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Senescence Processes in Leaf Abscission

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Abstract. **There is a large body of evidence which correlates the development of some phases of senescence with the ability of petioles to experience abscission. We have suggested that the change-over from stage 1 to stage 2 in the aging of bean petiole explants may be a reflection of initial stages of senescence in the pulvinar tissue. The abscission-inhibiting effect of auxin in interpretable as a retardation of pulvinar senescence. Senescence of cells in the separation layer has not been unequivocally established, and it seems unlikely that separation is itself a consequence of cellular senescence in the separation zone. More probably, senescence plays a role in the preparatory phases of abscission, that is, in the development of a condition of responsiveness to ethylene. In bean explants, ethylene responsiveness for abscission is associated with an ethylene-stimulated production of ethylene in the pulvinar tissues.**

Leaf abscission ordinarily takes place at a time when there are evident signs of senescence in the leaves. On the other hand, it has been generally recognized that active metabolic processes are necessary for the development of the separation, and in many cases even cell division occurs as a part of the separation process; as Carns (10) has pointed out, these features appear to be inconsistent with the concept of abscission as a consequence of cellular senescence at the separation zone. From an examination of the evidence available, we will suggest that the separation of the cells in abscission is not a senescence process, but that some progress toward the senescent state is apparently prerequisite for abscission. We will attempt to define this prerequisite for partial senescence in terms of ethylene responsiveness.

Abscission and Senescence. For many years it has been clear that leaves became increasingly ready for abscission with age. Myers (27) measured the time required for abscission of debladed *Coleus* leaves as a function of age, and established that with increasing age there was a progressive shortening of the time required for abscission. Similar observations have been made for cotton (21) bean (12) and lupine (11).

The greater facility of abscission in older leaves was attributed to a decline in auxin content by Myers (27), and similar measurements of the diffusible auxin from *Coleus* leaves of various ages led Wetmore and Jacobs (41) to the same conclusion. A striking correlation between the diffusible auxin content and the time required for abscission after debladding is obtained (fig 1).

The depressed auxin levels in leaves with increasing age may be related to the activity of indoleacetic acid oxidase and associated phenolic cofactors (35, 37). But the changing auxin relations of leaves with age are not simply a decreasing auxin content and hence a decreasing resistance to abscission. Chatterjee and Leopold (12) found that with increasing age, bean leaves showed a decreasing responsiveness to added auxin even when the auxin utilized was naphthaleneacetic acid which is not susceptible to the indoleacetic acid oxidase. The changing responsiveness to auxin will be discussed again in connection with the ethylene relationship to abscission.

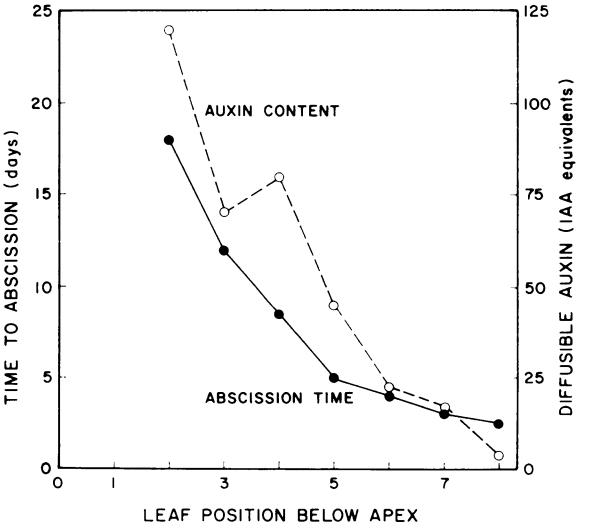

FIG. 1. With increasing age, *Coleus* leaves show a decline in the time required for the development of abscission upon being debladed, and an associated decline in diffusible auxin content. Leaf age is taken to be equivalent to the position of the leaf on the plant, leaf No. 1 being nearest the plant apex. Data of Myers (27).

