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Effect of 1-MCP on Cotton Plants under Abiotic Stress Caused by Ethephon

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Abstract

Many environmental stress factors have been identified to increase square and boll abscission and thus result in reduced cotton yield. Under stress conditions, ethylene is elicited. Ethylene peaks before abscission to promote the formation of the abscission layer and plays a major role in early season square and boll abortion in cotton (*Gossypium hirsutum* L.). In addition, ethylene stimulates the leaf senescence process. Thus, it is desirable to protect plants from ethylene-induced fruit loss and premature leaf senescence under stress conditions. The objective of this study was to evaluate the ability of 1-methylcyclopropene (1-MCP) to protect cotton plants against abiotic stress caused by ethephon (ethylene promoting effect). Field studies using a randomized complete block design with four replications were conducted in 2010 and 2011 at Texas A&M AgriLIFE Research Farm in Burleson County, TX. Eight treatments that consisted of two 1-MCP rates (0 and 10 g a.i. ha^{-1}) in combination with four ethephon rates (0, 146, 292, 438 mL·ha^{-1}) were imposed at the first flower (FF) stage of the development. 1-MCP increased plant height and number of main stem nodes in both years. In addition, 1-MCP-treated plants exhibited greater membrane integrity and increased photosystem II quantum efficiency and thus delayed senescence in both years. These potentials for yield increase were realized in 2011 with 1-MCP treatment exhibiting a higher lint yield. In 2012, although 1-MCP treatment increased number of open fruit and open fruit weight per plant significantly, no significant lint yield increase was detected.

Keywords

1-MCP, Ethephon, Yield Components, Yield Distribution, Leaf Senescence

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1. Introduction

Ethylene plays a primary role in the abscission of leaves [1]-[3] and fruit [4]. Because boll retention is a major concern for cotton yield improvement, the role of ethylene in cotton fruit shedding has been studied extensively. Ethylene promotes the abscission layer formation in the peduncle in cotton plants, thus leading to fruit abortion [4]. In cotton, research has demonstrated that ethylene production plays a major role in early season square and boll abortion [4]-[7]. Moreover, stress-induced ethylene synthesis can be elicited by temperature that is either high-temperature, freezing, or chilling, water stress including drought and waterlogging, chemicals including herbicides and insects salivary fluids, physical wounding including bruising, cutting and insect biting, and pathogens [8] [9]. Additionally, stresses may further decrease boll retention as confirmed by the fact that ethylene production accelerates induction of fruit shed of cotton plants under drought [2] [5] [10]. Due to the crucial role that ethylene plays in square and boll loss, it is advantageous to protect plants from ethylene-induced fruit loss.

Ethylene is also a mediator in the senescence process in which cells undergo programmed cell death induced by developmental and environmental signals [11]-[13]. When ethylene function was blocked, lower electrolyte leakage, indicating delayed senescence, was detected in flower petals [14]-[16] and leaves [17]. Enhanced chlorophyll degradation associated with ethylene production has been reported in many studies [18]-[21]. Leaf senescence often occurs during the boll filling stage in cotton [22]. At this critical stage, leaf senescence induced by ethylene caused a lower photosynthetic rate and less carbon accumulation and thereby decreased yield. Thus, as mentioned earlier, it is desirable to protect yield by reducing the ethylene effect which can reduce fruit shedding and lead to a delay of senescence.

The plant growth regulator 1-methylcyclopropene (1-MCP), which inhibits ethylene action, has been proven to be a valuable product in industry to improve quality and shelf life of horticultural products [23]. 1-MCP is a gas at room temperature with a formula of C_4H_6. 1-MCP occupies the ethylene receptor site and has an affinity 10 times greater for the site than that of ethylene [15] [23]. Thus, 1-MCP may inhibit ethylene action by competing with ethylene for the ethylene receptor to inhibit binding.

Ethephon (2-chloroethylphosphonic acid; Ethrel) is an ethylene-releasing compound that is metabolized to ethylene in plants. Ethephon is a widely used plant growth regulator since the 1960s. This compound is used to facilitate fruit ripening, senescence, abscission, flower induction in pineapple, and to also retard stem growth on cereal crops to reduce lodging. The primary use of this chemical is in cotton harvesting. Ethylene accelerates opening of cotton bolls and improves cotton responses to defoliants; thus ethephon usually makes up a part of defoliation programs [24] [25].

da Costa *et al*. (2011) [26] tested the effect of ethephon on 1-MCP treated cotton plants. Because we found that 1-MCP works more efficiently in stress conditions (water stress, heat stress, and ageing) (unpublished data), our present study was designed to test effect of 1-MCP under different stress levels applied as different rates of ethephon in the field conditions by assessing leaf senescence traits and yield related data.

