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Jasmonates Promote Abscission in Bean Petiole Explants: Its Relationship to the Metabolism of Cell Wall Polysaccharides and Cellulase Activity

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Abstract. Jasmonic acid (JA) and its methyl ester (JA-Me) promoted the abscission of bean petiole explants in the dark and light, and the activity of these compounds was almost same. JA and JA-Me did not enhance ethylene production in bean petiole explants in the light, indicating that the abscission-promoting effects of these compounds are not the result of ethylene. Cells in the petiole adjacent to the abscission zone expanded during abscission but not in the pulvinus, and JA-Me promoted cell expansion in the petiole and the pulvinus. JA-Me had no effect on the total amounts of pectic and hemicellulosic polysaccharides in 2-mm segments of the abscission region, which included 1 mm of pulvinus and 1 mm of petiole from the abscission zone. On the other hand, the total amounts of cellulosic polysaccharides in this region were reduced significantly by the addition of JA-Me in the light. JA-Me had no effect on the neutral sugar composition of hemicellulosic polysaccharides during abscission. The decrease in the endogenous levels of UDP-sugars in the petiole adjacent to the abscission zone was accelerated during abscission by the addition of JA-Me in the light. Cellulase activities of pulvinus and petiole in 10-day-old seedlings were enhanced by the addition of JA. These results suggest that the promoting effect of JA or JA-Me on the abscission of bean petiole explants is due to the change of sugar metabolism in the abscission zone, in which the increase in cellulase activity involves the degradation of cell wall polysaccharides.

Key Words. Abscission—Bean petiole—Cell wall polysaccharide—Cellulose—Jasmonate—*Phaseolus vulgaris*

Jasmonic acid (JA) and its methyl ester (JA-Me) are considered to be putative plant hormones for a number of reasons, including their wide occurrence in the plant kingdom, biologic, activities in multiple aspects at low concentrations, and their interaction with other plant hormones (for reviews see Parthier 1991, Hamberg and Gardner 1992, Sembdner and Parthier 1993, Ueda et al. 1994a). We have already reported that JA and JA-Me and C_{18}-unsaturated fatty acids, which are considered to be the substrates of the biosynthesis of jasmonates, are powerful senescence-promoting substances (Ueda et al. 1982b, 1991a). Senescence symptoms induced by these compounds are identical to those of natural senescence. Recently we have also found that JA inhibited indole-3-acetic acid (IAA)-induced elongation of oat (*Avena sativa* L. cv. Victory) coleoptile segments by inhibiting the synthesis of cell wall polysaccharides (Ueda et al. 1994b, 1995). These facts led us to study the mode of actions of JA and JA-Me on promoting abscission, which is considered the last dramatic phenomenon of senescence. In this paper we report that JA and JA-Me promote abscission in bean (*Phaseolus vulgaris* L. cv. Masterpiece) petiole explants and that the changes in the metabolism of cell wall polysaccharides in the petiole and the pulvinus adjacent to the abscission zone are involved in the promotive effects of these compounds.

Materials and Methods

Chemicals

JA was obtained by hydrolysis of JA-Me in 1 M methanolic NaOH solution followed by preparative thin layer chromatography developed with benzene:ethyl acetate:acetic acid (16:3:1, v/v/v) (Ueda et al. 1981, Ueda and Kato 1982a). In some experiments, JA (purchased from Sigma Chemical Co.) was used without further purification. Both authentic samples are racemic. Other chemical compounds used in this study were purchased from Sigma and Wako Pure Chemical Inc., and used without further purification.

Abbreviations: ABA, abscisic acid; ACC, 1-aminocyclopropane-1-carboxylic acid; DCB, 2,6-dichlorobenzonitrile; HPLC, high performance liquid chromatography; IAA, indole-3-acetic acid; JA, jasmonic acid; JA-Me, methyl jasmonate; MES, 2-(N-morpholino)ethanesulfonic acid, monohydrate; TCA, trichloroacetic acid; Tris, 2-amino-2-hydroxymethy-1,3-propanediole.

