1-Methylcyclopropene Has a Variable Effect on Adventitious Root Emergence from Cuttings of Two Sweetpotato Cultivars

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Abstract. This study aimed to investigate the effect of 1-methylcyclopropene (1-MCP) on adventitious rooting in two sweetpotato cultivars. Experiments with ‘Beauregard’ and ‘Evangeline’ sweetpotato cuttings revealed differential adventitious root (AR) emergence responses to 1-MCP application. ‘Beauregard’ AR count and length decreased with 1-MCP application in two of four experiments. In contrast, 1-MCP did not influence ‘Evangeline’ root count. However, ‘Evangeline’ root length decreased in three of four experiments. Trypan blue staining of ‘Beauregard’ nodal tissue with delayed AR primordia emergence showed localized dead tissue in the general area where ARs emerge. The degree of staining appeared to correspond with the stage of AR emergence with the staining becoming more intense around the time an AR primordium eventually emerged through a crack in the epidermis. This response agrees with reported results of ethylene-mediated AR emergence in other plant species. These results also appear to suggest that ‘Beauregard’ and ‘Evangeline’ cuttings differ in ethylene sensitivity. This represents the first evidence of genotype-specific ethylene involvement in adventitious rooting of sweetpotato cuttings.

The emergence of ARs in sweetpotato cuttings represents an important phase in plant establishment and represents the initial phase of storage root formation (Togari, 1950). The

knowledge of the influence of external and internal variables on adventitious rooting is important in identifying practical methods to optimize plant stand and production efficiency. The role of plant hormones in adventitious rooting has been a source of confusion not only in sweetpotatoes but in other plant species as well. In fact, Kays (1985) mentioned that although gibberellic acid, auxin, ethylene, cytokinin, and abscisic acid have been detected in sweetpotatoes, their specific roles have not been elucidated. Recently, Mortley et al. (2008) reported that 12 stem cuttings of the Whitley/Loretan cultivar produced $\approx 7 \text{ nL} \cdot \text{L}^{-1}$ of ethylene after 5 d. In other plant species, ethylene has been documented to promote, inhibit, or have no influence on adventitious rooting (Harbage and Stimart, 1996; Mudge and Swanson, 1978; Rapaka et al., 2008). The knowledge of the influence of ethylene in adventitious rooting is useful to identify commercially available technologies that can be used to improve quality and uniform establishment of cuttings. For example, Serek et al. (1998) used the ethylene inhibitors 1-MCP and silver thiosulfate to retard

storage-induced leaf yellowing in cuttings from *Dendranthema grandiflorum*, *Pelargonium zonale*, and *Hibiscus rosa-sinensis*. However, they observed reduced adventitious rooting in both fresh and stored cuttings. A follow-up study by Rapaka et al. (2008) determined that endogenous carbohydrate interacted with the action of ethylene to regulate leaf senescence and AR formation in *Pelargonium* cuttings. Mergemann and Sauter (2000) presented evidence that ethylene induced epidermal cell death at the site of AR emergence in rice (*Oryza sativa*), allowing preformed AR initials to emerge through the crack in the epidermis. The role of ethylene-induced cell death in AR emergence in sweetpotatoes has not been investigated. Experiments were conducted to assess the effect of 1-MCP in adventitious rooting in cuttings of two sweetpotato cultivars grown in Louisiana. A secondary objective was to investigate the possible role of epidermal cell death at the site of sweetpotato AR emergence, similar to the results described by Mergemann and Sauter (2000) in rice. Our hypothesis is that endogenous ethylene is involved in epidermal cell death at the site of AR emergence that results in appearance of ARs in sweetpotato cuttings.

Materials and Methods

Plant material. The greenhouse experiments were conducted in Chase, LA (lat. 32°6' N, long. 91°42' W). On 1 Oct. 2011, virus-tested ‘Beauregard’ and ‘Evangeline’ Generation 1 (G1) storage roots were bedded in washed river sand and served as a source of transplants for all experiments. In each experiment, cuttings with five to seven fully opened leaves and no visible emerged root primordia were obtained from each cultivar between 1400 to 1600 HR. It was observed that over the duration of the experiments (Nov. 2011 to Feb. 2012), the presence of nodes with emerged root primordia could not be avoided. Subsequently, later experiments (Jan. and Feb. 2012) included cuttings with nodes that showed visible root primordia. Cuttings were placed in plastic containers (volume = 99 L) within 10 min after harvesting for 1-MCP treatments.

