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Petal abscission in flower crops: A review

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Abstract
The flower is the organ with the shortest period of longevity. Petal shedding or petal abscission is a serious problem in many ornamental and commercial flower crops. Petal shedding may be regarded as the final stage of flower senescence. Senescence accomplishes through the changes that lead sooner or later to death of an organism or some part of it, while aging occurs in time without reference to death as a consequence. Petal senescence is an irreversible process and it has been the last phase of life in which, a series of normally irreversible events are initiated that lead to cellular breakdown and death. This article gives an idea about senescence, its types, causes and changes occurring during this process in the flower crops and the factor to control the abscission.

Keywords: Senescence, types, causes, flower crops, plant hormones

Introduction
Floral longevity is tremendously variable; ephemeral flowers may be open for only a few hours, while some flowers may remain open and receptive for many months. Flowers have very short life compared to most other plant organs, and their senescence is often precisely controlled by environmental or physiological cues. Senescence can be defined as those events leading to the death of cells, tissues, organs which include adverse water relation and floret abscission (Reid, 1988) [56]. Flower senescence or apoptosis is the terminal phase of developmental processes that lead to the death of flower, which include flower wilting, shedding and fading of petals. Leopold (1971) [38] has proposed types of senescence in plants which are overall senescence (entire plant dies after the development of fruit and seeds), top senescence (shoot system may die), deciduous senescence (all the leaves die but the bulk of the stem and root system remains viable) and progressive senescence (gradual death of old leaves from the base to the top of the plants).
Woltering and van Doorn (1988) [89] classified the petal senescence of 93 species into three types *viz.*, Type I- abscission mediated by ethylene, Type II- abscission not mediated by ethylene, Type III- abscission mediated by ethylene without any visible sign of wilting. As denoted by Yoshida (2003) [96], senescence has three stages of which first is the initiation of senescence followed by degradation and disassembly leading to third stage of death, which is due to decline in rate of anabolic processes and increase in rate of certain catabolic processes. Senescence in plants can be divided into two distinct processes namely aging of various tissue and organs as plant matures and the process of death of entire plant after pollination and fertilization called as monocarpic senescence as stated by Palavan-unsal *et al.*, 2005 [11].
Senescence in floral tissues occurs at various stages of development and can be characterised by distinct morphological changes and triggered by independent hormonal or another endogenous signal. At whole organ level, petals, anthers and stigma are not required after pollination and hence in many species, there is a mechanism for rescuing resources from the degenerative tissues and diverting them to other plant parts (Rogers, 2006) [59].
Programmed Cell Death (PCD) which is a synonym of senescence can be subdivided into three stages: Signalling phase, execution phase and dismantling phase (Depreatere and Golstein, 1988) [13]. PCD in plants has been classified into two main types based on morphological criteria i.e. vacuolar cell death and necrosis (or necrotic cell death). In vacuolar cell death, degradation of cellular components by an autophagy-like process and vacuolar hydrolases after tonoplast rupture occurs. It occurs mainly during tissue and organ formation and elimination.
In contrast, necrosis is characterized by swelling of mitochondria, early rupture of the plasma membrane, and shrinkage of the protoplast. Necrosis is mainly found during abiotic stress (van Doorn *et al.*, 2011; Shibuya *et al.*, 2016) [80, 67].

Senescence in flower crops

Senescence processes have been encountered in all stages of life cycle (Woolhouse, 1978) [90]. The senescence strategies have been found to vary with the flowers. In petunia (Gilissen, 1977) [21] and many orchids (Arditti, 1979) [3], the petals are found to be retained for months until pollination after which, they senesce and shrivel with a rapid fading of corolla in a day or by abscission as in Sweet Peas and Snapdragon. In morning glory (*Ipomoea caerulea*), the flowers are found to fade and collapse with in a day of bud opening as their contents break down and are withdrawn to the developing gynoecium. According to Shibuya *et al.* (2016) [67], floral longevity is species-specific and is closely linked to reproductive strategy. Petals in flowering plants senesce and eventually wilt or shed after pollination or some time following flower opening, regardless of the pollination event. Some flowers retain their petals after pollination whereas some flowers show immediate symptoms of senescence after pollination. In many rose cultivars, the petals abscise without senescence symptoms (van Doorn and Woltering, 2008) [83].

