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AGRONOMY AND PHYSIOLOGY

6-Benzyladenine Enhancements of Cotton Yields

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ABSTRACT

A recent greenhouse study suggested that cytokinin applied to young cotton seedlings may enhance overall performance and yield, especially in water-limited environments. The objective of this study was to evaluate the effects of a commercial formulation of cytokinin (6-benzyladenine) applied foliarly during the early stages of seedling development on Deltapine 444 BG/RR yields under water-deficit conditions. Field studies in 2005, 2006, and 2008 compared untreated controls with 6-benzyladenine treated seedlings at the cotyledon to two-leaf stage. Greenhouse studies determined that a range of concentrations up to 300 µmol/mol 6-benzyladenine enhanced rooting, hypocotyl thickness, and seedling growth at this developmental stage. Concentrations of 400 to 1000 µmol/mol resulted in stunting of the seedlings and phytotoxic lesions on the cotyledon surfaces at the higher concentrations. In the field, seedlings treated with 6-benzyladenine within two-weeks after planting exhibited increased hypocotyl diameters, increased lateral root proliferation, and a breaking of apical meristem dormancy. Increased cotton yields were observed in 2005 and 2008 compared with untreated controls. No yield enhancement was seen in 2006 possibly because of the severity of the drought experienced. This study showed that application of 6-benzyladenine to cotton early in development has the potential to increase yields and reduce water stress in cotton.

Field studies performed to date evaluated cytokinin foliar applications at the pinhead square stage or later (Bednarz and van Iersel, 1998; Cothren and Cotterman, 1980; Cothren and Oosterhuis, 2010; Guinn, 1986; Hedin and McCarty, 1994a, 1994b, 1997; Hofmann and Else, 1989; Mayeux et al., 1987). Responses ranged from yield enhancement to no effect. The lack of yield increases at some locations has been attributed to weather or other factors that masked the benefit of the product on the cotton plant. We hypothesized that the beneficial effects of cytokinin application would best be realized early in plant development before reproductive-induced changes in plant hormonal concentrations occurred. Burke (2009, 2011) evaluated the effects of a foliar application of a commercial formulation of cytokinin (6-benzyladenine) during the early stages of greenhouse-grown cotton seedling development, before the pinhead square stage, on enhancing the beneficial effects of cotton's hormonal response. The study reported increased hypocotyl diameter, breaking of apical dominance, increased lateral root formation, increased speed of lateral branch formations, a reduction in water use, and enhanced boll development. The time to first flower was reduced in the treated plants, and bolls were able to more fully develop compared to control plants. These findings suggested that cytokinin treatment of young cotton seedlings may enhance overall performance and yield, especially in water-limited environments. In the present study, we evaluated cotton yields over several years in response to an early application of cytokinin shortly after seedling emergence.

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METHODS AND MATERIALS

Greenhouse Cultural Practices. Deltapine 444 BG/RR (U.S. Patent 6838600) cotton seeds were planted into D40 Deepot cells (Stuewe & Sons, Inc., Tangent, OR) containing Sunshine Mix #1 soil (Sun Gro Horticulture Distributors Inc., Bellevue, WA). Three seeds were planted per Deepot cell, the cells were placed into a D20T tray (Stuewe & Sons, Inc., Tangent, OR), and the trays were placed on benches in a greenhouse set to provide a 31/27°C day/night cycle. Plants were thinned to one plant per pot seven days after planting to ensure seedling uniformity prior to hormone treatment. High-pressure sodium lights (430 W) (P. L. Light Systems, Beamsville. ON Canada) were used to maintain a 16/8 h photoperiod.

