Suppressing Green Mold Decay in Grapefruit with Postharvest Jasmonate Application

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ABSTRACT. Jasmonic acid (JA) and methyl jasmonate (MJ), collectively referred to as jasmonates, are naturally occurring plant growth regulators involved in various aspects of plant development and responses to biotic and abiotic stresses. In this study, we found that postharvest application of jasmonates reduced decay caused by the green mold *Penicillium digitatum* (Pers.: Fr.) Sacc. after either natural or artificial inoculation of grapefruit (*Citrus paradisi* 'Marsh Seedless'). These treatments also effectively reduced chilling injury incidence after cold storage. The most effective concentration of jasmonates for reducing decay in cold-stored fruit or after artificial inoculation of wounded fruit at 24 °C was 10 $\mu\text{mol}\cdot\text{L}^{-1}$. Higher and lower jasmonate concentrations were less effective at both temperatures. MJ at 10 $\mu\text{mol}\cdot\text{L}^{-1}$ also most effectively reduced the percentage of fruit displaying chilling injury symptoms after 6 weeks of storage at 2 °C and 4 additional d at 20 °C. When tested *in vitro*, neither JA nor MJ had any direct antifungal effect on *P. digitatum* spore germination or germ tube elongation. Therefore, it is suggested that jasmonates probably reduced green mold decay in grapefruit indirectly by enhancing the natural resistance of the fruit to *P. digitatum* at high and low temperatures.

Green and blue mold rots of citrus caused by *Penicillium digitatum* and *P. italicum* Wehmer, respectively, account for most of the postharvest losses of citrus fruit world-wide (Eckert and Brown, 1986). These pathogens are primarily controlled by extensive use of chemical fungicides (Eckert and Ogawa, 1985). Effective suppression of postharvest decay could also be achieved by storing the fruit at low temperatures. In grapefruit, however, storage below the optimal storage temperature (11 °C) results in the appearance of chilling injury (CI) symptoms, expressed as pitting of the fruit peel surface and increased attack by mold pathogens and stem end rots (Chalutz et al., 1981). To overcome this problem, relatively high concentrations of fungicides have been used to control postharvest decay (Schiffman-Nadel et al., 1975). In the search for alternatives to fungicides, several other methods have been employed to reduce CI and its consequent decay in citrus fruit; these include intermittent warming (Cohen, 1988; Wang, 1993), and hot water dips (Rodov et al., 1995). Treatments with methyl jasmonate (MJ) have also been reported to effectively reduce CI in grapefruit (Meir et al., 1996), as well as in other chilling-susceptible commodities (Wang and Buta, 1994; Meir et al., 1996).

Jasmonic acid (JA) and MJ, collectively referred to as jasmonates, are naturally occurring plant growth regulators that are widely distributed in the plant kingdom, and are known to regulate various aspects of plant development and responses to environmental stresses (Creelman and Mullet, 1995, 1997; Semblender and Parthier, 1993).

In addition, several lines of evidence suggest that jasmonates play an important role as signal molecules in plant defense responses against pathogen attack. First, JA accumulates in plant tissues or in cell cultures treated with elicitors of plant defense mechanisms (Doares et al., 1995; Gundlach et al., 1992; Nojiri et al., 1996). Second, jasmonates have been shown to activate genes

encoding antifungal proteins such as thionin (Andresen et al., 1992), osmotin (Xu et al., 1994), a novel ribosome-inactivating protein JIP60 (Chaudhry et al., 1994), and several other genes involved in phytoalexin biosynthesis (Creelman et al., 1992; Gundlach et al., 1992).

Moreover, modifying levels of jasmonates by exogenous applications of JA and MJ has effectively protected potato and tomato plants against infection by the late blight *Phytophthora infestans* (Mont.) de Bary (Cohen et al., 1993), and barley plants against infection by the powdery mildew *Erysiphe graminis* f. sp. *hordei* (Schweizer et al., 1993). Recently, it was reported that MJ can also be applied effectively, as a postharvest treatment, to suppress the gray mold rot caused by *Botrytis cinerea* Pers.: Fr. in strawberries (Moline et al., 1997) and in cut roses (Meir et al., 1998), and to reduce microbial contamination in celery and peppers (Buta and Moline, 1998).

