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MOLECULAR BIOLOGY AND PHYSIOLOGY

1-Methylcyclopropene Effects on the Physiology and Yield of Field-Grown Cotton

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ABSTRACT

Cotton (*Gossypium hirsutum* L.) is a major fiber crop; however, cotton yields are often limited due to its extreme sensitivity to environmental stress such as high temperature and drought. The current project was designed to evaluate the use of the plant growth regulator 1-methylcyclopropene (1-MCP) to alleviate the adverse effect of environmental stress on cotton yields. Three field studies were conducted in Arkansas in 2006 and 2007. An untreated control was compared with 1-MCP at 10 g ai ha^{-1} applied at first flower (FF), and another applied at FF and again two weeks later. Measurements were made of boll weight, boll number and yield, as well as on plant physiological and biochemical responses. During the period of cotton fruit development, the maximum temperatures for Marianna, AR in 2006 and 2007 were well above the optimum 30ºC temperature for cotton growth, indicating that cotton was under heat stress. Plants that received 1-MCP at FF and FF+2 weeks had significantly higher seed cotton and lint yields than the untreated control. This result was possibly due to a significant weight increase in 1-MCP treated bolls located in the middle of the plant canopy as no effect was observed on cotton fruit abscission. Applications of 1-MCP significantly decreased the stress levels of cotton plants as indicated by higher maximum quantum efficiency of Photosystem II and lower activity of the leaf antioxidant glutathione reductase. No 1-MCP effect on protein and malondialdehyde content in leaves was observed. The study showed that foliar application of 1-MCP has the potential to improve yields due to reduced plant stress.

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The USA average cotton (*Gossypium hirsutum* L.) lint yield in the past five-years was 877 kg ha^{-1} (USDA, NASS, 2007), which according to Baker and Hesketh (1969) is well below the theoretical maximum lint yield of 4,170 kg ha^{-1}. Another major concern of cotton producers and the cotton industry is the extreme year-to-year variability in yield (Lewis et al., 2000; Johnson and Bourland, 2003). Low and variable cotton yields have been mainly associated with environmental stress. The woody, indeterminate and perennial biology of the cotton plant is the main reason why under conditions of environmental stress the plant focuses on survival rather than seed production (Krieg, 2002). Among all stress factors, temperature and drought appear to play the most significant roles in decreasing crop yields (Sharp et al., 2004, Mittler, 2006). In August 2000 a combination of high temperature and dry weather was estimated to cause damage to US agriculture that extrapolated to a loss of US$4.2 billion (Mittler, 2006).

A common response of plants under stress is increased ethylene synthesis (Abeles et al., 1992). Ethylene is an endogenous phytohormone associated with senescence, abscission and pollination processes (Abeles et al., 1992). In cotton, ethylene is well known for its role in the regulation of the abscission process in cotton fruit (Guinn, 1982a and 1982b; Lipe and Morgan, 1972). The main components of cotton fiber yields are boll number per unit of land area and seed number per boll (Worley et al., 1974). Cotton typically abscises about 65 percent of the total bolls developed (Addicott, 1982) and this is one of the main reasons it does not reach its theoretical yield potential. Although the relationship of ethylene and boll abscission is well documented, the relationship of ethylene with seed set has not been documented. However the role of ethylene in flower senescence and pollination (Abeles et al., 1992) would indicate a possible effect on cotton seed development.

The product 1-methylcyclopropene (1-MCP) is an inhibitor of ethylene action that has been widely used to improve shelf life and quality of agriculture products (Blankenship and Dole, 2003). At room temperature and pressure, the 1-MCP molecule is a gas with a molecular mass of 54 g mol^{-1} and a formula of C_4H_6. This

gaseous molecule has been shown to occupy ethylene receptors inhibiting binding and initiating action (Sisler et al., 1999; Blankenship, 2001). Furthermore, the affinity of 1-MCP for the receptor sites is approximately 10 times greater than that of ethylene and, compared with ethylene, 1-MCP is active at much lower concentrations (Blankenship and Dole, 2003).