2. Materials and Methods

The study was conducted at the Texas A&M AgriLIFE Research Farm in Burleson County on a Westwood silt loam field (fine-silty mixed thermic Fluventic Ustochrept). Cotton cv. FM832LL was seeded on April 10th in 2011 and 2012 at a density of 11 seeds·m^{-2}. Each plot had four 1.02-m-wide rows that were 9.73 m in length. Furrow irrigation was used when necessary to water plants during the growing season. Fertility, disease prevention, insect and weed control were performed according to the Texas A&M AgriLIFE Extension Service local recommendations. Harvest aids (1.106 kg a.i. ha^{-1} ethephon plus 0.056 kg a.i. ha^{-1} thidiazuron and 0.421 kg a.i. ha^{-1} tribufos) were applied at approximately 60% open bolls.

2.1. Treatment Application and Experimental Design

Eight treatments were arranged as a randomized complete block design with four replications. They consisted of two rates of 1-MCP (0 and 10 g a.i. ha^{-1}) with a 0.0375% v/v surfactant Silwet L77 (Rohm & Hass, Philadelphia, PA) and four rates of ethephon (0, 146, 292, 438 mL·ha^{-1}) (PREP, Bayer Crop Science). At first flower stage of development, 1-MCP was applied according to specified treatments in July 7th 2011 and June 25th 2012. Ethephon was applied as a source of stress after 24 hrs. Foliar spray was applied according to treatments with 103 L·ha^{-1} water and a compressed air sprayer using 8002XR nozzles.

2.2. Data Collection

At 1, 3, and 5 days after ethephon application, electrolyte leakage and chlorophyll fluorescence measurements were taken at 11 a.m. Membrane leakage was measured to show the level of plasma membrane integrity using the method of Djanaguiraman *et al.* [27] with some modification. Five 1-cm-diameter leaf discs from the fifth fully extended uppermost leaf were sampled and incubated in 10-mL of double distilled water (ddH_2O) in glass tubes at room temperature. After 48 h of incubation, initial electrical conductivity (IEC) was taken using a calibrated conductivity meter (Oaklon CON11, EUTECH instrument, IL). Leaf discs were then autoclaved at 120˚C for 15 min. After the solution cooled to room temperature final electrical conductivity (FEC) was measured, and the membrane damage was calculated from the equation: Membrane damage = (IEC/FEC)*100.

Chlorophyll fluorescence was obtained in light adapted leaves at the fourth position from the uppermost fully-expanded leaves with a fluorometer (PAM-2100, Walz, Germany). The value of Yield (Φ_{PSII}), used to reflect photosystem II effective quantum efficiency, was the ratio of number of photons absorbed to number of photons emitted by fluorescence. Stressed plants usually exhibit lower Φ_{PSII} values because the number of photons absorbed tends to be lower under stressed conditions.

Immediately before machine harvest, 5 randomly chosen plants from the two center rows per designated plot were sampled to conduct box-mapping according to da Costa *et al.* [26]. Box mapping was used to determine number of vegetative, reproductive, and main-stem nodes, boll weight, plant height, and boll number by individual position and node to determine yield distribution within the canopy. Internode length was measured as the fraction of plant height to main-stem node number. Two weeks after harvest aid application, the two center rows were harvested with a two-row spindle picker.

2.3. Data Analysis

Data were subjected to analysis of variance using ANOVA of SAS 9.3 (SAS Institute, NC). Multiple mean comparisons were made using the LSD test at $P \leq 0.05$.