The aim of the present study was to examine further the possible applications of JA and MJ as alternative postharvest treatments to reduce decay in citrus fruit. MJ dipping has been previously demonstrated to markedly reduce CI incidence in 'Marsh Seedless' grapefruit, after cold storage (Meir et al., 1996). Therefore, we chose this citrus fruit as a model system, to examine the effects of jasmonates on the development of green mold decay, after either natural or artificial infection with *P. digitatum*.

Materials and Methods

PLANT MATERIAL AND FUNGAL CULTURES. Grapefruit (*Citrus paradisi* 'Marsh Seedless') were obtained from a local orchard and were used on the day of harvest. Before treatments, fruit were thoroughly washed with water and then air dried. Experiments were repeated two to four times, with 140 fruit replications for each postharvest treatment and six fruit per treatment for the artificial inoculation experiments. *P. digitatum* was obtained from an infected grapefruit and cultured on Potato Dextrose Agar (Difco, Detroit, Mich.). Spore suspensions were prepared by removing the spores with a bacteriological loop from the sporulating edges of a 2- or 3-week-old culture, and suspending them in sterile distilled

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Fig. 1. Effect of methyl jasmonate (MJ) on the incidence of postharvest decay (A) and on the percentage of grapefruit with chilling injury (CI) (B) after 6 weeks of low-temperature storage and simulated shelf life. Fruit were dipped for 30 s in water or various concentrations of MJ, and then stored at 2 °C for 6 weeks. Decay and CI were evaluated immediately after storage and after 4 d of simulated shelf life at 20 °C. Decay was also evaluated after 21 d of shelf life. Fruit with CI were defined as fruit with moderate to severe CI symptoms. Data are means of 140 fruit per treatment in three different experiments. An overall LSD at $P \leq 0.05$ is shown for means comparison.

water. The spore concentration was determined with a hemocytometer and adjusted as required.

PREPARATION OF JASMONATES. JA (Sigma) and MJ (Aldrich Chemical Co. Inc., Milwaukee, Wis.) were each prepared as a 100 mmol·L⁻¹ stock solution in 2 mol·L⁻¹ ethanol plus 500 mg·L⁻¹ of the surfactant L-77 (dimethyl polysiloxane modified with alkylene oxide) (Union Carbide Co., N.Y.). Jasmonates were then adjusted to their final concentrations for application by diluting in distilled water.

POSTHARVEST MJ TREATMENT AND STORAGE. For postharvest treatments, fruit were dipped for 30 s in various concentrations (1 to 50 μmol·L⁻¹) of MJ, and then air dried in the shade. Control fruit were similarly dipped in water containing 500 mg·L⁻¹ of L-77. The treated fruit were stored at 2 °C for 6 weeks, and subsequently transferred to 20 °C for 3 additional weeks; the relative humidity was 90% in both storage temperatures.

EVALUATION OF DECAY AND CHILLING INJURY. Evaluation of decay incidence was performed at the end of the 6-week cold storage, and after 4 and 21 d of subsequent shelf life at 20 °C. The total number of fruit manifesting decay symptoms (mainly green mold) was determined in each treatment and expressed as the

decay percentage. Evaluation of CI was performed at the end of the 6-week cold storage and after an additional 4 d at 20 °C. Grapefruit CI symptoms were manifested as rusty surface pitting. The severity of CI symptoms was assessed visually according to a four-stage scale, as follows: 1 = no pitting; 2 = a few scattered pits; 3 = pitting covering up to 30% of the fruit surface; and 4 = extensive pitting covering >30% of the fruit surface. The CI index was calculated according to the severity of symptoms (S) and the number of fruit affected (N) [Eq. [1]].

$$CI = \frac{\sum_{i=1}^4 (N_i \times S_i)}{\sum_{i=1}^4 N_i} \quad [1]$$

The percentage of injured fruit was defined as the percentage of grapefruit with moderate to severe CI index (stages 3 and 4); such fruit were considered as unacceptable for sale and consumption.