At the time of discovery of the ability of auxin to defer abscission, Laibach (20) noted that associated with the deferral of abscission, auxin brought about a stimulation of growth in the petiole above the abscission zone. He suggested that the deferral of abscission might be related to the restoration of growth by the applied growth substance. This relationship between the auxin effect on growth and on abscission has been taken up in some detail by Jacobs (16, 17, 18). He points out that as a leaf approaches senescence, petiole growth ceases; removal of the leaf blade terminates petiole growth, and deferral of abscission by auxin is associated with at least a temporary reinstatement of the growth activity in the tissues distal to the abscission zone.

Differences in growth activities of tissues above and below the abscission zone can apparently lead to the development of shearing forces across the abscission zone. Using explants from bean petioles, Leopold (22) observed that auxin treatments which deferred abscission maintained an active growth in diameter of the pulvinus, whereas ethylene treatments which hastened abscission led to a preferential diameter increase in the petiole which was not matched by growth of the pulvinus. The failure of lateral growth in the pulvinus when growth is proceeding in the petiole can cause shearing forces to build up at the abscission zone.

Another feature of leaf senescence which is associated with abscission development is the formation of abscission-accelerating substances. Osborne (29) was able to accelerate abscission of petiole explants by applying diffusates from the cut petioles of senescent leaves of several different species. The accelerating action was not obtained with materials diffused from non-senescent leaves. Similar results have been obtained in several laboratories (14, 19, 23). The isolation and identification of abscisic acid from cotton fruits (24, 28) has made this type of experiment much more meaningful. This compound has subsequently been isolated from leaves of several species (13). An apparent feature of each of the diffusible abscission accelerators is their ability to act as growth inhibitors. In view of the several lines of evidence that the termination of growth of the tissues distal to the abscission zone may contribute to abscission, it is a striking observation that abscisic acid is markedly more promotive of abscission when applied to the distal than to the proximal end of a petiole explant (5). Also, in view of the various evidences that leaf senescence phenomena are involved in the development of abscission, it is perhaps relevant to mention here that abscisic acid is effective in hastening the senescence of leaf discs (7).

It appears, then, that the increased tendencies toward abscission with increasing leaf age may be a consequence of A) lowered auxin levels, B) lowered auxin responsiveness, C) depression of growth in the distal tissues, and D) the production of abscission accelerators with increasing leaf age.

Mobilization and Abscission. The ability of kinetin to stimulate the mobilization of nutrients to a localized area in a leaf was discovered by Mothes (26); in subsequent experiments on the effects of kinetin applications on abscission, Osborne and Moss (31) found that when kinetin was applied to the abscission zone it prevented abscission, but applications at either end of a petiole explant resulted in accelerated abscission. They interpreted these results as indicating that mobilization of nutrients out of the abscission zone would hasten cellular senescence there, leading to accelerated abscission. Scott and Leopold (36) were able to measure the mobilization of nutrients from the distal to the proximal parts of petiole explants during the development of abscission. The distal tissues were found to lose substantial amounts of dry weight, chlorophyll, RNA, and protein; and these losses were ordinarily accompanied by increases in the proximal tissues (fig 2). When abscission was deferred by the application of auxin, this mobilization of materials out of the distal tissue was largely suppressed. The conclusion was offered that mobilization of nutrients out of the tissues distal to the abscission zone would hasten cellular senescence there, and provide a component in the development of abscission.

Examination of the ethylene effects on abscission led Abeles and Rubinstein (4) to the deduction that abscission stimulating effects of auxins and other growth regulators were attributable to stimulations of ethylene production, and that ethylene plays a