3. Results

3.1. Lint Yield

Treatment effect on lint yield was variable for the two years; there were also significant treatment and year interactions. Thus, data was analyzed by each year. Orthogonal contrast in 2011 showed a significant 1-MCP effect, with 1-MCP-treated plants exhibiting a higher lint yield than untreated plants (**Table 1**). It was noted that the yield enhancement effect of 1-MCP was more evident under ethephon stress rather than when ethephon was absent. In 2011, 1-MCP plus ethephon treatments increased lint yield by 11%, 15%, 18%, and 12% at ethephon rates of 0, 146, 292, and 438 $mL \cdot ha^{-1}$, respectively, compared to their corresponding ethephon treatment alone. The greatest contribution to this increase of yields was from 1-MCP treatment under the ethephon rate of 292 $mL \cdot ha^{-1}$. 1-MCP plus 292 $mL \cdot ha^{-1}$ ethephon treatment increased lint yield by 18% compared to 292 $mL \cdot ha^{-1}$ ethephon treatment alone. In contrast, the smallest contribution to the increase of yields was from 1-MCP treatment in absence of ethephon. 1-MCP effect was compromised in absence of ethephon (**Figure 1(a)**). A similar result was observed in the year 2012 with 1-MCP treatment exhibiting no effect on lint yield in absence of ethephon treatment. However, no 1-MCP effect in 2012 was detected by orthogonal contrast as in the year 2011 (**Table 1**). This observation was caused by the variant effect of 1-MCP under different ethephon rates in 2012. 1-MCP exhibited a positive effect on yield under 438 $mL \cdot ha^{-1}$ ethephon. 438 $mL \cdot ha^{-1}$ ethephon plus 1-MCP treatment increased lint yield significantly compared to the 438 $mL \cdot ha^{-1}$ ethephon treatment alone. In contrast, 1-MCP exhibited a negative effect on yield under 292 $mL \cdot ha^{-1}$ ethephon with the 292 $mL \cdot ha^{-1}$ ethephon plus 1-MCP treatment decreasing lint yield significantly in contrast to the 292 $mL \cdot ha^{-1}$ ethephon treatment alone (**Figure 1(b)**). However, the effect of 1-MCP under 292 $mL \cdot ha^{-1}$ ethephon contributed most to the overall lint increase caused by 1-MCP in 2011 (**Figure 1(a)**), this unexpected 1-MCP effect at the 292 $mL \cdot ha^{-1}$ of ethephon in 2012 disagrees with the 2011 results. There was not clear explanation for this result based on the collected data. The ethephon effect on lint yield was evident in 2012. Orthogonal contrast indicated that ethephon treatment decreased lint yield compared to all other treatments that did not receive ethephon application in 2012 (**Table 1**). Additionally, 438 $mL \cdot ha^{-1}$ ethephon treatment had a lower lint yield compared to the untreated control in 2012 (**Figure 1(b)**).

Table 1. The effect of 1-MCP and ethephon on cotton lint yield, open fruit weight per plant, open fruit weight per boll, open fruit number per plant in 2011 and 2012. Same letters within each column represent non-significant differences (P = 0.05).

Treatment	1-MCP	Ethephon	Lint yield		Open fruit weight		Open fruit number		Open fruit weight	
			2011	2012	2011	2012	2011	2012	2011	2012
	g a.i. ha^{-1}	$mL \cdot ha^{-1}$	$kg \cdot ha^{-1}$		$kg \cdot plant^{-1}$		no. $plant^{-1}$		$kg \cdot boll^{-1}$	
1	0	0	1115abc	1545a	70.49ab	69.33ab	15.60a	13.07ab	4.48a	5.29a
2	0	146	1109abc	1429abc	63.31ab	53.76bc	13.47a	10.67ab	4.71a	5.04a
3	0	292	1004bc	1505ab	63.52ab	57.13abc	13.67a	11.27ab	4.62a	5.07a
4	0	438	895c	1345bc	53.07b	49.99c	11.73a	9.87b	4.51a	5.07a
5	10	0	1238ab	1575a	71.79ab	65.27abc	15.47a	12.53ab	4.70a	5.20a
6	10	146	1278a	1425abc	82.83a	72.90a	16.67a	13.80a	4.96a	5.30a
7	10	292	1186ab	1306c	75.08ab	56.11abc	16.87a	11.13ab	4.41a	5.04a
8	10	438	1005bc	1560a	61.02ab	73.10a	13.13a	13.60a	4.88a	5.42a
LSD (0.05)			252	180	28.40	17.87	5.60	3.41	0.55	0.64
Orthogonal contrast										
Ethephon vs. ethephon + 1-MCP			*	NS	NS	*	NS	*	NS	NS
1-MCP vs. 1-MCP absent			*	NS	NS	*	NS	NS	NS	NS
Control vs. ethephon			NS	NS	NS	*	NS	NS	NS	NS
1-MCP vs. 1-MCP + ethphon			NS	NS	NS	NS	NS	NS	NS	NS
Ethephon vs. ethephon absent			NS	*	NS	NS	NS	NS	NS	NS

*Significantly different at P = 0.05.

The overall 1-MCP effect was noted in 2011 according to orthogonal contrast, but no significant effect was observed under each individual ethephon rate. This observation was likely due to the high variance of the lint yield data: the coefficient of variation (CV%) for 2011 lint yield data was 13.7% whereas the CV% for that of 2012 was 8.4%. Also in 2011 one outlier was removed which dropped the CV% from 15.9% to 13.7%. This high CV% observed in 2011 was likely associated with the drought and heat stress conditions of that year (**Figure 2**).

