Preplant Application of 1-Methylcyclopropene Improves Postplanting Performance of Tomato Transplants by Suppressing Ethylene-induced Stress Responses

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Additional index words. 1-MCP, abiotic stress, mechanical stress, *Solanum lycopersicum*, stand establishment, transplant shock

Abstract. Transplant shock is caused by various types of abiotic stress, limiting stand establishment and productivity of many vegetable crops. Although postplanting stress can be minimized under well-managed field conditions, mechanical stress is unavoidable during the transport and transplanting of seedlings. Mechanical stress stimulates ethylene production, which in turn, induces overall growth retardation as a stress adaptation strategy. We hypothesized that, under optimum field conditions, transplant shock is caused primarily by ethylene-induced stress responses, and that inhibiting ethylene action can reduce transplant shock by maintaining uninterrupted growth. In this study, a new spray formulation of 1-methylcyclopropene (1-MCP) was used to inhibit ethylene perception in tomato (*Solanum lycopersicum* L.) seedlings. A bioassay experiment demonstrated reduced ethylene sensitivity in 1-MCP-treated ($1 \text{ mg}\cdot\text{L}^{-1}$) seedlings using leaf epinasty and chlorosis as measured responses. Field experiments evaluated growth, physiological, and yield responses to preplant spray treatment of 1-MCP ($12.5\text{--}50 \text{ mg}\cdot\text{L}^{-1}$) under optimum field conditions. Postplanting growth modulation by 1-MCP at the flowering stage was characterized by enhanced height growth and suppressed stem diameter growth, indicating the inhibition of ethylene-induced stress responses. At the fruit harvest stage, preplant 1-MCP treatment increased shoot biomass by 23% and flower production by 22%, while improving photosynthetic capacity on a whole-plant basis. As a result, 1-MCP-treated plants produced 13% to 24% higher total marketable fruit yields than untreated plants in two consecutive growing seasons. Correlation analyses revealed that flower number increased proportionally to shoot biomass, and marketable fruit number increased proportionally to flower number. These results support our hypothesis and propose that preplant 1-MCP treatment is a new stress-management approach to reducing transplant shock. Importantly, this new technique is easily implementable by commercial transplant nurseries with no negative side effect on transplant quality and fruit development.

Transplanting results in transplant shock in seedlings, limiting stand establishment and productivity of many vegetable crops (Agehara and Leskovar, 2012; Vavrina,

2002). Transplant shock is caused by various types of abiotic stress occurring during the transport and transplanting of seedlings (Vavrina, 2002). Seedlings are also subjected to abiotic stress after transplanting, such as direct sunlight, wind, and temperature extremes. Common symptoms of transplant shock include leaf chlorosis, leaf abscission, impaired or stunted growth, wilting, and seedling mortality (Vavrina, 2002). The degree and duration of these stress symptoms can vary greatly depending on the type and severity of stress. Minimizing growth interruption caused by transplant shock is critical to successful stand establishment of vegetable seedlings.

Transplant shock is not simply physical damage in seedlings, but it is the consequence of adaptive stress responses regulated by multiple phytohormones to cope with dynamic changes in growing conditions

(Srivastava, 2002; Taiz and Zeiger, 2010). For example, mechanical stress during shipping and transplanting operations stimulates the synthesis of ethylene in seedlings (Druege, 2006). As a strong antagonist of gibberellic acid, increased production of this gaseous phytohormone inhibits stem elongation and leaf expansion, while promoting stem thickening (Biddington, 1986; Khan, 2006; Tholen et al., 2006). Other ethylene-induced responses include leaf epinasty and senescence (Ferrante and Francini, 2006; Ursin and Bradford, 1989). The resulting compact growth and overall growth retardation are morphological adaptations to withstand mechanical stress, such as physical contact, vibration, and wind (Biddington, 1986; Druege, 2006; Tholen et al., 2006). Absciscic acid is another phytohormone that induces physiological and morphological adaptive changes (Srivastava, 2002). Water uptake capacity in newly transplanted seedlings may be limited because of root injury during transplanting and disturbed root–soil contact (Burdett, 1990). Water deficit increases accumulation of absciscic acid in leaves, which in turn, induces stomatal closure to reduce transpirational water loss (Davies and Jones, 1991). Absciscic acid also limits plant water use by inhibiting leaf expansion and thus limiting increases in transpirational area (Van Volkenburgh, 1999).

Many chemical compounds have been evaluated for their effectiveness in reducing transplant shock (Berkowitz and Rabin, 1988; del Amor et al., 2010; Goreta et al., 2007; Iriti et al., 2009; Moftah and Al-Humaid, 2005). Antitranspirants can reduce plant water loss by limiting transpiration physically or physiologically (Park et al., 2016). The most popularly used physical antitranspirants are spray emulsions of latex, wax, or acrylic that form thin films over leaf surfaces and block stomata (Park et al., 2016). Other physical antitranspirants, such as kaolin clay, are reflective materials, which prevent the absorption of radiant energy, thereby reducing leaf temperatures and transpiration (Bittelli et al., 2001; Jifon and Syvertsen, 2003; Moftah and Al-Humaid, 2005). Absciscic acid acts as a physiological antitranspirant that reduces transpirational water loss by inducing stomatal closure and inhibiting leaf expansion (Davies and Jones, 1991; Taiz and Zeiger, 2010). Plants can also be acclimated to adverse growing conditions using priming agents that activate defense mechanisms in metabolic processes (Tuteja and Sarvajeet, 2012).