Cytokinin Concentration Determination for Cotton Seedlings at the Cotyledonary-Leaf Stage. The experiment was arranged in a completely randomized design with ten concentrations of 6-benzyladenine and a water control. Ten individual D40 Deepot cells containing a single seedling were treated to determine responses to increasing concentration of cytokinin. When the Deltapine 444 BG/RR plants reached the cotyledonary stage (Fig. 1, approximately seven days after planting) they were sprayed with 0 (water), 100, 200, 300, 400, 500, 600, 700, 800, 900 or 1000 µmol/mol 6-benzyladenine (MaxCel, Valent BioSciences, Chicago, IL). A single pass sprayer equipped with an 8003EV fan-tipped spray nozzle located in a safety hood was used in the hormone application at 20 PSI. Plants were placed 30 cm beneath the spray nozzle and allowed to sit at room temperature for one hour following the hormone application prior to being returned to the glasshouse. Phenotypic responses of the plants were evaluated eight days after treatment (Figure 2, the randomized seedlings were sorted by treatment prior to taking the photograph). Based upon the findings of this greenhouse study, subsequent field treatments received a single spray application up to 300 µmol/mol 6-benzyladenine at the cotyledonary stage. Seven days after treatment, cotton hypocotyl thicknesses of plants from the greenhouse were measured 2.54 cm above the soil surface using a 0-25 mm micrometer having 0.001 mm accuracy (Mitutoyo Corporation, Aurora, IL).

Figure 1. Deltapine 444 BG/RR seedling 7 days after planting in a D40 Deepot cell (Stuewe & Sons, Inc., Tangent, OR) containing Sunshine Mix #1 soil (Sun Gro Horticulture Distributors Inc., Bellevue, WA).

Crop Management: 2005. The soil type was an Amarillo fine sandy loam, and the fields were located in Lubbock, TX. Four 15 m rows of Deltapine 444 BG/RR cotton were planted in a North-South orientation per replication of a complete block design on Day of Year 158 (7 June 2005) using a John Deere 7300 MaxEmerge 2 VacuMeter Planter. The field was part of an annual sorghum-cotton rotation. The plots were pre-plant irrigated by furrow irrigation and only received rain there after. Seedlings were sprayed with 100 µmol/mol 6-benzyladenine (MaxCel, Valent BioSciences, Chicago, IL) on Day of Year 168 (17 June 2005). The plots were sprayed with Ginstar (Bayer CropScience, RTP, NC) and Prep (Bayer CropScience, RTP, NC) according to manufacturers instructions on Day of Year 280, and the plots were harvested on Day of Year 306. Three m of the center two rows of seven untreated (control) and seven 6-benzyladenine-treated replicate plots were hand harvested and evaluated for yield. Additionally, six m of outside row of three control and three 6-benzyladenine-treated plots were harvested with a John Deere 484 plot stripper and evaluated for yield.

Crop Management: 2006. The soil type was an Amarillo fine sandy loam, and the fields were located in Lubbock, TX. Four 30 m rows of Deltapine 444 BG/RR were planted per replication of a randomized complete block design in a North-South orientation on Day of Year 131 (11 May 2006) using a John Deere 7300 MaxEmerge 2 VacuMeter Planter. The field was part of an annual sorghum-cotton rotation. The plots were pre-plant irrigated by furrow irrigation and the three replications only received rain there after. Seedlings were sprayed with 150 µmol/mol 6-benzyladenine (MaxCel, Valent BioSciences, Chicago, IL) on Day of Year 145 (25 May 2006). The plots were sprayed with Ginstar (Bayer CropScience, RTP, NC) and Prep (Bayer CropScience, RTP, NC) according to manufacturers instructions on Day of Year 283, and the plots were

