Managing Cotton Growth and Development with Plant Growth Regulators

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ABSTRACT

Cotton is a perennial with an indeterminate growth habit and is very responsive to changes in environment and management. Plant growth regulators (PGRs) have been used to control growth and enhance yields. Plant growth regulators are organic compounds, other than nutrients that affect physiological processes of plants when applied in small concentrations. These compounds represent diverse chemistries and modes of action and provide numerous possibilities for altering crop growth and development. There is, however, a lack of published research on their use and mode of action in cotton. Their time of use extends from early season when they are applied in-furrow or as seed treatments at planting, to mid-season foliar applications and late in the season, preparing the crop for harvest. Overall benefits from PGR use in cotton include control of vegetative growth, yield enhancement, improved fiber quality and greater ease of harvest. More specific responses include alteration of carbon partitioning, greater root: shoot ratios, enhanced photosynthesis, altered nutrient uptake, improved water status and altered crop canopy shape. These responses are a reflection of the interaction of heritable characteristics, cultural inputs and environment. Because of this complex interaction, crop response to PGRs is not always predictable. Plant mapping techniques have been developed to monitor the crop growth and development, with specific emphasis on fruiting rates, fruit retention and distribution of fruit relative to PGR treatment. Increased boll retention at the early fruiting sites enhances crop maturity, allowing quicker harvest and improved lint quality. Strategies for using PGRs in cotton production include numerous options for beneficially modifying crop response to improve yield and crop management. Research has shown that PGRs can play a role in remedial management of stressed cotton. This may prove to be a valuable future management tool.

Introduction

Cotton (Gossypium hirsutum L.) is reputed to have the most complex growth habit of all major row crops (Mauney, 1985). Furthermore, the cotton crop is very responsive to changes in the environment and management, making it difficult to manage crop growth within a single season for optimum growth, seedcotton yield and fiber quality. This has led to interest in chemical plant growth regulators (PGRs) to manipulate and control plant growth, while maximizing yield potential. This review provides a summary of the uses of PGRs in cotton production and makes use of previous reviews by the authors (Cothren and Oosterhuis, 1993; Cothren, 1995).

In the last two decades many new compounds have been developed and used on cotton, often however, with variable and sometimes disappointing results. Part of the reason for this has been the extremely varied environments and crop conditions under which PGRs are used and also partly to the lack of understanding of the nature and performance of these chemical compounds (Oosterhuis, 1995). Furthermore, there are numerous inferior or inappropriate compounds being imposed on the agricultural community without any accompanying research data, or insufficient studies, to adequately support use of the chemical in crop production. In general, the biggest criticism of PGRs, particularly those aimed at yield enhancement, is that they have generally had inconsistent effects on growth and yield.

There have been many field evaluations of commercially available PGRs for their effect on the growth and yield of cotton (e.g. Thomas, 1972; Urwiler et al., 1988; Oosterhuis et al., 1995; Millhollin and Waters, 1997). However, the results of all these studies have usually been inconclusive and inconsistent. The consequence has been that most of these compounds have not been widely used or accepted by farmers. Numerous studies have been conducted on the optimal timing of PGRs, particularly with mepiquat chloride, including single applications, split applications and multiple low dose applications. Recently there have been some innovative suggestions about how to improve mepiquat chloride timing (Constable, 1995; Edmisten, 1995; Landivar et al., 1996) that will be discussed later. Unfortunately, there have been relatively few studies on the physiological effects and underlying mechanism of the more promising PGRs (Cadena et al., 1994; Oosterhuis,
1996). There have been some in depth studies on a few PGRs such as mepiquat chloride (Cothren et al., 1977; Gausman et al., 1978, 1979; Zhao and Oosterhuis, 2000) and PGR-IV (Oosterhuis, 1995). This type of information is necessary for improved use of the PGR concerned and results in more consistent and predictable results.

More recently there have been a number of innovative uses of PGRs proposed, such as for enhancement of nutrient uptake (Guo et al., 1994), improving drought tolerance (Zhao and Oosterhuis, 1997), improving carbohydrate status (Zhao and Oosterhuis, 2000), increasing photosynthesis (Cadena et al., 1994; Nepumoceno et al., 1997), increasing partitioning to the fruit (Zhao and Oosterhuis, 2000), late season applications for yield increases and earlier maturity (Cothren et al., 1996) and combinations with foliar fertilizers (Oosterhuis et al., 1992).

### Definition of Plant Hormones

#### Plant Hormones and Plant Growth Regulators

Plant hormones or phytohormones are organic compounds, other than nutrients that affect physiological processes of plants when applied in small concentrations. Plant hormones are often referred to in more popular terminology as plant growth regulators (PGRs) because of their role in agriculture. These compounds represent diverse chemistries and modes of action and provide numerous possibilities for altering crop growth and development. Some PGRs are plant hormones or their analogues, others are simply metabolic regulators. Since most plant growth and development processes are regulated by natural plant hormones, it is necessary to define the nature and role of plant hormones. The complexity and multiplicity of the known plant regulatory activities of plant hormones and their roles in plant growth and development was summarized in tabular form by Cothren (1995). The activities of the individual categories of hormones have been summarized by Cothren (1995) and in more detail by Davies (1995) and Arteca (1996) and will not be detailed in this review.

There are five major classes of phytohormones but recently, two additional groups of compounds, the Brassinoids and the Salicylates and possibly a third group, the Jasmonates, have been added to this list. A developmental process is ultimately controlled by the ratio of the promoter to inhibitor hormones. Furthermore, the regulatory activity of all five hormones are involved in many processes such as growth rate, flower initiation, abscission and senescence (Davies, 1995). The lack of an indication for the involvement of the hormone in a particular process may not be absolute but rather indicates that the hormone has not been positively identified with the process at present (Leopold, 1987).

**Auxins:** Auxins stimulate cell elongation and cause wall loosening, a term describing the more rapidly extensible or plastic nature of walls from cells treated with auxins (Salisbury and Ross, 1992). At least three mechanisms have been considered in the last 30 years to explain wall loosening. The most popular of these mechanisms, the acid-growth hypothesis, was treated in a review of wall loosening by Ray (1987). The hypothesis proposes that auxins cause receptor cells in stem sections to secrete H+ into their surrounding primary walls. These H+ ions result in a lowering of the pH so that wall loosening and fast growth occur. The low pH presumably allows certain cell wall-degrading enzymes that are inactive at a higher pH to function. Cell wall-degrading enzymes purportedly break bonds in wall polysaccharides, allowing the walls to stretch more easily. At the cellular level, auxin effects include increases in the nucleotides DNA and RNA and subsequent involvement in protein and enzyme synthesis; increases in proton exchange, membrane charge, and potassium uptake (Marre, 1977); and rapid changes in gene activity (Guilfoyle, 1986; Key, 1989).

**Gibberellins:** Since 1990, 84 gibberellins had been discovered in various fungi and plants (reviewed by Takahashi et al., 1990). Gibberellins exhibit many physiological effects, suggesting that they have more than one primary site of action. They stimulate cell division in the shoot apex (Liu and Loy, 1976), promote cell growth by inducing various hydrolyases (Noggle and Fritz, 1983) and often increase cell wall plasticity (Taylor and Cosgrove, 1989). Additionally, gibberellins are known for their effects on stimulation of internode growth, promotion of seed germination and their ability to increase leaf size of a number of different plant species.