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Abscission Assay

The abscission assay using bean (*P. vulgaris* L. cv. Masterpiece) explants with the junction between the petiole and the pulvinus in the primary leaves was carried out according to a method reported previously (Ueda et al. 1991a). Bean seeds were soaked in tap water for a few hours and germinated in sand sufficiently washed with running water. Seedlings were grown under a continuous white fluorescent light of 8.6 W/m^2 at 25°C for 10 days. Explants (segments) having the first abscission zone between the pulvinus and the petiole were prepared from the primary leaves of the seedlings. Pulvinus and petiole lengths were 3.0 and 7.0 mm, respectively. Ten to 30 such explants were placed horizontally on two layers of Toyo no. 2 filter paper moistened with test solutions containing 1% ethanol in a sterilized Petri dish. Ethanol at a concentration of 1% had no effect on the abscission of the explants. The Petri dishes were kept in a chamber in the dark or under a continuous white fluorescent light of 8.6 W/m^2 at 25°C. To avoid evaporation of the test solutions, the chamber was kept oversaturated. Abscission was measured by applying a constant pressure to the explants about constant hours after the treatment.

Gas Analysis

The experiments for gas analysis used ten explants incubated in a 10-mL vial containing two layers of Toyo no. 2 filter paper moistened with 0.25 mL of test solution. Each vial was sealed with silicon rubber caps and kept in a continuous white fluorescent light of 8.6 W/m^2 at 25°C. At 24 and 72 h after the incubation, 1 mL of the gas within the head space of the vial was sampled. Ethylene production was determined using a Hitachi 163 gas-liquid chromatograph fitted with a hydrogen flame ionizing detector. Porapack N packed in a glass column (3 mm × 2 m) was used. The carrier gas was N_2 (0.4 kg/cm^2). The column temperature and the temperature of the injection and detector part were 50 and 120°C, respectively. In these conditions, the retention times of the authentic samples of ethylene, ethane, and acetylene were 2.5, 3.2, and 4.6 min, respectively.

Analyses of Cell Wall Polysaccharides

Analyses of cell wall polysaccharides were done according to a method reported previously (Nishitani and Masuda 1981). Two-mm segments consisting of 1 mm of pulvinus and 1 mm of petiole adjacent to the abscission zone were prepared after a 64-h incubation with or without 10^{-4} M JA-Me. Each of the 40 segments was fixed with boiling methanol for several min. After fixation the segments were treated with Actinase E (Kaken Seiyaku Co., Japan) solution for 18 h at 37°C to remove proteins; they were then homogenized. The homogenates were washed sufficiently with cold water, acetone, and then chloroform-methanol solutions, successively. The homogenates were treated with α-amylase for 3 h at 37°C to remove starch and then centrifuged. The pellet was extracted with ammonium oxalate and then centrifuged. The supernatant contained pectic polysaccharide. The pellet residue was extracted with 4% KOH and then 24% KOH, each supernatant giving hemicellulose I and II fractions, respectively. The residue was recognized as an α-cellulose fraction. These hemicellulosic polysaccharide fractions were dried and hydrolyzed with 2 N trifluoroacetic acid at 120°C for 1 h. After centrifugation of this hydrolyzed material the supernatant was reduced with sodium borohydride and then acetylated with anhydride acetic acid. Acetylated sugars were identified and quantified by a Hitachi 163 gas-liquid chromatograph fitted with a flame ionizing detector according to a method already reported (Albersheim et al. 1967, Loescher and Nevins 1972). The sugar contents in pectic, hemicellulosic, and cellulosic polysaccharide fractions were determined by the phenolsulfuric acid method (Dubois et al. 1956).

Cellulase Extraction

Extraction procedures of cellulase in *P. vulgaris* L. cv. Masterpiece were carried out according to the method of Lewis and Koehler (1979) with modifications. Five g of plant parts was homogenized in 0.02 M Tris-MES buffer (pH 7.2) containing 0.3 M sucrose using a glass homogenizer. The homogenate was passed through cheesecloth to remove debris. The extract was centrifuged at 2,000 ×g for 20 min. Ammonium sulfate was added to the supernatant to obtain the recipitate containing soluble proteins. The precipitate was resuspended in the buffer for enzyme assay. The test solutions of chemical compounds at the appropriate concentrations were applied to the root system of 10-day-old seedlings of bean plant at 25°C for 48 h in the light. After the incubation, all of the parts of the seedlings were sampled and stored at −80°C before use.

