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MOLECULAR BIOLOGY AND PHYSIOLOGY

1-Methylcyclopropene Effects on Field-Grown Cotton: Physiological Characteristics

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ABSTRACT

Cotton (*Gossypium hirsutum* L.) is the lead cash crop in Texas, and its productivity is often challenged by stressful environmental conditions such as high temperatures and sub-optimal water supply. The objective of this investigation was to assess the impact of 1-methylcyclopropene (1-MCP) applications triggered by canopy temperature and forecasted ambient temperatures on field-grown cotton plants. Physiological responses to 1-MCP applications were investigated in field studies conducted during the summers of 2012-2014 at the Texas A&M University Field Laboratory in Burleson County, TX. During all three growing seasons, more than 65% of the days reached temperatures above 28 °C, which indicated great potential for high temperature stress. Daily plant canopy temperature, net photosynthesis, transpiration, and photosystem II quantum yield were affected by 1-MCP treatment when plants were irrigated, but not under dryland conditions. Positive effects of 1-MCP were found for fruit retention in 2013 and 2014, for both irrigated and dryland studies, although a negative impact was found in the 2012 irrigated study. Applications of 1-MCP affected physiological characteristics; however, it did not affect crop yield.

Plants living under natural conditions are often unable to express their full genetic potential due to unfavorable environmental conditions. According to Boyer (1982), atmospheric and/or soil moisture deficits along with high radiation and high temperature pose the biggest constraints for plant survival and crop productivity. Due to their intimate relationship, it is difficult to distinguish between drought and high temperature stress effects. It is important, however, to develop means to help mitigate the negative impacts of such stresses on crop productivity.

The hormone ethylene is a naturally occurring product of plant development (Gane, 1934), and widely known for its involvement in multiple physiological and developmental processes (Bapat et al., 2010; De Grauwe et al., 2005; Foo et al., 2006; Gniazdowska et al., 2010; Linkies et al., 2012; Mohapatra et al., 2006; Steffens et al., 2005). Although its effects may be different depending upon the plant and plant tissue, ethylene is known to affect plant growth at all developmental stages. More important for the scope of this project is ethylene's involvement in plant stress responses (Fluhr et al., 1996; Pierik et al., 2007; Sharp et al., 2002), especially those related to the abscission of vegetative and reproductive structures (Abeles et al., 1971; Jones et al., 1995; Morgan et al., 1992; Reid et al. 1992), and the potential of some ethylene inhibitors to help reduce stress-induced yield losses. The compound 1-methylcyclopropene (1-MCP) is an ethylene antagonist that works by binding to ethylene receptors in the plant, preventing and/or delaying the negative effects promoted by stress-induced ethylene (Sisler et al., 1997). Under controlled environments, it has been widely and effectively used in the fruits, vegetables, and ornamental flowers market to delay senescence and fruit ripening, thus significantly extending the shelf-life of various products (Hofman et al., 2001; Jiang et al., 2001; Ku et al., 1999; Wills et al., 2002).

Theoretically, under field conditions 1-MCP has the potential to mitigate the negative impacts of stress and positively influence cotton yield. Results from the limited literature are contradictory. Kawakami et al. (2010a) and de Brito et al. (2013) conducted field trials in Arkansas (USA) and Goiás (Brazil), respectively, and both concluded that 1-MCP increased cotton yield under field conditions.

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Kawakami et al. (2010a) attributed the increase in yield to decreased levels of stress (higher maximum quantum efficiency of Photosystem II + decreased glutathione reductase activity) and increased boll weight, while de Brito et al. (2013) provided no such explanation. On the other hand, in Texas, da Costa et al. (2011b) utilized ethephon (synthetic ethylene) as a source of stress applied one day after 1-MCP treatment, and reported that although 1-MCP improved growth and yield components (mainly in the upper canopy), no improvement in yield was found with either one of the rates tested (25 and 50 g a.i. ha^{-1}). In another field study conducted in Texas, Chen et al. (2014) reported that 1-MCP treatment delivered to plants at 10 g a.i. ha^{-1} decreased membrane damage, increased chlorophyll content and photosynthetic efficiency of subtending leaves (of tagged bolls), but that all these positive responses did not translate into higher yields.

The primary objective of this study was to assess the effects of 1-MCP applications triggered by different temperature thresholds, on field-grown cotton physiological parameters. To achieve this, canopy temperature, photosynthetic efficiency, transpiration, stomatal conductance, chlorophyll fluorescence, and pre-dawn leaf water potential were monitored and analyzed at three very distinct crop stages.

MATERIALS AND METHODS

Cultural practices. Two field trials (irrigated and dryland) were conducted at the Texas A&M AgriLife Field Laboratory in Burleson County (30°33'01.67" N, 96°26'07.07" W), approximately eight miles west of College Station, TX, on a Weswood silt loam soil (fine-silty, mixed, superactive, thermic, Udifluventic Haplustepts), during the 2012 – 2014 growing seasons. The study area was equipped with a sub-surface drip irrigation system installed at a depth of 0.457 m, with emitters spaced 0.457 m apart. Drip lines were spaced 1.02 m apart and were located at the center of each row (i.e. directly under the cotton plants). For the irrigated studies, water delivery was arbitrarily set at 80% evapotranspiration replacement (ET_r). Amounts were adjusted based on crop stage following guidelines by Fisher and Udeigwe (2012).

