Physiology of Olive Leaf Abscission Induced by Phosphorus

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Abstract. Adding Al_2O_3 to 8-hydroxyquinoline citrate (8-HQC) solution did not alter the sensitivity of the leaf abscission zone to external ethylene. Exogenous ethylene at $791 \text{ nl}\cdot\text{liter}^{-1}$ for 72 to 120 hours and at $193 \text{ nl}\cdot\text{liter}^{-1}$ for 120 hours induced leaf abscission, whereas no leaf abscission occurred at $47 \text{ nl}\cdot\text{liter}^{-1}$ for 72 to 120 hours. Ethylene at $791 \text{ nl}\cdot\text{liter}^{-1}$ for 72 to 120 hours increased ethylene evolution, but the amount of ethylene evolved from the explants does not seem to be enough to induce leaf abscission. Three different ethylene inhibitors—aminooxyacetic acid (AOA), CoCl_2 , and aminoethoxyvinylglycine (AVG)—were used to determine whether P-induced leaf abscission was mediated through elevated ethylene evolution. Although AOA and CoCl_2 failed to inhibit ethylene evolution from the explants stem-fed with NaH_2PO_4 , AVG inhibited ethylene evolution. Each inhibitor, except 5 mM CoCl_2 , promoted leaf abscission when administered alone or with P. Our results reveal that P-induced olive leaf abscission may occur without elevated ethylene evolution. At 40 or 75 mM NaH_2PO_4 , abscission did not occur until explants were removed from N_2 and placed in ambient air.

Studies of fruit loosening agents that facilitate mechanical olive harvest have been conducted for many years. Foliar sprays with ethylene-releasing compounds, such as 2-(chloroethyl)-phosphonic acid (ethephon), have induced fruit abscission (Ben-Tal and Lavee, 1976; Hartmann et al., 1970; Lang and Martin, 1987; Martin et al., 1981). However, these treatments have also caused excessive leaf abscission, which results in reduced yield and entry of olive knot bacteria the following season (Martin, 1986). No chemicals tested to date have performed satisfactorily due to lack of fruit abscission action or excessive leaf loss.

Recently, Banno et al. (1993) found that NaH_2PO_4 induced leaf and fruit abscission of olive explants in stem-feeding treatments. They also observed fruit abscission with minimal leaf loss after foliar spray treatment and suggested a potential strategy to loosen fruit for mechanical harvest using NaH_2PO_4 sprays.

Elevated ethylene levels resulted in olive leaf and fruit abscission (Lang and Martin, 1987, 1989; Weis et al., 1988), and the extent of leaf abscission was correlated with the early rate of ethylene evolution from individual leaves (Lavee and Martin, 1981a–c). Lavee and Martin (1981a) also indicated that a robust ethylene or ethephon treatment was required at least 50 h before olive leaf abscission was induced. In contrast, ethylene evolution from olive explants stem-fed with NaH_2PO_4 evolved ethylene coincidentally with leaf abscission (Banno et al., 1993; Burnik-Tiefengraber et al., 1994). Banno et al. (1993) also found that Al_2O_3 delayed phosphate- and ethephon-induced abscission. Al_2O_3 binds phosphate; however, it might also decrease abscission-zone sensitivity to phosphate treatment. Burnik-Tiefengraber et al. (1994) used aminooxyacetic acid (AOA), an ethylene inhibitor, to determine whether P elevated ethylene levels, which then enhanced abscission. They observed that AOA did not measurably affect leaf abscission or ethylene evolution induced by NaH_2PO_4 . Other investigators (Fuchs et al., 1981; Sobolewska and Plich, 1986) suggested that phosphate inhibited ethylene biosynthesis in some higher plants and that the site of its control was the conversion of 1-amino-cyclopropane-1-carboxylic acid (ACC) to ethylene.

The mechanism of P-induced abscission is unclear, although some suggestions have been provided by Banno et al. (1993) and Burnik-Tiefengraber et al. (1994). The purpose of our research was to test four hypotheses on the mechanism of P-induced leaf abscission as follows: 1) Al_2O_3 decreases abscission-zone sensitivity to ethylene; 2) a low level of external ethylene induces leaf abscission via increased endogenous ethylene evolution; 3) P-induced abscission is mediated through increased ethylene production; and 4) O_2 is required for P-induced leaf abscission.