3.2. Yield Components

Analysis of yield components showed that the number of open fruits than weight per boll contributed more to the difference of open fruit weight per plant caused by 1-MCP treatment (**Table 1**). In the year 2012, there was a significant 1-MCP effect on the number of open fruit. 1-MCP pretreatment increased number of open bolls under stress imposed by ethephon application according to the orthogonal contrast. This beneficial effect of 1-MCP on boll number, together with the numerical increase of weight per boll, contributed to higher boll weight per plant in 2012. However, the beneficial effect of 1-MCP on yield components in 2012 did not result in higher yield. This result was due to the unexpected 1-MCP effect on yield under 292 $mL \cdot ha^{-1}$ ethephon. In 2012, 1-MCP exhibited a negative effect on yield under 292 $mL \cdot ha^{-1}$ ethephon with the 292 $mL \cdot ha^{-1}$ ethephon plus 1-MCP treatment decreasing lint yield significantly in contrast to the 292 $mL \cdot ha^{-1}$ ethephon treatment alone. Thus, this negative effect of 1-MCP effect under 292 $mL \cdot ha^{-1}$ ethephon offset its positive effect on cotton yield under other ethephon rate. In addition, the orthogonal contrast also indicated a lower boll weight per plant for treatments receiving ethephon compared to the untreated ones in 2012 (**Table 1**). Previous reports also have shown that high rates of ethephon caused small bolls [28]. This result is consistent with the lint yield data which also exhibited a significant ethephon effect in 2012. In the year 2011, neither 1-MCP nor ethephon showed a significant effect on yield components. Although open fruit weight per plant in 1-MCP treated plants was numerically greater than corresponding untreated plants under all different ethephon rates, no significant difference was detected due to a comparatively large variance in sample data (**Table 1**).

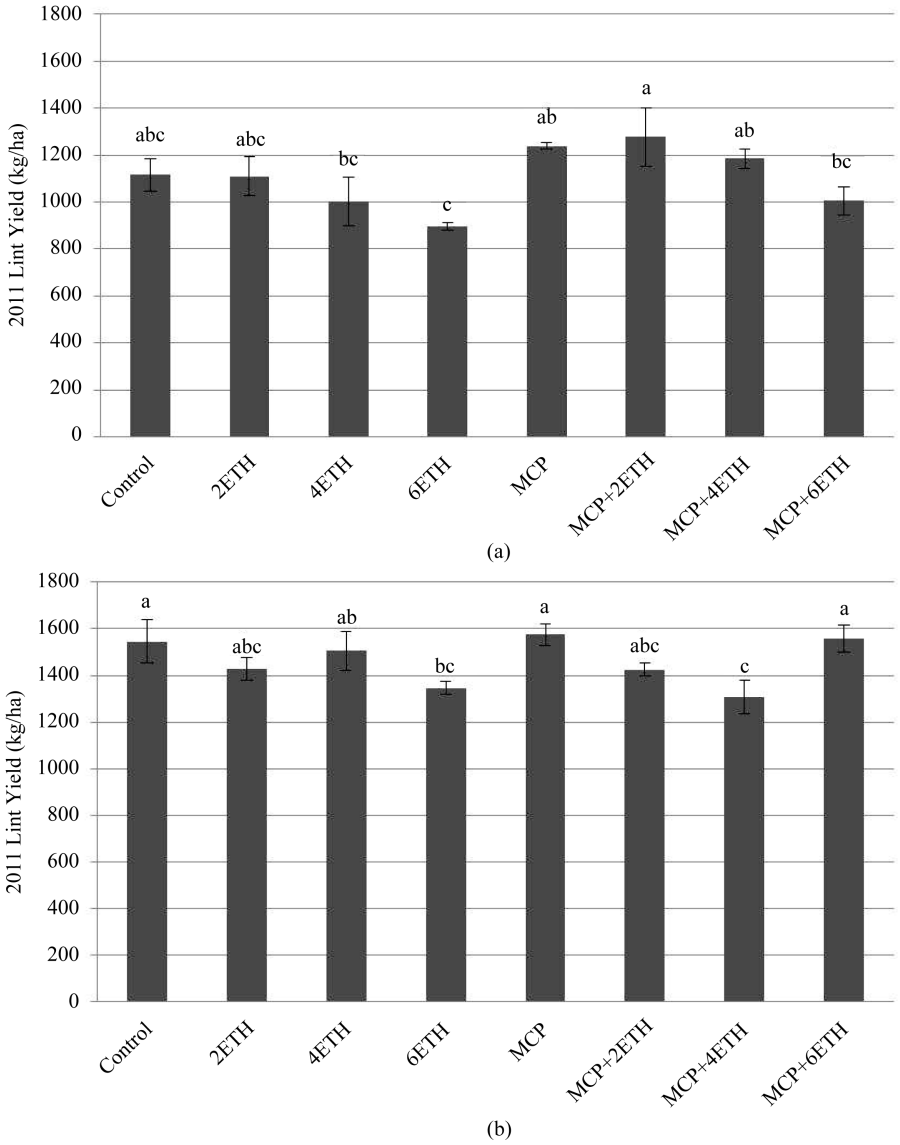

Figure 1. The effect of 1-MCP and ethephon on cotton lint yield in 2011 (a) and 2012 (b). Control = the untreated control; 2ETH = 146 mL·ha^{-1} Ethephon; 4ETH = 292 mL·ha^{-1} Ethephon; 6ETH = 438 mL·ha^{-1} Ethephon; MCP = 10 g a.i. ha^{-1} 1-MCP; MCP + 2ETH = 10 g a.i. ha^{-1}. 1-MCP + 146 mL·ha^{-1} Ethephon; MCP + 4ETH = 10 g a.i. ha^{-1} 1-MCP + 292 mL·ha^{-1} Ethephon; MCP + 6ETH = 10 g a.i. ha^{-1} 1-MCP + 428 mL·ha^{-1} Ethephon. Same letters above histograms represent non-significant differences (P = 0.05). Vertical bars indicate SE.

