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Review Article

The Effect of Pollination on Ethylene Production and Flower Senescence in Crop Plants

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Abstract

Flowering is the transition from the vegetative phase of a plant's lifecycle to the reproductive phase. The final stage of flowering is flower senescence, which leads to the termination of the flower. Flower senescence includes flower wilting and dehiscence (opening) of floral organs. Senescence of other parts of the plant is usually a gradual process, but flower senescence is generally much quicker. Ethylene, a simple gaseous hormone, is thought to be a key regulator of flower senescence. Ethylene is involved in many different aspects of plant development and growth, including fruit ripening. Studies of ethylene biosynthesis and signaling pathways in model and ornamental plants have provided tools for the study of ethylene effects in other systems, including crop plants. In ornamental plants, flower senescence has been shown to be ethylene dependent. Manipulation of the target genes for ethylene signaling or biosynthesis can improve flower longevity. This is an important area of research for the floriculture industry, as it could lead to the development of new varieties of flowers with longer vase life.

Keywords: *Crop Plant, Ethylene, Ethylene Signalling, Flower Senescence, Gene Expression, Pollination.*

Introduction

Flowers have an indispensable role in the life cycle of an angiosperm. They are responsible for seed production through sexual reproduction. Pollination can occur through self-pollination or through animal or wind-mediated cross-pollination. However, pollination is usually essential to produce seeds and fruit, and therefore it is a key element in the productivity of crops including cereals, pulses, fruits, and nuts. Flowers that senesce before pollination may represent a wasted opportunity for seed production and cost a plant energy and other resources to build. On the other hand, flowers that do not senesce following pollination may distract pollinators from unpollinated flowers and result in pollen limitation and reduced seed set. It is therefore to be expected that evolution would favour systems in which flower senescence is triggered by pollination and occurs rapidly thereafter but does not occur without pollination. Such a situation would also be optimal to maximise crop yield. There are flowers that persist for just a few hours while there are some that last for days or even weeks (Table 1). The control of flower longevity is of great interest to horticulturists as cut flowers with a longer vase life fetch more commercial value. Similarly, in agriculture the length of the flowering period and pollination period influences fruit and seed set.

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Table 1: Flower duration in horticulture is variable, as is its ethylene sensitivity

Flowers	Duration of opening (hours/ days)	Ethylene sensitivity	References
Hibiscus rosa-sinensis	3 h	Ethylene sensitive	Woodson, *et al.*, 1985
Tradescantia virginica	12 h	Ethylene sensitive	Trivellini, *et al.*, 2016
Mirabilis longiflora	7 h	Ethylene sensitive	Trivellini, *et al.*, 2016
Hemerocallis fulva	14 h	Ethylene insensitive	Chakrabarty, *et al.*, 2009
Dianthus caryophyllus	2 days	Ethylene sensitive	Satoh, 2011
Cyclamen europaeum	10 days	Moderate to highly ethylene sensitive	Halevy, *et al.*, (1984)

In principle, the duration of flower life could be modified by pollination, by fertilization and by environmental factors. Theoretically, regulating flower longevity by pollination is considered the most efficient of these options (Buchanan-Wollaston, *et al.*, 2005; Rogers, 2013). Once sufficient pollen has been deposited on the stigma then further pollination is a waste in terms of breeding potential. Also, excessive growth of pollen tubes might result in competition for stylar food reserves which are required for nourishing growing pollen tubes. Maintenance of elaborate floral structures is a costly process in terms of respiratory energy and water transpiration (Chapin and Jones, 2007; Jones, 2013). It is therefore likely that senescence of floral organs following pollination is under selective pressure.

