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Pollination-induced flower senescence: a review

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Abstract

Ethylene has long been implicated in the control of the senescence of many cut flower species, but the control of senescence in relation to wild species has received much less attention. The longevity of individual flowers varies greatly from species to species; in some each flower is open for just a few hours, whilst in others the flower may persist for several weeks, or even months. The functional life of the flower may be terminated by petal wilting, abscission or a colour change of all, or part, of the perianth. In some species pollination appears to reduce floral longevity whilst in others, particularly those species having short-lived flowers, the pattern of flower development and senescence appears unaffected by pollination.

Examples of the various pollination-induced strategies shown by plants are presented and the role of ethylene and other potential mediators of senescence in these processes discussed.

1. Longevity of flowers

As would be expected there is tremendous diversity in the longevity of individual flowers, Molisch [23] catalogued the duration of flower opening of a large number of plants. Some flowers persist for just a few hours, and this may be during the day or night; others last for about a day, yet others for several days or, in the case of the really long-lived flowers, the flowers may persist for several weeks (Table 1). The control of flower longevity is of interest to horticulturalists since cut flowers with a longer vase life will have a greater commercial value, whilst in agriculture the length of the pollination period will influence fruit and seed set. Ecologists too are interested in flower longevity for similar reasons, since the duration of flower opening influences seed set and therefore the fecundity of any given individual genotype. The pattern of flower senescence may also effect the frequency of self-pollination and thereby further influence seed set.

In the case of the longest lived flowers it is perhaps not surprising that flower longevity may be modified by environmental factors or more dramatically by fertilisation or pollination. The advantages to the plant for reducing flower longevity by pollination, as opposed to successful fertilisation, may be two-fold. Firstly, once sufficient pollen has been deposited upon the stigma for full seed set then further deposition of pollen is wasteful in terms breeding potential; furthermore, the growth of excessive pollen tubes may result in competition for stylar food reserves which are required to nourish the growing pollen tubes. Secondly, the maintenance of elaborate floral structures must be a costly process, both in terms of respiratory energy used and the transpiration of water, if this can be minimised it must be to the plants advantage. In the shorter-lived flowers it is of course unlikely that pollination, or other events, will influence floral longevity, nevertheless the internal control of the timing of senescence is of considerable interest.

2. Endogenous control of flower longevity in short-lived flowers

Of those species so far studied it would seem that the flowers of some species are ethylene sensitive and that in these endogenous production of ethylene terminates the effective period during which pollination can occur. In those species in which ethylene plays no part the control of flower senescence has not yet been elucidated.

Table 1. The longevity of the flowers, in either hours or days, of selected plants. Modified from [23]

	Duration of opening (h)		Duration of opening (days)
Flowers open by day		Dianthus prolifera	2
		Papaver somniferum	2
Hibiscus trionum	3	Potentilla formosa	3
Oxalis stricata	8	Escholitzia californica	5
Tradescantia virginica	12	Digitalia purpurea	6
Hemerocallis fulva	14	Oxalis lasiandra	6
		Parnassia palustris	8
Flowers open by night		Cyclamen europaeum	10
		Vanda coerulea	30
Cereus nycticalus	5	Phalenopsis grandiflora	50
Mirabilis longiflora	7	Phalenopsis shilleriana	90–135
Cereus grandiflorus	7	Dendrobium crassinode	422

Kende and Hanson [18] showed that in *Ipomoea* corolla rib segments behaved in a manner identical to the intact flower, clearly in such a case the developmental pattern of the corolla must be pre-programmed and therefore pollination is unlikely to influence flower senescence. The inrolling of corolla rib segments was accompanied by increased ethylene production, furthermore application of ethylene hastened inrolling as long as the flower from which the segments were removed was within a day of opening, younger flowers were not sensitive to exogenous ethylene. A similar situation exists in *Tradescantia* in which the flowers are only fully sensitive to ethylene on the day of anthesis [36]. The application of silver thiosulphate (STS) to *Ipomoea* flower buds, usually a very effective ethylene antogonist [38, 39], is ineffective at prolonging the open period because in blocking ethylene action flower opening is also prevented.

