Management of the Cotton Plant with Ethylene and Other Growth Regulators

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Reprinted from ADVANCES IN CHEMISTRY SERIES, No. 159
PLANT GROWTH REGULATORS
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The complexity and cost of production methods in cotton culture are increasing the need for and the feasibility of effective plant growth regulators to improve managerial control of the crop. Response goals include: (1) improved seedling vigor, (2) early flowering, (3) promotion of fruiting under conditions that favor excessive vegetative growth, (4) improved fruit set and translocation to fruit, (5) improved fiber and seed quality and yield, (6) early termination of flowering, and (7) improved harvest-aid systems. Current research centers on seedling vigor, plant height, flowering, fruit set, and early termination of flowering and growth. Manipulation of the ethylene physiology of plants can influence many responses, some of which are relevant to cotton production. Most other growth regulators and some plant hormones modify ethylene physiology, resulting both in problems and in opportunities to discover unique responses.

Cotton as a profitable crop is uniquely sensitive to competition from synthetic substitutes—the man-made fibers. For this and other reasons there is a particularly pressing need in the cotton production business for new ways to cut costs or to increase efficiency. Plant growth regulators may be a major avenue by which unit production costs can be reduced. It seems likely that systems for chemical manipulation of crop performance would be readily accepted by cotton producers.

Recent changes in crop production systems are increasing the feasibility of using chemical growth regulants. Cotton is experiencing many of these important changes. For example, the use of high-density populations of dwarf-type compact plants and the more conservative uses of
irrigation water and fertilizer will produce uniform plants in similar
growth stages with a compressed fruiting period. This condition is more
compatible with chemical management than an extended, indeterminate
fructing mode on large plants which results in a fruit load of variable
age and location. A shorter time interval from planting to harvest will
increase the need for uniform fruit maturity, efficient removal of leaves,
and effective regrowth control to facilitate mechanical harvesting.

This review is written from the position that both the potential for
successful development of growth regulator applications in cotton pro­
duction and the need for these applications have increased significantly
in recent years. The purpose is: (a) to analyze the types of responses
which would be beneficial, (b) to review recent studies, (c) to point
out the underlying importance of ethylene physiology to growth regu­
lator investigations, and (d) to present some potentials of ethylene as
an agricultural chemical. Ethylene physiology (1, 2, 3) and the manipu­
alation of ethylene as a strategy in agricultural production (4, 5) have
been reviewed recently in detail.

Desirable Plant Responses

How would the commercial producer manipulate the cotton plant
if he had his choice? An analysis of the possible responses and further
consideration of their potential value should aid in the development of
research objectives. That approach is used here.

Cotton is a tropical deciduous perennial from a Mediterranean
climate which is cultured as an annual. It is produced under divergent
environmental conditions which result in great differences in cultural
systems and management. For example, it is produced on dry land under
marginal levels of rainfall, in non-irrigated areas with usually abundant
rainfall (rainbelt), in areas with supplemental irrigation, and in arid
regions with complete irrigation. In addition, both conventional (40-in.)
and narrow (10-inch) row spacing and high and low plant densities are
now being used. The plant responses one would desire to control in a
certain culture system might be of little value in another. The following
analysis of the crop considers the major differences in how the crop
develops and how it is managed.

Seed Germination. Across the American cotton belt, cotton germi­
nates under environmental stresses such as low soil temperature, moisture
deficit or excess, oxygen deficits, and mineral extremes. Seed treatments
to increase tolerance to early season stresses would be very beneficial.
When large scale replanting depletes the best seed, lower quality seed
must be used. So any treatment which would improve the performance
of such seed, even under favorable environmental conditions, would be
valuable. In the future, plant breeders may select breeding lines for
those seed quality characteristics exclusively related to food value (resistance to weathering, etc.). If hard seed coat, physiological dormancy, or some other agronomically undesirable characteristic accompanied such genetic modification of the plant, it might be feasible to circumvent those characteristics chemically in planting seed. In doing so, one would be able to realize the benefits of increased food quality from that portion of the cottonseed which is processed.