**Cytokinins:** Cytokinins is a generic name for substances that typically stimulate cell division (cytokinesis). Several lines of evidence suggest cytokinins may have a role in nucleic acid metabolism and protein synthesis (Davies, 1995; Binns, 1994). Chemically, they are related to adenine, a purine base found in both DNA and RNA. Cytokinins have been isolated from meristematically active plant parts where vigorous nucleic acid and protein synthesis occurs. Application of cytokinins inhibits chlorophyll breakdown and thereby delays senescence (Richmond and Lang, 1957). These authors discovered that kinetin, a cytokinin, retards the senescence of detached leaves of cocklebur (Xanthium). Spraying solutions of kinetin directly onto leaves caused only those areas to which the chemical was applied to remain green. Furthermore, the treated areas of yellowing leaves actually became greener (Mothes and Englebrecht, 1961). Cytokinins also participate in the orderly development of embryos during seed development.

**Abscisic acid:** Abscisic acid (ABA) was isolated from cotton fruits in the early 1960s but was first identified and chemically characterized in 1963 by Addicott and...
his co-workers who were studying compounds responsible for abscission of cotton fruits (Ohkuma et al., 1963). It retards cell elongation, induces abscission, accumulates under stress (Wright and Hiron, 1972) and induces stomatal closure (Horton, 1971). ABA is also thought to be the main signal from roots to shoots concerning water shortages (Davis et al., 1994).

Jasmonates: Jasmonic acid, recognized for its growth inhibitory activity, has been shown to be widespread in the plant kingdom (Sembdner and Parthier, 1993). Bellrano et al. (1998) reported a hastening of leaf senescence in wheat. Renewed interest has focused on its ability to increase expression of specific plant genes, some of which occur in response to wounding (Hopkins, 1999). Jasmonic methyl ester was first isolated from Jasminum grandiflorum (Demole et al., 1962).

**Major Uses of PGRs in Cotton**

Although there are countless uses of PGRs in plant growth, the major roles in cotton were summarized by Cothren (1995) to include:

- Improved seed germination and emergence
- Enhanced seedling development
- Control of vegetative growth and improved canopy morphology
- Early flower production and increased fruit retention
- Improved fruit growth
- Improved leaf and canopy photosynthesis
- Improved partitioning between vegetative and reproductive growth
- Altered nutrient uptake
- Ethylene and fruit growth
- Crop termination and harvest aids
- Earlier maturity
- Environmental stress
- Enhanced yields

It should be remembered, however, that there is often more than one PGR involved in a particular growth process (Leopold, 1987), making research on that process complex and the results difficult to interpret.

**Application of PGRs to Cotton to Regulate Growth and Development**

The use of exogenously applied compounds to regulate cotton growth and development has previously been reviewed by Walhood and Addicott (1968), Namken and Gausman (1978), Cathey (1983), Guinn (1984), Cathey and Thomas (1986), Guinn (1986), Cothren and Oosterhuis (1993) and Cothren (1995). Cothren (1995) published a list updated from Cathey (1983) to illustrate the broad array of uses and times of application for PGRs. The following provides a discussion of the uses of PGRs in cotton production management. The information on harvest aids is limited to PGRs used as crop terminators, pre-conditioners and boll openers, with little coverage of defoliants and desiccants.

**Rate and Timing of PGRs**

Use of PGRs begins at the time of planting and continues through harvest. Timeliness of application, correct rates, and interaction with cultural inputs have a significant impact on the crop response and the potential for successful PGR use. There have been numerous reports of rates and timing of PGRs, particularly for mepiquat chloride. The rates vary depending on the cultural conditions and geographical location but overall there appears to be a small range over which a particular chemical works best. For example mepiquat chloride is usually applied at a low rate of 292-430 g/ha at first square and this rate steadily.
increases as plant height and growth progresses into flowering (Kerby, 1985; Landivar et al., 1992). PGR-IV is usually applied at 73-146 g/ha at planting, and 292 g/ha at pinhead square (PHS) or at first flower (Oosterhuis, 1995). A list of typical timing and rates used with some of the PGRs commercially available in the USA is given in Table 1.

The optimum timing of PGRs has proved to be much more difficult to determine. This is because the optimum timing varies with the condition of the crop and desired plant response of the PGR being used. This is particularly so with PGRs used to enhance a particular growth attribute. With a growth retardant such as mepiquat chloride, it has proved much easier to time the chemical for growth suppression. This has often been determined based on the plant height and more recently on the ratio of plant height to the number of main-stem nodes. If this ratio is greater than a certain predetermined maximum, e.g. 5 cm, then mepiquat chloride is applied. Recently, a modified ruler, the MPERT stick, was introduced (Landivar et al., 1996) to help determine when to apply mepiquat chloride. The MPERT stick is about 30 cm long and marked in green (0 to 10 cm), yellow (11-20 cm) and green (20 to 30 cm). The MPERT stick is placed in the axil of the sixth main-stem branch (petiole) and the position of the plant terminal against the MPERT stick determined. If the plant terminal is in the red area of the stick then no mepiquat chloride is required, whereas in the green area of the stick, mepiquat chloride is required. The yellow area is a warning of caution and a judgement call is needed based on the size and vigour of the cotton crop. The rate can be determined from a chart, calculated on theoretical mepiquat chloride concentrations needed in the plant in relation to total plant height and main-stem nodes (Landivar et al., 1996).

Constable (1995) introduced a sensitive method of scheduling mepiquat chloride based on the rate of change of the selected petiole length between two sampling dates. Johnson and Edmisten (1995) reported an innovative method based on running a large wick, set a desired height and soaked in mepiquat chloride, across a cotton field so as to only retard the taller, more vigorous plants. More recently, Edmisten (1995) based mepiquat chloride application on a plant monitoring point system.

**Methods of Application**

There are basically two methods of applying PGRs to cotton; foliar applications or applications made to the seed. Foliar sprays can be made by a variety of means including by aircraft, by tractor mounted or self-propelled motorized sprayers or by portable backpack sprays, depending on the acreage and nature of the production system. Seed treatments can be made in the hopper box or added to the seed prior to planting. Usually, however, a carrier of some sort is needed such as clay, talc powder or graphite to help the PGR adhere to the seed. A related method that has been used in the USA is to apply the PGR in the furrow with the seed at planting. Research has shown that seed treatment with PGRs may be superior to in-furrow planting PGR applications (Oosterhuis, 1996).

**Uses of PGRs in Cotton Production**

PGRs are widely used in cotton production for a variety of purposes. The following is a list of some of the more widely used purposes that have shown benefits to cotton growth or seedcotton yields.

**Germination and Emergence**

An important factor in producing a high yielding cotton crop is the establishment of a uniform and vigorous stand early in the season. However, cotton is often planted into cool, wet soils, such as occurs in the Mississippi River Delta that create unfavourable conditions for stand establishment and seedling growth. PGRs, in addition to fungicides and insecticides, offer an opportunity for enhancing early-season plant development.

The cotton plant is sensitive to chilling, and is adversely affected by low temperature at the early stages of growth. Because cotton is sensitive to chilling injury during germination, compounds that lead to improved seed germination and seedling vigour could contribute significantly to increased yield. Chilling temperatures during initial hydration of cotton seed can be extremely damaging. Chilling for as little as four hours at the onset of hydration can kill all seeds or can cause high incidence of aborted root tips (i.e. nub root); little injury occurs, however, if seed are hydrated to 12-13% moisture (Christiansen, 1967). Once the radicle has elongated 2-3 cm, chilling causes cortex sloughing, slowing of early growth and long-term growth reduction and flowering delay (Christiansen and Thomas, 1969). Broadening the base of adaptability to chilling injury with PGRs could enhance the yield potential. Although total yield may not be significantly influenced by chilling, the value of the crop is significantly reduced because of lower fiber quality (Christiansen and Thomas, 1969). Wanjura et al. (1996) correlated speed of cotton emergence and productivity; thus, rapid plant emergence and crop vigour are important factors in predicting crop yield. Not only is it important to generate adequate aboveground growth, establishment of a healthy root system for nutrient and water uptake is equally important.

