
Ethylene and Abscission

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Abscission (Latin: *ab*—from, *scindere*—to cut or sunder), is the process by which plants shed lateral organs. The fundamental event in all abscission is the secretion of enzymes which hydrolyze the cellulose “exoskeleton” and the pectin “cement” of the cells in the abscission zone. This hydrolysis often is accompanied by ingenious mechanisms to assist removal of the abscising organ. The early appearance of these processes in the fossil record (6) is evidence of the strong evolutionary advantage to plants of shedding organs, whether it be the removal of leaves to avoid snow load or drought stress, or the shedding of fruit or seeds to ensure their dispersal and continuation of the species.

Researchers have studied the biology of the processes leading to abscission for more than 130 years (51). It is not the purpose of this article to replicate the several recent and excellent reviews (2, 6, 9, 54, 60, 80, 99) of this extensive literature, but rather to present a consensus of the role of ethylene in abscission, and to describe the horticultural implications of that role. It seems appropriate,

however, to commence with a brief summary of our present understanding of the anatomy, biochemistry, and regulation of abscission.

Anatomy

In most plants, the processes of abscission occur in a rather specific part of the abscising organ called the abscission zone (Fig. 1). The zone may be apparent throughout the life of the plant, or may become much more obvious as the time of abscission approaches (6, 84), frequently as a lighter-colored, slightly swollen area. Typically, the zone comprises a plate of thin-walled, narrow cells which are differentiated clearly from the isodiametric cells of the cortex of the axis, and from the columnar cells of the petiole or pedicel. Cells of the abscission zone, sometimes now referred to as “target” cells (83), commence a phase of intense activity immediately prior to the start of physical separation of the abscising plant parts.

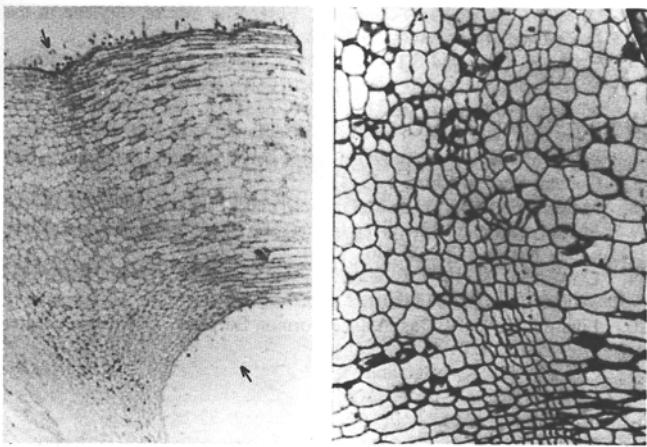


Fig. 1. Transverse section of the abscission zone in a *Coleus* explant. A. Low power view of abscising explant. B. Cells in the abscission zone of a freshly prepared explant.

Biochemistry

The start of the abscission process, whether natural or stimulated by application of exogenous ethylene, is marked by increased respiration (72, Fig. 2), which reflects a similar concurrent stimulation in the rates of RNA and protein synthesis (3, 47, 64). Electron micrographs (12, 65, 66, 100, 111) provide dramatic evidence of the metabolic upheaval resulting from ethylene treatment of sensitive abscission zones (Fig. 3a, b). A marked increase in the quantities of polyribosomes and rough endoplasmic reticulum (66, 100) is followed rapidly by the development of vesicles, presumed to contain the newly synthesized proteins (57). These vesicles move outwards, and, in the process of fusing with the plasmalemma (100), excrete their contents. Within hours the cell walls become swollen and cell separation commences. The cytoplasm loses its bounding membrane and starts to disintegrate (Fig. 3b).

The conclusion that RNA and protein synthesis is a normal prerequisite for abscission (3, 47, 64) is supported by studies with inhibitors of various steps of the protein synthetic sequence; α -amanitin, which inhibits transcription of messenger RNA (103),

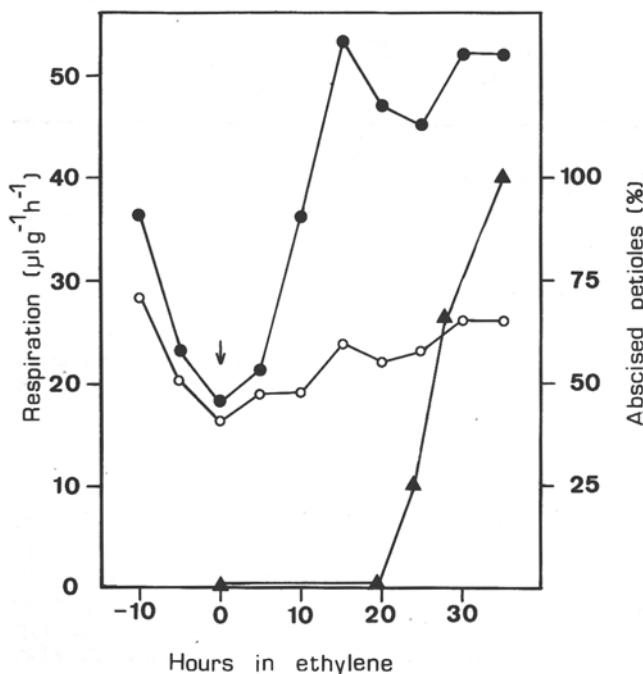


Fig. 2. Respiration of control (●) and ethylene-treated (○) *Coleus* explants. Means of 3 replicate explants per treatment. The arrow shows the start of the ethylene treatment (20 ppm). Petiole abscission (▲) was assayed on a further 10 replicate explants per treatment (Goszczynska and Reid, unpublished data).

cordycepin, which inhibits message processing (104), and cycloheximide, which inhibits protein synthesis (33). All retarded the abscission of *Coleus* explants treated with ethylene (Fig. 4).