The Machinery of Flower Senescence

From an evolutionary perspective, petals are derived from leaves (Friedman, *et al.*, 2004), and subsequently flower senescence shares common physiological and biochemical processes with leaf senescence, such as disintegration of intracellular structures, degradation of macromolecules and membrane systems, and recycling of substances (Xu and Hanson, 2000; Price, *et al.*, 2008). However, flower and leaf senescence are also distinct from each other in many respects (Price, *et al.*, 2008; Wagstaff, *et al.*, 2009). For instance, flower senescence is often activated or accelerated by pollination, and is thus tightly regulated by internal developmental signals, rather than by environmental signals, which contrasts with leaf senescence. Secondly, leaves are the primary site of photosynthesis, so nutrient remobilization is a critical event during leaf senescence (Maillard, *et al.*, 2015). While floral organs will contain some nutrients, this is likely to be a less critical element of flower senescence.

Flower senescence has been studied using a range of approaches, and a number of unexpected observations have been made. Flower senescence can be visualized as wilting, withering or abscission, and different studies have used different characters to define senescent organs. Interestingly, different floral organs are affected by senescence differently, senescing at different speeds (Ahmad and Tahir, 2015). The general outline of flower senescence diverges widely between different genera or even within species of the same genus. Depending on the species, flower senescence can be either dependent on ethylene or independent of this hormone and as such a distinction is made between ethylene dependent and independent flower senescence (van Doorn and Woltering 2008). In most species of the Geraniaceae, for example, the petals senesce whilst fully turgid, petal fall being sensitive to exogenous ethylene. In the Caryophyllaceae, the perianth is generally ethylene sensitive whereas in the Asteraceae it is usually

ethylene insensitive (van Doorn, 1997) (Table 1).

Flower senescence is important from the physiological point of view as it allows molecules from the wilting organs to be remobilized to emerging organs such as new flower buds or storage organs like tubers, bulbs etc (Fischer, 2012). Such molecules may include nutrients, regulatory proteins and stress related proteins, although it is thought that nitrogen-containing compounds may be the most significant resource that is recycled during senescence (Shahri and Tahir, 2014) (Fig 1). The period for which the flower remains open and functional (known as the floral longevity) is a key trait determining the reproductive strategy of a plant and the energy required for distributing resources and flower maintenance (Spiglar and Woodard, 2018).

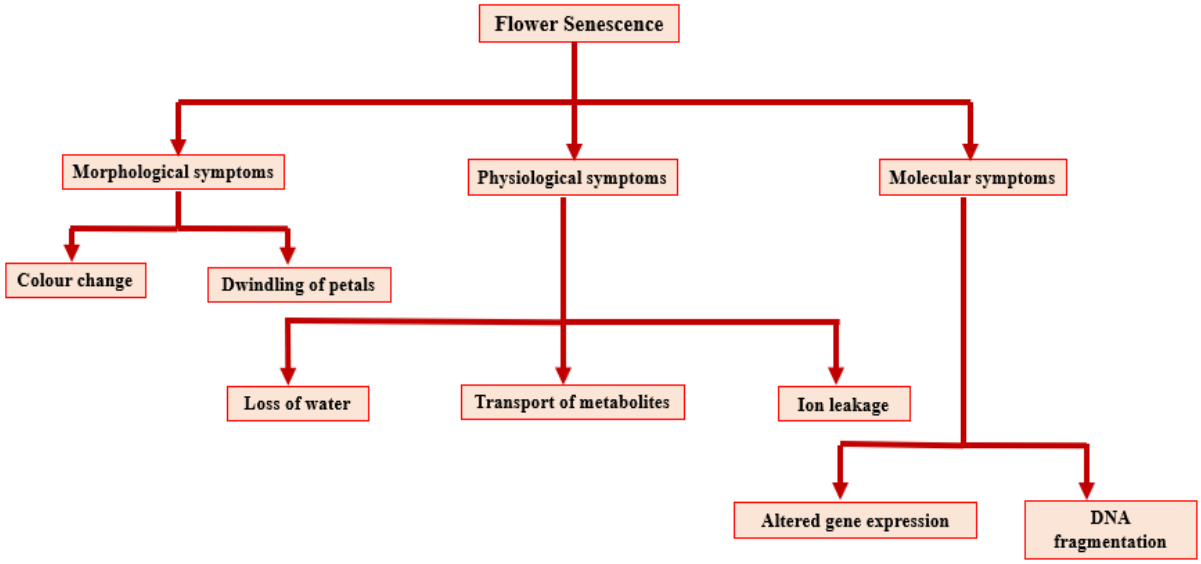

Figure 1: Understanding flower senescence. Various symptoms indicate flower senescence, including morphological, physiological and molecular symptoms.