Floricultural crops such as carnation, eustoma (*Eustoma grandiflorum*), petunia (*Petunia hybrida*), and sweet pea (*Lathyrus odoratus*) are sensitive to ethylene, and ethylene production increases during flower senescence. It was previously reported that petal wilting is induced by ethylene produced in the gynoecium and petals in carnation (Shibuya *et al.*, 2000) [66], while petal abscission is thought to be induced by ethylene produced in the pistils or receptacles in torenia (*Torenia fournieri*) and delphinium (*Delphinium* sp.) (Woltering and van Doorn, 1988) [89].

Ethylene concentration was high at full bloom condition and was increased after harvest in *R. bouboniana* and *R. damascena* (Shweta and Nagar, 2008) [68]. Ethylene concentration was high at full bloom condition and was increased after harvest in *R. bouboniana* and *R. damascena* (Shweta and Nagar, 2008) [68]. Different response for ethylene were observed with regard to floral organs. In all the stages, the production of ethylene was higher in the ovaries, followed by the style-stigma plus stamens and finally the petals. Hence, high concentrations of ethylene caused rose flowers either to open prematurely or drop their petals before the buds were open (Trivellini *et al.*, 2011) [76]. Cut dahlia flowers have a short vase life of 3–7 days, and some cultivars exhibit petal abscission, even inside of cardboard boxes during transport. This petal abscission is induced by ethylene in many cases.

Causes for senescence

In flower petals, senescence is caused by various factors such as hormonal changes namely ethylene and ABA concentration and also by up regulation and down regulation of various genes. Free radical formation also causes senescence. Plant hormones and other signalling molecules are implicated in the senescence process. During senescence, there is a reciprocal action of various hormones e.g., ethylene and ABA which plays important role in senescence.

a) Ethylene

Ethylene, a simple hydrocarbon gas act as a principal hormone in inducing senescence whereas other hormones affect the sensitivity to ethylene (Reid and Jiang, 2012) [58].

Sensitivity of flower crop for ethylene depends on the carbohydrate status of the tissue and on pre-harvest and post-harvest conditions (Mayak and Dilley, 1976) [41].

Flower crops are classified as ethylene sensitive and ethylene insensitive based on their sensitivity to ethylene. The classification of families based on their sensitivity to ethylene was carried out by Woltering and van Doorn (1988) [89] in which the family 'Rosaceae' fell in the high sensitivity class with the percentage of stimulation of abscission in the range of 66-99%.

The pathway of endogenous ethylene production has been elucidated in plants. Ethylene is synthesized in plant tissues from the amino acid precursor methionine (Adams and Yang, 1979) [1]. Steps in ethylene biosynthesis are the conversion of S-adenosyl methionine into 1-amino cyclopropane-1-carboxylic acid (ACC) and the conversion of ACC into ethylene (Yang and Hoffman, 1984) [95]. The processes are catalysed by ACC synthase (ACS) and ACC oxidase (ACO), respectively.

In many tissues, the application of ACC results in the rapid production of ethylene, suggesting that ACC synthase is a rate limiting step in the *in vivo* synthesis of ethylene (Yang and Hoffman, 1984) [95]. At the time of pollination, 1-amino cyclopropane-1-carboxylic acid (ACC), the immediate precursor of ethylene, is synthesized in the stigma and subsequently transported the petals (Halevy, 1986) [23].

