Chapter 7

COTTON FLOWERING AND FRUITING: CONTROL AND MODIFICATION WITH PLANT GROWTH REGULATORS

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INTRODUCTION

Cotton (*Gossypium hirsutum* L.), by nature, is a perennial woody shrub that possesses an indeterminate growth habit. Through breeding and selection, cotton has been adapted to an annual production system and is currently grown under both semi-arid and humid conditions. As such, the crop is often subjected to environmental extremes and exposed to various stresses that impact its yield. The crop may be more vulnerable to these stresses at key developmental stages, such as flower initiation and boll filling.

At present, cotton is not genetically limited for yield, but the ability to retain and mature the fruit that are produced remains a challenge. Because of the indeterminate growth habit, cotton produces fruit over an extended fruiting period. Thus, these fruit are developed under varying moisture, temperature, and light regimes. The fruiting habit of the crop normally proceeds from fruit production commencing at around the sixth node and proceeding upward and out on fruiting branches until it reaches a stage of development referred to as cutout. Each fruiting branch that is produced normally initiates from 1 to 4 fruiting sites, with fruiting continuing upward until around the eighteenth mainstem node. Previous research indicates that the majority of yield is produced from the first and second fruiting sites on main-stem nodes 9 through 14. Reports indicate that as much as 80% of the yield originates at these sites. The obvious question is, "why is this the case." A major contributor to this occurrence is that of source and sink. The first position fruit on a node constitutes a stronger demand for assimilates and if supplies are limited, the subsequent fruit produced on the fruiting branch suffer the consequences.

Because of these growth characteristics, ways to modify and control the flowering/fruiting of the cotton plants are often desirable. The alterations may be accomplished through the use of plant growth regulators (PGRs). An organic substance is considered a plant growth regulator if in low concentrations it promotes, inhibits, or modifies plant growth and development, eliciting responses similar to the ones observed from endogenous plant hormones. However, interactions with the environment and differences in cultural practices are mainly responsible for the complex responses generated by crops to PGRs. Lack of consistency in performance, and the fact that PGRs may not be economically beneficial are some of the limitations for PGR usage.

[3] Mention of proprietary products does not constitute an endorsement by Texas AgriLife Research or Dow AgroSciences LLC, nor are products mentioned inclusive of all plant growth regulators. Specific products are mentioned as examples of physiological potential for cotton growth and modification.

Since most control and modification of cotton flowering and fruiting processes are regulated by natural plant hormones, these processes may be manipulated either by modifying the hormonal concentrations within the plant or by altering the natural way plants sense/respond to their hormones. PGRs, diverse in both their chemistry and use, are part of the management tools that can be used to ensure efficient cotton production system.

PGRS AND COTTON MANAGEMENT

Management of cotton with plant growth regulators (PGRs) is a season-long process. A successful PGR program encompasses a systems approach that includes many crucial decisions. Because we cannot predict weather with 100% accuracy, it is important to minimize factors that contribute to stress as much as possible. Fine-tuning fertility programs, water management, and pest control are key in optimizing lint production. There are no substitutes for sound cultural practices. One way that producers can supplement these inputs is by judicious use of plant growth regulators. These compounds are not meant to be used as a salvage or rescue operation, but should be used to more efficiently manage the crop to adjust plant growth and to improve lint yield and quality. This can best be achieved through the use of well-adapted, high-yielding cultivars. Again, there is no substitute for genetics, but even the "best" cultivar cannot be expected to provide higher yields under all circumstances due to inconsistencies in the environment. PGRs and other stress management practices can be used in an effort to consistently produce higher yields.

Yield of the cotton plant is determined by a combination of factors: boll number, boll size, seed number per boll, and fiber/seed. These parameters are influenced by the physiological activity of the plant and its interaction with the environment. Due to the perennial nature of cotton, fruiting continues during its maturation, thus impacting any or all of these parameters. According to Mauney (1986), three nodes on each sympodium (fruiting branch) are most likely to mature. His scenario is that about 50 prime squares will be produced by the presence of 18 sympodia (3 squares/sympodium X 18 sympodia/plant = 54 squares/plant). If 50, 30, and 10% of the squares at fruiting position 1, 2, and 3, respectively, mature into open bolls with 1.5 grams of lint per boll, a population of 30,000 plants per acre would yield 1500 pounds of lint/acre. This data is reflective of work reported by Mauney (1986) for studies conducted at various locations in the U.S. from 1940 through 1982. A major portion of this yield is contributed by nodes 9 through 14 (Jenkins et al., 1990), depending on length of the growing season and other cultural inputs. According to the nutritional balance theory of fruiting, the cotton plant will set as many bolls as it can produce substrate for and maintain maximum growth (Guinn, 1976a). Seed number, mass and surface area, and lint mass, as well as fiber number, were recorded for the first fruiting position bolls located from nodes 9 and 14 in an irrigation by plant density study (Feng et al., 2010). In this study, individual seed surface area and mass increased with increases in irrigation and decreases in plant density. Seeds per locule responded in a likewise manner. Fiber number per unit seed surface, however, were not affected by any of the treatments suggesting this component was likely heritable.

Temperature

Two of the major abiotic stresses impacting cotton growth and development, and thus PGR usage are temperature and water stress. Temperature purportedly has only a small effect on canopy photosynthesis, but strongly influences vegetative growth and development, light capture during the vegetative period, and light conversion during much of the boll-filling period (Reddy and Hodges, 2006). Previ-

ous studies show that the minimum temperatures for cotton growth is about 15° C and the optimum is about 28° C (Reddy et al., 1992), which is well below commonly occurring air temperatures in most cotton growing areas. We know that cotton is capable of much higher productivity than typically observed even under the best management practices. Although photosynthesis is an important component of yield, it generally correlates poorly with dry matter production or harvestable yields because of the multiplicity of factors limiting yield (Evans, 1993) and the fact that this conclusion was drawn from instantaneous measurements (often on single leaves) conducted under standardized conditions rather than from seasonal measurements on canopy photosynthesis in the field (Zelitch, 1982). However, Cornish et al. (1991) reported that genetic advances in cultivated cotton types (Gossypium barbadense L.) were closely associated with increasing single-leaf photosynthesis rate and stomatal conductance, when grown under greenhouse conditions. One would assume that higher stomatal conductance increases CO2 diffusion into the leaf that would favor higher photosynthetic rates. In chambers with twice atmospheric [CO2] (720 µmol CO2 mol-¹ air) maximum photosynthetic rates were about 6 mg CO2 m-² s-¹ compared to maximum rates of about 4 mg CO2 m-² s-¹ at 360 µmol CO2 mol-¹ air (Reddy and Hodges, 2006). If these higher photosynthetic rates are sustained they could in turn favor higher crop yield. Previous work with advanced Pima cotton lines showed a higher photosynthetic capacity than older, low-yielding cultivars, but use of the same leaves used to measure stomatal conductance showed that photosynthetic rates in these same leaves were not positively correlated with yields (Radin, 1994). Therefore, it appears that higher stomatal conductance favors higher yields by a mechanism not directly related to photosynthesis. Studies by Lu et al. (1998) pointed out that selection for higher yields in irrigated crops at high temperature indirectly imposed selection pressure for higher stomatal conductance than lowered leaf temperature. Subsequently the deleterious effects of heat stress on critical flowering and fruiting stages were reduced, thus leading to higher crop yields.