Seed treatments have proved to be a successful means of applying PGRs in cotton production. However, the results have not always shown consistent benefits. Usually, an initial benefit can be shown in increased height and root development of seedlings but this has often not translated into yield increases at the end of the season (Egilla and Oosterhuis, 1996; Oosterhuis et al., 1996).
Although mepiquat chloride is not labelled as a seed treatment, it is capable of inducing physiological changes in the seed (Urwiler, 1981; Albers and Cothren, 1981; Zhang et al., 1990). Germination tests at a sub-optimal temperature regime (15°C) indicated that membrane permeability was influenced (less leaky) by mepiquat chloride treatment (Albers and Cothren, 1981). These authors showed that after cotton seed were germinated for 96 hours in germination paper at 15°C, mepiquat chloride-treated seed showed a significant increase (p= 0.10) in the number of germinating seed (radicle length >1 cm). Germination tests under simulated crusting conditions with high and low quality seed, selected by leachate screening tests, indicated that crusted emergence of cotton could be at least partially predicted by leachate analysis (Albers and Cothren, 1983). Mepiquat chloride treatment of the same seed enhanced emergence displacement for the treated seedlings when compared with untreated seedlings under controlled environments. In this study, chilling injury was lessened by mepiquat chloride seed treatment for only the more sensitive cultivars from the “unhardened” location.

Seedling Development

Cotton is notorious for slow seedling growth. Research has shown that seedling growth and development can be significantly enhanced by application of PGRs to the seed (Oosterhuis et al., 1996) or the foliage (Oosterhuis, 1996). The potential for enhancing seedling establishment exists in a number of commercially available chemical compounds, such as PGR-IV, ASA and Asset, but results have been very variable (Egilla and Oosterhuis, 1996). Recently, Becker et al. (1998) evaluated the effect of Arise, Cytoplex, Early Harvest, Maxon, PGR-IV, mepiquat chloride, Ryzup, Stimulate and Triggr on early season growth and found no significant stand improvement, root growth enhancement, or yield increase from any of the compounds tested.

Earlier, Urwiler and Oosterhuis (1986) showed that both indole butyric acid (IBA) alone, and mepiquat chloride plus IBA, stimulated early seedling root growth, whereas mepiquat chloride alone did not. It has also been shown that PGR-IV (Microflo Company, Memphis, TN) applied with the seed in-furrow at planting increased root length (+47%), total number of lateral roots (+23%) and root dry weight (+20%) (Oosterhuis and Zhao, 1994). In a subsequent study, seed treatment with PGR-IV was also shown to increase root growth (Oosterhuis et al., 1996). The use of PGR-IV as a seed treatment was shown to be superior to applications made in-furrow with the seed at planting (Oosterhuis, 1995). For example, in a growth chamber study using pots of sand, the average plant dry matter was increased 37% from seed treatment with PGR-IV at 8 oz/100 lb. seed, and 24% from in-furrow application at 2 oz/A, compared to the untreated control. Similarly, root length was increased 36% from seed treatment and 28% from in-furrow application, compared to the untreated control. Zhang et al. (1990) evaluated the effect of mepiquat chloride on early plant growth of cotton when seeds were treated with 0, 0.02, and 2.0 g a.i./ha. All treatments significantly decreased the number of nodes, leaves and squares, as well as the dry weight of leaves, stems and roots when compared with control plants at 28 days after emergence. Plant height and total leaf area of mepiquat chloride seed treatments were also significantly reduced compared with controls.

Asset (Helena Chemical Company, Memphis, TN) that is sold as a fertilizer additive with growth promoting properties, was reported to increased emergence and early seedling growth of cotton in growth-room studies at 144 ml/ha (Oosterhuis et al., 1996). However, subsequent field research failed to show a consistent significant effect on final yield (Robertson, 1999). Asset has proved more effective as an in-furrow application than as a seed treatment (Oosterhuis et al., 1996) possibly because it is more of a soil additive than a true PGR.

Control of Vegetative Growth and Improved Canopy Morphology

Plant growth regulators have been used successfully to reduce height, resulting in more desirable height-to-node ratios (Landivar et al., 1996), to reduce excessive leaf area (Walter et al., 1980; Stuart et al., 1984) and to alter partitioning of assimilates (Fernandez et al., 1991; Oosterhuis and Zhao, 1998). However, undesirable vegetative to reproductive ratios are often encountered due to excess nitrogen or insect induced fruit shedding. Under these circumstances, PGRs have been used with equal success in bringing about the same desired results. Typical plant growth retardants used in cotton include, mepiquat chloride, cycocel and Pox Plus (Table 1).

Mepiquat chloride has been widely used and tested for over two decades in the U.S. Cotton Belt to control excessive vegetative growth (e.g. McCarty and Hedin, 1994) with the restriction in vegetative growth usually resulting in improved partitioning to the reproductive component (Kerby, 1985; York, 1983). Its action has been determined as an anti-gibberellin by inhibiting two consecutive enzymes in the gibberellic acid biosynthetic pathway (Carlson, 1987). Through this mode of action, mepiquat chloride inhibits internode lengthening, causing shorter and more compact plants and reduced leaf expansion (Fernandez et al., 1992). A yield increase has often been associated with the changed plant structure and early fruit retention. Oosterhuis et al. (1991) reviewed data from 10 year’s of research with mepiquat chloride in Arkansas and showed that plant height was significantly reduced 100% of the time, earlier maturity was achieved 50% of the time, with an associated significant yield increase 25% of the time. Cycocel (chlomequat chloride or CCC) is used mainly to reduce height and lodging in cereals (Predko and Shapoval, 1978).
although the advent of short stunted cultivars has curbed its use. Cyoccel has been used in cotton (Oosterhuis, 1976) and is still used in many cotton producing countries (De Silva, 1971). However, in comparative tests, it has not proved as efficient as mepiquat chloride in controlling plant height and may have a negative yield effect (Oosterhuis and Zhao, 1998). Pix Plus, formerly MepPlus, (BASF Corp., Research Triangle Park, NC, USA), a new PGR incorporating Bacillus cereus with mepiquat chloride, has performed comparably to mepiquat chloride in reducing height, leaf area and stem dry matter, with a modest yield advantage (Parvin and Atkins, 1997; Zhao and Oosterhuis, 2000).

Increases in cotton yield have been primarily through changes in partitioning of dry matter from vegetative to reproductive structures. Generally, plant breeders have made considerable progress in improving partitioning in plants between vegetative and reproductive structures for a more efficient and higher yielding plant (Duncan et al., 1978). A comparison of five obsolete cotton cultivars with 20 more modern cultivars showed greater investment of dry matter into reproductive rather than vegetative structures by the modern cultivars that averaged 24% more lint (Meredith and Wells, 1989). These authors pointed out that the question confronting cotton breeders is whether further yield increases can be made through reproductive partitioning. Although their study suggested that yield increases through the use of conventional breeding methods were likely to be achieved through continued partitioning of dry matter from vegetative to reproductive structures, they did question the limits of this potential. They indicated that at some point, further reductions in leaves and stems will not result in improved yields, and that when this occurs, yield increases would need to be obtained only through some other source of variation, such as photosynthesis. Use of mepiquat chloride in cotton has been shown to alter partitioning of assimilates (Fernandez et al., 1991). Recently, Zhao and Oosterhuis (2000) showed that Pix Plus partitioned a greater percentage of total dry matter. Obviously, PGRs can also be expected to play a role in improved partitioning to reproductive sinks.