In striking contrast to ACC synthase, ACC oxidase is constitutively expressed in many tissues and is generally not regarded as rate limiting in the biosynthesis of ethylene (Kende, 1993) [32]. However, ACC oxidase transcripts have been shown to increase in response to a number of stimuli such as wounding (Balague *et al.*, 1993) [6], senescence (Tang *et al.*, 1994) [72] and ripening (Kim and Yang, 1994) [33].

Pollination, especially fertilization promotes petal abscission in several flowers and can be attributed to a rise in ethylene production (Salunkhe *et al.*, 1990) [62]. Ethylene caused rapid abscission of leaves, buds and even mature flowers from miniature rose plants (Serek *et al.*, 1995) [65]. Ethylene production in senescing carnation petals appears to be subjected to autocatalytic regulation (Woodson and Jones, 2003) [88].

Xue *et al.* (2008) [92] reported that ethylene receptors and downstream genes of ethylene signalling cascade may play important role in the progression of senescence. Ethylene regulates various genes which are shown to be up-regulated during flower senescence.

Ethylene promotes shedding of flower buds and petals in many flowers, including roses. CO_2 which is generally antagonistic in its effect to ethylene also promoted petal shedding. Ethylene coordinates the expression of a large number of senescence-associated genes expressed during petal senescence. It encourages protein turn over which expresses the balance between protein synthesis and protein degradation to move into more breakdown than protein synthesis symptoms. This causes loss of membrane integrity and vacuolar autophagy which means degradation and recycling of cellular components where cytoplasmic constituents are isolated within double-membraned vesicles known as an autophagosomes. The autophagosome then blind with a lysosome (spherical vesicles containing hydrolytic enzymes capable of breaking down virtually all kinds of biomolecules, including proteins, nucleic acids and carbohydrates) and therefore the cell components are degraded (Sakr, 2016) [61].

The process of petal separation in the fragrant rose, *Rosa*

bourboniana, is accompanied by the expression of two xyloglucan endotransglucosylase/hydrolase genes, RbXTH1, and RbXTH2. The sequences of the two genes show 52% amino acid identity but are conserved at the catalytic site. The genes are up-regulated soon after the initiation of the abscission process and their transcription is associated with the progression of abscission, being faster in ethylene-treated flowers but slower during field abscission. Transcription is ethylene responsive, with the ethylene response being tissue-specific for RbXTH1 but largely tissue-independent for RbXTH2. Expression is correlated with an increase in xyloglucan endotransglucosylase (XET) action in petal abscission zones of both ethylene-treated and field abscising flowers. Proximal promoters of both the genes drive b-glucuronidase expression in an ethylene-responsive and abscission-related manner in agrobacteria-infiltrated rose petals, indicating that cis-elements governing ethylene-responsive and abscission-related expression probably lie within the first 700 nucleotides upstream of the translational initiation codon (Singh *et al.,* 2011) [2].

b) Abscissic acid

Abscissic acid was now found to induce senescence in flower petals. ABA seems to be involved in the regulation of the senescence of ethylene-sensitive flowers. In rose and carnation, exogenously applied ABA modulates an early increase in ethylene production, enhancing the sensitivity to ethylene (Mayak and Halevy, 1972; Mayak and Dilley, 1976) [42, 41].

Exogenous ABA in daylily accelerated senescence-associated events, such as a loss of membrane permeability, and lipid peroxidation (Panavas *et al.*, 1998) [52].

In narcissus, exogenous ABA has been shown to lead to an early premature accumulation of senescence-associated transcripts in the tepals. The timing of ABA accumulation in petals suggests that the hormone co-ordinates the early events in the senescence signal transduction pathway in some flowers, whereas in others, it affects only the latter stages of senescence, perhaps serving to drive the process to completion (Hunter *et al.*, 2004) [29].

ABA is also a natural regulator of flower senescence (Reid and Chen, 2007) [57]. In flowers where the senescence process does not respond to ethylene, ABA has been envisaged as being the key factor regulating flower senescence through an early and continuous accumulation in various flower tissues.