Most of these chemicals aim to reduce postplanting water stress. Although their beneficial effects are reported in many previous studies, they appear to be pronounced mainly when plants are under severe water stress (Agehara and Leskovar, 2012; Berkowitz and Rabin, 1988; Moftah and Al-Humaid, 2005). Under optimum growing conditions, conversely, antitranspirants may have negative side effects. Stomatal closure reduces water stress at the expense of CO_2 supply to photosynthesis (Lawlor, 2002).

Received for publication 26 Nov. 2019. Accepted for publication 20 Feb. 2020.

Published online 19 March 2020.

I thank the Horticulture Laboratory staff at Gulf Coast Research and Education Center for their technical assistance. I also thank Kenny Lee for providing high-quality plant materials used in this study and Alan Green for his contribution on designing treatment and experiment protocols and participating in discussions. Funding was provided by AgroFresh.

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Fig. 1. Suppression of ethylene-induced leaf epinasty by 1-methylcyclopropene (1-MCP) in 'Florida 47' tomato at 3 d after ethephon and 1-MCP treatments (Expt. 1): (A) epinasty rating (1 = none; 2 = slight; 3 = moderate; 4 = severe), and (B) leaf epinasty induced by ethephon in tomato seedlings. Treatments were as follows: untreated water control, ethephon treatment at 1000 mg·L⁻¹, and 1-MCP treatment at 1 mg·L⁻¹ 1 h before ethephon treatment at 1000 mg·L⁻¹. Data are means ± 95% confidence intervals (n = 4). Means with the same letter are not significantly different (Tukey–Kramer test, $P < 0.05$).

Agehara and Leskova (2012) reported that stomatal limitation to photosynthesis by exogenous abscisic acid limited shoot dry matter accumulation in muskmelon seedlings. Other negative side effects of abscisic acid include leaf chlorosis, leaf abscission, and excessive inhibition in leaf expansion and stem elongation (Agehara and Leskova, 2014a, 2014b, 2015, 2017; Park et al., 2016). In addition, the performance of film-forming antitranspirants is limited primarily on the adaxial leaf surface and is dependent highly on spray coverage (Goreta et al., 2007).

In contrast to water stress, mechanical stress is unavoidable regardless of postplanting growing conditions. Mechanical stress occurs during the transport and transplanting of seedlings, as they are moved from a transplant nursery, vibrated in trays during shipment, pulled from trays, and planted into the soil (Cantliffe, 1993). It stimulates ethylene production in seedlings, which in turn, induces overall growth retardation as a stress adaptation strategy. Therefore, we hypothesized that, under well-managed field conditions, transplant shock is caused primarily by ethylene-induced stress responses, and that inhibiting ethylene action can reduce transplant shock by maintaining uninterrupted

Fig. 2. Suppression of ethylene-induced leaf chlorosis by 1-methylcyclopropene (1-MCP) in 'Florida 47' tomato at 3 d after ethephon and 1-MCP treatments (Expt. 1): (A) leaf chlorophyll index, and (B) leaf chlorosis induced by ethephon in tomato seedlings. Treatments were as described in Fig. 1. Data are means ± 95% confidence intervals (n = 4). Means with the same letter are not significantly different (Tukey–Kramer test, $P < 0.05$).

growth. This new stress-management approach will have large-scale applicability because its efficacy will not depend on the presence of postplanting stress.

In this study, a new spray formulation of 1-MCP was used to inhibit ethylene perception in tomato seedlings by inactivating ethylene receptors. The objective of this study was to examine the efficacy of preplant 1-MCP treatment to suppress ethylene-induced stress responses and its effectiveness in improving postplanting growth and yield of tomato.

Materials and Methods

Plant materials. A major commercial cultivar of fresh-market tomato in Florida, 'Florida 47', was used in this study. All tomato seedlings used in this study were grown in 128-cell polystyrene plug trays at a commercial transplant nursery (Quik-Starts, Ruskin, FL). Seedlings were grown for 28 to 30 d or until they reached the optimal size (10–13 cm in height) for transplanting according to the nursery's commercial standard.

1-MCP spray treatment. A powder formulation of 1-MCP, AFXRD-038 (Agro-Fresh, Spring House, PA), containing 3.8% of 1-MCP, was used in this study. Test solutions were prepared by adding the requisite amount of 1-MCP to deionized water in a spray tank. To minimize the loss of 1-MCP in a gaseous form before treatment, the tank was

gently swirled to dissolve the 1-MCP powder and spray treatments were performed within 30 min after preparing the test solutions. All spray treatments were performed using a CO₂-pressured backpack sprayer (model T; Bellspray, Opelousas, LA) between 11:00 and 12:00 AM.