In *Linum lewisii* flower buds open early in the morning and petal abscission occurs in mid-afternoon of the same day. Because of the speed and uniformity of behaviour Addicott [1] concluded that petal abscission occurred autonomously, without influence of either pollination or fertilisation. This work further showed that the rate at which abscission occurred could be modified by application of either abscisic acid or indole acetic acid (IAA) but no experiments were performed with ethylene.

The flowers of day lilies (*Hemerocallis fluva*) produce little ethylene either as buds, or later as the flower collapses. The maximum rate of ethylene production from the flower was less than 1 nl g^{-1} fresh weight (Stead, unpubl. results), whilst in *Petunia* and *Dianthus* the rate exceeds 20 nl g^{-1} fresh weight [41, 9]. As would therefore be expected neither STS nor the ethylene production inhibitor aminoethoxyvinylglycine (AVG) influence flower longevity in daylilies, neither do these compounds prevent the opening of flowers when applied to buds the day before flower opening. In this species however, cycloheximide (CHI) is very effective at prolonging the life of the flower as long as it is supplied just as the flower opens [21]. Application of CHI to younger buds prevents flower opening, thus CHI, and by inference protein synthesis, appears to regulate flower opening and flower senescence in daylilies.

The observation that CHI inhibits both petal senescence and protein degradation, whilst inhibitors of RNA biosynthesis are ineffective, implies that control of petal senecence in day lilies is dependant upon proteolysis. Electophoretic separation of the petal proteins from daylilly flowers of differing ages supports this contention (Lay Yee et al., in prep.).

3. Control of flower longevity in long-lived flowers

The greatest amount of information pertains to cut flowers and treatments which may increase their vase life. Although the floral longevity of some species is clearly controlled by ethylene there are many species in which the flowers appear to be insensitive to ethylene – just as occurs with short-lived flowers [44]. In roses for example vascular blockage, often due to bacterial infection at the cut

surface, appears to limit water uptake and therefore cause premature wilting of the flower relative to flowers left attached to the plant [37]. In many *Protea* species the flowers and subtending bracts blacken when left under low light conditions typical of those in which cut flowers may be placed; if left under high intensity illumination, however, the flowers remain fresh. Thus carbohydrate supply appears to limit the vase life in this species and indeed stems provided with a supply of carbohydrate will often remain acceptable as cut flowers for much longer (Reid, pers. comm.) In other species, however, the addition of sugars to the holding solution increases microbial contamination, causing vascular blockage which limits water supply and thereby accelerates flower senescence [37].

4. Pollination effects

In most cases pollination simply accelerates the pattern of floral senescence seen in unpollinated flowers.

If pollination is to deter further visit by pollination vectors, and so reduce pollen wastage, then a number of strategies can be envisaged which would accomplish this goal:

1. Reduction and/or modification of the composition of nectar.
2. Structural modification, particularly corolla wilting.
3. Modification of the colour of all, or part, of the flower.
4. Abscission of all, or part, of the corolla.

In fact there is evidence that all four strategies may exist in different plant species.

4.1 Nectar modification

The composition of nectar can certainly change in response to external stimuli. Gottsberger et al. [14] found that damaging the nectary tissue in *Hibiscus rosa-sinensis* caused an increase in the amino acid content of the nectar within 5 min; an increase due mainly to changes in the levels of asparagine. Willmer [42] and Corbet and Willmer [6] also found changes in the amino acid content in relation to insect visits and tissue damage. However, whilst there is clearly the capability for changes in nectar composition and quantity to occur, in order to influence pollinator behaviour the insect must be able to detect the presence, or composition, of the nectar before it enters the flower. So far studies on foraging behaviour suggests that insects predict the probable reward from the next flower to be visited by the reward received in the last flower visited [3]. In *Oenothera*, the flowers of which are relatively short-lived, pollination can accelerate both the collapse of the petals and a change in petal colour [10], but remarkably the removal of the nectar, without pollination, has a similar effect, however it remains unclear how nectar removal alone might influence flower senescence. The work to date has concentrated on the ecological aspects of any changes in the composition of the nectar but as yet there is no information concerning the physiological control of such changes. Clearly this is an area which warrants further research.