During the seedling and early vegetative stage, cotton often is subjected to cold weather; being of tropical origin, the plant suffers chilling injury which has long term growth and flowering effects (6, 7). Presently there is interest in substances to prevent or circumvent chilling injury, and such could be useful to cotton producers.

Vegetative Development—Flower Initiation. In the past, an accepted strategy for improving cotton yields was to increase early fruit set. That is no longer a complete or adequately specific solution. This goal is being reached, in a sense, in the narrow row or high density planting systems (8, 9). Plant competition forces earlier flowering and although individual plants have fewer bolls, the total acre yield can be more. Further, there are some records of increased fruit set without increased yield (10, 11); thus, in some circumstances fruit load may not limit yield. There are, however, several processes of the cotton plant during the pre-fruiting period which might be manipulated in a beneficial way, depending upon the nature of the cultural system involved. A major need is to prevent excessive vegetative growth in situations of luxuriant moisture and fertility. Managers have learned to moisture stress cotton marginally in the desert-irrigated regions to shift from vegetative to reproductive growth, but the problem is not limited to those areas. A mild chemical stress agent would be very useful; it should favor reproductive over vegetative growth while possibly shortening and strengthening the main stem. Vigorous early growth and fruit set are drought- and disease-escape mechanisms in drier, non-irrigated areas; however, they are unachieved because high density planting is not feasible under strong moisture limitations. In such areas a chemical which would set more fruit earlier could reduce the frequency of crop failures.

Fruiting. Once flowering starts, it is generally recognized that the crop should be set as quickly as possible. A regulator to improve fruit set could be useful, for example, to offset the effect of stresses such as heat, moderate moisture lack, minor insect damage, and cloudy weather. On the other hand, a better goal might be for a regulator to hasten resumption of flowering and fruit setting after the relief of stress.

Fruit Growth. Perhaps the most obvious growth regulator goal in cotton culture is to discover a way to promote fiber production chemi-
cally. This might be accomplished by: (a) improving mobilization of photosynthate in order to promote the rate of fiber elongation and secondary cell wall deposition, (b) prolonging the duration of fiber development, or (c) promoting initiation of a greater number of fibers per seed. New information on the interplay between elongation and secondary cell wall growth (12, 13) and the hormonal regulation of fiber development in tissue culture (14, 15) may aid efforts to develop longer, stronger fibers in the boll. There is evidence suggesting that photosynthesis alone does not limit yield. Perhaps mobilization of photosynthate to the boll is the key; if so, inhibition of translocation to and storage of starch in the stem and roots might improve translocation as effectively as a direct promotion of the mobilizing strength of the fruit.

Possibly one of the most interesting and potentially beneficial concepts now being explored is early termination of flowering—once achieved genetically in the strongly determinate varieties. The practice comes to our attention at this time primarily because of insect problems; once the main crop is set, if further flowering could be terminated, substantial savings in insecticides and other costs could be realized. This system has been demonstrated to be economically sound and feasible in Arizona where termination can be initiated by withholding water (16, 17). It seems that neither the use of highly determinate varieties nor the withholding of irrigation water is a generally satisfactory early termination system. Basically, the objective is a chemical regulator which will quickly bring fruiting meristems into dormancy or inactivity while not impairing the plant’s ability to channel most of the available energy into the fruit already present.

Harvest. With defoliation or chemical desiccation almost a universal practice and with economical, effective materials in established markets, this would appear to be one phase of the crop which can be ignored. Such is not the case. One persistent problem is regrowth after defoliation when rain or other weather delays harvesting. A good regrowth inhibitor to go along with the basic harvest-aid chemical would be useful on large acreages. Use of arsenicals may not always be permitted on stripper-harvested cotton, and an acceptable substitute is not apparent. Additional acres are harvested by stripper harvesters each year, and high-density, narrow-row culture systems may accelerate this trend. The harvest phase of cotton production could benefit from some new products.

Research Areas

Seed Treatments. Several efforts to improve seed germination chemically have been made in recent years. The inhibition of lateral root development in cotton seedlings which can result from exposure to the
herbicide trifluralin have been relieved with IAA or kinetin (18). Soil-incorporated D-a-tocopherol or oleic acid and cottonseed oil also reduced trifluralin damage (19). Many workers have reported that multiple treatments of cotton seeds with insecticides and fungicides can produce detrimental interactions (20, 21, 22), and any substance which would prevent this type of pesticide damage could be a valuable component of a seed treatment package.