Transplant bioassay (Expt. 1). A tomato transplant bioassay (Expt. 1) was conducted at the Gulf Coast Research and Education Center in Balm, FL, to examine the efficacy of 1-MCP to suppress ethylene-induced stress responses in tomato seedlings. Ethephon (Florel; Lawn and Garden Products, Inc., Fresno, CA), an ethylene-releasing compound, was used as exogenous ethylene. Treatments were untreated water control, ethephon treatment at 1000 mg·L⁻¹, and 1-MCP treatment at 1 mg·L⁻¹ 1 h before ethephon treatment at 1000 mg·L⁻¹. Treatment concentrations are based on active ingredients. Spray treatments were performed with a spray volume of 5.5 mL/plant.

The sensitivity of tomato seedlings to ethylene was assessed at 3 d after treatment based on the degree of leaf epinasty and chlorosis, both of which are typical ethylene-induced responses (Ferrante and Francini, 2006; Ursin and Bradford, 1989). Leaf epinasty is defined as downward bending of petioles. Leaf epinasty was rated using the first fully expanded leaf as follows: 1, none with less than 45° bending; 2, slight with 45 to 90° bending; 3, moderate with 90 to 135° bending; 4, severe with more than 135° bending. Leaf chlorophyll index was measured using a chlorophyll meter (SPAD-502; Konica Minolta Sensing, Tokyo, Japan) on the most matured true leaf. Two readings were taken per leaf on a leaf lamina between major leaf veins.

Field experiments (Expt. 2 and Expt. 3). Two field experiments were conducted at the Gulf Coast Research and Education Center to examine the effects of preplant 1-MCP treatment on postplanting growth and yield of tomato. The soil at the experiment site is classified as a Myakka fine sand siliceous hyperthermic Oxyaquic Alorthod. At preplant, surface (top 15 cm) soil had pH of 6.8 and organic matter of 15 g·ha⁻¹. Raised beds (20 cm high and 81 cm wide at the base) were fumigated with Pic-Clor 60 at 336 kg·ha⁻¹ and covered with a white-on-black polyethylene plastic mulch film. Two drip tapes with emitters spaced 30 cm apart and a flow rate per emitter of 0.91 L·h⁻¹ (Netafim, USA, Fresno, CA) were installed at 2-cm depth in each bed. Preplant fertilizers were applied at 177N–49P–294K kg·ha⁻¹ as soil incorporation and band applications during the bed preparation. Between the flowering stage and the first harvest, fertigation was performed to apply 47N–7P–52K kg·ha⁻¹ in six weekly applications. Standard cultural practices and pest management practices for commercial tomato production in Florida were followed.

The first field experiment (Expt. 2) was conducted in the 2014 Fall season. Treatments were three concentrations of 1-MCP

Table 1. Postplanting growth of 'Florida 47' tomato as affected by preplant spray application of 1-MCP (Expt. 2).^z

1-MCP ^y (mg·L ⁻¹)	Plant ht (cm)		Plant width (cm)		Stem diam (cm)	
	16 DAT	33 DAT	16 DAT	33 DAT	16 DAT	33 DAT
0.0	23.1	55.5 b	37.6	78.6	0.45	1.45 b
12.5	25.8	62.4 a	37.2	80.7	0.41	1.34 ab
50.0	25.5	59.3 ab	36.4	78.4	0.43	1.18 a
Mean (12.5 and 50 mg·L ⁻¹)	25.7	60.9	36.8	79.5	0.42	1.26
<i>P</i> value ^x						
1-MCP treatment	0.3202	0.0490	0.6619	0.4469	0.7535	0.0349
0 vs. 12.5 and 50 mg·L ⁻¹	0.1566	0.0279	0.5003	0.5705	0.5138	0.0260

^zMeans in a column with the same lowercase letter are not significantly different (Tukey–Kramer test, $P < 0.05$); 16 and 33 DAT corresponds to transplant establishment and initial flowering stages, respectively.

^ySpray treatments were performed with a spray volume of 15.6 mL/plant at 1 d before transplanting.

^xTreatment effects of 1-MCP were tested using the restricted maximum likelihood method. Orthogonal contrasts (0 vs. 12.5 and 50 mg·L⁻¹) were performed based on the following hypothesis: 12.5 and 50 mg·L⁻¹ are above the saturation concentration of 1-MCP to inactivate ethylene receptors; therefore, growth-modulating effects are equivalent at both concentrations.

1-MCP = 1-methylcyclopropene; DAT = days after transplanting.

Table 2. Growth of 'Florida 47' tomato at the harvesting stage as affected by preplant spray application of 1-MCP (Expt. 2).

1-MCP ^z (mg·L ⁻¹)	Shoot FW (kg)	Stem diam (cm)	Flower number (no./plant)
0.0	1.21	1.41	120
12.5	1.46	1.41	140
50.0	1.51	1.36	153
Mean (12.5 and 50 mg·L ⁻¹)	1.48	1.38	147
<i>P</i> value ^y			
1-MCP treatment	0.1093	0.3651	0.1643
0 vs. 12.5 and 50 mg·L ⁻¹	0.0448	0.4674	0.0863

^zSpray treatments were performed with a spray volume of 15.6 mL/plant at 1 d before transplanting.