Evidence is varied as to the nature and importance of the proteins synthesized and secreted by the cells of the abscission zone in response to ethylene treatment. There is substantial evidence for the changes in pectin metabolism suggested in 1918 by Sampson (95). Many workers have shown increased levels of the pectin-degrading enzyme, polygalacturonase (13, 39, 50, 79, 91), and others have seen a concomitant reduction in the activity of pectin methylesterase (74, 99), which is thought to reduce esterification and cross-linking of the cell "glue".

Electron micrographs (Fig. 3b) show considerable hydrolysis of the cell wall itself prior to abscission, and substantial increases have now been shown in cellulase, the enzyme presumed to be responsible for this hydrolysis, during abscission (1, 37, 39, 49, 50, 59, 63, 64, 88). It has now been demonstrated that only one of the 2 cellulase isozymes present in kidney bean abscission zones is directly involved in the abscission process (31, 58, 68, 88). As well as allowing separation of the cells in the abscission zone, hydrolysis of cellulose also would be necessary for the cell expansion which is thought to be involved in final separation (97), literally forcing the cells apart, especially in petal abscission (73, 98). It seems possible that this expansion is driven by increased turgor resulting from hydrolysis of starch in the abscission zone (20). Considerable increases in peroxidase activity are noted consistently in abscission zones (46, 112). The role of this enzyme in abscission is still uncertain, although there is evidence supporting the suggestions that it is involved in lignification, IAA oxidation, or disease resistance (99).

Regulation

Since the demonstration (70) that auxin applied to the distal end of petioles would prevent abscission of debladed *Coleus* explants, physiologists have been fascinated with the control of abscission by growth regulators. The attraction of these studies lies not only in the importance of the process under investigation, but also in the potent effects of growth regulators on it, the speed of the response (Fig. 2), and the uniformity and reproducibility of explants (short pieces of axis with stumps of abscising petioles attached) as an experimental tool (10). Using such explants as a bioassay, Addicott and his coworkers extracted from developing cotton fruit a compound which would stimulate abscission (24, 29) and which they called abscisin, now ABA. This regulator has since been shown to play important roles in the control of stomatal aperture and in the regulation of seed dormancy, but its role in abscission is probably not a primary one (86, 94).

The literature on abscission abounds with exceptions and special cases, but the results of many of the studies of the effects of environmental conditions and applied plant hormones are consistent with the following hypotheses:

- A gradient of auxin from the subtended organ to the plant axis maintains the abscission zone in a nonsensitive state (6). This gradient is itself maintained by factors which inhibit senescence of the organ. Thus, auxins (8, 70), cytokinins, light (107), and good nutrition all tend to reduce or delay abscission.

- Reduction or reversal of the auxin gradient causes the abscission zone to become sensitive to ethylene. Application of auxin proximal to the abscission zone (8), removal of the leaf blade (10), or treatments which accelerate its senescence [shading (71), poor nutrition (96), ethylene (71)] therefore hasten abscission. Ethylene, or stresses which enhance its production (40, 85), also may hasten abscission by reducing auxin synthesis and/or by interfering with its transport from the leaf (14, 16). Where ABA stimulates abscission (6, 7) it may do so by stimulating ethylene production (94), or by interfering with the production, transport, or action of auxin.

- Once sensitized, the cells of the abscission zone respond to low concentrations of ethylene (52, 53), whether exogenous or endogenous, by the rapid production and secretion of hydrolytic enzymes and subsequent shedding of the subtended organ.

Role of ethylene in natural abscission

Whereas the preceding hypotheses are consistent with much of the published information on regulation of the processes resulting

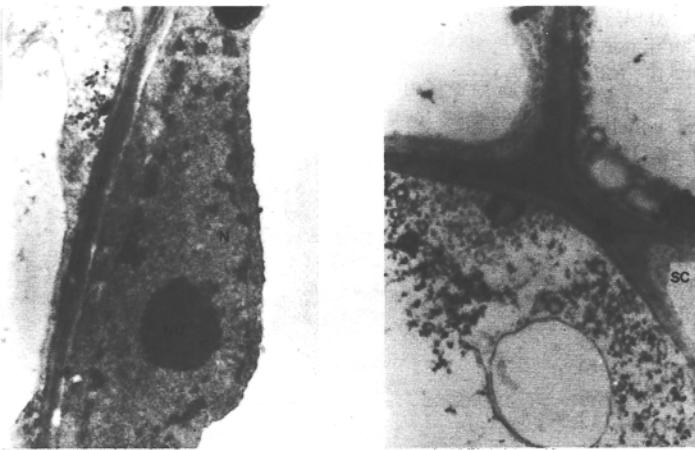


Fig. 3. Electron micrographs of cells in the abscission zone of *Coleus* explants. A. Control (freshly cut). B. Treated with ethylene for 8 hr. Labels show the nucleus (N), nucleolus (NU), mitochondrion (M), wall (W), middle lamella (ML), and separation cavity (SC) (from Morrison Baird, Gosczynska, Reid and Webster, in preparation).

in eventual abscission of plant organs, some workers have expressed reservations about the widely-held view that ethylene plays a major role in natural abscission. Addicott concluded his review of the evidence relating ethylene to abscission (6) by stating that "... it is a probable that ethylene is not essential to abscission". Nevertheless, the weight of the experimental evidence summarized hereafter supports the view that ethylene plays a more critical role in abscission than the "promotor" or "local coordinator" he ascribes to it.