Enzyme Assay

Cellulase activity was determined by measuring the total amount of reducing sugar released from 1.3% CM-cellulose as a substrate. All of the assay were run in the presence of 0.17% Triton X-100 according to the method of Lewis and Koehler (1979). The assay solution was incubated at 37°C for 18 h. The total amounts of reducing sugar released by cellulase were determined by the Somogyi-Nelson method (Somogyi 1952). The results are expressed as a unit of the enzyme.

Analyses of UDP-sugars

The analyses of UDP-sugars in bean petiole explants were carried out according to a method reported previously (Inouhe et al. 1987a, 1987b). One hundred of the bean explants consisting of 1 mm of pulvinus and 1 mm of petiole adjacent to the abscission zone of the first leaves treated with or without 10^{-4} M JA-Me in the presence of absence of 10^{-6} M IAA were sampled 45 h after treatment in the light. These segments were homogenized with a mortar and pestle in 1 mL of 20% methanol containing 8% trichloroacetic acid (TCA) at 0°C. The homogenate without debris was sufficiently washed with water-saturated diethyl ether to remove TCA. Aqueous residue containing UDP-sugars was lyophilized and dissolved in a small amount of distilled water. UDP-sugars were determined using HPLC (Shimadzu model LC-7A) with a Partisil 10-SAX anion exchange column (Whatman). Results are expressed as the average of two independent experiments.

Results

Effect of JA and JA-Me on the Abscission of Bean Petiole Explants

In our experimental conditions the explants incubated in the dark had a greater delay in abscission than those kept in the light, although the dark has been well known to

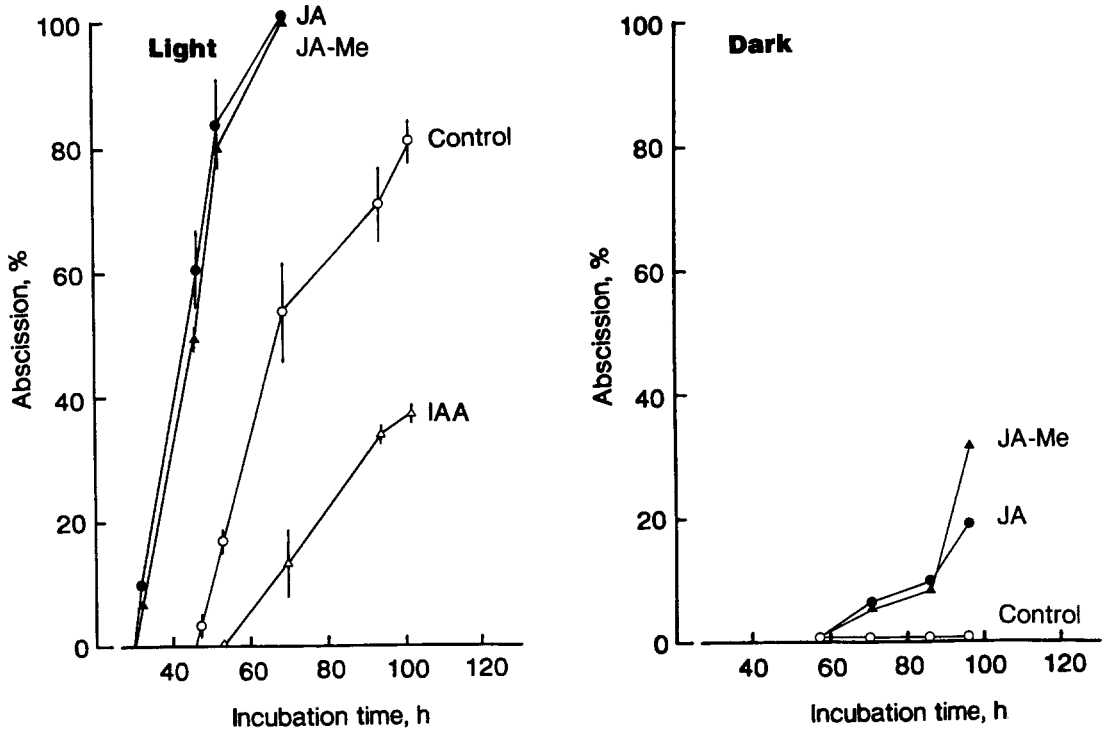

Fig. 1. Effects of JA, JA-Me, and IAA on the abscission of bean petiole explants. The concentrations of JA and JA-Me, and IAA were 3×10^{-5} M and 5×10^{-6} M, respectively. *Bars* indicate S.E.