^yTreatment effects of 1-MCP were tested using the restricted maximum likelihood method. Orthogonal contrasts (0 vs. 12.5 and 50 mg·L⁻¹) were performed based on the following hypothesis: 12.5 and 50 mg·L⁻¹ are above the saturation concentration of 1-MCP to inactivate ethylene receptors; therefore, growth-modulating effects are equivalent at both concentrations.

1-MCP = 1-methylcyclopropene; FW = fresh weight.

Fig. 3. Leaf chlorophyll status of 'Florida 47' tomato during establishment (16 d after transplanting) as affected by preplant spray application of 1-methylcyclopropene (1-MCP) (Expt. 2): (A) leaf chlorophyll index, and (B) plot photographs. Treatments were as follows: untreated water control, 1-MCP treatment at 12.5 mg·L⁻¹, and 1-MCP treatment at 50 mg·L⁻¹. Spray treatments were performed with a spray volume of 15.6 mL/plant at 1 d before transplanting.

(0, 12.5, and 50 mg·L⁻¹). Spray treatments were performed in a greenhouse 1 d before transplanting with a spray volume of 15.6 mL per plant. Seedlings were transplanted in one row per bed at a row spacing of 152 cm and an in-row spacing of 46 cm. Fruits were harvested twice at the mature green stage and graded using a commercial grading standard in Florida.

The second field experiment (Expt. 3) was conducted in the 2015 Fall season. Treatments were two concentrations of 1-MCP (0 and 50 mg·L⁻¹). Spray treatments, field management, harvesting, and grading criteria used in Expt. 2 were followed. The 1-MCP concentrations in the field experiments were determined based on the preliminary experiments performed by the manufacturer.

Plant growth and physiological measurements (Expt. 2). In Expt. 2, postplanting growth and physiological responses to preplant 1-MCP treatment were evaluated. Postplanting growth measurements were performed on four plants per replication at 16 and 33 d after transplanting, which were the transplant establishment and initial flowering stages, respectively. Plant height was measured from the soil surface to the top-most portion of the plant. Plant width was measured at the widest part. Stem diameter was measured at the widest part near the soil surface. Immediately after the final harvest, shoot fresh weight, stem diameter, and flower number were measured on three plants per replication.

Physiological measurements were performed on four plants per replication at 16 and 33 d after transplanting (transplant establishment and initial flowering stages, respectively). Leaf chlorophyll index was measured on the youngest fully expanded leaf by the method used in Expt. 1. Net CO₂ assimilation rate and stomatal conductance (g_s) were measured using an open-flow infrared gas analyzer (LI-6400; LI-COR, Lincoln, NE). The instrument was equipped with a 2 × 3-cm leaf chamber and a red plus blue light-emitting diode light source (6400-02B; LI-COR). During measurements, photosynthetically active radiation, reference CO₂ concentration, air flow rate, and block temperature were maintained constant at 1500 μmol·m⁻²·s⁻¹, 400 μmol·mol⁻¹, 500 μmol·s⁻¹, and 28 °C, respectively. Relative humidity in the sample chamber ranged between 50% and 70%.

Experimental design and statistical analysis. In Expt. 1, there were six replicated seedling trays for each treatment, which were arranged in a randomized complete block design. Each spray treatment was assigned randomly to an individual tray. In Expts. 2 and 3, there were four replicated field plots for each treatment, which were arranged in a randomized complete block design. Each plot consisted of 12 plants.

All data were analyzed using SAS (version 9.2; SAS Institute, Cary, NC), and *P* values less than 0.05 or 0.10 were considered statistically significant. In all experiments, treatment effects were tested using the restricted maximum likelihood method with the DDFM=KR option in the MIXED procedure. In Expts. 1 and 2, multiple comparisons of least squares means were performed by the Tukey–Kramer test in the MIXED procedure. In Expt. 3, multiple comparisons of least squares means were performed by the *t* test in the MIXED procedure.

In Expt. 2, linear relationship between two growth variables was tested using the REG procedure in SAS. The relationship was considered nonsignificant when the slope was not significantly different from zero ($P > 0.05$). A specific hypothesis (0 vs. 12.5 and 50 mg·L⁻¹) was also tested by an orthogonal contrast in the MIXED procedure. Based on our preliminary experiments suggesting that

the effectiveness of 1-MCP spray treatment can be maximized at 1 to 10 mg·L⁻¹ (data not shown), we hypothesized that both 12.5 and 50 mg·L⁻¹ are above the saturation concentration of 1-MCP to inactivate ethylene receptors; therefore, growth-modulating effects are equivalent at both concentrations.

Results and Discussion

1-MCP spray treatment suppresses ethylene-induced stress responses in tomato seedlings. The mechanism of action of 1-MCP involves its binding to ethylene receptors,

which in turn, inhibits ethylene perception and prevents ethylene-induced responses (Blankenship and Dole, 2003). Because 1-MCP is a volatile gas at standard temperature and pressure, the current commercial use of 1-MCP is limited primarily to post-harvest application, which is performed in enclosed spaces to maximize the contact of 1-MCP gas to ethylene receptors (Blankenship and Dole, 2003; Sozzi and Beaudry, 2007). The beneficial effects of 1-MCP on extending shelf life and maintaining postharvest quality are reported in many fruit, vegetable, and floriculture crops (Watkins, 2008).

