Journal of Experimental Botany, Vol. 48, No. 309, pp. 821–837, April 1997

Journal of Experimental Botany

REVIEW ARTICLE

Abscission of flowers and floral parts

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Received 8 May 1996; Accepted 31 October 1996

Abstract

The abscission of inflorescences, flowers, petals, sepals, styles, and stamens is discussed, with emphasis on the anatomy and ultrastructure of the abscission zones, and the role of cell wall degrading enzymes and hormonal control. Shedding of these parts is usually due to cell wall dissolution, but abscission of petals, stamens, and styles in some species occurs due to the forces generated by the growing fruit. Flower abscission is clearly regulated by ethylene, whilst auxins apparently decrease the sensitivity to ethylene. Petal, style and stamen abscission also seems to be controlled by endogenous ethylene. Auxin is apparently involved in abscission of styles and stamens, but in petals its role is at yet unclear. The ultrastructural data indicate high protein synthesis and high secretory activity of material toward cell walls of abscission zone cells. The physiological evidence indicates a role of both polygalacturonase and cellulase in cell wall dissolution, whilst the role of other cell wall degrading enzymes is still unknown. The physiological processes occurring in the walls of the separating cells should be distinguished from those relating to defence against microbial intrusion, such as deposition of lignin and suberin and tylose formation. Experimentation using mutants and transgenic plants may aid in separating these processes. Sequencing of the isoenzymes specific for the abscission zone and a search for abscission zone-specific promoters seems a requirement for the successful evaluation of the enzymes involved in cell wall degradation.

Key words: Abscission, anatomy, abscission zone, hormonal control, cell wall degrading enzymes, inflorescences.

Introduction

Abscission of plant parts is, by definition, due to dissolution of the cell walls, hence it is an active physiological process. The term abscission, derived from the Latin *abscindere*, 'to tear', is, therefore, appropriate, but in several plants some parts are shed due to growth of subtending parts, a process which also can be considered tearing, but which is to be distinguished from true abscission.

Abscission of plant reproductive organs, both inflorescences and individual flowers, is widespread and the fall of flower parts also occurs in many species; most conspicuous is petal[4] fall, but, depending on the species, floral parts such as sepals, styles, and stamens may also fall, and in some flowers the bracts that enclose the unopened bloom abscise.

Abscission of flower buds is also common and, although not covered in-depth in this review, its anatomy and physiology is similar to flower shedding (Crane *et al.*, 1982; Tripp and Wien, 1989; Wien *et al.*, 1989). When appropriate, some of the physiological work related to bud drop is also discussed.

This paper reviews the abscission of inflorescences, flowers and flower parts, with emphasis on (a) the anatomy and ultrastructure of the abscission zones, (b) the physiology of abscission, in particular the role of cell wall degrading enzymes and hormonal control, and (c) the (potential) use of transgenic plants to study the shedding of these parts.

Abscission of inflorescences and flowers

In several monoecious and dioecious trees the male flowers are borne in an inflorescence, called a catkin, that

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[4] In plants in which the perianth is not differentiated into a calyx and corolla, such as tulips, all perianth members are called tepals. These may either all abscise concurrently, but in some species the outer ring, which is analogous to the calyx, may do so just before the inner one. The fall of both petals and tepals will in this paper be indicated as petal abscission.

falls after pollen shedding (von Mohl, 1860). Examples are walnut (Juglandaceae) and several species in the Betulaceae. Inflorescences that show abscission can consist of bisexual flowers, e.g. in *Beloperone*, *Pachystachus* and olive (Woltering, 1987; Weis *et al.*, 1988). These inflorescences also often bear flower bracts, which in some species, such as *Pachystachus*, are leaf-like, and these fall with the inflorescence. Inflorescences usually fall when still fully turgid. Examples of inflorescence abscission are given in Table 1.

Gärtner (1844), in an exhaustive monograph about flowers and fertilization, described abscission of female and bisexual flowers in genera such as *Lychnis*, *Nicotiana* and *Verbascum*. Flower shedding was, in general, due to the absence of pollination or fertilization; in some species the presence of a single embryo prevented flower fall. It was concluded that in some species pollination, in the absence of fertilization, was sufficient to prevent flower fall (e.g. *Mimulus*, *Potentilla* and some *Nicotiana* species). Becquerel (1907), however, described that fertilization was a prerequisite for preventing flower fall in several other *Nicotiana* species. Similarly, in legume species the unfertilized flowers, at the top of the raceme, are often shed (Clifford *et al.*, 1992).

Fertilized flowers may also abscise, in legumes such as *Glycine max* (Abernathy *et al.*, 1977) and *Vicia faba* (Kambal, 1969; Chapman *et al.*, 1979; Gates *et al.*, 1981), for example. In cocoa (*Theobroma cacao*) up to 98% of fertilized flowers reportedly fall. The possible evolutionary reasons for investment in surplus flowers, and in fertilizing them, is discussed in detail by Stephenson (1981). Among hypotheses that have been proposed to explain the selective advantage is a larger floral display, which would reduce uncertainties in pollinator visits. Bisexual flowers may also fall when developing abnormally, for example in *Citrus* spp. 83% of abscised flowers shed had visible abnormalities, and in peach all flowers containing aborted pistils were found to be shed (Kaska, 1989).

Male flowers may fall before, during, or after they shed their pollen. In some aquatic plants the male flowers abscise, then float on the water and shed their pollen, for example, in a number of *Elodea* spp. and *Valisneria* spp. (Pfeiffer, 1927). Male flowers of *Mercurialis* spp. (Euphorbiaceae) abscise as the anthers open; and when these flowers fall their pollen is dispersed (von Wettstein, 1916). Von Mohl (1860) described male flower abscission in *Cucumis melo* and *Ricinus communis*, after the pollen had been shed.

Male flowers usually abscise when still fully turgid. Female or bisexual flowers may also fall when still fully turgid, but in many species the petals wilt prior to flower abscission, for example, unfertilized *Yucca filamentosa* (Agavaceae) and *Tritoma uvaria* (Liliaceae; Hannig, 1913), and several orchids, such as *Phalaenopsis*. True abscission may even occur when the entire distal part is desiccated, the abscission zone cells apparently remain alive and active. Several examples of flower abscission are included in Table 2.

The stem segment just underneath individual flowers, called the pedicel, often contains a morphologically distinct abscission zone. This zone is usually situated either at the top or base, but in some species it is just above the base (e.g. *Asparagus*; Gärtner, 1844; Hannig, 1913) or just below the top (*Citrus* spp.; Einset *et al.*, 1979). In several *Prunus* species it is located in the lower part of the floral cup, which consists of fused basal portions of sepals, petals and stamens (Simons, 1973). The location of the abscission zone in several other species has been described by Stephenson (1981), Woltering (1986), and McKenzie and Lovell (1992*b*). The presence of an abscission zone does not necessarily lead to abscission. In commercial cut rose flowers, for example, an abscission zone is present at the pedicel base, and although flowers usually remain unfertilized, only in a few cultivars does this zone become functional (van Doorn and Schröder, 1995).

Flower abscission is commercially important as it limits fruit set of plants such as walnut (*Juglans regia*; Catlin and Olsson, 1990), field bean (*Vicia faba*; Kambal, 1969), snap bean (*Phaseolus vulgaris*; Webster and Chiu, 1975), soybean (*Glycine max*; Huff and Dybing, 1980), mungbean (*Vigna radiata*; Poehlman, 1991), cowpea (*Vigna unguiculata*; Ojehomon, 1972), lemon, orange, mandarin, and grapefruit (*Citrus* spp.; Einset *et al.*, 1979). It is also often a limiting factor in the trade of several flowering potted plants (Cameron and Reid, 1981, 1983; Hoyer, 1982; van Leeuwen, 1985; Woltering, 1986).