IN VIVO ASSAYS WITH WOUNDED GRAPEFRUIT. Grapefruit rinsed under tap water were dried and wounded with a desiccating needle (1 to 2 mm deep) at three sites around the stem end, and aliquots of 25 μL of jasmonate solutions were pipetted into each wound. Wounds of control fruit were treated similarly with sterile-distilled water instead of jasmonates. Wounded sites were inoculated with 25 μL of spore suspension of *P. digitatum* (5 × 10⁴ spores/mL) after 24 h incubation at 24 °C. When dry, grapefruit were kept at 24 °C in plastic trays under humid conditions for 4 to 7 d before determining the percent of infected sites. Six fruit were used per treatment (total of 18 wounds), and each experiment was performed four times with JA and twice with MJ.

EFFECT OF JASMONATES ON *P. digitatum* IN VITRO. Spores of *P. digitatum* were suspended in 100 g·L⁻¹ potato dextrose broth (Difco, Detroit, Mich.) at a final concentration of 2 × 10⁴ spores/mL. Aliquots (450 μL) of spore suspensions were transferred to wells of tissue culture clusters (Corning Costar Corporation, Cambridge, Mass.), and 50-μL aliquots of the various jasmonate solutions were added to give final concentrations of 1 to 1000 μmol·L⁻¹. Samples of the various test solutions (30-μL drops), were placed on ethanol-washed microscope slides (three drops per slide) kept in petri dishes padded with moistened filter paper, and incubated for 24 h at 25 °C in darkness. Spore germination and germ tube elongation were measured in three microscope fields, each containing 40 to 50 spores, under a light microscope.

STATISTICAL ANALYSIS. Results were analyzed with the SigmaStat statistical software (Jandel Scientific Software, San Rafael, Calif.). Two-factor analysis of variance (ANOVA) and Student-Newman-Keuls multiple range tests were performed where indicated. Unless noted otherwise, only results significant at $P \leq 0.05$ are discussed.

Results

EFFECT OF POSTHARVEST DIP TREATMENTS WITH MJ. To examine the efficacy of MJ as a potential postharvest treatment to reduce decay in citrus fruit, we dipped grapefruit in MJ solutions of various concentrations (1 to 50 μmol·L⁻¹) and evaluated decay development and CI symptoms after 6 weeks of storage at 2 °C and 4 and 21 d of simulated shelf life at 20 °C. The results show that MJ appeared to reduce green mold decay that developed naturally immediately after cold storage and after 4 d of shelf life in a dose-dependent manner (Fig. 1A). However, after the prolonged simulation of shelf life (21 d), dipping in the highest concentration of MJ (50 μmol·L⁻¹) appeared to be less effective than dipping in 10 μmol·L⁻¹ MJ (Fig. 1A). In fruit treated with 10 μmol·L⁻¹ MJ, the

Table 1. Summary of statistical analysis of the effects of methyl jasmonate (MJ) concentration and shelf time at 20 °C on decay development and chilling injury (CI) in grapefruit after 6 weeks of storage at 2 °C. Mean values were derived from the data of Fig. 1.

Analysis	Decay (%)	CI index (1–4)	Fruit with CI (%)
MJ concn ($\mu\text{mol}\cdot\text{L}^{-1}$)			
0 (control)	7.6 a ^z	1.77 a	23.8 a
1	5.4 b	1.92 a	24.2 a
10	1.9 c	1.37 b	5.7 c
50	2.3 c	1.87 a	15.7 b
Time at 20 °C (d)			
0	1.7 b	1.56 b	10.2 b
4	3.2 b	1.91 a	24.5 a
21	8.0 a	ND ^y	ND
Two-factor analysis of variance			
MJ concn (C)	***	***	***
Time at 20 °C (T)	***	***	***
C $\times$ T	NS	**	NS

^zMeans within each column, followed by different letters are significantly different at $P = 0.05$ according to the Student-Newman-Keuls multiple range test.

^yND = not determined.