4.2 Structural changes

Amongst those species favoured by the Horticultural trade as cut flowers there are many species in which the end of the useful vase life is marked by petal wilting. In many of these species ethylene accelerates petal wilting whilst the natural senescence is accompanied by increased ethylene production. In these species pretreatment of the cut flowers with STS can increase the vase life considerably (Table 2).

In carnation (*Dianthus caryophyllous*) the senescence of flowers is characterised by the inrolling of the petal margins, this process is accelerated by ethylene and pollination [24]. Within 3 h of pollination the production of ethylene from the stigmas increased 10-fold [25] at which time a small increase in ethylene production from the ovary and receptacle was detectable. Only later (between 8 and 24 h after pollination) did the rate of ethylene production from the petals increase [25]. Because increased ethylene production occurs so rapidly after pollination it suggests that this is the result of an interaction between the growing pollen tubes and the stigmatic tissues, since fertilisation could not occur so soon after pollination and germinating pollen grains produce little or no ethylene when cultured *in vitro*.

In *Petunia hybrida* pollination can also bring

Table 2. Species for which treatment with silver is recommended for extending the vase life. Data from [26]

1. Species of cut flowers in which the vase life can be significantly enhanced by treatment with STS	
Aganpanthus spp.	Euphorbia fulgens
Alstromeria spp.	E. pulcherrima
Anthirrinium spp.	Freesia hybrids
Aster spp.	Gladiolus spp.
Consilida ambigua	Kniphofia spp.
Cyclamen spp.	Lathyrus odoratus
Delphinium spp.	Lillium spp.
Dianthus caryophyllus	Mattholia spp.

2. Species of cut flowers which are recommended to be treated with silver nitrate or silver-containing preservatives (other than STS)	
Anthurium spp.	Lobelia fulgens
Bouvardia spp.	Lysimachia clethroides
Callistephus chinensis	Phlox spp.
Campanula spp.	Phystegia virginiana
Chrysanthemum moriflorum	Rosa hybrida (some cultivars)
Eremurus spp.	Rudbeckia spp. Saponaria spp.
Forsythia spp.	Scabiosa spp.
Gerbera spp.	Silene spp.
Gyposophilia paniculata	Solidago spp.
Leucospermum cordiflorum	Trachelium spp.

3. Flowers known to be adversly affected by ethylene but for which treatment with silver is either not recommended or for which the effects of silver are not documented	
Aconitum spp.	Dendrobium spp.
Alstromeria spp.	Dianthus barbatus
Cattleya spp.	Paphiopedilum spp.
Cymbidium spp.	Prunus spp.

about the collapse of the corolla, early hypotheses suggested that the growing pollen tubes brought about a wounding-like response since corolla wilting also occurs if the stigma is removed or pierced with a needle [12]. All these treatments also elicit rapid ethylene production; indeed Pech et al. [27] have shown that ethylene production increases within 5 min of pollination. Other workers have demonstrated that, as a result of either wounding or pollination, a water soluble substance is translocated down the style within 4 h [13]. Although not identified, the eluates from detached, pollinated styles did not contain elevated levels of the ethylene precursor 1-aminocyclopropane 1-carboxylic acid (ACC). Despite this observation there was, until quite recently, the belief that ACC might be the transmitted signal in pollinated flowers (see below).

4.3 Perianth colour changes

The occurrence of perinath colour changes appears to be widespread with examples from over 50 Angiosperm families (M. Weiss, pers. comm.). Subtle pigmentation changes in parts of the inflorescence of, for example, *Phalenopsis*, after pollination were reported by Curtis [7]; in some *Cymbidium* blossoms, anthocyanins accumulate in the labellum after pollination or treatment with ethylene [2]. Many species of orchids have been shown to increase their rate of ethylene production after either pollination or emasculation, indeed Burg and Dijkman [5] reported two peaks of production, one a few hours after treatment the other about 40 h later. Woltering et al. [43] have subsequently shown that the first peak is associated with the labellum colour change and the later peak with the wilting of the petals and sepals.