Management practices such as fertility, disease prevention, weed and insect control followed the guidelines provided by the Texas A&M AgriLife Extension service for the region. Cotton (*G. hirsutum* L. cv. Phytogen 499 WRF) seed were sown on April 10 in 2012 and April 09 in 2013 and 2014, at a rate of 108,000 seeds ha^{-1} in northwest to southeast oriented rows, spaced 1.02-m apart. Plant growth regulator applications consisted of a combination of cyclanilide (1-(2,4-dichlorophenylaminocarbonyl)-cyclopropane carboxylic acid; 0.003 kg a.i. ha^{-1}) and mepiquat chloride (N,N-dimethylpiperidinium chloride; 0.012 kg a.i. ha^{-1}), which were applied as needed during the growing season.

Treatments and experimental design. The studies were arranged in a randomized complete block design. Plots were four rows wide, 9.73-m in length with a 3-m alley in between, and the four treatments (including an untreated control) were replicated four times. Treatments were sprayed using a four-row, compressed air small-plot sprayer with hollow cone nozzle tips spaced at 51 cm delivering 103 L ha^{-1} and consisted of 1-methylcyclopropene (1-MCP) at a single rate of 25 g ha^{-1} of active ingredient with no adjuvants or surfactants used. The 1-MCP formulation used was a soluble powder (3.8 % a.i.), which released 1-MCP gas when in contact with water. For each treatment, 1-MCP powder was mixed with water in the field immediately prior to application. All plots receiving 1-MCP were sprayed within 20 min. of mixing. Treatments were defined as:

1. Control (C): No 1-MCP application
2. Smartcrop™ (S): 1-MCP application triggered by a canopy stress temperature of 28°C, accumulated for at least five consecutive hours, starting at pinhead square stage
3. Ambient 35ºC (A95): 1-MCP application triggered by forecasted maximum daily temperature of 35ºC or higher for at least three consecutive days, up to 24 hours prior, starting at pinhead square stage
4. Ambient 37.8ºC (A100): 1-MCP application triggered by forecasted maximum daily temperature of 37.8ºC or higher for at least three consecutive days, up to 24 hours prior, starting at pinhead square stage

There was a window of at least 14 days between applications, regardless of forecasted temperatures within that time frame. Treatments started based on each of the specified triggers at the pinhead square stage, and continued until plants reached maturity (open boll stage), after which no more 1-MCP applications were made.

Canopy temperature. To monitor crop canopy temperatures (CT), one SmartCrop™ (Smartfield Inc., Lubbock, TX) infrared thermometer (IRT) sensor (± 0.6 °C accuracy) was installed in the middle of each plot, on the third row, pointing southeast. Sensors were deployed at 42, 59, and 64 days after planting (DAP) in 2012, 2013, and 2014, respectively. The IRT installation occurred later in both 2013 and 2014 due to unseasonably low temperatures following planting, which delayed the establishment and initial growth of the crop. Sensors were mounted on a bracket and attached to a 2-m perforated pole. The bracket maintained sensors at a fixed 45° angle from the soil surface and the perforated pole allowed changes in sensor height (Fig. 1). To account for crop growth, frequent adjustments in height were made during the growing season to maintain sensors 20 to 30-cm above the crop canopy at all times, which resulted in an approximate 0.5 m^2 field of view. Canopy temperature data were automatically collected every minute and 15-min averages were wirelessly transferred to a base station (SmartWeather™) and automatically uploaded to the CropInsight™ (Smartfield, Inc., Lubbock, TX) website (http://www.cropinsight.com/).

Figure 1. Smartcrop™ infrared sensors were installed on a 2 m perforated pole about half-way into each plot, on the third row, pointing southeast. Brackets mounted on the pole maintained sensors at a fixed 45° angle from the soil surface throughout the season. Constant adjustments in height were made to maintain sensors about 20-30 cm above the crop canopy, which resulted in an approximate 0.5 m^2 field of view.

Weather. Rainfall, ambient temperature, and wind speed data were collected by the SmartWeather™ weather station (Smartfield, Inc., Lubbock, TX) that also served as a base station to wirelessly gather data from the infrared thermometer sensors.

Soil water potential. Soil water potential was continuously measured using Watermark sensors model 200SS (Irrometer Company, Inc., Riverside, CA) and the SmartProfile™ system (Smartfield, Inc., Lubbock, TX). The SmartProfile™ system logged data from the sensors and wirelessly transferred them to the SmartWeather™ base station. Sensors were installed at depths of 15, 30, and 61 cm, approximately 10 cm from the center of the row at 80, 66, and 92 DAP in 2012, 2013, and 2014, respectively. One set of sensors (three depths) was installed per study (i.e. dryland and irrigated).