Table 1. *Examples of inflorescence abscission, as related to the plant families*

Data from Gärtner (1844), Wacker (1911), Namikawa (1926), Pfeiffer (1928), Weis *et al.* (1988), and Woltering (1987). Classification according to Cronquist (1988).

		Type of flowers borne on the inflorescence
Dicotyledons		
Acanthaceae	*Beloperone guttata*	Bisexual
	Pachystachus lutea	Bisexual
Betulaceae	*Alnus* spp.	Staminate
	Betula spp.	Staminate
	Carpinus spp.	Staminate
	Corylus spp	Staminate
Fagaceae	*Castanea* spp.	Staminate
	Fagus spp.	Staminate
	Quercus spp.	Staminate
Hippocastanaceae	*Aesculus* spp.	Staminate
Juglandaceae	*Juglans* spp.	Staminate
	Pterocarya spp.	Staminate
Myricaceae	*Myrica* spp.	Staminate
Oleaceae	*Olea europea*	Bisexual
Salicaceae	*Populus* spp.	Staminate
	Salix spp.	Staminate

Table 2. *Examples of families and species showing flower abscission*

Data from Gärtner (1844), von Mohl (1860), Wacker (1911), Pfeiffer (1928), Simons (1973), Woltering (1986; 1987). Classification according to Cronquist (1988).

Monocotyledons	
Agavaceae	*Aloe plicatis, Beschorneria yuccoides, Dianella nigra, Phormium tenax, Polianthes tuberosa, Sansevieria trifasciata, Yucca* spp.
Arecaceae	*Phoenix robelinii, Rhopalostylis sapida, Washingtonia robusta*
Cannaceae	*Canna* × *generalis*
Iridaceae	*Diplarrhena moraea, Iris wattii, Sisyrinchium striatum*
Liliaceae	*Arthropodium cirrhatum, Asparagus crispus, A. plumosa, Chlorophytum comosum, Gasteria verrucosa, G. picta, Haworthia attenuata, Hemerocallis fluva, H. flava, Hosta undulata, Kniphofia uvaria, Tritoma uvaria*
Maranthaceae	*Maranta leuconora*
Orchidaceae	*Cymbidium* spp. *Epidendrum candicans*
Dicotyledons	
Anacardiaceae	*Mangifera indica*
Asclepiadaceae	*Asclepias syriaca*
Balsaminaceae	*Impatiens* spp.
Begoniaceae	*Begonia* spp.
Bignoniaceae	*Campsis radicans, Catalpa speciosa*
Cactaceae	*Schlumbergera* spp.
Caprifoliaceae	*Lonicera segreciensis*
Caryophyllaceae	*Dianthus* spp., *Lychnis* spp
Cucurbitaceae	*Cucumis melo*
Euphorbiaceae	*Euphorbia fulgens, Hevea brasiliensis, Mercurialis* spp., *Ricinus communis*
Fagaceae	*Quercus alba*
Labiatae	*Salvia* spp., *Westringia longifolia*
Lythraceae	*Cuphea* spp., *Lythrum salicaria*
Malvaceae	*Hibiscus rosa-sinensis*
Nyctaginaceae	*Mirabilis* spp., *Oxybaphus viscosus*
Onagraceae	*Fuchsia* spp.
Papilionaceae	*Glycine max, Phaseolus multiflorus, Vigna radiata, Wisteria chinensis*
Primulaceae	*Anagallis* spp., *Primula* spp.
Proteaceae	*Macademia ternifolia*
Rosaceae	*Prunus* spp., *Pyrus malus, Rosa* spp
Rutaceae	*Citrus* spp.
Saxifragaceae	*Ribes* spp
Scrophulariaceae	*Verbascum* spp., *Veronica* spp.
Solanaceae	*Atropa belladonna, Browallia demissa, Capsicum annuum, Datura stramonium, Iochroma coccinea, Lycium europaeum, Lycopersicon esculentum, Nicotiana* spp., *Solanum tuberosum*
Sterculiaceae	*Theobroma cacao*
Verbenaceae	*Clerodendrun* spp.

Petal abscission

Several early authors noted that abscission of turgid petals is generally consistent at the family level (Gärtner, 1844; Darwin, 1877; Wacker, 1911; Pfeiffer, 1928). This was more recently confirmed (Woltering and van Doorn, 1988; McKenzie and Lovell, 1992*a*). The generalization does not apply to all families, though; in the Iridaceae, Ericaceae and Primulaceae, for example, abscission of turgid petals is found in some species and petal wilting, either clearly prior to abscission or not followed by abscission, in others.

Table 3A shows a number of families in which petals are usually shed while fully turgid. Interestingly, this is largely restricted to the dicots as petals abscising from monocots usually show signs of partial wilting or withering (McKenzie and Lovell, 1992*a*). Table 3B shows families in which petals generally wilt prior to their fall.

Reiche (1885) concluded that in several species the petals fell due to fruit growth rather than cell wall dissolution in an abscission zone. Shedding due to fruit growth was observed in some families in which most species drop their petals when still fully turgid, such as Boraginaceae (e.g. *Symphytum*, *Pulmonaria*), and some species in the Labiateae and Scrophulariaceae. It was also found in species where petal wilting precedes shedding, for example in several Convulvulaceae, Malvaceae and Solanaceae tested.

In some species the petals desiccate, but remain attached to the developing fruit. This occurs in several monocots, for example, in several Liliaceae and Iridaceae species, and in dicot families such as Cucurbitaceae, Gentianaceae, Hypericaceae, and Campanulaceae (Reiche 1885; Wacker, 1911; Pfeiffer, 1928). Petals may in some species also remain attached to the developing fruit, while staying fully turgid and showing growth, e.g. in several Polygonaceae studied by Reiche (1885). In *Rumex*, for example, the three innermost perigon leaves grow and surround the developing fruit. Similar observations were made in some monocots (*Eucomis punctata*,

Table 3. (A) *Examples of families containing several species showing shedding of turgid petals, and data on sepal fall in these families, when available*

Data from Gärtner (1844), Reiche (1885), Wacker (1911), Fitting (1921), Namikawa (1926), Pfeiffer (1928), Woltering (1986), Woltering and van Doorn (1988), and unpublished observations. n.a.: not applicable. The words 'some' or 'several' in the first column implies that other flowers from that family reportedly exhibit abscission after petal wilting or that the petals remain. Classification according to Cronquist (1988).

	Sepal abscission
Dicotyledons	
Apocynaceae	Sepals remain
Balsaminaceae	Sepals fall at about same time as petals
Boraginaceae	Sepals remain
Cistaceae	Sepals remain
several Ericaceae	Sepals remain
Geraniaceae	Sepals remain
Gesneriaceae	Sepals remain
Labiatae[a]	Sepals remain
Linaceae	Sepals remain
Lythraceae	Sepals remain
Magnoliaceae	n.a. (usually perigon)
Menyanthaceae	
Myrtaceae	
Nymphaeaceae	Sepals fall
some Onagraceae	Sepals fall
Papaveraceae	Sepals (calyptra) often fall before petals
Polygalaceae	Sepals fall
several Primulaceae	Sepals remain
Ranunculaceae	Sepals, when present, fall
Rosaceae	Sepals remain
Rutaceae	Sepals remain
Saxifragaceae	Sepals remain
Scrophulariaceae	Sepals remain, in some species they grow considerably (e.g. *Euphrasia*, *Mimulus*, *Pedicularis*, *Rhinanthus*)
some Solanaceae	Sepals of species showing petal abscission grow considerably (e.g. *Physalis*, *Nicandra*), forming a balloon-like structure

[a]The corolla of the Labiatae generally falls turgid, but in some species it falls (slightly) wilted.