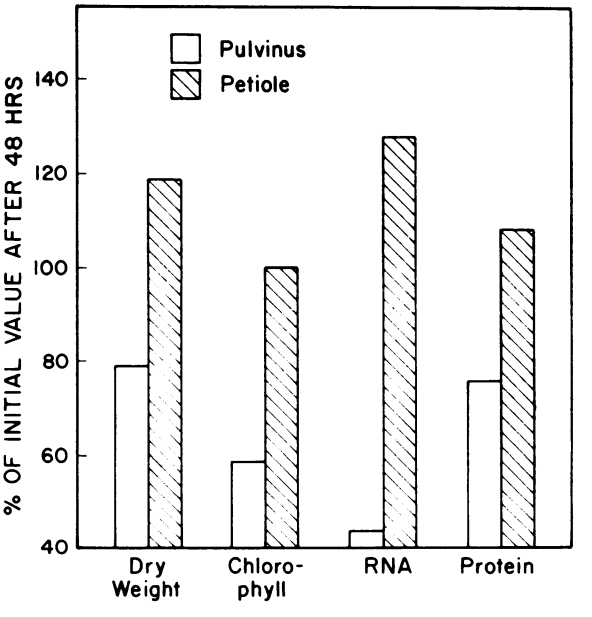

FIG. 2. Mobilization of materials in bean explants occurs during the development of abscission. Extensive losses of dry weight, chlorophyll, RNA, and soluble protein from the pulvinus may be reflected by increases in contents of the proximal petiolar tissue. These data are for 48 hours after cutting the explant. From Scott and Leopold (36).

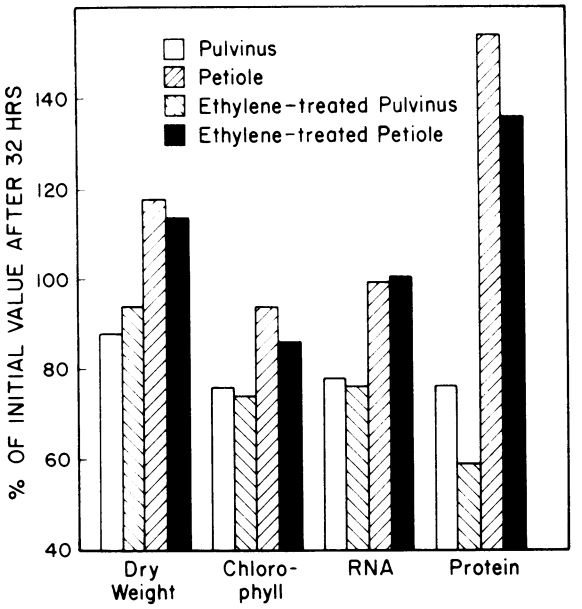

FIG. 3. Mobilization of materials from the pulvinus to the petiolar tissue in bean explants is not accentuated by ethylene treatment. As in figure 2, losses from the pulvinus may be reflected by increases in the proximal petiolar tissue, but treatments with ethylene (4 ppm) to stimulate abscission did not bring about an enhancement of the mobilization effect. These data are for 32 hours after cutting the explant. From Abeles, Holm and Gahagan (3).

central role in triggering abscission. Some convincing experiments by Abeles *et al.* (3) established that the ethylene stimulation of abscission did not involve an enhancement of mobilization from the distal to the proximal tissues (fig 3). They offered the conclusion that the mobilization processes were not related to the development of abscission, occurring in an independent but simultaneous manner. Experiments in our laboratory have confirmed that ethylene treatment does not have a detectable effect on the mobilization of nutrients from the distal to proximal tissue.

While cellular senescence, and its driving force of mobilization, are not stimulated by ethylene in the bean explant there is considerable experimental evidence suggesting that early stages of cellular senescence are prerequisite to the processes which are ethylene stimulated. The prior evidence of Osborne and Moss (31) and of Scott and Leopold (36) indicated that retardation of senescence in bean explants would prevent the development of abscission. The experiments of Abeles *et al.* (3) indicate that the ethylene-stimulated changes are prevented by treatments which prevent the development of senescence. Collectively, these facts suggest that ethylene responsiveness is achieved only after some early progress of senescence has been developed in the distal tissues, and that mobilization can promote abscission through the enhancement of such cellular senescence.

Senescence and Protein Changes. As leaf tissue enters into senescence, it experiences an extensive hydrolysis of protein components. Vickery *et al.* (39) described this hydrolytic activity and the associated increase in amides. A wide array of amino acids accumulates as a consequence of the protein hydrolysis, including especially glutamine, leucine, phenylalanine, and valine (32). Early work of Michael (25) established that the progress of leaf senescence was facilitated when the soluble amide products could be translocated out of the leaf tissues, and was retarded if this translocation was interfered with. In the abscission experiments with bean explants, extensive protein hydrolysis is taking place, especially in the pulvinar tissue (3, 36). Auxin treatments which suppress abscission also suppress this protein degradation. Severing the pulvinus from the petiole markedly suppresses protein degradation in the pulvinus (1).

