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Abscission-Inducing Properties of Methyl Jasmonate, ABA, and ABA-Methyl Ester and their Interactions with Ethephon, $AgNO_3$, and Malformin*

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Abstract. The biological activities of methyl jasmonate, ABA, methyl abscisate, and malformin were compared in a variety of *Vigna radiata* abscission tests. Although each compound diminished or completely negated the antiethylene properties of Ag^+, differences in potency were observed. ABA and ABA-Me stimulated leaf abscission in the dark, potentiated abscission with low concentrations of ethephon, and interacted synergistically with malformin, whereas methyl jasmonate was inactive in each of these tests. Methyl jasmonate was most active in potentiating leaf abscission induced by high ethephon concentrations and stimulated petiole abscission, whether applied proximally or distally, from debladed explants. In two tests, negation of Ag^+ activity and interaction with malformin, ABA concentrations as low as 0.1 μM were biologically active and indicated that ABA can be a highly active abscission-inducing compound. Based on differences in biological activity, it was concluded that the modes of action of methyl jasmonate, ABA, and malformin were different.

Jasmonic acid (JA) and methyl jasmonate (JA-Me) have been suggested as new phytohormones (Yamane et al. 1980, 1981, Ueda et al. 1981, Satler and Thimann 1981). The biological activity of both compounds resembles that of ABA with regard to the induction of senescence and stomatal closure (Ueda and Kato 1980, Satler and Thimann 1981), but some effects of JA are different from those of JA-Me. For example, JA but not JA-Me inhibited pollen germination

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(Yamane et al. 1982), whereas the activity of JA-Me was considerably greater than that of JA in inducing senescence in *Avena* segments (Ueda et al. 1981). Although both (−)-JA-Me and (+)-JA-Me inhibited the growth of rice seedlings, the naturally occurring (−)-form was most active (Yamane et al. 1981a). Inhibition of ABA uptake by JA-Me (Rubery and Astle 1982) suggests interactions between the two compounds.

Because the effect of JA-Me on abscission has not been examined, it was compared with ABA and ABA-Me in a variety of leaf and petiole abscission tests with bladed and debladed explants of *Vigna* (mung bean). Tests included the effects of light, ethephon, and the silver ion, an ethylene antagonist (Beyer 1976), on their biological activity. Interactions among the compounds were also examined, as well as with malformin, cyclo-D-cysteinyl-D-cysteinyl-L-valyl-D-leucyl-L-isoleucyl (Bodanszky and Stahl 1974), a potent abscission-inducing compound produced by the fungus *Aspergillus niger* (Curtis 1958, 1977).

Materials and Methods

Leaf Abscission from Bladed Explants

Bladed explants (8.0 cm stem) of *Vigna radiata* (L. Wilczek cv Jumbo) in the primary leaf stage were obtained from 14-day-old seedlings grown in a greenhouse under natural light (Curtis 1977). These were placed in 12-ml vials containing 10 ml of test solution (10 cuttings/vial) and placed in the dark (28 C) or in continuous white fluorescent light as described earlier (Curtis 1982a). Deionized water was added daily to maintain the volume at about 10 ml. Primary leaf abscission was determined at daily intervals after treatment by rotating the stems rapidly between the fingers to dislodge loosely attached leaves. Treatments were not identified until after abscission had been determined. Most experiments were performed three or four times and consisted of three or four determinations per treatment. To test the ability of the compounds to negate the antiethylene properties of $AgNO_3$, the cuttings were placed in vials containing water and sprayed to run-off with Tween 20 (0.1% v/v) with and without $AgNO_3$ (1.0 mM). After 24 h in continuous light, ethylene-induced abscission was obtained by transferring the cuttings to fresh vials containing 10 ml of ethephon (1.38 mM), an ethylene-releasing compound (2-chloroethylphosphonic acid), and various concentrations of the test compounds. The vials were placed in continuous light and leaf abscission was determined at daily intervals.