• Ethylene production increases prior to abscission in many abscising organs (2, 4, 72). This argument for the involvement of ethylene has been suggested to be inconclusive, inasmuch as abscission can occur in some tissues without increased ethylene production (2, 28). The controversy is remarkably similar to that which was, for years, the focus of physiologists studying the role of ethylene in fruit ripening. Relatively recently, the changing sensitivity of fruit tissues to endogenous ethylene was recognized as being more important than a simple increase in ethylene production in governing the timing of the onset of ripening in climacteric fruit (89). As in abscission, this sensitivity is now known to increase with advancing age of the fruit, and to be affected by many factors, including the balance of endogenous plant growth regulators (17). Few fruit physiologists now consider there to be qualitative differences between natural ripening and that induced by ethylene. In other plant responses, too, there is increasing support for the view that changing

sensitivity to plant hormones is at least as important as changes in their endogenous concentrations as a control mechanism (105). The importance of the balance of growth regulators in the control of abscission is emphasized by the interrelated effects of different plant hormones on the process (77, 78).

- Treatment of a wide range of plant species with ethylene (2) or with ethylene-releasing compounds (5) dramatically stimulates abscission. Abeles (2) noted that in some plants application of ethylene did not induce foliar abscission, and drew the reasonable conclusion that ultimate control of abscission in such species might depend on factors other than ethylene. It seems equally reasonable to postulate in such cases that the hormonal changes required to sensitize the cells of the abscission zone were not induced by the ethylene treatment, so that the cells simply were not receptive to ethylene under the experimental conditions utilized. In such instances, one might also draw parallels with fruit physiology. Avocado, a classic climacteric fruit, is insensitive to even high concentrations of ethylene when still attached to the tree (17).

- Silver ion, a potent and apparently specific inhibitor of the action of ethylene (15), inhibits not only ethylene-stimulated abscission (15, 22), but also abscission caused by other stresses (23, 107). Similarly, 2, 5-norbornadiene, a compound which is known to competitively inhibit ethylene binding in plants, has recently been shown also to inhibit abscission (Sisler and Goren, unpublished data). Analogs of rhizobitoxin which interfere with the biosynthesis of ethylene also inhibit natural abscission (110).

Horticultural Implications

Beneficial effects. In the years since the discovery of the potent effects of ethylene in stimulating abscission, there has been considerable interest in its use in commercial horticulture. Such use became practicable with the development of ethylene-releasing chemicals such as ethephon (2-chloroethyl phosphonic acid), which enables spray or dip applications of "ethylene" (30).

Removing leaves. Abscission-promoting effects of ethylene on foliage are of considerable value to agriculture in some circumstances. Leaves are removed prior to harvest of bare-root nursery stock (61), cotton (32), or in the management of a range of other crops (5, 36, 68), by the application of ethylene-releasing chemicals or of chemical poisons which presumably stimulate ethylene production by wounding the tissue (117).

Removing flowers or young fruit. Removal of flowers or young fruit, either selectively, as in tree fruit where hand thinning is no longer economically feasible, or totally, as in ornamentals, where dropping fruit is considered to be undesirable, has been achieved by spraying with several ethylene-releasing or stimulating chemicals (45, 56, 93, 106, 113, 114).

Removing mature fruit. The force required to detach maturing fruit from the tree, which decreases as ethylene production increases (109), has been used since antiquity as a means of assessing their maturity, and is still an important factor in the harvest of many

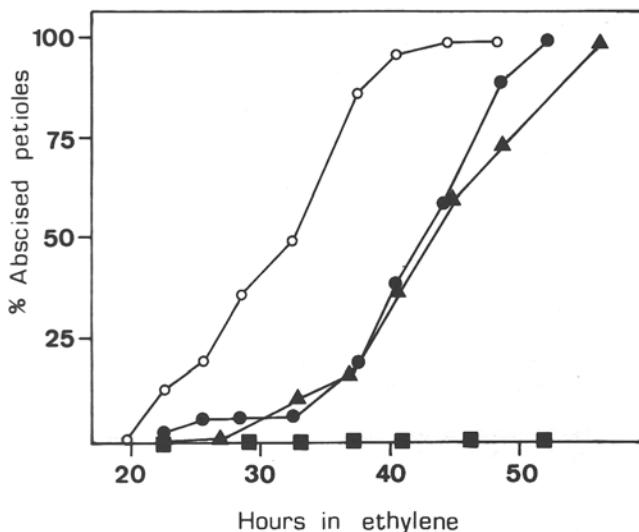


Fig. 4. Effect of inhibitors of protein synthesis on abscission of *Coleus* explants treated continuously with 10 ppm ethylene. Explants were treated prior to deblanding with solutions containing water (○), α -amanitin (Δ), cordycepin (\bullet), or cycloheximide (\blacksquare). Means of 30 petioles per treatment (Woods and Reid, unpublished data).

fruit. In melons, for example, the development of the "slip", the region of the abscission of the fruit from the vine, and an important maturity index in some cultivars, occurs at the time when the fruit's endogenous ethylene production is increasing (87).

Application of ethylene-releasing chemicals is used widely to reduce the strength of the abscission zone of mature fruit (18, 19, 21, 62, 67) and is of particular importance in facilitating the mechanical harvesting of sour cherries (81), and the shucking of walnuts (82, 101) and pecans. The application of low concentrations of cycloheximide (10–20 ppm) to citrus fruit has been shown selectively to wound the peel adjacent to the button (26, 116). Ethylene production in response to this wounding stimulates button abscission, a sequence of events which has been of some commercial value in the mechanical harvesting of Florida citrus (48, 116).

