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Flower Senescence Coordinated by Ethylene: An Update and Future Scope on Postharvest Biology in the "Buttercup" Family

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Abstract

Postharvest senescence of cut flowers is a stumbling impediment in harnessing their commercial potential. Consequently, the postharvest quality preservation of cut flowers is a crucial factor to allure buyers and maximize economic gains. Flower senescence being final phase of organ development is a key factor triggering postharvest quality deterioration. The process of flower senescence is closely regulated by developmental and environmental cues. The perception of these signals subsequently involves loss of membrane integrity, decreased activity of antioxidant enzymes, and upregulation of proteases and nucleases, which are key signatures of senescence and culminate in the death of petal tissues. Moreover, the developmental and environmental cues are synchronized by considerable turnover in different growth regulators, particularly cytokinins, abscisic acid, ethylene, and gibberellic acid, which act both antagonistically and synergistically to coordinate the senescence process in flowers. Among these growth regulators, ethylene has a crucial role in orchestrating petal senescence in ethylene-responsive systems, while, abscisic acid regulates petal senescence in ethylene-independent systems. Recent research on ethylene-sensitive flowers revealed that the crosstalk of ethylene with sugars and other growth regulators plays a crucial role in modulating senescence by affecting the expression of ethylene-responsive genes. Despite the plethora of postharvest studies conducted so far, considerable miss links still persist in understanding the intricacies of senescence regulating mechanisms, mainly in ethylene-responsive flowers. To this end, it is imperative to critically re-evaluate our current understanding of ethylene-dependent flower senescence to gain intricate inputs regarding the underlying senescence mechanisms, particularly in ornamental families like Ranunculaceae. This constitutes the pivotal gateway toward deciphering the enigmatic complexities governing senescence regulatory mechanisms, thereby forging a path for postharvest researchers to craft pioneering methodologies aimed at accentuating the longevity of commercially significant flowers, thereby yielding substantial economic ramifications.

Keywords Flower senescence · Ethylene · Abscisic acid · Postharvest longevity

Introduction

Flowers are incredibly intricate organs that have developed to improve the reproductive fitness of angiosperms. Petals being an integral part of flowers facilitate reproduction through pollination and eventually undergo senescence leading to the death of these tissues (Ma et al. 2018). Senescence is an active and crucial aspect of flower development, designed to maximize nutrient recycling from senescing petals to young parts of a flower. Flowers offer excellent model systems for senescence investigations as they possess uniform tissue, short lifespan, and easily manipulable chemically without suffering significant damage (Wagstaff et al. 2002). Petals, originated from leaves through an evolutionary process, manifest analogous physiological and biochemical characteristics during senescence, entailing disintegration of intracellular structures and degradation of membranes and macromolecules, along with salvage of essential substances. (Xu and Hanson 2000; Friedman et al. 2004). However, petal senescence varies from leaf senescence in certain aspects. Firstly, petal senescence is irreversible and progresses at different rates in the components of the flower, while still interconnected to each other. Leaf senescence on the other hand is reversible up to the

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"point of no return." In contrast to leaf senescence which is strictly regulated by environmental cues, petal senescence is particularly regulated by developmental signals, like pollination, fertilization, and fruit formation (Dar et al. 2014; Ahmad and Tahir 2015). Secondly, nutrient remobilization is of less importance in petals as they act as sinks, whereas nutrient remobilization is of key importance in leaves being active source organs performing photosynthesis (Chapin and Jones 2007a, b; Jones 2013; Maillard et al. 2015). Thirdly, petal senescence is relatively rapid as compared to leaf senescence, even in some species abscission of petals occur while still fresh (Woltering and van Doorn 1988; Yamada and Ichimura. 2007). The onset of petal senescence encompasses a multitude of physiological and biochemical changes, like dehydration of senescent tissues, increase in membrane fluidity, generation of reactive oxygen species (ROS), lipid peroxidation, and degradation of proteins and carbohydrates. (Tripathi and Tuteja 2007). These changes are orchestrated by turnover in different plant growth regulators especially, ethylene, abscisic acid, cytokinins, and gibberellic acid. Among these, ethylene and abscisic acid act synergistically to accentuate senescence (Costa et al. 2016; Dar et al. 2021), while cytokinins and gibberellic acid retard this process (Kumar et al. 2014; Lone et al. 2021a, b). Depending on their response to exogenous ethylene, the flowers may exhibit ethylene-sensitive or ethylene-insensitive senescence. Treatment of ethylene-responsive flowers with ethylene antagonists like silver thiosulfate has been found to delay the instigation of senescence in *Clarkia pulchella,* likewise, application of GA_3, an ABA antagonist reduced the impact of ABA action in *Gladiolus grandiflora* (Kumar et al. 2014; Dar and Tahir 2018). Besides hormonal regulation, several marker genes like *ETR1, DAD1*, and *SAG12* act as key regulatory switches during the process of flower senescence. The accumulation of *SAG12* transcripts in senescent tissues of *Nicotiana mutabilis* accelerates senescence by facilitating protein degradation (Jones et al. 2005). Meanwhile, *DAD1* and *ETR1* genes were upregulated during the open stage of flower development in *Petunia hybrida* flowers. *DAD1* is anti-senescent which encourages the glycosylation of nascent proteins to prevent their breakdown (Jeong et al. 2018). *DAD1* transcripts accumulate at higher levels in fresh petal tissues as observed in *Petunia hybrida* flowers, whereas higher transcript levels of *ETR1* signpost its potential role in the perception of ethylene signals (Nisar et al. 2021a, b). Modulating the expression levels of important genes such as cysteine protease and *DAD1* through postharvest treatments and biotechnological intervention may be an effective approach to enhance the longevity of significant cut flowers. Application of $CaCl_2$ retarded the expression of the cysteine protease gene, while the concomitant upregulation of the *DAD1* gene considerably improved the longevity in *Gladiolus* flowers (Sairam et al. 2012). Furthermore, altering ethylene output by reducing the expression levels of *ACC* synthase and *ACC* oxidase can act as a breakthrough in augmenting the postharvest longevity of commercially important ornamentals as realized in *Dianthus caryophyllus* (Savin et al. 1995). In this perspective, the current review focuses on understanding hormonal crosstalk during flower senescence and sheds light on recent developments in the modulation of senescence mechanisms through postharvest treatments and biotechnological approaches. All these strategies have considerable future technological implications for improving the postharvest longevity of commercially important ornamentals, often judged an extremely important parameter in assessing their quality.

From Order to Organized Disorder: How the Collapse of Structural Integrity Triggers Petal Senescence?

Petal senescence encompasses subtle changes in the structure of petal tissues. Modes of petal senescence vary widely between species. In some species, the petal senescence involves wilting followed by the abscission of floral tissues, while in others, the petals abscise while still turgid. The petals that abscise without undergoing wilting are generally sensitive to ethylene, whereas the petals that first undergo wilting and are eventually shed off, are usually non-responsive to ethylene. However, in some ethylene-insensitive flower systems, such as tulips, petals fall off before wilting (Van Doorn 2001). Senescence in petal cells includes both structural and metabolic transformations, along with the activation of catalytic machinery, which fosters nutrient recovery amassed during the growth phase (Rogers 2013; Shibuya and Ichimura 2016). The maintenance of the structural integrity of cells is vital for their survival and performance of metabolic processes (Ahmad and Tahir 2016a, b). Cell wall degeneration besides turgor loss and tonoplast rupture could be one of the factors contributing to cell death (Shibuya et al. 2016). In ethylene-sensitive flowers, ethylene and auxin mediate the abscission of petal tissues, while in ethylene-insensitive systems, INFLORESCENCE DEFICIENT IN ABSCISSION (IDA) peptide and HAE-HSL2 kinases mediate abscission of petal tissues. These genes encode for cell wall-degrading enzymes which lead to the abscission of floral organs (Meir et al. 2019). Studies on senescing petals of *Dianthus* and *Ipomea* have reported a decrease in cellulose and hemicellulose content in cell walls (Wiemken-Gehrig et al. 1974; De Vetten and Huber 1990). Cell wall degeneration has been attributed to the discharge of hydrolytic enzymes into the cell wall, before cell death. In *Iris* and *Dendrobium* flowers, swelling of cell walls has been observed in the senescing mesophyll cells. This swelling is ascribed to vesicle formation between the plasma membrane