NS, **, *** Nonsignificant or significant at $P = 0.01$ or 0.001 , respectively.

incidences of decay during cold storage (2 °C) and after 4 or 21 d of shelf life were only 0.9%, 1.9%, and 2.8%, respectively, compared with 4%, 7%, and 12% in untreated control fruit.

The statistical analysis, summarized in Table 1, indicated that this $10\text{-}\mu\text{mol}\cdot\text{L}^{-1}$ MJ dose was also the most effective concentration in protecting grapefruit against CI (expressed as percentage of pitted fruit) after cold storage and 4 d of shelf life (Fig. 1B). In this treatment, the percentage of fruit exhibiting CI during cold storage was only 3%, compared with 16% in the untreated control fruit. After 4 d of shelf life, the incidence of CI in $10\text{-}\mu\text{mol}\cdot\text{L}^{-1}$ MJ-treated fruit was 8.4%, compared with 31% in control fruit (Fig. 1B). The severity of CI, expressed as CI index, was also similarly reduced by $10\text{-}\mu\text{mol}\cdot\text{L}^{-1}$ MJ (Table 1), as previously reported (Meir et al., 1996). The statistical analysis (Table 1) shows that MJ may affect decay during cold storage in a different manner from the way it affects CI incidence. However, depending on the shelf-life duration, $10\text{-}\mu\text{mol}\cdot\text{L}^{-1}$ MJ seems to be the most effective concentration to reduce both parameters.

EFFECT OF JASMONATES ON ARTIFICIALLY INOCULATED FRUIT. To examine the possible effect of jasmonates on decay caused by artificial inoculation with the green mold, *P. digitatum*, in the absence of CI, we pretreated the fruit with several exponential concentrations of jasmonates applied through wounds, and monitored decay development at 24 °C after inoculation with the fungus. The results (Fig. 2) show that JA effectively reduced the amount of green mold decay that developed in the inoculated wounds in a concentration-dependent manner, with a peak of efficacy at $10\text{-}\mu\text{mol}\cdot\text{L}^{-1}$. Thus, at $10\text{-}\mu\text{mol}\cdot\text{L}^{-1}$ JA reduced decay to 47% of the amount that developed in nontreated control fruit, whereas 1 and $100\text{-}\mu\text{mol}\cdot\text{L}^{-1}$ JA reduced decay to only 59% and 78%, respectively. Higher or lower concentrations (0.1 or $1000\text{-}\mu\text{mol}\cdot\text{L}^{-1}$ JA) were completely ineffective in reducing decay (Fig. 2). Similar results of reduction of green mold rot after artificial inoculation of ‘Marsh Seedless’ grapefruit with *P. digitatum* were also obtained when MJ instead of JA was applied in the same concentration range (data not shown).

EFFECT OF JASMONATES ON *P. digitatum* IN VITRO. To examine whether the effects of JA and MJ in reducing decay caused by the green mold, *P. digitatum*, were due to their direct antifungal activity, we incubated a *P. digitatum* spore suspension in a growth medium containing various concentrations of jasmonates. We found that neither JA nor MJ, at all concentrations tested (1 to $1000\text{-}\mu\text{mol}\cdot\text{L}^{-1}$), had any inhibitory effect on *P. digitatum* spore germination and germ tube elongation (data not shown). Moreover, the high concentrations of JA or MJ even enhanced slightly germ tube elongation of the pathogen.

Discussion

Jasmonates are naturally occurring plant growth regulators, known to be involved in various aspects of plant development and responses to biotic and abiotic stresses (Creelman and Mullet, 1995, 1997). In the present study, we found that postharvest application of jasmonates reduced decay caused by the green mold, *P. digitatum*, after either natural (Fig. 1A) or artificial (Fig. 2) inoculation of ‘Marsh Seedless’ grapefruit.