The work of Abeles and coworkers (2, 15) has implicated a stimulation of protein synthesis in the ethylene induction of abscission. Examination of protein synthesis at the histological level has shown that the synthetic activity is the greatest in the cells at the separation zone and several cells proximal to this position (30, 40). A requirement for protein synthesis in the ethylene stimulation of abscission does not preclude an active hydrolysis of protein even in the same tissues (43).

A part of the effect of pulvinar tissue senescence in the abscission process might be the provision of amino acids from which ethylene may be synthesized. Numerous amino acids which accelerate abscission are also capable of stimulating ethylene synthesis (1). Valdovinos and Muir (38) have found that several D-amino acids were more effective in stimulating abscission than L-amino acids, and suggested that the D forms might act in part by inhibiting protein synthesis in the abscission zone. A more likely explanation would seem to be that the D-forms of at least some amino acids (alanine, methionine, glutamate) are more effective in stimulating ethylene synthesis (1).

Senescence and Ethylene Responsiveness. Using somewhat indirect evidence, we can say that as leaves grow older their responsiveness to ethylene increases. Chatterjee and Leopold (12) applied β-alanine to bean explants from leaves of various ages and showed an increasing abscission response with leaf age. The effects of β-alanine can be tentatively interpreted as ethylene effects, since this substance brings about abundant ethylene production in the bean petiole explant (1).

After the petiole explant has been cut, its responsiveness to ethylene can increase in a matter of hours. This important shift in ethylene responsiveness was first suggested by Yamaguchi (42) on the basis of very tentative data. Comparisons of freshly cut explants with those cut 24 or 48 hours before ethylene exposure have been made by Abeles (1, 4), who found that the freshly cut explants were essen-

tially unable to respond to ethylene, whereas explants aged for 24 or 48 hours were readily stimulated to abscission by ethylene.

More exacting measurements of the onset of ethylene responsiveness can be made by exposure of the explants to ethylene for brief periods and then removal of the ethylene by evacuation. The grams of force needed to bring about abscission 24 or 48 hours after cutting provides a quantitative measure of the progress of abscission over relatively short time periods. The data in figure 4 show that brief ethylene exposures during the first 10 hours after cutting result in no measurable enhancement of abscission; at about 12 to 14 hours after cutting ethylene responsiveness begins, and continues to increase after that. These data confirm the conclusion of Abeles (1) that some progress into senescence is prerequisite to ethylene responsiveness.

The effectiveness of auxin in preventing abscission is inverse to the ethylene effectiveness; it must be applied within the first 6 hours after cutting if inhibitory actions are to be obtained (34). Application of auxin to the pulvinar tissue is markedly more effective in preventing abscission than to the proximal petiole tissue (6). Abeles (1) has suggested that the auxin inhibition may result from the prevention of the onset of senescence in the explant. We would assign the auxin action more specifically to the inhibition of senescence in the distal tissue, that is, in the pulvinus. A comparison of ethylene responsiveness of bean explants placed in agar containing a range of auxin concentrations, with either the proximal or the distal tissue in contact with the agar, is shown in figure 5. After 20 hours on the auxin agar, ethylene was applied for 6 hours after which the force needed to cause abscission was measured. In the upper section of the graph it is seen that the promotive effects of ethylene were eliminated by 10^{-5} M indoleacetic acid when the auxin was applied at the distal end. In contrast, after auxin applications to the proximal or petiolar end of the explant (lower section of fig 5) no such prevention of ethylene responsiveness was evident.

A reasonable interpretation of the various experiments on ethylene responsiveness is that young