There are no detailed reports of PGRs changing partitioning within the cotton boll, i.e. between cellulose and oil. This would provide a useful management tool for improved utilization of assimilates and increased efficiency.

**Early Flower Production and Increased Fruit retention**

Historically, many PGRs have been tested in an attempt to increase flower production and particularly to decrease fruit abscission (e.g. Murty et al., 1976), with limited success. This was partly due to the complexity of these processes and the role of the environment in modifying them. Early flower production and increased fruit retention have become increasingly important with the acceptance of faster fruiting cultivars. With a narrower production window, less time exists for recuperation from any fruit loss, whether this is from environmental, cultural, or pest causes. Since a large percentage (66-75%) of the yield is produced on first position fruiting sites (Jenkins et al., 1990), retention and maturation of these bolls is critical. Increased boll retention at the early fruiting sites enhances crop maturity, allowing quicker harvest and improved lint quality. Growth retardants such as mepiquat chloride have been shown to retain more early fruit (Kerby, 1985), leading to earlier maturity.

**Ethylene and Fruiting Modification**

In cotton, ethephon has been used to raise the node level of the first flower in Pima cotton to a higher position, thus potentially increasing the efficiency of mechanical harvesting (Pinkas, 1972). Recently, interest has also been directed toward early-season application of ethephon in cotton to induce early fruiting square loss (Pettigrew et al., 1993). This has been suggested as a way of depriving overwintering insects of a food source and possibly delaying the development of certain insect infestations (Bariola et al., 1988; Henneberry et al., 1988). An additional reason for examining early fruit removal is that cotton has been shown to compensate for the loss of early squares by increasing the subsequent rate of square initiation (Kletter and Wallach, 1982; Kennedy et al., 1986; Ungar et al., 1987). Holman (1996) reported that cotton could compensate for up to 19% square removal (by insects) after which there was a yield decrease. Sheng et al. (1988) suggested that the increased rate of square initiation permitted cotton to overcompensate for early-season square abscission induced by ethephon application and sometimes produce greater yields. However, this is not always the case. Yield results with early square removal have been variable with responses depending on the year or the degree of fruit removal (Kletter and Wallach, 1982; Ungar et al., 1987). Pettigrew et al. (1992) concluded that early square removal should not be used in current production practices. It is generally accepted that early-season square removal, despite enhanced subsequent square initiation, will result in later crop maturity that could be critical in short-season locations such as the Mississippi river delta.

**Yield Response**

Mepiquat chloride has been shown to increase yields (Erwin et al., 1979a), to increase yield in some tests while decreasing yields in others (Armstrong, 1982; York, 1983a, 1983b), to have little effect on yield (Heilman, 1981; Stuart et al., 1984) or to reduce yield (Thomas, 1975; Crawford, 1981). In Arkansas, yield was significantly increased 50% of the time when mepiquat chloride was used (Oosterhuis et al., 1991). Results from 35 experiments conducted over a five-year period in the San Joaquin Valley of California
indicated that yield responses occurred only when control plant heights exceeded 1.10 m at maturity, or when the length of the growing season was short (Kerby, 1985). Plant mapping from eleven experiments conducted from 1981 to 1984 in the San Joaquin Valley of California showed that mepiquat chloride treatment produced 3.1% fewer fruiting positions than untreated plants (Kerby et al., 1986). However, it stimulated early boll load as number of bolls increased to a peak at nodes nine and ten, then declined continuously above node ten. This decrease in late season boll load was apparently due to increased abortion of fruiting forms rather than to a limited initiation of fruiting positions.

Numerous field tests have been conducted across the U.S. Cotton Belt comparing select PGRs for affect on yield. In Arkansas, replicated field comparisons of major commercially available PGRs have been conducted yearly since 1983 to compare existing PGR’s for effect on cotton yield (e.g. Urwiler et al., 1987; Oosterhuis and Janes, 1994; Oosterhuis and Zhao, 2000). Most of the PGRs tested have failed to significantly or consistently increase yields. Consequently, most of these compounds have not been recommended or widely used.

**Root Growth and Nutrient Uptake**

Increased yields and faster fruiting rates have also emphasized the need for enhanced nutrient uptake. Efforts to increase flowering and boll retention cannot be realized unless the plant has the ability to supply sufficient nutrients to these sinks to meet their demands. Increases in root:shoot ratios could potentially benefit the plant by providing a larger root mass to meet the needs of the aboveground biomass. Increasing the physiological activity of the root for nutrient uptake would also be beneficial. Total root length continues to increase as the plant develops until the maximum plant height is achieved as fruit begin to form (Taylor and Klepper, 1974). Root growth begins to decline as the developing boll load becomes the dominant sink and older roots die (Cappy, 1989). Synchronization of root activity with fruit production is critical for optimum productivity. Increased root activity during the later stages of boll filling is important for supplying needed minerals and water to the developing fruit, but prolonged activity can lead to serious problems with late-season vegetative growth near to, or following, defoliation, complicating leaf removal at harvest and introducing the potential for regrowth.

PGRs have been shown to increase root activity of seedlings but there are no reports of increased root activity once flowering and boll development commences. Oosterhuis and Zhao (1994) reported an increase in root growth of seedlings with PGR-IV, but this effect gradually decreased from a 47% increase in root length one week after germination to 8% at pinhead square. Increased root length was associated with a significant increase in the uptake of copper, potassium and iron.

Nutrient deficiency has often been a limiting factor in obtaining higher cotton yields. This may be caused by insufficient or unavailable mineral nutrients in the soil, or by the inability of the plant to take up the nutrient from the growth media. The former can be corrected by fertilization, while the latter may possibly be improved by nutrient uptake stimulants. Certain PGRs have been reported to enhance the nutrient uptake of crop plants from hydroponic root media. An increased dehydrogenase activity in cotton roots by PGR-IV has been reported (Clark et al., 1992), indicating an increased capability for nutrient uptake. Guo et al. (1994) demonstrated that the nutrient uptake of cotton seedlings can be enhanced by selected plant growth regulators. For example, PHCA was more effective in promoting cation uptake, while Cytokin can increase the uptake of nutrients when applied with Microplex or calcium chelate. The increased nutrient uptake by PGR-IV was probably related to enhanced root growth and activity (Oosterhuis and Zhao, 1994).

Alteration and change in the distribution of nutrient uptake by mepiquat chloride-treated cotton plants has been reported (Cothren et al., 1977; Heilman, 1985; Zhang et al., 1990), although the changes reported for specific ions have not always been consistent. Increases of calcium, magnesium, potassium and phosphorus were reported in cotton plant tissues from mepiquat chloride foliar treatments (Cothren et al., 1977). Nester (1978) also reported that calcium, magnesium and phosphorus increased in the leaves of plants treated foliarly with mepiquat chloride; potassium and phosphorus increased in the roots. Seed and foliar treatments of mepiquat chloride, applied singly or in combination, generally increased levels of calcium, potassium and magnesium in seed (Cothren et al., 1983). Heilman (1985) showed that nitrogen and phosphorus concentrations in leaves were unaffected by mepiquat chloride treatments, but percent of calcium and magnesium was significantly increased.