Photosynthetic activity and transpiration. Physiological parameters such as net photosynthesis (A), transpiration (E), stomatal conductance (g_s), and difference in vapor pressure between leaf and air (Δe) were measured with a portable photosynthesis system model Li-Cor 6400 XT (LI-COR, Inc., Lincoln, NE). Each measurement series began at 10:00 and concluded by 14:00 at three distinct crop stages; early bloom (EB), full bloom (FB), and open boll (OB). Three random plants and one leaf per plant per plot were used. Measurements were made on the third uppermost fully-expanded leaf (Patterson et al., 1977). A photosynthetic photon flux density (PPFD) of 2,000 µmol m^{-2} s^{-1} was generated by a Red/Blue Light Source 6400-02B (Li-COR Inc., Lincoln, NE) on the adaxial surface of the leaf being measured. The closed leaf chamber of the equipment had an area of 6 cm^2 and a constant reference cell carbon dioxide (CO_2) concentration of 400 µmol mol^{-1} was maintained throughout the measurements. Leaf adaptation to the conditions inside the closed chamber were monitored using the coefficient of variation (CV) on the instrument's display and values were not recorded until measurements were stable, which usually took around 60 to 360 s.

Chlorophyll fluorescence. Chlorophyll fluorescence was measured using a portable chlorophyll fluorometer model PAM-2100 (Heinz Walz GmbH, Effeltrich, Germany) between the hours of 10:00 and 14:00 and completed within 30 min of recording the first data point. Five random plants per plot were measured using the third uppermost fully-expanded leaf. Chlorophyll fluorescence measurement indicates the quantum efficiency of the photosystem II by measuring the excess energy being re-emitted as light (Maxwell et al., 2000). Actual quantum yield of pho-

tosystem II (ϕ_{PSII}) was measured using the saturation pulse method in light adapted leaves and calculated as $Y = (F_m' - F_t) / F_m'$, where F_m' is maximum fluorescence intensity and F_t is fluorescence at a given time.

Leaf water potential. To examine the effect of 1-MCP on crop water status and assess the efficiency of the irrigation system in creating two distinct growing conditions, pre-dawn leaf water potential (ψ_{wl}) was measured with a pressure chamber (PMS Instrument Co., Corvallis, OR) between 4:30 and 6:30 using the method described by Scholander et al. (1965). Three plants per plot were sampled to collect data using the third uppermost fully-expanded leaf, at three distinct crop stages (EB, FB, and OB). About a third of the leaf petiole was cut using a razor at an approximate 45° angle. Leaves were placed within the chamber usually within three min of their removal from the plant. The pressure chamber was then slowly pressurized at a rate of approximately 0.03 MPa s^{-1} as suggested by Turner (1988).

Statistical analysis. Data were analyzed using JMP Pro, Version 11.0.0, SAS Institute Inc. (2007). Analysis was performed on a yearly basis since significant Year x Treatment interaction was found. Data were subjected to analysis of variance considering replication and treatment as random and fixed effects, respectively. Means were separated using Fisher's LSD at the 5% probability level. Means comparisons were made between treatments within each irrigation regime (e.g. dryland or irrigated) and data were combined over years whenever permissible.

RESULTS AND DISCUSSION

In-season rainfall totals were 503, 325, and 635 mm, and accounted for 48, 32, and 50% of total annual rainfall for 2012, 2013, and 2014, respectively (Table 1). In 2012, the majority of daily rainfall totals were in the 2 – 10 mm range but were very well distributed throughout the growing season. Frequent, smaller (< 25 mm) rainfall events, coupled with fewer but stronger (> 25 mm) events were able to maintain reasonable amounts of water in the soil profile during the period studied (Table 1). During the 2013 growing season (between planting and harvest), plants received only about 65% of the amount of rain that fell in 2012, for roughly the same time period. Also, significant rainfall events during periods of high water demand (e.g. flowering to boll filling) were not as frequent in 2013 as they were in 2012. In 2014 the trial received unusually high amounts of rainfall between planting and harvest dates and events were also very well distributed along the season.

Fifteen-minute average measurements of soil water matric potential indicated that the 15 to 61-cm profile were kept above permanent wilting point (-1.5 MPa) for the irrigated treatments during all years studied. The 15-cm depth of the dryland treatments reached permanent wilting point for the first time at 120, 91, and 163 DAP for 2012, 2013, and 2014, respectively. The remaining depths (30 and 61-cm) did not reach -1.5 MPa in either of the years studied for the dryland treatments.

Table 2 shows a summary of 1-MCP applications for all three years studied based on treatment triggers. During all three growing seasons, more than 65% of the days reached temperatures above the midway point of the thermal kinetic window (TKW) of 28 °C, which indicated great potential for high temperature stress. The TKW represents the temperature range in which the apparent Michaelis-Menten constant (K_m) remains within 200% of the minimum value for optimum enzyme function (Burke et al., 1988). Additionally, the average maximum temperature during all three seasons was greater than the upper TKW threshold of 31 °C. The highest temperatures occurred between 12:00 and 17:00. Daily maximum temperatures relative to the TKW are shown in Figure 2.