3.3. Yield Distribution

To further analyze the yield distribution, boll set and weight were analyzed by fruiting position on sympodial branches and different node positions. According to orthogonal contrast, 1-MCP treatment increased boll weight on the second fruiting position for both years (**Table 2**). Additionally, in the year 2011, 1-MCP plus ethephon treatments impacted boll weight on main-stem nodes 11 to 15 compared to ethephon treatments alone. Thus, 1-MCP treatment increased boll weight in the second fruiting position and nodes 11 - 15 in cotton plants. Since the second position and nodes 11 - 15 contributes to an important part of the cotton yield, an improvement at these sites could make a significant difference in yield. Orthogonal contrast showed ethephon treatments decreased first position boll weight compared to the untreated control in 2012 (**Table 2**). This may partially explain the significant decrease in overall boll weight per plant and final lint yield caused by ethephon.

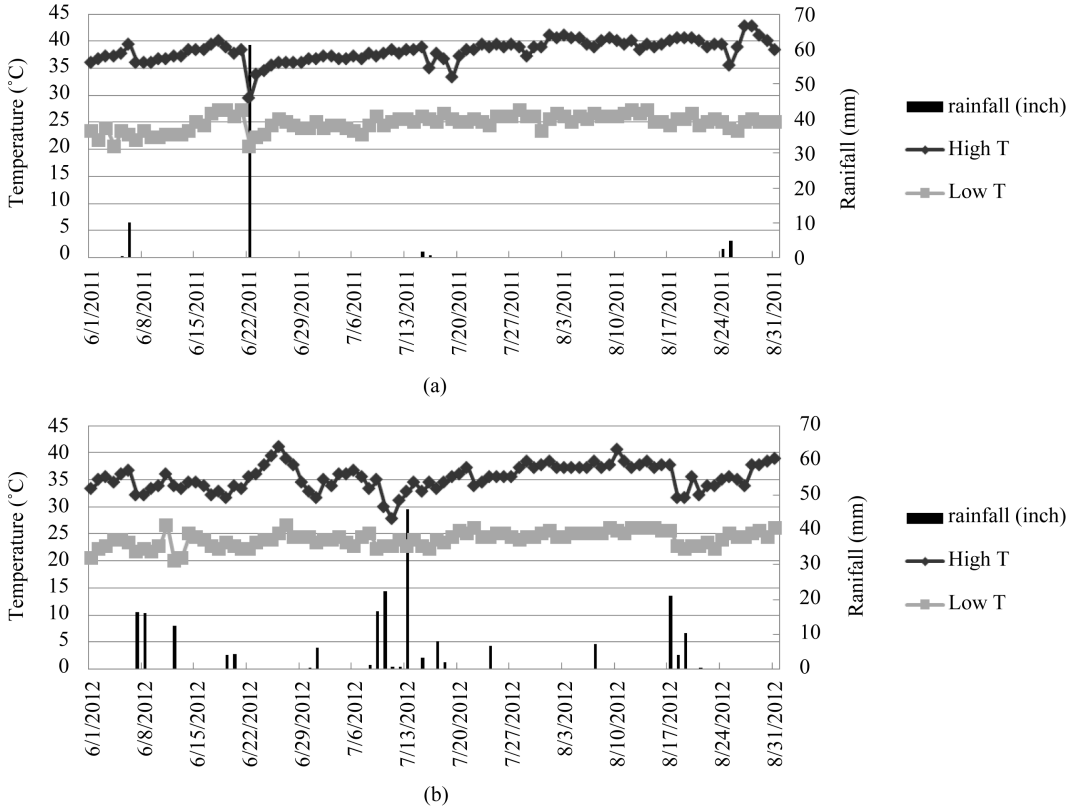

Figure 2. Weather data for 2011 (a) and 2012 (b).

Table 2. The effect of 1-MCP and ethephon on cotton boll weight on first position and second position of sympodial branches, node 6 - 10, node 11 - 15, node 16 - 20 of the main stem in 2011 and 2012. Same letters within each column represent non-significant differences (P = 0.05).