In daylilies, the ABA content of the petals increases before the increases in activities of hydrolytic enzymes and before flower opening (Panavas and Rubinstein, 1998) [52], whereas in roses, the ABA content increases comparatively late in the petals,

2 days after the surge in ethylene production (Mayak and Halevy, 1972) [42].

c) Free radicals

Free radicals' formation may also increase the petal senescence. Free radicals like O_2^- and H_2O_2 are involved in the wilting of ethylene insensitive gladiolus perianth (Dhindsa *et al.*, 1981). The superoxide radicals or their derivatives have been reported to induce degradation of membrane lipids in carnation petals (Mayak *et al.*, 1983) [43].

Free radicals and anti-oxidative enzymes are involved in the wilting of daylily petals (Panavas and Rubinstein, 1998) [52].

Accelerated generation and or accumulation of ROS (Reactive Oxygen Species) have emerged as important signals in the activation of plant PCD, including petal cells in some species (Rubinstein, 2000; Hoeberichts and Woltering, 2002; De Pinto *et al*., 2006) [60, 14].

d) Other causes

External factors such as shaking, injury, adverse temperatures, certain plant gases and growth substances have been known to induce rapid petal shedding in sensitive species.

Physiological, biochemical and morphological changes during senescence

Senescence causes various morphological, biochemical and physiological changes in petals. Plant produces various signals to induce senescence or apoptosis of cells.

One of the signals for apoptosis is decrease in mitochondrial transmembrane potential, aberrant exposure of phosphatidylserine in the plasma membrane followed by activation of proteases, phospholipase and phosphatase enzymes.

Two metabolic events occur in senescing petals i.e. increase in respiration and hydrolysis of cell components. Lay-Yee *et al*. (1992) [37] showed that respiration, i.e. CO_2 generation increased in petals of opening flowers and decreased after the onset of senescence. The enzymatic changes which occur during senescence are mainly associated with these two processes.

Yamada *et al*. (2003) [94] found drastic change from a sink to a source in the petals of opening flowers. This phenomenon acted as a trigger of petal senescence.

a) Physiological changes

During maturation and senescence, disappearance of the ribosomes was observed as in the order-first of the free, single ribosomes, then of those aggregated into clusters and finally of those attached to the endoplasmic reticulum which vesiculates. This pattern of changes in ribosomes is very similar to that found in other plant tissues (Butler and Simon, 1971) [10]. It is followed by a reduction in the numbers of Golgi bodies, mitochondria, and other organelles.

Wiemken *et al.* (1976) [86] used iris petals as a model plant to study the changes during senescence. As noted by them, closure of plasmodesmata was the earliest change, allowing transfer of small molecules like sugars, hormones and RNA molecules between adjacent cells when open and when closed, transport gets halted.

The first observed sign of aging in cells is the invagination of tonoplast, which indicates the autophagic activity of vacuoles. It is mainly due to loss in membrane integrity. Eradication of compartments and release of hydrolytic enzymes results in cell death. Cytoplasmic streaming ceases immediately after the disruption of the vacuole (Groover *et al*., 1997) [22].

Petal cell death involves rupture of the vacuolar membrane, and subsequent complete degradation of the plasma rather than gradual increase in cell leakiness resulting from progressive degradation of the plasma membrane (van Doorn and Woltering, 2005) [82].

The developmental events that take place during senescence also involve physiological changes such as loss of water from the senescing tissue, leakage of ions, transport of metabolites to different tissues, and biochemical changes, such as generation of reactive oxygen species (ROS), increase in membrane fluidity and peroxidation, hydrolysis of proteins,

nucleic acids, lipids and carbohydrates (Tripathi and Tuteja, 2007) [77]. Increased activity of hydrolytic enzymes, DNA laddering and the appearance of apoptotic bodies was also observed by van Doorn and Woltering (2010) [84].

