soil, and the topography are the fundamental factors governing the runoff process. Certain of these are susceptible to modification by cultural or other management practices.

To discuss the effects of such practices on surface runoff, rather than the primary factors themselves, is the purpose of this presentation. For a more complete discussion of runoff hydrology, see Wisler and Brater (1949), Harrold and Dreibelbis (1951), and Meinzer (1942).

Interest in the effects of management on watersheds centers on somewhat different problems in humid and in subhumid and arid regions. In the former, major attention is given to erosion control, with water yield usually a secondary consideration. In drier regions, however, major emphasis is given to the yield of water for off-site storage and use.

Many studies conducted on agricultural land show the effect of vegetative cover on runoff and erosion (Colman, 1953). The data summarized in Table X, although representing a rather wide range of soils, slopes, and climatic conditions, all indicate that the average annual runoff from clean-tilled row crops is frequently 50 to 100 per cent greater than from a three- or four-year rotation containing small grains and meadow crops, and around ten times that from permanent sod. Soil losses show
even greater responses to cropping practices than do runoff volumes. In both phenomena, however, the seasonal occurrence and intensity of the precipitation greatly modify the effects of vegetation. A high percentage of both runoff and erosion result from only a relatively small number of the storms that themselves make up a small part of the total precipitation.

The reader is referred to the references listed in Table X for additional details concerning the data summarized, and for discussions of other factors, such as length of slope, row direction, fertilization, crop sequence, residue management, etc., that modify the main effects of vegetative cover on soil and water losses.

In the humid regions, extensive studies have also been conducted on contouring, strip cropping, and terracing as means of controlling runoff and erosion. A summary of the results of experiments with contouring shows that it reduced runoff more than 30 per cent in 15 of 21 cases. However, field experience did not show as great an effect, because of the practical difficulties of maintaining true contours. The weighted average crop yield increase from contouring was 11 per cent (Stallings, 1945). Strip cropping has not shown a consistent effect on runoff, but in controlled experiments in six states gave an average reduction of soil loss of 49 per cent (Stallings, 1945). Soil movement occurs within the strips, but, because of shorter slopes, the losses are reduced. Field terraces also effectively reduce slope length, reduce runoff, and decrease erosion. Runoff peaks were reduced 54 per cent in watershed comparisons at Bethany, Missouri (Smith et al., 1945).

The development of good physical conditions in the surface soil through fertilization, residue management, and cropping practices is of greater over-all benefit in increasing infiltration and reducing soil and water losses than are the supplemental practices discussed above.

Despite its local effects on runoff and erosion, land management is considered of little importance in downstream flood prevention. Leopold and Maddock (1954) pointed out that 20 to 50 per cent reductions in peak runoff rates apply to moderate storms, and that the quantities of runoff so affected are in tenths of inches. Major floods are usually associated with high rainfall coupled with a saturated or frozen soil having little or no residual moisture storage. In the absence of such storage capacity, runoff occurs from sloping land largely independent of the crop cover. In contrast with the foregoing, watershed management at the headwaters of mountain streams in Utah has proved to be a major factor in determining flood damage (Bailey et al., 1947).

The management of rangeland has important effects on runoff and erosion. Studies in Idaho (Craddock and Pearse, 1938) showed that runoff
increased 0.4 to 60.8 per cent when overgrazing created a shift from wheat grass to annual weed cover. Soil losses increased from 0.003 to 7.8 tons per acre per year. More recent studies (Packer, 1951) indicated the importance of both total ground cover and the maximum size of unvegetated spaces in determining both runoff and soil loss. Results from 97 sites typical of the mountain ranges of Utah, summarized by Bailey et al. (1947), indicated a runoff of about 5 per cent when the normal plant cover and litter were present. On deteriorated areas, runoff increased to values ranging from 20 to 80 per cent as the density of cover decreased.

Brush removal by burning is widely practiced for range improvement in the Western States. Replacement of deep-rooted woody species that draw on soil moisture throughout the entire summer by shallower-rooted grasses and forbs that mature and stop growth in the early summer increases water yield by reducing the amount of water required for subsoil recharge (Adams et al., 1947). Such effects are not observed on soils having little deep-storage capacity. Where a suitable grass cover is established after burning, infiltration is not impaired nor is erosion increased, and water losses due to interception are reduced. A summary and discussion of the hydrologic consequences of brush burning appears in the article by Adams et al. (1947).

Forests occupy large parts of the areas that yield water for irrigation and other off-site uses. Therefore the hydrologic effects of forest management are of importance (Kittredge, 1948). Water yield is increased by watershed deforestation, but maximum discharge rates may rise to destructive levels during periods of excess rainfall or snow melt, and fall to zero during seasons of greatest off-site demands. Thus, forests provide flood protection and stability of yield at the expense of increased evapotranspiration. Snow is an important source of water for off-site use in the western United States. There is evidence that water yield from the snow pack in forests can be increased significantly by proper cutting and forest-management practices (Colman, 1953).