Table 3. *(B) Examples of families containing several species showing petal shedding shortly after they wilt, and some data on sepal fall in these families*

Data from Reiche (1885), Wacker (1911), Fitting (1921), Namikawa, (1926), Pfeiffer (1928), and unpublished observations. n.a.: not applicable. The words 'some' or 'several' in the first column implies that other flowers from that family exhibit abscission of turgid petals or that petals remain. Classification according to Cronquist (1988).

	Sepal abscission
Monocotyledons	
Cannaceae	Sepals remain
Commelainceae	Sepals remain
some Iridaceae	n.a. (perigon)
some Liliaceae	n.a. (perigon)
Dicotyledons	
Asteraceae	Sepals usually remain
Berberidaceae	Sepals fall
Convulvulaceae	Sepals remain
Cruciferae	Sepals fall or remain
some Cucurbitaceae	Sepals fall
Hypericaceae	Sepals remain
Malvaceae	Sepals remain
some Onagraceae	Sepals fall together with petals, when having a common abscission zone, or sepals fall after the petals when abscission zones are separate
Polemoniaceae	Sepals remain
Portulacaceae	Sepals fall or remain
Rutaceae	Sepals remain
several Solanaceae	Sepals fall or remain
Umbelliferae	Sepals remain
Verbenaceae	Sepals remain
Violaceae	Sepals remain

Paris quadrifolia, *Veratrum nigrum*, and *V. album*; all Liliaceae) by Wacker (1911).

In a few species pollination is assisted by petal abscission. In *Mimulus guttatus* (Scrophulariaceae) the stamens are connected to the corolla, which is shed fully turgid. As the anthers touch the stigma this results in selfing (Dole, 1990). However, similar suggestions by Darwin (1877) in respect to *Digitalis* were not confirmed in more recent studies (Stead and Moore, 1983).

Petal abscission is often hastened by pollination or fertilization. Gärtner (1844), for example, showed earlier petal shedding after pollination in a range of species. However, in several other species tested, no effect of pollination on the time to abscission was found, in *Geranium molle* and in *Linum* species, for example (Fitting, 1911).

Petal abscission is an important factor in potted plants trade, where several species show extensive petal shattering (Woltering, 1986). Precocious petal abscission is also a characteristic of many cut flowers (Fischer, 1949; Woltering and van Doorn, 1988). Without a treatment that reduces petal fall, for example with anionic silver thiosulphate complex (STS, an inhibitor of ethylene action), most of these flowers would not be marketable (van Doorn and Woltering, 1991).

Sepal abscission

Wacker (1911) and Fitting (1921) noted that sepals may fall prior to petals in plants such as Papaveraceae, at the same time, as in several Cruciferae, or, most commonly, after petal fall. In many other plants only the petals fall, whilst the sepals remain attached, for example, in many Rosaceae species.

In the Papaveraceae, for example *Chelidonium* and *Eschscholzia*, the sepals remain united at their top, forming a cap (Wacker, 1911; Addicott, 1982) which is abscised as the flower opens. In *Eucalyptus* spp. a similar cap (calyptra) occurs, which, depending on the species, may be derived from sepals, petals, or from both. The calyptra falls upon flower opening (Addicott, 1982).

In most plant families the sepals remain attached and desiccate. In a few plants (some Scrophulariaceae, for example) the sepals grow, following fertilization, thereby covering the ovary. or, as in *Physalis* (Solanaceae), form

a structure at some distance from the ovary (Reiche, 1885). Sepal growth is observed in several species of the Asteraceae, Dilleniaceae, Malvaceae, and Labiatae (Endress, 1994), where the sepals take part in fruit development. Data on sepal abscission are included in Table 3A and B. The type of sepal abscission is often consistent within families, though in some families both falling and persistent sepals occur.

Abscission of stamens and styles

Depending on flower morphology, stamens may fall separately, or with the petals when they are epipetalous. Generally, stamens that are not attached to the petals wilt and remain attached, irrespective of the type of petal senescence (abscission or wilting). In these instances the dried stamens can be observed attached to the fruit. If the stamens are shed it occurs when they are either fully turgid, partially or completely wilted or even after desiccation (Table 4). When the stamens fall after desiccation it may relate to mechanical tearing by the growing fruit rather than true abscission.

In a few species the anthers may also abscise from the filament, for example, in *Geranium* spp. where the filaments subsequently desiccate and remain attached (Table 4). In other species an abscission zone is found at the filament base (von Mohl, 1860).

The styles of many plants desiccate and remain attached to the developing fruit, but in some families they abscise (von Mohl, 1860; McKenzie and Lovell, 1992*a*). Abscission may occur when styles are still fully turgid, for example in some Liliaceae, Rutaceae (*Citrus* spp.) and Rosaceae, or after wilting, e.g. in *Eucalyptus* species (Moncur and Boland, 1989). Styles may also fall after desiccation, in Boraginaceae and Onagraceae for example, but it is not clear whether in these cases their fall is due to true abscission or a mechanical effect by the growing fruit (Wacker, 1911). Examples of style shedding are given in Table 5. Families in which the styles generally are not shed include Linaceae, Polemoniaceae, Scrophulariaceae, Verbenaceae, and Violaceae.

The style abscission zone is usually located at its base, e.g. in apple (Simons *et al.*, 1970) and *Prunus* species (Simons, 1973). In other species the zone is located just above the base (e.g. *Geum*; Hannig, 1913, and *Citrus*; Einset *et al.*, 1979). The position of the style abscission zone is variable in the genus *Eucalyptus* and in some species it is absent (von Guttenberg, 1926).

Abscission zone anatomy and ultrastructure

Details of the development and anatomy of the abscission zone in male catkins were presented by Namikawa (1926). The abscission zones in pedicels have been described e.g. by Hannig (1913) and petal abscission zones by Reiche (1885) and Pfeiffer (1928).

These authors identified, on the basis of cell anatomy, three types of abscission zone.

(a) *Cells of the abscission zone smaller than adjacent cells but predominantly isodiametric* observed in certain inflorescences or individual flowers, for example, in the pedicel of *Salvia* species or *Solanum nigrum* flowers, and in male inflorescences of *Quercus robur*. The abscission zone cells often have a thinner wall than the neighbouring ones. Similarly the abscission zone of petals from numerous species, e.g. *Pelargonium* (Evensen *et al.*, 1993*b*), *Linum lewisii* (Wiatr, 1978) and *Geranium robertianum* (Sexton *et al.*, 1983), the filaments of *Calodendrum*, *Dictamnus*, *Lilium*, and *Liriodendron*, and the styles of *Lilium* and *Lonicera* all have small isodiametric cells (Pfeiffer, 1928).

Table 4. *The relationship of stamen fall with plant families*

As the number of genera investigated in each family is small, the indication of a family does not imply that the phenomenon is of general occurrence in that family. When some species from a family show a phenomenon the word 'some' is used. Data from Wacker (1911), and unpublished observations. Classification according to Cronquist (1988).

Monocotyledons
Fall while fully turgid or somewhat wilted, with the petals (some Liliaceae)
Fall following desiccation, but prior to petal fall (some Liliaceae)
Dicotyledons
Fall of the anthers; the filaments desiccate but remain (some Geraniaceae)
Fall of stamens while fully turgid, before petal abscission (Balsaminaceae; some Papaveraceae)
Fall of stamens while turgid or somewhat wilted with or shortly after the (almost) turgid petals (Acanthaceae, Boraginaceae, Gesneraceae, Labiatae, some Papaveraceae, Rutaceae, Scrophulariaceae)
Stamens fall when wilted, with the wilted petals (Convulvulaceae, Cruciferae, Malvaceae, Polemoniaceae, Portulacaceae, Solanaceae, Verbenaceae)
Stamens desiccate, then fall with or after the petals (Berberidaceae, Onagraceae, Ranunculaceae, Violaceae)

Table 5. *The relationship of style shedding with plant families*

As the number of genera investigated in each family is small, the indication of a family does not imply that the phenomenon is of general occurrence in that family. When some species from a family show a phenomenon the word 'some' is used. Data from Wacker (1911), and unpublished observations. Classification according to Cronquist (1988).