Comparisons between cotton seed treated with 0.0, 0.2, 1.0 and 2.0 g a.i. mepiquat chloride showed that, in general, the highest rate of mepiquat chloride produced greater concentrations of calcium, phosphorous and nitrogen in leaves and stems and higher concentrations of magnesium, phosphorous and nitrogen in roots than control plants (Zhang et al., 1990). It seems likely that PGRs may play a role in improving the efficiency of crop fertility management.

**Crop Termination and Harvest Aids**

Producers strive for the proper balance between nutrients, especially nitrogen and water and a good fruit load to facilitate an easier, acceptable harvest. Provided management decisions are correct, the crop usually depletes water and nitrogen sources by the end of the season, preparing the crop for easier defoliation and harvesting.
Plant growth regulators are used at the end of the growing season for different purposes. One is for chemical termination. Chemical termination is a term used for the technique of applying certain PGRs to terminate plant fruiting, remove late-season green bolls and reduce the number of diapausing pink bollworm [Pectinophora gossypiella (Saunders)] and overwintering bollworm / budworm (Heliothis; Helicoverpa spp.) larvae (Bariola et al., 1976; Thomas et al., 1979; Bariola et al., 1990). Chemical termination combined with early irrigation cutoff produces acceptable yields and reduced bollworm populations when applications are properly timed (Bariola et al., 1981). Ethephon and thidiazuron are effective for terminating plant fruiting (Hopkins and Moore, 1980; Bariola et al., 1986). Eleven cultivars of upland cotton grown under a short-season system were evaluated for their response to ethephon and thidiazuron, applied as chemical terminators (Bariola and Chu, 1988). Yield was unaffected by the chemical treatments and all treatments significantly reduced the number of green bolls at harvest. Leaf shed was significantly greater in treatments with thidiazuron or with thidiazuron plus ethephon than in the untreated control or those treated with ethephon alone. Kittcock et al. (1973) reported that ethephon caused an 87-96% decrease in diapausing pink bollworm larvae by reducing the number of green bolls remaining after harvest by more than 90%. The rates used, however, were excessive and declines in yield and quality were too severe to warrant further consideration.

A second use of PGRs at the end of the season is for boll opening and preconditioning the plant for defoliation. The indeterminate growth habit of cotton often forces producers to harvest more than once or to postpone harvest for several weeks. Ethephon has been used successfully and is widely accepted as a harvest aid to accelerate boll dehiscence prior to harvesting (Cathey et al., 1982). Application of ethephon causes the concentration of ethylene to increase inside bolls, leading to weakening and dissolving of cell walls. A build-up of internal pressure causes carpels to split apart. They immediately start to dry and fold backwards, allowing bolls to open naturally. Ethephon causes immature bolls to open, resulting in a greater percentage of the crop harvested at first harvest or in once-over harvest (Cothren, 1980; Weir and Gaggero, 1982; Sawan et al., 1984). Dunster et al. (1980) reported that rates of ethephon from 1.12 to 2.24 kg a.i. ha⁻¹ applied when 20-60% of the mature bolls were open, consistently caused unopened bolls to dehisce. Effects of ethephon on fiber quality and yield have been varied. It effected a greater percent first harvest, resulting in reduced micronaire and boll and seed weight in bolls that were unopened at the time of treatment (Cathey and Luckett, 1980). In Louisiana, Crawford (1980) reported that ethephon did not affect seed cotton yields, but tended to reduce micronaire at approximately the last 10% of the total yield in treatments where a significant acceleration of boll opening occurred. Over several years in Arkansas, ethephon applied with 12-25% open bolls did not reduce seed cotton yields relative to application to cotton with 48-72% opened bolls (Smith et al., 1986), nor were any consistent detrimental effects on fiber quality detected in first or once-over harvest cotton. However, Williford (1992) reported that when used to accelerate boll opening, ethephon significantly reduced yield and grade if applied at the 40% or 60% open stage, but had no detrimental effect on yield or grade if applied at the 80% open stage. Vories et al. (1991) reported that ethephon (Prepn®) effectively opened bolls even when applied as early as 10% open bolls with no effect on yield and only a small effect on lint quality.

Vegetative regrowth frequently presents problems at the end of the growing season, especially following chemical defoliation. Terminal and axillary buds of actively growing plants are often activated following defoliation. New, juvenile leaves are less responsive to defoliation treatments and can contribute significantly to problems with picking efficiency and increased green stain of lint. The cotton defoliant thidiazuron shows excellent regrowth suppression (Taylor, 1981). Glyphosate (N-phosphonomethyl glycine) was shown to suppress regrowth for as long as seven weeks when used alone or in combination with a defoliant (Cathey and Barry, 1977). Effectiveness of defoliant chemicals was also enhanced with glyphosate, but deleterious effects on seeds of immature bolls were found at the rates used in this study. Sub-lethal rates (282 g ai/ha) of glyphosate were recently shown to suppress regrowth for up to 55 days (or more) after application at 10% open boll, without a significant effect on lint yield or fiber quality (Landivar et al., 1994).

**Early Maturity**

Early crop maturity without any significant delays in crop development is a desirable production goal. This is to prevent excessive production inputs (e.g. insecticides) and to ensure that the crop is ready to harvest before the advent of inclement weather, e.g. in the Mississippi river delta. However, this is often not achieved because of delays due to excess fruit shed from insects, adverse weather or other crop stresses during the season. One of the advantages often touted with PGRs is earlier maturity. This has been shown to occur with growth retardants such as mepiquat chloride and cycoceol but not usually with growth enhancers such as PGR-IV. Early Harvest or Cytokin. Oosterhuis et al. (1991) reported that in Arkansas, earlier maturity was only achieved 50 % of the time when mepiquat chloride was used. Recently it was reported that the application of mepiquat chloride or PGR-IV late in the season, four weeks after first flower, resulted in significantly earlier maturity due to enhanced partitioning of assimilates into upper canopy bolls that subsequently matured more rapidly (Cothren...
et al., 1996; Oosterhuis et al., 1997). More research is needed to understand this use of PGRs.

**Cultivar Response**

Numerous studies on cultivar response to mepiquat chloride have been conducted, including those of Briggs (1981), York (1983), Bader and Niles (1986), Niles and Bader (1986), Landivar et al. (1992), Boquet and Coco (1993) and Viator et al. (1999). A three-year study conducted in eight environments with 14 cultivars indicated that cultivar selection should not be a consideration in deciding whether to apply mepiquat chloride (York, 1982). Cultivar by mepiquat chloride interaction for yield, micronaire, fiber strength, and fiber length uniformity were observed in only one of eight environments. Similar conclusions were made in Mississippi (Cathey and Meredith, 1988). A study of the changes in morphological and phenological variables for short- and full-season cotton cultivars to mepiquat chloride suggested that full-season types are more flexible than short-season types in their response in maturity modification, despite having similar changes in morphological characters following treatment (Bader and Niles, 1986). In this study, mepiquat chloride exhibited a trend for increased yield in the full-season cultivar, but a reduced yield for the short-season cultivar (Niles and Bader, 1986). Accordingly, a simulation model to determine the timing and rate of mepiquat chloride application indicated that maintaining a mepiquat chloride concentration of between 6-12 ppm for DPL-51 and 5-10 ppm for CAB-CS should prove beneficial for the Lower Coastal Bend of Texas (Landivar et al., 1992).