Treatment	1-MCP	Ethephon	First position boll weight		Second position boll weight		Node 6 - 10 boll weight		Node 11 - 15 boll weight		Node 16 - 20 boll weight	
			2011	2012	2011	2012	2011	2012	2011	2012	2011	2012
	g a.i. ha^{-1}	$mL \cdot ha^{-1}$	$g \cdot plant^{-1}$									
1	0	0	45.25a	42.44a	17.01ab	9.52b	24.21a	21.27a	26.86ab	24.58ab	10.24ab	11.18ab
2	0	146	41.33a	35.90ab	11.25ab	10.54ab	25.18a	19.77a	20.40ab	22.61ab	8.71b	6.18bc
3	0	292	40.64a	34.41ab	13.00ab	11.01ab	21.34a	17.64a	20.54ab	21.75b	13.14ab	8.97abc
4	0	438	36.74a	30.84b	10.11b	10.17b	19.85a	14.51a	18.89b	24.93ab	8.80ab	6.13bc
5	10	0	44.03a	34.93ab	17.47ab	16.12ab	26.22a	22.94a	24.37ab	27.30ab	13.42ab	5.79bc
6	10	146	50.85a	40.51ab	19.55a	15.17ab	23.70a	20.82a	30.63a	30.81a	16.26a	9.58abc
7	10	292	43.16a	35.03ab	19.04a	13.20ab	24.03a	23.71a	24.95ab	21.20b	15.99ab	4.13c
8	10	438	38.97a	34.78ab	11.24ab	17.82a	20.65a	17.62a	23.85ab	28.70ab	8.73b	13.08a
LSD (0.05)			18.41	9.72	8.49	7.43	8.29	9.72	10.85	8.56	7.50	6.12
Orthogonal contrast												
Ethephon vs. ethephon + 1-MCP			NS	NS	*	*	NS	NS	*	NS	NS	NS
1-MCP vs. 1-MCP absent			NS	NS	NS	**	NS	NS	NS	NS	NS	NS
Control vs. ethephon			NS	*	NS	NS	NS	NS	NS	NS	NS	NS
1-MCP vs. 1-MCP + ethphon			NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Ethephon vs. ethephon absent			NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

*, **Significantly different at P = 0.05 and 0.01, respectively.

3.4. Plant Growth Parameters

Plant growth parameters were also recorded to test the effects of 1-MCP treatment. Orthogonal contrast revealed a significant 1-MCP effect on plant height and number of main-stem nodes for both years of the study. 1-MCP treated plants were taller with more main-stem nodes compared to the plants that did not receive 1-MCP treatment. However, treatments failed to show any ethephon effect on plant growth parameters for either year of the study (**Table 3**).

3.5. Leaf Senescence

Electrolyte leakage and chlorophyll fluorescence were measured to assess physiological parameters of the treated plants. These two traits are good indicators of leaf senescence. Fluorescence yield is measured to show the quantum efficiency of photosystem II [29]. The orthogonal contrast indicated that 1-MCP exhibited a beneficial effect on photosynthetic efficiency. The 1-MCP treated plants had a higher fluorescence yield than untreated ones in both years. In the year 2011, orthogonal contrast also showed an ethephon effect on fluorescence yield. Ethephon treatment decreased fluorescence compared to treatments receiving no ethephon (**Table 4**). Whereasethephon had a deleterious effect on photosystem II efficiency, 1-MCP treatment positively influenced the plants' ability to overcome the ethephon effect. In 2011, 1-MCP plus ethephon-treated plants had significantly higher fluorescence yield compared to their corresponding ethephon treated plants under the ethephon rate of 0, 146, and 292 mL/ha. However, when the ethephon rate was too high (as at 438 mL/ha), 1-MCP failed to show the protective effect on photosynthesis (**Table 4**).

Similar results were detected in membrane leakage data. Ethephon detrimentally affected membrane integrity and increased membrane damage (**Table 4**). Significant 1-MCP and ethephon effects were detected in both years of the present study. 1-MCP treated plants showed a lower membrane damage percent, which indicated better membrane integrity, compared to untreated plants according to orthogonal contrast. In the year 2012, ethephon plus 1-MCP treatments decreased membrane leakage compared to their corresponding ethephon treatments at all ethephon rates (**Table 4**). Thus, ethephon accelerated senescence while 1-MCP had the ability to delay senescence.

Table 3. The effect of 1-MCP and ethephon on plant height, and number of main stem nodes in 2011 and 2012. Same letters within each column represent non-significant differences (P = 0.05).