The significance of such changes is well illustrated by a study on several Australian shrubs [19] in which it was shown that insect pollinators showed a strong preference for flowers with white or yellow flowers whilst flowers which had changed to various shades of red were visited very infrequently. This change in colour occurred at the same time that stigma receptivity declined and may have been linked to fertilisation.

In *Lupinus albifrons* flowers the banner spot of the standard changes from white or pale yellow to magenta a few days after opening. This colour change is accelerated by either pollination or treatment with ethylene, moreover the maximum rate of ethylene production coincides with when the banner spot is changing colour [35]. The increase in ethylene production appears to be derived not from the banner spot or the adjacent tissues, but almost entirely from the keel and ovary. Furthermore, once the colour change is complete, the production of ethylene by the standard decreases significantly (Figure 1). There was a 10-fold increase in ethylene production from either the keel plus pistil or the pistil alone, as the banner spot changes colour. However, on a fresh weight basis the rate of production from the pistil is much greater (approximately 100 nl $gFW^{-1} h^{-1}$). This situation is identical to other species in which the pistil, and in particular the style, has the highest rate of ethylene production per unit fresh weight of all the floral tissues [15, 24, 36].

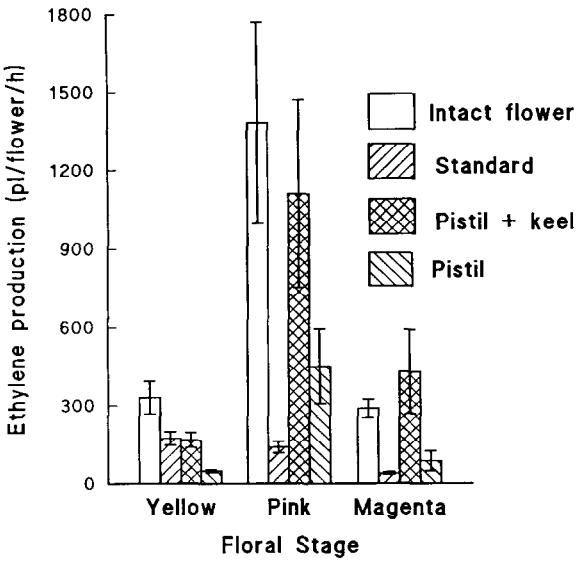

Fig. 1. Ethylene production from isolated lupin flowers and dissected parts of the flower at three developmental stages defined by the colour of the banner spot. Measurements were taken from a minimum of 20 replicates; data shown with standard errors.

4.4 Abscission of perianth parts

In members of the Scrophulariaceae in particular, pollination brings about the rapid abscission of the corolla without any loss of either water or corolla constituents. Following pollination in *Digitalis*, for example, the corolla abscises within 24 h and at this time there is no detectable change in fresh weight, protein content or membrane permeability between the corollas of pollinated and unpollinated flowers (Table 3). The corollas of unpollinated flowers remain attached for about six days following stigma opening and there is gradual decline in corolla constituents and, especially in the last 24 h before corolla abscission, a rise in membrane permeability and respiration (Table 3). Ethylene production rapidly increases after pollination and the force required to detach the corolla decreases, such that abscission is complete within 24 h of pollination, whereas the corollas of unpollinated flowers remain attached for several days after the stigmatic lobes separate and become receptive [33]. The eventual abscission of the still-turgid corolla from unpollinated *Mimulus* flowers, another member of the Scrophulariaceae, brings about self-pollination thus ensuring seed set [8]. It has also been suggested that by shedding large coloured perianth parts the plant may be less attractive to herbivores and may also reduce the possibility of attack by fungal pathogens.

In *Papaver rheas* too flower longevity is greatest when seed set is lowest (Stead, unpubl.). Thus during winter months, even when grown in environmental chambers, pollinator activity is low and therefore few seeds are set and petals only abscise 4–5 days after flower opening. In summer, when numerous small insects pollinate the flowers, seed set is high and petals abscise within 1–2 days of flower opening.