Ethylene-induced abscission is a common problem in the post-harvest handling of vegetables (55), fruit, and ornamentals (11, 42, 71). Even at storage temperatures, ethylene can accelerate abscission of leaves of cabbage, cauliflower, celery and similar vegetables (69). Loss of the button from lemons, limes, and other citrus also can result from ethylene exposure during marketing. Abscission effects of ethylene in ornamentals were noted long before ethylene was proved the causal factor. Abscission of florets from cut flowers and potted flowering plants (23), and of leaves from potted foliage plants (71), are common symptoms of exposure of these crops to ethylene-polluted environments. The rapid abscission of many florets following the presence of an errant bee in a snapdragon greenhouse or the pollination of foxgloves under laboratory conditions (102) provides another example of ethylene-mediated abscission. Pollen contains ACC (1-aminocyclopropane-1-carboxylic acid) in high concentrations (115), and this ethylene precursor, is transported from the stigma to other parts of the flower (90).

Preventing ethylene-induced abscission

The commercial implications of the unwanted abscission of leaves, flowers, or fruit in horticultural crops have aroused considerable interest in devising ways of avoiding the problem. In most respects, the techniques employed are similar to those described for overcoming other undesirable effects of ethylene.

Avoiding exposure to ethylene. Many of the problems after harvest can be avoided by eliminating sources of ethylene (such as internal combustion engines, ripening fruit, fungi, and poorly vented fossil fuel heaters), and by proper ventilation of environments likely to be contaminated with ethylene.

Reducing the sensitivity of plants to ethylene. The danger of premature abscission can be reduced by ensuring that the abscission zone remains insensitive to ethylene by providing adequate nutrition and illumination, avoiding desiccation, or treating the plants with synthetic auxins. This latter treatment is important in preventing abscission of some fruit crops, such as apples (35) and citrus (25). It also has proved useful in reducing leaf abscission in English holly (92) and flower abscission in some ornamentals, including bougainvillea (41), Geraldton wax flower (43), and Lily of the Nile (75).

Use of specific ethylene inhibitors. Silver ion (15) has no place in preventing abscission in food crops, but it is already in widespread use (formulated as the stable, relatively nonphytotoxic and mobile thiosulfate complex) in preventing the abscission of flowers of ornamental plants (22, 23, 75, 76, 107, 108). Spraying zygocactus plants with 0.2 mM STS (silver thiosulfate) at the stage when buds were starting to show color completely prevented subsequent flower abscission in response to low concentrations of ethylene (22). A 4 mM STS spray similarly prevented ethylene-accelerated abscission of leaves from foliage plants (Fig. 5).

STS appears to move considerable distances in plants. In geranium, spraying tight buds prevented abscission not only of their petals, but also of those of flowers developing several weeks later (23).

Silver ion appears to inhibit ethylene effects at a very early stage in the events leading to abscission. Electron micrographs of cells in abscission zones from Coleus explants treated with STS and then with ethylene are indistinguishable from those of freshly-cut control explants (Fig. 3). The curious interactions between light, silver ion,

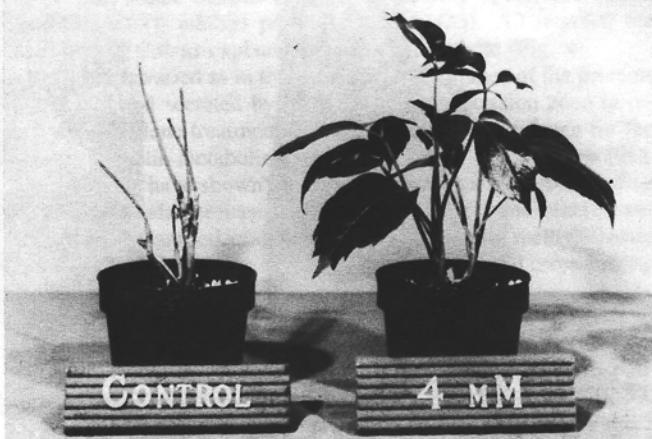


Fig. 5. Effect of prior spray application of 4 mM STS on abscission of leaflets from plants of *Brassaia actinophylla* treated with 2 ppm ethylene for 7 days (Goszczynska and Reid, unpublished data).

ethylene and abscission observed by Curtis (27), do not yet appear to have been explained satisfactorily.

Whereas inhibitors of ethylene production prevent floret abscission in some flowers (110), the practical implications of this finding are limited, since these compounds have little or no effect on the response of plant tissues to exogenous ethylene.

Future Research

The horticultural implications briefly outlined in this report are a clear indication of the importance of ethylene-mediated abscission. We already possess a great deal of information on the anatomy, biochemistry, and physiology of the process, and we have an armory of chemical agents to stimulate or inhibit it with varying degrees of commercial success. In the future, we may hope for modification of abscission behaviour by genetic manipulation of sensitive plants. This goal will not be achieved without further fundamental research into the means by which ethylene acts.

Two interesting and relatively unattended reports may provide useful experimental systems for such studies. Fitting's observation in 1911 (34) that brief exposure of geranium flowers to ethylene will cause almost immediate abscission suggests that in these flowers the depression of the genome, which is implied in most other abscission systems (Fig. 4), is not involved in the abscission response. Further studies of this system (98) might reveal a more direct effect of ethylene which would provide important information about the modulation of cell behavior by this hormone. In 1958, Haney (44) showed the sensitivity of snapdragon floret abscission to ethylene to be due to a single gene locus. Identification of the product of this gene using modern genetic techniques also might yield important information about the control of abscission by ethylene.