Chilling injury to Pima S-4 cotton seedlings during germination was reduced by preconditioning seed before planting with either water alone, aqueous GA, or cyclic AMP (23). Germination of cottonseed was inhibited by ABA; furthermore, ethephon, GAs, and kinetin all partially overcame the inhibition by ABA (24). No desirable result was recognized from soaking seeds in NAA prior to planting, and the highest concentrations tested reduced stands and delayed maturity (25). Gibberellic acid applied to cottonseeds promoted lipase activity. Presumably the endogenous gibberellins do the same (26). Aflatoxins inhibited germination and lipase activity (26).

Oil seeds, cotton, and peanuts, in particular, produce ethylene at rather high rates during and immediately following germination (27). High germinability and seedling vigor are correlated with high ethylene production during germination (27); however, there is as yet no published evidence that ethylene or ethephon will improve germination of cottonseeds.

Flowering, Fruit Set, and General Plant Development. Much of the current research on cotton involves applications of materials before initiation or during flowering to modify fruiting. One recognized problem is that the insecticide, methyl parathion, delays the maturity of cotton and reduces yields, at least under some environmental conditions, by raising the nodal position of the first fruiting branch (28, 29, 30). The delay can further complicate late season insect control problems and illustrates that there may be a potential for improvement in cotton by making the crop mature earlier. During extended, very favorable growing seasons, however, methyl parathion does not delay maturity and actually increases yields (31, 32, 33). Similar inconsistency can be expected in responses sought for beneficial results. Practices may be possible for specific areas and culture systems which will not be effective worldwide. On some sites, Pima S-4 cotton sets its first fruit too low for efficient mechanical picking, and lower flower buds could be removed with ethephon. The node level of the first fruit was raised about four nodes (34).

The problem of cotton "going vegetative" can result from high soil fertility, abundant moisture, loss of early flowers to insects, or combinations of these factors. The result is usually rank vegetative growth and low yields. Even if fruit set is acceptable, excessively tall cotton can
lodge, be subject to excess boll rot, and be difficult to harvest. Currently
there is interest in controlling height and vegetative growth. In cases
where little fruit set would occur without this practice, yield would
hopefully be increased. However, in other cases where average yields
would occur, it might be acceptable if the regulator simply reduces
height and does not lower yields. The growth retardants, CCC (2-
chloroethyltrimethylammonium chloride) and CMH (N-dimethyl-N-\(\beta\-
chloroethylhydrazonium chloride), were used on Acala cultivars in Israel
and reduced that height growth which occurred after application as much
as 50% without reducing yield (35). Applications were made during the
first week of flowering, and the results were improvements over earlier
efforts cited by the authors. African Upland variety SATU 65 in Uganda
responded to CCC with a reduction in both yield and height (36). Growth inhibitors BAS 0660W (dimethylmorpholinum chloride) and
BAS 0640W (dimethyl-N-(\(\beta\)-chloroethyl)hydronium chloride) effectively
reduced plant height and increased earliness and ginning percentage
without damaging fiber quality, but the effect was less on irrigated than
on rain-grown cotton (37). The most serious lodging problem occurs
with the irrigated cotton (37).

One of the early efforts to limit height of the cotton plant with CCC
was in Mississippi where undesirable yield reductions occurred (38);
however, in recent experiments, Thomas was able to reduce height 16 in.
with CCC without a significant reduction in yield (39). Unsuccessful
efforts have been made to modify cotton yield with sub-lethal applications
of simazine (S-triazine) and terbacil (3-tert-butyl-5-chloro-6-methylura-
cil) (40). Freytag and Wendt (41) found that soil-injected ethylene
increased yields of cotton in some but not all moisture-tension regimes.
Reduced height was obtained with TIBA (2,3,5-triiodobenzoic acid),
but it lowered the yield (42).