We hypothesized that 1-MCP sprayed on cotton plants will inhibit the action of ethylene during stress, resulting in less fruit abscission which could contribute to higher yields. The objective was to evaluate the possible use of 1-MCP to alleviate the adverse effect of environmental stress experienced during the season on square and boll development, and thereby reduce yield variability and result in higher yields.

MATERIALS AND METHODS

A field study was conducted in 2006 and 2007 at the University of Arkansas Cotton Branch Station at Marianna, AR. In 2007 the experiment was also conducted at the Arkansas Agricultural Research and Extension Center in Fayetteville, AR. The planting date for all three experiments was in mid May with the cotton (*Gossypium hirsutum* L.) cultivar DP444BG/RR. Fertilizers were applied according to preseason soil tests and recommended rates. Weed and insect control were performed according to state extension recommendations. The plot size was 4 rows by 15 m, with a row spacing of 0.96 m and plant density of 10 plants m^{-1}. The experiment was arranged in a randomized complete block design with five replications. Treatments consisted of: (T1) an untreated control, (T2) 10 g ai ha^{-1} of 1-MCP applied at the first flower (FF) stage, and (T3) 10 g ai ha^{-1} of 1-MCP applied at FF followed by a second application two weeks later (FF+2). All 1-MCP treatments were sprayed with a backpack CO_2 sprayer calibrated to deliver 187 L ha^{-1}. The 1-MCP formulation used was AFxRD-038 WP manufactured by AgroFresh Inc., Philadelphia, PA. Adjuvant AF-400 (Rohm Hass, Philadelphia, PA) was added to the spraying solution at a rate of 0.375% v/v. The cotton crop reached the first flower stage on July 20, July 10, and July 18 for the studies in Marianna 2006, Marianna 2007, and Fayetteville 2007, respectively.

Yield parameters were calculated from a 1 m length of row located in the middle of the plot. The total number of bolls was counted and harvested for determination of seed cotton yield, boll size, gin turnout and lint yield. Seed production was calculated by weighing 600 seed from each plot, and the number of seed per sample was estimated by dividing the weight of the total amount of seed by the average individual seed weight.

The experiment conducted in Fayetteville in 2007 was also used to study the effect of 1-MCP on the treated flowers. Ten white flowers from the first sympodial fruiting position of main-stem nodes 6 for the treatment T3 and 12 for the T2 treatment were tagged on the day of 1-MCP application, and bolls were collected at the end of the experiment. For the node position determination the cotyledonary node was considered node 1. Measurements consisted of percentage boll abscission, boll weight and number of seeds per boll.

Cotton fiber samples from studies conducted in Marianna were sent for fiber analysis to the Louisiana State University Cotton Fiber Testing Laboratory, Baton Rouge, LA. The following parameters were analyzed: micronaire, length, strength, color, uniformity, short fiber index, and elongation.

Chlorophyll fluorescence measurements were made one week after 1-MCP application for both treatments (FF+1 and FF+2 weeks) on the upper most fully-expanded main-stem leaf at the fourth node below the terminal of the plant, using a Modulated Fluorometer OS1-FL (Opti-Science, Tyngsboro, MA) with light adapted leaves. Measurements were conducted in the two studies of 2007, no data were collected in 2006. Values of chlorophyll fluorescence were calculated as Yield (Φ_{PSII}) according to the equation $\Phi_{PSII} = (Fms-Fs)/Fms$, where Fms is the amount of monochromatic radiation that the fluorometer emits to the sample, and Fs is the amount of radiation reemitted by the plant. Stressed plants show lower Yield values because under stress conditions plants exhibit high values of Fs. The measurements of chlorophyll fluorescence were used as a tool to quantify the quantum use efficiency of the Photosystem II.