Literature Cited

1. Abeles, F.B. 1969. Abscission: role of cellulase. *Plant Physiol.* 44:447–452.
2. Abeles, F.B. 1973. Ethylene in plant biology. Academic Press, N.Y.
3. Abeles, F.B., G.R. Leather, L.E. Forrence, and L.E. Craker. 1979. Abscission: regulation of senescence, protein synthesis, and enzyme secretion by ethylene. *HortScience* 6(4):371–376.
4. Adato, I. and S. Gazit. 1977. Role of ethylene in avocado fruit development and ripening. I. Fruit drop. *J. Exp. Bot.* 28:636–643.
5. Addicott, F.T. 1976. Actions on abscission, defoliation and related responses, p. 191–217. In: L.J. Audus (ed.). *Herbicides, physiology, biochemistry, ecology*, 2nd ed, vol 1. Academic Press, London.
6. Addicott, F.T. 1982. *Abscission*. Univ. of California Press, Berkeley.
7. Addicott, F.T. 1983. Abscisic acid in abscission. In: F.T. Addicott (ed.). *Abscisic acid*. Praeger, N.Y.
8. Addicott, F.T. and R.S. Lynch. 1951. Acceleration and retardation of abscission by indoleacetic acid. *Science* 114:688–689.
9. Addicott, F.T. and J.L. Lyon. 1973. Physiological ecology of abscission, p. 85–124. In: T.T. Kozlowski (ed.). *Shedding of plant parts*. Academic Press, N.Y.