A final example of the role of management on water yield is that of the control of riparian vegetation. The water used by phreatophytes growing along streams and on river flood plains having high water tables has been estimated to amount to over 20 million acre-feet per year in the seventeen Western States (Robinson, 1952). Clearing a 2000-foot channel on a 70-mile section of the Salt and Gila rivers of Arizona was estimated to give a 75 per cent net reduction of evapotranspiration, amounting to a saving of 16,000 to 22,000 acre-feet of water per year (Turner and Skibitzke, 1952). Croft (1948) reported diurnal fluctuations of 25 per cent in stream flow caused by evapotranspiration of riparian vegetation along the stream courses. Mechanical removal, chemical treatment, and
lowering of the flood-plain water table are the techniques used to control undesirable phreatophytes. To date, however, the cost of such control limits this water-conservation practice to situations where a high value is placed on the water.

VII. Summary and Conclusions

The asymmetric distribution of the charge in the water molecule is the fundamental cause of the highly significant properties—high dipole moment and hydrogen bonding—that are primarily responsible for such unique properties of water as its high heat of vaporization, viscosity, surface tension, and solvent properties. Those and other physical properties, all arising from the tendency of water molecules to associate with one another and with other molecules, are responsible for the observed behavior of the unique and ubiquitous compound—water.

The average annual precipitation received in the United States is about 30 inches, of which about 8 inches returns to the ocean as runoff. Neither of these quantities is uniformly distributed, either geographically or seasonally. Annual precipitation exceeds potential evapotranspiration in areas east of the 95th meridian, and in some of the mountain areas of the West. In much of the humid region, and especially in the subhumid and arid regions, the seasonal distribution of precipitation is not in phase with seasonal water use by crops. Soil storage and irrigation are two principal ways of bringing water supply and crop demands into balance. Total ground-water reserves and lakes are equivalent to about thirteen years of precipitation. Aquifer recharge, usually by water-spreading, is used in some areas to correct depletion of ground water by excessive pumping.

Water use by crops is primarily an energy-dependent process. The rate of vapor transfer away from the evaporating surface, and, in certain cases, the rate at which liquid water is supplied to such a surface, serve to modify the energy dependence of evapotranspiration from the soil and leaf surfaces. Water use can be estimated from losses from standardized evaporationimeters, from calculations based on the energy balance of vegetated surfaces, from aerodynamic measurements of energy and vapor fluxes, and from "inventory" calculations based on precipitation and soil moisture records.

Soil properties reflect current and antecedent moisture regimes in many important ways. Weathering, leaching, profile differentiation, and erosion are water-induced processes that greatly affect the agricultural potentialities of soils. The capacity of soils to store water for plant use is primarily a function of their porosity and depth. The affinity with which
soil moisture is held and the ease with which it moves through the unsaturated soil are both determined by the moisture content and texture of the soil. These properties largely determine the availability to plants of water in the rooting zone.

The nature and extent of root development are major factors governing plant responses to moisture conditions. Plants vary genetically in rooting characteristics, but also are highly responsive to the physical and chemical properties of the soil. Aeration, temperature, nutrient supply, and soil compaction strongly influence root growth. Insects, nematodes, and diseases often seriously reduce the extent and effectiveness of root systems, thereby altering plant responses to moisture conditions.

Water makes up 85 to 90 per cent of the fresh weight of actively growing plants, is an essential ingredient in many of the biochemical reactions, serves as a medium of transport within the plant, and by means of turgor pressure imparts mechanical strength to plant tissues. When the rate of transpiration exceeds the rate of water intake, plants develop internal water deficits, and characteristic metabolic changes and anatomical responses result. Cell enlargement, photosynthesis, respiration, transpiration, and biochemical composition are altered in plants subjected to water deficit. Water content, relative turgidity, diffusion-pressure deficit, and stomatal opening are measures that have been used to determine water deficit in plants.

Plants show large differences in drought tolerance. Such differences reflect the ability of the plant (1) to avoid internal water stress by effectively balancing water intake and water loss or (2) to adjust physiologically to such stress. Drought injury is believed to be caused by mechanical disruption of the protoplasm rather than by the loss of water per se.

Inadequate aeration is the principal explanation of crop response to excessive water. Plants that tolerate water-logged conditions have morphologic and physiologic adaptations enabling them to function in an anaerobic root environment. Roots of other plants cease growth and are unable to absorb water or nutrient ions in a normal manner in the absence of oxygen sufficient for aerobic respiration.

Crop responses to different soil moisture regimes have been extensively studied, but, because of the many interactions between the soil, plant, and climatic factors involved, few generalizations concerning field response have been established. Vegetative production is more responsive to moisture differences than is the production of reproductive parts or storage products. Crop yields are invariably reduced if the plant undergoes wilting for extended periods, the responses of certain crops being conditioned by the stage of growth at which the moisture deficiency
occurs. Some plants, particularly perennials growing on deep permeable soils, show no significant growth response to changes in soil moisture content between field capacity and the permanent-wilting percentage. By contrast, responses are expected with annual crops, crops having poorly developed root systems, and crops subjected to high transpiration demands. Under highly controlled conditions, various growth and metabolic processes have shown differential response to moisture differences throughout the range from field capacity to the permanent-wilting percentage.