Monocotyledons
Fall while fully turgid or somewhat wilted (some Liliaceae and Iridaceae)
Fall following desiccation (some Liliaceae)
Dicotyledons
Fall while fully turgid or somewhat wilted (some Rosaceae, some Rutaceae, some Solanaceae)
Fall following wilting, together with wilted petals and stamens (Convulvulaceae, Malvaceae)
Fall after desiccation (Boraginaceae, Berberidaceae, Onagraceae)

(b) *Cells of the abscission zone smaller than adjacent cells but predominantly oblong*, for example, the cells of the abscission zone of *Aesculus* inflorescences and the pedicel of *Begonia* flowers which are oblong in the direction of the zone. These cells are often club-like at their poles, for example in petals of several *Fuchsia* species (Hannig, 1913; Pfeiffer, 1928).

(c) *Cells of the abscission zone of similar size to adjacent cells*, for example, in flowers of *Nicotiana* and *Solanum* species and *Phaseolus vulgaris* (Hannig, 1913; Pfeiffer, 1928; Yager, 1957; Lieberman *et al.*, 1983; Webster and Chiu, 1975), tomato (Roberts *et al.*, 1984). In sepals of *Magnolia* (Wacker, 1911), for example, and in petals and styles, of several species (Pfeiffer, 1928), the abscission zone cells are similar in size to the adjacent cells.

Light and electron microscopy on petal abscission zones of *Geranium robertianum* (Sexton *et al.*, 1983) and *P.* × hortorum (Evensen *et al.*, 1993*b*) showed that the volume of intercellular space increased as the flowers developed. Just before abscission the middle lamella was extensively degraded and in transverse sections, some cells in the zone eventually appeared to have no point of contact with most of their surrounding cells (Evensen *et al.*, 1993*b*).

The role of changes in cell size during abscission is as yet unclear. A drop in osmotic potential in abscission zone cells has been observed, and expansion of the separation zone cells has been extensively reported (Kendall, 1918; Pfeiffer, 1928; Sexton and Roberts, 1982). Cell swelling has been suggested to assist in breaking of the vascular strands. In abscission zones of soybean (Oberholster *et al.*, 1991) and field bean (Gates *et al.*, 1981) flowers, cell swelling has also been observed, but such swollen cells were apparently not present in the separation zone of tobacco and tomato pedicels (Jensen and Valdovinos, 1968), nor in pedicels of *Phaseolus* flowers (Webster and Chiu, 1975). It is, however, not always clear from reports in which no swollen cells were noted whether the authors had sought to prevent cell collapse. In a study on Solanaceous plants, Kendall (1918) relates turgor increase and cell swelling to the presence of starch grains in the separation layer cells, which are present in some but absent in other species.

Starch deposition in abscission zone cells was observed in flower pedicels of *Hibiscus* (Gilliland *et al.*, 1976). The number of amyloplasts in abscission zone cells of *Phaseolus* pedicels was higher than in adjacent cells (Oberholster *et al.*, 1991). Amyloplasts were also observed in the abscission layer of *Citrus* (Shiraishi and Yanagisawa, 1988) and *Magnolia* petals, in the latter they were found to disappear just prior to abscission (Addicott and Lynch, 1955). Accumulation of amyloplasts occurred in 1–3 cell layers on each side of the separation zone in *Magnolia* sepals (Wacker, 1911). In *Crocosmia* petal abscission zones, however, the number of amyloplasts was lower than in the neighbouring cells (McKenzie and Lovell, 1992*b*), which indicates that starch accumulation is not a prerequisite for abscission.

Cell division may be absent prior to abscission, as in the pedicel of tobacco (Kendall, 1918; Jensen and Valdovinos, 1967), tomato (Jensen and Valdovinos, 1967; Roberts *et al.*, 1984), and several other solanaceous genera (Kendall, 1918), in *Begonia* flowers (Hänisch ten Cate *et al.*, 1973) and *Phaseolus vulgaris* (Webster and Chiu, 1975), but small cells were observed in soybean (*Glycine max*) flowers stalks (Oberholster *et al.*, 1991), reminiscent of leaf abscission zones where cell division may precede cell wall dissolution in some species (Webster, 1968; Sexton and Roberts, 1982; Sexton *et al.*, 1977). Cell division was also observed catkin stalks of *Salix* and *Castanea*. In *Salix*, division occurred not in the actual separation layer, but in a layer beneath it. In *Betula* catkins, cell division was observed on the proximal surface, after abscission. The newly formed cells became lignified and suberized. These results suggested that cell divison is not universal, but when it occurs it is often located outside the actual separation layer and concerned with the formation of protecting tissue (Namikawa, 1926). Ethephon treatment stimulated abscission in *Glycine max* flowers, but it inhibited secondary cell division (Oberholster *et al.*, 1991), which also indicates that cell division is not essential to the separation process.

Abscission is often accompanied by the formation of tyloses, i.e. balloon-shaped outgrowths of ray cells, sometimes of paratracheal parenchyma cells, into the lumen of xylem conduits (Chattaway, 1948). Tyloses may aid in protecting distal plant parts from pathogen invasion (Lee, 1911). Tylose formation has often been observed in leaf abscission (Lee, 1911; Brown and Addicott, 1950; Leinweber and Hall, 1959; Scott *et al.*, 1964; Bornman *et al.*, 1967), and has also been found in soybean pedicels (Oberholster *et al.*, 1991), but has apparently not been reported in abscission zones of floral parts.

In an excellent series of papers, the group of Valdovinos and Jensen described the ultrastructure of the abscission zone cells in tobacco and tomato pedicels. Numerous rough endoplasmatic reticulum profiles were found at an early stage and probably relate to synthesis of proteins involved in wall breakdown. Along the entire cell wall the plasma membrane showed invaginations; it was suggested that this was due to microbodies depositing material into the cell wall region. Cell separation started at the middle lamellae in both tobacco and tomato, and in tobacco evidence for degradation of the primary wall was also found. During degradation, cell walls appeared to swell, then invaginated (Jensen and Valdovinos, 1967, 1968; Valdovinos and Jensen, 1968; Valdovinos *et al.*, 1972). Similar observations were made in pedicel abscission zones of *Phaseolus vulgaris* (Webster and Chiu, 1975) and soybean (Oberholster *et al.*, 1991) flowers.

Transmission electron microscopy on *Pelargonium* × hortorum showed that cells at the proximal fracture face were seemingly senescent, as the tonoplast and plasma membrane were no longer intact and the cells were almost devoid of recognizable organelles. The cells at the distal fracture face (the petal base) were somewhat less disrupted, but also showed signs of senescence such as a low number of intact organelles (Evensen *et al.*, 1993*b*).

From these observations, and those on cells in leaf abscission zones (Webster, 1973; Osborne and Sargent, 1976; Sexton *et al.*, 1977; Bonghi *et al.*, 1993), the picture emerges that the earliest changes in abscission zone cells are an increase in rough endoplasmatic reticulum and the number of ribosomes, both indicating increased protein synthesis. Cell wall degradation, particularly at the middle lamella, occurs next, followed, in some species, by partial or complete autolysis of the cell contents. Cell swelling seems an integral part of abscission, in some species at least.