1-Methylcyclopropene treatment and growing conditions. 1-MCP solution was prepared by adding SmartFresh™ research tablets (AgroFresh Inc., Springhouse, PA) to a plastic release vial containing an activator tablet and 18 mL activator solution. Treatment levels were 1 and 2 $\mu\text{L} \cdot \text{L}^{-1}$. The release vial was placed adjacent to a battery-powered fan (5 cm in diameter). The plastic container was sealed within 30 s with plastic tape and stored in dark conditions. Temperatures ranged from 24 to 27 °C during the treatments. Untreated cuttings were also placed in sealed plastic containers. After the 24 h of 1-MCP treatments, cuttings were set by burying two to three nodes under the growth medium (washed river sand) contained in 10 cm-diameter polyvinyl chloride pots (height = 30 cm) with detachable plastic bottoms. Cuttings were watered with 200 mL distilled water. At the conclusion of each

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rooting experiment (4 d), growth substrate moisture content was $\approx 50\%$ of field capacity [$\approx 7\%$ volumetric water content as measured with ECH₂O soil moisture sensors (Model EC-5; Decagon Devices Inc., Pullman, WA)] inserted vertically at the 2- to 7-cm depth. Fertilizer application consisted of 0.76 g of 5N–20P–20K per pot. The greenhouse temperature regime was 29 °C for 14 h (day) and 18 °C for 10 h (night), and relative humidity (RH) averaged 60%. Temperature and RH were monitored at the canopy level using an integrated temperature and RH sensor (Model RHT; Decagon Devices Inc.). Photosynthetic photon flux (PPF) for all experiments ranged from 150 to 1133 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Supplementary lighting was provided using white fluorescent lights ($\approx 42 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPF) for 14 h per day. PPF was measured at the canopy level with a quantum sensor (Model QSO-S; Decagon Devices Inc.).

Data collection and experimental design. In all experiments, plants were grown for 4 d after which near-intact root systems were collected. In previous work, we have determined that ‘Beauregard’ formed ARs that underwent rapid initial growth after 5 d (Villordon et al., 2009). Harvesting at an earlier date permitted characterization of initial AR root emergence. At harvest, the detachable plastic bottoms were removed and the pot was tilted and the growth substrate was gradually removed using a stream of water. The planting dates were 10 Nov. 2011, 17 Nov. 2011, 26 Jan. 2012, and 10 Feb. 2012. There were five replicates (one plant per pot = one replicate) in each experiment. All experiments were arranged as randomized complete blocks repeated across planting dates. As a result of the variability of the number of ARs per plant, there were unequal subsample sizes. In all experiments, intact ARs were floated on waterproof trays and scanned using a specialized Dual Scan optical scanner (Regent Instruments Inc., Quebec, Canada). The acquisition and image analysis software was WinRHIZO Pro (Version 2009c; Regent Instruments Inc.). Debris removal among scanned images was performed manually using the WinRhizo Pro Edition working mode. Debris consisted mainly of images of sand particles. The length of the AR main axis was measured using ImageTool (Univ. of Texas Health Science Center at San Antonio, available from <ftp://maxrad6.uthscsa.edu>). Entire node sections with non-emerged roots were excised and subjected to trypan blue staining (Desmond et al., 2008) to determine the presence of cell death at the site of adventitious root emergence (Mergemann and Sauter, 2000). Entire node sections were immersed in 0.4% trypan blue (Sigma Chemical Co., St. Louis, MO) for 3 min and washed with water. Microscopic analysis of staining patterns was performed immediately using a stereo microscope. To verify ethylene production by ‘Beauregard’ and ‘Evangeline’ cuttings during the application of experimental treatments, a CI-900FK portable ethylene gas analyzer equipped with a field kit (CID Bio-Science Inc., Camas, WA) was used. Modifications were made on containers

(volume = 99 L) by installing sampling ports on the covers to allow access of the CI-900FK sampling wand. In all experiments, five cuttings of each cultivar were weighed and immediately placed in containers within 5 min of harvesting for the imposition of experimental treatments. Sampling was performed every 6 h by attaching the CI-900FK sampling wand to the sampling ports and recording the ethylene concentration after the instantaneous readings stabilized (≈ 10 min). Calibration was verified using an ethylene analytical standard (Sigma-Aldrich Inc., St. Louis, MO). There were three replicates per cultivar $\times$ treatment combination.

Statistical analysis. As a result of the variability of the state of AR primordia emergence across varieties and time, rooting experiments were analyzed separately by variety and experiment. Root length and count data were transformed using log 10 and square root transformation, respectively, to normalize the residuals. The unbalanced data sets were analyzed using SAS Proc Mixed (SAS Version 9.1; SAS Inc., Cary, NC).