Petiole Abscission from Debladed Explants

The effect of JA-Me, ABA, and ABA-Me on petiole abscission of debladed explants was also examined. Explants were prepared from untreated bladed explants or bladed explants that had been sprayed 24 h prior to use with control or $AgNO_3$ solutions as described above. They consisted of two opposite petioles (approximately 2 mm long) subtended by a stem (approximately 8 mm

long) and were prepared by excising the primary leaf blades from the distal end of the petioles and the stem 8 mm below the junction of the petioles and stem. The explants were inserted stem end down (proximal treatment) or petiole ends down (distal treatment) into aluminum planchets (3.1 cm O.D., 0.2 cm deep, 20 explants/planchet) containing 2.0 ml 1% (w/v) water agar containing the test compounds. Planchets were placed in pyrex baking dishes (2.7 l) lined with moist paper towels, covered with aluminum foil and placed in the dark. Petiole abscission was determined at various intervals by counting the number of petioles that broke off when subjected to a 5.0-g weight placed briefly on the end of the petiole.

Chemicals

Malformin was isolated from culture filtrates of *A. niger* as described earlier (Takahashi and Curtis 1961). (±)-ABA was purchased from Calbiochem-Behring Co. (San Diego, California, USA), and (±)-ABA-Me from Sigma Chemical Co. (St. Louis, Missouri, USA). (±)-JA-Me was used because it is more stable at room temperature than JA (N. Takahashi, personal communication) and was a generous gift from Prof. N. Takahashi (Dept. of Agricultural Chemistry, University of Tokyo, Bunkyo-ku, Tokyo, Japan). Ethephon (Ethrel) was a gift from Amchem Products, Inc. (Ambler, Pennsylvania, USA).

Results

Leaf Abscission from Bladed Explants in Dark and Light

In the dark, ABA, ABA-Me, and malformin stimulated leaf abscission (Fig. 1). Malformin was most active in terms of concentration and response rate. Little difference was noted in the activity of ABA and ABA-Me, although the response to ABA was slightly faster. JA-Me was completely inactive and even delayed abscission slightly. The activity of all compounds was virtually abolished when they were used in the light. In preliminary experiments, ABA (100 μM) and malformin (10 μM) also stimulated abscission in the dark when applied as a leaf spray, but JA-Me (100 μM) remained inactive.

Negation of Antiethylene Properties of $AgNO_3$ in Bladed Explants

To determine the ability of the compounds to negate the antiethylene properties of $AgNO_3$, bladed explants sprayed 24 h earlier with $AgNO_3$ (1.0 mM) were placed in solutions of ethephon (1.38 mM) with or without the test compounds and placed in the light. Explants sprayed with Tween 20 solutions and treated only with ethephon served as a secondary control (non-Ag^+ control). In the absence of Ag^+, ethephon induced rapid abscission, but Ag^+-treated explants did not respond to ethephon (Fig. 2). Both malformin and ABA completely negated the antiethylene properties of Ag^+, but malformin activity was ob-

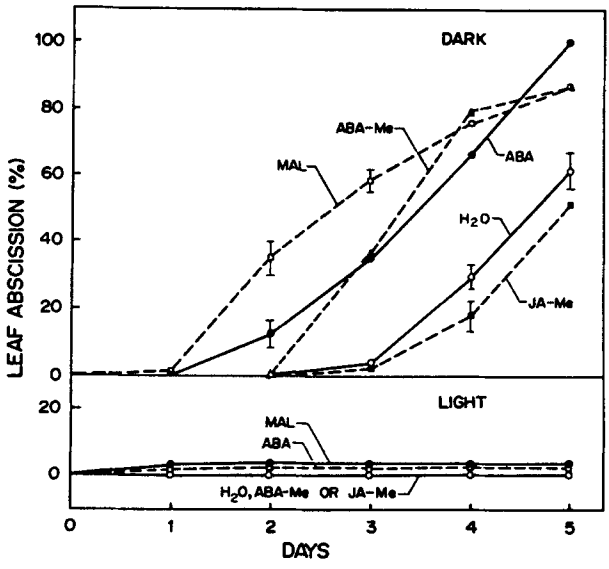

Fig. 1. Leaf abscission from *Vigna* bladed explants placed in vials containing H_2O, 100 μM JA-Me, ABA, ABA-Me, or 10 μM malformin and placed in the dark or continuous white light. Leaf abscission was determined at daily intervals. Vertical bars = ± S.E.

