Effect of Time of Harvest on Postharvest Leaf Abscission in Lantana (*Lantana camara* L. 'Dallas Red') Unrooted Cuttings

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Abstract. This study investigated the preharvest carbohydrate status and postharvest ethylene action of unrooted shoot-tip cuttings of lantana 'Dallas Red' harvested at three times during the day (0800, 1200, and 1600 HR) in relation to subsequent leaf abscission, shoot apices blackening, and adventitious root formation. The cuttings harvested at various times during the day were stored in darkness at 20 ± 1 °C for 4 days in sealed polyethylene bags. The cuttings harvested at 0800 HR had lowest total nonstructural carbohydrate concentrations; however, the amount of ethylene production during postharvest storage was similar among harvest times and increased during the storage period. After 4 days of storage, 69% of the leaves of cuttings harvested at 0800 HR abscised, but only 22% and 8% of the leaves abscised in cuttings harvested at 1200 and 1600 HR, respectively. Application of 1-methylcyclopropene (1-MCP) increased ethylene production and suppressed leaf abscission regardless of the harvest time, but cuttings harvested at 0800 HR developed blackened shoot apices. Leaf abscission was negatively correlated with total nonstructural carbohydrate concentration in the leaves, but no relationship was found with ethylene production. These results indicate that a high endogenous carbohydrate status decreases the postharvest ethylene sensitivity in unrooted shoot-tip cuttings of lantana. Time of harvest influenced subsequent rooting response; however, 1-MCP application did not inhibit rooting. Among various storage treatments, the best rooting response was observed in cuttings harvested at 1600 HR and treated with 1-MCP. Therefore, significant improvement of postharvest storage quality in vegetative lantana cuttings could be achieved by harvesting cuttings late in the day and treating with 1-MCP.

The production of shoot-tip cuttings for the greenhouse ornamental industry in the United States primarily occurs in South and Central America. Therefore, the success of U.S. growers has become increasingly dependent on their ability to receive high-quality cuttings from offshore production facilities. However, shipment of cuttings usually takes 2 or 3 d from the time they are harvested from stock plants and are available for rooting. In addition, shipment often occurs under unfavorable conditions such as temperature extremes and exposure to ethylene (Purer and Mayak, 1988). Ethylene production is stimulated by many forms of stress, which

eventually results in leaf senescence and abscission (Abeles et al., 1992). As a result, rooting in propagation can be inhibited after quality deterioration during shipment.

Although ornamental plants propagated from vegetative cuttings have become increasingly important, little is known about the postharvest physiological processes that occur in unrooted cuttings of many species. Most of the published research has focused on methods for improving the storage longevity of cuttings by delaying postharvest leaf abscission and senescence. Investigations include the use of cold storage treatments (Behrens, 1988) and application of ethylene action inhibitors such as 1-methylcyclopropene (1-MCP), silver nitrate, and silver thiosulfate (Blankenship and Dole, 2003; Faust and Lewis, 2005; Kadner and Druege, 2004; Paton and Schwabe, 1987; Serek et al., 1998). Additional studies include

application of gibberellins (Purer and Mayak, 1988) and thidiazuron (Mutui et al., 2005).

Lantana camara L. 'Dallas Red' is an evergreen shrub valued for its colorful flowers ranging from yellow to red. Lantanas are mainly produced as mixed bedding, border, and container plants. In lantana, leaf abscission and shoot apices blackening are frequent quality problems usually observed during postharvest shipment or storage of cuttings.

Studies on tomato seedlings (*Lycopersicon esculentum* Mill.) have shown that chilling sensitivity was highest at the end of the diurnal dark period (King et al., 1988). Furthermore, in different species of fresh herbs or leafy green vegetables, it was demonstrated that the shelf life of leaves can be extended by harvesting at the end of the photoperiod (Clarkson et al., 2005; Lange and Cameron, 1994). Those responses were attributed to the endogenous carbohydrate levels of the tissue. In plants, carbohydrates have conventionally been viewed as resources for respiration, metabolic intermediates, and osmotic functions as well as structural or storage components. However, carbohydrates also modulate gene expression (Koch, 1996) and several other vital processes that are also controlled by hormones (Sheen et al., 1999). There are studies indicating an interaction between carbohydrates and ethylene signal transduction pathway (Leon and Sheen, 2003; Zhou et al., 1998). For example, Yanagisawa et al. (2003) demonstrated that glucose enhances the degradation of the ethylene-insensitive 3, a key transcriptional regulator in ethylene signaling. In addition, external loading of sucrose decreased ethylene responsiveness in harvested broccoli (*Brassica oleracea* L.) florets and carnation (*Dianthus caryophyllus* L.) flowers (Nishikawa et al., 2005; Verlinden and Garcia, 2004). However, no similar ethylene studies have been reported on vegetative cuttings.