Table 1. Average soil water matric potential (ψ_m) measured at depths of 15, 30, and 61 cm for dryland (Dry) and irrigated (Irr.) studies. Total rainfall for each year of the study and their respective in-season accumulations are also shown

Year	ψ_m (Dry)			ψ_m (Irr.)			Rainfall	
	15 cm	30 cm	61 cm	15 cm	30 cm	61 cm	Total	Season
	MPa	MPa	MPa	MPa	MPa	MPa	mm	mm
2012	-0.47	-0.19	-0.27	-0.18	-0.11	-0.04	1,046	503
2013	-1.18	-0.41	-0.32	-0.35	-0.26	-0.10	998	325
2014	-0.44	-0.19	-0.14	-0.12	-0.07	-0.03	744	635

Table 2. Table shows timing of 1-methylcyclopropene (1-MCP) application based on different temperature thresholds (treatments). All applications were made using a powder formulation of 1-MCP at a single rate of 25 g a.i. ha^{-1} with a small-plot sprayer and occurred for both dryland and irrigated studies on the same dates

Treatment[Z]	1-MCP Applications		
	2012	2013	2014
S	5-Jul	27-Jun	2-Jul
	5-Aug	11-Jul	24-Jul
		25-Jul	8-Aug
A95	5-Jul	11-Jun	10-Jul
	5-Aug	27-Jun	24-Jul
		11-Jul	8-Aug
		25-Jul	
A100	5-Aug	27-Jun	8-Aug
		11-Jul	
		25-Jul	

[Z]Smartcrop™ (S), Ambient 35°C (A95), and Ambient 37.8°C (A100)

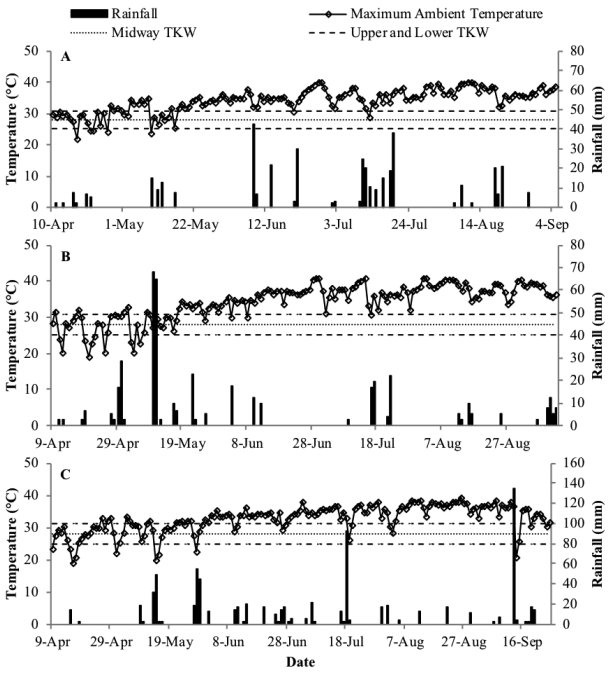

Figure 2. Daily maximum ambient temperature and rainfall during the season for 2012 (A), 2013 (B), and 2014 (C). Dashed horizontal lines represent the lower and upper bounds of the TKW (25 and 31 °C), and the dotted line represent the midway temperature of the TKW (28 °C). Notice the difference in rainfall scale for 2014 compared to 2012 and 2013.

Rainfall was plentiful and well-distributed in 2012 and 2014, which maintained an adequate amount of water in the soil profile, even for the dryland study throughout most of the season (Table 1 and Figs. 2A and 2C). As a result, differences in leaf water potential between the dryland and irrigated studies were only found at the OB stage for both 2012 and 2014 (Figs. 3A and 3C). During the 2013 season, however, reduced rainfall lowered soil available moisture (Table 1), such that differences in leaf water potential were found throughout the growing season, from EB through OB (Fig. 3B). Across all three years, the irrigated study had lower leaf water potential at the OB stage (Fig. 3). Based on single measurements at midday, Kawakami et al. (2010b) reported an increase in stomatal resistance (decrease in stomatal conductance) five days after 1-MCP treatment in water-stressed cotton plants, which led to lower leaf water potential when compared to the untreated control also under water stress. Our studies found no impact of 1-MCP on differences in pre-dawn water potential between treatments in any of the three growth stages or years (Table 3).