The upper fully-expanded main-stem leaf, four nodes below the terminal of the plant, was collected and stored at -80°C. Samples were collected one week after each 1-MCP application (FF+1 week and FF +3 weeks) and the leaf extraction procedure enzyme described by Gomez et al. (2004) was followed. Leaf samples of 1 g were ground under liquid nitrogen using a mortar and pestle and placed in a 35-ml centrifuge tube. The extraction solution consisted of 50mM PIPES buffer, 6mM cysteine hydrochloride, 10mM D-isoascorbic acid, 1mM EDTA, 1% PVP-10, 0.3% Triton X-100, and adjusted to pH 6.8. To the tube containing the leaf sample, 0.5 g of polyvinylpyrroline, one drop of antifoam A, and 4 ml

of extraction solution was added and homogenized for 3 min with a Polytron homogenizer (Brinkmann Instruments Inc., Palo Alto,CA). The samples were centrifuged for 20 min at 21000 g at 4°C in a Hermle centrifuge (Labnet International, Inc, Edison, NJ). The supernatant was collected and desalted by passing it through a PD-10 column (GE Healthcare, United Kingdom). Extracted solutions were stored at -80°C until the day of the enzyme quantification.

The glutathione reductase (GR) assay of Schaedle and Bassham (1977) was followed. The assay was initiated by placing 950 µl of a reaction solution and 50 µl of plant extract in a 1-ml quartz cuvette. The reaction solution was prepared by dissolving 0.303 g of Tris (50mM) (Sigma Company, St. Louis, MO), 0.007 g of NADPH+H (0.15 mM) (Sigma Company, St. Louis, MO), 0.016 g of oxidized glutathione (0.5mM) (Sigma Company, St. Louis, MO), and 0.031 g of $MgCl_2$ (3mM) (Sigma Company, St. Louis, MO), in 40 ml of distilled water. The pH was adjusted to 7.5 and the final volume was adjusted to 50 ml with distilled water. The GR activity was measured according to the oxidation of NADPH+H with a Biospec 1601 UV/VIS spectrophotometer (Shimadzu, Columbia, MD). The instrument was regulated to display a wavelength of 340 nm and measurements were made during a period of 1 min. Glutathione quantities were expressed as mmol $g^{-1}$of fresh weight (FW).

Membrane decomposition was measured with a modification of the method of Heath and Packer (1968). A 1-ml solution of enzyme extract was mixed with a 4-ml solution of 20% trichloroacetic acid (TCA) (Sigma Company, St. Louis, MO) containing 0.5% 2-thiobarbituric acid (TBA) (Sigma Company, St. Louis, MO). The mixture was heated at 95°C for 30 min and then quickly cooled in an ice-bath. After centrifugation at 22615 x g for 10 min the absorbance of the supernatant was measured at 532 nm and 600 nm. The malondialdehyde (MDA) concentration was calculated according to the following equation: MDA equivalents (nmol mL^{-1}) = $[(A_{532}-A_{600})/155000]10^6$ where A_{532} and A_{600} are the absorbance at 532 and 600 nm, respectively. Total MDA content was expressed as nmol g^{-1} FW. Measurements of MDA were made from the leaf samples collected from the two experimental locations in 2007.

The software JMP version 7 (SAS Institute Cary, NC) was used to perform the statistical analyses. Mean and standard error values were calculated to assemble graphs using the Sigma Plot software version 10 (MMIV Systat Software, Inc., San Jose, CA). Analysis of Variance and LSD test (α=0.05) were exploited to analyze statistical significance between means. A probability less than 0.05 was considered significant.

RESULTS

Yield Parameters. Statistical analysis of cotton yield did not indicate a significant interaction effect between 1-MCP treatments and experiments. Since there was no interaction effect the results of 1-MCP treatments were averaged across experiments. The combined analysis of the yield data from the three experiments showed that treatment T3 (1-MCP at FF and FF+2) exhibited significantly higher seed cotton yield (P=0.007), lint yield (P=0.011) and seed production (P=0.006) compared to the untreated control (T1) (Fig.1). The 1-MCP at FF and FF + 2 treatments had 228 kg ha^{-1} higher lint yield and 320 kg ha^{-1} higher seed yield than the control. Neither, 1-MCP application timings caused a significant increase in number of bolls (Fig. 2) and or boll weight (Fig. 3).