5. Pollination-induced signals

In experiments such as those of Nichols et al. [25] with carnations it is apparent that following pollination a wave of increased potential for production

Table 3. The levels of certain constituents and physiological activity in *Digitalis* corollas at the time of stigma opening and when abscissed (both pollinated and unpollinated). Data modified from [33]

	Floral stage		
		Corolla just abscissed	
	Stigma opening	Pollinated	Unpollinated
Fresh weight (mg)	521.5	519.5	530.6
Dry weight (mg)	63.4	61.9	50.2
RNA (μg)	108.9	97.1	104.5
Protein (μg)	2.42	2.20	1.75
Respiration ($\mu l O_2 h^{-1}$)	20.85	23.28	16.64
Solute leakage from pre-frozen corollas (mho)	7.13	8.06	24.25
from fresh corollas as a % of pre-frozen corollas	35.6	35.1	69.1
Ethylene production (nl flower^{-1} h^{-1})	0.48	5.72	1.85
Corolla detachment force	131.3	0	8.4

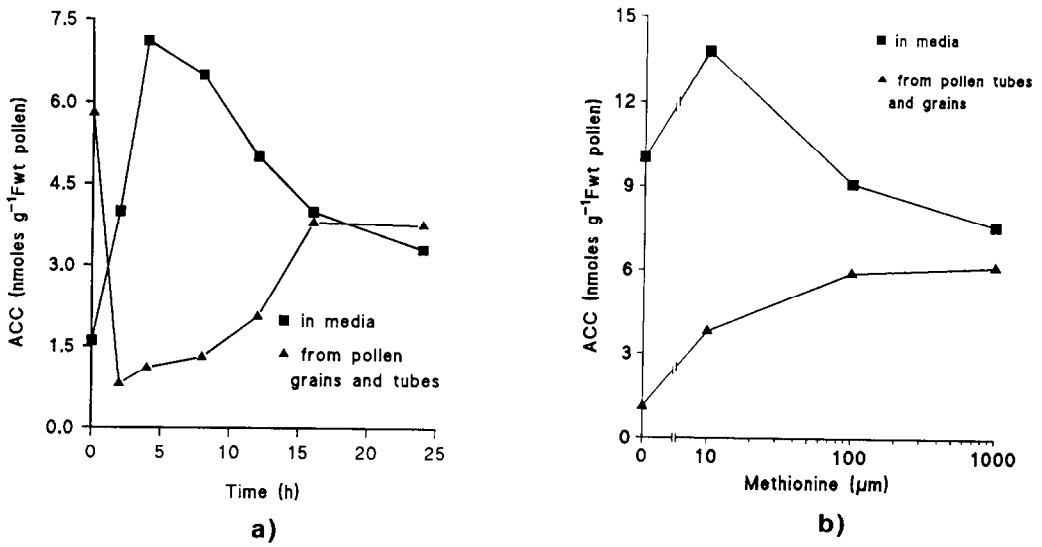

Fig. 2(a). The production of ACC by *Digitalis* pollen germinating *in vitro* in Kwacks medium. ACC in the media (■——■) and in the pollen grains/tubes (▲——▲). (**b**) similar but with germination media supplemented with methionine and ACC determined in the media (■——■) and pollen grains/tubes after 10 h (▲——▲). ACC measured according to the method of [16].

of ethylene passes through the tissue. Removal of various tissues following pollination also indicate that pollination-induced signals are generated within floral tissues and that these are transmitted through the style [32]. The strength of any such signals is probably related to the amount of pollen applied. In *Digitalis* increasing amounts of pollen cause more and more seeds to be set and reduce the time to corolla abscission. The amount of ethylene produced by the flowers of both *Digitalis* and *Nicotiana* is also related to the amount of pollen applied [34, 16].

In previous experiments [5] it has been suggested that pollen-held auxin causes an increase in ethylene production from the column and that it is the intercellular movement of this gaseous ethylene that acts as an autocatalytic trigger for further ethylene production. More recently it has been suggested that ACC maybe translocated between the flower parts [40] as it is in response to waterlogging in tomato plants [4]. In carnation however Nichols et al. [25] found that the levels of ACC in the various tissues only increased after they detected increased ethylene production, furthermore they found that the relationship between ACC content and ethylene production was very different between the stigmas and the remaining floral tissues, indicating that some aspect of the biosynthesis of ethylene must differ between these tissues.