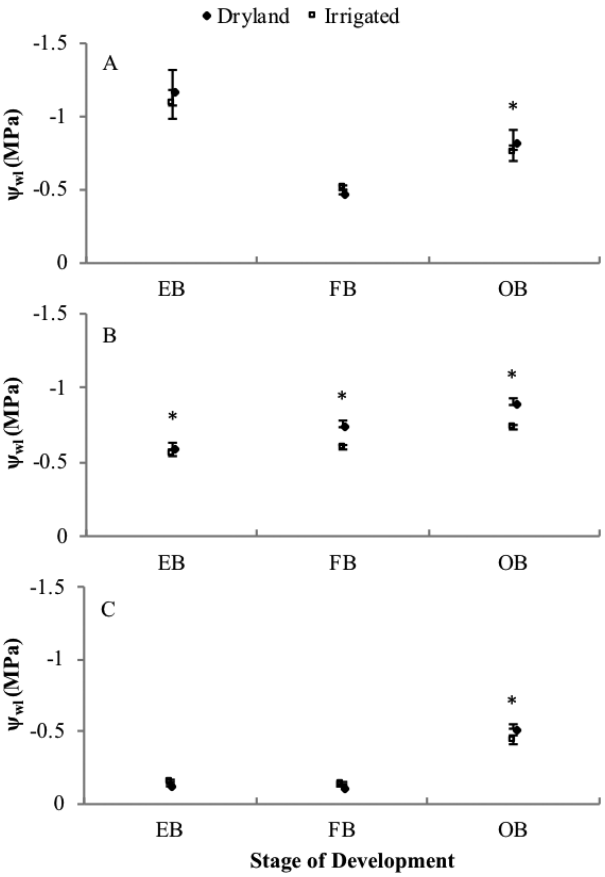

Figure 3. Pre-dawn leaf water potential (ψ_{wl}) measurements are shown for cotton grown during the summers of 2012 (A), 2013 (B), and 2014 (C). Values are averages of all four treatments combined within each growth stage (n = 48): early bloom (EB), full bloom (FB), and open boll (OB). Error bars represent ± SE, and * represents statistical significance between studies at the 5% probability level within each growth stage.

Table 3. Effect of 1-methylcyclopropene (1-MCP) on leaf water potential (ψ_{leaf}) at early bloom (EB), full bloom (FB), and open boll (OB) growth stages of field cotton grown during the summers of 2012, 2013, and 2014 under irrigated (Irr.) and dryland (Dry) conditions. Values are averages of three samples and four replications per treatment (n = 12)

Year	Treatment[Z]	ψ_{leaf} (EB)		ψ_{leaf} (FB)		ψ_{leaf} (OB)	
		Irr.	Dry	Irr.	Dry	Irr.	Dry
		MPa					
2012	C	-1.08	-1.20	-0.51	-0.49	-0.75	-0.84
	S	-1.09	-1.30	-0.50	-0.54	-0.75	-0.88
	A95	-1.13	-1.23	-0.50	-0.55	-0.81	-0.92
	A100	-1.01	-1.19	-0.52	-0.51	-0.72	-0.83
	Sig.[Z]	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
2013	C	-0.56	-0.61	-0.60	-0.76	-0.73	-0.91
	S	-0.56	-0.61	-0.61	-0.74	-0.75	-0.88
	A95	-0.57	-0.58	-0.56	-0.75	-0.73	-0.87
	A100	-0.53	-0.62	-0.57	-0.78	-0.75	-0.92
	Sig.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
2014	C	-0.15	-0.14	-0.13	-0.13	-0.45	-0.53
	S	-0.14	-0.15	-0.18	-0.15	-0.43	-0.48
	A95	-0.17	-0.15	-0.16	-0.13	-0.47	-0.46
	A100	-0.12	-0.14	-0.16	-0.16	-0.48	-0.49
	Sig.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

[Z] Control (C), Smartcrop™ (S), Ambient 35°C (A95), and Ambient 37.8°C (A100)

[Y] Significance (Sig.) of differences between treatments at the 5% probability level. Not significant (n.s.)

Canopy temperatures for each treatment in the dryland plots were consistently higher than those found in irrigated plots (Figs. 4A and 4B). Those differences were more pronounced in the drier 2013 season than they were in the other two growing seasons (2012 and 2014). The higher CT exhibited by water stressed plants when compared to the ambient or non-stressed plants is a well-known plant response (Idso et al., 1977; Jackson et al., 1977).

When daily plant CT was averaged within each season, no effect of 1-MCP treatment was found in any of the years when the plants were grown under dryland conditions (Fig. 4A). P-values were 0.852, 0.293, and 0.287 for 2012, 2013, and 2014, respectively. Under irrigation, however, 1-MCP impacted CT in all three years tested (Fig. 4B). P-values for such analyses were 0.025, 0.027, and < 0.0001, for 2012, 2013, and 2014, respectively. In 2012, the highest CTs were found for the S treatment which were higher than both the C and A95. In 2013, all 1-MCP treatments had significantly higher CTs when compared to the C. In 2014, the A100 treatment had higher CT than both the C and A95.