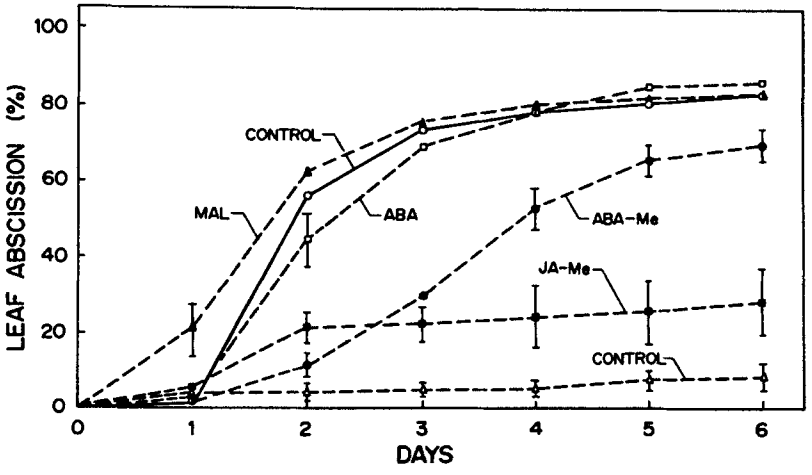

Fig. 2. Effect of JA-Me, ABA, ABA-Me, and malformin on the antiethylene properties of $AgNO_3$. Bladed explants of *Vigna* were sprayed with Tween 20 (0.1%) containing $AgNO_3$ (1.0 mM), incubated for 24 h in continuous light, transferred to solutions of ethephon (1.38 mM) with and without (control, △---△) 100 μM JA-Me, ABA, ABA-Me, or 10 μM malformin, and placed in continuous light. A secondary control (non-Ag^+-treated, ○—○) was sprayed with Tween 20 (0.1%) and also treated with ethephon after 24 h. Leaf abscission was determined at daily intervals. Vertical bars = ± S.E. Solid line = non-Ag^+-treated cuttings; broken line = Ag^+-treated cuttings.

Table 1. Effect of ABA, ABA-Me, and malformin on the antiethylene activity of Ag^+ in bladed explants of *Vigna*.

Treatment and concentrations (μM)[a]	Leaf abscission (%)
Non-Ag^+-treated	
Control	82.5 ± 4.8
Ag^+-treated	
Control	6.4 ± 2.3
ABA 1.0	9.2 ± 4.9
ABA 10.0	20.7 ± 3.6
ABA 100.0	86.0 ± 3.8
ABA-Me 1.0	4.7 ± 1.0
ABA-Me 10.0	8.7 ± 3.3
ABA-Me 100.0	69.5 ± 4.9
Malformin 0.1	14.8 ± 5.1
Malformin 1.0	22.4 ± 4.1
Malformin 10.0	76.6 ± 2.6

[a] Bladed explants sprayed with Tween 20 (0.1%) with or without $AgNO_3$ (1.0 mM), and incubated for 24 h in white light. Controls were then treated with ethephon only (1.38 mM). ABA, ABA-Me, and malformin were incorporated into identical ethephon solutions. Results after six days.

served earlier (after one day). ABA-Me also negated Ag^+ activity, but acted at a considerably slower rate than either ABA or malformin. Initially, JA-Me negated Ag^+ activity more rapidly than ABA-Me, but then the rate leveled off and failed to reach the degree of activity of the other compounds.

In similar experiments, various concentrations of ABA, ABA-Me, and malformin were compared (Table 1). Of the concentrations tested, the minimum concentration of ABA-Me, ABA, and malformin that decreased the antiethylene properties of Ag^+ were 100, 10, and 0.1 μM, respectively. Concentrations of JA-Me below 100 μM were inactive (data not given).

Potentiation of Ethephon Activity in Bladed Explants

In these experiments, performed with previously untreated bladed explants in continuous light, two concentrations of ethephon were used, one that induced only a trace of abscission (0.138 mM), and another that induced rapid and abundant abscission (1.38 mM). At the lower concentration, ABA, ABA-Me, and malformin potentiated ethylene-induced abscission when added to the ethephon solution (Fig. 3). Although ABA, ABA-Me, and malformin by themselves induced little or no abscission in the light (Fig. 1), they reacted synergistically with ethephon. Kinetics of the synergistic reaction were considerably different, malformin reacting most rapidly, ABA after a lag period of about 24 h, and ABA-Me beginning about 48 h after treatment. JA-Me was inactive at the lower ethephon concentration. In dosage-response studies the lowest concentration of ABA, ABA-Me, and malformin that potentiated the action of ethephon (0.138 mM) was 10, 10, and 1.0 μM, respectively. None of these