10. Addicott, F.T., R.S. Lynch, G.A. Livingston, and J.K. Hunter. 1949. A method for the study of foliar abscission *in vitro*. *Plant Physiol.* 24:537-539.
11. Armitage, A.M., R. Heins, S. Dean, and W. Carlson. 1980. Factors influencing flower petal abscission in the seed propagated geranium *Pelargonium hortorum*. *J. Amer. Soc. Hort. Sci.* 105(4):562-564.
12. Baird, L.A.M., P.D. Reid, and B.D. Webster. 1978. Ultrastructural modifications associated with the induction of abscission in *Coleus blumei*. *Bot Gaz.* 139:165-170.
13. Berger, R.K. and P.D. Reid. 1979. Role of polygalacturonase in bean leaf abscission. *Plant Physiol.* 63:1133-1137.
14. Beyer, E.M., Jr. 1975. Abscission: The initial effect of ethylene is in the leaf blade. *Plant Physiol.* 52:322-327.
15. Beyer, E.M., Jr. 1976. Silver ion: A potent antiethylene agent in cucumber and tomato. *HortScience* 11(3):195-196.
16. Beyer, E.M., Jr. and P.W. Morgan. 1971. Abscission. The role of ethylene modification of auxin transport. *Plant Physiol.* 48:208-212.
17. Biale, J.B. and R.E. Young. 1981. Respiration and ripening in fruits—retrospect and prospect, p. 1-39. In: J. Friend and M.J.C. Rhodes (eds.). *Recent advances in the biochemistry of fruit and vegetables*. Academic Press, London.
18. Blumenfield, A., E. Epstein, and Y. Ben-Tal. 1978. Ethylene treatment and abscission of olive fruits. *HortScience* 13(1):47-48.
19. Bondad, N.D. 1976. Response of some tropical and subtropical fruits to pre- and post-harvest applications of ethephon. *Econ. Bot.* 30:67-80.
20. Bornmann, C.H., F.T. Addicott, and A.R. Spurr. 1966. Auxin and gibberellin effects on cell growth and starch during abscission in cotton. *Plant Physiol.* 41:871-876.
21. Browning, G. and M.G.R. Cannell. 1970. Use of 2-chloroethyl phosphonic acid to promote the abscission and ripening of fruit of *Coffea arabica* L. *J. Hort. Sci.* 45:223-232.
22. Cameron, A.C. and M.S. Reid. 1981. The use of silver thiosulfate anionic complex as a foliar spray to prevent flower abscission of zygocactus *Schlumbergera truncata*. *HortScience* 16(6):761-762.
23. Cameron, A.C. and M.S. Reid. 1983. Use of silver thiosulfate to prevent flower abscission from potted plants. *Sci. Hort.* 19:373-378.
24. Carns, H.R., J.L. McMeans, and F.T. Addicott. 1959. An abscission-accelerating hormone in cotton and some of its interactions with auxin and with gibberellie acid. *Proc. 9th Intl. Bot. Congr.* 2:60.
25. Coggins, C.W., Jr. 1973. Use of growth regulators to delay maturity and prolong shelf life of *Citrus*. *Acta Hort.* 34(1):469-472.
26. Cooper, W.C. and W.H. Henry. 1967. The acceleration of abscission and coloring of citrus fruit. *Proc. Fla. State Hort. Soc.* 80:7-14.
27. Curtis, R.W. 1981. Light requirement for silver nitrate inhibition of ethrel induced leaf abscission from cuttings of *Vigna radiata* cultivar Jumbo. *Plant Physiol.* 68:1249-1252.
28. Davenport, T.L., P.W. Morgan, and W.R. Jordan. 1976. Stress-induced foliar abscission: no enhanced ethylene production by leaf petioles. *Plant Physiol.* 57(suppl.):97. (Abstr.)
29. Davis, L.A. and F.T. Addicott. 1972. Abscisic acid: correlations with abscission and with development in the cotton fruit. *Plant Physiol.* 49:644-648.
30. DeWilde, R.C. 1971. Practical applications of (2-chloroethyl) phosphonic acid in agricultural production. *HortScience* 6(4):364-370.
31. Durbin, M.L., R. Sexton, and L.N. Lewis. 1981. The use of immunological methods to study the activity of cellulase isozymes in bean leaf abscission. *Plant Cell Environ.* 4:67-73.
32. Elliott, F.C., M. Hoover, and W.K. Porter Jr. (eds.). 1968. *Advances in production and utilization of quality cotton: principles and practices*. Iowa State Univ. Press, Ames.
33. Ellis, R.J. and I.R. MacDonald. 1970. Specificity of cycloheximide in higher plant systems. *Plant Physiol.* 46:227-232.
34. Fitting, H. 1911. Untersuchungen über die vorzeitige Entblätterung von Blüten. *Jahrb. f. wiss. Bot.* 49:187-263.
35. Gardner, F.E., P.C. Marth, and L.P. Batjer. 1939. Spraying with plant growth substances to prevent apple fruit dropping. *Science* 90:208-209.
36. Gerds, M.H., G.L. Obenhauf, J.L. LaRue, and G.M. Leavitt. 1977. Chemical defoliation of fruit trees. *Calif. Agr.* 31(4):19.
37. Goren, R. and M. Huberman. 1976. Effects of ethylene and 2,4-D on the activity of cellulase isoenzymes in abscission zones of the developing orange fruit. *Physiol. Plant.* 37:123-30.
38. Gorter, C.J. 1964. Studies on abscission in explants of *Coleus*. *Physiol. Plant.* 17:331-345.
39. Greenberg, J., R. Goren, and J. Riov. 1975. The role of cellulase and polygalacturonase in abscission of young and mature Shamouti orange fruits. *Physiol. Plant.* 34:1-7.