Hodges et al. (1993) showed that high temperatures strongly influence numbers of vegetative and reproductive branches in cotton. Vegetative branches increased and fruiting branches decreased with high temperatures. In this study, number of fruiting sites increased by 50% as temperature was increased from 30 to 40˚ C; however, number of squares and bolls decreased dramatically above 35˚ C to a value of zero at 40˚ C. Later work by Bibi et al. (2008) and Snider et al. (2009) indicated that photosynthesis in cotton is highly sensitive to temperatures above 35˚ C which detrimentally affects quantum efficiency of the photosynthetic apparatus and decreases chlorophyll content (Snider et. al., 2010). The temperature effect is especially important with respect to rubisco activase, which is necessary for activation of ribulose-1, 5-bisphophate carboxylase/oxygenase (Rubisco) (Crafts-Brandner and Salvucci, 2000). As temperatures increased, the rate of Rubisco deactivation exceeded the capacity of activase to promote activation. This results from activase being inhibited by a lower temperature than that for Rubisco. Rubisco activation decreased when leaf temperature exceeded 35˚ C, whereas activities of isolated activase and Rubisco were highest at 42˚ C and >50˚ C. Studies in Arkansas using membrane leakage and fluorescence as techniques for determining tolerance of cotton germplasm to high temperature failed in most instances to show significant differences, but a few lines were identified with appreciable temperature tolerance (Oosterhuis et. al., 2009). Similar measurements were made in a multi-level determination of heat tolerance in cotton under field conditions by Cottee et. al. (2010).The most rapid and reliable screens for heat tolerance in this study with high yielding cotton included electron transport rate, membrane integrity, and enzyme viability. Kawakami et. al. (2010) showed that 1-methylcyclopropene treatment to cotton at first flower and first-flower plus two weeks significantly increased seed cotton and lint yield in a two-year study compared to the untreated control. In both years of this study, maximum temperatures were well above the optimum 30˚ C temperature for cotton at the study location, indicating that cotton was under heat stress. Therefore, PGRs

have shown potential for increased yield under stress conditions. Efforts to identify increased thermotolerance and tolerance to water limitation remain high priorities for improving yields in cotton.

Water-Deficit Stress

Temperature and water stress often occur simultaneously in cotton producing areas, and the ability to identify crop response to either one in solo is difficult. Wanjura et al. (1984) investigated the use of canopy and air temperature differences to compute a crop water stress index (CWSI) for assessing plant water status using cotton crop canopies that fully or partially covered the ground. The results showed that the slope of the non-stressed baseline of the CWSI for a cotton crop with a canopy which had about 50% ground cover was approximately one-half of that reported for full canopies. The study emphasized the importance of complete canopy for calculating CWSI values by either "theoretical" or "empirical" procedures. CWSI calculated under complete canopy condition agreed more closely for the two procedures than when they were calculated under a partial canopy situation. Since the effective use of plant growth regulators is often stress based, we continue to search for methods that serve as more reliable triggers of stress. Similar to the work of Wanjura et al. (1984), Howell et al. (1982) previously found that canopy temperature in cotton was a sensitive indicator of water stress caused by either soil water deficit or soil osmotic stresses. Recent work (Conaty et al., 2012) indicated that a plant-based thermal optimum approach to irrigation scheduling provides potential benefits when water applications are scheduled on basis of plant response to water stress. The ability of the plant to maintain its optimum temperature (Topt) range uses the principle that plant performance is maximized when a plant is maintained at this temperature. Methods of achieving continuous measurement of plant canopy temperature in agricultural settings can be achieved with a low-cost wireless temperature monitoring system compared to that of higher-cost industrial-grading sensors, thus potentially making them a viable alternative in many agricultural settings (Mahan et al., 2010). Mahan et al. (2010) stated there are conditions where plants cannot evaporate fast enough to maintain their temperature below the Topt, regardless of how well they are supplied with water. Although cotton is considered to be a drought-tolerant crop, sensitivity varies greatly among genotypes (Igbal et al., 2011) Moreover, for successful breeding of cotton cultivars to drought, there must be significant variability to water stress and this variation must be genetically controlled (Mitra, 2001). The occurrence of variation for drought tolerance within G. hirsutum has been shown (Pettigrew, 2004a; Basal et al., 2005), but less is known about the genetic mechanism that controls this variation in drought tolerance of G. hirsutum (Singh and Singh, 2004). These factors further complicate achieving consistent responses to PGR use, but PGRs have shown a potential to partially alleviate the detrimental effects of water stress on specific physiological activities of cotton growing under growth chamber conditions (Fernandez et al., 1992; Zhao and Oosterhuis, 1997). The more we understand of the complex interaction of the different plant stresses with PGRs, especially water and temperature, the more successful we can become in knowing when and in what quantities PGRs can be used to effectively reduce these stresses.

Plant Hormones

Plant hormones are plant-made (endogenous) growth regulators that alter growth and development. According to Davies (2010), the concept of plant hormones was first defined in a 1937 publication based on animal physiology. Plant hormone was described as an organic compound that was synthesized in one part of a plant and translocated to another part, where it caused a physiological response. Currently, the concept based on animal physiology clearly no longer applies to the definition of a plant hormone,

since the synthesis of hormones in plants can either be localized as in animals or occur in a wide range of tissues. The site of action may or may not coincide with the site of synthesis. Ethylene, the only plant hormone that is a gas, causes physiological changes at the site of synthesis, and has no need of being transported. Transport is only required if the hormone sites of action and synthesis do not coincide.

Plant hormones serve as chemical messengers to coordinate growth, development, differentiation and environmental responses. Plant hormones at very low concentrations are able to cause responses through a signal transduction pathway that produces a cascade effect. The five classical major plant hormones are auxins, gibberellins, cytokinins, abscisic acid and ethylene (Gaspar et al., 1996). The search to identify new plant hormones is ongoing, resulting in the recognition of five additional new compounds as plant hormones: brassinosteroids, jasmonates, salicylic acid, polyamines, and peptides (Davies, 2010). In reality, plant hormones do not perform alone, but rather in conjunction or opposition to each other resulting in plant growth/development changes. The following presents an abbreviated summation of the major plant hormones and their physiological roles in crop growth and development.

Auxins

Decapitated grass coleoptiles were recognized as being able to bend after having their growth stimulated by agar blocks saturated with diffused substances from the tips of grass coleoptiles (Went, 1926). The substance that was diffused to the agar blocks was later named auxin, constituting the first plant hormone ever discovered (Davies, 2010). It was subsequently demonstrated that auxin was synthesized in the tips of grass coleoptiles and moved basipetally, i.e. from the tip to the base (Wildman, 1997). The most important representative in the auxin group is indole-3-acetic acid (IAA) since it is one of the main auxin molecules present in the majority of plants (Davies, 2010). The IAA molecule is not only found in its original form, but is also present in plants in various conjugated forms. Auxin has little transport in xylem and phloem. Auxin transport is mainly polar and proceeds from the apex to the base (basipetally) in the shoots. In roots, besides having a basipetal transport, auxins are also transported acropetally (base to tip). The leaf apex, young leaves, as well as developing seeds, serve as the primary sites for auxin biosynthesis, which can occur from tryptophan-dependent or tryptophan-independent pathways (Bartel, 1997). Genetic and biochemical studies, however, have indicated that tryptophan is the main precursor for IAA in plants (Woodward and Bartel, 2005; Zhao, 2010). Auxins promote cell enlargement, stem elongation, apical dominance (repressing growth of lateral buds), vascular differentiation (xylem and phloem), tropistic responses (root and shoot response to light and gravity), and growth of flower parts, as well as delaying senescence. Auxins induce fruit set and growth in some fruit, delay fruit ripening, and stimulate flowering in bromeliads. At high concentrations, this plant hormone inhibits root growth (Chadwick and Burg, 1967).