Some effects of growth regulators on fiber properties have been
studied. An increased yield of one Indian cotton, MCU-1, was achieved
with CCC, but it had no effect or reduced yields of three other varieties
(43). Some abnormal bolls were produced, and the lint from these bolls
was coarser and stronger. Bhatt et al. (44) studied the effects of several
growth regulators on fiber quality in India. NAA increased fiber fineness
at a low concentration and had the reverse effect at higher ones. IAA
improved length slightly and improved fineness. SADH (1,1-dimethyl-
aminoureaic acid) increased length and Phosfon (2,4-dichlorobenzyl-
tributylphosphonium chloride) increased fineness. At a lower concen-
tration, tested CCC increased fiber coarseness, but higher concentrations
increased length and fineness while decreasing strength, maturity, and
yield. Gibberellic acid applied to the Indian variety PRS-72 did not
reduce seed cotton yield but increased fiber length significantly (45).
On Laxmi cotton in India, GA₄ did not increase fiber length or change other fiber characteristics (46). Studies on natural growth substances on cotton fibers suggest that there may be specific fiber elongation hormones (47), and thus, failure to achieve a major, consistent improvement in fiber properties to date may simply be the result of the failure to test the right compound. For that reason, the potential for chemically improving fiber length should not be ignored.

Early Termination. Work is underway to develop a system for chemical termination of flowering. Thomas (39) applied CCC and DPX-1840 [3,3a-dihydro-2-(p-methoxyphenyl)-8H-pyrazolo[5,1-a]isoindol-8-one] in order to retard late season flowering and found the latter material more effective. Additional studies revealed that DPX-1840 was readily absorbed and translocated to stem tips where it eventually retarded growth without serious effects on flower or boll development (48). In Arizona, studies were undertaken to reduce food (cotton flower buds) for the pink bollworm larvae and thus reduce the population going into diapause (49). Results indicated that 2,4-D (2,4-dichlorophenoxyacetic acid), CCC, chlorflurenol (methyl-2-chloro-9-hydroxyfluorene-9-carboxylate), Pennwalt TD 1123 (3,4-dichlorothiazole), and Basf 0860 (N-dimethylmorpholine chloride) showed promise. Ethephon, DPX-1840, cecodylic acid (hydroxydimethylarsine oxide), Sustar 2-S MM [3′-(trifluoromethylysulfonyamido)-p-acetotoluidide], and Dalapon were not promising. Treatments which reduced green bolls remaining at harvest also reduced the number of pink bollworm larvae. This work was extended in 1974 with several mixtures of the above compounds acting very effectively; the most effective termination treatments reduced larvae 93–97% with less than 5% yield reduction (50). Although 2,4-D is apparently the most effective compound tested, its translocation into seed and very high damage potential on seedlings makes its use questionable. Thus, additional work is needed to perfect an acceptable early termination system.

Defoliation. Interest in defoliation has been low in recent years. One relatively new development is the "wiltant" which is applied only shortly before harvest (51). As an outgrowth of some basic studies, several auxin transport inhibitors, TIBA, DPX-1840, Alsanap (N-1-naphthylphthalamic acid), and morphactins (2-chloro-9-hydroxyfluorene-9-carboxylic acid), were shown to promote ethylene- and ethephon-mediated leaf abscission (52, 53). Subsequently, GA₄ was found to be even more active in promotion of ethylene-induced abscission (54). It now appears that the GA₄ counteracts the inhibitory effect of auxin on ethylene-induced leaf abscission (55); thus, GA₄ might improve the performance of any defoliant that achieves part of its action by stimulating stress-induced ethylene production and lowering the natural auxin content of the dam-
aged leaves. From a slightly different approach, Sterrett et al. (56) have shown a synergistic effect of ethephon and the defoliant endothall (7-oxabicyclo[2.2.1]heptane-2,3-dicarboxylic acid) at levels at which neither is effective alone. Field work is currently underway to condition cotton for defoliation (57). Miller (58) has devised a new technique for improving the efficiency of desiccants which involves application to the stem so that the chemical enters the transpiration stream and moves internally to the leaf.