The physiology of abscission of flowers and flower parts

Mineral nutrition, carbohydrates, water stress

In several species the proportion of pollinated flowers that set fruit decreases as the number of pollinated flowers on an individual plant or an inflorescence increases. The physiological causes of resource-limited abscission of flowers is, however, still largely unknown. Ovules fertilized first may have a temporal advantage and may prevent the fertilization of other ovules, which may then be abscised with the rest of the reproductive parts (Lee, 1988). Abscission of fertilized flowers may also be regulated by the availability of resources (Lee, 1988; Stephenson, 1981). Increasing the available mineral nutrients in *Pisum sativum* decreased flower bud abscission by 75% (Nightingale and Farnham, 1936). In citrus a higher rate of flower abscission was correlated with a lower level of micronutrients such as zinc (Kaska, 1989).

Carbohydrate partitioning in abscising structures has only been investigated in a few species. Photosynthate competition between reproductive and vegetative sinks has been suggested to play a role in the abscission of *Vicia faba* flowers (Aufhämmer *et al.*, 1987). Similarly, the results of Turner and Wien (1994) and Aloni *et al.* (1996) indicate that competition for assimilates between flowers and the adjacent young leaves may partially determine flower fall in pepper. Pate and Farrington (1981) noted that, prior to abscission, flowers of *Lupinus angustifolius* accumulated less ^{14}C assimilate than flowers which would not later abscise. Flower abscission in walnut has also been suggested to be related to competition for carbohydrates (Deng *et al.*, 1991), although previously several years of field measurements failed to establish such a relationship (Catlin *et al.*, 1987). Petal abscission in roses is insensitive to petal carbohydrate levels (van Doorn and Voginovic, 1996).

A decrease in water potential could increase abscission, due to increased ethylene synthesis (Apelbaum and Yang, 1981), whilst a further decrease in water potential may decrease abscission, due to inhibited metabolism. In abscission of rose petals, a decrease in water potential was, however, not found to advance abscission, and inhibition of abscission occurred only at a rather extreme water potential (below −2.0 MPa within 5 d following flower opening; van Doorn and Vojinovic, 1996).

Protein synthesis

Abscission apparently requires *de novo* protein synthesis, as treatment with cycloheximide, an inhibitor of translation, strongly inhibited tobacco flower abscission (Valdovinos and Jensen, 1973) and petal abscission in *Pelargonium* × hortorum (Evensen *et al.*, 1993*a*). Actinomycin D, an inhibitor of mRNA synthesis, reduced petal abscission in *Pelargonium* × hortorum to about one-quarter of that of the controls (Evensen *et al.*, 1993*a*), but had no effect on petal abscission in *P.* × domesticum (Evensen *et al.*, 1993*a*), nor on tobacco flower abscission (Henry *et al.*, 1974). The absence of an actinomycin D effect in some systems may relate to inadequate transport to and/or uptake by nuclei of abscission zone cells or, alternatively, the mRNA maybe synthesized much earlier.

Protein levels, expressed per unit fresh weight, doubled just prior to petal abscission in *Pelargonium* × hortorum, and several new proteins were found (Evensen *et al.*, 1993*b*), indicative of active protein synthesis.

Cell wall modification

Cell wall degradation in abscission zones has mainly been studied in leaves, and even for leaves it has not been characterized in detail. Prior to leaf abscission, levels of insoluble wall pectins decreased and the level of soluble pectic acids increased (Osborne, 1989). This led to the hypothesis that pectins are degraded and their bonds with other molecules cleaved, by hydrolytic enzymes. Cell wall disassembly may also involve cleavage of cellulose and hemicellulose.

A number of the enzymes involved in cell wall degradation have been characterized in relation to fruit ripening and include pectin esterase (PE; sometimes called pectinmethyl esterase), endo-polygalacturonases (PG), exo-polygalacturonase, rhamnogalacturonidase, α-galactosidase and β-galactosidase, hemicellulases, and cellulase. The latter, endo-1,4-β-D-glucanase—usually called cellulase although it is not certain that it can use cellulose as a substrate—hydrolyses β-1,4-D-glucosyl bonds which occur, apart from cellulose, in xyloglucans and other type of glucans. Xyloglucan, an important hemicellulose, can

be hydrolysed by a number of enzymes, e.g. xyloglucan endotransglycosylase (XET). Exo-polygalacturonase has been related to the late stages of peach ripening (Downs *et al.*, 1992), rhamnogalacturonidase may be involved in early stages of cell wall degradation in tomatoes (Melotto *et al.*, 1994), and both α-galactosidase and a β-galactosidase with exo-galactanase activity may be involved in cell wall degradation in tomato fruits (Carey *et al.*, 1995; Carrington and Pressey, 1996). XET activity increases considerably during kiwi (Redgwell and Fry, 1993) and tomato (Machlachlan and Brady, 1994) fruit ripening. The biochemistry and physiology of a number of these wall-degrading enzymes, in relation to fruit ripening, have been reviewed (Fischer and Bennett, 1991; Tucker and Mitchell, 1993; Seymour and Gross, 1996). Cellulase, PE, and PG have been implicated in abscission, whereas the role of other enzymes has as yet not been evaluated.

Cellulase: An increase in activity has been reported to be associated with leaf abscission (Lewis and Varner, 1970), and with flower abscission in tobacco (Lieberman *et al.*, 1983), and tomato (Tucker *et al.*, 1984). Two isoforms of the enzyme were found, one with an isoelectric point (pI) of 4.5, the other of 9.5. Gene expression of the latter occurred prior to leaf abscission (Lewis and Varner, 1970; Tucker *et al.*, 1988; Tucker and Milligan, 1991) and prior to flower abscission in soybean (Kemmerer and Tucker, 1994). Evidence for a role of this enzyme in leaf abscission followed from the work of Sexton *et al.* (1981) who introduced an antibody to this protein in the abscission layer and found that abscission was prevented. Immunoblotting showed that the pI 9.5 enzyme of bean leaf abscission zone was present in the abscission zone of soybean flowers (Kemmerer and Tucker, 1994). In bean leaves the pI 9.5 isoform was also present in the stele next to the abscission zone (del Campillo *et al.*, 1990). Its presence a few millimetres from the zone probably relates to tylose formation, which often occurs in the xylem adjacent to the abscission zone (Klein, 1923; Chattaway, 1948). Degradation of the pit membrane, which mainly consists of cellulose, is required for tylose formation.

In tomato pedicels two genes coding for endo-1,4-β-D-glucanase were found, one being highly expressed both within the abscission zone and distal to the zone, and another mainly confined to the abscission zone. It is not clear how these transcripts relate to the pI 9.5 enzyme in soybean pedicels (Lashbrook *et al.*, 1994). Subsequently, four additional transcripts were isolated from tomato pedicels, two being homologous to fruit pericarp tissue and two were novel genes whose expression was correlated with flower shedding. The mRNA of two of the six cellulase genes isolated from the pedicel was reduced to 1% when the pedicel was treated with indole-3-acetic acid, which resulted in virtually no abscission. Another cellulase gene, in contrast, increased slightly following this auxin treatment, indicating that repression of specific cellulase genes is also integral to the abscission process (del Campillo and Bennett, 1996).

Tucker *et al.* (1984) assessed the possible role of endo-1,4-β-D-glucanase in abscission, using two tomato mutants in which fruit ripening is delayed or does not occur, called *rin* (ripening inhibitor) and *Nr* (never ripe), respectively. In *rin* plants, flower abscission was as in controls, but the mutant showed a delayed increase in enzyme activity, and lower peak activity. In the *Nr* mutant, now known to be a mutation in the ethylene receptor, similar to *etr1* in *Arabidopsis* (Lanahan *et al.*, 1994), the increase of enzyme activity was more delayed than in *rin*, and peak activity was much lower than in *rin*, which correlates with a delay in flower abscission. These data indicate that endo-1,4-β-D-glucanase activity is essential in flower abscission. Similar studies have not been reported with regard to the fall of floral parts.