There are only a few reports of exogenously applied jasmonates actually protecting plants against disease development: in potato (*Solanum tuberosum* L. ‘Alpha’) and tomato (*Lycopersicon esculentum* Mill. ‘Baby’) plants, jasmonates protected against *Phytophthora infestans* (Cohen et al., 1993); in barley (*Hordeum vulgare* L. ‘Golden Promise’) plants JA protected against *Erysiphe graminis* (Schweizer et al., 1993); in cut roses (*Rosa hybrida* L. ‘Mercedes’) and strawberries (*Fragaria xananassa* Duch. ‘Delmarvel’) MJ protected against *Botrytis cinerea* (Meir et al., 1998; Moline et al., 1997); and in fresh-cut celery (*Apium graveolens* L.) and peppers (*Capsicum annuum*) MJ reduced microbial contamination (Buta and Moline, 1998).

In a similar manner to our findings in grapefruit (Figs. 1A and 2), $10\text{-}\mu\text{mol}\cdot\text{L}^{-1}$ JA or MJ was the most effective concentration in reducing decay also in strawberries (Moline et al., 1997) and in fresh-cut celery and peppers (Buta and Moline, 1998). However,

Fig. 2. Effect of exponential concentrations of jasmonic acid (JA) on green mold decay development after artificial inoculation of grapefruit with *Penicillium digitatum*. Surface wounds were treated with $25\text{-}\mu\text{L}$ of various concentrations of JA, and then inoculated with $25\text{-}\mu\text{L}$ of a spore suspension of *P. digitatum* (5×10^4 spores/mL). Decay was evaluated after incubation for 4 d at 24 °C. Data represent means of 72 wounds from 4 different experiments. An overall LSD at $P \leq 0.05$ is shown for means comparison.

in the other plant systems examined, much higher jasmonate concentrations were required. For example, the most effective concentrations for reducing decay were 200 $\mu\text{mol}\cdot\text{L}^{-1}$ MJ in cut roses (Meir et al., 1998), 300 $\mu\text{mol}\cdot\text{L}^{-1}$ jasmonates in potato and tomato plants (Cohen et al., 1993), and 4.8 $\text{mmol}\cdot\text{L}^{-1}$ JA in barley plants (Schweizer et al., 1993). Similar to our present findings in grapefruit (Figs. 1A and 2), MJ is most effective in cut roses in reducing decay when applied in the pulsing solution at an optimal concentration (200 $\mu\text{mol}\cdot\text{L}^{-1}$), but is less effective at either higher or lower concentrations (Meir et al., 1998).

We have demonstrated previously that postharvest application of MJ could significantly reduce CI after cold storage of various chilling-susceptible fruit, such as avocado (*Persea americana* Mill. 'Hass'), grapefruit and bell pepper (Meir et al., 1996). A similar MJ protection against CI was reported previously for zucchini squash (*Cucurbita pepo* L.) also (Wang and Buta, 1994). The results of the present study further confirm that 10 $\mu\text{mol}\cdot\text{L}^{-1}$ MJ was the optimal concentration for reducing CI in grapefruit after 6 weeks of cold storage and 4 additional d of shelf life (Fig. 1B, Table 1). It is well known that low-temperature stresses render the commodity to become more susceptible to postharvest pathogens (Bramlage and Meir, 1990). Indeed, storage of grapefruit at temperatures lower than 11 °C has resulted in CI, expressed as peel pitting of the fruit, increased attack by mold pathogens and stem end rots (Chalutz et al., 1981). In addition, the present statistical analysis clearly shows that the effects of MJ on CI and decay development depend on concentration and duration of the shelf life (Table 1). Therefore, it could be speculated that the inhibitory effect of MJ on the decay of cold-stored fruit (Fig. 1A) may be a result of its inhibitory effect on CI (Fig. 1B), which enhances fruit susceptibility to fungal attack. However, our findings strongly suggest that this is not the case. Firstly, there was no strict correlation between the MJ dose dependency of the two processes: 50 $\mu\text{mol}\cdot\text{L}^{-1}$ MJ, which was the most effective concentration for decay reduction after 6 weeks of cold storage and 4 d of shelf life, was much less effective for CI reduction during this period (Fig. 1 and Table 1). On the other hand, 10 $\mu\text{mol}\cdot\text{L}^{-1}$ MJ was the optimal concentration for decay reduction after 21 d of shelf life (Fig. 1A). At this time, CI could not be evaluated because of the high percentage of decayed fruit, and because the sporulated fungus has completely covered the fruit surface. Secondly, this 10 $\mu\text{mol}\cdot\text{L}^{-1}$ MJ (or JA) concentration was also the most effective dose to protect grapefruit against decay caused by artificial inoculation with *P. digitatum* at 24 °C (Fig. 2). It appears therefore, that this dose of jasmonates is the optimal one to induce fruit resistance against decay in general, regardless of storage temperature.