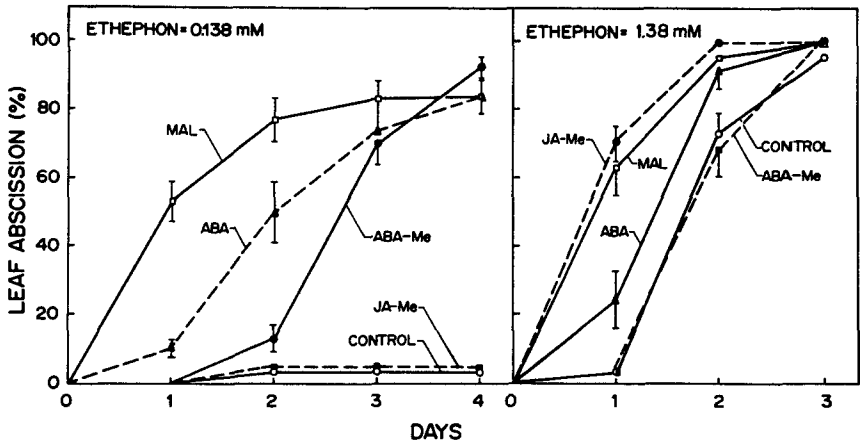

Fig. 3. Potentiation of ethylene-induced leaf abscission by JA-Me, ABA, ABA-Me, and malformin. Bladed explants of *Vigna* treated in continuous light with 0.138 or 1.38 mM ethephon in the absence (control) or presence of 100 μM JA-Me, ABA, ABA-Me, or 10 μM malformin. Leaf abscission was determined at daily intervals. Vertical bars = ± S.E.

compounds were active when ethephon concentration was decreased to 0.014 mM (data not given).

When the ethephon concentration was increased (1.38 mM), JA-Me and malformin were most active in potentiating ethylene-induced abscission (Fig. 3), whereas ABA appeared to have only moderate activity and ABA-Me appeared to be inactive. The apparent diminished activity of ABA and ABA-Me is probably misleading, and it seems likely that their slower action, shown at the lower ethephon concentration (0.138 mM), was masked by the rapid abscission induced by ethephon at the higher concentration (1.38 mM).

Interactions Between JA-Me, ABA, ABA-Me, and Malformin in Bladed Explants

When bladed explants were treated in the light, ABA, ABA-Me, JA-Me, and malformin induced little or no leaf abscission (Fig. 1). When ABA or ABA-Me were combined with malformin, abscission was rapid and approached 100% in four days (Fig. 4). As in the previous experiments, the effect of ABA-Me lagged behind that of ABA. No significant abscission occurred when ABA, ABA-Me, or malformin were combined with JA-Me. Dosage-response curves of the interaction between ABA and malformin were determined (Fig. 5). When the concentration of malformin was 10μM, the addition of as little as 0.1 μM ABA resulted in a stimulation of abscission. At a concentration of 1.0 μM malformin, an interaction occurred only when the concentration of ABA was 100 μM. At no concentration did either ABA or malformin induce abscission when tested alone.

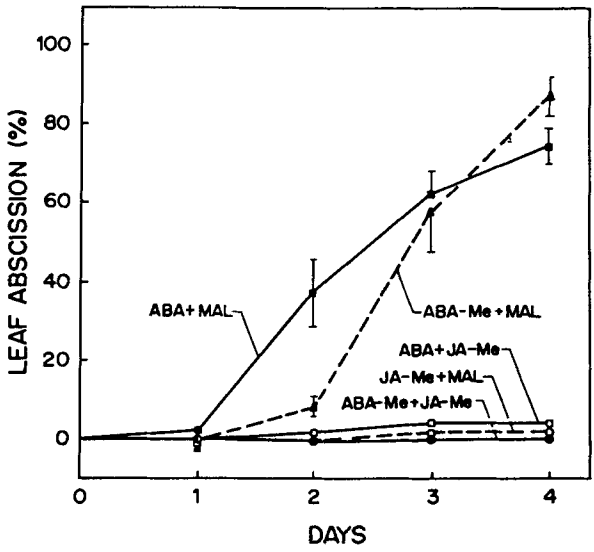

Fig. 4. Interactions between ABA, ABA-Me, JA-Me, and malformin with regard to leaf abscission from bladed explants of *Vigna*. Bladed explants were treated in vials containing various combinations of the growth regulators and placed in continuous white light. Abscission was determined at daily intervals. Vertical bars = ± S.E. When applied individually, none of the compounds induced leaf abscission (data not given). Concentrations of ABA, ABA-Me, JA-Me = 100 μM; malformin = 10 μM.