and cell wall, which secrete hydrolytic enzymes, resulting in cell wall degradation (Kamdee et al. 2015). After cell wall degradation, the integrity of the membrane is compromised, which is unraveled through the microscopic investigations of senescent cells. This loss of integrity impairs their prime functions (Yamada et al. 2009; Shahri and Tahir 2011a). Senescence causes an upsurge in the activity of phospholipases and acyl hydrolases and replaces phospholipids with neutral lipids thereby increasing the membrane outflow. The loss of membrane phospholipids is a crucial index of lipid metabolism in senescing petals (Rubinstein 2000; Van Doorn and Woltering 2008). The loss of membrane integrity is followed by subtle changes in cytoplasm, which undergoes structural alterations characterized by the accumulation of electron-dense globules on the surface of the plastids. These globules are thought to originate from plastoglobules that form within the plastid (Mulisch and Krupniska 2013). These globules consisting of proteins and lipids increase in size toward the senescent stage as observed in the epidermal cells of Iris petals. Reportedly, these enlarged globules participate in the degradation of plastids by breaking down proteins in the proteasome and lipids in the peroxisome (Shibuya et al. 2016). In addition, intercellular connections, such as plasmodesmata, involved in the movement of RNA, carbohydrates, and phytohormones also get closed before the onset of flowering. The closure of plasmodesmata is the primary structural modification as noticed in the petal cells of *Iris*, which prevents the transport of sugars into cells, ultimately causing their demise due to the exhaustion of ATP (Van Doorn et al. 2003). In addition, autophagic structures have been noticed in petal cells of *Ipomea*, *Dianthus* and *Hemerocallis*, which contain acid phosphatases and other hydrolytic substances and function as lytic vacuoles. (Phillips and Kenede 1980; Smith et al. 1992; Stead and Van Doorn 1994; Marty 1999). These vacuoles increase in size by combining with other vacuoles and participate in cytoplasmic degradation. In addition plastids and mitochondria of senescing petals also function as lytic vacuoles (van Doorn et al. 2011). The plastids of *Dendrobium* petals plastids have been found to degrade the engulfed portion of cytoplasm owing to their intrinsic proteolytic and lipolytic activity (Kato et al. 2005; Barsan et al. 2010). The nucleus is the sole cell organelle that survives till the last stage of flower senescence. It undergoes various morphological changes, like nuclear fragmentation and chromatin condensation. Chromatin condensation is followed by DNA degradation due to the depolymerization of F-actin, which is the most commonly assessed criterion during petal senescence. The process of petal senescence has been linked to DNA fragmentation (Wagstaff et al. 2003; Arora and Singh 2006; Yamada et al. 2006). In case of pea petals, DNA degradation is characterized by a laddering pattern of DNA fragments on the agarose gel. Moreover, the application of Ca^{2+} has been found to upregulate Dnase activity and hence DNA laddering. DNA degradation being a hallmark of PCD is also imitated by the emancipation of Cyt c from the inner membrane space of mitochondria since the timing of this release of Cyt c is coupled with the initiation of DNA laddering (Xu and Hanson 2000).

What Causes a Flower to Die?

Flower senescence is a complex tripartite process involving initiation, disassembly, and nutrient remobilization. The disassembly phase entails the breakdown of structural integrity, giving way to prominent biochemical transformations, including proteolysis, nucleic acid degradation, carbohydrate catabolism, lipid peroxidation, and compromised activity of antioxidant enzymes. These biochemical alterations collectively facilitate the efficient transfer of nutrients from petal tissues to sink tissues. The key biochemical events are described as follows:

Senescence and Proteolysis: Two Processes, Single Destiny

Proteolysis being a hallmark of petal senescence fosters protein degradation and enables the transfer of amino acids to the sink (Solomon et al. 1999). The protein content of petal tissue acts as a decisive factor in flower senescence, as the decrease in protein concentration truncates the vase life of cut flowers (Rezvanypour and Osfoori 2011). Proteins not only improve relative water content but also act as a substitute energy source during sugar depletion (Shan and Zaho 2015; Hirota et al. 2018). Protein enrichment improves the performance of antioxidant enzymes and encourages the production of stress-specific proteins that stimulate defense systems, leading to an increased ability to resist postharvest deterioration and thus extending the postharvest longevity (Doganlar et al. 2010; Promyou et al. 2012). The characteristic feature of senescence is elevated proteolytic activity due to an upsurge in the expression of the cysteine protease gene (Jones et al. 2005). Earlier studies linked the cysteine protease gene with the petal senescence of ethylene-sensitive flowers (Jones et al 1995). However, later findings confirmed its role in insensitive flowers as well (Wagstaff et al. 2002; Arora and Singh 2004; Pak and Van Doorn 2005). Proteases being abundant and best characterized cell death proteins hydrolyze proteins by internal peptide bonds (Beers et al. 2000). Protein degradation takes place in multiple organelles, such as proteasomes, vacuoles, mitochondria, and the nucleus, but the majority of it ensues within vacuoles. Proteasomal-based degradation involves the breakdown of misfolded

proteins via ubiquitination (Van Doorn and Woltering 2008). Delay of senescence signs via silencing of the Ring domain of E3 protein in *petunia* and chemical inhibition of proteases in *Iris* indicates the implication of Proteasomal action in petal senescence (Xu et al. 2008). Proteins are also degraded independent of Proteasomal action in vacuoles, mitochondria, plastids, and the nucleus. However, the bulk of protein degradation occurs in vacuoles as most of the proteases are localized in them (Van Doorn and Woltering 2008).

Sugar Starvation and Flower Senescence

Sugars act as an important energy source to maintain cellular homeostasis and regulate water levels by elevating the concentration of osmotic solutes (Van Doorn 2004; Van Doorn and Woltering 2008). Depletion of sugars is regarded as the key feature of senescent petal tissues, orchestrating petal senescence either by regulating metabolites or by modulating the action of ethylene Van Doorn 2004; Van Doorn and Woltering 2008; Shahri et al. 2010). Sugars are recognized for their ability to enhance the postharvest quality of cut flowers and prolong their vase life (van Doorn 2004; Eason 2006). Detachment of flowers from their mother plant truncates their carbohydrate supply, subsequently triggering physiological alterations that eventually lead to cell death. (Halevy and Mayak 1979). Also, cut flowers cannot assimilate sufficient carbon as they receive light intensity below the compensation point, hence leading to fast depletion of carbohydrate reserves (Pun et al. 2016). Sugar starvation fosters protein and lipid breakdown which act as alternate respiratory substrates for sustaining key physiological processes. Low sugar content also induces expression of senescence-associated genes which are otherwise suppressed by sugars (Morkunas et al. 2012). Sugars and sugar-metabolizing enzymes effectively counter oxidative stress (Bolouri-Moghaddam et al. 2010). The synergistic interaction of sugars and sugar-like compounds including phenols form an important part of the redox system, which quenches ROS and therefore confers stress tolerance. Sugars being important signaling molecules perform differently in different flower systems. In ethylene-sensitive flowers, like *Dianthus*, sucrose treatment delays the climacteric rise in ethylene by reducing the expression of ACC synthase and ACC oxidase, thereby suppressing ethylene biosynthesis (Pun et al. 2016). Likewise, glucose and mannitol treatments prevented the abscission of flowers in *Delphinium* (Ichmura et al. 2000). Thus, sugars serve as important energy substrates besides modulating the ethylene pathway, thereby regulating petal senescence.

From Bright to Bleach: Anthocyanin Degradation

Discoloration and color fading are core causes of quality deterioration in cut flowers. The primary pigments contributing to the vibrant color of the flowers include anthocyanins, carotenoids, and betalains. Anthocyanins being the largest class of plant pigments form red, violet, and blue colors. The accumulation of anthocyanins is determined by the degree of expression of various biosynthetic genes, like Chalcone synthase (CHS), chalcone isomerase (CHI), phenylalanine ammonia-lyase (PAL), and flavonoids 3-hydroxylase (F3H). Studies conducted on *Petunia, Malus, Antirrhinum,* and *Rosa* have revealed that the expression of these genes peaks in the initial stages of flower development and declines toward advanced stages (Cavaiuolo et al. 2013). The color formation by anthocyanins is under the regulation of pH. Under low pH, anthocyanins produce red color while at high pH, anthocyanins produce blue color (Avila-Rostant et al. 2010). In *Ipomea tricolor*, flower petals are characterized by low pH upon bud opening, but as the development proceeds the pH increases resulting in the blue color of petals (Yoshida et al.1995). Besides pH, high temperatures and low light also reduce the pigment level in petals as a result of degeneration and downregulation of anthocyanin biosynthetic genes (Gonzalez 2009). In ethylene-sensitive flowers, exogenous ethylene inclusion induced color fading in *Vanda* flowers. Ethylene-induced color bleaching was due to an increase in peroxidase activity, responsible for anthocyanin degradation. Pretreatment of spikes with 1-MCP (1-Methylcyclopropene) prevented color blenching and degradation of anthocyanins. Moreover, MCP-treated inflorescences exhibited vibrant color of petal tissues relative to control (Khunmuang et al. 2019).