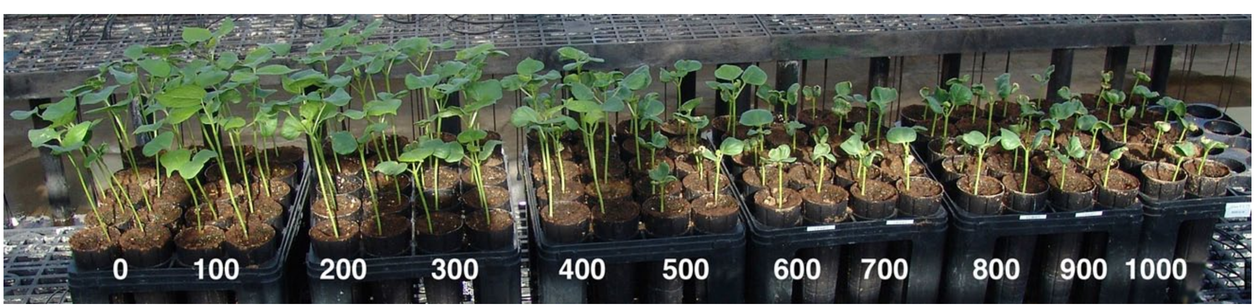

Figure 2. Photograph of seedling responses to different 6-benzyladenine concentrations for cotyledon spraying of DPL444BR seedlings. When Deltapine 444 BG/RR plants reached the cotyledonary stage they were sprayed with 0 (water), 100, 200, 300, 400, 500, 600, 700, 800, 900 or 1000 µmol/mol 6-benzyladenine (MaxCel, Valent BioSciences, Chicago, IL). The seedlings were evaluated for phenotypic responses 8 days after treatment with 6-benzyladenine.

harvested on Day of Year 291. Fifteen m of the center two rows of eight untreated (control) and eight 6-benzyladenine-treated replicate plots were harvested with a John Deere 484 plot stripper and evaluated for yield.

Crop Management: 2008. The soil type was an Amarillo fine sandy loam, and the fields were located in Lubbock, TX. Thirty-two 61 m rows of Deltapine 444 BG/RR were planted in a North-South orientation on Day of Year 151 (May 30, 2008) using a John Deere 7300 MaxEmerge 2 VacuMeter Planter. The plots were pre-plant irrigated by furrow irrigation, and only received rain there after. Seedlings were sprayed with 300 µmol/mol 6-benzyladenine (MaxCel, Valent BioSciences, Chicago, IL) on Day of Year 161 (8 June 2008). The plots were sprayed with Ginstar (Bayer CropScience, RTP, NC) and Prep (Bayer CropScience, RTP, NC) according to manufacturers instructions on Day of Year 290, and the plots were harvested on Day of Year 317. Three untreated (control) and three 6-benzyladenine replicates (four rows wide and 61 meters long) from a complete block design were harvested with a John Deere 7160 four-row cotton stripper equipped with a field cleaner. Seed cotton weights were taken in the field with a boll buggy equipped with load cells. Grab samples were collected from the boll buggy to determine turnout.

Meteorological Measurements. The United States Department of Agriculture-Plant Stress and Water Conservation (USDA – PSWC)- Meteorological Tower is located immediately adjacent to the experimental plots. Five-minute measurements of rainfall (mm), and temperature (C) were collected and hourly averages calculated.

RESULTS

Cytokinin Concentration Determination for Cotton Seedlings at the Cotyledonary Stage. Greenhouse studies compared untreated controls with 6-benzyladenine treated seedlings at the cotyldeonary stage. When the Deltapine 444 BG/RR cotton seedlings reached the cotyledonary stage (Fig. 1, approximately seven days after planting) they were sprayed with 0 (water), 100, 200, 300, 400, 500, 600, 700, 800, 900 or 1000 µmol/mol 6-benzyladenine. Figure 2 is a photograph of the seedlings eight days after treatment. Plants treated with 100 or 200 µmol/mol 6-benzyladenine were 17% taller than the control seedlings (Figure 3). Plants treated with 300 and 400 µmol/mol 6-benzyladenine were similar in height to control seedlings. Concentrations of 500 µmol/mol and above showed significant stunting of the plants and phytotoxic lesions at the highest concentrations. Hypocotyl diameters increased from an average of 3.040 mm for control seedlings to an average of 3.869 mm for 100 µmol/mol 6-benzyladenine treated seedlings (Figure 4). Higher 6-benzyladenine concentrations showed similar enlargement of the hypocotyls to those of the 100 µmol/mol 6-benzyladenine treated seedlings.