Senescence is usually described as a progressive temporal event. In most flowers studied to date, including petunia, carnation and orchids, flower senescence occurs at the same time as a rise in endogenous ethylene production and flower senescence can be delayed by inhibiting ethylene production (Jones, 2008, Chun In, *et al*., 2013, Ichimura, *et al*., 2009, Almasi, *et al*., 2012, Meir, *et al*., 2019). The ability to inhibit flower senescence by inhibiting ethylene production suggests a direct link between ethylene and senescence, and also provides a mechanism to enhance the shelf life of ornamental flowers. Shibuya, *et al.,* (2000) reported that ethylene production in petals did not increase following the removal of gynoecia. This may suggest that floral ethylene is produced in gynoecia of this system, or alternatively that gynoecia trigger ethylene production in petals or other organs of carnation flowers, possibly in response to detecting pollen arriving at the stigma. In *Digitalis* flowers, petals abscise upon exposure to ethylene. In these flowers, ethylene production in gynoecia increases with the progression of flower senescence, but ethylene production in petals does not (Stead and Moore, 1983, Goto, *et al*., 1999). In this example, ethylene produced in the gynoecium appears to act at the petal abscission zone, leading to petal loss.

Different floral organs function for different periods of time. While it is usual to think about floral longevity in relation to the need for pollination and ovule fertilisation, flowers also have the ability to continue to function as male parents even after their ovules have been fertilised (Ishii & Sakai 2000). For example, in *Erythronium japonicum* (Asian fawnlily), floral longevity was almost constant

irrespective of on which of days 1 to 12 post-anthesis flowers were pollinated (Ishii & Sakai 2000). This 12 day period was subsequently shown to be necessary for *E. japonicum* flowers to shed most of their pollen (Ishii & Sakai 2001). Based on these results, Ishii & Sakai (2001) proposed that flowers have a genetically determined minimum longevity that functions to facilitate male reproductive function, not just female receptivity. They reported that flower senescence is advanced by the deposition of pollen grains on the stigma but that there exists a minimum longevity during which the flower never shows senescence, even if it is pollinated with a sufficient number of pollen grains.

Different floral organs play diverse roles and hence they senesce at different rates and may also respond differently to senescence signals. It is therefore important to have specific coordination between signals for senescence among different floral parts. Rieu, *et al.,* (2003) revealed that, in tobacco, ethylene regulates petal senescence but at the same time the ovary develops without any interruption, so must be insensitive to ethylene. In a normal flower, petals, anthers and the stigma are no longer required following pollination, whereas the ovary will mature to nurture the developing seeds, so it may often be the case that the ovary develops insensitivity or resistance to senescence-causing signals such as ethylene. In many species there is also a mechanism for rescuing resources from the degenerating organs such as petals, and diverting them to other parts of the plant such as the developing ovary (Stead and van Doorn, 1994). Wagstaff, *et al.,* (2003) showed that petal margins start degenerating before the centre position of the petal, suggesting that there is a gradient of the senescence signal or sensitivity to it across a single floral organ.

The overall pattern of flower senescence varies widely between different genera. Depending on the species, flower senescence is visibly shown either by wilting followed by abscission or simply by abscission. Wilting is due to turgor loss of petals, and is often accompanied by a colour change. In species that show wilting of the perianth, an important function of senescence may be to allow remobilization of key metabolites from the senescing organs back into the developing ovary (Chapin & Jones, 2007), developing flower buds (Bieleski, 1995, Wojciechowska, *et al*., 2017) or tuber formation (Fischer, *et al*., 1998).