Complete degradation of mesophyll cells occurs prior to visible senescence due to the closure of plasmodesmata whereas epidermal cells remain intact (Battelli *et al*., 2011) [8]. Rapid and progressive cell-autonomous degradation of organelles including nuclei, vacuoles, plastids, mitochondria and endoplasmic reticulum and at maturity loss of plasma membrane and some parts of the cell was also observed. Respiration efficiency was gradually reduced due to inability of mitochondria to utilize the sugar substrate. Most noticeable changes during development and senescence takes place in plastids which show invaginations in plastid membrane.

b) Biochemical changes

Enzymes like glucose-6-phosphate dehydrogenase and glutamate dehydrogenase activity was increased in tulips, whereas their activity was decreased in *Phalaenopsis* (Trippi and Van, 1971) [78]. Proteases are also involved in the autolytic processes. Increase in peroxidase activity was found in petals of tulip (Carfantan and Danssant, 1975) [11]. Increased activity of peroxidase is related to an increase in release of peroxides and free radicals which react with cellular constituents and involved in promotion of petal senescence.

Activities of acid, alkaline pyrophosphatase and RNase increased with age in rose (Parups, 1976) [53]. During the senescence process, the level of macromolecules like starch, proteins, nucleic acids and cell wall polysaccharides was decreased. Increase in pH of the vacuole and decrease in cytoplasm pH was also observed. Since the pH of the normal cytoplasm is always neutral and that of vacuole is acidic, the disruption of the tonoplast may cause leakage from the vacuole, thus reducing the cytoplasm pH and increase in vacuole pH. Decrease in pH was also caused by increase in the level of organic acids like malic acid. This may be due to dark fixation of CO_2 into organic acids which was well demonstrated by Schnabl and Mayer (1976) [63] in rose petals.

Rubinstein (2000) [60] stated that PCD can be predicted by the biochemical changes i.e. increases in hydrolytic enzymes and respiratory activity which causes breakdown of macromolecules.

Reduction in the level of phospholipids enhances the permeability of plasma membrane and causes the cell prone to leakage. Another important event that leads to loss of membrane permeability is oxidation of membrane lipids (lipid peroxidation) due to lipoxygenases in day lily and carnations. Hossain *et al*. (2006) [28] reported the role of lipooxygenase in promoting senescence in gladiolus.

The ratio of saturated and unsaturated fatty acids was tend to increase during flower senescence (Hopkins *et al.*, 2007) [27].

Proteases degrade proteins by hydrolyzing internal peptide bonds and are one of the best characterized cell death proteins in plants. PCD-promoting signals induce inactive zymogens to active proteases and trigger irreversible proteolysis cascade causing death. Among all the proteases, the cysteine proteases are the most frequent and well characterized (Tripathi and Tuteja, 2007) [77]. Azeez *et al*. (2007) [5] reported the expression of specific serine proteases during senescence-associated proteolysis in gladiolus flowers. During the senescence, serine protease activity also increases up to 2/3 of total proteases activity.

ROS is produced from hydrogen peroxide, thus the hydrogen peroxide level regulating enzymes showed differential expression during senescence. In some flowers, an increase in ROS due to a decrease in activity of catalase and increased activity of superoxide dismutase (SOD) was observed. In carnation petals, catalase and ascorbate peroxidase (APX) activities increased during flower senescence. Decreased levels of natural antioxidants were reported in several flowers. In gladiolus petals, the decrease in APX activity was noted as prerequisite for flower senescence resulting in an increase of the endogenous H_2O_2 level (Rani and Singh, 2014) [55].