40. Guinn, G. 1976. Water deficit and ethylene evolution by young cotton bolls. *Plant Physiol.* 57:403-405.
41. Hackett, W.P., R.M. Sachs, and J. DeBie. 1972. Growing bougainvillea as a flowering pot plant. *Calif. Agr.* 26(8):12-13.
42. Halevy, A.H. and S. Mayak. 1981. Senescence and post-harvest physiology of cut flowers, part 2. *Hort. Rev.* 3:59-143.
43. Halevy, A.H., R. Shillo, A. Borochov, Y. Kirscholtz, and T. Tirosh. 1974. Geraldton wax flower: growth and post-harvest treatments. *Ann. Rpt Dept. Orn. Hort. Hebrew Univ. for 1973-74*, p. 89-92. Rehovot.
44. Haney, W.J. 1958. Snapdragons that are shatter resistant. *Flor. Exchange* 130:17.
45. Hedberg, P.R. and P.B. Goodwin. 1980. Factors affecting natural and ethephon induced grape *Vitis vinifera* berry abscission. *Amer. J. Enol. Vitic.* 31:109-113.
46. Henry, E.W., J.G. Valdovinos, and T.E. Jensen. 1974. Peroxidases in tobacco tissue. II. Time course studies of peroxidase activity during ethylene-induced abscission. *Plant Physiol.* 54:192-196.
47. Holm, R.E. and F.B. Abeles. 1967. Abscission: the role of RNA synthesis. *Plant Physiol.* 42:1094-1102.
48. Holm, R.E. and W.C. Wilson. 1977. Ethylene and fruit loosening from combinations of *Citrus* abscission chemicals. *J. Amer. Soc. Hort. Sci.* 102(5):576-579.
49. Horton, R.F. and D.J. Osborne. 1967. Senescence, abscission and cellulase activity in *Phaseolus vulgaris*. *Nature* 214:1086-1088.
50. Huberman, M. and R. Goren. 1979. Exocellular and endocellular cellulase and polygalacturonase in abscission zones of developing orange fruits. *Physiol. Plant.* 45:189-196.
51. Inman, T. 1848. The causes that determine the fall of leaves. *Proc. literary and philosophical soc., Liverpool, 36th Session, No. IV*:89-92.
52. Jackson, J.M. and D.J. Osborne. 1970. Ethylene, the natural regulator of leaf abscission. *Nature* 225:1019-1022.
53. Jackson, J.M., C. Hartley, and D.J. Osborne. 1973. Timing abscission in *Phaseolus vulgaris* by controlling ethylene production and sensitivity to ethylene. *New Phytol.* 72:1251-1260.
54. Jacobs, W.P. 1962. Longevity of plant organs: internal factors controlling abscission. *Annu. Rev. Plant Physiol.* 13:403-436.
55. Kays, S.J., C.A. Jaworski, and H.C. Price. 1976. Defoliation of pepper transplants in transit by endogenously evolved ethylene. *J. Amer. Soc. Hort. Sci.* 101(4):449-451.
56. Knight, J.N. 1982. Regulation of cropping and fruit quality of Conference pear by the use of gibberellie-acid and thinning 2. The effect of ethephon as a flower thinner when used in conjunction with gibberellie-acid application. *J. Hort. Sci.* 57:61-68.
57. Koehler, D.E., R.T. Leonard, W.J. Vanderwoude, A.E. Linkins, and L.N. Lewis. 1976. Association of latent cellulase activity with plasma membranes from kidney bean abscission zones. *Plant Physiol.* 58:324-330.
58. Koehler, D.E., L.N. Lewis, L.M. Shannon, and M.L. Durbin. 1980. Purification of cellulase from kidney bean abscission zones. *Phytochemistry* 20:409-412.
59. Kossuth, S.V. and R.H. Biggs. 1977. Fruit removal force cellulase and ethylene production in release and ethephon treated oranges. *J. Amer. Soc. Hort. Sci.* 102:609-612.
60. Kozlowski, T.T. (ed.). 1973. *Shedding of plant parts*. Academic Press, N.Y.
61. Larsen, F.E. and G.D. Lowell. 1977. Tree fruit nursery stock defoliation with harvest aide chemical and surfactant mixtures. *HortScience* 12(6):580-582.
62. Lavee, S. and G.C. Martin. 1981. In-vitro studies on ethephon induced abscission in oliver *Olea europaea* cultivar Manzanillo. 2. The relation between ethylene evolution and abscission of various organs. *J. Amer. Soc. Hort. Sci.* 106(1):19-26.
63. Lewis, L.N. and D.E. Koehler. 1979. Cellulase in the kidney bean *Phaseolus vulgaris* seedling. *Planta* 146:1-6.
64. Lewis, L.N. and J.E. Varner. 1970. Synthesis of cellulase during abscission of *Phaseolus vulgaris* leaf explants. *Plant Physiol.* 46:194-199.
65. Lieberman, S.J., J.G. Valdovinos, and T.E. Jensen. 1979. Ultrastructural localization of cellulase during ethylene induced abscission and natural abscission of *Nicotiana tabacum* flower pedicels. *Plant Physiol.* 63:132. (Abstr.)
66. Lieberman, S.J., J.G. Valdovinos, and T.E. Jensen. 1983. A morphometric study on the effect of ethylene treatment in promoting abscission of tobacco *Nicotiana tabacum* cultivar Little-Turkish flower pedicels. *Plant Physiol.* 72:583-585.
67. Lipe, J.A. and P.W. Morgan. 1972. Ethylene: role in fruit abscission and dehiscence processes. *Plant Physiol.* 50:759-764.
68. MacConnell, W.P. and L. Kenerson. 1964. Chemi-pruning northern hardwoods. *J. For.* 62:463-466.
69. McKeown, A.W., E.C. Lougheed, and D.P. Murr. 1978. Compat-