This study demonstrated high efficacy of 1-MCP spray treatment as a new stress-management tool for vegetable transplants. First, high efficacy of 1-MCP to inhibit ethylene-induced responses was indicated in Expt. 1. When tomato seedlings were treated with only ethephon, which is an ethylene-releasing compound, severe leaf epinasty was induced, with the epinasty rating measured at 3 d after treatment increasing, compared with untreated plants, from 1.17 to 3.83 (Fig. 1). Leaf epinasty is defined as downward bending of petioles, and the degree of petiole bending is generally proportional to the amount of ethylene produced in the plant tissue or exogenous ethylene (Ursin and Bradford, 1989). Pretreatment of 1-MCP reduced the magnitude of this ethylene-induced response by 65% (3.83 vs. 2.50) (Fig. 1). Another typical ethylene-induced response is leaf chlorosis (Van Volkenburgh, 1999). In the ethephon-treated seedlings, leaf chlorosis was clearly visible, with leaf chlorophyll index decreasing by 12% compared with untreated seedlings (38.0 vs. 33.6) (Fig. 2). Pretreatment of 1-MCP maintained leaf chlorophyll index at the same level as in untreated seedlings. These results suggest that 1-MCP spray treatment is effective in inhibiting ethylene perception in tomato seedlings.

Second, postplanting growth modulation by 1-MCP indicated the suppression of ethylene-induced stress responses in Expt. 2 (Table 1). Preplant spray treatment of 1-MCP increased plant height by up to 12% (55.5 vs. 62.4 cm) but reduced stem diameter by up to 29% (1.45 vs. 1.18 cm) at the flowering stage (Table 1). Increased ethylene production inhibits stem elongation and leaf ex-

pansion, while promoting stem thickening (Druege, 2006). Therefore, the morphological changes observed in Expt. 2 suggest that ethylene-induced growth modulation was suppressed by preplant spray treatment of 1-MCP.

Stem thickening and inhibition of stem elongation are morphological adaptations to mechanical stress, such as physical contact, vibration, and wind (Biddington, 1986; Druege, 2006; Khan, 2006; Tholen et al., 2006). Although the suppression of these morphological changes can increase the risk of plant lodging, it is not likely a problem for commercial fresh-market tomato production, as plants are typically grown on stakes. In Expts. 2 and 3, plants were tied on wood stakes at the early flowering stage and no lodging was observed throughout the experiments. Furthermore, stem diameter measured at the harvest showed no treatment difference (Table 2), suggesting that the suppression of stem diameter growth by 1-MCP is only transient. As plants grow, new plant tissues produce new ethylene receptors that can respond to ethylene (Sisler et al., 2006). It is likely that 1-MCP-treated plants regained sensitivity to ethylene and resumed normal stem diameter growth after establishment in the field.

Transplant shock is caused by various types of abiotic stress occurring during the transport and transplanting of seedlings (Vavrina, 2002). For example, newly transplanted seedlings can suffer water stress, especially when root water uptake is limited because of root injury, disturbed root-soil contact, and delayed irrigation (Agehara and Leskovar, 2012). In this study, however, typical water stress symptoms, such as leaf chlorosis, leaf abscission, and wilting, were not observed, and all treatments established healthy leaf chlorophyll status at 16 d after transplanting (Fig. 3). Furthermore, gas exchange measurements showed steady increases in both net CO₂ assimilation rate (Fig. 4A) and g_s (Fig. 4B) after transplanting in all treatments, suggesting that water stress was minimal. The minimal water stress in this study was probably because optimum soil moisture was maintained using plastic mulch and daily irrigation via drip tapes. Nonetheless, postplanting growth showed

Fig. 4. Postplanting gas exchange of 'Florida 47' tomato as affected by preplant spray application of 1-methylcyclopropene (1-MCP) (Expt. 2): (A) net CO₂ assimilation rate, and (B) stomatal conductance. Both gas exchange variables showed steady increases after transplanting. Treatments were as described in Fig. 3. Orthogonal contrasts (0 vs. 12.5 and 50 mg·L⁻¹) were performed based on the following hypothesis: 12.5 and 50 mg·L⁻¹ are above the saturation concentration of 1-MCP to inactivate ethylene receptors; therefore, growth-modulating effects are equivalent at both concentrations. DAT, days after transplanting.

Table 3. Marketable yield of 'Florida 47' tomato as affected by preplant spray application of 1-MCP (Expt. 2).^a

1-MCP ^b (mg·L ⁻¹)	Extra-large fruit yield			Total marketable yield		
	(no./plant)	(g/fruit)	(t·ha ⁻¹)	(no./plant)	(g/fruit)	(t·ha ⁻¹)
0.0	2.47 b	215	7.7	11.9	145	24.5
12.5	3.74 a	215	11.5	13.6	155	30.0
50.0	3.16 ab	209	9.3	15.1	143	30.7
Mean (12.5 and 50 mg·L ⁻¹)	3.45	212	10.4	14.4	149	30.4
			<i>P</i> value ^c			
1-MCP treatment	0.0202	0.8743	0.0696	0.2603	0.3446	0.0691
0 vs. 12.5 and 50 mg·L ⁻¹	0.0120	0.8004	0.0412	0.1562	0.5682	0.0291

^aMeans in a column with the same lowercase letter are not significantly different (Tukey–Kramer test, *P* < 0.05).