Pectinesterase and polygalacturonase: In tobacco flower abscission zones, no change was found in PE activity (Moline *et al.*, 1972), but PG activity increased (Tucker *et al.*, 1984). A gene for PG has been isolated from tomato flower pedicel abscission zones, which was regulated in co-ordination with flower abscission (Kalaitzis *et al.*, 1995). In the *rin* tomato mutant, PG activity in the flower abscission zone increased as in the wild type (and flower abscission was also unaltered), whilst in the *Nr* mutant, both the increase in PG activity and the onset of abscission were delayed with respect to wild type (Tucker *et al.*, 1984). This close correlation does suggest that PG may be involved in cell wall separation in flowers.

Peroxidase: A good temporal correlation was found between abscission zone weakening in *Phaseolus* pedicels and increased peroxidase activity (Henry and Jensen, 1973; Henry *et al.*, 1974). Increased activity was apparently mainly due to *de novo* synthesis, as cycloheximide treatment prevented it (Valdovinos and Jensen, 1973; Valdovinos *et al.*, 1985). The precise role of peroxidase in the zone is as yet not clear (Henry, 1979). One function of peroxidase is polymerization of lignin monomers, and this may well be the reason for the considerable increase in peroxidase activity because at the proximal side of the separation zone, cell walls become heavily impregnated with both lignin and suberin, and tylose formation must also involve synthesis of these compounds.

Role of Ca^{2+} and pH changes: Osborne (1989) noted that Ca^{2+} was lost from walls of leaf abscission zone cells, and that the affinity for added calcium ions decreased as abscission progressed. At the same time, abscission could be blocked by applying a high dose of calcium ions. The role of added calcium is, however, not unequivocal as calcium may have several effects on the physiology of

abscission zone cells. Kubart (1906) and Kendall (1918) found an acid reaction from the abscised corolla base in *Nicotiana*, and Kendall (1918) noted increased acidification in the base of *Datura* corollas at abscission. Osborne (1989) drew attention to the possibility that cell wall loosening may simply occur as a result of wall acidification. A drop in pH may release calcium ions from the walls. However, the low pH of separation zones may also be due to the presence of free pectic acid and, therefore, be a result, rather than a cause, of separation processes. Kendall (1918) also noted that in *Nicotiana* an acid reaction of the abscission zone can sometimes be found in controls, considerably prior to abscission, and that no acidity was detected in abscised *Nicotiana* pedicels. The role of free calcium and changes of acidity in the cell walls, therefore, is as yet unclear.

Hormonal control: ethylene

Inflorescences and flowers: The role of ethylene in abscission is well established. Exposure of plants to exogenous ethylene hastened inflorescence abscission in plants such as olive (Weis *et al.*, 1988), *Beloperone* and *Pachystachus* (Woltering, 1987), and flower fall in several other species (Cameron and Reid, 1981; Hoyer, 1985*a*, *b*; van Leeuwen, 1985; Rewinkel-Jansen, 1985).

The rate of ethylene production often increases prior to flower abscission, for example in the male flower of *Ecballium elaterum* (Jackson *et al.*, 1972), and in flowers of tomato (Roberts *et al.*, 1984) and *Lathyrus odoratus* (Mor *et al.*, 1984*b*). Silver thiosulphate (STS), an inhibitor of ethylene action, reduced flower abscission to zero in several species (Cameron and Reid, 1981; Mor *et al.*, 1984*a*, *b*; van Leeuwen, 1985; Hoyer, 1985*a*, *b*; Joyce, 1989; Sexton *et al.*, 1995). Amino-oxyacetic acid (AOA), which inhibits ethylene synthesis, also delayed the onset of flower abscission (Furutani *et al.*, 1989; Dostal *et al.*, 1991). Recently, some cyclic olefins have been found to inhibit ethylene action; one of these (diazocyclopentadiene, DACP) inhibited flower abscission in sweet pea (Sexton *et al.*, 1995), and another (1-methylcyclopropene, MCP) had the same effect on flower abscission in Geraldton wax flower (Serek *et al.*, 1995). The effects of these inhibitors strongly indicate that the natural abscission of flowers is controlled by endogenous ethylene.

Darkness or shade often increases flower fall (Jiang and Egli, 1993). In *Begonia* and *Hibiscus* plants, the effect of darkness was alleviated by STS, indicating mediation of the effect through endogenous ethylene (Hoyer, 1985*a*, *b*). Wien *et al.* (1989) observed increased ethylene production in *Capsicum annuum* flowers, in plants placed in 80% shade. Various other environmental factors, such as elevated temperatures (*Phaseolus vulgaris*, Monterroso and Wien, 1990; Konsens *et al.*, 1991; *C. annuum*, Rylski and Sigelman, 1982; Wien 1990), and low soil water potential (Cochran, 1936) are also known to stimulate flower abscission. Ethylene production in plants is generally increased by these factors (Abeles *et al.*, 1992). High temperature-induced flower abscission in *C. annuum* was inhibited by STS (Aloni *et al.*, 1995).

Petals and sepals: Fitting (1911) exposed flowers of numerous *Geranium* species and other members of the Geraniaceae (*Erodium*, *Pelargonium*) to illuminating gas and tobacco smoke and found that this resulted in rapid petal abscission. The effect of illuminating gas is now known to be due to ethylene. The response time to the treatment decreased with the age of the flowers. Rapid response times were later also found in *Pelargonium* hybrids (Deneke *et al.*, 1990; Evensen, 1991; Evensen *et al.*, 1993*b*).

The rate of ethylene production increased prior to petal abscission in *Digitalis* (Stead and Moore, 1983), banana (*Musa* sp.; Israeli and Blumenfeld, 1980), and *Rubus* (Burdon and Sexton, 1993). In two rose cultivars, one abscising its petals several days earlier than the other, a peak in ethylene production (by flowers) preceded abscission by about 2 d (Mayak *et al.*, 1972). Some experiments also showed increased ethylene production in *Pelargonium* (Wallner *et al.*, 1979; Deneke *et al.*, 1990), although this was not always confirmed (Armitage *et al.*, 1980).

STS reduced or prevented petal abscission in numerous species (Rewinkel-Jansen, 1985; Agnew *et al.*, 1985; Woltering and van Doorn, 1988; McKenzie and Lovell, 1992*b*). Aminoethoxyvinylglycine (AVG), an inhibitor of ethylene synthesis, was reported to prevent petal shattering in potted *Pelargonium* × hortorum (Miranda and Carlson, 1982), *Anthirrinum* (Wang *et al.*, 1977), *Digitalis* (Stead, 1985), and raspberry (*Rubus idaeus*; Burdon and Sexton, 1993).

Styles and stamens: Style abscission in lemon flowers was delayed after a spray with AVG (Sipes and Einset, 1982), indicating that abscission of this floral part, too, is regulated by endogenous ethylene.

Hormonal control: auxins

As leaf abscission is generally increased by removal of the distal leaf part, an effect alleviated by applying auxin at the cut end, it has been hypothesized that normal continuous auxin production by the distal leaf part prevents abscission (Osborne, 1989). A similar mechanism may occur in inflorescences, flowers and flower parts.

Inflorescences: Female catkins of *Alnus japonica* do not normally abscise, but when they were cut off at the upper end of the stalk, the remaining stalks were shed, indicating that fall is normally prevented by the presence of the distal parts (Namikawa, 1926), a situation reminiscent of the effect of the distal parts in leaf abscission. The fall of male catkins in *Alnus glutinosa* and *Corylus avellana* was

delayed by spraying with an aqueous solution of the synthetic auxin α-naphthaleneacetic acid (NAA), or by placing cut branches in aqueous solution of NAA or indole-3-acetic acid (IAA). In some experiments with cut branches placed in water the catkins did not abscise and remained turgid for 3 months following this treatment (Aarts, 1957). Inflorescence abscission in olives was also reduced by auxin (2,4-dichloroacetic acid) treatment (Addicott and Lynch, 1955).