The low pH is optimal for hydrolases like RNase or phospholipase. This attributed to proteolysis and an increase in asparagine as the major amino compound in old petals, followed by accumulation of free ammonia. Increase in the activity of phospholipase causes a decreased level of phospholipids. The main phospholipid degrading enzymes are phospholipase D, phospholipase C, lipolytic acyl hydrolase and lipooxygenase which degrade fatty acids and up regulates the senescence process (Rani and Singh, 2014) [55].

c) Other changes

In addition to the physiological changes occurring during PCD, characteristic processes of apoptosis, such as DNA fragmentation, chromatin condensation and nuclear fragmentation have been detected in senescing petals of both ethylene-sensitive

(Orzaez and Granell, 1997) [50] and ethylene-insensitive flower species (Yamada *et al*., 2001) [93].

The breakdown products of the cell macromolecules are transported out of the petals to other parts of the plants or to the developing gynoecium. In the final stage of senescence, petals lose fresh weight leading to drying and shriveling. In some flowers, blackening and browning of petals occurs which is due to the oxidation of flavones, leucoanthocyanins and other phenols and the accumulation of tannins. Degradation of anthocyanins during senescence is possibly related to oxidative process. A significant increase in antioxidant activity is correlated with the rate of anthocyanin degradation.

Role of plant hormones in controlling abscission

Plant bio-regulators are unique plant producing hormone which is produced in one part of the plant and transported to the other parts to do their respective action. They are also produced artificially and applied as aqueous sprays to a variety of plant surfaces to do their desired response. Bio-regulators in plants are always produced at very low concentration. They are often called as Plant hormones.

a) Auxin

Auxin is the first identified plant growth hormone (Went, 1928) [87]. There are two types of auxins *viz.*, natural auxin (e.g., IAA, IBA) and artificially produced synthetic auxin (e.g., NAA, 2,4-D). Auxins are primarily synthesized in the shoot apex and move in a polar, basipetal fashion through the stem, and acropetally in the root, with a transition to basipetal flow from the root tip, often described as a fountain-like flow. They are transferred from cell to cell through vascular cambium, procambial strands and also in epidermal cells but transferred to root through phloem cells (Swarup and Bennett, 2003) [71].

Auxin has various physiological effects on plant cells. The major effect is to stimulate the elongation of cells. It also increases the osmotic solutes of the cell, reduce wall pressure, increase the permeability of cells to water and increase the wall synthesis. Thimann and Skoog (1934) [74] pointed that apical dominance is under the control of auxin which is produced at the terminal bud and transported downward through the stem to the lateral buds and hinders their growth.

French and Beevers (1953) [20] stated that auxin may increase the respiration rate indirectly through increased supply of ADP (Adenosine diphosphate) by rapidly utilizing the ATP in the expanding cells. It also involves in vascular differentiation.

Halevy and Kofranek (1976) [24] showed the positive effect of NAA on flower bud abscission in roses. NAA increased the longevity of bougainvillea when applied at later stages of bract development and prevents the dropping of mature bracts (Chang and Chen, 2001) [91].

Meir *et al.* (2006) [45] reported that basipetal polar auxin flux through the abscission zone prevents abscission by causing the abscission zone to be insensitive to ethylene. If the source of auxin is removed, the abscission zone becomes sensitive to ethylene, resulting in the initiation of abscission.

Higher concentration of auxin inhibits the elongation of root but increases the number of lateral roots and hence most of the cuttings are treated with auxin for better rooting. Auxin also induces parthenocarpic fruit. It also increases the respiration rate. In tissue culture, auxin and cytokinin ratio influence the shoot and root development. If higher concentration of auxin was found, it causes the root development and vice versa.

The important effect of auxin related to the experiment was delaying abscission of leaves, flowers and fruits. Among all auxins, NAA (Naphthalene Acetic Acid) is commonly used to reduce the senescence or abscission. Yumoto and Ichimura (2010) [97] suggested that auxin pulse treatment was effective in increasing fresh weight in cut Eustoma flowers.

b) Brassinolide

In addition to already established five phytohormone classes, there are newly formed substance which regulates plant growth and development namely phenolics, polyamines, methyl jasmonates and brassinosteroids. Among these substances, brassinosteroids are considered as sixth class of phytohormone.