^bSpray treatments were performed with a spray volume of 15.6 mL/plant at 1 d before transplanting.

^cTreatment effects of 1-MCP were tested using the restricted maximum likelihood method. Orthogonal contrasts (0 vs. 12.5 and 50 mg·L⁻¹) were performed based on the following hypothesis: 12.5 and 50 mg·L⁻¹ are above the saturation concentration of 1-MCP to inactivate ethylene receptors; therefore, growth-modulating effects are equivalent at both concentrations.

1-MCP = 1-methylcyclopropene.

significant responses to preplant 1-MCP treatment as discussed previously, suggesting that mechanical stress is a limiting factor on postplanting performance of vegetable transplants.

Fig. 5. Linear correlation between shoot fresh weight and flower number of 'Florida 47' tomato at the harvest (Expt. 2). The slope was significantly different from zero ($P > 0.05$). Treatments were as described in Fig. 3. Data variation is due mainly to preplant treatment of 1-methylcyclopropene (1-MCP), which increased both shoot fresh weight and flower number (Table 2).

Fig. 6. Linear correlation between flower number and fruit set of 'Florida 47' tomato (Expt. 2). The slope was significantly different from zero ($P > 0.05$). Flower number data were collected at the harvest. Treatments were as described in Fig. 3. Data variation is due mainly to preplant 1-methylcyclopropene treatment, which increased both flower number and fruit set (Tables 2 and 3).

Improved postplanting growth by preplant 1-MCP treatment increases fruit set and yield. Significant growth promotion by preplant 1-MCP treatment was observed at the harvest stage in Expt. 2 (Table 2). Compared with untreated plants, 1-MCP-treated plants had, averaging across two 1-MCP concentrations, 23% greater shoot biomass ($P = 0.0448$, 1.21 vs. 1.48 kg/plant) and 22% more flowers ($P = 0.0863$, 120 vs. 147/plant), suggesting that suppression of ethylene-induced stress responses by 1-MCP during establishment has long-term growth-promoting effects. Furthermore, postplanting gas exchange measurements showed an increasing trend in response to preplant 1-MCP treatment: 1-MCP-treated plants had up to 17% and 61% higher net CO_2 assimilation rate and g_s than untreated plants, respectively (Fig. 4A and B). Therefore, 1-MCP-treated plants likely had greater photosynthetic capacity on a whole-plant basis than untreated plants. The increased flower production resulted in increases of similar magnitude in both marketable fruit number per plant and yields (Table 3). Averaging across two 1-MCP concentrations, preplant 1-MCP treatment increased extra-large and total marketable fruit yields by 36% (7.7 vs. 10.4 t·ha⁻¹) and 24% (24.5 vs. 30.4 t·ha⁻¹), respectively. Correlation analyses revealed that flower number increased proportionally to shoot biomass (Fig. 5), and fruit set increased proportionally to flower number (Fig. 6). Furthermore, the average fruit weight was unaffected by preplant 1-MCP treatment, indicating that yield increases by preplant 1-MCP treatment were due mostly to improved fruit set (Table 3).

Similar yield increases by preplant 1-MCP treatment were observed in Expt. 3 (Table 4), although treatment effects were statistically significant only at $P < 0.10$. Preplant treatment of 1-MCP at 50 mg·L⁻¹ increased extra-large and total marketable fruit yields by 21% (31.0 vs. 37.5 t·ha⁻¹) and 13% (49.4 vs. 55.6 t·ha⁻¹), respectively. In both seasons, yield increases by preplant 1-MCP treatment appeared to be more pronounced in extra-large fruit yields than in total marketable fruit yields (Tables 3 and 4). The explanation for this observation can be that the suppression of ethylene-induced stress responses by 1-MCP advanced plant growth and development, thereby extending the period for fruit expansion. Because extra-large tomatoes generally receive price pre-

miums (Bierlen and Grunewald, 1995; Davis and Gardner, 1994), preplant 1-MCP treatment may improve the profitability of fresh-market tomatoes by increasing not only yields but also the price received by growers.

Transplant shock is not simply physical damage in seedlings, but it is the consequence of active stress responses regulated by multiple phytohormones to cope with dynamic changes in growing conditions (Srivastava, 2002; Taiz and Zeiger, 2010). Although mechanical stress is unavoidable during the transport and transplanting of seedlings (Cantliffe, 1993), the magnitude of postplanting stress depends on field conditions. In this study, we suspect that postplanting stress was minimal to mild, because tomato seedlings were transplanted under well-managed field conditions, and no significant stressful weather events occurred during establishment. Moreover, untreated plants did not display any noticeable symptoms of transplant shock. Nonetheless, the results of this study demonstrated that preplant 1-MCP treatment is effective in improving the postplanting performance of tomato seedlings. We propose that the mode of action of preplant 1-MCP treatment can be explained as illustrated in Fig. 7. First, 1-MCP inhibits ethylene perception in seedlings by inactivating ethylene receptors. The reduced sensitivity to ethylene suppresses stress adaptive responses (e.g., leaf chlorosis, leaf epinasty, stem thickening, and inhibition in stem elongation and leaf expansion) that could be otherwise induced by mechanical stress during the transport and transplanting of seedlings. The suppression of ethylene-induced stress responses maintains uninterrupted growth, thereby improving stand establishment of seedlings. Finally, improved postplanting growth leads to yield increases.