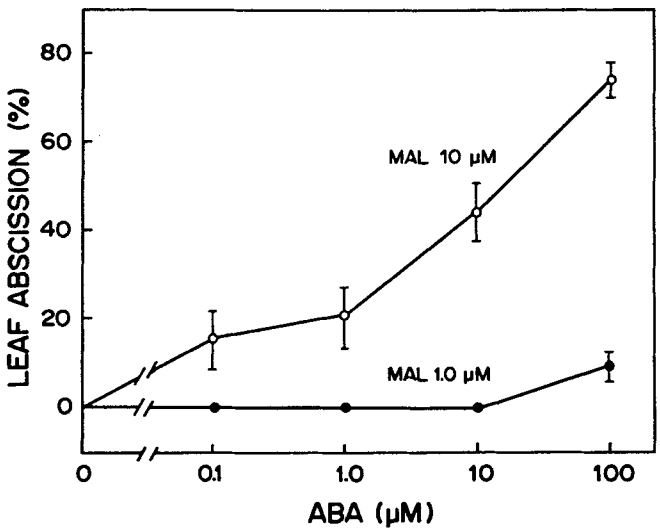

Fig. 5. Interaction between ABA and malformin in inducing leaf abscission from bladed explants of *Vigna*. Cuttings treated in light as described in Fig. 4. Results after six days.

Petiole Abscission from Debladed Explants

Proximal treatment of explants obtained from untreated *Vigna* cuttings indicated that JA-Me, ABA, and ABA-Me stimulated petiole abscission (Fig. 6). JA-Me was least active, stimulating petiole abscission only at the highest concentration (100 μM). ABA stimulated petiole abscission more and at a lower

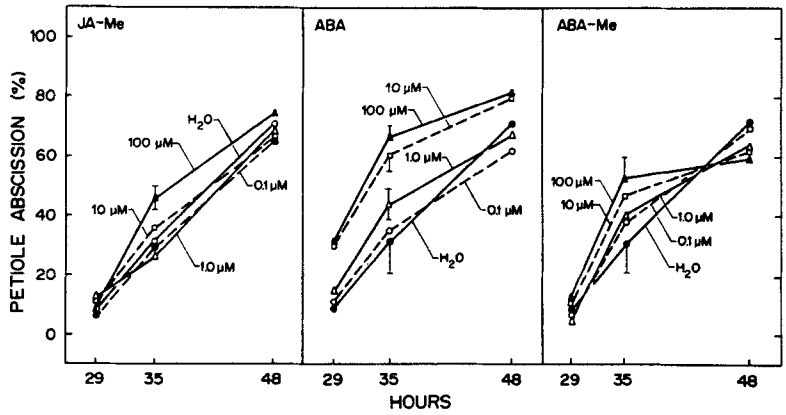

Fig. 6. Petiole abscission from debladed *Vigna* explants treated proximally with JA-Me, ABA, and ABA-Me. Explants prepared from untreated bladed explants were inserted stem end down into water-agar containing test compounds. Abscission determined by counting the number of petioles that broke off when subjected to a 5.0 g weight placed briefly on the end of the petiole. Vertical bars = ± S.E.