Treatment	1-MCP	Ethephon	Plant height		Main stem nodes	
			2011	2012	2011	2012
	g a.i. ha^{-1}	$mL \cdot ha^{-1}$	cm			
1	0	0	71.53b	73.42bc	28.87b	24.67bc
2	0	146	75.20ab	72.32bc	28.67b	24.13c
3	0	292	71.67b	72.50bc	28.60b	24.07c
4	0	438	71.20b	70.58c	27.47b	23.93c
5	10	0	73.60ab	74.27ab	28.80b	25.93a
6	10	146	77.40a	71.70bc	30.93a	24.47c
7	10	292	75.13ab	73.72abc	29.27ab	25.13abc
8	10	438	74.60ab	77.30a	29.20ab	25.80ab
	LSD (0.05)		5.08	1.45	2.00	1.25
	Orthogonal contrast					
	Ethephon vs. ethephon + 1-MCP		*	*	**	**
	1-MCP vs. 1-MCP absent		*	*	*	*
	Control vs. ethephon		NS	NS	NS	NS
	1-MCP vs. 1-MCP + ethphon		NS	NS	NS	NS
	Ethephon vs. ethephon absent		NS	NS	NS	NS

*, **Significantly different at P = 0.05 and 0.01, respectively.

Table 4. The effect of 1-MCP and ethephon on leaf chlorophyll fluorescence yield and membrane damage in 2011 and 2012. Same letters within each column represent non-significant differences (P = 0.05).

Treatment	1-MCP	Ethephon	Fluorescence yield		Membrane damage	
			2011	2012	2011	2012
	g a.i. ha^{-1}	$mL \cdot ha^{-1}$			100%	
1	0	0	0.539cd	0.670ab	9.95abc	9.92d
2	0	146	0.537cd	0.665ab	10.30abc	11.95ab
3	0	292	0.532d	0.662ab	11.53ab	11.96ab
4	0	438	0.534cd	0.660b	11.96a	12.06a
5	10	0	0.562a	0.677a	8.79c	10.88c
6	10	146	0.550b	0.676a	9.70bc	10.43cd
7	10	292	0.543bc	0.666ab	9.62bc	11.14bc
8	10	438	0.536cd	0.675ab	10.97ab	11.02c
	LSD (0.05)		0.011	0.016	2.06	0.92
	Orthogonal contrast					
	Ethephon vs. ethephon + 1-MCP		**	*	NS	**
	1-MCP vs. 1-MCP absent		**	*	*	*
	Control vs. ethephon		NS	NS	NS	**
	1-MCP vs. 1-MCP + ethphon		**	NS	NS	NS
	Ethephon vs. ethephon absent		**	NS	*	**

*, **Significantly different at P = 0.05 and 0.01, respectively.

4. Discussion

The overall lint yield in 2012 was much higher than that of 2011 (**Table 1**). This phenomenon was likely the result of weather differences as bolls were set and developed under different environments for each year. It has also been reported that ethephon interaction with temperature impacts immature fruit shedding, cotton defoliation, and cotton boll opening [30]. Weather data showed that high temperature existed through the entire boll development period in 2011. In addition, cotton experienced a drought year in 2011. In 2012, temperature was lower during the boll development stage compared to 2011. These temperatures, however, were still considered to be high for cotton, but more precipitation was detected. Thus, cotton plants were under drought and greater heat stress in 2011 (**Figure 2**). In 2011, daily maximum and minimum temperature at application day was 37˚C and 23˚C, respectively, and the average daily maximum and minimum temprerature in the following week was 38˚C and 25˚C with no precipitation. In the year 2012, the daily maximum and minimum temperature at the application day was 39˚C and 24˚C, and the average daily maximum and minimum temprerature in the following week was 36˚C and 24˚C. There was a precipitation of 0.25 and 6.35 mm,respectively, at 5 and 6 days after application. Thus, the average weekly high temperature after application was 2˚C higher in the year 2011 than in the year 2012. Because one week after application is a critical time for the chemical effect, the constant high temperature after application in the year 2011 also impacted the potential beneficial effect of 1-MCP. The ideal temperature is 28˚C ± 2˚C for cotton growth [31]. High temperature during reproductive development adversely affects cotton growth and development and ultimately yields [32] [33]. The lower yield is caused by reduced boll size [32] [34], pollen infertility, and thus low seeds per boll [33], as well as a high fruit shedding rate [32] [34] [35]. In addition to these factors, with an increase intemperature, more biomass was allocated to roots, leaves, and stems because of reduced boll set [32]. Heat stress also impacts vegetative growth of cotton plants, with stressed plants typically exhibiting a reduced number of branches per plant with a lower branch length, shorter internodal length and fewer nodes [32]. High day temperatures may result in direct damage to components of leaf photosynthesis, thereby limiting photosynthetic potential and ultimately yield [32] [36].

The protective effect of 1-MCP on lint yield was more evident at the 292 $mL \cdot ha^{-1}$ ethephon treatment in 2011 (**Figure 1(a)**), whereas in 2012 the effect was more evident at the 438 $mL \cdot ha^{-1}$ ethephon (**Figure 1(b)**). This indicated that the higher degree of weather stress in 2011 combined with a lower ethephon rate equals the stress

level of the lower degree of weather stress in 2012 combined with a higher ethephon rate. These data suggest that 1-MCP works more efficiently under some degree of stress. It also raises questions about the abiotic stress study: What is the internal stress level in the plants? How can we define the overall stress level? Is use of infrared thermometry (IRT) a good way to make this determination?