Cell elongation as well as cell wall loosening (plastic nature of walls from cells) is caused by auxins (Salisbury and Ross, 1992). The most popular mechanism that explains cell wall loosening is the acid-growth hypothesis (Ray, 1987) This hypothesis proposes that auxins cause receptor cells in stem sections to secrete H+ into their surroundings. Secreted H+ ions eventually reduce the pH, presumably allowing activation of certain cell wall-degrading enzymes which are inactive at a higher pH. The activity of these enzymes breaks bonds in the wall polysaccharides resulting in wall loosening and accelerated growth through increased cell turgor pressure.

Gibberellins

Investigations in plant diseases led researchers to the discovery of gibberellins (GAs). The name gibberellin originated from the fungus Gibberella fujikuroi, from which culture filtrates allowed

scientists to gain chemical identification of this group of plant hormones (Davies, 2010; Wildman, 1997). Gibberellins contain over 136 compounds identified in various fungi and plants (MacMillan, 2002), with all containing the ent-gibberellane structure (Davies, 2010). Among these already identified GA compounds, gibberellic acid (GA3), a fungal product, is the one most widely available, with GA1 being the most important GA in plants. The vast majority of the GAs are precursors or inactivation products of the biologically growth-active form of GA1.

Gibberellins are mainly synthesized in young seeds and tissues of the shoot tissues from glyceraldehyde-3-phosphate via isopentenyl bisphosphate taking place initially in chloroplasts followed by activities in the cytoplasm (Davies, 2010). Gibberellins exhibit many physiological effects, suggesting that they have more than one primary site of action. More specifically, GA1 stimulates cell elongation and division in the stem, which together with cell turgor pressure, causes its elongation (Davies, 2010). Gibberellin causes bolting in long-day plants such as cabbage, germination in seeds that require cold/light to break dormancy, production of enzymes such as amylase that is required during seed germination, and fruit setting and growth as in grapes treated with GA (Taiz and Zeiger, 2010). Gibberellins also are linked to changes in juvenility and flower sexuality through induction of maleness in dioecious flowers, and are known to increase leaf size of a number of different plants (Taiz and Zeiger, 2010). The most important bioactive agents for vegetative growth and development are probably GA1 and GA4. In most species that have been investigated, GA1 is the predominant bioactive (Hedders, 1999).

Cytokinins

Tissue culture experimentation led scientists to the discovery of cytokinins (Davies, 2010; Wildman, 1997). The chemical identification of this group of plant hormones was made possible with the use of autoclaved herring sperm DNA (Davies, 2010). Cell division is known as cytokinesis, which has resulted in the term cytokinin being assigned to substances that typically stimulate cell division. Cytokinin synthesis derivates from adenine, a purine base found in RNA/DNA, and is most abundant in the young, rapidly dividing cells of the shoot and root apical meristems. Cytokinin transport is mainly through the xylem system. Besides being involved in cell division (either in tissue culture in the presence of auxin, or in crown gall tumors, or in actively dividing tissues), cytokinins participate in seed and chloroplast development (exogenous application of cytokinins leads to accumulation of chlorophyll and conversion of etioplasts to chloroplasts) , chloroplast maturation, leaf senescence delay and expansion, cell enlargement, and embryo development (Davies, 2010; Hare et al., 1997). Cytokinins stimulate the synthesis of specific chloroplast proteins that are encoded by nuclear genes and synthesized by cytoplasmic ribosomes (Binns, 1994; Taiz and Zeiger, 2010).

Abscisic Acid

Studies on abscission control and dormancy led to the finding of abscisic acid (ABA) (Davies, 2010; Wildman, 1997) which is a single compound isolated from cotton fruits in the early 1960s. Addicott and colleagues first identified ABA while studying compounds related to cotton fruit abscission (Ohkuma et al., 1963). Since it was believed that ABA was involved in abscission, the compound was then named abscisic acid (Addicott et al., 1968). Nowadays, it is known that in fact ABA has little effect on abscission which is mainly driven by ethylene. ABA is synthesized via isopentenyl diphosphate and carotenoids from glyceraldehyde-3-phosphate in almost all cells that contain plastids in roots and mature leaves (Davies, 2010). ABA, which is classified as a growth inhibitor (since exogenous applications do

inhibit growth in plants) (Davies, 2010), inhibits auxin-induced cell growth by preventing cell loosening (Zeevaart and Creelman, 1988). ABA also inhibits growth by interfering with nucleic acid synthesis, reducing the rate of cell enlargement, and reducing the rate of cell division. ABA is a promoter of bud and seed dormancy, and mutants that are deficient in ABA are viviparous (Pilet and Barlow, 1987). In addition, ABA is considered the plant's signal for water stress. The root synthesizes more ABA under water stress which is translocated to the shoot. ABA levels of the leaf can increase 50-fold during water stress (Christmann et al., 2005). The increased concentration of ABA in turn induces the closure of the guard cells of the stomata because high concentrations of ABA cause potassium and other ions to leave the guard cell. After the ions leave the guard cell, the guard cell loses turgidity and the stomata close (MacRobbie, 1997). In addition to closing stomata, ABA increases hydraulic conductivity of the root and increases the root:shoot ratio at low water potentials (Taiz and Zeiger, 2010).

Ethylene

The burning of the gas used for public and private illumination during the 19th century led to the discovery of ethylene (Davies, 2010; Wildman, 1997). Chemical identification of ethylene was possible through study of this illumination gas (Davies, 2010). Ethylene is a gaseous plant hormone involved in a wide range of physiological processes that range from seed germination to apoptosis (cell death). Although its concentration in plants is normally low, levels are greatly increased during particular physiological processes such as leaf and flower abscission, fruit ripening, as well as in responses to a wide range of biotic and abiotic stimuli (Lin et al., 2009). The capability of higher plants to produce ethylene is evident in all tissues. The rate at which ethylene is synthesized varies among plant tissues and is affected by the age of the respective tissue (Mattoo and Suttle, 1991).

Ethylene Synthesis

Two key enzymes are involved in the ethylene synthesis pathway. The first enzyme ACC-synthase (ACS) converts S-adenosylmethionine (SAM), which originates in the methionine cycle, to 1-aminocyclopropane-1-carboxylic acid (ACC). ACC is then oxidized to ethylene by ACC-oxidase (ACO) (Chaves and Mello-Farias, 2006; Kende, 1993; Zarembinski and Theologis, 1994). Tissues that do not produce significant levels of ethylene have low ACS activity, but upon stimulation ACS activity can be quickly induced (Chae et al., 2003). Both ACS and ACO can be induced upon stress (Morgan and Drew, 1997). Unlike ACS, ACO has a constitutive activity present in most tissues. Thus, one of the major steps during ethylene induction is ACS, which is a rate-limiting enzyme (Chae et al., 2003). The ACS6 gene encodes for one of the ACS proteins and is part of a multi-gene family (Fluhr and Mattoo, 1996; Kende, 1993; Tsuchisaka and Theologis, 2004) in which all genes are independently regulated (Fluhr and Mattoo, 1996). *ACO2* also belongs to a multi-gene family encoding ACO proteins (Barry et al., 1996; Kende, 1993). Ethylene perception occurs when the plant hormone binds to an ethylene receptor (ETR). ETRs are a family of membrane receptors (Chang et al., 1993), and the ETR5 gene encodes for a membrane protein which is part of this multi-gene family. Ethylene perception and its signal transduction pathway that follows are feedback regulated (Urao et al., 2000).