Ethylene-Ethephon: Potential in Growth Regulation

In recent years ethylene has enjoyed a rather glamorous state among the plant hormones. It has been considered in a relative flood of papers and has been implicated in a wide array of plant processes. Ethylene is also enjoying a growing status as a practical plant growth regulator. This probably stems from three major reasons: (a) ethylene has relatively minor residue problems, (b) ethylene is involved in many naturally regulated plant processes, and (c) the number of options for regulating ethylene physiology is large and increasing (4, 5).

Ethylene promotes a large array of responses in seeds, plants, and fruits (Table I), some similar to and some dissimilar to effects of auxins. Those with actual or potential commercial application include: (a) growth promotion of seedlings (rice), (b) inhibition of height growth, (c) root initiation, (d) chlorophyll destruction (citrus), (e) flower initiation (pineapple, bromeliads), (f) stimulation of fruit growth (figs),

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(g) fruit ripening and loosening, (h) promotion of storage material hydrolysis, (i) promotion of secretion (rubber), (j) leaf, fruit, and flower abscission, (k) release of lateral buds from apical dominance, and (l) release of seed and bud dormancy. The potential is limited because some effects are known in only isolated species noted in parentheses above. Also, desirable and undesirable responses may occur simultaneously. On the other hand, much work with ethylene has been done with high concentrations or long durations which may have obscured desirable responses. A range of ideas has been considered relative to the use of ethylene in cotton, including; (a) improving seedling vigor, (b) enhancing early-season branching and flowering, (c) termination of flowering, (d) defoliation and (e) boll opening (4). None of these uses has been achieved on a commercial scale.

Ethylene physiology of the plant can be manipulated in a variety of ways. In the past, the use of ethylene was limited to exposure of plants to the gas in containers; thus, field applications were impractical. This limitation was removed by the discovery and commercial development of ethephon in which the liquid active ingredient, 2-chloroethyl phosphonic acid, is converted to ethylene by the plant (59). Other means of modifying ethylene physiology have been recognized and discussed (4, 5).

It is possible to stimulate ethylene synthesis with auxins (60, 61, 62, 63), abscisic acid (64), defoliants (65), ascorbic acid (66), cycloheximide (66), and iron salts (66), among other compounds. A number of physical, environmental, microbial, and insect stresses increase ethylene synthesis, including moisture stress (67) and air pollutants (68).

In some cases it might be desirable to inhibit ethylene synthesis chemically to prevent responses mediated by naturally produced ethylene or stress-produced ethylene. Although some substances do inhibit ethylene production modestly—e.g. TIBA (69)—no outstanding regulator of this nature has been discovered. Another possibility is to promote or inhibit ethylene action. Promotion can be accomplished by auxin transport inhibitors and GA in cases where auxins and ethylene have opposite effects (52, 53, 54, 55). Recently, silver ion was found to be a potent inhibitor of ethylene action (70). Ethylene action also can be inhibited by lowering the temperature and O₂ level or increasing the CO₂ level (2). These manipulations are not usually practical in the field. An effective inhibitor of ethylene action might be a useful growth regulator. Removal of ethylene significantly delays natural ethylene responses such as fruit ripening (71), but the procedure requires putting the plant or fruit in a container in which a partial vacuum can be sustained. It is thus only applicable to harvested fruit and vegetables, potted plants, and similar items.
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Ethylene Physiology in All Growth Regulator Applications

Since many growth regulators modify ethylene synthesis and responses to ethylene (2, 72), including many of the substances listed in the previous section, it is possible that some failures to achieve desired responses in past studies could have been the result of secondary effects on the ethylene physiology of the plant. Some of these problems might be alleviated when their causes are recognized. It seems desirable, then, to know how new growth regulators modify ethylene physiology in cotton prior to field testing. Stress effects on hormone physiology also need more attention in the future. Some of the inconsistency of the effects of several growth regulators on fruit set, for example, may result from differences in environmental stresses immediately before or at the time of the treatment.

The attention focused on ethylene physiology in this section has another message. Perhaps this is a case where basic understanding of hormonal-environmental interactions can contribute, in the long run, to improved agricultural practices. While there is still no way to custom design a regulator to do a certain job, we are learning more about the secondary effects and interactions which must be considered. Ethylene, both ubiquitously present and uniquely phytoactive, seems to be critical to many goals of growth regulator technology.

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