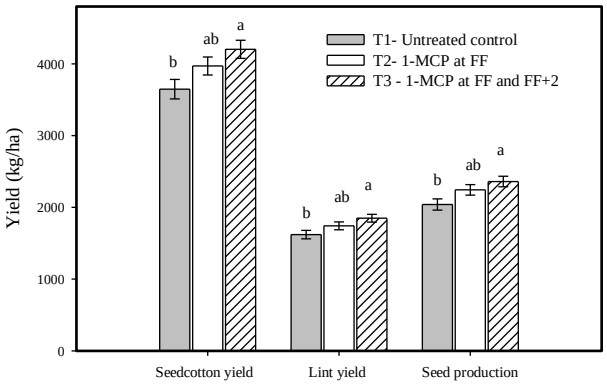

Figure 1. Effect of 1-MCP on cotton yield, results from combined data of the three experiments. Groups of columns with the same letter are not significantly different (P=0.05). Error bars represent ± one standard error.

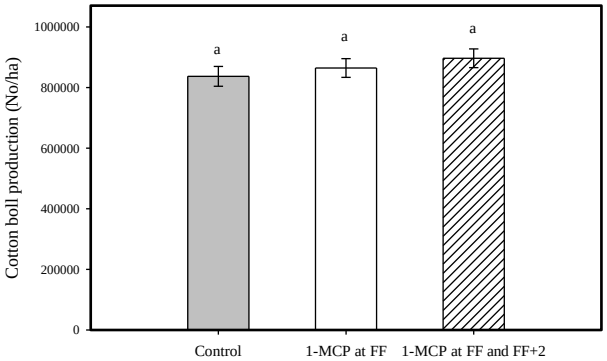

Figure 2. Effect of 1-MCP the number of cotton bolls, results from combined data of the three experiments. Columns with the same letters are not significantly different (P=0.05). Error bars represent ± one standard error.

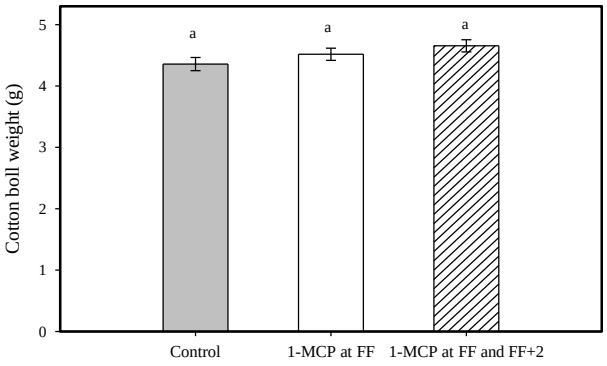

Figure 3. Effect of 1-MCP on cotton boll weight; results from combined data of the three experiments. Columns with the same letters are not significantly different (P=0.05). Error bars represent ± one standard error.

Boll weight and number of seeds per boll, in the lower half of the canopy, were significantly influenced by applications of 1-MCP at the white-flower stage (Fig. 4 and 5). Bolls from main-stem node 6 that received 1-MCP (T2) exhibited a significant increase in boll weight compared to the untreated control (P=0.05) (Fig.4). This effect was mainly due to the significantly higher amount of seeds produced by the treatment (P=0.024) (Fig. 5).

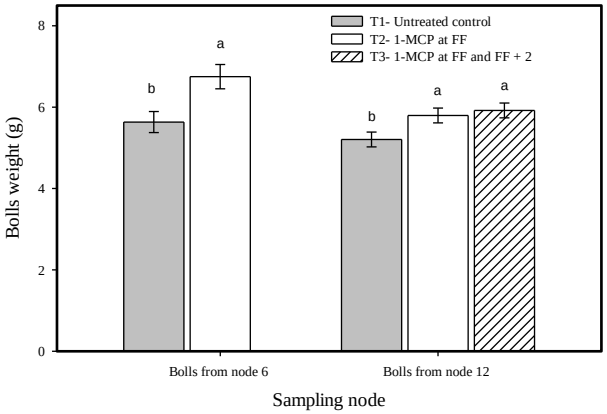

Figure 4. Effect of 1-MCP on cotton boll weight from the experiment conducted in Fayetteville, AR, 2007. Groups of columns within each sampling node with the same letter are not significantly different (P=0.05). Error bars represent ± one standard error.