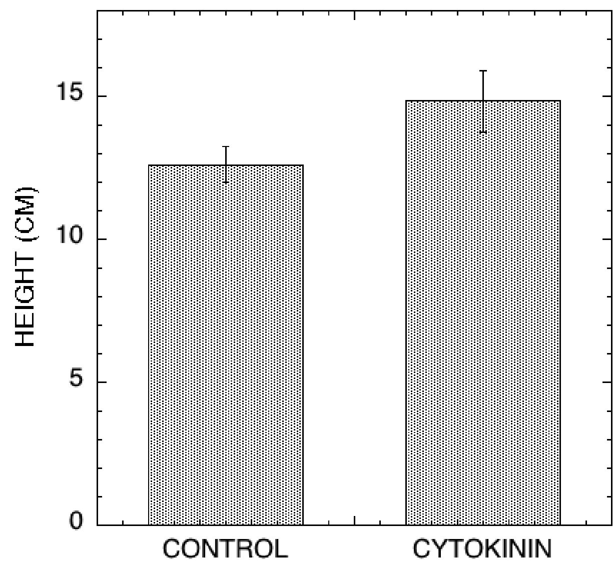

Figure 3. Graph of control and 100 µmol/mol 6-benzyladenine treated Deltapine 444 BG/RR seedling heights. Error bars represent standard errors.

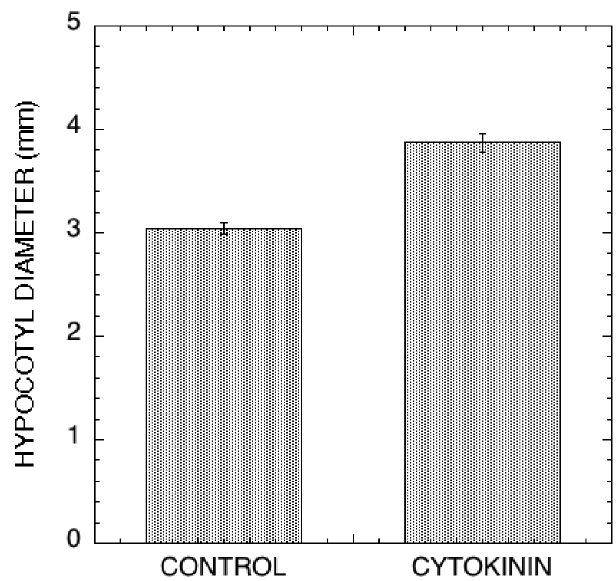

Figure 4. Graph of hypocotyl diameters of control and 6-benzyladenine treated Deltapine 444 BG/RR seedlings. Hypocotyl thickening following treatment with 6-benzyladenine was observed at all concentrations evaluated. Error bars represent standard errors.

Response of Cytokinin-treated Cotton Seedlings during the 2005 Growing Season. Field evaluation of Deltapine 444 BG/RR cotton treated with 100 µmol/mol 6-benzyladenine at the cotyledon stage was initiated in 2005. Because of variability of seedling emergence in the field, treatment was withheld until ten days after planting. The seedling morphology primarily consisted of the two cotyledons and a primary leaf that was beginning to expand (Figure 5). Random plants were pulled from control and cytokinin-treated plots on 9 August 2005 to provide a cursory look for phenotypic changes previously reported for greenhouse grown plants treated with cytokinin (Burke, 2011). The phenotypic responses included enhanced lateral root proliferation and earlier boll set. The photographs in Figure 6 show increased lateral rooting in the cytokinin-treated plants. Additionally, an increase in boll number and boll size was observed. Lint yields were determined at crop maturity for both hand-harvested and stripper-harvested samples (Figure 7). The hand-harvested control (untreated) samples averaged 1234.1 kg ha^{-1} of lint, while the cytokinin-treated samples averaged 1394.5 kg ha^{-1}. The plot stripper harvested control samples averaged 794.4 kg ha^{-1} of lint, while the cytokinin-treated samples averaged 1110.0 kg ha^{-1}. The lint increases were significant for both the hand-harvested (P-Value = 0.0008) and stripper harvested (P-Value = 0.005) samples.

Figure 5. Photograph of 2005 field-grown Deltapine 444 BG/RR seedlings immediately prior to spraying with 6-benzyladenine.