Brassinosteroids are steroidal hormones which regulates the growth and development of plants in many ways. It was the first plant steroid to have hormonal activities (Srivastava, 2002) [70]. Brassinosteroids were first isolated and characterized from the pollen of rape plant, *Brassica napus* L. Subsequently, the occurrence of the hormone has been reported from 44 plants and are regarded probably ubiquitous in the plant kingdom. Brassinosteroids are highly effective in stimulating growth in young vegetative tissues and retarded abscission of leaves of citrus (Iwahari *et al*., 1990) [30].

Brassinosteroids have been characterized from 44 plant species, which include 37 angiosperms (nine monocots and 28 dicots), five gymnosperms, one pteridophyte and one algae. Leubner–Metzger (2001) [40] proposed that the gibberellin and brassinosteroid acted in distinct pathways in seed germination. He proposed that gibberellin and light act in a common pathway, whereas brassinosteroids directly enhances the growth of the emerging embryo independent of gibberellin and that particularly β-1,3-glucanase.

Brassinosteroids are considered as hormones with pleiotropic effects, as they influence varied developmental processes like growth, germination of seeds, rhizogenesis, flowering and senescence. The initial studies with brassinolide were concentrated around its ability to induce cell elongation, swelling, curvature and splitting of the second internode and such activity is called 'brassin activity' (Seeta *et al*., 2002) [64].

It enhances sink strength and phloem un-loading (Jenneth and Sasse, 2003) [31]. Application of brassionlide in jujube fruit delayed postharvest senescence processes by significantly reducing ethylene production and the respiration rate (Zhu *et al*., 2010) [101].

These growth-promoting steroidal hormones were extracted from pollen grains, anthers, seeds, stems, leaves, roots, flowers, and other organs. In addition, brassionosteroids were isolated from insect and crown galls of plants such as the Japanese chestnut (*Castanea crenata*) (Kutschera and Wang, 2012) [34]. Young growing tissues contain higher levels of brassinosteroids than mature tissues. They were found physiologically active in very low concentrations. Brassinosteroids are highly mobile in the plant system.

c) Salicylic acid

Salicylic acid extended vase-life of cut rose flowers by regulating water uptake. Improved water balance may be due to possible germicidal activity of salicylic acid as an antimicrobial compound acting by inhibiting vascular blockage and/or positive regulatory role on stomatal closure which regulates the rate of transpiration and increases the water-retaining capacity of leaves and petals (Mori *et al*., 2001) [48].

Salicylic acid influence various growth and development processes such as seed germination, vegetative growth, photosynthesis, respiration, thermogenesis, flower formation, seed production, senescence, local and systemic response against microbial pathogens. SA could contribute in maintaining cellular redox homeostasis through the regulation of antioxidant enzymes activity (Slaymaker *et al*., 2002) [69] and induction of the alternative respiratory pathway (Moore *et al*., 2002) [47] and regulating gene expression by inducing an RNA-dependent RNA polymerase which is important for post-transcriptional gene silencing (Xie *et al*., 2001) [91].

Salicylic acid has been recognized as a regulatory signal mediating plant response which affects leaf and chloroplast structure (Uzunova and Popova, 2000) [79], osmotic stress (Borsani *et al*., 2001) [9], chilling response activity of enzymes such as RuBisCO (ribulose-1, 5-bisphosphate carboxylase/oxygenase) and carbonic anhydrase (Slaymaker *et al*., 2002) [69], heat response (Larkindale *et al*., 2005) [36], affects chlorophyll and carotenoid contents (Fariduddin *et al*., 2003) [18], abiotic stresses such as drought (Chini *et al*., 2004) [12] and heavy metal tolerance (Freeman *et al*., 2005) and stomatal closure (Melotto *et al*., 2006) [46].