Lipid Peroxidation and Loss of Membrane Integrity

Petal senescence involves significant structural and biochemical changes in the cell membrane. The key biochemical changes include loss of membrane phospholipids and increase in neutral lipids and sterol to phospholipid ratio, as well as an increase in the ratio of saturated to unsaturated fatty acids (Lesham 1992; Thompson et al. 1998). This alteration in membrane constituents are induced by membrane-degrading enzymes, like phospholipase C, Lipolytic acyl hydrolase, and Lipoxygenase, which are localized in membrane microsomes. Membrane lipids particularly polyunsaturated fatty acids are prone to oxidation by enzymatic means, like lipoxygenase (LOX). Lipoxygenase activity is positively correlated with membrane damage and promotes

senescence in flowers, like *Gladiolus* (Peary and Prince 1990; Hossain et al. 2006). Membrane degradation causes ion leakage and the release of hydrolytic enzymes from the vacuoles to induce the breakdown of cellular components and hampers the exchange of metabolites as signaling molecules between neighboring cells. Thus, the collapse of the tonoplast and subsequent execution of cell death as a result of mass lipid degradation during senescence may be caused by membrane degradation. Besides degrading membrane lipids, lipid peroxidation produces many toxic aldehydes and ketones resulting in the breakdown of macromolecules (Wilhelmova et al. 2006). Membrane breakdown is directly linked to free radical production induced by ethylene (Carlos et al. 1996). Studies conducted in *Dianthus* revealed that inhibition of ethylene production improves vase life by preventing lipid peroxidation, indicating a link between ethylene production and free radical generation (Brochov et al. 1997). Previous investigations demonstrated that treatment of cut carnations with sodium benzoate (free radical scavenger) can improve their vase life by inhibiting ethylene burst (Baker et al. 1977). In addition, alteration in membrane fluidity of microsomes is linked with an increase in superoxide radical production, wherein exogenous application of free radical scavenger, propyl gallate prevented such changes in microsomes (Mayak et al. 1983). Thus, ethylene is a potent inducer of membrane degradation in ethylene-sensitive flowers.

Loss of Synchronization Between ROS Production and Antioxidant Machinery

The aging process in plants, including their individual parts, often involves oxidative stress caused by the abundant production of reactive oxygen species (ROS such as superoxides (O_2–) and hydrogen peroxide (H_2O_2) by the cells (Saeed et al. 2014). The primary sources of ROS in petals are believed to be peroxisomes, mitochondria, and the apoplast. To manage ROS levels during senescence, plants produce antioxidant compounds and increase the activity of antioxidant enzymes. Non-enzymatic antioxidants such as ascorbic acid and tocopherol are vital ROS regulators. Studies have demonstrated that ascorbic acid plays a crucial role in regulating genes associated with senescence. A reduction in ascorbic acid levels has been found to induce senescence by increasing the expression of senescence-associated genes (Barth et al. 2004). Tocopherols, which are linked to thylakoid membranes, protect cells against oxidative stress by eliminating ROS, primarily by impeding the spread of lipid peroxidation via scavenging of lipid peroxyl radicals (Falk and Munné-Bosch 2010). In addition, phenolic compounds including anthocyanins and flavonols act as important antioxidant compounds in plants. Flavonols have been found to protect the flowers from the harmful exposure of UV-B rays, thus preventing ROS generation, while anthocyanins have been found to improve the longevity of flowers, like *Petunia* and *Hibiscus* (Kumar et al. 2008; Trivellini et al. 2007). During senescence, plant cells stimulate different ROS scavenging enzymes by activating specific signaling pathways, which include superoxide dismutase (SODs), catalase (CATs), and ascorbate peroxidase (APX) (Rogers 2012; Kou et al. 2014). The activity of SOD and CAT is important for stabilizing the lipid bilayer and averting the oxidation of unsaturated fatty acids (Saeed et al. 2014). In *Iris versicolor*, a decrease in antioxidant enzyme activity has been found to induce senescence (Ahmad and Tahir 2016a, b), while an increase in the activity of these antioxidant enzymes has been shown to improve the vase life of *Consolida ajacis* (Haq et al. 2022a, b). Thus, during the onset of aging process, the antioxidant defense system is upregulated. However, the production of ROS beyond the scavenging capacity of an antioxidant system leads to oxidative damage, which ends up in the death of petal tissue. All these events are summarized in Fig. 1.

Modulation of Ethylene Pathway for Extending the Longevity of Climacteric Flowers

The longevity of flowers is a crucial component in quality evaluation. Therefore, extending vase life is an important factor to convince customers to repurchase flowers (Vehniwal and Abbey 2019). Vase life is considered to be terminated with the appearance of senescence symptoms, like wilting, color fading, and abscission of petals (Olsen et al. 2015). In cut flowers particularly in ethylene-responsive systems, application of anti-ethylene treatments has been found to improve the vase life to a greater extent; however, a more viable approach to enhance the quality of cut flowers is the exploitation of alternative means ranging from conventional cross-pollination to advanced molecular methods, which involve direct modulation of the ethylene biosynthetic pathway (Table1). In *Dianthus caryophyllus*, repeated crossing doubled the flower longevity (Onozaki et al. 2011). The expression analysis revealed that the ethylene biosynthetic enzyme *DcACS1* and *DcACO2* exhibited low expression in these cultivars due to repeated crossing and selection, hence, improved longevity due to low ethylene production (Tanase et al. 2013). Moreover, hybridization through the interspecific crossing resulted in heterogeneous progeny with higher ethylene tolerance has been achieved in various *Leptospermum* species and *Grevillea and Chamelaucium* species (Bicknell 1995; Beal and Joyce 1999; Macnish et al. 2004). However, a significant drawback of this method is that it is not a practical strategy for improving existing cultivars,

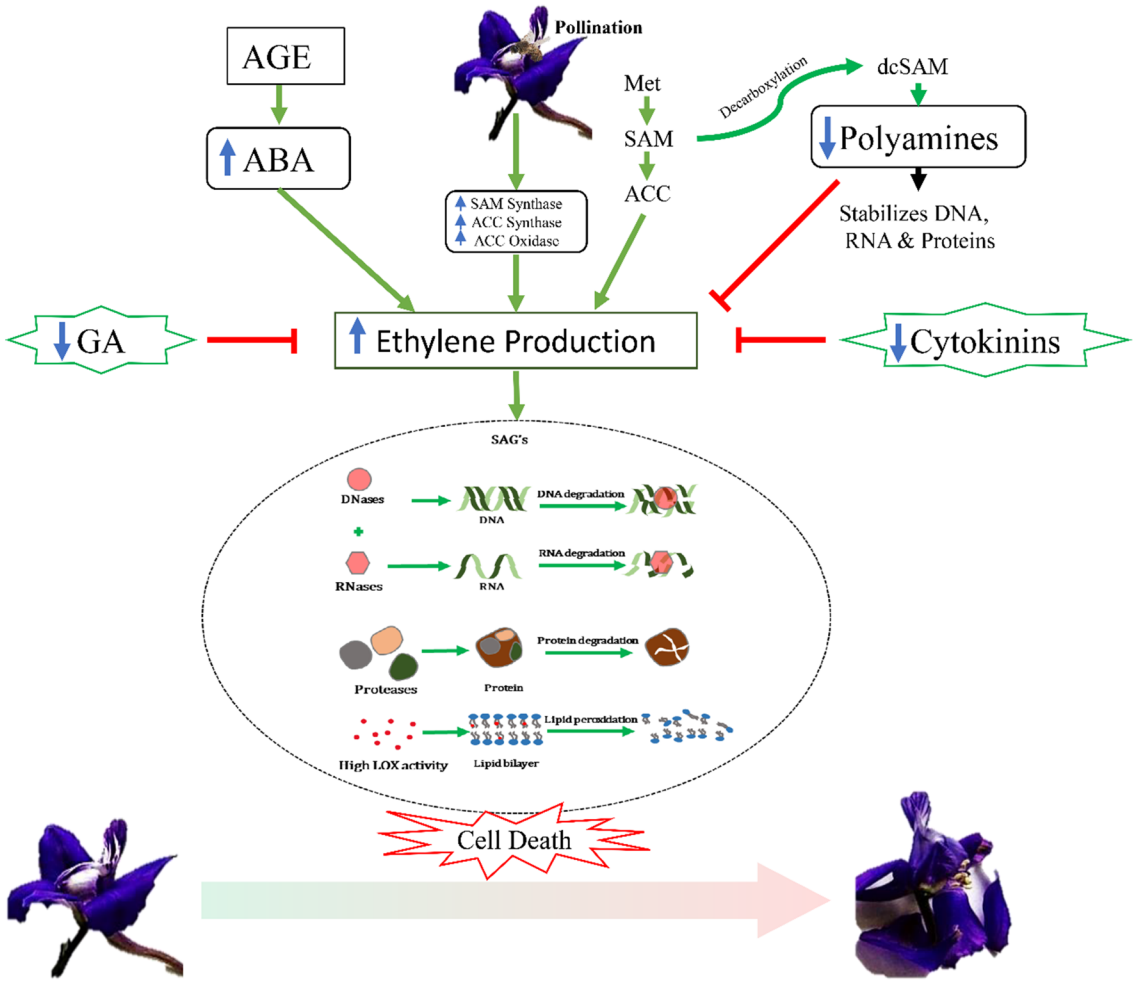

Fig. 1 A summarized representation of hormonal crosstalk and ethylene-mediated senescence in ethylene sensitive flowers (blue color arrows show increase and decrease in growth regulators, whereas red lines indicate inhibition of ethylene by different growth regulators) (Color figure online)

Table 1 Modes of modulation of ethylene pathway for improving postharvest longevity