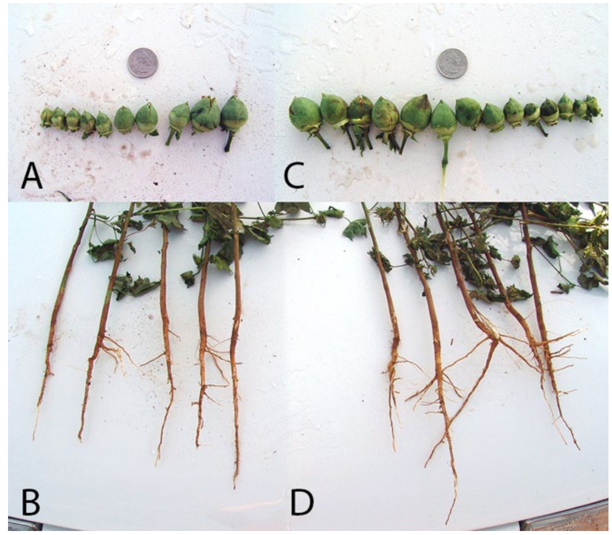

Figure 6. Photograph of roots and bolls from 5 randomly selected control (A, B) and 6-benzyladenine-treated (C, D) DPL444BR on August 9, 2005. Increased lateral root development, boll numbers, and boll maturity were observed in the 6-benzyladenine-treated DPL444BR.

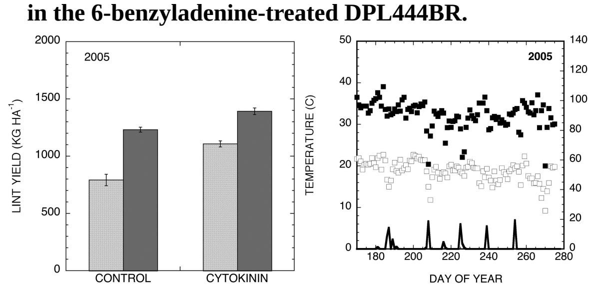

Figure 7. Graph of cotton lint yields from control and 6-benzyladenine-treated DPL444BR grown in 2005. Maximum - minimum temperatures and daily rain accumulations are provided in the graph to the right. Samples harvested with a John Deere 484 two-row plot stripper are represented by the light grey bars and samples harvest by hand are represented by the dark grey bars. Error bars represent standard errors.

Response of Cytokinin-treated Cotton Seedlings during the 2006 Growing Season. Field evaluation of Deltapine 444 BG/RR cotton treated with 150 µmol/mol 6-benzyladenine at the cotyledon stage was initiated in 2006. Because of cool temperatures the first week after planting (average air temperature of 21.5°C) the emergence of the cotton was delayed and it took longer to reach the desired development stage. This is why the seedlings were sprayed 14 days after planting instead of the ten days used in 2005. Unlike 2005 (Figure 7), little rainfall occurred during May, June or July of the 2006 season (Figure 8). Additionally, maximum air temperatures increased to high levels centering between 34 and 38°C during June and July. Significant rain events did not occur until mid-August and September. The stripper-harvested control samples averaged 559.86 kg ha^{-1} of lint, while the cytokinin-treated samples averaged 589.41 kg ha^{-1}. Although there was a numerical increase of five percent more lint in the cytokinin-treated plots, the lint increase was not significant (P-Value = 0.290).

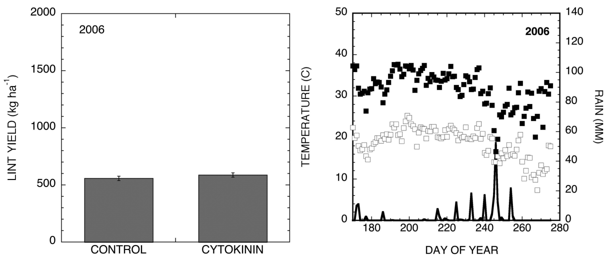

Figure 8. Graph of cotton lint yields from control and 6-benzyladenine-treated DPL444BR grown in 2006. Maximum - minimum temperatures and daily rain accumulations are provided in the graph to the right. Error bars represent standard errors.

Response of Cytokinin-treated Cotton Seedlings during the 2008 Growing Season. Field evaluation of Deltapine 444 BG/RR cotton treated with 300 µmol/mol 6-benzyladenine at the cotyledon stage was initiated in 2008. This study evaluated large-scale plot sizes (four rows 61 meters long per replicate) and the use of a commercial four-row cotton stripper. Excellent stand establishment occurred and the seedlings were treated ten days after planting similar to the 2005 study. Daily maximum-minimum temperatures in 2008 were similar to those of 2005, and rainfall quantities were greater in 2008 compared with 2005 (Figure 9). Seedlings treated with 300 µmol/mol 6-benzyladenine were less green in the developing leaves eight-days after treatment compared to the untreated controls (Figure 9). The untreated seedlings are on the left and the cytokinin-treated seedlings are on the right side of the photographs (Figure 10A and 10B).