The objectives of this study were (1) to determine whether harvest time would influence subsequent storage quality of unrooted lantana cuttings, (2) to determine the effect of preharvest carbohydrate status of cuttings on postharvest ethylene action, and (3) to evaluate the effect of 1-MCP treatment on postharvest storage quality and final rooting response.

Materials and Methods

Plant material. Rooted cuttings of *Lantana camara* 'Dallas Red' were transplanted on 21 Oct. 2005 into 7.5-L standard plastic pots containing a commercial peat-based growing media (Middle weight Mix # 3-B; Fafard Co., Anderson, S.C.) and were maintained as stock plants in growth chambers (Conviron, E-15; Controlled Environments Ltd., Winnipeg, Man., Canada). The temperature was set to 22.5 °C and cool white fluorescent (Cool White Sylvania, 160 W; Mississauga, Ont., Canada) and incandescent lamps (Sylvania, 90 W) provided a photosynthetic photon flux (PPF) of 463 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for 12 h (from

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0800 to 2000 HR) resulting in daily light integral (DLI) of 20 mol·m⁻²·d⁻¹. The PPF distribution between the incandescent and fluorescent lamps was 1:5.8. The stock plants were irrigated manually and provided with constant liquid fertilization at 250 mg·L⁻¹ N using a 15N-2.2P-12.5K fertilizer (Peters Excel 15-5-15; Scotts-Sierra Horticultural Products Co., Marysville, Ohio). The stock plants were grown for 7 to 8 weeks in the growth chambers and then cuttings were removed for experimental use. The experiments were conducted at Clemson University, Clemson, S.C.

Effect of harvest time. Shoot-tip cuttings with four leaves and a 4-cm stem length were harvested from stock plants at three different times during the day: 0800, 1200, and 1600 HR. At each harvest time, 111 cuttings were removed from the stock plants and wrapped in wet paper towels. After the harvest, cuttings were transferred immediately to a laboratory kept at 20 ± 1 °C and 50% relative humidity with 10 μmol·m⁻²·s⁻¹ PPF from cool white fluorescent lamps and assigned to treatments as described subsequently. The air in the laboratory was ethylene-free. Cuttings were separated into three replications, each replication consisting of 37 cuttings. From each replication, seven cuttings were used for analyzing the carbohydrate status at harvest, 10 cuttings for studying rooting response in the greenhouse without storage, and the other 20 cuttings were placed in sealed polyethylene bags, 10 per bag (volume: 0.946 L, thickness: 68.6 μm; Ziploc; S.C. Johnson & Son, Inc., Racine, Wis.). A wet paper towel was also placed inside each bag to humidify the postharvest environment to avoid desiccation. In one of the bags, 2.0 mg of a 1-MCP commercial powder formulation (Ethylbloc; Floralife, Waltherboro, S.C.) was placed using a plastic weighing vessel, whereas the other bag remained without 1-MCP. The ambient moisture within the plastic bags combines with the 1-MCP powder to release 0.7 μg·L⁻¹ 1-MCP gas within 20 to 30 min (Blankenship and Dole, 2003). The cuttings were stored at 20 ± 1 °C in darkness for 4 d. Ethylene concentration in the headspace of the bags was measured at 24-h intervals during 4 d of storage. At the end of the storage period, cuttings were removed from the bags and evaluated for leaf abscission and shoot apices blackening, and then inserted in the rooting media for studying the subsequent rooting response in a greenhouse. The experiment was performed twice during Dec. 2005 and Jan. 2006 (harvests 1 and 2, respectively).