Table 1. Cell size of the pulvinus and the petiole adjacent to the abscission zone in bean petiole explants. Samples were harvested 64 h after treatment with or without 10^{-4} M JA-Me. Each cell was considered to be a circle, and the lengths of the longitudinal (upper) and transverse (lower) axes were measured. Data are expressed in μm.

	Initial	Control	JA-Me
Pulvinus	52.7 ± 3.0	51.0 ± 2.8	57.2 ± 1.2
	52.7 ± 3.3	50.2 ± 2.1	57.3 ± 1.1
Petiole	101.1 ± 2.9	108.2 ± 6.1	113.7 ± 7.8
	99.1 ± 3.3	101.4 ± 3.9	112.0 ± 3.1

promote senescence (Ueda and Kato 1981) and/or abscission (Osborne 1968) (Fig. 1). IAA was effective in inhibiting abscission in the light. The inhibitory effect of auxin is almost same as that in another assay system using bean petiole explants, in which the explants are arranged in agar plates with the petiolar end down (Osborne 1968). Therefore, our assay system is suitable for the abscission test as well. Fig. 1 also shows the promotive effect of JA and JA-Me on bean petiole abscission in the light and dark. JA and JA-Me had almost the same effect on promoting the abscission in the light. These compounds were effective at concentrations of 10^{-5} M and more in the light (data not shown).

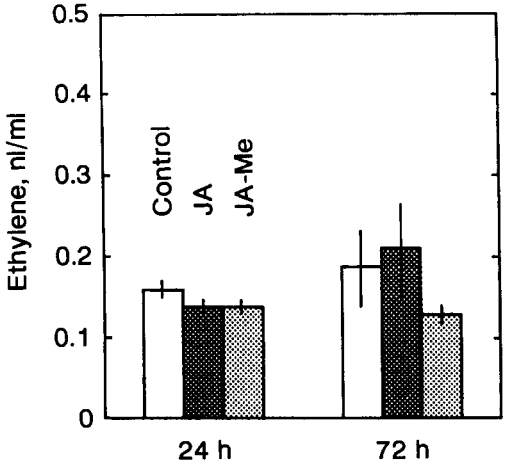

Fig. 2. Effects of JA and JA-Me on the production of ethylene from bean petiole explants in the light. One mL of the gas from the head space of the vial in which the explants were kept was sampled at 24 and 72 h after treatment. The concentration of JA and JA-Me was 10^{-4} M. *Bars* indicate S.E.

JA-Me-induced Cell Expansion of Pulvinus and Petiole Adjacent to Abscission Zone

The cell size of the pulvinus and petiole adjacent to the abscission zone was measured using longitudinal sections of the segments. As shown in Table 1, cells of the

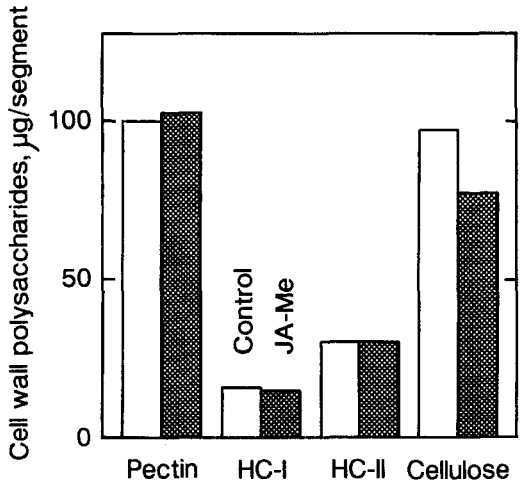

Fig. 3. Effects of JA-Me on the total amounts of cell wall polysaccharide. The segments consisting of the petiole (1 mm) and the pulvinus (1 mm) adjacent to the abscission zone of bean petiole explants were sampled at 64 h after the treatment in the light. The concentration of JA-Me was 10^{-4} M. Results are expressed as the average of two independent experiments. HC-I and HC-II, hemicellulose I and II, respectively.