This mode of action proposes a new stress-management approach to reducing transplant shock. Most stress-management techniques reported in previous studies aim to reduce postplanting water stress by limiting transpiration (Berkowitz and Rabin, 1988; del Amor et al., 2010; Goreta et al., 2007; Iriti et al., 2009; Moftah and Al-Humaid, 2005) or by activating defense mechanisms in molecular processes (Tuteja and Sarvajeet, 2012). The main drawback of these techniques is that their beneficial stress control effects are limited under optimum field conditions (Agehara and Leskovar, 2012; Berkowitz and Rabin, 1988; Moftah and Al-Humaid, 2005). By contrast, preplant 1-MCP treatment is effective in reducing transplant shock in the absence of postplanting stress, because it is targeted to mechanical stress, which is unavoidable during the transport and transplanting of seedlings. This stress-management approach also differs from the field application of 1-MCP, which has been tested for postplanting stress control in several agronomic crops (Below and Uribe-larrea, 2009; Dahmer et al., 2007).

Preplant 1-MCP treatment does not affect fruit ripening and quality. Ethylene plays an important role in tomato fruit ripening (Nath

Table 4. Marketable yield of 'Florida 47' tomato as affected by preplant spray application of 1-MCP (Expt. 3).^z

1-MCP ^y (mg·L ⁻¹)	Extra-large fruit yield			Total marketable yield		
	(no./plant)	(g/fruit)	(t·ha ⁻¹)	(no./plant)	(g/fruit)	(t·ha ⁻¹)
0.0	10.2 B	212	31.0 B	19.6	177	49.4 B
50.0	12.5 A	211	37.5 A	22.1	178	55.6 A
<i>P</i> value ^x						
1-MCP treatment	0.0511	0.7962	0.0856	0.1621	0.9733	0.0791

^zMeans in a column with the same uppercase letter are not significantly different (*t* test, $P < 0.10$).

^ySpray treatments were performed with a spray volume of 15.6 mL/plant at 1 d before transplanting.

^xTreatment effects of 1-MCP were tested using the restricted maximum likelihood method.

1-MCP = 1-methylcyclopropene.

Fig. 7. Mode of action of preplant treatment of 1-methylcyclopropene (1-MCP) for reducing transplant shock in vegetable seedlings. First, 1-MCP inhibits ethylene perception by inactivating ethylene receptors. The inhibited ethylene perception suppresses ethylene-induced growth modulation (e.g., leaf chlorosis, leaf epinasty, stem thickening, and inhibition in stem elongation and leaf expansion) during the transport and transplanting of seedlings. The suppression of ethylene-induced stress responses maintains uninterrupted growth, thereby improving stand establishment of seedlings.

et al., 2006; Pech et al., 2008). Commercially, ethylene is applied to fresh-market tomatoes harvested at the mature green stage, often at a packinghouse before shipping, to initiate ripening and shorten the ripening time (Chomchalow et al., 2002). Conversely, tomato fruit ripening can be inhibited when fruits are treated with 1-MCP (Guillén et al., 2007; Tassoni et al., 2006). In this study, fruits harvested from 1-MCP-treated plants showed normal ripening and sugar accumulation compared with those from untreated plants (data not shown). The absence of inhibition in fruit ripening is probably because plants were treated with 1-MCP only once at the young seedling stage. Plants treated with 1-MCP often regain sensitivity to ethylene as new plant tissues produce new ethylene receptors (Sisler et al., 2006). Therefore, 1-MCP treatment at the young seedling stage does not appear to affect important functions of ethylene involved at later stages of development, including fruit ripening.

Practical implications. 1-MCP rapidly volatilizes and deteriorates on dissolving in water (Rizzolo et al., 2005). To maximize the contact of 1-MCP gas to ethylene receptors, therefore, commercial postharvest application of 1-MCP is performed using a gas generator in enclosed spaces, such as coolers, storage facilities, and shipping containers (Watkins, 2008). The product label of a commercial 1-MCP registered as SmartFresh (AgroFresh, Philadelphia, PA) recommends 1-MCP concentrations at 0.2 to 1 $\mu\text{L}\cdot\text{L}^{-1}$ and exposure time for 12 to 24 h, depending on the plant produce subjected to the treatment. Postharvest immersion treatment of 1-MCP has been tested for several fruit commodities