It is desirable to protect yield by preventing fruit loss induced by the peak in ethylene prior to abscission. Thus the need for alternatives that could reduce or prevent abortion of cotton bolls under stress is worthwhile. Heitholt et al. (1993) suggested that preventing loss of flowers and young fruit is essential in cotton yield enhancement; thus ethylene inhibitors may provide an alternative for reducing the loss of reproductive structures in an effort to improve cotton yield.

Water-Deficit Stress and Ethylene

In recent years drought stress tolerance has become one of the main points of interest to agronomic research since major crops such as cotton are experiencing drier years than normal due to changes in weather patterns (Gowda et al., 2007; Pettigrew, 2004a). As a result, declining irrigation reserves are occurring together with an increase in costs associated with irrigation (Gowda et al., 2007). This is due to dwindling water supplies from aquifers that have had less recharge (Howell et al., 2004). Water-deficit stress detrimentally impacts cotton production (Howell et al., 2004; Mooney et al., 1991; Pettigrew, 2004b). Although cotton is able to maintain a leaf turgor potential by osmotic adjustment while facing moisture deficit (Oosterhuis and Wullschleger, 1987), it eventually faces a reduction in leaf water potential under dry conditions (Nepomuceno et al., 1998; Turner et al., 1986). In response to drought, stomata tend to close reducing their conductance which consequently affects leaf photosynthesis (Ephrath et al., 1990; Faver et al., 1996; Genty et al., 1987). Under water-deficit stress, the overall dry matter accumulation in cotton plants decreases (Mooney et al., 1991) and expansion of leaf blades and plant growth is reduced, thus promoting stunted growth (Ball et al., 1994; Gerik et al., 1996). Limited water availability causes cotton plants to generate fewer flowers resulting in reduced boll production (Guinn and Mauney, 1984).

The variable which contributes most to lint yield is the number of bolls per unit area (Boquet et al., 2004; Worley et al., 1974; Wu et al., 2005). Therefore, increased boll abortion in plants under severe stress during their reproductive development consequently reduces lint yield (Gerik et al., 1996; Pettigrew, 2004a; Turner et al., 1986). One of the factors interacting with stress is hormones. A burst in ethylene synthesis that lasted four days was observed prior to occurrence of boll abscission (Morgan et al., 1992). The authors suggested that this peak in ethylene synthesis may be the signal necessary to initiate cell wall hydrolysis in the abscission zone followed by abscission of that particular structure.

Diverging opinions exist on the impact of water deficit on ethylene synthesis. Reports of increased ethylene synthesis due to water stress were based on detached plant parts being subjected under a rapid dry down period and then stored in closed chambers while air samples were collected for ethylene measurements (Adato and Gazit, 1974; Aharoni, 1978; Apelbaum and Yang, 1981; Ben-Yehoshua and Aloni, 1974; Bergner and Teichmann, 1993; Hoffman et al., 1983; Huberman et al., 1993; McKeon et al., 1982; McMichael et al., 1972; Michelozzi et al., 1995; Narayana et al., 1991; Tudela and Primo-Millo, 1992; Wright, 1977; Wright, 1981). On the other hand, ethylene emission studies which exposed plants to a gradual dry down period by terminating watering and collecting air samples from intact plants or plant parts placed in closed chambers, with or without constant air flow, indicated that water-deficit stress did not increase ethylene production (Ben-Yehoshua and Aloni, 1974; Eklund et al., 1992; Feng and Barker, 1992; Hubick et al., 1986; Morgan et al., 1990; Narayana et al., 1991).

Brassinosteroids

Brassinosteroids were discovered in Brassica pollen extracts. Their properties in plant growth were demonstrated through bioassay in bean petioles (Davies, 2010). Brassinosteroids include over 60 steroidal compounds (Davies, 1995) that are classified as growth promoting substances accelerating cell division and cell elongation (Adam and Marquardt, 1986; Clouse and Sasse, 1998). In addition, brassinosteriods are also involved in light-regulated development, and brassinosteroid-induced cell growth is light dependent (Li et al., 1996). Kasukabe et al. (1999) filed a patent on the production of cotton fibers with improved fiber characteristics by treatment with brassinosteroids. Subsequent work by Sun et al. (2005) showed that exogenous applications of the brassinosteroid brassinolide (BL)

promoted fiber elongation while treatment with brassinazole (Brz), a brassinosteroid biosynthesis inhibitor, inhibited fiber development. When cotton floral buds were treated with Brz, fiber differentiation was completely absent. In addition, expression of fiber genes associated with cell elongation increased in ovules treated with BL and was suppressed by Brz treatment, establishing a correlation between brassinosteroid-regulted gene expression and fiber elongation (Sun et al., 2005).

Jasmonates

Jasmonic acid and its methyl ester, substrates of the biosynthesis of jasmonates, are considered powerful senescence-promoting substances (Gross and Parthier, 1994; Ueda et al., 1991). Jasmonates accelerate senescence by reductions in chlorophyll content and degradation of chloroplast proteins, especially Rubisco (ribulose 1,5-bisphosphate carboxylase/oxygenase) (Beltrano et al., 1998; Creelman and Mullet, 1995). They are also known to promote tuber formation, fruit ripening, pigment formation, and tendril coiling while inhibiting growth and seed germination (Davies, 1995; Gross and Parthier, 1994). Recent work has focused on the role of jasmonate in promoting abscission. Jasmonic acid and its methyl ester affect sugar metabolism in the abscission zone in bean petioles through an increase in cellulase activity involved in the degradation of cell wall polysaccharides (Ueda et al., 1991). In addition, jasmonates are involved in the plant's defense against water stress, wounding, insect attack, and pathogen attack (Baron and Zambryski, 1995; Creelman and Mullet, 1995; Creelman and Mullet, 1997). Jasmonates also induce ethylene formation (van Loon et al., 1998).

Salicylic Acid

Salicylic acid, which is chemically related to aspirin, belongs to a diverse group of plant phenolics (Raskin, 1995). Like jasmonates, salicylic acid may be involved in the resistance to pathogens because it induces the production of pathogenesis-related proteins. However, the salicylic acid defense pathway is independent of the jasmonate defense pathway (van Loon et al., 1998). Pathogenesis-related proteins are protein compounds with antimicrobial and antifungal activities; eleven pathogenesis related protein families have been characterized (Sticher et al., 1997). Transgenic tobacco plants lacking the ability to produce salicylic acid were unable to induce a resistance mechanism, called systemic acquired resistance, to certain plant diseases (Baker et al., 1997; Delaney et al., 1994; Hammerschmidt and Becker, 1997; Ryals et al., 1996). Salicylic acid also enhances flower longevity, inhibits ethylene biosynthesis, inhibits seed germination, blocks the wound response, and reverses the effects of ABA (Davies, 1995; Gross and Parthier, 1994).