The discovery of abundant ACC in the pollen of

Table 4. Levels of IAA in pollinia of two orchid species as determined by ELISA. Data from [11] using a goat anti-IAA antibody kindly supplied by DDS, Copenhagen and similar to that used by [22]. Pollinia were placed in 80% methanol at 4 °C for 24 h; after centrifugation the supernatent was assayed either directly or after solvent partioning with ethyl acetate according to [29]. The pellet was re-extracted by homogenisation in 80% methanol and again either assayed directly or purified by solvent partioning. All figures corrected for percentage recovery determined by the addition of ^{14}C IAA to the original material; in all cases % recovery of label exceeded 90%

	IAA immunoreactive material μg IAA/g Fwt.					
	Original Crude extract			Purified IAA fraction		
	Diffusate	Pellet	Total	Diffusate	Pellet	Total
Onchidium splendidum	24	3	27	23	3	26
Lemboglossum bictoniense	104	46	150	108	5	113

many species [40, 34] certainly supported the view that ACC could be the transmissable signal in some species. In those species in which the pollen does not contain abundant ACC it was suggested that the pollen might synthesise ACC upon hydration or germination [34]. Experiments in which *Digitalis* pollen, a species which normally contains very little ACC, was germinated *in vitro* showed that low levels of ACC did accumulate in the germination media (Figure 2a). The levels of ACC produced were however very low, even when the very basic germination media was supplemented with methionine (Figure 2b), although no attempt was made to supplement the media with other compounds which might be essential for the biosynthesis of ACC.

Even in those species with abundant pollen-held ACC it is obvious that the amount of ACC likely to be deposited on the stigma at pollination is small compared to the ethylene produced. In *Nicotiana*, for example, the amount of ACC derived from pollen would sustain floral ethylene production for no more than 5 h [16], further synthesis of ACC must therefore occur within either the stylar tissues or the growing pollen tubes. That *de novo* synthesis of ACC occurs in the style after pollination has now been established by Hoekstra and Weges [17]. Furthermore, Pech et al. [27] demonstrated that whilst ACC could be easily washed from *Petunia* pollen into water, when placed in a solution of equivalent osmotic potential to that of the stigmatic secretions, little or no ACC was eluted from the pollen.

Although early reports suggested abundant auxin within orchid pollen, an observation we are now able to confirm by the use of a highly sensitive immunoassay (Table 4), the only other evidence for the involvement of auxin in the control of flower senescence comes from the application of exogenous auxins to either the standing solution used for cut flowers or by application to the stigma surface.

In *Dianthus* application of greater than 10^{-6} M IAA to isolated petals causes increased production of ethylene and rapid petal inrolling [45], however it would seem unlikely that such high levels of auxin would occur naturally within the petals. Similarly applications of both IAA and 2,4-D to the stigma cause increased ethylene production and accelerated petal inrolling but once again it is unlikely that such high concentrations would occur naturally. In *Digitalis* various methods of applying IAA to the stigma failed to induce corolla abscission [32].

Other suggestions as to the nature of the transmitted signal have included some form of membrane pertubation manifested by changes in the electrical potential [30], although in the experiments reported it would seem that the electrodes were placed such that the physical disruption to the stylar tissue, by the growing pollen tubes, could have been responsible for the changes seen. More recently there have been reports that the sensitivity to ethylene may be increased after pollination, indeed Whitehead and Halevy [41] have suggested that the "sensitivity factor" is a fatty acid, since they were able to show that after pollination in *Petunia* the senescence of the corolla is hastened by ethylene to a greater extent than in unpollinated flowers. Furthermore, short chain fatty acids, such as octanoic and decanoic acid, increased after pollination and application of small droplets of these chemicals to the stigma, increased the sensitivity of the flowers to ethylene in a manner similar to pollination.

Far from suggesting that wounded or pollinated stigmas produce a compound which accelerates senescence Lovell et al. [20] suggested that the intact stigma may produce a compound which prevents senescence and that it is the removal of the source of this compound, by either wounding or pollination, that brings about accelerated wilting.

Given these various observations it is evident that the transmittable signal, produced, or metabolised, in response to pollination, still remains to be identified.

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