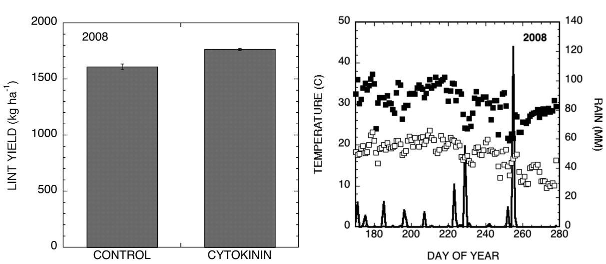

Figure 9. Graph of cotton lint yields from control and 6-benzyladenine-treated DPL444BR grown in 2008. Maximum - minimum temperatures and daily rain accumulations are provided in the graph to the right. Samples were harvested with a John Deere 7160 four-row cotton stripper equipped with a field cleaner. Seed cotton weights were taken in the field with a boll buggy equipped with load cells. Grab samples were collected from the boll buggy to determine turnout. Error bars represent standard errors.

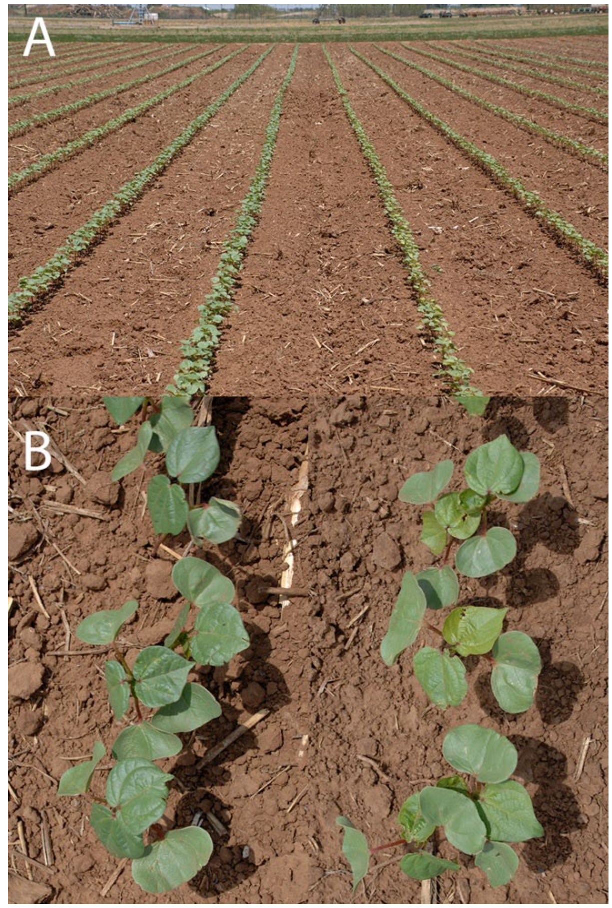

Figure 10. Photographs of seedlings treated with 300 µmol/mol 6-benzyladenine exhibiting lower chlorophyll levels in the developing leaves 8-days after treatment compared to the untreated controls. The untreated seedlings are on the left and the cytokinin-treated seedlings are on the right side of the photographs (Figure 9A and 9B).

The observation that developing leaves were not as green as controls prompted us to evaluate the water-stress levels in these plants. It has been shown previously that water-stressed cotton increases leaf thickness, reduces leaf area, and increases chlorophyll per unit area (Burke et al., 1985). If the higher chlorophyll levels in the untreated cotton is related to water-stress, then this should be detectable using the bioassay described by Burke (2007). Burke reported that sucrose levels were lower in non-stressed cotton at sunrise compared to water-deficit stressed cotton, potentially predisposing the non-stressed tissue to succumb more rapidly when subjected to a prolonged elevated respiratory demand in the dark. Figure 11 shows the response of 50 untreated seedlings (closed circles) and 50 cytokinin-treated seedlings (open circles) in this bioassay. The untreated seedlings exhibited significantly greater stress levels than the cytokinin-treated seedlings. This is evident from the higher chlorophyll fluorescence values in the untreated seedlings following the bioassay challenge.