Despite inconsistent results for stomatal conductance measurements (tables 4, 5, and 6), evidence of a 1-MCP-induced increase in stomatal resistance (Kawakami et al., 2010b), reduction in stomatal conductance (da Costa et al., 2011a), and decrease in respiration rates (Cefola et al., 2010) may help explain the CT results shown on Figures. 4A and 4B. While grown under irrigation at least one 1-MCP treatment displayed significantly higher CT when compared to the untreated control. Although research on the effects of 1-MCP in cotton shows that its effects are only temporary (da Costa et al., 2011a; Kawakami et al., 2010b; Su et al., 2012), it is possible that multiple 1-MCP applications during the season were capable of affecting the in-season average CT by temporarily reducing transpiration and thus the plants' transpirational cooling which may have led to higher CT. Furthermore, da Costa and Cothren (2011a) found a decrease in stomatal conductance and transpiration coupled with increased leaf temperature in 1-MCP-treated cotton plants grown in a greenhouse when the plants were grown in well-watered conditions. Plants grown under water deficit stress did not exhibit the same responses to 1-MCP application.

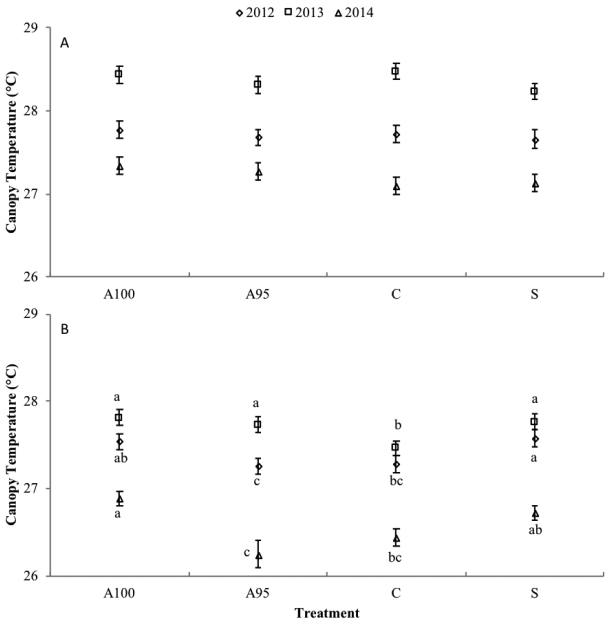

Figure 4. Effect of 1-methylcyclopropene (1-MCP) on different treatments for cotton grown during the summers of 2012, 2013, and 2014 under dryland (A) and irrigated (B) conditions. Values are shown as the average of daily canopy temperature throughout the season. Bars represent ± SE when greater than the symbols. Different letters within years represent significance at the 5% level of probability between treatments.

Physiological parameters measured were not affected by 1-MCP application when cotton was grown under dryland conditions in any of the three crop stages and years studied (Tables 4, 5, and 6). In general, under dryland conditions net photosynthesis was higher early and during the peak reproductive phases (EB and FB), and substantially decreased by the time the crop reached the late reproductive phase (OB stage). These reductions in photosynthetic activity as the crop matures were not unexpected and have also been reported elsewhere (Bauer et al., 2000; Peng et al., 1991; Pettigrew et al. 1993). Transpiration also followed the same trend, such that ~ 50% decrease in transpiration was detected towards the latter part of the growing season when late season (OB) measurements were compared to early-season measurements (EB and FB).

During the 2013 season, all parameters measured showed differences among irrigated treatments at the FB stage (Table 5). Net photosynthesis, stomatal conductance, and transpiration for the S and A100 treatments were higher than those of the control plots at FB. The Δe was higher in C plots when compared to the higher temperature threshold treatment (A100). At the FB stage in 2013, S and A100 treatments had received one 1-MCP application while the A95 treatment had received two 1-MCP applications, on 27 June and 11 and 27 June, respectively (Table 2). In 2014, there were no differences between treatments in any of the three crop stages (Table 6). Results were not consistent within years and/or across growth stages, which may possibly be attributed to the transient effects of 1-MCP. Previous studies of 1-MCP effects on cotton plants and cotton plant parts showed that its effects usually lasted less than 72 hr (da Costa et al., 2011a; Su et al., 2012). Indeed, measurements showed that although some differences among treatments were found in the FB growth stage in 2013, those differences were undetectable by the time the crop reached the latter phase of its reproductive stage (OB).

Photosystem II quantum yield (ϕPS_{II}) measurements showed differences early in the season (EB) for irrigated plots in 2013 and 2014 (Table 7). In 2013 ϕPS_{II} measurements were higher for the A95 when compared to the C plots, whereas in 2014, C plots showed higher ϕPS_{II} when compared to the S treatment. However, at the time of EB measurements treatment A95 in 2013 was the only treatment that had received 1-MCP application, which happened two weeks prior to measurements. No 1-MCP applications had been made prior to ϕPS_{II} measurements in 2014 (Table 2). In the 2013 irrigated study, 1-MCP increased ϕPS_{II} at EB when compared to the C. Differences found early at the EB stage in the 2014 irrigated study may not be attributed to 1-MCP since the first application did not occur until July 2, post EB measurements. Throughout the rest of the growing season (FB and OB), no differences were found between treatments within each study and growth stage. In general, higher ϕPS_{II} values were found early in the season at the EB stage, and declined as the season progressed, such that the lowest values were found at the OB stage. Furthermore, cotton plants in the irrigated study were able to maintain sligthly higher ϕPS_{II} throughout the growing seasons than those in the dryland study. This is not unexpected, since previous research has shown that drought stress may affect chlorophyll fluorescence in several plant species, including faba bean (*Vicia faba* L.), mung bean (*Vigna radiata*), mango (*Mangifera indica*), and chickpea (*Cicer arietinum* L.) (Abid et al., 2017; Batra et al., 2014; Elsheery et al., 2008; Rahbarian et al. 2011).