Since one of the main functions of senescence is to recycle nutrients from fading parts of the flowers to the developing fruits, grains and rest of the plant (Gan and Amasino, 1997), a better understanding of the key regulators of senescence will help to maximize crop yield and improve quality of fruits, vegetables and cut flowers. However, there are other reasons why an understanding of floral senescence is important in optimising crop yield. For example, broccoli is a commonly used vegetable with floral heads comprised of immature florets arranged in whorls on an edible fleshy stem. Each floret consists of an immature flower bounded within sepals (containing chlorophyll). Chlorophyll degradation within these sepals results in the rapid yellowing of the heads during storage (Pogson, *et al*., 1995, Page, *et al*., 2001). In broccoli inflorescences, chlorophyll degradation is the first visual sign of senescence and reduces the shelf life and value of this important crop plant (Tripathi and Tuteja, 2007).

Bridging Ethylene, Pollination and Senescence

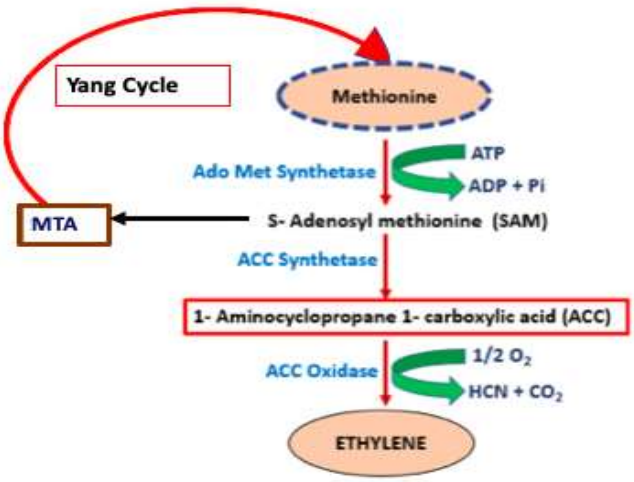

Figure 2: Ethylene biosynthesis pathway, ACC is the rate limiting substrate. Yang (1984) demonstrated the central role of methionine as a precursor of ethylene.

The biosynthesis of ethylene, and its perception, has been studied in depth, most notably in model systems such as Arabidopsis (Klee, 2004). Confirmation of *S*-adenosylmethionine (*S*-AdoMet) and ACC as ethylene precursors was considered to be the breakthrough in understanding the ethylene synthesis pathway (Yang and Hoffman , 1984, Kende, 1993, Wang, *et al*., 2002, Iqbal, *et al*., 2017). S-AdoMet is a fundamental building block of protein synthesis, acts as a major methyl donor in plants and is used as a substrate for many biochemical pathways, including polyamines and ethylene biosynthesis (Ravanel, *et al*., 1998). In addition, S-AdoMet is responsible for methylation reactions that modify lipids, proteins, and nucleic acids. Methionine is converted to *S*-AdoMet (SAM) by the enzyme *S*-AdoMet synthetase (SAM synthetase) at the expense of ATP utilization (Ravanel, *et al*., 1998, Wang, *et al*., 2002). Aminocyclopropane synthetase (ACS) then converts SAM into aminocyclopropane carboxylic acid (ACC). In addition to ACC, ACC synthase (ACS) also produces 5′-methylthioadenosine (MTA) in this reaction, which is then transformed into methionine by using a modified methionine cycle (Bleecker and Kende, 2000). This retrieval pathway conserves the methyl group for another round of ethylene production. Therefore, ethylene can be produced continuously without demanding an increasing pool of methionine. At the same time, the sulphur group of the methionine is also conserved. Finally, ACC is oxidized by ACC oxidase to form ethylene, CO2, and cyanide, which is detoxified to β-cyanoalanine by β-cyanoalanine synthase (β-CAS) to avert toxic effect of accumulated cyanide during the process of ethylene synthesis. ACC is further oxidized by another enzyme, ACC oxidase (ACO), to form ethylene (Yang and Hoffman, 1984, Lin, *et al*., 2009). (Figure 2).