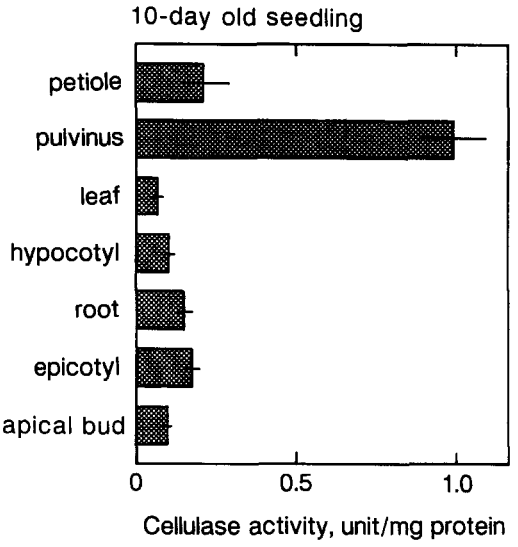

Fig. 4. Cellulase activity in 10-day-old bean seedlings. Cellulase activities are expressed as units/mg of protein. *Bars* indicate S.E.

pulvinus as well as the petiole adjacent to the abscission zone were significantly expanded by the addition of JA-Me.

Production of Ethylene from Bean Petiole Explants

Fig. 2 shows the production of ethylene from bean petiole explants incubated in the presence or absence of 10^{-5} M JA and JA-Me in the light. These compounds were not effective on ethylene production for 24 and 72 h.

Effects of JA-Me on Polysaccharide Contents and Neutral Sugar Compositions of Cell Walls in the Abscission Region of Bean Petiole Explants

Fig. 3 shows the total amounts of cell wall polysaccharides in 2-mm segments consisting of 1 mm of pulvinus and 1 mm of petiole adjacent to the abscission zone incubated with or without 10^{-4} M JA-Me for 64 h in the light. JA-Me had no effect on the total amounts of cell wall polysaccharides in noncellulosic (pectic, hemicellulosic I and II) fractions. On the other hand, JA-Me at a concentration of 10^{-4} M decreased significantly the total amount of cell wall polysaccharides in the cellulosic fraction of the segments.

The neutral sugar composition in 2-mm segments consisting of 1 mm of pulvinus and 1 mm of petiole adjacent to the abscission zone incubated with or without 10^{-4} M JA-Me for 64 h in the light was determined. Rhamnogalacturonan and arabinogalactan, and glucuronoarabinoxylan and xyloglucan were, respectively, the major components in pectic and hemicellulosic polysaccharides of the segments. The neutral sugar composition of these pectic and hemicellulosic polysaccharides in the segments was not affected by the addition of JA-Me (data not shown).

Cellulase Activity in Bean Plants

Cellulase activities were detected in all of the tissues of 10-day-old seedlings of bean plants. The highest activity of cellulase in the seedling was observed in the pulvinus of the first leaves (Fig. 4). Relatively high activities in the petiole region of the seedlings were also detected. Cellulase activities in pulvinus and petiole of the first leaves in the seedlings were reduced by cycloheximide treatment (Fig. 5), suggesting that the cellulase detected was newly biosynthesized. Simultaneous addition of IAA significantly inhibited cellulase activities in the regions of the pulvinus and petiole of the first leaves in the seedlings. On the contrary, JA and ABA promoted these activities extremely well (Fig. 6). These results suggest that JA and ABA enhance the biosynthesis of cellulase in the seedlings, and IAA reduces it.

Effect of JA-Me on the Levels of UDP-sugars in the Abscission Region of Bean Petiole Explants

Fig. 7 shows the effect of JA-Me on the levels of UDP-sugars in the 2-mm region consisting of 1 mm of pulvinus and 1 mm of petiole adjacent to the abscission zone

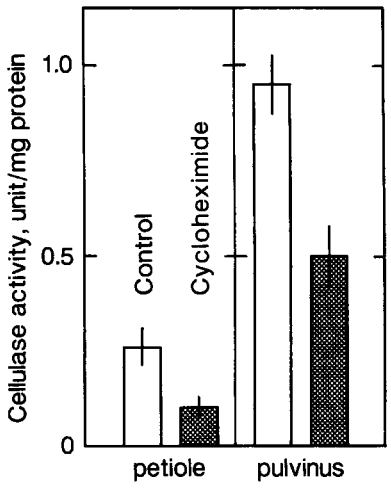

Fig. 5. Effect of cycloheximide on cellulase activity in the petiole and the pulvinus of the primary leaves of 10-day-old bean seedlings. The concentration of cycloheximide was 10^{-6} M. *Bars* indicate S.E.