Table 4. Net photosynthesis (A), transpiration (E), stomatal conductance (g_s), and difference in vapor pressure between leaf and the air (Δ_e) at three crop stages for dryland (Dry) and irrigated (Irr.) cotton in 2012. The third uppermost fully-expanded leaf was used for the measurements. Values are averages of three random plants per plot and four replications per treatment per growth stage (n = 12)

Treatment[Z]	Growth Stage[Y]	Dry	Irr.	Dry	Irr.	Dry	Irr.	Dry	Irr.
		A		E		g_s		Δ_e	
		umol CO_2 m^{-2} s^{-1}		mmol H_2O m^{-2} s^{-1}		mol H_2O m^{-2} s^{-1}		kPa	
C	EB	36.23	36.68	9.29	9.79	1.75	2.10	0.80	0.81
S	EB	35.71	35.82	9.07	9.33	2.03	1.90	0.82	0.84
A95	EB	36.32	37.55	9.10	9.58	1.79	3.02	0.86	0.69
A100	EB	37.72	37.41	9.42	9.52	2.64	2.99	0.73	0.74
C	FB	37.40	38.10	10.64	10.95	1.72	1.78	1.00	1.04
S	FB	35.43	37.69	10.22	11.13	1.70	1.70	1.08	1.03
A95	FB	39.43	38.96	10.80	11.15	1.88	1.82	0.95	0.98
A100	FB	36.80	39.00	10.66	11.20	1.70	2.13	1.00	0.93
C	OB	15.65	17.60	5.56	5.97	0.20	0.25	3.13	3.03
S	OB	15.53	18.87	5.44	6.39	0.21	0.25	3.06	2.85
A95	OB	16.49	20.21	5.69	7.15	0.20	0.35	3.05	2.67
A100	OB	15.52	16.87	5.56	6.35	0.20	0.23	3.11	3.06
ANOVA									
EB		0.252	0.655	0.494	0.727	0.162	0.101	0.087	0.010
FB		0.257	0.625	0.679	0.651	0.838	0.182	0.324	0.220
OB		0.956	0.614	0.990	0.667	0.996	0.331	0.980	0.329

[Z]Control (C), Smartcrop™ (S), Ambient 35°C (A95), and Ambient 37.8°C (A100)

[Y]Early Bloom (EB), Full Bloom (FB), and Open Boll (OB)

Table 5. Net photosynthesis (A), transpiration (E), stomatal conductance (g_s), and difference in vapor pressure between leaf and the air (Δ_e) at three crop stages for dryland (Dry) and irrigated (Irr.) cotton in 2013. The third uppermost fully-expanded leaf was used for the measurements. Values are averages of three random plants per plot and four replications per treatment per growth stage (n = 12)

Treatment[Z]	Growth Stage[Y]	Dry	Irr.	Dry	Irr.	Dry	Irr.	Dry	Irr.
		A		E		g_s		Δ_e	
		umol CO_2 m^{-2} s^{-1}		mmol H_2O m^{-2} s^{-1}		mol H_2O m^{-2} s^{-1}		kPa	
C	EB	28.89	33.19	10.89	11.47	1.20	1.74	1.30	1.13
S	EB	27.35	30.10	10.73	10.83	1.23	1.32	1.26	1.31
A95	EB	28.74	29.08	10.52	11.03	1.16	1.15	1.37	1.44
A100	EB	29.59	29.27	10.57	10.89	1.13	1.21	1.38	1.37
C	FB	21.88	22.17	8.38	9.13	0.73	1.09	1.51	1.25
S	FB	23.62	28.19	8.08	10.54	0.72	1.54	1.59	1.11
A95	FB	21.95	24.78	7.60	9.86	0.58	1.33	1.70	1.12
A100	FB	23.16	28.44	8.49	10.77	0.76	1.87	1.56	0.97
C	OB	19.69	31.53	6.04	11.32	0.28	1.02	2.53	1.49
S	OB	20.98	29.67	6.86	11.11	0.36	1.02	2.33	1.48
A95	OB	23.07	32.36	7.85	11.20	0.45	1.09	2.19	1.44
A100	OB	21.91	34.24	6.76	12.09	0.33	1.23	2.44	1.40
ANOVA									
EB		0.696	0.186	0.881	0.709	0.935	0.112	0.408	0.112
FB		0.736	0.011	0.545	0.001	0.557	0.005	0.680	0.050
OB		0.284	0.075	0.210	0.212	0.142	0.252	0.372	0.631