Plant species	Mode of modulation	Gene targeted	References
Petunia hybrida	CRISPR/Cas9 technology	*PhACO1*	Xu et al. (2020)
Leptospermum sp., *Grevillea sp.*, *Chamelaucium sp.*	Interspecific hybridization	*ACS/ACO*	Bicknell (1995), Beal and Joyce (1999) and Macnish et al. (2004)
Lotus japonica	Carbon ion beam irradiation	*ETR1*	Du et al. (2021)
Petunia hybrida	Expression of a sense RNA (PhEIN2-sense) and RNA interference (PhEIN2-RNAi) sense PhEIL2	*PhEIN2 EIN3*	Shibuya et al. (2004) and Shibuya and Clark (2006)
Dianthus caryophyllus	Transformation with antisense ACC oxidase gene	*ACC* oxidase	Savin et al. (2019)
Petunia hybrida	Transformation with PSAG12 promoter	*PSAG12-IPT*	Chang et al. (2003a, b)
Campanula carpatica, Chrysanthemum, Pelargonium zonale, Kalanchoe blossfeldiana	Transformation with mutated etr-1	*ETR1*	Sumitomo et al. (2008), Sanikhani et al. (2008), Mibus et al. (2009) and Gehl et al. (2018)
Dianthus caryophyllus	Crossing and selection	*DcACS1* and *DcACO2*	Tanase et al. (2013)

as substantial backcrossing with the parent plant may be required (Shibata 2008). Inducing mutations through irradiation is another viable approach to modulate ethylene output. Mutations induced in *Lotus japonica* by carbon ion beam significantly improved the flower longevity. These mutations altered the ethylene biosynthetic pathway and resulted in minimal ethylene production (Du et al. 2021). Besides irradiation, a more sophisticated way to introduce mutations in the desired genes is the CRISPR/Cas9 technology. This technology holds potential to edit the gene loci involved in ethylene biosynthesis as achieved in *Petunia* and ensures stable transmission of mutant alleles to the subsequent generations (Xu et al. 2020). Moreover, genetic engineering has significantly focused on targeting the ethylene pathway to enhance the lifespan of cut flowers. The transfer of mutated ethylene receptor gene etr1 from *Arabidopsis thaliana* in various ornamental plants, such as *Campanula carpatica, Chrysanthemum, Kalanchoe blossfeldiana,* and *Pelargonium zonale*, reduced their susceptibility to ethylene (Winkelmann et al. 2016; Gehl et al. 2018). In addition to receptors, the longevity of flowers has been improved by targeting specific elements in the ethylene signaling pathway, such as *EIN2* and *EIN3* (Shibuya et al. 2004; Shibuya and Clark 2006). Furthermore, inhibition of ethylene production in carnation by transforming with antisense *ACC* oxidase gene has proven to be effective (Savin et al. 1995). It is noteworthy that the ethylene sensitivity can also be altered by increasing cytokinin levels, through transformation with cytokinin biosynthesis gene *PSAG12-IPT* as achieved in petunia (Chang et al. 2003a, b). Thus, manipulation of the ethylene pathway presents a substantial avenue for enhancing postharvest quality in climacteric ornamental plants.

Conventional Ethylene Antagonists and Their Cost-Effective and Eco-Friendly Substitutes

Ethylene is a key hormone modulating senescence in ethylene-sensitive flowers. The ability of ethylene to induce flower senescence has developed naturally as a way to aid changes brought in by pollination (Chapin and Jones 2007a, b). Depending upon the mode of senescence, petal senescence can be ethylene regulated or ethylene independent (Dar et al. 2021). The response of climacteric flowers to ethylene varies among species and varieties (Wu et al. 2017). In ethylene-sensitive flower systems, an upsurge in endogenous ethylene triggers senescence and the exogenous application of the same speeds up the process. On the contrary, ethylene hardly influences senescence in ethylene-independent flowers. Non-climacteric flowers typically produce little ethylene and do not respond to exogenous treatment (Wang et al. 2020a, b). However, the interaction of ethylene with other hormones either promotes or hinders its production or action (Iqbal et al. 2017; Shibuya 2018). The ethylene biosynthesis pathway involves the following steps.

L-methionine → S-adenosyl-L-methionine (SAM) → 1-aminocyclopropane-1-carboxylate (*ACC*) → Ethylene ($CH_2=CH_2$).

The enzymes accountable for ethylene biosynthesis are *ACC* synthase (ACS) and *ACC* oxidase (ACO). ACS converts SAM to ACC, while *ACO* converts *ACC* to ethylene. These genes have been identified in different flowers (Shibuya and Ichimura 2016). The mRNA transcripts of these genes are inversely related to the postharvest life of ornamental flowers (Tanase and Onozaki 2016). The ethylene signal is detected by the *ETR1* receptor, a negative regulator of the ethylene response pathway. *ETR1* then transmits the signal to downstream signaling components, such as *CTR1, EIN2, EIN3*, and *ERF'S*. These signaling components induce the expression of ethylene-responsive genes, such as proteases and lipoxygenases (Ceusters and Van de Poel 2018), which trigger the breakdown of proteins and membrane lipids, leading to the initiation of senescence (Hong et al. 2000; Jones et al. 2005). Ethylene burst also leads to respiratory upsurge which induces the degradation of carbohydrates and thus truncates vase life of flowers (Gonzalez-Candelas et al. 2010). However, exogenous sourcing of sugars such as glucose, trehalose, and mannitol accentuated the vase life of ethylene-responsive flowers, like *Delphinium* and *Dianthus* (Ichimura et al. 2000; Dar et al. 2014). Molecular studies revealed that sucrose treatments reduced ethylene production by curtailing ACO and ACS transcripts in climacteric flowers (Pun et al. 2016). Apart from sucrose, application of anti-ethylene substances like silver nanoparticles (Nag), aminooxyacetic acid (AOA), silver thiosulfate (STS), and 1-methylcyclopropene (1-MCP) treatments considerably diminished the deleterious effects of ethylene by inhibiting the accumulation of ACS and ACO transcripts in *Dianthus* and hybrids of *Mokara* Orchid (Naing et al. 2021; Wongjunta et al. 2021). Interestingly salicylic acid, a phenolic compound, has been suggested as a potential postharvest therapy to extend the lifespan of several types of cut flowers, including *Rosa hybrida*, *Dianthus caryophyllus*, *Lillium pumilum*, and *chrysanthemum* (Phi et al. 2021). Salicylic acid regulates petal aging in *Nicotiana plumbaginifolia* by enhancing the sugar and protein content of the petals. (Nisar et al. 2021a, b). In addition, molecular studies revealed that salicylic acid enhances the vase life by the diminishing activity of ACC oxidase besides, conferring membrane stability and improving water uptake (Kazemi et al. 2012). Convincingly, studies conducted on various cut flowers suggested a considerable role of Nitric oxide (NO) in mitigating postharvest senescence by multiple modes of action (Haq et al. 2021). Nitric oxide given as sodium nitroprusside (SNP) sustains optimal hydration

of flower petals and inhibits the peroxidation of membrane lipids to minimize membrane effusion (Hassan et al. 2020). NO mitigates senescence in both ethylene-responsive as well as non-responsive systems. In ethylene-independent systems, NO ameliorates display life mainly by scavenging reactive oxygen species, while in ethylene-responsive systems, it accentuates the longevity of cut flowers by reducing the ethylene production (Liao et al. 2013; Naing et al. 2017; Lone et al. 2021a, b). Quite recently, role of novel postharvest treatments such as selenium and hydrogen nanobubble has been implicated in the regulation of postharvest senescence particularly in ethylene-sensitive systems. In climacteric flowers, endogenous ethylene production inhibits cell expansion via regulation of aquaporins involved in water transport through the cell membrane (Ma et al. 2008; Xue et al. 2020). Consequently, this results in a negative water balance, which limits the postharvest longevity of cut flowers (Van Meeteren and Aliniaeifard 2016). Moreover, ethylene-induced respiratory upsurge depletes primary respiratory substrates like carbohydrates and leads to oxidative stress via ROS production (John-karuppiah and Burns 2010; Bayanati et al. 2019). On the contrary, application of Selenium (Se) downregulated ethylene biosynthetic genes, which in turn inhibited the initiation of senescence-associated events, like respiratory upsurge, sugar depletion, ROS production, and petal wilting (Costa et al. 2020). Thus, Se can offer an economically viable and environmentally acceptable alternative to the existing conventional ethylene antagonists used for ethylene-sensitive cut flowers. Hydrogen-rich water (HRW) is another novel postharvest treatment reported to alleviate the deleterious effects of ethylene on cut flowers. Application of HRW reduces the accumulation of 1-aminocyclopropane-1-carboxylic acid (ACC) as well as inhibits the activity of ACC synthase (Wang et al. 2020a, b). HRW also prevents the degradation of proteins and nucleic acids by inhibiting proteases and nucleases, the key executioners of senescence (Li et al. 2021). HRW can accentuate the longevity of cut lilies by stimulating NO, which acts as a downstream signaling molecule (Huo et al. 2018). This suggests that HRW can not only reduce ethylene production but can serve as a strong inhibitor of nucleases and proteases besides, activating signaling molecules like NO which can ameliorate the display life of precious ornamentals. Boric acid is yet another cost-effective and eco-friendly substitute for conventional ethylene antagonists, like Silver thiosulfate (STS). Boric acid as a vase solution has been reported to preserve the quality of *Tuberose* and *Jasmine* cut flowers by delaying senescence symptoms (Manimaran et al. 2018; Baidya et al. 2020). Exogenous inclusion of Boric acid not only impedes ethylene biosynthesis but also improves other biochemical attributes, like proteins and sugars (Farooq et al. 2021a, b). Besides boric acid, ethanol is also used in the preservation of postharvest quality of horticultural produce owing to its safe and eco-friendly properties (Lin et al. 2020). Exogenous inclusion of ethanol has been found to improve the longevity of various cut flowers, effected by the ethylene and water stress (Pun et al. 2013; Sadeghi and Hashemabadi 2016). Ethanol being antimicrobial and anti-ethylene compound prevents microbial proliferation in vase solutions and impairs the activity of ACC synthase. Thus, ethanol reduces xylem occlusion and ethylene biosynthesis as reported in Alstroemeria and Rosa (Yaghoubi and Yadegri 2016; Manzoor et al. 2021; Nekouyar and Emani 2022). The aforementioned ethylene antagonists and their mechanism of action has been summarized in Table 2.