- ibility of cabbage, carrots, and apples in low pressure storage. *J. Amer. Soc. Hort. Sci.* 103(6):749-752.
70. Mai, G. 1934. Korrelationsuntersuchungen an entspreiteten Blattstielen mittels lebender Orchideenpollinien als Wuchsstoffquelle. *Jahrb. Wiss. Bot.* 79:681-713.
 71. Marousky, F.J. and B.K. Harbaugh. 1979. Interactions of ethylene temperature light and carbon dioxide on leaf and stipule abscission and chlorosis in *Philodendron scandens* ssp *oxycardium*. *J. Amer. Soc. Hort. Sci.* 104(6):876-880.
 72. Marynick, M.C. 1977. Patterns of ethylene and carbon dioxide evolution during cotton explant abscission. *Plant Physiol.* 59:484-489.
 73. Miranda, R.M. and W.H. Carlson. 1981. Anatomy physiology and chemical control of petal abscission of hybrid geraniums *Pelargonium hortorum*. *HortScience* 16:428. (Abstr.)
 74. Moline, H.E., C.E. LaMotte, C. Gochnauer, and A. McNamer. 1972. Further comparative studies of pectin esterase in relation to leaf and flower abscission. *Plant Physiol.* 50:655-659.
 75. Mor, Y., A.H. Halevy, A.M. Kofranek, and M.S. Reid. Prevention of flower shattering in *Agapanthus*. *J. Amer. Soc. Hort. Sci.* 109(4):494-497.
 76. Mor, Y., M.S. Reid, and A.M. Kofranek. 1984. Use of silver thiosulfate to extend vase life of sweet pea (*Lathyrus odoratus*). *J. Amer. Soc. Hort. Sci.* 109(4):866-868.
 77. Morgan, P.W. 1976. Gibberellic acid and IAA compete in ethylene-promoted abscission. *Planta* 129:275-276.
 78. Morgan, P.W. and J.I. Durham. 1975. Ethylene-induced leaf abscission is promoted by gibberellic acid. *Plant Physiol.* 55:308-311.
 79. Morre, D.J. 1968. Cell wall dissolution and enzyme secretion during leaf abscission. *Plant Physiol.* 43:1545-1549.
 80. Morrison Baird, L.A. and B.D. Webster. 1979. The anatomy and histochemistry of fruit abscission. *Hort. Rev.* 1:172-203.
 81. Olien, W.C. and M.J. Bukovac. 1982. Interaction between temperature and ethylene in sour cherry (*Prunus cerasus* cultivar Montmorency) fruit abscission. *HortScience* 17(5):795-796.
 82. Olson, W.H., G.S. Sibbett, G.L. Carnhill, and G.C. Martin 1977. Lower ethephon rates effective in walnut harvest. *Calif. Agr.* 31(7):6-7.
 83. Osborne, D.J. 1977. Ethylene and target cells in the growth of plants. *Sci. Prog.* 64:51-63.
 84. Osborne, D.J. and J.A. Sargent. 1976. The positional differentiation of abscission zones during the development of leaves of *Sambucus nigra* and the response of the cells to auxin and ethylene. *Planta* 132:197-204.
 85. Peterson, J.C., J.N. Sacalis, and D.J. Durkin. 1980. Promotion of leaf abscission in intact *Ficus benjamina* by exposure to water stress. *J. Amer. Soc. Hort. Sci.* 105(6):788-792.
 86. Porter, N.G. 1977. The role of abscisic acid in flower abscission of *Lupinus luteus*. *Physiol. Plant.* 40:50-54.
 87. Pratt, H.K. 1971. Melons, p. 207-232. In: A.C. Hulme (ed.). The biochemistry of fruits and their products, vol. 2. Academic Press, London.
 88. Reid, P.D., P.G. Strong, F. Lew, and L.N. Lewis. 1974. Cellulase and abscission in the red kidney bean *Phaseolus vulgaris*. *Plant Physiol.* 53:732-737.
 89. Reid, M.S. 1974. The role of ethylene in the ripening of some unusual fruits. In: Facteurs et regulation de la maturation des fruits. Colloques Intl. CNRS 283:177-182. Paris.
 90. Reid, M.S., D.W. Fujino, N.E. Hoffman, and C.S. Whitehead. 1984. ACC—the mobile stimulus in pollinated flowers? *J. Plant Growth Reg.* (In press)
 91. Riov, J. 1974. A polygalacturonase from *Citrus* leaf explants. Role in abscission. *Plant Physiol.* 53:312-316.
 92. Roberts, A.N. and R.L. Ticknor. 1970. Commercial production of English holly in the Pacific Northwest. *Amer. Hort. Mag.* 49:301-314.
 93. Robitaille, H.A., F.H. Emerson, and K.S. Yu. 1977. Thinning ap-
 - ples with ethylene releasing chemicals. *J. Amer. Soc. Hort. Sci.* 102(5):595-598.
 94. Sagee, O., R. Goren, and J. Riov. 1980. Abscission of *Citrus* leaf explants. Interrelationships of abscisic acid, ethylene, and hydrolytic enzymes. *Plant Physiol.* 66:750-753.
 95. Sampson, H.C. 1918. Chemical changes accompanying abscission in *Coleus blumei*. *Bot. Gaz.* 66:32-53.
 96. Seeley, J.G. 1950. Potassium deficiency of greenhouse roses. *Proc. Amer. Soc. Hort. Sci.* 56:446-470.
 97. Sexton, R. and A.J. Redshaw. 1981. The role of cell expansion in the abscission of *Impatiens* leaves. *Ann. Bot.* 48:745-757.
 98. Sexton, R., W.A. Struthers, and L.N. Lewis. 1983. Some observations on the very rapid abscission of the petals of *Geranium robertianum*. *Protoplasma* 116:179-186.
 99. Sexton, R. and J.A. Roberts. 1982. Cell biology of abscission. *Annu. Rev. Plant Physiol.* 33:133-162.
 100. Sexton, R., G.G.C. Jamieson, and M.H.I.L. Allan. 1977. An ultrastructural study of abscission zone cells with special reference to the mechanisms of enzyme secretion. *Protoplasma* 91:369-387.
 101. Sorber, D.G. and M.H. Kimball. 1950. Use of ethylene in harvesting the Persian walnut (*Juglans regia*) in Calif. USDA. Tech. Bul. 996.
 102. Stead, A.D. and K.G. Moore. 1983. Studies on flower longevity in *Digitalis purpurea*. The role of ethylene in corolla abscission. *Planta* 157:15-21.
 103. Strain, G.C., K.P. Mullinix, and L. Borogard. 1971. RNA polymerases of maize: nuclear RNA polymerases. *Proc. Natl. Acad. Sci.* 68:2647-2651.
 104. Takegami, T. and K. Yoshida. 1975. Remarkable retardation of the senescence of tobacco leaf disks by cordycepin, an inhibitor of RNA polyadenylation. *Plant and Cell Physiol.* 16:1163-1166.
 105. Trewavas, A. 1981. How do plant growth substances work? *Plant Cell Environ.* 4:203-228.
 106. Unrath, C.R. 1978. The development of ethephon's thinning potential for spur 'Delicious' apples. *Acta Hort.* 80:233-243.
 107. VanMeeteren, U. and M. DeProft. 1982. Inhibition of flower bud abscission and ethylene evolution by light and silver thiosulfate in *Lilium* cultivar Enchantment. *Physiol. Plant.* 56:236-240.
 108. Veen, H. 1983. Silver thiosulfate: an experimental tool in plant science. *Sci. Hort.* 20:211-224.
 109. Walsh, C.S. 1977. The relationship between endogenous ethylene and abscission of mature apple fruits. *J. Amer. Soc. Hort. Sci.* 102(5):615-619.
 110. Wang, C.Y., J.E. Baker, R.E. Hardenburg, and M. Lieberman. 1977. Effects of 2 analogs of rhizobitoxine and sodium benzoate on senescence of snapdragons. *J. Amer. Soc. Hort. Sci.* 102:517-520.
 111. Webster, B.D. 1974. Characteristics of abscission in *Phaseolus* plants treated with 2-chloroethylphosphonic acid. *R. Soc. N.Z. Bul.* 12:863-869.
 112. Webster, B.D., T.W. Dunlap, and M.E. Craig. 1976. Ultrastructural studies of abscission in *Phaseolus*: localization of peroxidase. *Amer. J. Bot.* 63:759-770.
 113. Weinbaum, S.A., C. Guilivo, and A. Ramina. 1977. Chemical thinning ethylene and pre-treatment fruit size influence enlargement, auxin transport and apparent sink strength of French prune and Andross peach. *J. Amer. Soc. Hort. Sci.* 102(6):781-785.
 114. Weinbaum, S.A. and T.T. Murooka. 1978. Chemical thinning of prune. Relation of assimilate deprivation to ethylene mediated fruit abscission. *HortScience* 13(2):159-160.
 115. Whitehead, C.S., D.W. Fujino, and M.S. Reid. 1983. Identification of high concentrations of ACC in pollen. *Sci. Hort.* 21:291-297.
 116. Wilson, W.C., G.E. Coppock, and J.A. Attaway. 1982. Growth regulators facilitate harvesting of oranges. *Proc. Intl. Soc. Citriculture* 1:278-281.
 117. Yang, S.F. and H.K. Pratt. 1978. Wound ethylene production, p. 595-622. In: G. Kahl (ed.). *Biochemistry of wounded plant storage tissues*. De Gruyter, Berlin.