The commercial release of transgenic cultivars is one of the more recent advancements in cotton production. These cultivars give producers an alternative management strategy to conventional pest and weed control but the effects of genetic alteration on the physiology of the crop has not been documented. Thus, concern has arisen over the application rate for PGRs, especially mepiquat chloride. Some researchers and producers claim that more mepiquat chloride may be required to elicit the same response as in conventional cultivars (Wrona et al., 1997; Jones et al., 1996). Viator et al. (1999) stated that planting herbicide-resistant cultivars, such as BXN® and Roundup Ready® cotton, should not affect implementation of PGR strategies. Furthermore, the concentration of mepiquat chloride based on plant biomass required to suppress vegetative growth did not differ between the insect-resistant cultivar DPL 35a® (Bt cotton) and its conventional parent DPL 5415a®. Although the transgenic cultivars were numerically taller, no differences in the growth rate were detected between the transgenic and conventional cultivars (Underbrink et al., 1999). In fact, the optimum mepiquat chloride concentration of 8-12 ppm for conventional cotton (Landivar et al., 1995) also served as the optimum mepiquat chloride concentration for the transgenic cultivar (Underbrink et al., 1999).

**Row Spacing**

The effect of row spacing and mepiquat chloride treatment on earliness of eight cotton cultivars was inconsistent (Boquet and Coco, 1993). Earliness of Deltapine 20 was unaffected by row spacing without mepiquat chloride, but with mepiquat chloride, maturity was earlier at the 30 inch row spacing versus the 40 inch row spacing. In contrast, Stoneville LA 887 matured earlier in 40 inch rows than in 30 inch rows when treated with mepiquat chloride.

More recent studies are re-investigating the use of ultra-narrow row spacing to improve light interception and to enhance yield potential. Post-emergence weed control has been a major limitation to ultra-narrow row cotton (UNRC) production in the past, but the availability of transgenic cultivars, such as BXN® and Roundup Ready® cotton, has alleviated this problem (Snipes, 1996; Gerik et al., 1998). PGRs, especially mepiquat chloride, have reduced the problems associated with harvesting and rank growth by suppressing vegetative growth in UNRC (Atwell, 1996). Thus, UNRC production is becoming a more attractive alternative for producers. UNRC production allows for rapid canopy closure. Jost et al. (1998) estimated that cotton planted in 7.5-in. rows approached 50% canopy closure by match-head square compared to 10% closure at conventional spacing. Accelerated canopy closure and rapid early-season leaf area development in UNRC reduce weed competition, increase light interception and decrease soil water evaporation (Heitholt et al., 1992). Decreasing plant spacing reduces plant height, boll size, number of bolls per plant and number of nodes (Fowler and Ray, 1997). Decreasing the number of bolls per plant may lead to an earlier harvest for UNRC because the bolls are set earlier in the season (Buxton et al., 1979). PGRs obviously constitute an integral part of UNRC production.

**Plant Density and Fertility**

Other inputs for obtaining optimum lint yields include higher plant populations and nitrogen (N) fertility. Although high N rates and high plant populations should increase cotton yields, research has shown that optimum N rates and plant populations exist and that yield may be decreased if these optima are exceeded (Smith et al., 1979). Since both higher populations and higher N rates result in excessive vegetative growth, it seemed logical that mepiquat chloride should be used with these inputs to control excessive growth and possibly increase yields. A three-year study at eight locations in North Carolina showed that mepiquat chloride did not alter the optimum N rate or plant population (York, 1983). The results suggested that mepiquat chloride had no adverse effects when
populations were below those necessary for optimum yield, but might sometimes overcome the detrimental effects of above optimum populations when environmental conditions favoured excessive vegetative growth and delayed maturity.

Robertson and Cothren (1991) reported that lint yields were influenced by the interaction of mepiquat chloride, row spacing and N rate. Gordon et al. (1986) found that mepiquat chloride increased yield, but these increases were similar for all N rates. Heilman (1981, 1985) also failed to show N rate by mepiquat chloride interactions in his studies, but there was no response to mepiquat chloride and optimum N rates were not exceeded. Although Kerby et al. (1982) reported a greater yield response to mepiquat chloride at higher N rates, optimum N rates again were not exceeded. When above optimum N rates were used in Texas, the only significant interaction for mepiquat chloride and N application rate was for the highest N rate (180 kg ha-
1) and the control where no N was added (Han et al., 1990). Petiole nitrate-N concentration of mepiquat chloride-treated cotton was higher than for untreated cotton at three sampling dates, suggesting an improved fertility status of the crop (Maples, 1981). McConnell et al. (1992) and Boman and Westerman (1994) failed to show significant interactions for nitrogen rates and mepiquat chloride treatment.

**Planting Date**

Studies with mepiquat chloride and date of planting suggest mepiquat chloride mitigates the adverse effects caused by delayed planting (Cathey and Meredith, 1988). Mepiquat chloride by planting date interactions occurred for plant height, flower production, lint yield, and seed index. For three planting dates (mid-April, early May and mid-May), mepiquat chloride reduced lint yield by 4.5% in the early planting and increased yield by 5.4 and 12.7% in the optimum and late plantings, respectively. Boll weight was increased by mepiquat chloride treatment at all planting dates, but flower production was increased only in the late planting and seed index was increased and lint percentage reduced in all mepiquat chloride-treated plots from the three dates of planting.

**Insecticides as Growth Regulators**

Ample information suggests that some insecticides can have physiological effects that alter the growth and development of cotton (Brown et al., 1962; Roark, et al., 1963; Lincoln and Dean, 1976; Campbell et al., 1979). However, testing insecticides for plant growth regulation is often difficult because it is hard to distinguish between plant responses to the chemical *per se* and to the control of insects. In early reports on the growth regulating properties of insecticides, some hydrocarbons were shown to increase fruit set and early maturity and some organophosphates tended to induce lateness (Brown et al., 1962; Roark et al., 1963). Early-season applications of the insecticide chlordimeform [N'-4-chloro-o-toly-N, N.dimethylformamidimine] increased cotton lint yields above those expected from the pesticidal properties of the chemical (Lincoln and Dean, 1976; Benedict, 1986). Campbell et al. (1979) reported a 25% increase in yield for chlordimeform-treated cotton and described the effects as a combination of insecticidal control and physiological yield enhancement. Other researchers have found no influences of chlordimeform on cotton growth and development, concluding that the product did not increase yields beyond that associated with actual pest control (Cathey and Bailey, 1987; Durant, 1989). Because of potential environmental hazards, chlordimeform was voluntarily removed from the market.

Cytokinin-like activity were reported for several agricultural chemicals, including soil applications of the photosynthesis-inhibiting triazine, uracil and phenylurea herbicides that retard senescence in intact maize (*Zea mays* L.) leaves at subtoxic dosages (Hiranpradit and Foy, 1973); the cotton defoliant thidiazuron (N-phenyl-N'-1,2,3-thidiazol-5-yl urea) that promotes growth of sieva bean (*Phaseolus lunatus* L.) callus culture (Mok et al., 1982) and the fungicide triadimefon [1-(4-chlorophenoxyl)-3, 3-dimethyl-1(1H-1, 2, 4-triazol-1-yl)-2-butanone] that exhibits cytokinin-like activity in detached barley (*Hordeum vulgare* L.) leaves (Forster et al., 1980).