Synergistic or Antagonistic: Crosstalk of Ethylene with Other Growth Regulators During Petal Senescence

Petal senescence being a tightly regulated complex biological process is modulated by several phytohormones. There is a complex interplay between different growth regulators during petal senescence. Usually, cytokinins have an inhibitory effect on senescence, whereas ethylene and ABA show a stimulatory effect (Ma et al. 2018; Chen et al. 2018a, b). The role of auxins concerning petal senescence is somewhat contradictory and elusive. Treatment of carnation petals with auxin-induced senescence by stimulating ethylene production, while as auxins delayed senescence in *Delphinium* by reducing the ethylene sensitivity (Wulster et al.1982; Jones and Woodson 1999). Senescing carnation petals indicated a transient spike in the mRNA abundance of an AUX/IAA gene, whereas Aux/IAA genes were shown to be down-regulated in *Mirabilis jolapa* during petal senescence (Xu et al. 2007; Price et al. 2008). The instigation of senescence in some flowers like *Hemerocallis*, *Ipomoea*, *Ranunculus*, and *Lilium longiflorum* has been reported to occur without any alterations in endogenous levels of auxin (Ahmad and Tahir 2016a, b). Gibberellic acid (GA) is known to act as an ethylene antagonist and thus delays senescence in some cut flowers, like roses and carnations (Chen et al. 2021). Gibberellic acid-mediated delay in senescence can be attributed to the decrease in climacteric ethylene production (Saks et al. 1992). GA treatment has been found to reduce the accumulation of ACC in carnation petals (Ma et al. 2018). Senescence in rose petals was expedited by silencing the GA_{20} oxidase gene *RhGA20ox1* involved in GA biosynthetic pathway (Lü et al. 2014). Gibberellic acid delayed senescence in peony cut flowers via reduction in expression of MYB transcription factor gene *PlMYB308*, which otherwise leads to the accumulation of ABA and ethylene (Ji et al. 2022). The application of GA_3 considerably improved the postharvest attributes and activity of antioxidant enzymes in non-climacteric gladiolus flowers by antagonizing ABA

Table 2 Shows the effect of various postharvest treatments and their mechanism of action in ornamentals of different families

Plant species	Treatment	Mode of action	Family	References
Dianthus caryophyllus	Sucrose	Reduced ethylene production by curtailing *ACO* and *ACS* transcripts	Caryophyllaceae	Pun et al. (2016)
Mokara sp.	Aminooxyacetic acid (AOA), silver thiosulfate (STS) 1-methylcyclopropene (1-MCP)	Inhibited the accumulation of ACS and ACO transcripts	Orchidaceae	Wongjunta et al. (2021)
Nicotiana plumbaginifolia	Salicylic acid (SA)	Enhanced the sugar and protein content of the petals	Solanaceae	Nisar et al. (2021a, b)
Dianthus caryophyllus	Sodium nitroprusside (SNP)	sustained optimal hydration of flower petals and inhibited the peroxidation of membrane lipids	Caryophyllaceae	Hassan et al. (2020)
Consolida ajacis	Sodium nitroprusside (SNP)	Enhanced activity of antioxidant enzymes and improved the protein and sugar content	Ranunculaceae	Haq et al. (2021)
Rosa sp.	Hydrogen-rich water (HRW)	Inhibits the activity of ACC synthase	Rosaceae	Wang et al. (2020a, b)
Digitalis purpurea	Boric acid	Impedes ethylene biosynthesis, improves protein and sugar content	Scrophulariaceae	Farooq et al. (2021a, b)
Alstroemeria sp.	Ethanol	Reduces xylem occlusion and ethylene biosynthesis	Alstroemeriaceae	Yaghoubi and Yadegri (2016)
Rosa sp.	Ethanol	Reduces xylem occlusion and ethylene biosynthesis	Rosaceae	Nekouyar and Emani (2022)

effects (Costa et al. 2016). However, GA treatment does not affect endogenous ACC levels or the longevity of ethylene-sensitive flower Grevillea (Irving et al. 2006). Thus, anti-aging effect of GA cannot be generalized but seems to be species specific.

Polyamines (PAs) have a vital role in plant juvenility by fostering cell proliferation, growth, and the postponement of senescence (Galston and Kaur-Sawhney 1995). The most prevalent polyamines in plants include putrescine, spermidine, and spermine. The interaction between ethylene and polyamines seems to regulate floral growth and senescence. More specifically, the balance between these two plant hormones determines whether the process of senescence will occur or not (Valero 2009). Polyamines are purported anti-senescent because of their ability to prevent senescence in climacteric flowers like *Dianthus* and *Nicotiana* by inhibiting ethylene biosynthesis (Ahmad and Tahir 2016a, b). Polyamines and ethylene compete for the same precursor S-adenosyl methionine (SAM). Therefore, an upsurge in polyamine biosynthesis limits the biosynthesis of ethylene, hence delaying the execution of senescence. Thus, owing to their common precursor SAM, ethylene and polyamines exhibit antagonistic roles in relation to petal senescence (Davarynejad et al. 2021). Application of polyamines prevents protein breakdown by downregulating protease activity and stabilizing proteins via binding of amine groups (Nisar et al. 2015). Polyamines also maintain the membrane integrity of petal tissue by attenuating lipoxygenase activity, hence preventing lipid peroxidation (Yousefi et al. 2019). Given the available data, polyamines are known to play a significant role in climacteric flowers, but their function in non-climacteric systems remains unclear. Abscisic acid (ABA) is believed to be the main regulator of aging in non-climacteric flowers (Da Costa et al. 2016). Investigations carried out on *Narcissus pseudonarcissus* indicated that the conversion of carotenoids to ABA leads to an increase in ABA concentration during flower senescence (Hunter et al. 2002). Treatment with ABA hastened the senescence process in *Gladiolus* by reducing water uptake and fresh weight and enhancing membrane seepage (Kumar et al. 2014). In climacteric flowers, ABA accelerates senescence by stimulating ethylene production or by increasing sensitivity to ethylene (Ronen and Mayak 1981; Muller et al. 2000). On the contrary, application of ABA in *Hibiscus rosa-sinensis* masked the expression of ethylene perception (*HrsETR* and *HrsERS*) and ethylene biosynthetic genes (*HrACS* and *Hr ACO*) (Trivellini et al. 2011). Silencing of *PhHD-Zip* in petunia decreased the expression of ethylene biosynthetic genes and curtailed ethylene output. Decrease in ethylene output impaired the expression of the ABA biosynthesis gene *NCED* (9-cis-epoxycarotenoid-dioxygenase). This indicates mediation of crosstalk by PhHD-Zip between ABA

and ethylene (Chang et al. 2014). Cytokinins act as anti-senescent agents both in ethylene-responsive as well as ethylene-independent flower systems. In ethylene-independent flowers, cytokinins defer senescence by impeding ABA synthesis, while as in ethylene-responsive systems, cytokinins prevent senescence instigation by reducing ethylene output (Van Doorn and Woltering 2008; Trivellini et al. 2015). Application of cytokinin inhibits the initiation of senescence by maintaining sugar and protein content and reducing the membrane outflow of petal tissues (Iqbal et al. 2017; Chen et al. 2018a, b). In *Nicotiana plumbaginifolia*, exogenous inclusion of cytokinins retards the senescence execution by improving the activity of antioxidant enzymes (Tahir et al. 2018). Several studies have reported a negative correlation between senescence instigation and the cytokinins content (Hönig et al. 2018). On the contrary, increase in ethylene content has been positively correlated with cytokinin breakdown via O- glycosylation, thereby inducing senescence (Chang et al. 2003a, b). Isolated petunia petals treated with cytokinins exhibited decreased ethylene sensitivity and application of 6-methylpurine, a cytokinin oxidase inhibitor, dramatically reduced ethylene production and postponed flower senescence (Taverner et al. 2000). Transformation of miniature rose with cytokinins biosynthesis gene *IPT* (isopentenyl transferase) under the regulation of *SAG12* promoter reduced ethylene sensitivity and retarded petal senescence (Zakizadeh et al. 2013). These results indicate antagonistic interaction between ethylene and cytokinins in the modulation of petal senescence.