Salicylic acid serves as a trigger for increasing the activity of alternative respiration (Kapulnik et al., 1992). Alternative respiration refers to a minor respiratory pathway in plants that is not sensitive to cyanide, unlike conventional respiration. Alternative respiration represents approximately 27 to 30% of the electron flow through the electron transport chain (Lennon et al., 1997; Ordentlich et al., 1991). Because alternative respiration does not produce much energy in the form of ATP, most of the energy produced in alternative respiration is released as heat. The heating of plant tissue caused by an increase in alternative respiration is coined thermogenecity. Thermogenecity plays a key role in increasing the temperature of Araceae (Arum family) inflorescences by as much as 25° C. Increasing the temperature of the inflorescence volatilizes amine compounds, and the odor given off from the amines attracts insect pollinators (Taiz and Zeiger, 2010). The alternative oxidase associated with alternative respiration has been implicated in various biochemical processes including a role in lowering mitochondrial reactive oxygen production in tobacco cells (Ribas-Carbo et al., 2000) to alleviate stress, as

an avenue for improving tolerance to chilling injury, and as a means for improving resistance to various pests. Bi et al. (1997a) had previously indicated that insect herbivory on cotton induced resistance to the cotton bollworm (Helicoverpa zea). Since abundant evidence had accumulated showing that salicylic acid plays a key role in coordinating the expression of systemic acquired resistance against phytopathogens (Vernoolj et al., 1994), Bi et al. (1997b) investigated whether herbivory impacted production of foliar salicylic acid and hydrogen peroxide, a frequently observed response following pathogenesis. In cotton, herbivory enhanced foliar catalase and ascorbate peroxidase activities, but the application of salicylic acid or methyl salicylate to cotton plants did not affect foliar resistance to H. zea. Studies by Heitholt et al. (2001) also failed to show a response to exogenously applied salicylic acid relative to flower production, boll retention, and yield.

Polyamines

Polyamines are not only crucial components in DNA, but are also vital substances present in all forms of life. Polyamines are classified as a plant hormone group since they promote plant growth and development at small concentrations (Davies, 2010). Polyamines are generally antagonistic to abscisic acid and are indispensable to plants at the time of flowering, as well as at the time of early fruit development (Kloareg et al., 1986). Thus, a deficiency of polyamines during flowering and early fruit development causes direct negative effects on the reproductive development of plants. Bibi et al. (2010) examined the effect of putrescine, one of the most common polyamines, on ovary development and seed set of cotton under high temperature stress (day/night temperature of 38/20° C) and controlled environmental conditions. Putrescine was applied to floral buds of cotton 24 hours prior to anthesis. Increased temperature in this study decreased seed set in cotton flowers which was ameliorated by the exogenous application of putrescine. Putrescine application led to increased levels of putrescine in cotton flowers, which was associated with increased seed set despite the negative effect of increased temperature.

Peptides

To date, four peptide signal molecules have been discovered in plants: systemin, endo40, cyi1a, and sulfokine (Franssen, 1998), although plants appear to possess the receptors for a plethora of peptide signals (Schaller, 2001). Plant peptides are active in the nanomolar to picomolar range (Van de Sande, 1996). The peptide signal molecule systemin behaves as an active factor that is transported out of the wounds of wounded tomato plants to distal tissues inducing the expression of two well characterized wound-inducible proteinase inhibitor encoding genes (Pearce et al., 1991). As such, these genes are systemically induced in tomato plants as part of the inducible defense repertoire of the plant. Endo40 was reportedly isolated as a gene that is activated during root nodule formation on legumes as a result of the interaction of these plants with soil-borne Rhizobium bacteria (Yang et al., 1993). Additional studies suggest that the function of endo40 is not restricted to nodule formation (Franssen, 1998), but that it may also play a role in cell proliferation, which in most cases is controlled by an auxin-cytokinin balance. Miklashevichs et al. (1997) suggest that cyi1a encodes a peptide which participates in the events downstream of a junction point of cytokinin and auxin action that leads to cell division. Three of the four peptides that have been isolated thus far appear to have a role in cell division and proliferation, these being enod40, sulfokins, and cyi1a. Of these three, enod40 and cyi1a seem to interact with the activity of the classical hormones auxin and cytokinins; sulfokins, however, work independently of these hormones (Franssen, 1998).

PLANT GROWTH REGULATORS

Several plant growth regulators (PGRs) are available in the market for cotton production systems. These growth regulators are organized into groups based on the stages of development at which they trigger a response: germination, seedling, vegetative, reproductive developments, and harvest aids. Our discussion of the PGRs will focus mainly on vegetative and reproductive stages and cotton flowering and fruiting aspects to positively influence cotton production.

Gibberellins and Auxins

In a study with four concentrations (50, 100, 150, 200 mg/l) of gibberellic acid (GA3), cotton sprayed just before anthesis (five-week-old plants) produced a significantly greater number of flowers (at the two highest concentrations) than did the control (Mathur and Mittal, 1964). Although all four concentrations of gibberellic acid increased the number of flowers shed during the eight-week-period, the highest concentration still retained more flowers than the untreated control. The potential for increasing yield through increased flower production is more importantly reflected in the components of the mature boll (boll size, boll weight, ovules (seed)/boll, fibers/seed, and weight per fiber). Yield may be increased through a single increase in a given input or by a multiple additive effect. Miller and Rawlings (1967) reported that as yield increased by selection, lint percentage and seeds per boll increased while boll and seed size decreased. If boll size is decreased, the number of bolls produced per acre and the total surface area of seed therein becomes more important. Experiments by Giavalis and Seagull (2001) demonstrated changes induced by hormone application can increase fiber initiation. Significant increases in fiber production, relative to untreated controls, were found with an exogenous application of either indole-3-acetic acid or gibberellic acid. The largest increase in fiber initiation was realized with a pre-anthesis treatment of indole-3-acetic acid. These authors suggested 1) that manipulation of the hormone level might cause an increase in the proportion of epidermal cells that differentiated as fibers or 2) that hormone treatments might induce cell division, resulting in more epidermal cells that could potentially lead to a greater number of fiber cells. Berlin (1986) reported that fiber number per ovule varied among species and cultivars. Examination of ovule surfaces on the day of anthesis by scanning electron microscopy revealed about 60,000 cells per ovule regardless of the cotton type. This number increased from about 1,000 epidermal cells at 23 days preanthesis to the 60,000 at anthesis and to nearly 350,000 cells at 6 days postanthesis. Initial ovule fiber cell members were controlled primarily by additive gene effects in a study by Bowman et al. (2001) suggesting that positive combining ability of some cultivars for that trait would make them good parents in a breeding program for improving fiber cell numbers. Reports of the proportion of epidermal cells that develop into fibers vary from 10% (Ryser, 1999) to 25% (Beasley, 1975). The good news is that the development cues for fiber production appear to be present over a considerable time frame, so there may be a long "window of opportunity" over which development can be manipulated to increase fiber production (Seagull and Giavalis, 2004).

Although the data for the timing of fiber initiation is varied, most reports indicate that initiation begins several hours to several days before anthesis (Berlin, 1986; Joshi et al., 1967; Stewart, 1975). Chen and Guan (2011) reported that increasing auxin levels at the right time and place during ovule and fiber development improves the yield and quality of cotton fibers. Their contention is that biotechnology succeeded in increasing cotton yields through introduction of transgenes for herbicides and insecticides. However, the ability to improve cotton quality has not been possible without penalty in fiber yield or seed size or number. Simultaneous improvement in yield and quality of cotton fiber was

obtained by over-expression of a gene responsible for the synthesis of the auxin indole-3-acetic acid (Chen and Guan, 2011). The question is whether these same responses can be elicited by exogenous foliar applications of auxins.