Materials and Methods

Plant materials. One-year-old vegetative shoots on “off-year” ‘Manzanillo’ olive trees were collected as needed from March to July 1993 from the orchard at the Univ. of California, Davis. Excised shoots were placed in buckets of water for transport to the laboratory. Shoots with five pairs of leaves were recut under water to 20 to 25 cm long, and four shoots were placed in a 50-ml flask of either the control solution containing $200 \text{ mg}\cdot\text{liter}^{-1}$ 8-hydroxyquinoline citrate (8-HQC) (Burnik-Tiefengraber et al., 1994) or treatment solutions with 8-HQC. Using 8-HQC extends explant vitality by several weeks.

Aluminum oxide effect. Explants continuously stem-fed with 8-HQC or 8-HQC + $100 \text{ mg}\cdot\text{liter}^{-1}$ Al_2O_3 (saturated) were exposed to three ethylene concentrations (1, 2, and $4 \mu\text{l}\cdot\text{liter}^{-1}$) plus air only (control) in the gas-flow system (Lang and Martin, 1989). High humidity was maintained by laying wet paper towels at the bottom of the jar and passing air alone or air mixed with ethylene through the jar. Eight shoots in two flasks were provided for each treatment and placed in the jar. Explants were removed from the flow-through system to ambient laboratory conditions at 20C in the same room after the treatment periods described in detail in the footnote of Fig. 1 to observe leaf abscission for the following 7 days. Cumulative leaf abscission was recorded every day as the number of leaves that abscised naturally and those that separated by the gentle touch of a finger.

Low concentration of ethylene treatment. Using the gas-flow system described above, shoots stem-fed with 8-HQC solutions were exposed to ethylene at 0, 47, 193, and $791 \text{ nl}\cdot\text{liter}^{-1}$ for 72, 96, or 120 h. Explants were removed from the jars and placed in the same controlled-temperature room at 20C after ethylene treatment. Leaf abscission was measured every 24 h after removing the

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explants from the flow-through system for 3 to 5 days depending on treatment duration. A flask containing four shoots per treatment was transferred into a 1.88-liter jar with a stopper for 2 h, and then a 10-ml gas sample was taken from each jar for ethylene analysis by gas chromatography (Goren et al., 1988). Ethylene was measured 2, 6, and 24 h after removing the explants from the external ethylene treatments.

Ethylene biosynthesis inhibitors. Shoots were prepared in the same way as described above, and four shoots per treatment were put in a flask and continuously stem-fed with solutions containing 8-HQC, 8-HQC + 40 mM NaH_2PO_4 , or 8-HQC + 75 mM NaH_2PO_4 combined with AOA, CoCl_2 , or aminoethoxyvinylglycine (AVG) at 1.25, 2.5, or 5.0 mM. Explants were placed in the laboratory at 20°C, and leaf abscission and ethylene evolution from the explants were measured every day for the 10 days of treatment in the same manner as described before. Ethylene production was no longer measured when the percentage of leaf abscission attained 90% or more, because even the small amount of evolved ethylene from the shoot stems might affect the ethylene evolution calculated on a per-

leaf basis. The experiment was repeated five times during June to early July.

Nitrogen gas effect. Explants stem-fed with 8-HQC, 8-HQC + 40 mM NaH_2PO_4 , or 8-HQC + 75 mM NaH_2PO_4 were placed in the jars connected with the gas-flow system described above. Since N_2 gas severely damaged leaves under high humidity in a preliminary experiment, humidity was not adjusted in this experiment. Shoots were exposed to air or 100% N_2 gas in the flow-through system for 5 days. After the gas treatments, shoots were placed on the bench top in the controlled-temperature room at 20°C to observe leaf abscission.

Results

Aluminum oxide effect. In the treatment of $1 \mu\text{l}\cdot\text{liter}^{-1}$ ethylene for 72 h, shoots in the solution containing Al_2O_3 abscised a few more leaves than those without Al_2O_3 after 3 days of posttreatment observation (Fig. 1B). There was no clear difference in leaf abscission among the other ethylene treatments with or without Al_2O_3 (Fig. 1).