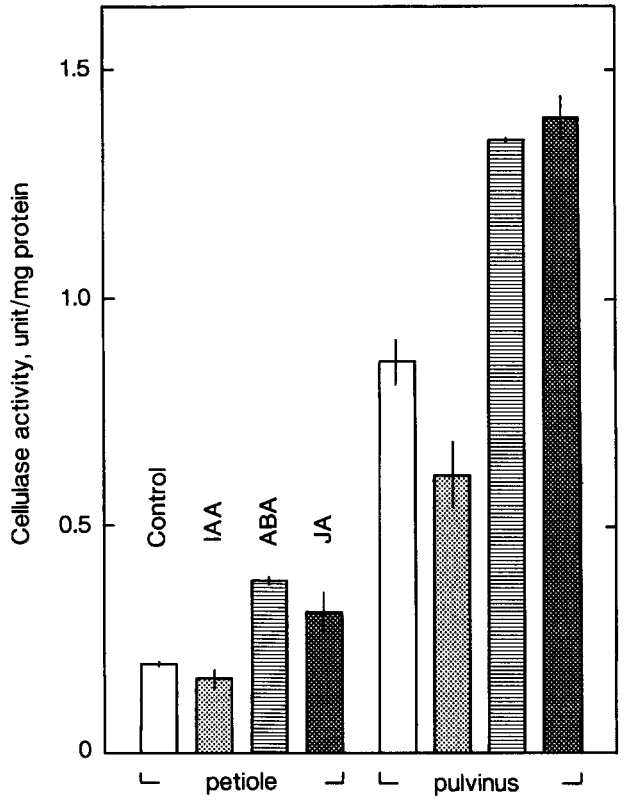

Fig. 6. Effects of JA, ABA, and IAA on cellulase activity in the petiole and pulvinus of the primary leaves of 10-day-old bean seedlings. The concentrations of JA and ABA, and IAA were 3×10^{-5} M and 5×10^{-6} M, respectively. *Bars* indicate S.E.

at 45 h after treatment in the light. The levels of UDP-sugars in the explants decreased during incubation in the light. In the presence of JA-Me at 10^{-4} M, the levels of

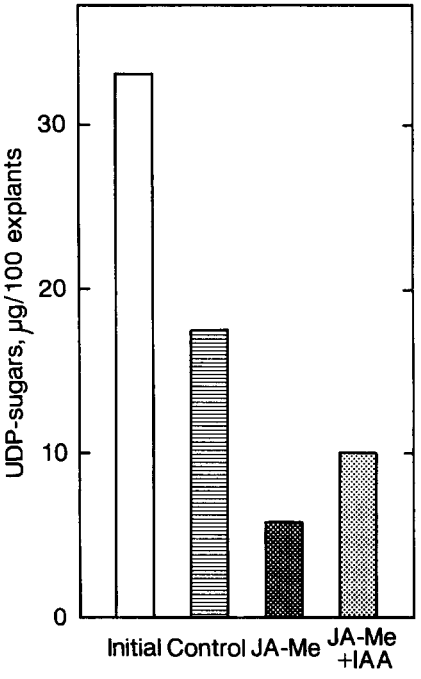

Fig. 7. Effects of JA-Me on the levels of UDP-sugars in bean petiole explants in the light. The explants were sampled at 45 h after treatment. Determinations of UDP-sugars in the explants were made by HPLC as described in the Materials and Methods section. The concentration of JA-Me and IAA were 10^{-4} m and 10^{-6} M, respectively. Results are expressed as the average of two independent experiments.

Table 2. Effect of DCB on the abscission of bean petiole explants. The concentration of DCB was 10^{-6} M.

	Abscission (%)	
	52 h	64 h
Control	17.5 ± 2.9	55.0 ± 7.5
DCB	60.0 ± 13.3	95.0 ± 3.3

UDP-sugars in the explants decreased rapidly. The addition of 10^{-6} M IAA to the incubation medium in the presence of 10^{-4} M JA-Me inhibited the decrease of the levels of UDP-sugars during the incubation.