Petal Senescence in *Ranunculaceae*

The family Ranunculaceae possesses a rich repository of beautiful ornamentals that could significantly transform the floriculture sector. Ranunculaceae is commonly known as the "buttercup family" or "crowfoot family." The flowers of this family exhibit protogyny, which encourages cross-pollination or outbreeding. It comprises of 2500 species and 55 genera that exhibit great variation in floral morphology (Delpeuch et al. 2022). The key ornamentals of Ranunculaceae include *Conslida sp.*, *Anemone sp., Clematis sp.*, *Helleborus sp.*, *Ranunculus sp.*, *Delphinium sp., nigella* (Love-in-mist), and *Aquilegia* with considerable potential for use as a cut flower in the floriculture market; however, the family's potential in the floricultural industry has not been fully explored from the perspective of cut flowers. Ranunculaceae is a highly ethylene-sensitive family with the level of sensitivity falling in the range of '3–4' as per Van Doorn and woltering classification (1988). Higher ethylene sensitivity truncates the vase life of cut flowers by inducing petal abscission. Extensive postharvest studies have not been carried out on Ranunculaceae, resulting in a lack of precise regulatory mechanisms and standardized chemical formulations to enhance the postharvest longevity of these elegant flowers. Therefore, this article summarizes the preliminary postharvest studies conducted on some ornamentals of Ranunculaceae, which will provide a precise understanding of senescence mechanisms and identify the areas for further investigation.

Helleborus

Helleborus is a ravishing perennial ornamental that blooms in the winter or early spring. It has gained considerable commercial significance for usage as cut flowers and interior potted plants (Dhooghe et al. 2018). The widely grown ornamental species of *Helleborus* include *Helleborus niger* L. (Christmas rose) and *Helleborus orientalis* (Lenten Rose) (Rice and Strangman 1993). *Helleborus niger* flowers from mild winters (on Christmas) up to april, while *Helleborus orientalis* flowers from late winter to early spring (Salopek-Sondi and Magnus 2007; Shahri et al. 2011a, b). *Helleborus* flower consists of showy creamy white petaloid sepals. Whereas, petals are reduced to nectaries present at the base of flowers also called honey leaves (Dhooghe et al. 2018). It can act as a model system owing to its unique mode of senescence. Senescence studies conducted by shahri et al. (2011a, b) in *Helleborus orientalis* revealed that the flower senescence involves layer-by-layer stamen abscission surrounding the pistils, which is followed by the browning of nectaries at the base and finally the creamy white sepals harden and turn greenish. These sepals persist till the seed set is complete after which the complete flower abscises from the plant. Besides morphological changes, the various biochemical changes documented during the flower senescence include a decrease in sugars and proteins with an increase in protease activity. These persistent sepals become photosynthetically active during seed development. It is considered as important ecophysiological adaptation in *Helleborus*. Since *Helleborus* flowers in winter, therefore its leaves although green are covered by snow and debris. Moreover, they regularly deteriorate at their late stage with the formation of new leaves which are not photosynthetically active. Thus, green sepals are considered as the most reliable and direct source for providing assimilates to the developing seeds and fruits. The greening of sepals is induced by the stimulation of GA biosynthesis due to signals emanating from the developing fruits (Ayele et al. 2010). The protein extract of *Helleborus orientalis* analyzed through SDS-PAGE, demonstrated an increase in low-molecular weight proteins "so-called death proteins" and a decrease in high-molecular weight proteins during flower senescence. Thus in this flower system, senescence mechanisms and their post-transcriptional regulation can be better understood by analyzing the nature of these proteins (shahri et al. 2011a, b).

Helleborus orientalis being an elegant cut flower has been least studied in terms of postharvest perspective. Recently, Abdulla and Çelikel (2018) reported that sucrose pulsing of *Helleborus orientalis* accentuated its postharvest longevity by via improving water uptake and fresh weight of flowers. Consequently, the positive response of *Helleborus* cut flowers to sucrose pulsing suggests a huge scope for postharvest quality improvement in Helleborus cut flowers using suitable postharvest treatments.

Anemone

Anemone is commonly known as "wind flower." It occurs in various hues and colors, like red, blue, purple, and white. They are short-stemmed and spring flowering. Among the various species, *Anemone coronaria* is mostly used for cut flower production on large scale (Laura and Allavena 2007). They are usually harvested when buds are fully colored and half open. Anemones are highly sensitive to ethylene and exhibit ethylene-dependent mode of senescence (Reid 2004). The key senescence symptoms include petal in rolling and stem bending. The average lifespan of an individual flower in distilled water is about 5 days. Application of GA_3 has been found to accentuate longevity and improve flower quality by preventing neck bending. Moreover, the inclusion of anti-ethylene treatments like $AgNO_3$ in vase solutions improved the postharvest performance and flower quality of cut anemone flowers by reducing endogenous ethylene production (Sharifani, et al. 2004). Pulsing with ethylene action or synthesis inhibitors like STS (Silver thiosulfate) or MCP also reduced quality deterioration and improved their display life (Reid 2004). Moreover, Cyclodextrin nanosponges (CD-NS) synthesized by hydrolysis of starch are used for sustained release of 1-MCP (an ethylene biosynthesis inhibitor) (Manzoor et al. 2020). The use of CD-NS structure for sustained release of 1-MCP significantly improved the vase life of *Anemone coronaria* as compared to gaseous MCP (Seglie et al. 2013). The combination of treatments like BA (Benzyl adenine) and growth-retardant Paclobutrazol was also found to be effective in improving postharvest attributes, like preventing membrane leakage, improving anthocyanin content and inhibiting stem bending (Chernov et al. 2007). Thus anti-ethylene treatments and growth retardants can significantly mitigate the postharvest losses in *Anemone* cut flowers.

Clematis

Clematis is known for its profuse blooming and large elegant flowers measuring 20 cm in diameter (Rabiza-Świder et al. 2017). It is successfully cultivated as a cut flower in the U.S.A. on large scale (Greer and Dole 2009). Xylem occlusion leading to negative water balance is regarded as a key factor limiting the vaselife of clematis flowers. The first noticeable symptoms of senescence include loss of fresh weight and petal wilting (Rabiza-Świder et al. 2017). The root cause for the xylem occlusion was found to be tyloses and bacterial proliferation. Application of 8HQC (8-hydroxyquinoline citrate) and 2% sucrose reduced the bacterial proliferation and growth of xylem tyloses (Jedrzejuk et al. 2012). Moreover, the effect of the treatments including 8-hydroxyquinoline citrate (8HQC, 200 mgL^{-1}) and a standard preservative (SP) solution comprising 200-mgL^{-1} 8HQC and 20-gL^{-1} sucrose (S) on vase life was found to be cultivar specific. In cultivars like 'General Sikorski,' both treatments accentuated vase life by about 30% as compared to the control, however, in 'Mazury' cultivar, vase life was increased by about 40% as compared to the control, by the standard preservative solution only. On the contrary, in jalka and pillu cultivar, no effect was found on the vaselife by the application of these two solutions. These vase solutions also differentially affected the water uptake rates in different cultivars. The water uptake was significantly increased by both the vase solutions in 'General Sikorski,' while in 'Piilu' cultivar both the vase solutions reduced the water uptake as compared to control (Rabiza-Świder et al. 2017). Apart from 8HQC, the inclusion of other biocides like $Al_2(SO4)_3$, NaOCl and $Ca(OCl)_2$, or citric acid as acidifier did not have any significant impact on the vase life of cut clematis flowers, thereby confirming the fact that the effect of biocides varies with different species and cultivars (Rabiza-Świder et al. 2017; Tekalign et al. 2011). Although *clematis* flowers do not produce measurable amounts of ethylene but they were highly responsive to exogenous ethylene treatment leading to shortening of vaselife. On the contrary, application of STS (Silver thiosulfate) and MCP significantly improved their vase life. MCP caused a maximum increase in vase life. The presence of silver ions in the STS complex hinders the ethylene effect by competing for the same active site (Rabiza-Świder et al. 2017). Moreover, the antimicrobial effect of STS improves water uptake and enhances flower longevity (Rezvanypour and Osfoori 2011). The cultivar-specific differences in terms of responding to different preservatives were also reflected in senescence mechanisms at the ultrastructural level. PCD studies conducted in two cultivars of clematis 'Popieluszko and Andromeda' revealed temporal differences in the degradation of different organelles during their cell death. In the long-lived cultivar, 'Popieluszko' symptoms of organelle degeneration were initiated at the open stage, while in the short-lived cultivar, 'Andromeda' symptoms of organelle degeneration were already initiated at the bud stage. This temporal difference in the initiation of senescence mechanisms may be the underlying reason for different longevity in different cultivars. Nuclear degradation being one of the earliest signs of PCD was well advanced in a short-lived cultivar at the bud stage while in

long-lived cultivar, nuclei were found stable up to the last stage of development. The senescence process is usually intensified once the flowers are detached from the parent plant. However, application of preservatives has been found to retard the same (Lone et al. 2021a, b). Surprisingly, long-lived cultivars of clematis cut flowers held in preservative solutions had the same rate of chromatin degradation as that of control ones held in distilled water. In opposite to this, chromatin degradation was arrested in short-lived cultivars treated with preservatives. Mitochondria and plastids which are stable organelles were visible in wilted flowers of long-lived varieties as well as in short-lived cultivars treated with preservative (sucrose + 8HQC). The cell wall is one of the structures that degraded during the end phase of senescence. In long-lived cultivars, preservatives could not arrest cell wall degradation, whereas in short-lived cultivars, cell wall degradation was arrested by the application of preservatives (Rabiza-Świder et al. 2016). From the above studies, it can be concluded that although clematis is a beautiful cut flower with high market demand, but the selection of a suitable cultivar and optimization of appropriate postharvest treatments is the only means to commercialize it on large scale.