Carbohydrate analysis. To study the pre-harvest carbohydrate status of cuttings, carbohydrates were quantified in leaf lamina and stem of cuttings immediately after the harvest. Seven cuttings per harvest time and replicate were used for the analysis. Leaves and stems were separated, immediately frozen in liquid nitrogen, and stored at -70 °C until samples were lyophilized. Dry weights were then recorded and leaf and stem tissues were minced and soluble sugars were

extracted from 50 mg of tissue with 12 methanol:5 chloroform:3 water (by volume) as described by Miller and Langhans (1989). Mannitol (1 mg) was added as an internal standard. Clear supernatant was removed and passed through an ion exchange column (Amberlite IRA 8 and Dowex 50 W; Sigma Chemicals, St. Louis, Mo.) and eluted with 1 methanol:1 water (by volume). Filtrate was evaporated to dryness in vacuo at 40 °C, and the residue was dissolved in 1 mL high-purity water (18.2 MΩ cm⁻¹, NANOpure Diamond; Barnstead International, Dubuque, Iowa). Sucrose, glucose, and fructose were separated using a Dionex DX-300 High Performance Liquid Chromatography system with a 4 × 250 mm CarboPac column and detected with an electrochemical detector (Dionex, Sunnyvale, Calif.). Quantification of sugars was based on the calibration curves obtained from their respective standards. Starch in dried residue, following soluble sugar extraction, was determined using enzymatic hydrolysis of starch using amyloglucosidase (from Rhizopus mold, EC 3.2.1.3; Sigma Chemicals) into glucose (Haissig and Dickson, 1979).

Measurement of ethylene concentration and determination of leaf abscission and shoot apices blackening. For measurement of ethylene concentration, air samples were removed at 24, 48, and 72 h after the beginning of the storage treatment with syringes through a silicon patch stuck onto each polyethylene bag. Ten cuttings per treatment and replicate were used for the measurement. The concentration was analyzed using gas chromatography (Shimadzu GC-9A, Kyoto, Japan). After 4 d of dark storage, number of leaves abscised per cutting and cuttings with blackened shoot apices were counted.

Rooting environment and determination of adventitious rooting response. For determining the rooting response, unstored and stored cuttings from various harvest times were propagated in a greenhouse. Ten cuttings per treatment and replicate were inserted in a sphagnum peatmoss-based commercial growing media (SuperFine Germinating Mix; Fafard Co., Anderson, S.C.) and were placed on a mist propagation bench in the greenhouse. The mist system was operated continuously (6 s every 6 min) during the first 24 h and then only during daylight hours for the remainder of the propagation period. Temperature set points for greenhouse heating/ventilation of 23/26 °C and bench heating of 25 °C provided an average air and soil temperature of 23.5 °C and 23 °C, respectively. The relative humidity in the greenhouse averaged 55%. Cuttings were shaded using retractable curtains when the global radiation outside the greenhouse exceeded a PPF of 517 μmol·m⁻²·s⁻¹, and the average DLI measured inside the greenhouse was 4.2 mol·m⁻²·d⁻¹. No rooting hormones were applied.

Rooting assessment was carried out after 4 weeks of propagation. The percentage of cuttings decayed as a result of leaf and shoot

necrosis was determined. The adventitious rooting response of cuttings was visually analyzed using the following scoring systems: 5 = substrate maintains container shape with uniform rooting; 4 = substrate maintains container shape with nonuniform rooting; 3 = substrate partly maintains container shape with few roots; 2 = substrate shape not maintained and three or four visible roots; 1 = substrate shape not maintained and one or two visible roots; and 0 = dead.

Statistical analysis. Experiments were conducted with three replications and repeated twice. Data were analyzed with analyses of variance and regression modules of the SPSS 13.0 software program (SPSS for Windows, release, 13.0.1; SPSS, Chicago; 12 Dec. 2004). The effect of time of harvest on carbohydrate status and the effect of both time of harvest and 1-MCP application on ethylene concentration, leaf abscission, and rooting response were tested by analysis of variance. Harvest dates were considered as replicates (n = 6) because they did not influence results. If significant effects were found, comparison of mean values was determined between times of harvest using the Tukey's test with significance level of $P \leq 0.05$. For analysis of linear regressions between the number of leaves abscised and carbohydrate status or ethylene concentration, replicates were considered individually (n = 18) to account for all variation.