Similar results occurred in bolls collected from main-stem node 11 (T2 and T3), which also exhibited significantly larger bolls (P=0.032) (Fig. 4) and higher number of seeds (P=0.037) (Fig. 5). As expected, smaller bolls with fewer seeds were observed on node 11 in contrast to bolls from node 5. On the other hand 1-MCP did not have any significant influence on the process of cotton fruit abscission (Fig. 6), and results of fiber quality analysis did not indicate any significant effect on fiber parameters (data not shown).

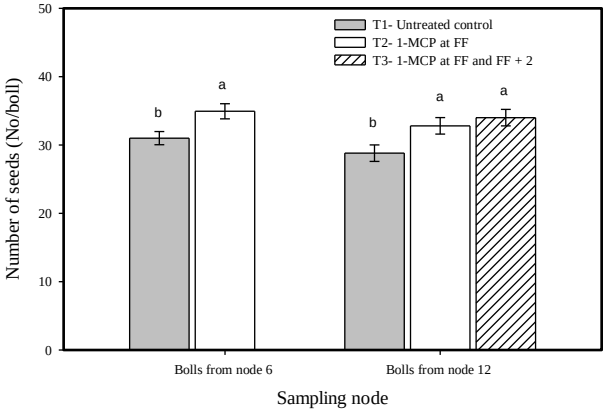

Figure 5. Effect of 1-MCP on number of seeds per boll from the experiment conducted in Fayetteville, AR, 2007. Groups of columns within each sampling node with the same letter are not significantly different (P=0.05). Error bars represent ± one standard error.

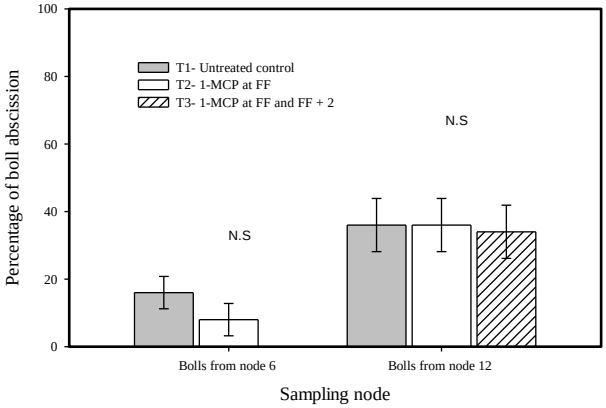

Figure 6. Effect of 1-MCP on boll abscission, results from the experiment conducted in Fayetteville, AR, 2007. N.S= non significant (P=0.05). Error bars represent ± one standard error.

Glutathione Reductase Activity, MDA, and Protein Content. No interaction occurred among 1-MCP treatments and experiments for the GR activity measurements. Averaged across the three experiments, there was significantly lower GR activity in the 1-MCP treatments than the untreated control (Fig. 7). Leaves collected one week after FF application of 1-MCP showed a significantly lower level of GR activity in the T2 (1-MCP at FF) treatment in comparison to the T1 (untreated control) treatment (P=0.008) (Fig. 7). Similarly, leaves collected one week after FF+2 application of 1-MCP showed significantly lower GR activity in both 1-MCP treatments (T2 and T3) in comparison to the untreated control (T1) (P=0.042) (Fig. 7).

Measurements of MDA and protein content did not show any significant differences in the comparison of 1-MCP treatments with the untreated control (Table 1).

Table 1. Effect of 1-MCP on malondialdehyde MDA and protein concentration. Results from combined data of the experiments conducted in Marianna and Fayetteville AR, 2007. Data averaged across location.