Chaperone

Chaperone is a PGR containing the nitrophenolates sodium 5-nitroguaiacolate, sodium ortho-nitrophenolate, and sodium para-nitrophenolate. These active ingredients, termed nitrophenolates, are found naturally in plants and have been shown to stimulate plant growth by altering the activity of specific antioxidant enzymes, such as superoxide dismutase (SOD), catalase (CAT), and peroxidase (POX) (Djanaguirman et al., 2004). These enzymes are involved with scavenging reactive oxygen species, such as superoxide ions, hydrogen peroxide (H2O2), hydroxyl (OH-), and singlet oxygen (O2-). Reactive oxygen species can attack proteins, nucleic acids, and polysaccharides (Matysik et al., 2002) and are increased in response to plant stress (Apel and Hirt, 2004; Gill and Tuteja, 2010). As a result of their overproduction, more are produced than are metabolized and oxidative stress occurs (Dhindsa et al., 1981). Therefore, the ability to lessen the impact of ROS on the physiology and yield of crop species is desirable. As early as 1995, Guo and Oosterhuis (1995) stated that Atonik, the former name of Chaperone, may enhance cotton growth and yield through increased assimilation of nutrients, nitrate reduction, and photosynthesis, as well as improved translocation, cytoplasmic streaming, and increased cell integrity. Guo and Oosterhuis (1995) also reported that Atonik hastened cotton maturity by 7 days compared to the non-treated cotton, but failed to show differences in lint yield. In years such as the 2001 growing season in Arkansas, which was a favorable year for cotton production, Atonik failed to show significant differences between treatments for yield or components of yield when applied alone or in combination with mepiquat chloride (Oosterhuis et al., 2001). Accordingly, spray application of other PGRs also failed to show significant yield responses. Subsequent work by Oosterhuis and Brown (2003) suggested that Chaperone may be a viable means for enhancing lint yields in cotton through enhancement of plant protein levels with concomitant increase in endotoxin levels. Increases in bollworm mortality were recorded for growth-chamber and field studies; all Chaperone treatments showed increased bollworm mortality that was increased with increasing rates of Chaperone. The results of two field studies (Study 1 - 2004 and 2005 in 28 locations in Texas at the commercially recommended rate of 0.43 g ai ha-1 and Study 2 - 8 locations from 2001-2005 in Burleson County, Texas at three rates: 0.43 g ai ha-1, 0.86 g ai ha-1, and 1.72 g ai ha-1) showed no differences in lint yield in Study 1 between Chaperone treated and the untreated control. However, in Study 2, across all experiments, Chaperone at 1.72 g ai ha-1 increased lint yield by 7.5% over the untreated control (Bynum et al., 2007). Results from this study did not support the use of Chaperone in cotton at its current recommended rate. Field studies were conducted from 2002 to 2005 in India (Djanaguiraman et al., 2010) to evaluate foliar spray of Atonik on cotton boll abscission rate by monitoring various reactive oxygen species (ROS) contents, antioxidant content, and antioxidant enzyme activity from 1 to 9 days after anthesis. This work suggested that the nitrophenolate (Atonik) sprayed plants counteracted deleterious effects of ROS by a peroxide/phenolics/ascorbate system, resulting in reduced boll abscission and increased yield. Yield responses to the nitrophenolate PGR have been inconsistent in tomato (Lycopersicon esulantum L.) and strawberry (Fragaria X ananassa) plants (Djanaguiraman et al., 2004; Zurawicz, 2004). Investigations with peanut (Arachis hypogaea L.) showed no effect on pod yield, percent extra-large kernels, percent total sound mature kernels, and crude protein levels of seed under a range of environmental and edaphic conditions with four cultivars.

PGR-IV

Another example of a combination of compounds in a PGR includes PGR-IV, which is a combination of gibberellic acid, indolebutyric acid, and a propriety fermentation broth. Various responses were observed for yield enhancement in studies by Oosterhuis and Zhao (1994). Foliar application gave yield enhancement that was associated with increases in leaf growth, nutrient uptake, and boll number, whereas yield enhancement from a soil application was associated with enhanced root growth and nutrient uptake. Subsequent work indicated that PGR-IV application made to plants grown in growth chambers with water stress imposed had the ability to partially alleviate the detrimental effects of water stress on photosynthesis and dry matter accumulation (Zhao and Oosterhuis, 1997). Additional studies were conducted to determine if PGR-IV was beneficial for increasing fruit retention of shaded cotton (Zhao and Oosterhuis, 1998). Shade shelters provided a 63% sunlight reduction. Shading during early squaring did not affect yield; however, shading after the first flower stage significantly increased leaf chlorophyll concentration and fruit abscission and also decreased leaf photosynthetic rate, nonstructural carbohydrate concentrations, and lint yield. An application of PGR-IV to the foliage before shading gave a numeric increase of 6 to 18% in lint yield compared with shaded plants not treated with PGR-IV. Guinn (1976a, 1982) had previously reported that ethylene and abscisic acid contents increased dramatically under low-light conditions resulting in boll abscission. A study by Biles and Cothren (2001) in Texas examined the use of PGR-IV and mepiquat chloride on cotton flowering when applied alone or used in sequential applications. The mepiquat chloride and PGR-IV + mepiquat chloride treatments caused plants to have a season-long average of 0.55 and 0.48 more flowers m-1 of row day-1, respectively, than the untreated plants. Earlier work (Oosterhuis and Zhao, 1993; Robertson and Cothren, 1995) suggested that yield increases resulted from increased boll numbers and boll weight (Faircloth, 2007).

Mepiquat-Based PGRs

One of the most widely used PGRs in cotton production is mepiquat chloride (MC) and similar products (Table 1).

Table 1. Mepiquat and Mepiquat-like growth regulators.

Common Name	Trade Name	Company
Mepiquat chloride	Mepex	DuPont™
Mepiquat chloride + kinetin	Mepex Ginout	DuPont™
Mepiquat chloride + cyclanilide	Stance	Bayer
Mepiquat pentaborate	Pentia	BASF

The original intent of this product was to suppress vegetative growth and reduce plant height. In situations where excess moisture and nitrogen were problems, this compound effectively reduced plant height in most instances (Nuti et al., 2006; Zhao and Oosterhuis, 1999), but was not necessarily associated with yield increases (Heilman, 1981; Boman and Westerman, 1994). Mepiquat chloride acts as an anti-gibberellic acid compound, thus decreasing cell elongation and usually reducing number of main-stem nodes (Kerby et al., 1986; Pettigrew and Johnson, 2005), although this is not always the case (Zhao and Oosterhuis, 1999). Earlier maturity has also been reported from mepiquat chloride use (Gwathmey and Craig, 2003; Oosterhuis et al., 1991).

Dodds et al. (2010) reported that a Beltwide evaluation of numerous mepiquat-based products showed reduced end of season plant height with application of all MC and MC-type PGRs examined.