Fig. 1. Effect of Al_2O_3 added to 8-hydroxyquinoline citrate (8-HQC) solution on leaf abscission induced by external ethylene in 'Manzanillo' olive explants. $\circ$ and ∇ = 200 $\text{mg}\cdot\text{liter}^{-1}$ 8-HQC without Al_2O_3 ; $\bullet$ and $\blacktriangledown$ = 200 $\text{mg}\cdot\text{liter}^{-1}$ 8-HQC with 100 $\text{mg}\cdot\text{liter}^{-1}$ Al_2O_3 . (A) $\circ$ and $\bullet$ = 72 h air. (B) $\circ$ and $\bullet$ = 72 h ethylene; ∇ and $\blacktriangledown$ = 96 h ethylene. (C) $\circ$ and $\bullet$ = 48 h ethylene; ∇ and $\blacktriangledown$ = 72 h ethylene. (D) $\circ$ and $\bullet$ = 48 h ethylene; ∇ and $\blacktriangledown$ = 72 h ethylene.

Low concentration of ethylene treatment. At 791 nl·liter⁻¹ ethylene for 72 h, ethylene evolution was low until 6 h after removal from ethylene treatment (Fig. 2A). By 24 h after removal from ethylene treatment, ethylene production increased up to 2.4 nl/leaf per h and then returned to <0.5 nl/leaf per h. Leaves in this treatment started to abscise 72 h after removal from ethylene (Fig. 2D). Ethylene evolution from the shoots treated with 791 μ l·liter⁻¹ ethylene for 96 h was similar to that treated for 72 h, except that it remained at 0.8 to 1.0 nl/leaf per h after the peak of ethylene evolution of 2.5 nl/leaf per h at 24 h after removal from ethylene (Fig. 2B). At the time of removal from 96 h of 791 μ l·liter⁻¹ ethylene, 20% of the leaves had abscised and abscission gradually increased subsequently (Fig. 2E). At 791 μ l·liter⁻¹ ethylene for 120 h, ethylene evolution 2 h after removal from treatment was already higher than that at 72 or 96 h (Fig. 2A and B vs. C). However the maximum ethylene evolution was 2 nl/leaf per h (Fig. 2C). Leaf abscission at 791 μ l·liter⁻¹ ethylene for 120 h was 48% at the time of removal from treatment and gradually increased during post-treatment observation (Fig. 2F). Treatment with ethylene at 193 nl·liter⁻¹ for 120 h led to elevated ethylene evolution by 24 h after

removal from treatment, and, after another 72 h, <0% leaf abscission occurred (Fig. 2C and F). Ethylene at 193 nl·liter⁻¹ for 72 and 96 h and at 47 nl·liter⁻¹ for 72 to 120 h did not affect subsequent ethylene evolution and/or leaf abscission when removed from treatment (Fig. 2A–F).

Ethylene biosynthesis inhibitors. The control containing 8-HQC alone resulted in no leaf abscission and ethylene evolution remained at 0.1 nl/leaf per h for 10 days (Fig. 3A and D). At 40 mM NaH₂PO₄, there was a slight increase of ethylene evolution at 8 and 9 days of treatment, while leaf abscission started to occur at 4 days of treatment and attained 50% abscission by 10 days (Fig. 3B and E). At 75 mM NaH₂PO₄, leaf abscission started at 3 days of treatment and increased up to 80% by 10 days (Fig. 3F). Ethylene production at 75 mM NaH₂PO₄ was 0.4 nl/leaf per h by 2 days of treatment and then increased to 1.6 nl/leaf per h at 6 days (Fig. 3C). At 7 days, ethylene evolution decreased and then gradually increased by 10 days to the level attained previously at 6 days. These results formed the control P-induced abscission comparison against which subsequent ethylene biosynthesis inhibitors could be compared.