Flowers: Auxins may also be involved in flower drop. Flower removal in tomato (Roberts *et al.*, 1984) and pepper (*Capsicum annuum*; Wien and Zhang, 1991) resulted in rapid pedicel abscission, but application of NAA on the cut surface alleviated this effect, at least in pepper. Seasonal fluctuations in the abscission of cotton flowers (Chatterjee and Chatterjee, 1971) and *Begonia davissii* flower buds (Hänisch ten Cate *et al.*, 1975) were correlated with the level of extractable IAA in abscission zones.

Drop of unfertilized flowers may relate to low endogenous auxin production in the ovary. Yager and Muir (1958) showed that ovary auxin production in unpollinated tobacco flowers was low compared to production in pollinated flowers. Floral abscission in *Cleome hassleriana* was found to be partially controlled by the presence of anthers, which apparently had this affect by virtue of their continued production of auxin (Koevenig, 1973).

Several reports show that exogenously applied auxins can prevent or delay flower abscission, for example, in *Lupinus* sp. (Warne, 1947; Aarts, 1957), apple (Osborne and Wain, 1951; van Overbeek, 1952), *Begonia*, dogwood (*Cornus florida*), cherry, *Phaseolus* (Addicott and Lynch, 1955), cotton (Chatterjee, 1977), and Geraldton wax flowers (*Chamelaucium uncinatum*; Joyce, 1989). Spraying with auxins is, however, not always successful (Burkholder and McCown, 1941; Wien and Zhang, 1991; Struckmeyer and Roberts, 1950). At certain concentrations auxin may increase rather than decrease abscission, but it is well established that excess auxin stimulates ethylene production (Abeles *et al.*, 1992). Furthermore, in experiments in which auxins were used as foliar sprays a surfactant was usually included in the spray solutions. Many surfactants are toxic to plants and can stimulate ethylene synthesis (Lownds and Bukovac, 1989; Knoche and Noga, 1991; van Doorn *et al.*, 1993).

IAA reduced pedicel abscission in soybean flowers, an effect which could not be overcome with a treatment with ethephon, an ethylene releasing compound (Oberholster *et al.*, 1991). Treatment with auxin reduced abscission in rose pedicels, furthermore it reversed the enhanced - abscission observed after placing stems in a solution of 1-aminocyclopropane-1-carboxylic acid (ACC) (Goszczynska and Zieslin, 1993). Both these results indicate that auxin is strongly able to decrease the sensitivity of abscission zone cells to ethylene.

Application of 2,3,5-triiodobenzoic acid (TIBA), an inhibitor of auxin transport, on the pedicel of pepper flowers hastened pedicel abscission (Wien *et al.*, 1992). This results may indicate that auxin is indeed an endogenous regulator of pedicel abscission.

Petals: Little is known about auxin effects in petal abscission. Armitage *et al.* (1980) noted that auxin did not delay petal abscission in *Pelargonium* × hortorum, and McKenzie and Lovell (1992*b*) found hastening of petal abscission by auxin in *Crocosmia*. In contrast, auxin in lanolin paste, placed on the adaxial surface of *Linum lewisii* petals, delayed the onset of petal abscission by about 5 h (Addicott, 1977). When the distal petal half was trimmed off and auxin in lanolin paste was placed on the edges, abscission was also delayed. In these experiments, the lanolin-treated petals, however, showed earlier, and more rapid, abscission than untreated control petals, an effect thought to be due to flower manipulation. The results of Addicott (1977) are therefore inconclusive.

Styles and stamens: Stylar abscission has been inhibited by auxin treatment: in cherry, plum, *Lilium*, *Oenothera*, and *Petunia* (Addicott and Lynch, 1955), and *Citrus* species (Einset *et al.*, 1979). The anthers in *Cleome hassleriana* were found to delay filament abscission, apparently through their supply of auxin (Koevenig, 1973; Koevenig and Sillix, 1973). Abscission of these floral parts may, therefore, also be regulated by endogenous auxins.

Hormones other than auxin and ethylene

Inflorescences and flowers: The possible regulating effect of other hormones is as yet unclear. Application of gibberellin on the pedicel of cotton flowers after severing the flower hastened pedicel abscission (Chatterjee, 1977). In *Begonia*, in contrast, gibberellic acid had no effect on flower abscission, and cytokinins did not have an effect either (Hänisch ten Cate and Bruinsma, 1973). Flower fall of *Capsicum annuum* could nevertheless be completely overcome by a combination of gibberellic acid and a cytokinin (Wien and Zhang, 1991).

The level of free ABA in the abscission zone of *Hibiscus* (Swanson *et al.*, 1975) and *Lupinus luteus* (Porter, 1977) flowers increased prior to abscission. Treatment of *Vitis vinifera* flowers with abscisic acid (ABA) resulted in early abscission (Weaver and Pool, 1969), and an application of ABA on the pedicel of cotton flowers, after flower removal, also promoted pedicel abscission (Chatterjee, 1977). In contrast, application of ABA had no effect on flower fall in *Begonia* (Hänisch ten Cate and Bruinsma, 1973) or *Lupinus luteus* (Porter, 1977). When exogenous ABA increased abscission in leaves it also generally increased the rate of ethylene production (Jackson and

Osborne, 1970; Abeles *et al.*, 1992), thus any effect may be indirect.

Petals: Petal abscission in *Pelargonium* × hortorum was inhibited by a spray with an aqueous mixture of gibberellins A4 and A7 (Miranda and Carlson, 1982). In *Leptospermum scoparium* (Zieslin and Gottesman, 1983) and in Golden Wave roses (Mayak and Halevy, 1970) petal abscission was delayed after treatment with a cytokinin; in *Leptospermum* this was related to a decrease in ethylene production (Zieslin and Gottesman, 1983). Intact plants of Golden Wave roses shed their petals earlier than Lovita roses, and the level of extractable cytokinins in the former was lower (Mayak and Halevy, 1970).

ABA concentrations in petals of cut roses increased prior to abscission, this rise also occurred earlier in a cultivar showing early abscission than in one with late abscission (Mayak *et al.*, 1972). In Shamouti orange (*Citrus sinensis*) a small increase in ABA concentration was found in the petals prior to their abscission (Goldschmidt, 1980). Addicott (1977) applied ABA in lanolin paste to the adaxial surface of *Linum lewisii* petals and found little effect of ABA, as compared to the pronounced enhancement of abscission by lanolin paste alone. Similarly, ABA application had no effect on petal abscission in *Crocosmia* (McKenzie and Lovell, 1992*b*).

Styles: Although a large increase was found in the endogenous concentration of ABA in styles of *Citrus limon* prior to abscission (Goldschmidt, 1980), style abscission in this species was not affected by ABA treatment (Einset *et al.*, 1979).

Phytochrome

Preliminary results from experiments in which soybean plants were locally shaded or treated with white or red light indicated that red light affected flower abscission (Heindl and Brun, 1983). More detailed experiments showed that about 80% of the flower buds of *Hibiscus rosa-sinensis* abscised when plants were held in darkness for several days (Force *et al.*, 1988; van Lieburg *et al.*, 1990). Dark-induced abscission of flower buds was much reduced by treatment with red light of low photon fluence, and the effect of red light was reversed by far red light, clearly implicating phytochrome as a regulator of dark-induced abscission (van Lieburg *et al.*, 1990). In other systems red light has often been reported to reduce the rate of ethylene production (Goeschl *et al.*, 1967; Samimy, 1978).