Results

Effect of harvest time on carbohydrate status. Carbohydrate levels in both leaf and stem tissues were influenced by the harvest time (Fig. 1). Leaf glucose, fructose, and sucrose concentrations increased from 0800 to 1200 HR. However, at 1600 HR, all individual sugar fractions decreased (Fig. 1A). In contrast, starch levels increased marginally during the first 4 h and substantially during the next 4 h of photoperiod (Fig. 1B). As a result, total nonstructural carbohydrate levels (TNC: glucose + fructose + sucrose + starch) increased from 0800 to 1200 HR but then remained at similar levels at 1600 HR.

Stem glucose and fructose increased from 0800 to 1200 HR and then decreased to the initial levels at 1600 HR (Fig. 1C). Stem sucrose was similar at the three harvest times (Fig. 1C). Stem starch did not increase during the initial 4 h of the photoperiod but increased during the next 4 h (Fig. 1D). As a result, stem TNC increased from 0800 HR through 1200 HR but subsequently decreased at 1600 HR. In general, stem total sugar concentrations (TNC - starch) were higher and starch concentrations were lower when compared with those corresponding carbohydrate concentrations in the leaf tissue (compare Fig. 1C, D and 1A, B).

Effect of harvest time and 1-methylcyclopropene on ethylene production. Harvest time had no influence on postharvest ethylene production during storage (data not presented). For untreated control cuttings, ethylene concentration in the bags increased

Fig. 1. Effect of harvest time on (A, C) glucose, fructose, sucrose, and (B, D) starch concentrations in (A, B) leaf and (C, D) stem tissues of lantana shoot-tip cuttings grown in growth chambers. Concentrations are expressed on a dry weight basis. Vertical bars represent $\pm$ SE (n = 6).

between 24 and 48 h of storage and then the concentrations remained at similar levels until 72 h of storage (Fig. 2). Application of 1-MCP resulted in a substantial increase in ethylene production by the cuttings, and the ethylene concentration in those bags increased throughout the storage period (Fig. 2).

Effect of harvest time and 1-methylcyclopropene on leaf abscission. In the untreated control, harvest time influenced the number of subsequently abscised leaves per cutting after 4 d of storage (Fig. 3). As the harvest time advanced during the photoperiod, the number of leaves abscised per cutting decreased from 2.8 to 0.3 (Fig. 3). No shoot apices blackening was observed in the cuttings harvested at various times (data not shown). In 1-MCP-treated cuttings, no leaf abscission occurred irrespective of the harvest time (Fig. 3). However, 40% of the cuttings harvested at 0800 HR developed black shoot apices; this response was not observed in cuttings harvested at 1200 or 1600 HR (data not shown).

The increase in the preharvest TNC levels in leaves and the decrease in the subsequent leaf abscission as the harvest time advanced during the photoperiod were negatively correlated (Fig. 4). Negative correlations were also calculated with leaf sucrose and starch levels and stem fructose, starch, and TNC levels; however, those correlations were low (Table 1). Because ethylene produced by the cuttings was not influenced by harvest time, there was no correlation calculated between ethylene production and leaf abscission.

Effect of harvest time and 1-methylcyclopropene on adventitious rooting response. No further significant leaf abscission was observed during the subsequent 4 weeks of propagation period irrespective of

Fig. 2. Effect of 1-methylcyclopropene [1-MCP] treatment on ethylene concentration in the headspace of bags at 24, 48, and 72 h after the beginning of the storage treatment. Ten cuttings per sealed bag (volume: 0.946 L) were stored in darkness at $20 \pm 1^\circ\text{C}$. Mean values of three harvest times are presented (n = 6 per harvest time). Vertical bars represent $\pm$ SE.

the harvest time and storage treatment. However, in 0800 HR-harvested stored cuttings, 100% of untreated control and 10% of 1-MCP-treated cuttings decayed (Table 2). In unstored cuttings, irrespective of the harvest time, the rooting response was similar. However, in stored cuttings, harvest time influenced the rooting response (Table 2). Application of 1-MCP did not inhibit rooting response irrespective of the harvest time. Furthermore, 1-MCP-treated cuttings harvested at 1600 HR had the best rooting response among various storage treatments (Table 2).