AOA alone resulted in ethylene evolution and leaf abscission

Fig. 2. Effect of low concentration of exogenous ethylene on ethylene evolution (A–C) and leaf abscission (D–F) in 'Manzanillo' olive explants stem-fed with 8-hydroxyquinoline citrate solution. The ethylene treatment duration is shown for each column as follows: (A and D) 72 h, (B and E) 96 h, and (C and F) 120 h.

after 5 days of treatment (Fig. 4 A and D). At 40 mM and 75 mM NaH_2PO_4 with AOA, leaf abscission began by 3 days of treatment and achieved 100% leaf abscission by 5 or 9 days depending on AOA concentration (Fig. 4 B, C, E, and F). In all cases, ethylene evolution increased coincidentally with the increase of cumulative leaf abscission. In most cases, 5 mM AOA promoted leaf abscission and ethylene evolution slightly more than 2.5 mM AOA.

Cobalt chloride alone at all three concentrations induced ethylene evolution and leaf abscission (Fig. 5 A and D). At 5 mM CoCl_2 , ethylene induction at 3 nl/leaf per h was greater than for any other treatment in these experiments (compare Figs. 3–6), yet it resulted in <20% leaf abscission (Fig. 5 A and D). When CoCl_2 was combined with 40 or 75 mM NaH_2PO_4 , ethylene evolution was <1.5 nl/leaf per h (Fig. 5 B and C). The latter treatments at 1.25 and 2.5 mM CoCl_2 led to 100% leaf abscission by 6 or 7 days, whereas 5 mM CoCl_2 combined with NaH_2PO_4 resulted in less leaf abscission than NaH_2PO_4 alone (Fig. 3 vs. 5).

Either alone or with NaH_2PO_4 , AVG accelerated leaf abscission even though ethylene evolution remained <0.5 nl/leaf per h in each treatment (Fig. 6 A–F).

Nitrogen gas effect. Leaf abscission was induced by 5 days of NaH_2PO_4 treatment when in ambient air, whereas no leaf abscission occurred when exposed to 100% N_2 gas (Table 1). By 3 days of posttreatment, leaf abscission on explants stem-fed with 40 and 75 mM NaH_2PO_4 and exposed to air increased to 55% and 95%, respectively. Delayed leaf abscission was evident in N_2 treatments combined with NaH_2PO_4 until exposed to ambient air. Leaf abscission in the N_2 -treated population began 24 h after removal from treatment, achieving 57.5% and 52.5%, respectively, by 3 days of posttreatment observation (Table 1). Nitrogen gas alone did not induce leaf abscission by 3 days of posttreatment.

Discussion

Banno et al. (1993) showed that adding Al_2O_3 to a solution of ethephon or NaH_2PO_4 delayed leaf abscission compared with ethephon or NaH_2PO_4 alone. These authors maintained that this result was evidence that Al_2O_3 in the treatment solution directly affected leaf abscission by adsorbing P. It can also be argued that Al_2O_3 temporarily decreased the sensitivity of the abscission zone

Fig. 3. Effect of 8-hydroxyquinoline citrate solution containing different concentrations of NaH_2PO_4 (0, 40, and 75 mM) on ethylene evolution (A–C) and leaf abscission (D–F) in 'Manzanillo' olive explants. Bars show SE.

to ethylene, delaying abscission. We tested that interpretation by adding Al_2O_3 to 8-HQC using several concentrations of external ethylene for different durations. Leaf abscission occurred at a similar rate with or without Al_2O_3 , a result indicating that Al_2O_3 does not affect the sensitivity of the abscission zone to ethylene in olive explants.

The data reported here and elsewhere suggested that ethylene concentrations $<50 \text{ nl}\cdot\text{liter}^{-1}$ have little or no effect on olive leaf abscission. The effect of low concentrations of external ethylene on olive leaf abscission was investigated by Burnik-Tiefengraber et al. (1994), but they did not determine endogenous ethylene evolution from explants after ethylene treatment. We measured ethylene production after exogenous ethylene treatment to determine whether subsequent leaf abscission was influenced by endogenous ethylene evolution. Leaf abscission occurred at the end of 96 or 120 h ethylene at $791 \text{ nl}\cdot\text{liter}^{-1}$, whereas ethylene evolution after 96 h ethylene at $791 \text{ nl}\cdot\text{liter}^{-1}$ was very low until 6 h after removal from treatment. Goren et al. (1988) applied a wide range of exogenous ethylene concentrations to detached olive leaves and