Delphinium

Delphinium is a fascinating ornamental with elegant spikes, mostly used as a cut flower (Ichimura et al. 2009). The spikes bear flowers of vibrant colors ranging from white to pink. *Delphiniums* are sensitive to ethylene but the sensitivity varies between the species and cultivars. In *Delphinium* hybrid cv. Bellamosum, ethylene sensitivity is age dependent, i.e., flowers become sensitive to ethylene toward the advanced stage of development (Ichimura et al. 2009). In *Delphinium* inter-organ signaling has been proposed to coordinate the senescence process within the flower similar to that of carnation (Shibuya et al. 2000). Interestingly, the climacteric upsurge of ethylene has not been observed in sepals and petals but in receptacle and gynoecium. The activity of ACC synthase and ACC oxidase was many folds higher in the gynoecium as compared to a receptacle, indicating production of ethylene in gynoecium signals the receptacle to produce ethylene and induce abscission of *Delphinium* sepals as they are directly connected to it rather than gynoecium (Ichimura et al. 2009). Moreover, wounding of the gynoecium and receptacle has also been found to induce sepal abscission as wounding leads to ethylene production in the receptacle (Yang and Hoffman 1984). The sepal abscission was however dramatically inhibited by the pulse treatment with STS (Silver thiosulfate) and AVG (Aminoethoxy vinyl glycine), but AVG inhibited the sepal growth of *Delphinium* flowers. Surprisingly, other ethylene antagonists like AOA (Aminooxyacetic acid) and 1-MCP (1-Methylcyclopropene) were found to be ineffective in inhibiting the abscission of sepals in cut *Delphinium* (Ichimura et al. 2009). This might be attributed to the accumulation of these inhibitors in insufficient concentration at the active site (Ichimura et al. 2002). Thus, STS is the only ethylene antagonist recommended to accentuate the quality of cut *Delphinium* flowers. Moreover, studies conducted in *Delphinium grandiflorum* revealed that the ethylene production was high in gynoecium and receptacle from day zero of harvest as compared to *D. belladonna*. During senescence, ethylene production exhibited a substantial increase in the receptacle as compared to gynoecium. Also, pollination induced the upsurge in ethylene production in gynoecium and receptacle, however, *ACS* and *ACO* transcripts were least abundant in gynoecium, while *DgACO3* transcripts were highly abundant in the receptacle. This indicates the differential regulation of *ACS* and *ACO* in the gynoecium and receptacle (Okamoto et al. 2022). Mannitol is a key soluble carbohydrate in *Delphinium*. In addition, mannitol is also a major soluble carbohydrate of Scrophulariaceae, Oleaceae, Rubiaceae, and Umbellifereae (Bieleski 1982). The application of exogenous mannitol exhibited multifaceted effects on *Delphinium*, manifesting not only in the retardation of sepal abscission but also in the mitigation of ethylene responsiveness and the attenuation of the climacteric surge in ethylene synthesis. Mannitol treatment induced augmented concentrations of glucose and fructose within the sepal tissues, concomitant with the rise in mannitol levels in the sepals (Ichimura et al. 2000). These results indicate that mannitol is metabolized into readily usable forms of carbohydrates like glucose and fructose by mannitol dehydrogenase, which in turn reduce the climacteric upsurge in ethylene production and thus prevent the sepal abscission (Kikuchi et al. 1999). A combination of STS pulse and 4% sucrose treatment significantly accentuated the longevity of *Delphinium elatum* flowers, besides enriching the anthocyanin content of sepal tissues (Kuroshima et al. 2017). Likewise, in *Delphinium malabaricum*, treatment of sucrose along with $AgNO_3$ significantly extended the vase life of *Delphinium* flowers. Sucrose not only acts as an osmoticum and respiratory substrate but also reduces ethylene sensitivity. Also, $AgNO_3$, a broad-spectrum bactericide, markedly inhibited bacterial proliferation and maintained the solution flow through the xylem vessels and hence improved the postharvest attributes (Kolar et al. 2017).

Ranunculus

Ranunculus is commonly known as "buttercup." It is a highly demanding crop in the global cut flower industry. *Ranunculus* cultivation is suitable for small-scale growers as it requires minimal space with huge economic returns as one bunch consisting of 10 *Ranunculus* stems costs $12.50 to $26.00 in the international market (Rauter et al. 2022). *Ranunculus* is an excellent model system for

studying flower colorations because of its wide variety of petal colorations, including white, yellow, red, green, black, and brown (Liu et al. 2019). Senescence studies conducted on *Ranunculus asiaticus* revealed that the membrane integrity decreases with the progression of flower development. Moreover, the other biochemical attributes like sugars, proteins, and phenols also witnessed a sharp decrease as the flower development proceeded from the open to the senescent stage (Shahri and Tahir 2011a, b). The visible symptoms of senescence symptoms in *Ranunculus asiaticus* are wilting and then abscission of petals toward the end phase of senescence. The color of the petals also changes from dark red to brick red with the loss in luster and turgidity. The flowers usually last for five days from the day of blooming. (Shahri et al. 2010). *Ranunculus asiaticus* exhibits ethylene-independent mode of senescence. Although the flowers produce a climacteric rise in ethylene production but they are not sensitive to exogenous ethylene. Moreover, the *ACC* level was found to be constant with age (Kenza et al. 2000). Application of anti-ethylene treatments were ineffective in improving the quality of cut flowers, thereby, indicating that flowers need not be shielded from ethylene exposure (Shahri et al. 2011a, b). The anti-senescent postharvest treatments like GA_3 significantly improved the vase life by maintaining higher carbohydrate content in petal tissues. Likewise, the application of salicylic acid and combination treatment of (sucrose + HQS + Citric acid) improved the postharvest performance of *Ranunculus* cut flowers by improving various biochemical attributes, like carbohydrate content, anthocyanin content, and water balance of petal tissues (Al-Hasnawi et al. 2018). Notably, individual sucrose treatments were found to be ineffective in delaying the senescence in cut flowers of *Ranunculus asiaticus* (Shahri et al. 2010). HQS being antibacterial prevents vascular occlusion by inhibiting bacterial growth, while citric acid maintains the pH of the preservative solution to facilitate absorption of all its constituents via xylem vessels (Al-Hasnawi et al. 2018). Moreover, salicylic acid and sucrose induce anthocyanin biosynthesis, thereby improving the display quality of these precious cut flowers (Hatamzadeh et al. 2012; Kazemi et al. 2011). Besides growth regulators, treatment of *Ranunculus* cut flowers with protein synthesis inhibitor 'Cyclohexamide' (CHI) has been reported to delay the execution of senescence by improving various postharvest attributes like membrane integrity and the content of soluble proteins in petal tissues through attenuation in protease activity. Moreover, carbohydrate content was also found to be higher in CHI-treated petal tissues, which may be attributed to a decrease in respiratory activity in petal tissues by application of CHI (Shahri and Tahir 2010a, b), as it reduces respiratory activity in higher plants. (Ellis and Macdonald 1970).