**Pest Resistance and PGRs**

Plant growth regulators may be effective in reducing pest populations by altering the morphological and biochemical characteristics of cotton (Graham et al., 1987). As discussed earlier, PGRs have been used both early and late in the season for chemical termination of cotton to remove vegetative and reproductive components, thus denying insects food and shelter. The application of PGRs may also alter the biosynthesis of compounds such as secondary plant constituents that are detrimental to pests. Zummo et al. (1984) reported that mepiquat chloride applied at rates used for control of excessive vegetative growth increased resistance to bollworm [*Helicoverpa zea* (Boddie)] damage in cotton. The increased resistance was attributed, in part, to increased tannin and terpenoid production from the mepiquat chloride treatment. Mulrooney et al. (1985), on the other hand, concluded from larval growth studies in the laboratory that mepiquat chloride does not enhance cotton’s resistance to second stage tobacco budworm (*Heliotis virescens* F.), but may actually increase larval growth and decreases natural resistance in an ideal growing season. Growth rates of second and third stage tobacco budworm larvae increased slightly when grown on leaves treated with mepiquat chloride at either the recommended or twice the recommended rate. Jenkins et al. (1987) did not believe the changes in allelochemic levels from mepiquat chloride treatments were sufficient to increase the natural resistance to tobacco budworm. In their study, gossypol was significantly increased in squares and leaves in two of
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three years, but was coupled with decreases in anthocyanin and flavonoids. Hedin and McCarty (1991) showed that mepiquat chloride treatment alone or with a commercial cytokinin preparation significantly increased gossypol and one or more of the other allelochemicals in cotton. Subsequent studies with natural bioregulators (kinetin, kinetin riboside, indole-3-acetic acid and gibberellic acid) did not appear effective for increasing yield or allelochemicals (Hedin and McCarty, 1994).

**Cytokinin Activity**

Several cytokinin and cytokinin-like compounds (e.g., Burst, Cytozyme, Cytokin, Triggrr) have been tested for PGR activity in cotton. Specific modes of action have not been elucidated, but these compounds theoretically promote fruit set and retention and increase the ability of the plant to fill existing fruit (sinks). Studies in Arkansas with a mixture of complexes containing various bacterially active cytokinins, auxins and amino-acid chelated minerals showed trends toward increased yields, but these changes were not significantly different from untreated controls in either year of a two-year study (Cothren and Cotterman, 1980). Laboratory tests with the product in controlled environment chambers revealed appreciable decreases in foliar nitrogen loss and increases in carbon dioxide fixation (Cotterman and Cothren, 1979). When Namken (1984) applied single and multiple foliar applications of a cytokinin product to cotton at first one-third-grown square and at first flower, the treated cotton produced a significantly higher lint cotton yield than the untreated control. Foliar application of this cytokinin product was reported to promote bud initiation and development that caused an increase in plant fruitfulness and increased efficiency of the plant to develop and fill that fruit (Mayeux et al., 1985). Significant increases in boll number and retention of bolls in first position fruiting sites (Mayeux and Kautz, 1992) were also reported. A comprehensive review of results with a similar product showed increases in cotton yields that averaged 49 kg lint/ha in 83 trials conducted in nine states over a nine-year period (Parker and Salk, 1990). In Arkansas, Cytokin significantly increased yields compared to the untreated control in two out of five years (Oosterhuis and Zhao, 1998; Table 2).

**Multiple Entity PGRs**

In the last decade a number of multi-entity PGRs have been introduced, e.g. PGR-IV and Early Harvest. PGR-IV is a multiple entity PGR that contains indolebutyric acid (IBA) and gibberellic acid (GA) in a nutrient solution blend. The purported mode of action of PGR-IV is through an alteration of plant hormone balance that affects growth. Various effects of PGR-IV on plant growth have been reported, including increases in shoot dry matter, nutrient uptake and number of squares retained (Oosterhuis and Zhao, 1995). Root growth was also significantly increased by in-furrow applications of PGR-IV in growth-room studies (Oosterhuis and Zhao, 1994). There have been reports of increased photosynthesis following PGR-IV application (Oosterhuis and Zhao, 1995), related to improved translocation of assimilates to the developing bolls. This report was corroborated by Cadena et al. (1994) who reported increased carbon uptake and respiration of PGR-IV treated plants at 20°C. PGR-IV has been shown to decrease the detrimental effects of mild stress, including water deficit, flooding and shade compared to unstressed plants (Zhao and Oosterhuis, 1997, 1998). Increased boll retention has also been reported for PGR-IV-treated plants (Robertson and Cothren, 1993). These favourable growth responses have resulted in lint yield increases (Urwiler et al., 1988; Cothren and Oosterhuis, 1993; Livingston and Parker, 1994; Oosterhuis, 1995).

Plant mineral elements have often been added to PGRs in an effort to improve their activity although it is then difficult to determine which component of the compound is responsible for any positive response on plant growth or yield. Recently, the soil bacterium *Bacillus cereus* was added to mepiquat chloride (Parvin or Atkins, 1997) to improve the activity of the PGR. Research so far has shown that the new PGR (Pix Plus) is similar to mepiquat chloride in effect on vegetative growth but may have a small yield advantage (Parvin and Atkins, 1997; Zhao and Oosterhuis, 2000).

**Remediation of Stress with PGRs**

Temperature stress (both high and low) can adversely affect the physiology and subsequent productivity of cotton. Chilling cotton plants caused reduced growth at later favourable temperatures that was directly proportional to the duration of chilling at 10°C (Christiansen, 1963, 1964). Mepiquat chloride reportedly increases heat and cold tolerance of cotton (Huang and Gausman, 1982). Electrolyte leakage (used as an indicator of membrane integrity) from leaf discs of treated and untreated plants showed that untreated discs leaked two times more electrolytes than mepiquat chloride-treated plants (Huang and Gausman, 1982). Ultrastructural observations revealed that in the mepiquat chloride-treated leaf the plasma membrane was altered by protein aggregation, but most of the plastidal envelope and the thylakoidal system were intact. These three membrane systems in the non-treated leaf showed extensive degeneration. Cotton plants previously treated with mepiquat chloride and exposed to 55°C showed increased heat resistance compared with the untreated control (Huang and Gausman, 1982). The mepiquat chloride-treated leaves had larger starch grains in their chloroplasts than control leaves, suggesting a difference in photosynthetic activity. Urwiler (1981) suggested that mepiquat chloride held potential for use as a cryoprotectant. Cadena et al. (1994) with whole plant
assimilation studies of PGR-IV treated plants at 20°C showed increases of 29, 37 and 24% in gross carbon uptake, respiration, and net carbon uptake, respectively, suggesting better growth at lower temperatures.

Water shortages are the leading cause of low yields in most field crops, including cotton. While there are only limited management options to try and overcome the detrimental affects of water deficit on cotton growth and yield, the use of PGRs may offer some limited relief. Xu and Taylor (1992) reported an increase in drought tolerance of cotton seedlings treated with mepiquat chloride. Livingston et al. (1992) reported that the percentage increase in yield from foliar application of PGR-IV was greater under dryland than under well-watered conditions. Recently, Zhao and Oosterhuis (1997) demonstrated that PGR-IV has the potential to alleviate partially the detrimental effects of water stress on photosynthesis and dry matter accumulation and to improve the growth and nutrient absorption of growth-chamber grown cotton plants. Similarly, Zhao and Oosterhuis (1994) showed that application of PGR-IV decreased the harmful effects of flooding on cotton growth and improved photosynthesis and dry matter production of flooded cotton plants. Shading from excessive vegetative growth or overcast weather often causes increased fruit abscission and yield losses in the Mississippi delta. PGR-IV also has the ability to assuage the detrimental affect of shade by significantly lowering fruit abscission and increasing non-structural carbohydrates in floral buds due to improved assimilate translocation (Zhao and Oosterhuis, 1998). The ability of PGRs to enhance nutrient uptake has already been addressed and will not be covered again under this section on stress remediation with PGRs. The use of PGRs to partially alleviate mild stress conditions may be an innovative way to improve crop management efficiency.