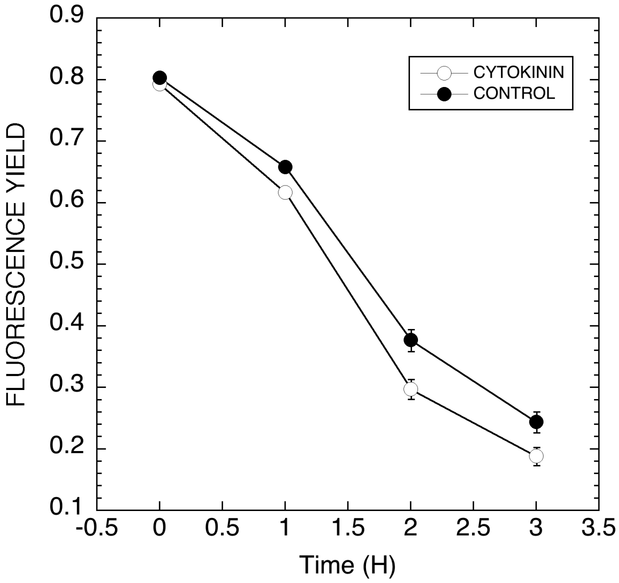

Figure 11. Graph showing the response of 50 untreated seedlings (closed circles) and 50 cytokinin-treated seedlings (open circles) in the chlorophyll fluorescence bioassay described by Burke (2007). The untreated seedlings exhibited significantly greater stress levels than the cytokinin-treated seedlings. This is evident from the higher chlorophyll fluorescence values in the untreated seedlings following the bioassay challenge. Error bars represent standard errors.

The 2008 yield data from the cotton harvested with a John Deere 7160 four-row cotton stripper equipped with a field cleaner is shown in Figure 9. Control samples averaged 1624.73 kg ha^{-1} of lint, while the cytokinin-treated samples averaged 1766.2 kg ha^{-1}. The average 8.7% increase in yield in the cytokinin-treated cotton was statistically significant (P-Value = 0.035).

DISCUSSION

Greenhouse studies showed cotton yield enhancements when seedlings were treated with 6-benzyladenine at the two to four leaf stage (Burke, 2011). This study investigated ways to transfer this technology from controlled greenhouse conditions to the variable environments common to field studies. The determination of optimal cytokinin concentrations for treating cotton seedlings at the cotyledon stage in the field showed that concentrations from 100-300 µmol/mol 6-benzyladenine provided enhanced root development, thickening of the hypocotyl, and improved seedling development. Concentrations above 400 µmol/mol 6-benzyladenine resulted in seedling stunting and phytotoxic lesions on the cotyledons. The concentrations used at the cotyledon stage for optimal response were four to ten times greater than those used in an earlier study of 6-benzyladenine treatment of greenhouse grown cotton treated at the two to four leaf stage (Burke, 2011). The higher concentrations to elicit the same responses may be required because of the reduced area for hormone absorption at the cotyledon stage of development. Differences in cuticular wax composition or amount between cotyledons and leaves (Oosterhuis, 2010) might be another possible explanation for the observed differences in sensitivity to 6-benzyladenine.

The initial field evaluation of Deltapine 444 BG/RR cotton treated with 100 µmol/mol 6-benzyladenine at the cotyledon stage was initiated in 2005 and completed in 2008. The plot sizes increased annually from 15 meters in 2005 to 62 meters in length in 2008. Increased lateral root development, boll numbers, and boll maturity were observed in the 6-benzyladenine-treated DPL444BR at mid-season (Figure 5). This observation was similar to that reported for the greenhouse-grown cotton by Burke (2011). Lint yields in 2005 of the hand-harvested control (untreated) samples averaged 1234.1 kg ha^{-1} of lint, while the cytokinin-treated samples averaged 1394.5 kg ha^{-1} (Figure 6). The plot stripper harvested control samples averaged 794.4 kg ha^{-1} of lint, while the cytokinin-treated samples averaged 1110.0 kg ha^{-1}. The lint increases were significant for both the hand-harvested (P-Value = 0.0008) and stripper harvested (P-Value = 0.005) samples. The 13% lint increase in the hand-harvested cytokinin-treated plots verifies the findings of increased boll weights reported for greenhouse-grown cotton treated with 25 µmol/mol 6-benzyladenine (Burke, 2011). The stripper-harvested cotton had yield increases of 39% in the 6-benzyladenine-treated plots. The difference in yields between the hand-harvested and the mechanically-harvested plots may point to inefficiencies in the mechanical harvester because of the overall reduction in yields (Figure 6). Another explanation for the observed reduction in lint yields may relate to partially open bolls that would be harvested by hand, but not by the mechanical harvester.