[Z]Control (C), Smartcrop™ (S), Ambient 35°C (A95), and Ambient 37.8°C (A100)

[Y]Early Bloom (EB), Full Bloom (FB), and Open Boll (OB)

Table 6. Net photosynthesis (A), transpiration (E), stomatal conductance (g_s), and difference in vapor pressure between leaf and the air (Δ_e) at three crop stages for dryland (Dry) and irrigated (Irr.) cotton in 2014. The third uppermost fully-expanded leaf was used for the measurements. Values are averages of three random plants per plot and four replications per treatment per growth stage (n = 12)

Treatment[Z]	Growth Stage[Y]	Dry	Irr.	Dry	Irr.	Dry	Irr.	Dry	Irr.
		A		E		g_s		Δ_e	
		umol CO_2 m^{-2} s^{-1}		mmol H_2O m^{-2} s^{-1}		mol H_2O m^{-2} s^{-1}		kPa	
C	EB	41.26	39.48	13.93	13.28	1.97	1.85	1.20	1.17
S	EB	40.20	40.76	13.83	13.73	2.11	1.93	1.14	1.18
A95	EB	41.18	39.18	13.79	13.44	2.21	2.01	1.08	1.16
A100	EB	39.95	40.33	13.50	13.14	2.03	1.69	1.16	1.22
C	FB	33.15	31.44	13.02	12.67	2.02	1.83	1.09	1.14
S	FB	33.42	31.13	13.14	12.71	2.02	1.88	1.09	1.10
A95	FB	31.75	29.18	12.96	12.76	1.97	1.80	1.10	1.13
A100	FB	32.16	31.05	12.95	12.65	2.02	1.73	1.08	1.20
C	OB	21.59	33.71	6.20	11.82	0.32	1.65	2.43	1.19
S	OB	21.78	33.79	5.88	11.98	0.29	1.79	2.44	1.11
A95	OB	22.56	32.63	6.49	11.63	0.36	1.58	2.29	1.16
A100	OB	19.61	33.28	5.67	11.49	0.41	1.42	2.51	1.24
ANOVA									
EB		0.447	0.725	0.455	0.195	0.683	0.308	0.259	0.739
FB		0.585	0.359	0.858	0.988	0.986	0.838	0.984	0.302
OB		0.817	0.667	0.875	0.516	0.741	0.306	0.881	0.477

[Z] Control (C), Smartcrop™ (S), Ambient 35°C (A95), and Ambient 37.8°C (A100)

[Y] Early Bloom (EB), Full Bloom (FB), and Open Boll (OB)

Table 7. Effect of 1-methylcyclopropene (1-MCP) on the quantum yield of photosystem II (ϕPS_{II}) for cotton grown during the summers of 2012, 2013, and 2014. Quantum yield of PSII was measured using the saturation pulse method in light adapted leaves and calculated as $Y = (F_m - F_t) / F_m$, where F_m = maximum fluorescence and F_t = fluorescence at given time. Data is presented for both irrigated (Irr.) and dryland (Dry) studies as a mean of 5 plants per plot per treatment (n = 20). Data was collected at early bloom (EB), full bloom (FB), and open boll (OB)

Year	Treatment[Z]	EB		FB		OB	
		Irr.	Dry	Irr.	Dry	Irr.	Dry
2012	C	0.649	0.670	0.426	0.419	0.516	0.360
	S	0.659	0.646	0.450	0.398	0.529	0.409
	A95	0.641	0.667	0.401	0.383	0.586	0.375
	A100	0.663	0.664	0.393	0.395	0.572	0.363
	Sig.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
2013	C	0.498b	0.560	0.548	0.534	0.513	0.596
	S	0.554ab	0.594	0.580	0.512	0.503	0.620
	A95	0.607a	0.558	0.584	0.514	0.515	0.614
	A100	0.545ab	0.546	0.542	0.515	0.535	0.594
	Sig.	*	n.s.	n.s.	n.s.	n.s.	n.s.
2014	C	0.508a	0.469	0.448	0.481	0.367	0.342
	S	0.453b	0.433	0.456	0.469	0.376	0.334
	A95	0.473ab	0.429	0.463	0.433	0.390	0.339
	A100	0.477ab	0.438	0.436	0.437	0.381	0.415
	Sig.	*	n.s.	n.s.	n.s.	n.s.	n.s.

Significance (Sig.): * significant at $P \leq 0.05$, not significant (n.s.)

[Z] Control (C), Smartcrop™ (S), Ambient 35°C (A95), and Ambient 37.8°C (A100)

CONCLUSIONS

Results of this study indicated that 1-MCP had little to no significant effect on physiological parameters of field grown cotton at different stages of crop development. The 1-MCP treatment had no impact on predawn leaf water potential for either dryland or irrigated conditions. Average daily plant CT, net photosynthesis, stomatal conductance, transpiration, and photosystem II quantum yield were affected by 1-MCP treatment when plants were grown under irrigation, but not under dryland conditions. In conclusion, the effects of 1-MCP applications during the different seasons were variable and somewhat inconsistent.

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