found that $>960 \text{ nl}\cdot\text{liter}^{-1}$ external ethylene induced autoenhancement of endogenous ethylene 96 or 120 h after exposure to ethylene. They also reported no relationship between the autoenhancement of ethylene and leaf abscission. Our data also showed a similar lag time of 120 h before autoenhancement of ethylene production, a time by which 50% abscission was already taking place. The shoots exposed to $791 \text{ nl}\cdot\text{liter}^{-1}$ ethylene for 72 or 96 h had a peak of ethylene evolution at 24 h after ethylene treatment. Lavee and Martin (1981d) showed that short-term ethylene evolution induced by pulse-feeding ACC had a very limited effect on leaf abscission. Thus, these short-duration peaks of ethylene evolution do not seem to induce leaf abscission, even when magnitudes of order higher in concentration. Lavee and Martin (1981b) reported 50% leaf abscission with $9.3 \text{ nl}\cdot\text{g}^{-1}$ fresh weight per h ($2 \text{ nl}/\text{leaf per h}$) ethylene evolution measured after 120 h of continuous stem-feeding with $50 \text{ mg}\cdot\text{liter}^{-1}$ ethephon. In our studies, 1.7 to $1.9 \text{ nl}/\text{leaf per h}$ endogenous ethylene evolution 24 to 72 h after $791 \text{ nl}\cdot\text{liter}^{-1}$ ethylene for 120 h may induce further leaf abscission. In both experiments, abscission may have resulted

Fig. 4. Effect of AOA in 8-hydroxyquinoline citrate (8-HQC) solution with or without NaH_2PO_4 on ethylene evolution (A-C) and leaf abscission (D-F) in 'Manzanillo' olive explants. The concentration shown at the top of each column indicates the concentration of NaH_2PO_4 in 8-HQC solution. Bars show SE.

from continuous treatment with ethephon or ethylene without relation to evolved endogenous ethylene.

The leaf abscission response to P treatment reported by Banno et al. (1993) and Burnik-Tiefengraber et al. (1994), occurred at lower P concentrations than results reported here. They achieved 100% leaf abscission after 6 days of 25 mM NaH_2PO_4 or 8 days of 75 mM NaH_2PO_4 , respectively. This may, in part, reflect the recovery of the trees used in these studies from the severe freeze damage of December 1990. During the 1991 growing season, leaf abscission was common even on trees without apparent freeze damage. We suggest that explants taken from those trees during 1991 would contain leaves that were more likely to abscise when treated with NaH_2PO_4 . It is well known that exposure to ethylene gas or ethephon is required to precede leaf abscission (Lang and Martin, 1987, 1989; Lavee and Martin, 1981a, 1981b, 1981d). Banno et al. (1993) doubted the dependence of P-induced abscission on ethylene production, because in their experiment ethylene evolution following P stem-feeding paralleled rather than preceded leaf abscission. In our experiments, ethylene evolution from the explants stem-fed with 75 mM NaH_2PO_4 increased coincidently

with the increase of cumulative leaf abscission, a result that agrees with the results of Banno et al. (1993) and Burnik-Tiefengraber et al. (1994). In our studies, olive explants stem-fed with 40 mM NaH_2PO_4 did not increase ethylene evolution until after 8 days of treatment, when only a slight increase of ethylene at <0.5 nl/leaf per h occurred and by which time 40% leaf abscission had occurred. This suggests the independence of P-induced leaf abscission from that of P effects on ethylene production.