Use of mutants and transgenic plants

The abscission zone often consists of only a few layers of cells, and the actual abscission occurs between the cell walls of only two layers of cells. Physiological studies should, ideally, distinguish between the enzymatic activities in the separating cells and their walls on one hand, and other changes occurring close to this cell layer, such as in the deposition of material involved in prevention of pathogen invasion (including tylose formation). Thus far, the biochemical approach has not always led to a clear distinction between these two processes, mainly because of the problems with accurately separating the various cell layers and the paucity of material. Molecular methods seem now sensitive enough to distinguish between these type of cells.

Two mutants have been important in the evaluation of ethylene perception in abscission (Patterson *et al.*, 1994; Lanahan *et al.*, 1994). Both are point mutations in the membrane spanning parts of the ethylene receptor (Bleecker and Schaller, 1996), one, *etr1–1* in *Arabidopsis* (cysteine^{65} replaced by tyrosine), was produced using chemical mutagenesis (Bleecker *et al.*, 1988), whereas the other, *Nr* in tomato (isoleucine^{69} replaced by phenylalanine) was found growing in the field (Rick, 1956). The *Nr* mutant shows a delay in flower abscission with respect to the wildtype and was found to have reduced PG and cellulase activity (Tucker *et al.*, 1984), indicating that the increase in activity of both enzymes is regulated by ethylene. Ethylene is also crucial to the abscission of petals, sepals, and stamens, at least in *Arabidopsis*, as in the *etr1–1* mutant the shedding of these parts is delayed. In the wildtype both petals and sepals abscised when still fully turgid, whilst in the mutant these organs fell after they had become wilted (Patterson *et al.*, 1994), which may relate to growth of the subtending parts, hence may not be true abscission.

The production of mutants or transgenic plants may be an important tool in the study of the physiology of cell wall separation, as it has been in fruits. Transgenic plants with over-expressed or repressed activity of enzymes such as PG (Smith *et al.*, 1988; Giovannoni *et al.*, 1989), PE (Tieman *et al.*, 1992; Hall *et al.*, 1993), cellulase (Lashbrook, personal communication, 1996) and peroxidase (Lagrimini *et al.*, 1990) have been constructed. Similar constructs could be used for investigations on the role of these enzymes in abscission processes. Transgenic plants thus far showed the absence of a role of various enzymes such as PG, PE, and cellulase, when studied in isolation, on fruit softening in tomato, although some of these enzymes seem involved in the last stages of fruit degradation. Although this is at present unknown, these last stages may bear more relationship with cell wall dissolution during abscission than the early stages of fruit softening. Moreover, when an enzyme by itself seems not essential for abscission, cell wall separation can be due to the concerted action of several enzymes, hence constructs with a blocked activity of combinations of enzymes are just as important as studies on individual enzymes.

Delayed abscission of flowers, petals and styles have been reported in the tomato *Nr* mutant (Tucker *et al.*, 1984; Lanahan *et al.*, 1994) and in tomato ACC antisense plants (Atkinson, personal communication, 1996), but since similar delays have not been reported in plants that were transgenic for cell wall PE and PG it may be concluded that the effects on abscission were not obvious. At least in the PE antisense plants reported by Hall *et al.* (1993) no clear changes in flower, petal and style abscission have been noted (Bird, personal communication, 1996). Similarly, transgenic tomato plants with an antisense construct for a β-galactosidase having exo-1,4-galactanase activity showed clearly reduced enzyme activity in the fruits, but no obvious changes were observed in the abscission of flowers, petals, and styles (Verhoeyen, personal communication, 1996). The absence of effects on abscission may be due to a different isozyme profile in fruits and abscission zones. In the antisense plants used by Hall *et al.* (1993), for example, the activity of PE in the leaves remained unaffected, whereas that of fruits was reduced by 93%. The cauliflower mosaic virus 35S promoter was expressed in the leaves, hence is was suggested that the leaf PE isozyme profile is different from that in the fruits. Similarly, PE and PG isozymes in the fruits may be different from those in the abscission zones, and antisense plants constructed for the study of abscission must be based on the sequences of the isozymes found in the zones. Absence of effects on abscission in transgenic plants may also be related to the specificity of promoters. Giovannoni *et al.* (1989), for example, expressed PG against a mutant background in which PG is not expressed, using a fruit-ripening specific promoter. In several antisense constructs the 35S promoter was used (PG: Smith *et al.*, 1988; PE: Tieman *et al.*, 1992; Hall *et al.*, 1993). Although it is often assumed that 35S is a constitutive promoter, it is not always expressed; thus it remains to be evaluated whether it will be expressed in the abscission zones. If this is not the case, a search for abscission zone specific promoters has to precede experimentation with transgenic plants.

The role of hormones can also be studied using transgenic plants. In tomato, an ACC antisense construct was found to delay abscission of both petals and stamens, clearly indicating a role of ethylene synthesis in the shedding of these parts (Atkinson, personal communication, 1996). The role of auxins and cytokinins can be studied using constructs that result in over-expression of these hormones (Hamill, 1993). Auxin over-expression often results in increased ethylene production, but a combination of auxin over-expression and genes conferring ethylene insensitivity can separate the effects of auxin and ethylene (Romano *et al.*, 1993). The *ipt* (isopentenyl transferase) gene, which catalyses the rate-limiting step in cytokinin synthesis, is widely used for cytokinin over-expression (Gan and Amasino, 1995). In tomato, such an *ipt* transgenic plant had increased endogenous zeatin riboside levels (Groot *et al.*, 1995), but no differences were found in petal and style abscission (van Doorn and Groot, unpublished results), indicating no major role of cytokinins in the abscission process.

Conclusions

The fall of inflorescences, flowers, and flower parts is usually due to cell wall dissolution. However, shedding of petals, stamens, and styles may, in some species, occur solely owing to the forces generated by the growing fruit, not to cell wall dissolution. This may occur particularly following wilting or desiccation, but Reiche (1885) even claimed that the fall of turgid petals was, in several species, only due to fruit growth, an observation that warrants reevaluation.

The anatomical evidence shows that abscission zones are generally formed during organ growth, not after an environmental stimulus. Without exception, the ultrastructural data on abscission of inflorescences, flowers, and flower parts indicate high protein synthesis and high secretory activity of material toward cell walls of abscission zone cells, indicating the release of enzymes involved in cell wall separation. Both the anatomical and physiological data indicate that flower abscission is the result of active middle lamella solubilization; and in some species also of breakdown of the primary wall.

The physiological evidence indicates that both endopolygalacturonase and cellulase are involved in cell wall separation, whilst the role of a range of other enzymes that may be involved in cell wall degradation during fruit ripening, such as PE and galactosidases, in cell wall separation during abscission is as yet unclear. Experiments with mutants and antisense constructs, or other constructs in which the function of one or more enzymes is blocked, may shed more light on cell wall separation, but requires information on the sequence of the isoenzymes present in the abscission zone and, possibly, the use of abscission zone specific promoters.

The hormonal physiology of abscission indicates a role of both auxins and ethylene. Hormonal relations in flower abscission has been studied only in a few species. This limitation may also be advantageous as at least in these species (bean, tobacco and tomato) the results can be interrelated. Flower abscission is advanced by ethylene. A decrease in endogenous auxins, for example, when the flower remains unfertilized, may be a trigger of abscission, owing to an increase in ethylene sensitivity. Petal abscission is also clearly regulated by ethylene, but a role of auxin is at yet unclear. The available evidence, although scarce, also indicates that style and stamen abscission is controlled by endogenous auxin, whilst in styles at least ethylene is apparently involved. The hormonal control of sepal abscission has apparently not been investigated, but

may be similar to that in leaves, where at least both auxin and ethylene are involved.

As the initial results are promising, many of the physiological questions relating to the processes occurring in the cells and the cell walls involved in the separation process, as distinct from the processes relating to defence against microbial intrusion, may become solved by the production of mutants and transgenic plants.

Acknowledgements

The authors are grateful to Ernst Woltering and Johan Bruinsma for critically reading of the manuscript.

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