Promotive Effect of DCB on Abscission

Table 2 shows the effect of DCB, which is a potent inhibitor of the synthesis of cellulosic polysaccharides on the abscission of the petiole explants in the light. DCB at 10^{-6} M promoted abscission, suggesting that inhibition of the synthesis of cellulosic polysaccharides promotes abscission in the light.

Discussion

In this experiment, jasmonates (JA, JA-Me, and related compounds) promoted the abscission of bean petiole explants. Since JA has already been identified in bean seedlings (Meyer et al. 1984 and our unpublished results), it is suggested that these compounds have an important role in promoting abscission in this plant. However, the mode of action of these compounds in promoting abscission is not yet clear.

Ethylene has been well known as an important active compound in promoting abscission. As already reported (Ueda et al. 1991a), the ACC (1-aminocyclopropane-1-carboxylic acid)-dependent pathway to ethylene is apparently operative in bean petiole explants, indicating that ethylene is also an active principle in promoting abscission of bean petiole explants. However, the production of ethylene from bean explants was not influenced by the addition of jasmonates in this experiment. These results suggest that jasmonates are considered to be the active principles in promoting senescence of pulvinus and petiole in bean petiole explants of the first leaves, but their effects are not the result of ethylene.

As soon as the petiole explants are excised, symptoms of senescence appear in the pulvinus. Soon, a few layers of cells constituting the cortex and pith of the petiole adjacent to the abscission zone were expanded by treatment with JA-Me suggesting that this compound changes sugar metabolism in relation to cell wall polysaccharides. In fact, the total amount of cellulosic polysaccharides in pulvinus and petiole adjacent to the abscission zone was reduced substantially by JA-Me (Fig. 3).

Cellulase (β-1,4-glucanase) is considered one of the most important enzymes for the degradation of cell wall polysaccharides (Osborne 1973). In 10-day-old seedlings of bean plant, cellulase activities were detected in all parts of these seedlings. The highest activity among them was found in the pulvinus region. Cellulase activity in the petiole region was also relatively high. Considering these results together with the fact that the first leaves of bean plants abscise about 20 days after germination in this experimental condition, it is suggested that cellulase detected in the region of the pulvinus and petiole of the first leaves in the seedlings is involved substantially in the abscission of the first leaves of bean plants. Since cell expansion of the segments during senescence was found in the pulvinus and petiole sides, cellulase detected in these tissues seems to involve the degradation of cell wall polysaccharides and cell wall loosening.

The inhibitory effect of cycloheximide on cellulase activities in the seedlings suggests that cellulase might be newly biosynthesized by triggering unidentified signals in this plant, supporting the idea of Campillo et al. (1990). The effect of IAA on the inhibition or JA and ABA in the promotion of abscission also suggests that these plant growth regulators might not inactivate or activate cellulase that already exists in cells but might control the biosynthesis of the protein of this enzyme so as to affect the signal transduction pathway of this plant. It has already been reported that the synthesis of cell wall-degrading enzyme was affected directly by IAA and ABA in the abscission zone when these compounds inhibited or accelerated abscission (Reddy et al. 1988, Rasmussen 1974).

The levels of UDP-sugars in the regions of the pulvinus and petiole adjacent to the abscission zone, which are considered to be important substrates of the synthesis of cell wall polysaccharides (Feingold and Avigad 1980), were decreased significantly by treatment with JA-Me. Furthermore, DCB, which is a specific inhibitor of cellulosic polysaccharide synthesis (Hogetsu et al. 1974, Montezinos and Delmer 1980), was as effective in promoting abscission as were jasmonates. These results suggest that the biosynthesis of cell wall polysaccharides, especially in relation to cellulose in the pulvinus and petiole adjacent to the abscission zone, is required for the inhibition of abscission, and jasmonates inhibit this process. From the evidence in this study together with the results of the effects of jasmonates on the change of sugar metabolism (Ueda et al. 1994a, 1994b, 1995), jasmonates promote the degradation of cellulosic polysaccharides and inhibit the synthesis of them in the petiole adjacent to the abscission zone, resulting in cell wall expansion and abscission.

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