ACC is the rate limiting substrate in the ethylene biosynthesis pathway; therefore regulation of ACS has been extensively studied (Wang, *et al*., 2002). ACC synthase (ACS) is encoded by a multigene family in most plants, for example there are 12 ACS genes in Arabidopsis, six in rice and 10 have been reported in grapevine (Xu and Wang, 2012). Genes encoding the enzymes have been isolated from many ornamental plant species (Shibuya and Ichimura 2016). ACS-encoding genes have been isolated, for example, from carnation (Tanase, *et al*., 2015), geranium (Xiaoli, *et al*., 2015), petunia (Lindstrom, *et al*., 1999, Wang, *et al*., 2018), morning glory (Frankowski, *et al*.,2009), tree peony (Zhou, *et al*., 2013), and orchids (Shi and Liu 2016).

Considering the role of ethylene in flower senescence, Woltering and van Doorn (1988) recognised three types of flower life termination; petal wilting, withering (that

could possibly be either ethylene-sensitive or insensitive) and abscission of turgid petals (ethylene-sensitive) from their experiments. van Doorn (2001) re-examined the above experiment with 200 different species and proposed a classification system to measure ethylene sensitivity across those species. The effects were expressed as the reduction in the time period taken for the symptoms to appear following ethylene treatment, compared to untreated controls. These percentages were then grouped according to five classes as follows (Table 2).

Table 2: Classification of ethylene sensitivity in flowers depending on flower senescence (van Doorn, 2001)

Class	Ethylene effect (Percentage)	Classification
0	0 (no response)	insensitive
1	Up to 33%	Low sensitivity
2	Between 33- 66%	Intermediate sensitivity
3	Between 66-99%	High sensitivity
4	100%	Very high sensitivity

A successful pollination event is responsible for initiation of a series of post-pollination events in the flower that contribute to ovary growth, pigmentation alteration and eventually flower senescence (Stead, 1992). In *Nicotiana tabacum* flowers, ethylene plays an important role in triggering the post-pollination events which begin from the pistil and seemingly facilitate the passage of pollen tubes (Wang, *et al*., 1996, van Doorn and Woltering, 2008). More than 30 different genera have been shown to experience pollination-induced senescence, and most of these are presumed to be ethylene sensitive (Table 3, Woltering 1986,1987; van Doorn and Stead, 1997). Pollination-triggered developmental processes are initiated at the stigma, where the pollen is first detected, but the flower senescence usually begins in petals (Rogers, 2006).

In some species flowers have a prolonged life when they are not pollinated, but they wither shortly after pollination (Primack, 1985). Evident signs of petal senescence include colour change, rolling, and wilting (Ma, *et al*., 2005), while functional changes including collapse of mesophyll cells can occur before the visible morphological changes (Bailly, *et al*., 2001; Wagstaff, *et al*., 2003) (Table 4). This suggests that inter-organ communication occurs and transmits pollination signals to other floral parts. Table 4 explores the relationship between pollination-induced floral senescence and ethylene-induced floral senescence in a number of species. To move from these correlations to a causal relationship requires direct experimentation. Satoh (2011) reported that, in carnation, flower senescence is characterized by autocatalytic ethylene production from petals. However, it has also been reported in the same plant that the initial ethylene burst is independent of the pollen grain's compatibility. A second burst of petal-derived ethylene is reported only when a compatible pollination event takes place (Singh, *et al*., 1992). Ethylene produced from the pollinated stigma has been shown to be translocated via the style and ovary to the petals where it up-regulates ethylene biosynthetic genes and induces the production of ethylene in the petals (Have & Woltering, 1997).

Table 4: Comparing the effect of exogenous ethylene and pollination on flower form and colour prior to flower senescence. The flowers may show permanent closure (closure), colour change (colour), wilting, withering or abscission of turgid petals as the first symptom of senescence.