A basic difficulty encountered in interpreting most experiments involving crop response to moisture conditions is the fact that the observed effects represent an integration, over the entire growth period and throughout the entire rooting volume, of a moisture condition that is variable in both time and space. The rate at which water moves through the soil-plant-atmosphere continuum, and short-term hysteresis effects in the soil adjacent to the absorbing root, are also believed to be important in explaining some of the differences observed in plant responses to soil moisture treatments.

The over-all efficiency of water use in crop production is low. In irrigated regions, low use efficiency reflects the water losses incurred in collection, storage, conveyance, and field application. Economic factors, administrative practices, and on-farm water-management methods, as well as soil and crop characteristics, have an influence on the efficiency with which water is used. In subhumid areas, surface evaporation and use by nonagricultural vegetation are the chief causes of low water-use efficiency. Such losses account for 70 to 80 per cent of the precipitation in fallow years, and perhaps 50 per cent in crop years. The central problem of such areas is to increase subsoil water storage at depths where it will be safe from evaporative loss.

The water-use efficiency of crops can be increased by breeding varieties the period of growth of which nearly coincides with the period of greatest precipitation or lowest potential evapotranspiration. Varieties or strains having more extensive rooting are more effective in meeting their water needs. Since water-use efficiency is normally improved by increasing acre yields, all breeding and management practices producing such increases indirectly lead to greater efficiency of water use. Breeding for specific morphologic or physiologic traits depends on establishing both the significance of such traits and the nature of their genetic dependence.

Runoff and erosion, although largely determined by soil, climatic, vegetative, and topographic factors, also respond to management practices. Maintaining high infiltration capacity and increasing the infiltr-
tion period are key objectives for the control of runoff and erosion. These are achieved by practices that increase the supply of readily decomposable organic matter, provide a protective canopy over the soil surface, and reduce the number of tillage operations, particularly during periods of high soil moisture. Grazing practices on rangeland, and forest-management practices in timbered areas, have important effects on both water yield and distribution of the runoff intensities of watersheds.

In conclusion it may be repeated that water, because of its unique properties, intimately affects nearly all of the physical and biological processes of plants and animals. The water that enters the soil, is absorbed by plant roots, and is returned to the atmosphere, has been the main focus of this review. This quantity, huge though it is for an area such as the United States, represents but a small component of the total hydrologic cycle, which encompasses both long- and short-term cycles, involving the interchange and movement of quantities of water and energy so enormous as to defy comprehension.

The supply of water and the demand for it imposed by vegetation vary widely, both geographically and seasonally. Acting as a reservoir, the soil serves to bring supply and demand into phase, and irrigation serves to correct both geographic and seasonal inequalities. In both cases, however, serious losses of water, due to evaporation, runoff to the sea, deep percolation, or use by nonagricultural vegetation, place strict limits on the efficiency with which present-day practices are able to effect a balance between water supply and crop demands.

To understand the complex behavior of plants under different water regimes and environmental conditions, it is essential to recognize the continuity and dynamics of water through the entire soil-plant-atmosphere system. Only confusion results from neglecting the complete system in attempting to explain the field behavior of plants. Proper consideration must be given not only to the intensity and capacity, but also to the rate factors of each of the component parts of the soil-plant-atmosphere system before useful generalizations concerning plant response to the hydrologic environment can be developed. Except for specific situations, it is unlikely that any meaningful and consistent relation can be developed between a particular soil moisture parameter and plant growth.

As the total fresh-water resources of the United States are more completely developed, agricultural use will face increasing competition from industrial and other uses that have a considerable economic advantage. In irrigated regions particularly, this represents an important long-range agricultural problem the solution of which will require a major increase in the over-all efficiency with which water is used in crop production. In
humid and subhumid regions, solving the problem will probably involve increasing the efficiency of natural precipitation through improved soil-moisture storage and utilization.

Long-range improvement of the competitive position of agriculture for water would seem to center on the two major areas of water supply— including collection, storage, distribution, application—and plant-use efficiency. In each area, more specific and quantitative information concerning the basic physical and biological processes is needed, together with the development of practical methods of modifying the phenomenon in the desired manner.

More specific examples of major research areas include: runoff and ground-water hydrology; the physics of, and methods for, modifying evaporation from water, soil, and plant surfaces; improvement of the water-intake and storage properties of soil; the dynamics of water in living plants; and the effects of water status on specific metabolic processes.

Since water is an active participant in all experiments involving growing plants, it is also important that greater attention be given to a more complete description of the moisture regime followed in all plant experiments. There usually are strong interactions between moisture and the treatments being studied. Therefore, the absence of relevant information on the moisture regime often prevents a full understanding of results.

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128 WATER AND ITS RELATION TO SOILS AND CROPS


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WATER AND ITS RELATION TO SOILS AND CROPS


WATER AND ITS RELATION TO SOILS AND CROPS