However, the PGR applications did not impact lint yield, micronaire, or uniformity in any region of the study (Dodds et al., 2010). Of the four products evaluated, no single product provided superior performance with regard to growth regulation, yield, or fiber quality. Several have reported acceleration of maturity whereas others have indicated that mepiquat chloride had no effect on earliness (Stewart et al., 2000). Gwathmey and Craig (2003) found that mepiquat chloride significantly hastened time to cutout, defined as NAWF=5 (Bourland et al., 2001), but the cultivars examined differed in this response as well as in the treatment regime. Comparisons across cultivars indicated that cutout occurred four to six days earlier with MC than in the untreated control. However, a single application of MC did not hasten flowering progress in STV 132, the earliest cultivar, relative to the untreated control. Low-rate multiple applications suggest that the growth habit of later cultivars which are more indeterminate may be shifted more by MC than earlier, more determinate types. Bader and Niles (1986) reported similar responses for cotton cultivars. Mepiquat chloride has also been used in efforts to improve carbohydrate source-sink relations to enhance efficiency of yield formation in cotton (Gwathmey and Clement, 2010). The understanding of carbon partitioning in cotton is not straight forward, as each boll can receive photosynthate from multiple sources (Pace et al., 1999). Autoradiography work by Brown (1968) showed photosynthate to a boll was provided by its bract, boll wall, subtending leaf, main-stem leaf subtending the sympodium and depended mainly on the subtending and other nearby leaves. Others found that the subtending leaf was the primary source for the boll (Ashley, 1972; Benedict et al., 1973), but Wullschleger and Oosterhuis (1990) contend that the total carbon needs of most bolls could not be supplied by the subtending leaf.

The premise of Gwathmey and Clement (2010) was that by increasing plant population density (PPD) through planting in narrower rows, boll retention would be reduced more than leaf area. Thus, leaf-to-boll ratio would be increased and the concentration of residual starch in stem tissue would be increased during boll filling. However, higher PPD tended to reduce bolls per plant more than leaf area per plant in narrower rows. They also hypothesized that application of MC would effectively decrease leaf-to-boll ratio and stem starch reserves, thus promoting yield formation at higher PPD. Their finding supported the hypothesis that boll set and yield formation in narrow-row systems benefit from a reduction in LAI. In this situation MC increased boll set percentage.

1-Methylcyclopropene (1-MCP)

The compound 1-methylcyclopropene (1-MCP) is a gaseous ethylene antagonist that blocks ethylene receptors, consequently inhibiting its perception and preventing ethylene effects in the plant tissues (Blankenship and Dole, 2003; Sisler and Serek, 1997). The affinity of 1-MCP to ethylene receptors is 10x greater than the affinity of ethylene to its receptors (Blankenship and Dole, 2003). 1-MCP is widely used in horticultural production (Fan and Mattheis, 2000). Studies in horticulture mainly focused on post-harvest physiology of climacteric fruit to counter the detrimental effects of ethylene. Its beneficial impact has been conclusively documented in fruit production and processing (Vilas-Boas and Kader, 2006; Zhou et al., 2006) as well as in flower quality (Porat et al., 1995; Reid and Celikel, 2008). These studies showed that the compound impacts a variety of physiological processes, such as decreasing ethylene synthesis (Blankenship and Dole, 2003; Dong et al., 2001; Jeong et al., 2002), respiration (Blankenship and Dole, 2003; Dong et al., 2001; Fan and Mattheis, 2000), and chlorophyll degradation (Blankenship and Dole, 2003; Fan and Mattheis, 2000; Jiang et al., 2002), thus extending shelf-life (Fan and Mattheis, 2000).

Ethylene, a plant stress hormone, is known to increase under environmental stresses such as high temperature (Davis et al., 1990) and water deficits (Pettigrew 2004a and 2004b). Morgan et al. (1992)

observed a burst in ethylene levels that lasted four days before abscission and concluded that this peak in ethylene may have been the necessary signal to initiate cell wall hydrolysis in the abscission zone followed by abscission. Since ethylene plays an important role in abscission (Guinn, 1976a) and young cotton fruit are more vulnerable to abscission than older fruiting forms, it is desirable to protect yield by preventing fruit loss induced by a peak in ethylene synthesis before abscission. Although squares can abscise at any age, most do so during the first seven days after appearance (Crozat et al., 1999). However, opinions vary as to the most susceptible stage for vulnerability to shedding. The most susceptible boll stage has been cited as occurring during the week following anthesis (open-flower stage) (Crozat et al., 1999), whereas for modeling purposes Hearn and da Roza (1985) assumed bolls were not susceptible to shedding 10 days after anthesis (flowering). Moreover, according to Guinn (1998), bolls are almost immune to shedding only after three weeks following anthesis. Since yield in cotton is generally associated with the number of bolls produced per unit area (Boquet et al., 2004; Wu et al., 2005), regardless of genotype and environment (Wells and Meredith, 1984), any means of reducing boll loss is important relative to increases in yield. Thus, if ethylene is a causal factor in boll abscission or in leaf senescence (Grbic and Bleecker, 1995), or other physiological processes, reducing the impact of ethylene on these processes provides a potential for increasing yield, and 1-MCP provides a mechanism for obtaining this goal. However, knowing the appropriate time to apply 1-MCP is critical for optimizing responses for reducing stress responses.

With the aforementioned information, da Costa and Cothren (2011a) established studies to investigate how drought affects plant growth/development and yield components of 1-MCP-treated cotton plants during the peak of reproductive phase under greenhouse conditions. A secondary objective was to determine if gas exchange, plant growth/development and yield component responses to drought could be altered by the presence of 1-MCP treatment. The compound 1-MCP was delivered as a gas one day before water-deficit stress was imposed as a protection agent to the fruiting sites already present. Utilizing plant mapping, dry matter partitioning and chlorophyll content data analyses, da Costa and Cothren (2011a) observed that water-deficit stress reduced plant height, internode length, nodes above white flower, total leaf area and weight, vegetative weight, number of squares, reproductive growth, number and retention of bolls. On the other hand, drought increased specific leaf weight, chlorophyll content, and harvest index. 1-MCP treatments had little or no positive effect on plant mapping, dry matter partitioning and chlorophyll content. The application of 1-MCP decreased the number of vegetative nodes, and increased the number of squares and reproductive nodes by 9% when plants were well-watered and by 17%, when under stress. The 1-MCP treatment showed a potential to improve lint yield in cotton, as it increased reproductive nodes per plant basis mainly for cotton under water stress during its reproductive phase. However, this greater number of reproductive nodes did not lead to a better harvest index, since 1-MCP caused high fruit abscission. In unpublished data (da Costa and Cothren, 2008 and 2009), it was observed that 1-MCP temporarily increased ethylene emission in cotton leaves above the untreated control one day after its application. Because ethylene is one of the main stimuli in abscission, it was speculated that this increase of ethylene early in the reproductive stage was one of the major factors for the high fruit shed that was observed 22 days after 1-MCP application. Loka and Oosterhuis (2011) reported that 1-MCP application to water-stressed cotton had no alleviating effect on stomatal conductance, leaf photosynthesis, and respiration. Similarly, leaf and pistil carbohydrate content remained unaffected by 1-MCP application with the exception of pistil sucrose content where 1-MCP decreased sucrose accumulation due to water-deficit stress.

Additional work has been completed with timing of application of 1-MCP (Kawakami et al., 2010) temperature conditions where the maximum temperatures during the period of cotton fruit development were well above the optimum 30° C temperature for cotton. Plants receiving 1-MCP at first

flower and first flower plus 2 weeks had significantly higher seed cotton and lint yields than the untreated control. Since no effect on cotton fruit abscission was observed, one possible reason offered for the yield increase was that the 1-MCP treated bolls in the middle of the plant canopy had significant increases in boll weight. Stress levels were also decreased by 1-MCP treatment; a higher maximum quantum efficiency of Photosystem II and lower activity of the leaf antioxidant glutathione reductase were noted as well. Loka and Oosterhuis (2011) were unable to show that 1-MCP alleviated the effects of water-deficit stress on leaf photosynthesis, respiration, and stomatal conductance. Work continues to refine the use of 1-MCP in cotton production systems.