Species	Family	Symptom (post pollination)	Ethylene response	Sensitivity class
Solanum lycopersicum	*Solanaceae*	Wilting followed with abscission	Wilting followed by abscission	3-4
Nicotiana tabacum	*Solanaceae*	Wilting	Wilting followed by abscission	3-4
Lotus corniculatus	*Fabaceae*	Colour	Wilting	0
Dianthus caryophyllus	*Caryophyllaceae*	Closure, colour, wilting	Wilting, closure	4
Allium cernuum	*Liliaceae*	Petal abscission	Wilting	0
Erythronium americanum	*Liliaceae*	Closure, wilting	Wilting followed by abscission	3
Primula sp	*Primulaceae*	Petal abscission	Wilting followed by abscission	2-3
Geranium pyrenaicum	*Geraniaceae*	Abscission	Abscission	4

It has long been known that huge differences exist between cultivars of carnation in their ethylene biosynthetic ability and the affinities of their receptors to ethylene (Wu, *et al*., 1991). By using simple cross pollinations between ethylene tolerant and ethylene sensitive cultivars (a heritable trait), Onozaki and co-workers (Onozaki, *et al*., 2011) achieved significant improvement in the longevity of carnation flowers. Their original material had flower longevity of 5 to 7 days (Onozaki, *et al*., 2004) but through repeated crossing, the sixth generation had increased its mean flower life to 15 days (Onozaki, *et al*., 2011) An investigation into the cause of this increase revealed that the genes encoding ethylene biosynthesis enzymes DcACS1, DcACS2, and DcACO1 were all expressed at extremely low levels in cultivars with good longevity, and ethylene production was also very low (Tanase, *et al*., 2015).

Possible Role of Floral Senescence in Crop Plants:

In cereal crops, there has been extensive debate on whether grain yield is determined by sink (the developing grain) or by source (the photosynthesizing vegetative tissues) (Gregersen, *et al*., 2013). The majority of agriculture scientists believe that sink strength is the key restraining factor for yield, particularly in small-grain cereals such as wheat (Fischer 2008) and, hence, that physiological events predominantly in the period around seed setting are critical for influencing yield levels.

Flower production, development and senescence in crop plants play a pivotal role in ensuring optimal yield. In seed crops, floral transition is a key developmental switch that determines the production of dry matter. In vegetative crops, such as cabbage (*Brassica oleracea*), sugar beet (*Beta vulgaris*) or fodder grasses (*Lolium perenne*), early bolting and flowering can limit the potential for yield increases or interfere with harvest operations (Jung and Müller, 2009). The two key flowering time related genes, *Heading date 1* (*Hd1*) and *Early heading date 1* (*Ehd1*) are reported to affect rice yield (Endo-Higashi and Izawa, 2011, Wei, *et al*., 2016). This suggests a strong potential connection between genes involved with flowering and strategies for improving the yield of crop plants.

Pollination in crops usually reduces the period of female receptivity and initiates earlier seed maturation. This is a likely adaptation to minimize the cost of floral maintenance, while maximizing the chances

for late pollination in unpollinated flowers (Ashman and Schoen, 1994; Sato, 2002).

Seed production via late pollination is assumed to be fewer and smaller than that obtained by early pollination. Hildesheim, *et al*., 2019 reported that in *Dalechampia scandens*, old flowers exhibit reduced seed production because of seed set failure. In their experiment seed mass also deteriorated with the delay in pollination, suggesting that flower senescence affects not only maternal performance, but also individual offspring quality. Reductions in seed number or quality with flower age have been reported in other species (Arathi, *et al*., 2002).

Flower senescence is the last phase of any crop plant's floral journey, which can strictly limit plant output (biomass, seed yield) when it is induced prematurely or delayed. Flower senescence can be manipulated into an advantageous phenomenon for crop productivity if the process is correctly timed relative to the time of anthesis and to the time of pollination, with these 2 factors contributing different weight according to the mating strategy of the plant (Bogard, *et al*.,2011, Egli 2011 and Parrott, *et al*.,2012). It is through the manipulation of ethylene production and sensitivity, and their link to the processes of anthesis and pollination, that agricultural scientists can begin to utilize molecular breeding to alter flower life in crop plants with the target of enhancing yield.

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