1-MCP treated plants were taller with more main-stem nodes compared to the plants that did not receive 1-MCP treatment (**Table 3**). These growth data also contribute to the explanation of the improved lint yield. Cotton lint yield is related to increases in plant height [37], and node number, since taller plants have a potential for producing more nodes which provide sites for development of reproductive branches to generate more bolls. Treatments failed to show any ethephon effect on plant growth parameters for either year of our study. In contrast, ethephon-treated plants were reported to exhibited height similar to or lower than the control, indicating a deleterious effect of ethephon on plant growth [28]. da Costa *et al*. (2011) [26] also found the detrimental effect of ethephon on plant growth: ethephon (292 $mL \cdot ha^{-1}$) reduced the number of reproductive nodes, which in combination with 1-MCP overcame this deleterious effect.

In our study, plants exposed to higher levels of ethylene exhibit premature senescence in the terms of increased membrane damage and lower photosynthetic quantum efficiency, while plants protected from ethylene effects show delayed senescence. When ethylene function was blocked, lower electrolyte leakage that is reflective of delayed senescence was detected in flower petals [14]-[16] and leaves [17] [20]. Reddy *et al*. (2004) [38] attributed the higher membrane damage to membrane lipid peroxidation in mulberry (*Morusalba* L.). Moreover, electrolyte leakage has been reported to be correlated with lipid peroxidation [39]. Our study confirmed that 1-MCP treatment lowered lipid peroxidation in stressed (heat stress and drought stress) cotton plants (unpublished data). Decreased malondialdehyde (MDA) level was also detected in 1-MCP treated soybean [27]. Another possible explanation for detected decreased membrane leakage is that ion transporters may also have been affected by 1-MCP treatment, impacting regulation of ion transport and thus impacting conductivity in the test solution. Further study is needed to test this hypothesis.

Ethephon or ethylene has been reported to decrease photosynthesis in soybean (*Glycine max* L. Merr.), mustard (*Brassica juncea* L.), and cotton [40]-[43]. A relation between decreased photosystem I and II activity to increased proteolysis and decreased chlorophyll content was found by using ethephon-treated isolated chloroplasts [44]. Thus, ethephon detrimentally affected photosynthesis, and ultimately carbon accumulation and the final yield in previous studies. Plants need oxygen for respiration and energy release. CO_2 fixation is limited by environmental stresses, such as cold and high temperature, drought, and salt stress which reduce $NADP^+$ regeneration and thus induce accumulation of ROS including hydrogen peroxide (H_2O_2), superoxide radical (O^{2-}), and hydroxyl radicals (OH^-) in leaves [45] [46]. Previous cotton research showed that premature leaf senescence, reflected as aggregated membrane damage, lipid peroxidation, and decreased photosynthesis, is a result of imbalance of ROS metabolism. Under these conditions, more ROS are generated than removed [39]. 1-MCP increased the antioxidant potential in pear (*Pyrusmalus* L. cv. Blanquilla) by reducing ROS and increasing enzymatic antioxidant potential [47]. 1-MCP-treated plants exhibited less membrane damage and greater antioxidant enzyme activities of superoxide dismutase (SOD) and glutathione reductase (GR) in cotton and soybean [27] [48]. Thus the reduced leaf senescence traits in 1-MCP treated plants were probably due to less impact from ethylene activity and enhanced ROS scavenging ability of antioxidant enzymes.

There are some problems in using ethephon as the source of ethylene. Ethephon is converted to ethylene when pH values are larger than 8. Ethephon decomposition results in the release of chloride, ethylene, and phosphate, which means non-ethylene responses may exist. In weed seed germination studies only a small portion of ^{14}C-labeled ethephon was released as ethylene [45]. Others have also shown low and inconsistent ethephon conversion efficiency [46] [49]. Thus, the application of ethephon may not always mimic ethylene treatment.

5. Conclusion

1-MCP treatment showed the potential to increase cotton yield. First, 1-MCP treated plants were taller and had more nodes in both years of the study suggesting that plants can produce more branches to set more bolls, although it could also suggest that the more robust plants were caused by a lack of boll set. Second, 1-MCP treated plants exhibited higher photosynthetic efficiency and less membrane damage in both years reflecting delayed senescence and a longer photosynthetically active period to produce more assimilates for boll development. Third, 1-MCP treatment increased number of open fruit and open fruit weight per plant in 2012. These

potentials for yield increase were realized in 2011 with 1-MCP treatment exhibiting higher lint yield. However, no significant yield increase was detected in 2012.

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