Results and Discussion

‘Beauregard’ and ‘Evangeline’ cuttings treated with 1-MCP showed variable AR emergence and length across four experiments that were conducted over time (Table 1). In ‘Beauregard’, cuttings had delayed AR emergence in the first two experiments, as exemplified by the results from the second experiment shown in Figure 1. In ‘Evangeline’, AR count did not vary among 1-MCP treatments across all experiments, which was similar to the results from the second experiment shown in Figure 1. However, ‘Evangeline’ AR length was significantly shorter in three of four experiments at the 2 $\mu\text{L}\cdot\text{L}^{-1}$ level. In general, these results are similar to those reported by Serek et al. (1998) where ethylene inhibitors reduced AR count and length in *Dendranthema*, *Pelargonium*, and *Hibiscus* cuttings. Trypan blue staining of ‘Beauregard’ nodal

sections with delayed AR emergence showed variable staining responses ranging from no visible stained epidermal tissue (Fig. 2A), patchy staining (Fig. 2B), contiguous tissue-specific staining (Fig. 2C), and staining of cracked epidermal tissue at the periphery of a protruding AR primordium (Fig. 2D). Figure 2 depicts the progressive death of epidermal tissue at the site of AR primordium emergence and is very similar to that observed by Mergemann and Sauter (2000) in ethephon-treated rice nodal epidermis. They proposed that ethylene-mediated adventitious rooting is an adaptive mechanism in deepwater rice where the emergence of AR primordia is dependent on an appropriate signal, i.e., submergence, which in turn is mediated by ethylene. Mortley et al. (2008) first reported ethylene emission by sweetpotato cuttings in a closed system after a period of 5 d. Although our ethylene measurements were taken over a 24-h period, the data generally indicate a trend toward a lower concentration in the control treatment at the end of the sampling period, in part confirming the observations by Mortley et al. (2008) (Fig. 3). During the application of 1-MCP in sealed containers, ‘Evangeline’ and ‘Beauregard’ cuttings showed differential ethylene accumulation depending on 1-MCP treatment level. Ethylene concentration in ‘Beauregard’ control and 1 $\mu\text{L}\cdot\text{L}^{-1}$ treatments showed an initial increase during the first 6 h but declined thereafter with the control treatment showing relatively higher ethylene concentration at the end of the treatment period. In ‘Beauregard’ cuttings exposed to the 2 $\mu\text{L}\cdot\text{L}^{-1}$ treatment, ethylene concentration was initially similar compared with the other treatment levels but showed a relatively higher accumulation rate over the next 18 h followed by a decline in the last 6 h of the treatment period. Ethylene concentrations in ‘Evangeline’ were initially similar during the first 12 h regardless of treatment levels. Starting at 18 h, ethylene accumulation varied with the control and 2 $\mu\text{L}\cdot\text{L}^{-1}$ levels showing a relatively higher accumulation rate compared with the 1 $\mu\text{L}\cdot\text{L}^{-1}$

Table 1. Adventitious root count and length at 4 d after transplanting among ‘Beauregard’ and ‘Evangeline’ sweetpotato cuttings subjected to 1-MCP pretreatments.^z

PD ^y	1-MCP ^x	Count		Length (cm)	
		BX	EV	BX	EV
1	0	4.0 $\pm$ 3.3 a	4.4 $\pm$ 3.6 a	1.7 $\pm$ 0.9 a	1.0 $\pm$ 0.8 a
	1	0 $\pm$ 0 b	4.8 $\pm$ 3.7 a	0 $\pm$ 0 b	0.9 $\pm$ 0.8 ab
	2	0 $\pm$ 0 b	2.6 $\pm$ 2.6 a	0 $\pm$ 0 b	0.7 $\pm$ 0.5 b
2	0	3.0 $\pm$ 3 a	6.2 $\pm$ 3.9 a	1.6 $\pm$ 0.9 a	1.8 $\pm$ 1.1 a
	1	0 $\pm$ 0 b	8.6 $\pm$ 14 a	0 $\pm$ 0 b	1.5 $\pm$ 1.2 a
	2	0.4 $\pm$ 0.8 a	9.4 $\pm$ 8.9 a	0.5 $\pm$ 0.7 a	1.4 $\pm$ 0.8 a
3	0	0.6 $\pm$ 1.3 a	6.6 $\pm$ 5 a	0.7 $\pm$ 1 a	1.1 $\pm$ 0.7 a
	1	1.8 $\pm$ 1.3 a	5.4 $\pm$ 3.4 a	0.9 $\pm$ 0.5 a	1.2 $\pm$ 0.6 a
	2	2.0 $\pm$ 1 a	5.2 $\pm$ 1.6 a	1.2 $\pm$ 0.6 a	0.7 $\pm$ 0.3 b
4	0	1.6 $\pm$ 2.3 a	6.2 $\pm$ 4.3 a	1.5 $\pm$ 1.8 a	1.7 $\pm$ 0.9 a
	1	3.2 $\pm$ 2.8 a	1.6 $\pm$ 1.5 a	2.3 $\pm$ 1.2 a	0.8 $\pm$ 0.6 b
	2	2.4 $\pm$ 0.5 a	5.8 $\pm$ 3.9 a	1.7 $\pm$ 0.9 a	1.3 $\pm$ 0.8 ab