at concentrations ranging from 150 μg to 10 $\text{mg}\cdot\text{L}^{-1}$ (Agehara et al., 2018; Choi and Huber, 2008; Manganaris et al., 2007; Pereira et al., 2013). In this study, a new spray formulation of 1-MCP was applied at relatively high concentrations (1 to 50 $\text{mg}\cdot\text{L}^{-1}$) to tomato seedlings in a greenhouse. High spray volumes at 5.5 to 15.6 mL/plant were used to simulate treatments by irrigation booms commonly used at commercial transplant nurseries. Using such application procedures, this study demonstrated that even a single foliar spray of 1-MCP is highly effective in suppressing ethylene-induced responses and improving the postplanting performance of tomato seedlings. The high efficacy of this 1-MCP application method despite the short exposure time in an open space may be due partly to the high density of tomato seedlings in a plug tray, which could slow down the volatilization of 1-MCP and increase the contact of diffused 1-MCP gas to seedling shoots. The fact that 1-MCP gas can penetrate plant tissues also may help improve the efficacy of this method (Blankenship and Dole, 2003; Sisler and Serek, 1997).

The tested formulation of 1-MCP has several key features for the successful commercial application as a new stress-management tool for vegetable transplants. First, it has a favorable safety profile and leaves no detectable residue according to the manufacturer. Second, its application is easy and flexible, as it can be applied with irrigation water using standard irrigation booms and injection systems. Third, it will not modify the final transplant quality or appearance, as it is recommended to be applied within a few days before the transport of

transplants. Finally, it does not have any negative side effects on postplanting growth or fruit ripening. To maximize the beneficial stress-management effects of 1-MCP, it is important to perform the treatment within a few days before the transport of transplants. Otherwise, plants will have more newly grown tissues with new ethylene receptors (Sisler et al., 2006) that can respond to ethylene by the time of shipment, increasing the sensitivity to mechanical stress.

The mode of action of preplant 1-MCP treatment involves the maintenance of uninterrupted growth in the field by preventative suppression of ethylene-induced stress responses, as discussed previously (Fig. 7). Ethylene action can be suppressed by inhibiting either ethylene perception using 1-MCP or 1-aminocyclopropane-1-carboxylic acid (ACC) synthesis using aminoethoxyvinyl glycine or silver thiosulfate (Taiz and Zeiger, 2010). Although the efficacy of the two approaches was not compared in this study, inhibition of ethylene perception by 1-MCP may be a more advantageous approach because it has a favorable safety profile and it can avoid potential negative side effects of suppressing ACC production. It is reported that ACC is involved in the local and long-distance transport mechanism of ethylene, and that it may function as a signal itself (Van de Poel and Van Der Straeten, 2014).

Most previous stress-management approaches to reduce transplant shock focused on minimizing water stress using physical or physiological antitranspirants. The major drawback of antitranspirants is that their beneficial effects are pronounced only under severe water stress conditions (Agehara and Leskovar, 2012; Berkowitz and Rabin, 1988; Moftah and Al-Humaid, 2005). Under optimum growing conditions, conversely, antitranspirants can have negative side effects, as excessive stomatal closure limits CO_2 supply to photosynthesis (Lawlor, 2002). For example, Agehara and Leskovar (2012) reported that stomatal limitation to photosynthesis by exogenous abscisic acid limited shoot dry matter accumulation in muskmelon seedlings. Other negative side effects of abscisic acid include leaf chlorosis, leaf abscission, and excessive inhibition in leaf expansion and stem elongation (Agehara and Leskovar, 2014a, 2014b, 2015, 2017; Park et al., 2016). In addition, the performance of film-forming antitranspirants is limited primarily on the adaxial leaf surface and is dependent highly on spray coverage (Goreta et al., 2007). By contrast, preplant 1-MCP treatment can improve postplanting performance of vegetable seedlings even when postplanting stress is minimal in the field, and it has no negative side effects. This new stress-management approach will have large-scale applicability, because it is targeted specifically to mechanical stress, which is unavoidable during the transport and transplanting of seedlings. On the other hand, when severe stress or water stress is expected immediately after transplanting, preplant 1-MCP treatment may not be an ideal stress-management

strategy, as ethylene-induced stress responses (e.g., compact growth and overall growth retardation) may play an important role in plant survival.

Conclusion

Under well-managed field conditions, transplanting may not cause apparent stress symptoms, such as leaf chlorosis, leaf abscission, and wilting. Nonetheless, preplant 1-MCP treatment can improve postplanting growth and yields in tomato. It is likely that, under mild plant stress, the field establishment of tomato seedlings is limited in part by ethylene-induced stress responses induced. The results in this study suggest that preplant suppression of ethylene perception is an effective strategy to reduce transplant shock by maintaining uninterrupted growth after transplanting. This stress-management approach is completely new in that it maximizes the performance of vegetable seedlings by preventing them from reacting to stress, rather than by reducing stress or improving stress tolerance. Preplant 1-MCP treatment has several key features for the successful commercial application, including the favorable safety profile, easy and flexible application for commercial transplant nurseries, and minimal negative side effect on transplant quality and field performance. Preplant 1-MCP treatment is not a recommended practice when severe stress or different types of abiotic stress (e.g., water stress) are anticipated. Rather, it is a recommended practice under well-managed field conditions, and it can minimize the negative impact of mechanical stress occurring during the transport and transplanting in vegetable seedlings.

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