Treatment	1week after FF		1 week after FF+2	
	Protein	MDA	Protein	MDA
	mg g^{-1} FW	nmol g^{-1} FW	mg g^{-1} FW	nmol g^{-1} FW
T1- Untreated Control	**2.97**	**0.43**	**3.19**	**1.40**
T2 – 1-MCP at FF	**3.03**	**0.35**	**2.92**	**1.16**
T3 – 1-MCP at FF and FF+2	**-**	**-**	**3.36**	**1.20**
P-value (0.05)	**N.S**	**N.S**	**NS**	**N.S**

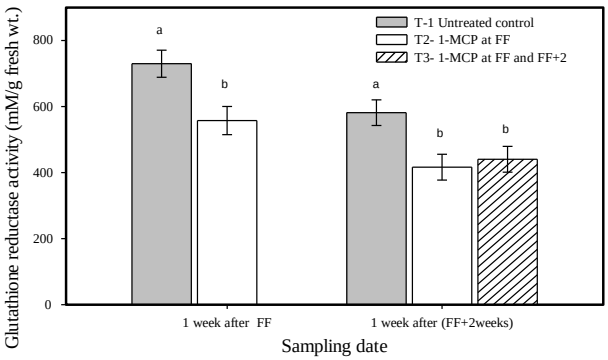

Figure 7. Effect of 1-MCP glutathione reductase activity; results from combined data of the three experiments. Groups of columns within each sampling day with the same letter are not significantly different (P=0.05). Error bars represent ± one standard error.

Chlorophyll Fluorescence. Chlorophyll fluorescence (Fig. 8), showed similar results to the glutathione reductase activity data (Fig.7), with 1-MCP having a significant effect. One week after FF, T2 (1-MCP at FF) had a significant effect on values of Φ_{PSII} compared to T1 (untreated control) (P=0.006). Measurements collected one week after FF+2 showed that both T2 and T3 had significantly higher Φ_{PSII} values than the untreated control (P=0.007).

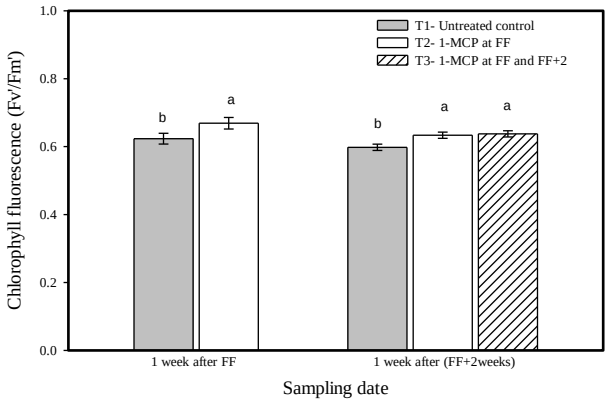

Figure 8. Effect of 1-MCP on chlorophyll fluorescence (Quantum Yield Φ_{PSII}); results from combined data of the experiments conducted in Marianna and Fayetteville AR in 2007. Groups of columns within each time interval with the same letter are not significantly different (P=0.05). Error bars represent ± one standard error.

DISCUSSION

High temperature stress is one of the main causes yield reduction and year-to year variability in yield of cotton (Oosterhuis, 2002). The optimum temperature for cotton growth and development is around 30ºC (Reddy et al., 1992); however in the US Cotton Belt during the reproductive stage of cotton, temperatures frequently to reach levels above 35ºC (Reddy et al., 1991; Boykin et al., 1995 cited by Pettigrew, 2008). In Marianna, AR in 2006 and 2007, the temperatures during cotton fruit development were well above 30ºC (Fig. 9), with the maximum temperature recorded during this period being 39.4ºC (Fig. 9). Under high temperature stress, changes in physiology, growth and yield of cotton crop are known to occur (Burke et al., 1988; Bibi et al., 2008; Snider et al., 2009).

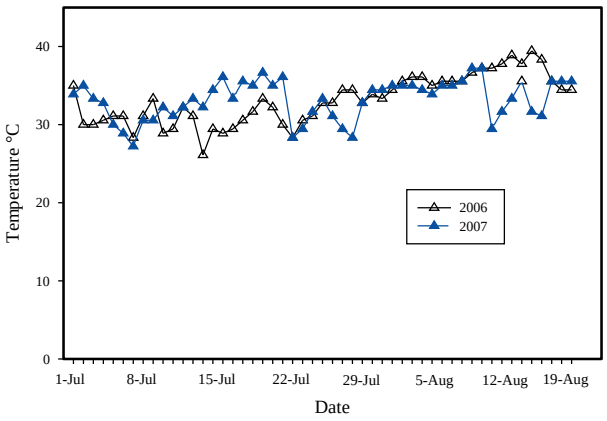

Figure 9. Record of maximum daily temperature during the period of cotton fruit development in Marianna, AR, for 2006 and 2007.