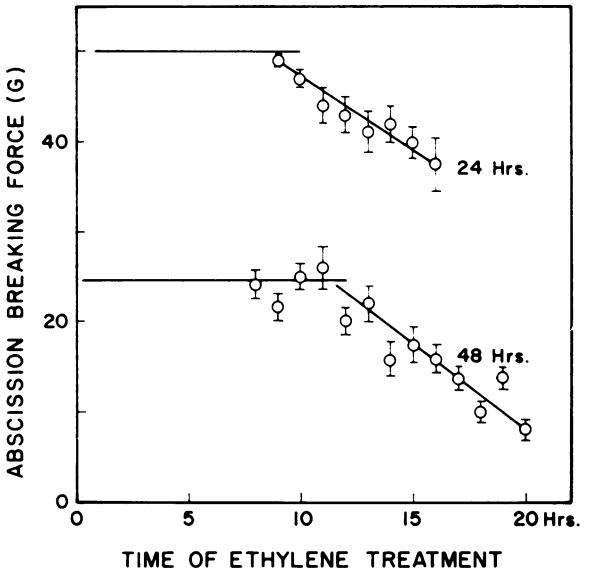

FIG. 4. Ethylene treatment was ineffective in altering the force needed to separate the pulvinus from the petiole in bean explants unless it was made more than 10 or 12 hours following excision. Ethylene exposure (500 ppm) was given at various times after cutting the explant; 2 hours later the gas was removed and the explants evacuated for 2 periods of 3 minutes each at 480 mm Hg. After the treatment the explants were placed together in a large plastic chamber aerated with moist air. The abscission breaking force was determined at 24 and 48 hours after excision. The force needed to separate the pulvinus from the petiole was measured with a laboratory balance, holding the pulvinus lightly wtih a pair of blunt forceps with the adaxial side down, and the petiole end pressed at about a 45° angle against the balance pan. Twenty explants were used for each determination and the standard error is indicated as a vertical line through each datum.

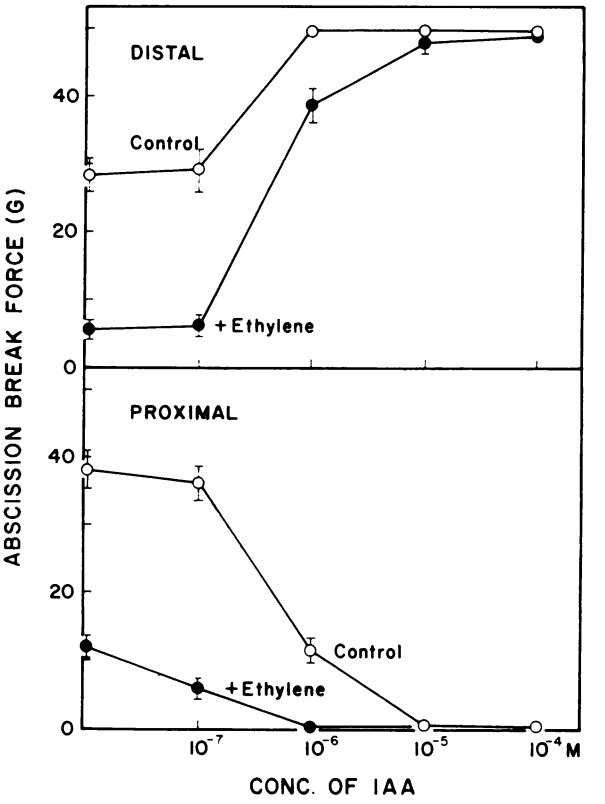

FIG. 5. Application of indoleacetic acid at the distal end can completely inhibit the abscission-promoting effect of ethylene on bean explants. Freshly cut explants were placed in 1.5 % agar containing the auxin. Ethylene (10 ppm) was given 20 hours after excision, and after 6 hours exposure the abscission breaking force was determined as in figure 4. Twenty explants were used for each determination.

leaves are relatively unresponsive and that, with aging, the passage from the auxin-inhibited to the non-inhibited condition (stage 1 to stage 2 of Rubinstein and Leopold, 34) is equivalent to the passage from an ethylene-insensitive to an ethylene-sensitive condition. Auxin applied to explants of any age will cause ethylene production (4), but responsiveness to ethylene is not achieved until a measure of senescence has been achieved. The gradual forshortening of the stage 1 requirement with leaf age (12) may represent the natural development of the early stages of senescence with leaf age.

The relatively greater sensitivity of the distal tissue to agents which will enhance senescence (*e.g.* abscisic acid) or defer senescence (*e.g.* indoleacetic acid) supports the concept that the senescence of the distal tissue is critical to the onset of ethylene responsiveness.