1-MCP and Synthetic Ethylene

Field studies were conducted by da Costa and Cothren (2011b) to evaluate 1-MCP capabilities to ameliorate the negative effects (if any) of ethephon, an ethylene-releasing chemical, as a source of abiotc stress on growth and yield components of cotton plants. Cotton plants are known to have the ability to compensate for early season fruit loss (Stewart *et al*., 2001), however, nothing is known regarding such a loss later in the season. Thus, the authors also investigated to what extent cotton plants can compensate for fruit loss during the late season as a secondary objective. Following manufacturer's recommendations at that time, 1-MCP was applied prior to the stress event in combination with a surfactant. One day later, ethephon was delivered as the source of stress.

Nodes above white flower (NAWF) value refers to the number of mainstem nodes that are above a sympodial (reproductive) branch. In order to be counted, such branch has to have a white flower in its 1st fruiting position. NAWF assessment provides researchers the progression of the reproductive stages, and where the plant is relative to its maturity development (Pettigrew, 2004a). Both rates of 1-MCP detrimentally effected NAWF in the absence of the surfactant resulting in an acceleration of crop maturity, meaning that the reproductive phase was shortened (Table 2; da Costa and Cothren, 2011 b). Such shortening was also supported by a low number of square (flower buds) counts. On the other hand, when both rates of 1-MCP were applied together with the surfactant (as recommended by the manufacturer) and compared against untreated-control, such combination ameliorated the negative effects of 1-MCP rates on NAWF and preserved the normal rhythm of the crop maturity.

It is important to highlight that vegetative nodes have minimum contribution in the overall lint yield. Reproductive nodes, which originate on sympodial branches, account for the vast majority of the cotton lint yield (da Costa and Cothren, 2011b). Ethephon alone reduced the number of reproductive nodes while all treatments with 1-MCP were not different than the untreated-control, demonstrating that 1-MCP overcame the unfavorable effect of ethephon on the number of reproductive nodes (da Costa and Cothren, 2011 b). This ability of 1-MCP to improve the number of reproductive nodes on stressed plants was also observed when cotton plants were under water deficit. Our associated studies showed that 1-MCP increased the number of reproductive nodes per plant basis by 17% when compared to untreated plants also under water deficit (da Costa and Cothren, 2011b).

Such an improvement in the number of reproductive nodes caused by 1-MCP treatments, however, did not generate greater lint yields. When applied alone, 1-MCP had the lowest lint yields. While in combination with the surfactant, 1-MCP lint yield was not different than the untreated-control (da Costa and Cothren, 2011 b). Therefore, 1-MCP alone showed a negative effect on lint yield. Numerically, the treatment with the highest lint yield, however, was ethephon alone (da Costa and Cothren, 2011 b). Ethephon alone also caused the greatest fruit abscission (Table 2). Such abscission consequently favored the formation of more bolls as it was demonstrated by the linear relationship (r^2 = 0.89) between fruit shed and green bolls over the 2 yr experiments (Fig. 1).

Table 2. Effects of 1-MCP, surfactant and ethephon on plant height, internode length, counts of vegetative, reproductive, and mainstem nodes, and nodes above white flower (NAWF) per plant 50 days after treatments were initiated at the Texas AgriLife Field Laboratory in Burleson County, TX, 2007-2008 (adapted from da Costa and Cothren, 2011 b).

1-MCP	Surfactant 0.37% v v^{-1}	Ethephon 292 mL ha^{-1}	Lint yield	Abscised fruit number	Square number	Reproductive nodes	NAWF
g a.i. ha^{-1}			Kg ha^{-1}				
0.0	-	-	1348ab	21.6ab	0.34ab	15.5a	1.1a
0.0	-	+	1440a	26.2a	0.41ab	13.9b	1.1a
0.0	+	+	1359ab	19.6b	0.60ab	14.9ab	0.8a
25.0	-	+	1170c	21.8ab	0.09b	14.6ab	0.0b
25.0	+	+	1208bc	23.4ab	0.84a	15.8a	1.3a
50.0	-	+	1083c	21.3ab	0.19b	15.2a	0.0b
50.0	+	+	1207bc	20.9b	0.54ab	15.1a	1.3a

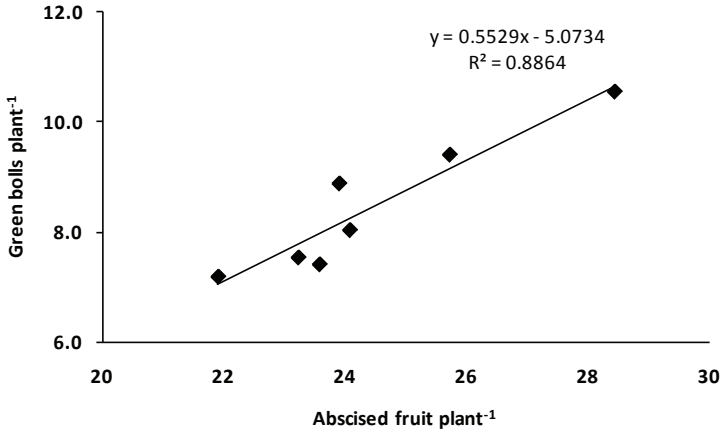

Figure 1. Relationship between the number of green bolls and abscised fruit per plant at 50 days after treatments were initiated at the Texas AgriLife Field Laboratory in Burleson County, TX, 2007-2008 (adapted from da Costa and Cothren, 2011 b).

Even though 1-MCP treatments favored the formation of reproductive nodes on stressed cotton plants, lint yields were not improved. The most logical question is to investigate why such yields were not improved as well. In order to address such a logical question, yield components were investigated at harvest. It was observed that both rates of 1-MCP favored the formation of fruit set in the upper canopy. Nevertheless, this increase in the total fruit number in the upper canopy did not lead to increased lint yield because the majority of this fruit increase was due mainly to a 76% improvement (data not shown) in the number of what appeared to be full size but still yet immature bolls (not cracked). Thus, both rates of 1-MCP showed potential to increase lint yield, but this potential was not converted into lint yield because the extra bolls set did not open in time for the mechanical harvest. Ethephon alone, on the other hand, had greater total number of fruit located in the lower portion of the canopy. Most of these bolls were already opened during harvest, granting ethephon treatment with the highest lint yield. Thus, these findings demonstrated that cotton plants treated with ethephon were still able to compensate for the fruit loss occurred later in the season (mid-bloom; da Costa and Cothren, 2011 b).

SUMMARY

From the previous discussion, it is obvious that cotton yield is affected by a number of factors. Although we can partially control some of these factors through cultural inputs, our ability to control the environment is often beyond our control. Two of the major environmental constraints limiting yield are temperature and water supply. When moisture is available through irrigation, we can effectively remove the water limitation. However, a large portion of cotton is grown under dry land production, and these areas are often prone to temperature stress as well. Plant growth regulators are used during the fruiting cycle of cotton in an effort to overcome the constraints of water stress and high temperature. The mepiquat chloride products can effectively reduce overall plant growth through reductions in plant height and leaf area and have been shown to benefit the crop by changes that lead to more efficient water uses. Other PGRs have also shown potential for increasing flower production, lint yield, and tolerance to water and temperature stresses. Means of more effectively monitoring the stress level of the crop also show utility for better timing and use rate in the crop.

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