Consolida

Consolida ajacis, also known as "Doubtful Knight's spur or Rocket larkspur," blooms from May to July. It is a magnificent ornamental with promising potential as a cut flower because of its fascinating spikes of various hues and colors, adding charm to gardens and interior spaces (Haq et al. 2022b). The characteristic feature of *Consolida ajacis* flowers are hood and spur formed by the upper petaloid sepals. Flower senescence in *Consolida ajacis* is characterized by the withering of anthers and projection of the pistil out of the protective hood formed by upper petals, followed by wilting and abscission of tepals (Shahri and Tahir 2011a, b). The senescence process in *Consolida ajacis* involves a decrease in sugar and protein content of tepal tissues and increase in membrane seepage and protease activity. Moreover, SDS-PAGE analysis of the protein extract of *Consolida ajacis* revealed increase in low-molecular weight proteins and decrease in high-molecular weight proteins during flower senescence. Consequently, elucidating the nature of these polypeptides can provide vital insights about the post-transcriptional regulation of senescence mechanisms within this flower system. (Shahri and Tahir 2011a, b). *Consolida ajacis* is a highly ethylene-sensitive flower which limits its postharvest longevity. Application of sucrose and ethylene antagonists like STS (silver thiosulfate) significantly alleviated senescence symptoms in *Consolida ajacis* spikes by reducing the ethylene action and preventing climacteric rise in ethylene production (Ichmura et al. 2000, Finger 1999; Shahri et al. 2010). In addition to anti-ethylene treatments, pulsing with protein synthesis inhibitor Cyclohexamide (CHI) has been found to be highly efficacious in mitigating postharvest senescence in cut spikes of *Consolida ajacis*. Pulsing of spikes with CHI maintained higher fresh mass and dry mass of flowers by reducing respiratory loss. Moreover, higher protein content was detected in flowers pulsed with CHI relative to untreated ones. This may be attributed to diminished protease activity by CHI pulsing and hence prevent protein degradation (Shahri and Tahir 2010a, b). Recent studies entrench the extensive role of growth regulators like salicylic acid, cytokinins, and polyamines and in accentuating the marketability of *Consolida ajacis* cut spikes by delaying the execution of senescence. Salicylic acid being a phenolic compound is highly effective in orchestrating postharvest senescence in cut spikes of *Consolida ajacis* (Haq et al. 2022a). In another study, the role of nitric oxide was also envisaged in improving display quality in cut spikes of *Consolida ajacis* (Haq et al. 2021). These studies demonstrated that lipid peroxidation and vascular occlusion are the primary factors responsible for senescence instigation in *Consolida ajacis.* Salicylic acid and nitric oxide treatments improved the solution uptake by decreasing bacterial proliferation and maintained membrane integrity of flower tissues

by attenuating lipoxygenase activity. In addition, these postharvest treatments significantly accentuated the activity of antioxidant enzymes to counter ROS involved in senescence instigation (Haq et al. 2021, 2022a). Owing to their multifaceted role in senescence regulation, these treatments can be recommended as effective anti-senescent therapies for mitigating postharvest losses in cut flowers of *Consolida ajacis*. Moreover, the implication of polyamines on various biochemical aspects of flower senescence in *Consolida ajacis* cut spikes was also tested. The investigation revealed that polyamines orchestrated the flower senescence by augmenting the antioxidant response, essential for ROS scavenging. The study also unveiled that Polyamines prevented the breakdown of protein and sugars besides, warranting the membrane stability of the tepal tissues. Thus, the depletion of sugars and Proteins, besides attenuation of antioxidant system was found to be the primary factors leading to senescence initiation in *Consolida ajacis* cut spikes (Farooq et al. 2021a). Cytokinins including Benzylamino purine (BAP), Kinetin (KIN), and cytokinin-like substances thidiazuron were also assessed in delaying the onset of senescence *Consolida ajacis* cut spikes. Inclusion of these postharvest treatments considerably improved the quality of cut spikes by augmenting phenolic content, besides maintaining optimum protein and sugar content in tepal tissues (Haq et al. 2022b). The aforementioned postharvest treatments have been summarized in tabulated form as shown in Table 3.

Conclusion and Future Perspectives

Ranunculaceae is an ethylene-responsive family, therefore the postharvest investigations conducted on cut flowers of this family have mostly evaluated the efficacy of conventional anti-ethylene treatments in alleviating postharvest senescence. However, using novel eco-friendly and cost-effective anti-ethylene substitutes over conventional ethylene blockers could be highly beneficial in preventing the onset of senescence. Moreover, earlier studies on senescence have entrenched the extensive role of growth regulators in accentuating the lifespan of cut flowers. As a result, exogenous sourcing of growth regulators such as cytokinins, salicylic acid, and polyamines can offer substantial opportunity for postharvest quality improvement in *Ranunculus* cut flowers. Ethylene being crucial in regulating flower senescence in Ranunculaceae, consequently elucidating crosstalk between ethylene and other phytohormones could be a promising strategy for modulating senescence in climacteric flowers. Senescence studies conducted on ornamentals of Ranunculaceae have primarily concentrated on understanding the biochemical mechanisms regulating their longevity. However, in recent years, significant advancements have been achieved in tagging the genes instigating senescence in various flowers, like *Dianthus, Petunia, and Gladiolus*. This has been achieved through gene expression studies, transcriptome profiling, and microarray technology. Extending the use of these technologies can be of immense help in tagging the genes responsible for senescence regulation in the ornamentals of Ranunculaceae. In addition, the antisense-RNA technology can help us to combat senescence in climacteric flowers by suppressing the transcripts of ethylene forming genes as achieved in *Dianthus*. Furthermore, the recent CRISPR technology can have far better implications in regulating the senescence process as it ensures the desirable fine tuning of senescence-associated genes along with their stable transmission to subsequent generations. Moreover, gaining insights into the crosstalk between the signaling cascades and the hormones can immensely widen our future understanding relating to postharvest physiology of flowers and as such the family Ranunculaceae can serve as a model system in this regard. Achieving successful outcomes in employing these strategies necessitates meticulous adherence to appropriate experimental designs, such as employing randomized designs to assess the potency of ethylene antagonists and growth regulators. Additionally, unraveling hormonal crosstalk and gene expression patterns of senescence markers demands judicious application of factorial and time series experimental designs to furnish insightful results. However, the application of the aforementioned methodologies is not devoid of hurdles. Concerns pertaining to environmental implications and potential adverse effects arising from the use of growth regulators may impede progress in these endeavors. Furthermore, implementing CRISPR technology to regulate senescence-associated genes in Ranunculaceae confronts the formidable challenge of mitigating off-target effects and the unintended modification of non-target genes, thereby necessitating stringent validation and optimization of the CRISPR-Cas9 system.

Table 3 Different postharvest treatments and their mode of action in delaying senescence in flowers of Ranunculaceae

Flower	Treatment	Mode of action	References
Anemone sp.	GA_3	prevented neck bending	Sharifani et al. (2004)
	AgNO3	Improved vaselife and reduced ethylene production	Sharifani et al. (2004)
	Cyclodextrin nanosponges (CD-NS)	Reduced ethylene production and improved postharvest quality	Seglie et al. (2013)
	BA (Benzyl adenine) and growth-retardant Paclobutrazol	Prevented membrane leakage, improved anthocyanin content of petal tissues, and inhibited stem bending	Chernov et al. (2007)
Clematis sp.	8HQC (8-hydroxyquinolin citrate) and 2% sucrose	Reduced the bacterial proliferation and growth of xylem tyloses	Jedrzejuk et al. (2012)
	STS and MCP	Accentuated vase life, reduced the ethylene effect, and STS improved the water uptake	Rezvanypour and Osfoori (2011) and Rabiza-Świder et al. (2017)
Helleborus sp.	Sucrose pulsing	Improved water uptake and fresh weight of flowers	Abdulla and Çelikel (2018)
Delphinium sp.	STS (silver thiosulfate)	Inhibited sepal abscission	Ichimura et al. (2009)
	Mannitol	Inhibited sepal abscission and reduced sensitivity to ethylene	Ichimura et al. (2000)
	STS pulse and 4% sucrose	Accentuated the longevity of *Delphinium elatum* flowers, enriched the anthocyanin content of tepal tissues	Kuroshima et al. (2017)
	Sucrose and $AgNO_3$	Reduced ethylene sensitivity and microbial proliferation	Kolar et al. (2017)
Ranunculus sp.	GA_3	Maintained higher carbohydrate content in petal tissues	Al-Hasnawi et al. (2018)
	(Sucrose + HQS + citric acid)	Maintained carbohydrate content, anthocyanin content, and water balance of petal tissues	Al-Hasnawi et al. (2018)
	HQS	Reduced microbial proliferation and prevented xylem occlusion	Al-Hasnawi et al. (2018)
	Salicylic acid and sucrose	Improved anthocyanin content	Kazemi et al. (2011) and Hatamzadeh et al. (2012)
	Cyclohexamide (CHI)	Improved carbohydrate content and soluble proteins, reduced protease activity and respiratory upsurge	Shahri and Tahir (2010a, b)
Consolida ajacis	Sucrose and STS	Reduced the ethylene action and prevented ethylene production	Finger (1999), Ichmura et al. (2000) and Shahri et al. (2010)
	Cyclohexamide (CHI)	Maintained higher protein content in tepal tissues	Shahri and Tahir (2010a, b)
	Salicylic acid and Nitric oxide	Improved the solution uptake, decreased bacterial proliferation, maintained membrane integrity, attenuated lipoxygenase activity	Haq et al. (2021) and Haq et al. (2022a)
	Polyamines	Augmented antioxidant system, maintained protein and sugar content in tepal tissues	Farooq et al. (2021a)
	BAP, KIN, and TDZ	Increased phenolic content and maintained protein and sugar content in tepal tissues	Haq et al. (2022b)

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Declarations

Conflict of interest The authors affirm that they have no conflicts of interest about this manuscript.

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