In 2006, plot sizes were increased and more replicate plots were harvested. The meteorological data provided in Figure 7 shows that these plants experienced a severe drought and high temperatures during flowering and boll set. Because of the drought cotton yields harvested control samples averaged 559.86 kg ha^{-1} of lint, while the cytokinin-treated samples averaged 589.41 kg ha^{-1}. Although there was a numerical increase of five percent more lint in the cytokinin-treated plots, the lint increase was not significant (P-Value = 0.290). The advantage provided by the larger root systems in the cytokinin-treated seedlings is dependent upon the availability of soil water. Without sufficient rain the plants will experience water-deficit stress responses regardless of the size of the root system. Clearly, the two-fold decrease in lint production in 2006 compared to 2005 illustrates the severity of the water-deficit stress experienced by the crop.

In an effort to identify the potential water-deficit stress avoidance provided by the 6-benzyladenine enhancement of root development, we monitored stress levels of control (untreated) and treated cotton as described by Burke (2007). The control seedlings showed a slower decline in fluorescence yield (closed circles) than the cytokinin-treated seedlings (open circles) (Figure 10). The slower decline in fluorescence yield in the untreated seedlings suggests that they experienced more water stress than the cytokinin-treated seedlings. Burke (2007) reported that sucrose levels were lower in non-stressed cotton at sunrise compared to water-deficit stressed cotton, potentially predisposing the non-stressed tissue to succumb more rapidly when subjected to a prolonged elevated respiratory demand in the dark. Significant differences were observed with the one hour measurement having a P-value = 0.001, the two hour measurement a P-value = 0.02, and at three hours a P-value = 0.08.

In 2008, seedlings were treated with 300 µmol/mol 6-benzyladenine to maximize cytokinin uptake without the detrimental effects on seedling growth observed at higher 6-benzyladenine concentrations. Unlike the low yields experienced in 2006, the 2008 study averaged 1624.73 kg ha^{-1} of lint for the untreated controls, while the cytokinin-treated samples averaged 1766.2 kg ha^{-1}. The average 8.7% increase in yield in the cytokinin-treated cotton was statistically significant (P-Value = 0.035).

The benefits of water stress avoidance on cotton growth have been previously reported (Burke et al., 1985). The severity of the soil water deficit was analyzed by monitoring changes in growth parameters of photoperiodic cotton strains T185 and T25 at 106 DAP. The magnitude of the reduction in plant height, leaf area index, plant dry weight, and leaf number between irrigated and dryland was greater in T185 than T25 treatments. T25 previously was identified as a drought resistant cotton line exhibiting enhanced stress avoidance because of elevated lateral root production (Quisenberry et al., 1981). Significant correlations between root characteristics and dry-matter yield under dryland conditions suggested that overall root vigor allowed T25 to be a better competitor for limited soil water. They concluded that root morphology and root growth potentials appear to be important for the adaptation of cotton to conditions where limited soil-water availability is a major growth constraint. In the present study, cytokinin resulted in an enhancement of lateral root development, and the treated plants exhibited reduced water-deficit stress levels based upon the chlorophyll fluorescence bioassay and the timing of boll opening. Cotton lint yields were increased 13% and 8.5% in the 6-benzyladenine treated plants in 2005 and 2008. A five percent increase in lint production was observed in 2006, however the difference between the control and treated plants was not significant. The results of these studies suggests that a treatment of cotton seedlings with 6-benzyladenine early in seedling development will aid in water-deficit avoidance and in enhancement of lint production.

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