In some cases of ethylene responses, there appears to be an entrainment of ethylene production resulting from the ethylene treatment. For example, ethylene treatment of mature fruits results in further ethylene production by the fruits (8); a similar entrainment

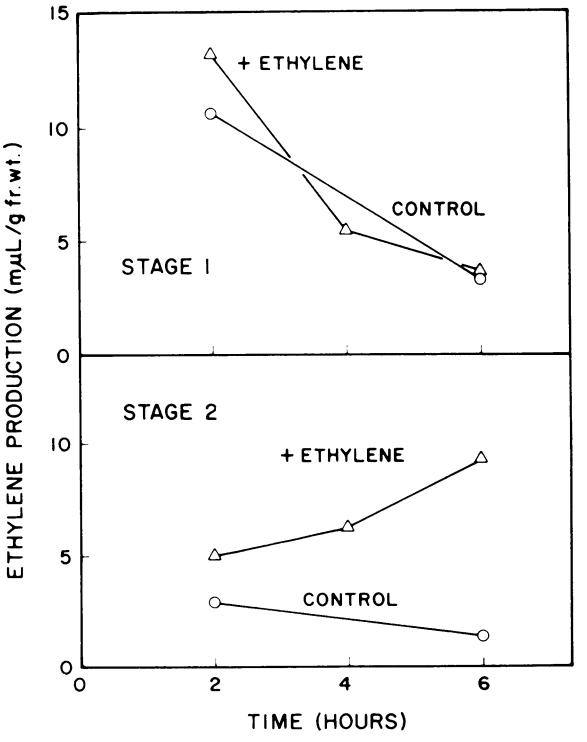

FIG. 6. Ethylene production is induced by ethylene treatment only in stage 2 explants. Explants were treated with ethylene directly after excision (stage 1, above) or 22 hours after excision (stage 2, below). Ethylene (10 ppm) was provided for 6 hours and then withdrawn by two 3 minute evacuations at 480 mm Hg. Controls were similarly evacuated. Fifteen explants from each treatment were placed on 1.5% agar in 17 ml vials covered with a vaccine cap and ethylene production measured at 2 hour intervals.

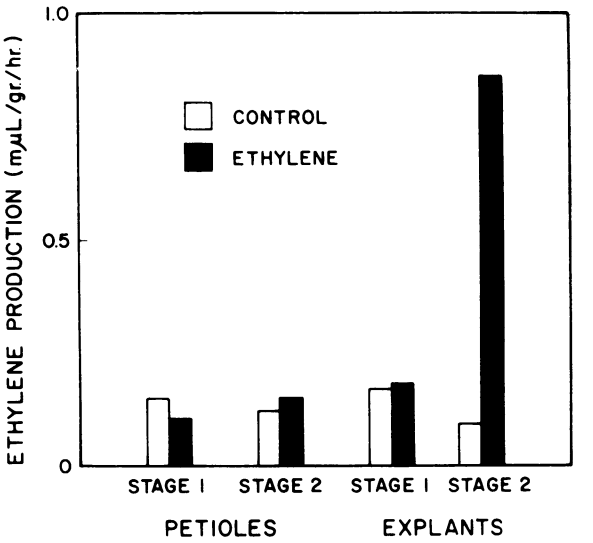

FIG. 7. Ethylene production is maximally stimulated by ethylene in stage 2 explants in tthe presence of the pulvinus. Comparison of ethylene production by 10 mm sections of petiole only and by the conventional 10 mm explant containing 6 mm of petiole and about 4 mm of pulvinus. Treatments are similar to those of figure 6. Ethylene production was measured for 12 hours after ethylene treatment and evacuation.

appears to occur following ethylene treatment of orchid flowers (9). Such an effect by ethylene can be readily observed in bean petiole explants as shown in figure 6. In this experiment, ethylene productions by explants with or without brief ethylene treatment, during stage 1 or stage 2, are compared. In the upper section of the figure it is seen that freshly cut explants (Stage 1) do not show a consistent response to ethylene in terms of ethylene production; however, in the lower section of the figure, stage 2 explants are seen to respond to ethylene exposure with a large amount of ethylene production over a 6 hour period.