Discussion

Harvest time during the day influenced the postharvest storage quality of lantana

Fig. 3. Effect of harvest time and 1-methylcyclopropene [1-MCP] application on number of leaves abscised by cuttings after 4 d of dark storage in sealed polyethylene bags. Ten cuttings per bag (volume: 0.946 L) were stored in darkness at $20 \pm 1^\circ\text{C}$. Vertical bars represent $\pm$ SE (n = 6).

Fig. 4. Linear regression drawn between total nonstructural carbohydrate (TNC) concentrations in leaf tissue of cuttings at harvest as independent variable and the number of subsequently abscised leaves as dependent variables (n = 18). R^2 of harvest 1 (H 1) and harvest 2 (H 2) were 0.96 and 0.57, which were significant at $P \leq 0.001$ and $P \leq 0.01$, respectively. Carbohydrate concentrations are expressed on a dry weight basis.

unrooted cuttings; leaf abscission substantially decreased and subsequent rooting response increased with later harvest during the photoperiod. Although commercial cutting producers harvest most cuttings early in the morning to reduce exposure to heat and to enable the product to be shipped on the same day, the quality and performance of unrooted shoot-tip cuttings of lantana, and perhaps other species, can be substantially improved by delayed harvest during the day.

1-MCP is an effective gaseous ethylene antagonist of ethylene perception that competitively and irreversibly blocks ethylene receptors (Sisler and Serek, 1997). In the present study, application of 1-MCP during postharvest storage of cuttings completely prevented leaf abscission irrespective of time of harvest. These results indicate that stress-induced ethylene is involved in leaf abscission of unrooted lantana cuttings during storage. Application of 1-MCP substantially increased ethylene production by the cuttings. Similar results showing enhanced ethylene production by vegetative tissues were

Table 1. Correlation coefficients calculated between carbohydrate concentrations at harvest in leaf and stem tissues of lantana 'Dallas Red' cuttings as independent variables and the number of subsequently abscised leaves as dependent variables (n = 18).

Carbohydrate concn	Tissue	Leaf abscission R ²
Glucose (G)	Leaf	NS
	Stem	NS
Fructose (F)	Leaf	NS
	Stem	0.27*
Sucrose (Su)	Leaf	0.37**
	Stem	NS
Starch (St)	Leaf	0.58***
	Stem	0.36**
Total nonstructural carbohydrates (TNC)	Leaf	0.70***
	Stem	0.23*

TNC: G + F + Su + St.

NS,*,**,***Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

previously reported for cuttings of geranium, *Pelargonium × hortorum* L.H. Bailey (Kadner and Druge, 2004), and poinsettia, *Euphorbia pulcherrima* L. (Faust and Lewis, 2005). In vegetative tissues, ethylene biosynthesis is controlled by autoinhibition (Philosoph-Hadas et al., 1985), but application of 1-MCP relieves the autoinhibition of ethylene (Lomaniec et al., 2003). Mullins et al. (2000) reported a similar stimulating effect of 1-MCP on ethylene production in grapefruit (*Citrus paradisi* Macf.), in which 1-MCP increased 1-aminocyclopropane-1-carboxylic acid (ACC) synthase gene transcripts in the respective tissues. Consequently, ACC content in the tissue increased, thereby leading to enhanced ethylene production.

Photosynthesis acts to replenish carbohydrates that are mobilized or metabolized overnight. In the present study, carbohydrates accumulated in both leaf and stem tissues during the photoperiod, exhibiting a diurnal phenomenon (Sicher et al., 1984). Photosynthetically fixed carbon was partitioned toward sugars in the morning, and after reaching a certain level, starch accumulated in the later part of the photoperiod. This is shown by the significant increase in all individual sugar concentrations and a concurrent marginal increase in starch concentrations from 0800 to 1200 HR and a substantial increase only in starch concentrations at 1600 HR. Sucrose levels increased during the initial 4 h and decreased during the latter 4 h, whereas starch increased steadily during the 8-h photoperiod, indicating that starch is the major temporary storage carbohydrate in lantana. A similar response was also observed in the leaves of sugar beet, *Beta vulgaris* L. (Fondy and Geiger, 1982). The maintenance of leaf TNC at a higher level and a concurrent decrease in stem TNC between 1200 and 1600 HR indicates that most of the photosynthate was retained by the leaves and only a small quantity was allocated for export during the afternoon.