Using ethylene biosynthesis inhibitors led to unexpected results in the olive explant system. Although Burnik-Tiefengraber et al. (1994) used AOA to determine whether P caused leaf abscission by elevating ethylene evolution, AOA did not affect P-induced leaf abscission or ethylene evolution. Since the response and sensitivity to a certain inhibitor may change depending on the tissue treated and application method (Yang, 1980), we tried AOA, AVG, and CoCl_2 applied via the stem in solution. Each inhibitor had different effects on ethylene evolution from explants stem-fed with P or inhibitor alone. All of these inhibitors except 5 mM CoCl_2 , however, promoted leaf abscission with or without P. In contrast to the report by Burnik-Tiefengraber et al. (1994), AOA accelerated leaf

Fig. 5. Effect of CoCl_2 in 8-hydroxyquinoline citrate (8-HQC) solution with or without NaH_2PO_4 on ethylene evolution (A-C) and leaf abscission (D-F) in 'Manzanillo' olive explants. The concentration shown at the top of each column indicates the concentration of NaH_2PO_4 in 8-HQC solution. Bars show SE.

abscission in the solutions with P and AOA alone. Since in their experiment with P leaf abscission occurred more rapidly than in our experiments, this positive effect of AOA could have been masked in their experiment. Cobalt chloride is known as an ethylene inhibitor that blocks the conversion of ACC to ethylene (Lau and Yang, 1976; Yang, 1980). Adding CoCl_2 at three concentrations with P or CoCl_2 alone increased ethylene evolution at 2 days of treatment, and the amount of ethylene at that time was positively related to the concentration of CoCl_2 . Development of necrosis on the leaves and promotion of ethylene evolution indicated that CoCl_2 was a phytotoxic compound rather than an ethylene biosynthesis inhibitor in olives. Inhibition of leaf abscission with severe necrosis and desiccation at 5 mM CoCl_2 also supports this contention and coincides with the same phenomenon on olive inflorescence treated with high ethephon concentrations (Weis et al., 1988).

It was reported that AVG inhibited ethylene evolution induced by wounding in detached olive leaves (Lavee and Martin, 1981c). In our results, even though AVG almost completely inhibited ethylene evolution, AVG promoted leaf abscission alone or with P.

This observation clearly separates the leaf abscission action of P from the requirement for ethylene evolution. Abeles and Wydoski (1987) indicated a promotive effect of AVG on lettuce root growth in air and in the presence of ethylene. They also showed that AVG, AOA, and L-canaline inhibited root elongation at high concentrations, although those compounds strongly inhibited ethylene production. These observations and the data reported here suggest that ethylene biosynthesis inhibitors have their own action on growth and abscission in addition to inhibiting ethylene evolution (Abeles and Wydoski, 1987).

Leaf abscission occurred in the shoots stem-fed P in ambient air but did not occur in 100% N_2 gas at 5 days of treatment. The quick response of leaf abscission when transferred from N_2 to aerobic conditions, however, suggests that the amount of P retained in the explant was enough to induce leaf abscission and that O_2 was required for P-induced abscission.

In conclusion, four hypotheses were tested and we interpret our results as follows: 1) Al_2O_3 does not decrease the sensitivity of the abscission zone to ethylene treatment, 2) ethylene at 47 or 193 $\text{nl}\cdot\text{liter}^{-1}$ for 4 days does not induce leaf abscission or endogenous

Fig. 6. Effect of AVG in 8-hydroxyquinoline citrate (8-HQC) solution with or without NaH_2PO_4 on ethylene evolution (A-C) and leaf abscission (D-F) in 'Manzanillo' olive explants. The concentration shown at the top of each column indicates the concentration of NaH_2PO_4 in 8-HQC solution. Bars show SE.

Table 1. Effect of N₂ gas treatment on P-induced leaf abscission in 'Manzanillo' olive explants.

NaH ₂ PO ₄ concn (mM)	Gas	Leaf abscission (%) ^z		
		5 Days of treatment	1 Day of posttreatment	3 Days of posttreatment
0	Air	0	0	0
	N ₂	0	0	0
40	Air	12.5	25.0	55.0
	N ₂	0	35.0	57.5
75	Air	45.0	62.5	95.0
	N ₂	0	52.5	52.5

^zExplants were treated for 5 days in jars, then removed to ambient conditions in the laboratory at 20C for postharvest treatment observation.

ethylene evolution and leaf abscission that occurred at 791 nl·liter⁻¹ ethylene does not seem to be induced by endogenous ethylene, 3) P-induced leaf abscission occurs independent of endogenous ethylene evolution, and 4) O₂ is required for P-induced leaf abscission.

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