MJ dipping of grapefruit seems to provide systemic protection against the green mold rot, *P. digitatum*, by eliciting resistance responses in the treated fruit. This conclusion is based on the following findings of the present study. a) Postharvest application of MJ to grapefruit significantly reduced the natural development of green mold decay during cold storage and subsequent shelf life at 20 °C (Fig. 1A, Table 1). b) The optimal dipping dose of MJ obtained for rot inhibition in these fruit was 10 $\mu\text{mol}\cdot\text{L}^{-1}$ (Fig. 1A and Table 1). c) This 10 $\mu\text{mol}\cdot\text{L}^{-1}$ MJ (or JA) concentration was also the optimal effective dose in reducing disease incidence after artificial inoculation of grapefruit with *P. digitatum* at 24 °C (Fig. 2). and d) Jasmonates had no inhibitory effect on *P. digitatum* *in vitro*, even at high concentrations. It appears therefore, that the effects of jasmonates in reducing decay development in grapefruit were indirect, and operated through enhancement of the fruit natural defenses.

Indeed, in the literature, it is well established that jasmonates

induce disease resistance and related responses in a wide variety of plants and cell cultures (Andresen et al., 1992; Chaudhry et al., 1994; Creelman et al., 1992; Creelman and Mullet, 1997; Doares et al., 1995; Farmer and Ryan, 1990; Gundlach et al., 1992; Nojiri et al., 1996; Xu et al., 1994). However, the mode of action of jasmonates in reducing disease development seems to differ among the various plants and pathogens examined. As in grapefruit, jasmonates reduce *Phytophthora infestans* in tomato and potato plants at much lower concentrations (300 $\mu\text{mol}\cdot\text{L}^{-1}$) than those required (3.5 to 5 $\text{mmol}\cdot\text{L}^{-1}$) for direct inhibition of the fungus (Cohen et al., 1993), and it was, therefore, suggested that jasmonates might protect the plants through the induction of host resistance responses (Cohen et al., 1993). In barley plants, however, JA reduces *Erysiphe graminis* only at high concentrations that inhibit appressoria formation and therefore, probably directly inhibit the fungus growth (Schweizer et al., 1993). On the other hand, in cut roses we previously showed that low MJ concentrations (200 $\mu\text{mol}\cdot\text{L}^{-1}$) provide systemic protection against *Botrytis cinerea* by enhancing petal resistance, whereas 400 $\mu\text{mol}\cdot\text{L}^{-1}$ MJ completely inhibits spore germination and germ-tube elongation of the fungus *in vitro* (Meir et al., 1998). Overall, it seems that the effects and mode of action of jasmonates in reducing disease development differ among the various crops and pathogens examined.

Another possible explanation for the mode of action of jasmonates in inducing disease resistance, may be by their induction of ethylene synthesis (Porat et al., 1993; Saniewski and Czapski, 1985). Especially, since it is known that ethylene induces the resistance of citrus fruit to *P. digitatum* (El-Kazzaz et al., 1983). However, there are also other cases in which jasmonates inhibit ethylene production (Nojavan-Asghari and Ishizawa, 1998). In cut roses, we found that jasmonate-induced resistance to pathogens is not ethylene mediated, since the MJ treatment was assayed in the presence of an ethylene antagonist (Meir et al., 1998). The possible effects of jasmonates on ethylene production in grapefruit were not evaluated in the current study.

In summary, our results clearly suggest that, when applied at low concentrations, jasmonates are potential postharvest treatments to enhance natural resistance and to reduce decay and CI in grapefruit. Since they are naturally occurring compounds and are given in low doses, jasmonates may provide a more environmentally friendly means to reduce the current massive use of chemical fungicides to control postharvest decay of grapefruit.

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