concentration than ABA-Me. Maximum stimulation of abscission for all of the compounds was observed 35 h after treatment. Distal treatment resulted in greater stimulation of abscission by all compounds (Fig. 7) and lowered the minimum active concentration of JA-Me to 10 µM. Although the dosage-response curves of ABA and ABA-Me were similar, the activity of ABA was slightly greater. Kinetics of the abscission stimulation process were similar for the three compounds, and a prominent lag phase for ABA-Me activity was not observed. When similar explants were obtained from bladed explants sprayed 24 h *prior* to use with $AgNO_3$, and the petiole abscission rate compared with that obtained using explants from untreated cuttings, Ag^+ inhibited abscission markedly (Table 2). Although distally applied JA-Me, ABA, and ABA-Me all negated the inhibition of abscission induced by Ag^+, differences in activity were observed with regard to concentrations required, degree of negation, and time required. Concentrations of JA-Me below 100 µM were inactive, whereas ABA and ABA-Me were active at 1.0 µM. The degree of negation was greatest for ABA, followed by ABA-Me and JA-Me. Despite these differences, each of the three compounds was capable of completely negating the activity of Ag^+. When applied proximally, JA-Me was inactive but the activity of ABA and ABA-Me remained about the same (data not given).

Discussion

In general, the activities of JA-Me, ABA, ABA-Me, and malformin in various abscission tests were diffferent. In only one test, negation of the antiethylene properties of $AgNO_3$ in bladed explants (Fig. 2), were all of the compounds active. Even in this test the activity of JA-Me was considerably lower than

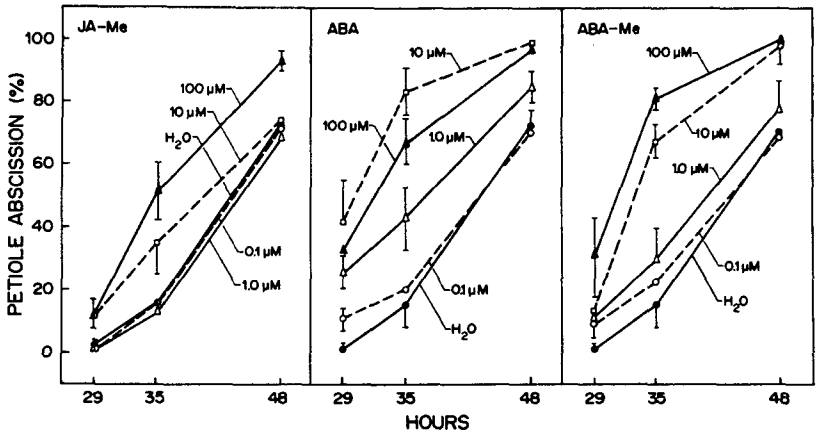

Fig. 7. Petiole abscission from debladed *Vigna* explants treated distally with JA-Me, ABA, and ABA-Me. Methods as for Fig. 6, except the explants were inserted petiole ends down.

Table 2. Effect of distally applied JA-Me, ABA, and ABA-Me on petiole abscission from debladed explants of *Vigna* obtained from Ag^+-treated bladed explants.

Treatment[a]	Abscission (%)	
Control explants	*48 h*	*72 h*
H_2O	71.5 ± 5.2	82.0 ± 5.2
Ag^+-treated explants		
H_2O	10.7 ± 1.5	60.7 ± 5.2
JA-Me 10 µM	10.0 ± 3.7	55.0 ± 3.7
JA-Me 100 µM	40.0 ± 1.2	80.7 ± 1.5
ABA 0.1 µM	12.5 ± 1.5	87.5 ± 3.7
ABA 1.0 µM	60.0 ± 3.7	91.2 ± 3.8
ABA 10.0 µM	65.0 ± 1.5	90.7 ± 5.7
ABA 100.0 µM	67.5 ± 6.2	80.7 ± 1.5
ABA-Me 0.1µM	13.7 ± 3.7	56.2 ± 1.2
ABA-Me 1.0µM	40.0 ± 7.5	86.2 ± 1.2
ABA-Me 10.0 µM	43.2 ± 4.2	76.5 ± 8.0
ABA-Me 100.0 µM	64.0 ± 3.0	89.0 ± 5.5

[a] Debladed explants obtained from control or $AgNO_3$-treated bladed explants as described in *Methods*, inserted petiole ends down into water-agar containing the test compounds and placed in the dark.

that of the other compounds. The differences in activity between JA-Me, ABA, and malformin were sufficient to suggest different modes of action for each compound. For example, JA-Me did not stimulate leaf abscission in the dark (Fig. 1), potentiate abscission by low concentrations of ethephon (Fig. 3), or interact with malformin (Fig. 4), whereas ABA and ABA-Me were active in each of these tests. In one test, potentiation of abscission by high concentrations of ethephon (Fig. 3), JA-Me and malformin were more active than either