^zValues represent means ($\pm$ SEM). Means within columns within planting dates followed by a common letter are not significantly different based on Fisher’s least significant difference mean separation test ($P \leq 0.05$). Counts were square root transformed, whereas lengths were log₁₀ transformed. Corresponding non-transformed values are shown. Scoring of adventitious root emergence was performed four days after planting. BX = Beauregard; EV = Evangeline.

^yPD = planting date, PD 1 = 10 Nov. 2011; PD 2 = 17 Nov. 2011; PD 3 = 26 Jan. 2012; PD 4 = 10 Feb. 2012.

^x1-MCP = 1-methylcyclopropene treatment levels; 0 = control; 1 = 1 $\mu\text{L}\cdot\text{L}^{-1}$; 2 = 2 $\mu\text{L}\cdot\text{L}^{-1}$.

Fig. 1. Differential adventitious rooting of 'Beauregard' and 'Evangeline' cuttings in response to 1-methylcyclopropene (1-MCP) treatment levels after 4 d of growth. Cuttings were treated in sealed containers for 24 h before planting. This experiment was planted on 17 Nov. 2011 and harvested on 21 Nov. 2011.

Fig. 2. Progressive emergence of adventitious roots depicted by trypan blue staining of epidermal tissue covering the primordia in buried 'Beauregard' nodes with non-emerged adventitious roots. (A) No detectable staining of epidermis; (B) patchy staining of epidermis; (C) near-contiguous tissue-specific staining of epidermis; (D) stained tissue includes cracked epidermis with emerging root initial. Descriptions of staining patterns are based on the work by Mergemann and Sauter (2000). Scale = 1.5 mm.

treatment. The initial increase of ethylene production by 'Beauregard' and 'Evangeline' cuttings (control treatment) between 6 and 18 h is similar to the pattern of wound ethylene accumulation in newly harvested pelargonium cuttings that were stored in sealed containers and monitored continuously with a photoacoustic trace gas detector (Kadner et al., 2000). They reported that wound ethylene production reached a maximum after 4 to 12 h and was completed in 24 h. Genotypic and temporal variability in plant tissue responses to 1-MCP treatments have been documented previously, for example in potted foliage plant genotypes (Macnish et al., 2011) and *Arabidopsis* accessions (Millenaar et al., 2005). Mao et al. (2007) reported that the presence of 1-MCP reduced wound ethylene in fresh-cut 'Fuji' apples (*Malus sylvestris*). In contrast, it has also been documented that the presence of 1-MCP increased ethylene production in pelargonium (*Pelargonium × hortorum*) cuttings (Rapaka et al., 2008). In wounded mature leaf blades of

citrus (*Citrus sinensis*), ethylene evolution was similar regardless of the presence or absence of 1-MCP (Pozo et al., 2004) during the first 48 h but was subsequently higher in 1-MCP-treated wounded leaves. To our knowledge, very little work has been done to investigate the role of exogenous and endogenous ethylene in sweetpotato cuttings and how ethylene interacts with other hormones, carbohydrate status, and external variables like temperature. Kadner et al. (2000) documented that storage temperature influenced ethylene emission by pelargonium cuttings. Rapaka et al. (2008) also reported that ethylene interacts with the carbohydrate status of pelargonium cuttings to help determine adventitious rooting capacity. In their experiments, Rapaka et al. (2008) harvested cuttings at 0800 and 1600 HR to represent lowest or highest carbohydrate export capacity of source leaves, respectively. Kays et al. (1987) have previously documented that the export pool of photosynthates in sweetpotato leaves is greater during the early forenoon and late afternoon periods. In our