We have implicated the senescence of the pulvinus as being specifically involved in the onset of ethylene responsiveness of explants. The role of the pulvinus tissue in ethylene responsiveness can be demonstrated by comparison of ethylene production after ethylene exposure when the sections are exclusively composed of petiole tissue and when sections contain the pulvinar tissue. Such an experiment is shown in figure 7, from which it is evident that the responsiveness to brief ethylene exposure, indicated by ethylene production, is not only restricted to Stage 2 explants, but also to explants in which pulvinar tissue is present.

The overriding effect of the pulvinus in the explant response to ethylene (in terms of ethylene production) suggests that the senescing pulvinus may be the principal site of the ethylene stimulation in the bean explant. Since the senescence of the pulvinus is markedly influenced by the proximal

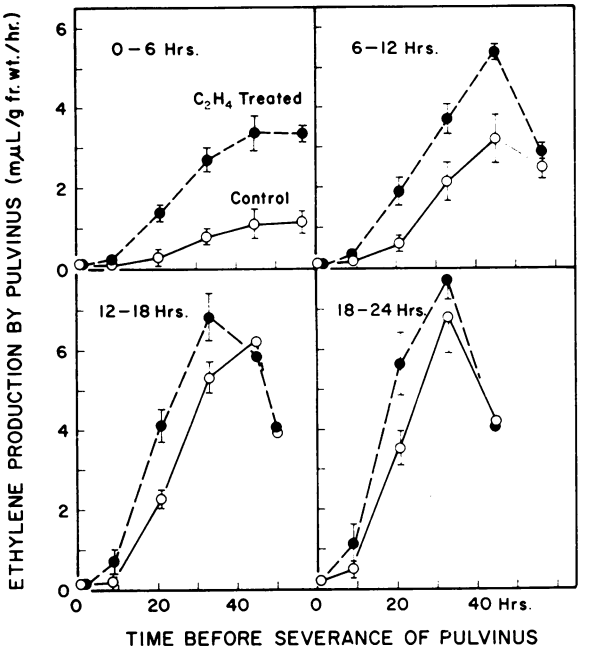

FIG. 8. Ethylene production by the pulvinus is increased by an action of the petiole. Severing the pulvinus from the petiole at later times after excision results in greater ethylene production and enhanced responsiveness to applied ethylene (10 ppm, 6 hr). Evacuation and the measurement of subsequently produced ethylene were carried out as in figure 6. Ethylene production was determined every 6 hours, followed by aeration with compressed air after each determination. Standard errors from 4 replications are indicated.

petiolar tissue (3), experiments were carried out varying the period of time over which the petiolar tissue remained connected to the pulvinus. A large group of explants was placed on plain agar; groups of 15 were removed after various intervals of time, and each explant was separated into pulvinar and petiolar tissue by breaking at the abscission zone. Both types of tissue were then exposed to ethylene (10 ppm) for 6 hours, evacuated in air 3 times, and subsequent ethylene production was followed over 6 hour intervals. The ethylene production by treated and control pieces is shown in figure 8, plotting the ethylene production (ordinate) against the length of time over which the petiole tissue remained intact with the pulvinar tissue (abscissa). Only pulvinar data are plotted, since petiole tissue in every instance produced less than 0.6 mμl/g/hr. Three conclusions can be drawn from the data in figure 8: A) ethylene exposure can bring about an early stimulation ot ethylene production by the pulvinar tissue; B) the longer the period of time over which the petiole tissue remained connected to the pulvinar tissue (abscissa, fig 8), the greater was the ethylene stimulation, and C) if the petiolar tissue was removed in the first 9 hours after cutting the explant, ethylene responsiveness was not detectable.

We suggest the following interpretation of the data in figure 8. Newly cut explants are essentially unresponsive to ethylene in terms of ethylene production; activity by the petiole half of the explant initiates the early stages of senescence in the pulvinar tissue, probably through the mobilization of nutrients out of the pulvinus; when a partially senescent state has been achieved (between 10 and 20 hr after cutting), the pulvinus becomes ethylene responsive in a manner parallel to stage 2 of the bean explant abscission. This interpretation implies that the pulvinus is a principal site of ethylene responsiveness, and that a partially senescent state in that tissue is prerequisite to ethylene responsiveness in the bean explant.

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