**Methanol as a PGR**

Nonomura and Benson (1992) reported that foliar sprays of aqueous 10-50% methanol caused striking increases in growth and development of C₃ crop plants in arid environments. Cotton, a C₃ plant, treated with a foliar application of 30% methanol under high noon direct sunlight, exhibited increased leaf turgidity within four hours and an approximate 15% increase in height over untreated controls within two weeks. Methanol also enhanced maturation and allowed irrigation to be terminated 15 days earlier than for an untreated field. Plants with C₃ metabolism did not increase productivity in response to methanol treatment. Subsequent to this report, studies were established throughout the US Cotton Belt to determine the response of cotton to foliar methanol treatments. Faver and Gerik (1994) reported that solutions of methanol up to 30% did not alter leaf area and cumulative water use, but photosynthesis, total biomass, fruit number, fruit weight and specific leaf weight were higher for methanol-treated plants than for untreated plants; however, these results were not repeatable. Results from most field studies in 1993 failed to show differences in photosynthesis or photorespiration (Husman et al., 1994; Nelson et al., 1994), water relations (Heitholt et al., 1994), plant growth and development (Husman et al., 1994; Nelson et al., 1994) or lint yield (Nelson et al., 1994) of methanol-treated cotton compared with untreated controls. Trends toward increased plant height, boll numbers, and fruiting sites from methanol treatment were reported by Barnes and Houghton (1994), but lint yield appeared to be adversely affected. A two-year, three state study by Van Iersel et al. (1995) also reported no effect on photorespiration, dry matter production or yield. Similar conclusions were reported by Gerik et al., (1996).

**Compatibility of PGRs**

Producers are often tempted to combine agricultural chemicals in the same tank to save on application costs. Questions have arisen about the compatibility of PGRs, particularly mepiquat chloride and PGR-IV since the first works as an anti-gibberellin and the latter contains gibberellin. Field research has shown that these two PGRs can be safely applied together without any harmful effect on yield, although the reduction in plant height from mepiquat chloride may be slightly decreased (Guo and Oosterhuis, 1994).

**Interpretation of PGR Responses**

Interpretation of results from these and other PGR studies is difficult because experimental inputs are confounded by differences in cultural inputs and environmental conditions. Cotton responds differently when production variables are changed, and adding a PGR as another variable further complicates the expression of the crop’s genetic potential. Conclusive evidence for increased boll set and retention and for changes in individual boll weights are especially difficult due to the inherent variability of individual plants.

Furthermore, as stated earlier in this review, cotton has a complex growth habit and the crop is very responsive to changes in the environment and management, making it difficult to predict growth and yield responses, especially with the added response to a PGR.

**Conclusions**

Plant growth regulators are organic compounds, other than nutrients that affect physiological processes of plants when applied in small concentrations. These compounds represent diverse chemistries and modes of action and provide numerous possibilities for altering crop growth and development. The possible benefits and uses of PGRs in cotton production include control of vegetative growth, increased boll retention,
earlier crop maturity, preparation of the crop for harvest and increased yields. More specific responses include alteration of carbon partitioning, greater root:shoot ratios, enhanced photosynthesis, altered nutrient uptake, improved water status and altered crop canopy shape. These responses are a reflection of the interaction of heritable characteristics, cultural inputs and environment. Because of this complex interaction, crop response to PGRs is not always predictable and results, especially with yield enhancement, have often been disappointing, with variable and inconsistent results.

Strategies for using PGRs in cotton production include numerous options for beneficially modifying crop responses to improve yield and management of the crop. Research has shown that PGRs can play a role in enhanced nutrient uptake and remedial management of stressed cotton and these may prove to be a valuable future management tools. Additional studies are needed on the physiological mechanisms of PGRs as this will allow better use and more synchrony with developmental events and management inputs for more predictable crop responses and greater economic returns. PGRs are widely used in cotton for improved management and yield increases. This use should expand in the future with improved understanding of PGRs and more consistent and reliable results.

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Table 1. Plant growth regulator common names, chemical makeup, timing, and rates of commercially available PGRs.

<table>
<thead>
<tr>
<th>PGR</th>
<th>Chemical makeup</th>
<th>Company</th>
<th>Timing</th>
<th>Rate:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Atonik</td>
<td>Na salts of ortho-nitrophenol, papra-nitrophenol, and 5-nitro-guaiaicol</td>
<td>Asahi Chem. Mfg. Co.</td>
<td>PHS, FF, FF+3 wks</td>
<td>1235 ml/ha, 1440 ml/ha</td>
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<tr>
<td>Crop+2</td>
<td>protein digest extract</td>
<td>Cytozyme Labs Inc.</td>
<td>3–4 leaf, PHS, FF</td>
<td>1,168 ml/ha per application</td>
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<tr>
<td>Cycocel</td>
<td>chlormequat chloride</td>
<td>Wilbur Ellis Company</td>
<td>PHS, FF</td>
<td>125 g/ha per application</td>
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<tr>
<td>Cytokin</td>
<td>Natural cytokinins</td>
<td>PBT Inc.</td>
<td>PHS, FF, FF+3 wks</td>
<td>292 ml/ha, 584 ml/ha</td>
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<tr>
<td>Early Harvest</td>
<td>IBA, gibberellin, cytokinin</td>
<td>Griffin Corporation</td>
<td>IF, PHS, FF</td>
<td>146 ml/ah, 292 ml/ha, 292 ml/ha</td>
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<tr>
<td>Pix Plus</td>
<td>mepiquat chloride and <em>Bacillus cereus</em></td>
<td>BASF Company</td>
<td>PHS, FF</td>
<td>584 ml/ha per application</td>
</tr>
<tr>
<td>PGR-IV</td>
<td>IBA, GA and a fermentation broth</td>
<td>Microflo Company</td>
<td>IF, PHS, FF</td>
<td>73 ml/ha, 292 ml/ha, 292 ml/ha</td>
</tr>
<tr>
<td>PHCA</td>
<td>polyhydroxycarboxylic acid</td>
<td>Microflo Company</td>
<td>PHS, FF, FF+3 wks</td>
<td>584 ml/ha, 1,168 ml/ha</td>
</tr>
<tr>
<td>Mepiquat chloride</td>
<td>1,1-dimethylpiperidinium chloride</td>
<td>BASF, Microflo, Griffin</td>
<td>PHS, FF</td>
<td>584 ml/ha per application</td>
</tr>
</tbody>
</table>

† Average rates used according to published literature or manufacturer recommendations.

‡ IF = in-furrow, PHS = pinhead square, FF = first flower.

Table 2. Effect of commercially available Plant Growth regulators on lint yield 1993 to 1999 in Arkansas.

<table>
<thead>
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<td>885</td>
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<td>1232</td>
<td>1453</td>
<td>1241</td>
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<td>1259</td>
<td>1192i</td>
<td>1500i</td>
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<tr>
<td>Cytokin</td>
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<td>1300</td>
<td>1151</td>
<td>1418</td>
<td>1257</td>
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<td>Early Harvest</td>
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<td>Pix Plus*</td>
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</tr>
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<td>1016</td>
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<tr>
<td>Bacillus cereus</td>
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<td>------</td>
<td>------</td>
<td>------</td>
<td>1203</td>
</tr>
<tr>
<td>LSD (0.05)</td>
<td>82</td>
<td>60</td>
<td>159</td>
<td>77</td>
<td>NS</td>
<td>NS</td>
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</tr>
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</table>

† Not evaluated in that year.
‡ Crop+2 was used in 1995 and 1996.
* MepPlus was renamed Pix Plus in 1999.