In the present study, postharvest ethylene production was similar among cuttings har-

Table 2. Effect of time of harvest and application of 1-methylcyclopropene (1-MCP) on subsequent cutting decay and rooting response of cuttings after 4 weeks of propagation (n = 6).^z

Time of harvest (HR)	Treatment	Decayed cuttings (%)	Rooting rate
0800	Unstored	0 c	4.4 bc
	Stored (control)	100 a	0.0 a
	Stored + 1-MCP	10 b	4.1 b
1200	Unstored	0 c	4.6 c
	Stored (control)	3 bc	4.2 bc
	Stored + 1-MCP	3 bc	4.5 bc
1600	Unstored	0 c	4.5 bc
	Stored (control)	2 c	4.4 bc
	Stored + 1-MCP	0 c	4.7 c
Analysis of variance			
Time of harvest		*	*
Treatment		*	*
Time of harvest × treatment		*	*

Different letters indicate significant interaction between time of harvest and treatments.

^zRooting response of cuttings was visually determined using a scoring system ranging from 0 to 5.

*Significant at $P \leq 0.001$.

vested at various times during the day; nevertheless, the number of leaves that subsequently abscised decreased as the harvest time advanced during the photoperiod. Although ethylene was involved in leaf abscission, the lack of correlation between postharvest ethylene production and number of subsequently abscised leaves may indicate that ethylene sensitivity varied among different harvest times. Furthermore, the negative correlation between preharvest leaf TNC of the cuttings harvested at various times during the day and number of subsequently abscised leaves suggests that ethylene sensitivity decreased with the increase in endogenous carbohydrate levels. Therefore, it can be inferred that postharvest leaf abscission decreases in lantana shoot-tip cuttings as the endogenous carbohydrate status increases.

1-MCP treatment completely suppressed leaf abscission in all cuttings, including those harvested at 0800 HR that had the lowest leaf preharvest TNC concentration but developed black shoot apices. Cuttings harvested at the onset of the photoperiod with a lower preharvest carbohydrate status, which was further depleted during dark storage (Rapaka et al., 2005) for metabolic processes, may have been subject to hydrolysis of phenolic glycoside esters by glycosidase enzymes (McConchie et al., 1994; Stephens et al., 2005). The cleavage of phenolic glycoside esters results in the production of a free sugar and a reactive phenolic moiety (Dey and Dixon, 1985), which can undergo nonenzymatic oxidation resulting in leaf blackening. Therefore, these results suggest that higher ethylene sensitivity incited by low endogenous carbohydrate status of the cuttings can be overcome by blocking ethylene action; however, other postharvest storage quality problems, in this case shoot apices blackening, that are directly associated with carbohydrate status cannot be eliminated.

In 0800 HR-harvested stored cuttings, the survival rate of untreated control and 1-MCP-treated was 0% and 90%, respectively. These responses can be attributed to the substantial leaf loss in untreated control and shoot apices blackening and consequent necrosis in

1-MCP-treated cuttings. Although 1-MCP has proven to be beneficial in alleviating the postharvest ethylene damage in ornamental cuttings, its role in subsequent adventitious root formation is found to be different among different species. It was observed that 1-MCP inhibited rooting response in geranium (*Pelargonium zonale* L.), hibiscus (*H. rosa-sinensis* L.), chrysanthemum [*Dendranthema grandiflorum* (Ramat.) Kitamura], and croton [*Codiaeum variegatum* (L.) Blume] cuttings (Kadner and Druge, 2004; Muller et al., 1998; Serek et al., 1998) and had no effect on rooting response in pothos [*Epipremnum pinnatum* (L.) Engl.] cuttings (Muller et al., 1997). In addition, in the present investigation, the lack of any inhibitory affect of 1-MCP on rooting response of lantana cuttings indicates that this is a species-dependent response.

In conclusion, this investigation has demonstrated that harvest time during the day influences the postharvest storage quality of shoot-tip cuttings of lantana. Application of 1-MCP improved the storage quality of the cuttings by suppressing leaf abscission and did not inhibit subsequent rooting. However, the postharvest storage quality and subsequent rooting response of lantana cuttings was most improved with both the rescheduling the time of harvest and the application of 1-MCP.

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