experiments, all cuttings were harvested between 1400 and 1600 HR to minimize possible variation in temperature and carbohydrate status effects. In commercial operations, cuttings are harvested regardless of the time of day (Thornhill, personal communication). Our results help to underscore the need to gain an understanding of the significance of ethylene activity in sweetpotato propagation. Preliminary replicated field studies appear to show that 1-MCP-treated cuttings had similar storage root yields relative to untreated cuttings (data not shown). Follow-up studies might focus on the possible interactive effects of 1-MCP treatment with carbohydrate status, storage temperature and duration, and transplanting conditions to identify conditions that might lead to increased survivability of cuttings. For example, Hammet (1983) presented evidence that 'Jasper' cuttings held for 3 d before planting had 15% more total marketable yield relative to cuttings that were obtained and planted on the same day. A possible explanation for these results is that cuttings were planted around the time the ARs were emerging, thereby reducing the exposure of cuttings to the drying effects of sun and wind. On the other hand, high temperatures (35 to 40 °C) have been shown to inhibit ethylene production (Yu et al., 1980) and this could conceivably influence plant establishment. It has also been shown that under drought conditions, ethylene endogenously regulates plant homeostasis and results in reduced root and shoot growth (Glick et al., 2007).

Based on the findings by Mergemann and Sauter (2000), it could be interpreted that the physical cutting of a sweetpotato stem section from the source plant is a necessary step in the signaling process for the emergence of pre-formed AR initials. In rice, a follow-up study appears to suggest that ethylene interacts with abscisic acid and gibberellin in initiating programmed cell death of epidermal cells that cover AR primordia (Steffens and Sauter, 2005). This work can also be used as a methodological model for conducting follow-up studies to determine if a similar mechanism exists for sweetpotato. Auxin is also implicated in AR emergence signaling (Li et al., 2009). An enhanced knowledge of the role of these hormones in adventitious rooting could lead to the development of practical methods that optimize plant establishment, reduce stand loss, and increase efficiency in sweetpotato production. The differential response between 'Beauregard' and 'Evangeline' cuttings to the 1-MCP treatments provides evidence for a presumptive genotypic component not only in ethylene-mediated AR emergence signaling, but possibly in other tissue-specific ethylene-mediated responses as well. 1-MCP selectively binds ethylene receptors such that ethylene cannot bind and elicit action (Blankenship and Dole, 2003). If an ethylene receptor undergoes mutation, similar to the *Arabidopsis etr1-1* ethylene receptor mutation, then ethylene perception is blocked (Gamble et al., 2002). An ethylene receptor mutation can also prevent 1-MCP from blocking the effects of ethylene. A similar mechanism might help to explain the apparent lack of differences in AR emergence

Fig. 3. Ethylene accumulation by 'Beauregard' and 'Evangeline' cuttings subjected to different 1-methylcyclopropene (1-MCP) treatment levels in sealed containers. Data shown are means $\pm$ SE of three replicates.

in 'Evangeline' cuttings treated with 1-MCP. Further studies are needed to characterize the non-response and presumptive differential perception of ethylene in 'Evangeline'. Clearly, the knowledge of the basis and effects of differential ethylene sensitivity among sweetpotato varieties can lead to the development of genotype-specific practices not only for optimizing propagation, but postharvest practices as well. In sweetpotatoes, ethylene has been implicated in wound healing (St. Amand and Randle, 1989) and loss of quality during storage (Kitinaja, 1987). In experiments with low levels of ethylene exposure during storage (0.1, 1.0, and 10 $\mu\text{L L}^{-1}$), the loss of quality was not detected until the sweetpotatoes were baked (Kitinaja, 1987). This result underscores the need to understand the implications of differential ethylene sensitivity and its role in sweetpotato cultivar storage performance.

In conclusion, our work provides evidence of the variable effect of 1-MCP on adventitious rooting in two sweetpotato cultivars. 'Beauregard' AR count and length varied in two of four experiments, but 'Evangeline' AR count was unaffected in all experiments. Blocking ethylene perception resulted in the delay of epidermal cell death that resulted in delayed emergence of AR primordia in 'Beauregard' sweetpotato cuttings. Ethylene appears to be involved in the death of nodal epidermal tissue at the site of AR emergence, similar to a mechanism previously described in rice. These results suggest that 'Beauregard' and 'Evangeline' cuttings differ in ethylene perception. Our data provide evidence of the role of endogenous ethylene in

adventitious rooting of sweetpotato cuttings. Our results also represent the first evidence for genotype-specific ethylene involvement in adventitious rooting of sweetpotato cuttings.

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