Our findings have shown that 1-MCP improved the yield of field-grown cotton under high temperature stress. This result was due to the effect of 1-MCP increasing the weight of cotton bolls located in the lower half of the plant canopy; i.e., bolls that were in the white flower stage (i.e., when pollination and fertilization occur) at the timing of 1-MCP application

(Fig. 4). The high boll weight in 1-MCP treatments was related to an increased number of seeds per boll. High temperature negative effect on boll weight has been previously reported by Reddy et al. (1999). Pettigrew (2008) found that high temperature treatments advanced crop maturity and decreased cotton yield mainly due to the smaller boll size caused by the fewer number of seeds per boll. The decrease in seed number is related to the effect of heat-stress hindering the success of cotton ovule fertilization, due to decrease in photosynthesis, adenosine triphosphate (ATP), soluble carbohydrates, and nicotinamide adenine dinucleotide phosphate (NADPH) oxidase activity (Snider et al., 2009a).

Quantifications of plant stress in our experiments using antioxidant enzyme activity and chlorophyll fluorescence indicated that 1-MCP reduced the level of stress in the cotton plant. Cotton is very sensitive to environmental stresses (Krieg, 2002), and therefore, the ability to reduce the impact of abiotic stress with 1-MCP application should be of major importance in cotton production for protection of yield. In cotton high temperature has been reported to increase GR activity (Snyder et al., 2009a, 2009b) and in our study, application of 1-MCP resulted in a decrease of GR levels. Chlorophyll fluorescence measurements showed that 1-MCP application increased the plant photosynthetic efficiency of PSII and high temperature has been documented to lower the photosynthetic efficiency of cotton leaves (Bibi, et al., 2008; Snider et al., 2009b). Lower GR activity and high leaf photosynthetic efficiency could result in additional production of photosynthates, which could help explain the positive effect of 1-MCP on cotton yield.

Surprisingly, 1-MCP did not have an effect on the abscission of cotton bolls (Fig. 6). Possibly, applications of 1-MCP did not sufficiently inhibit ethylene action to prevent fruit abscission. Studies have shown that application of 1-MCP reduced leaf abscission of mung beans (*Phaseolus aureus*) (Sisler et al., 1999) and citrus (*Citrus sinensis* L.) (Sisler et al., 1999; Pozo and Burns 2000; Zhong et al., 2001). In addition, 1-MCP also has been shown to affect the process of fruit abscission in cherry tomatoes (*Lycopersicon esculentum*) (Moualem et al., 2004), apples (*Malus sylvestris*) (Dal Cin et al, 2005; Byers et al., 2005), and citrus (*Citrus sinensis* L.) (Pozo et al., 2004). However, application of 1-MCP in the current study had no significant influence on boll number indicating no effect on boll abscission.

There was no effect of 1-MCP treatments on MDA, suggesting that 1-MCP applications lowered GR activity without affecting cell membranes integrity. Possibly untreated plants needed to increase GR activity to protect their cell membranes from oxidative damage. In addition, the chlorophyll fluorescence results demonstrated that 1-MCP application increased the maximum quantum use efficiency of Photosystem II. This could lead to an increase of photosynthetic rate of the plants, which would increase plant productivity.

In conclusion, the use of 1-MCP proved to have a positive effect on the physiology and yield of field-grown cotton. Significant yield increases were observed in the treatments where 1-MCP was applied twice (i.e., at FF and FF+2). This effect could be explained by the fact that applications of 1-MCP lowered cotton stress responses exhibited by low antioxidant activities and higher quantum yield and consequently increased boll weight and seed number per boll.

ACKNOWLEDGEMENTS

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