ABA or ABA-Me. Since JA-Me was most active in potentiating leaf abscission induced by high ethephon concentrations, yet least active in negating the antiethylene properties of Ag^+ (Fig. 2), it seems unlikely that negation of Ag^+ activity is induced by increasing the sensitivity of the cuttings to ethylene. Malformin was previously shown to potentiate the abscission-inducing activity of ethylene (Curtis 1970) and to negate the antiethylene properties of Ag^+ (Curtis 1981b). ABA increased the sensitivity of carnation flowers to senescence induced by ethylene but did not prevent Ag^+ from inhibiting senescence in carnation flowers (Ronen and Mayak 1981).

Although JA-Me did not induce leaf abscission from bladed explants (Fig. 1), it stimulated petiole abscission from debladed explants, whether applied proximally or distally (Fig. 6, 7). JA-Me was only slightly active in negating Ag^+ activity in bladed explants (Fig. 2) but completely negated Ag^+ activity in 72 hours on debladed explants (Table 2). The difference in activity cannot be attributed to slower translocation rates in the bladed explants, since JA-Me potentiated abscission induced by high ethephon concentrations in 24 h (Fig. 3).

Differences in activity indicate that the modes of action of ABA and malformin are also different. Malformin acts more rapidly in stimulating dark abscission (Fig. 1), negating Ag^+ activity in bladed explants (Fig. 2), and potentiating abscission in the presence of low ethephon concentrations (Fig. 3). In most of the tests malformin was active at lower concentrations than ABA. Although malformin is more rapid and potent than JA-Me, ABA, and ABA-Me in negating the antiethylene activity of Ag^+ in bladed explants, malformin does not negate Ag^+ activity in debladed explants (Curtis 1982b), whereas the other compounds are active (Table 2). From these differences it seems likely that malformin negates Ag^+ activity in bladed explants by promoting the formation, liberation or activity of another Ag^+ antagonist in the leaves. Based on the present results this antagonist is probably not JA-Me or ABA.

In bladed explants, the antiethylene activity of Ag^+ with regard to leaf abscission is lost in the dark (Curtis 1981a) but can be recovered in the dark by removing the leaf blade (Curtis 1982b). It was proposed that a substance in dark-treated leaves was responsible for loss of Ag^+ activity in the dark, but attempts to demonstrate the presence of this substance in crude leaf macerates failed. From present results, JA-Me does not appear to be responsible because it negates Ag^+ activity only slightly in bladed explants (Fig. 2), whereas Ag^+ activity is completely lost in the dark (Curtis 1981a). ABA or analogs of ABA similar to ABA-Me cannot be excluded from the present results.

The ability of ABA-Me to negate the antiethylene properties of Ag^+ in bladed explants (Fig. 2) and of JA-Me to negate Ag^+ activity in debladed explants (Table 2) indicates that a free carboxyl group is not necessary for this activity. In every test in which ABA-Me was compared with ABA, however, the activity of ABA-Me lagged behind that of ABA. Such a lag might be expected if the ester was converted to the free acid. In bean plants, the methyl ester of ABA is slowly hydrolyzed (Milborrow 1974). Similar comparisons between JA and JA-Me might be helpful, but JA appears to be less stable than JA-Me in aqueous solutions (N. Takahashi, personal communication).

Clarification of the role of ABA in abscission has been slow to develop (Milborrow 1974, Walton 1980; but see Addicott 1983), however, the present study demonstrates that under appropriate conditions ABA can have a powerful influence on abscission processes. In the presence of 0.138 mM ethephon, which induced little or no abscission, the addition of 100 μM ABA greatly stimulated abscission (Fig. 3). In bladed explants, 10 μM ABA reduced the antiethylene properties of Ag^+ (Table 1), and when applied distally to the petioles of debladed explants obtained from Ag^+-treated bladed explants, a concentration of ABA as low as 0.1 μM completely negated the inhibition of abscission induced by Ag^+ (Table 2, 72-h results). In the presence of 10 μM malformin, the addition of as little as 0.1 μM ABA stimulated abscission (Fig. 5). Under certain conditions in *Vigna radiata*, ABA can be ranked as a highly promotive abscission compound.

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