Salicylic acid (SA) is a new phenolic phytohormone, which participates in the regulation of different physiological processes in plants. Salicylic acid can reduce quantity of superoxide radicals by affecting SOD activity (Zhang *et al*., 2003) [100]. Salicylic acid is synthesized through two distinct and compartmentalized pathways that employ different precursors: the phenylpropanoid route in the cytoplasm initiates from phenylalanine, and the isochorismate pathway

takes place in the chloroplast (Hayat and Ahmad, 2007) [25].
Ezhilmathi *et al.* (2007) [16] reported that 5-sulfosalicylic acid as a salicylate derivative was effective in extending vase life of cut gladiolus. Salicylic acid inhibits the antioxidant enzymes catalase and ascorbate peroxidase, thus contributing to stabilizing H_2O_2 levels. Salicylic acid increased water uptake and fresh weight of cut rose flowers and thereby, caused a delay in decline of fresh weight and senescence of gladiolus spikes.
Mei-hua *et al.* (2008) [44] showed that salicylic acid can extend the vase life of cut flowers by decreasing ROS activity and ethylene activity. Salicylic acid scavenges ROS leads to decreasing lipid peroxidation. Salicylic acid increases the enzyme antioxidant activity thereby delaying the hydrolysis of cell components; reduce ROS production and ACC-oxidase activity.
Fan *et al*. (2008) [17, 44] showed that the treatment of salicylic acid extended the vase life and improved flower quality with reduced respiration rate, delay senescence and decrease lipid peroxidation. Yuping (2009) [98] reported that treatment with salicylic acid significantly extends the vase life of gerbera.
Hayat *et al*. (2010) [26] reported that antioxidants and active oxygen-scavenging enzyme systems such as SOD are regulated either directly or indirectly by salicylic acid. They also reported that exogenously applied salicylic acid at moderate concentrations enhances antioxidant system efficiency.
Salicylic acid is a well-known phenol that can prevent ACC-oxidase activity which is the direct precursor of ethylene and decrease ROS with increase in the enzyme antioxidant activity (Zamani *et al*., 2011) [99]. Most of the salicylic acid synthesized in plants is glucosylated and/or methylated. Salicylic acid decreases the permeability of plasma membrane of floret cells and improves the structure of chloroplasts which were badly damaged by ethylene. It was also shown to retard the reduction of catalase activity. It decreases rate of transpiration and evaporation of tissues, as well as decreases respiration which prevents the loss of fresh weight in cut flowers. It showed an enhanced vase life of lisianthus flowers by higher activity of SOD enzyme and reducing deteriorative enzyme activity such as LOX during flower senescence Bahrami *et al*. (2013) [7].

d) Gibberellin

Gibberellins were first isolated from the pathogenic fungus *Gibberella fujikuroi* from which they derive their name. Gibberellins are known to regulate seed germination, stem growth, induction of flowering, pollen development, senescence and fruit growth.
There are about 136 gibberellins being identified but few of them have a biological activity.
GA_1 has been identified in 86 plants and GA_3, which is also known as gibberellic acid, has been identified in 45 plants. It is the major GA accumulating in *G. fujikuroi*, from which it is produced commercially. Gibberellic acid is used to promote seed germination, stem elongation, and fruit growth in a variety of agronomically and horticulturally important plants. GA induces the production of enzyme to digest the endosperm, which causes barrier for seed germination. It provides de-etiolated condition for the plants.
Gibberellins act as secondary messengers in processes induced by long photoperiods. It induces flowering in short day plants. Gibberellins induce bolting and flowering under noninductive conditions in many plants that require low temperature for flower initiation. Applying GA_3 to carnation petals delayed senescence to limited extent. The observations suggested that decline in the GA_3 content may be a factor in determining the onset of senescence.
GA_3 treatment in carnation flowers showed delayed senescence and also showed decline in climacteric rise in ethylene. In reproductive development, GA has essential functions in stamen/anther formation, pollen formation, and pollen tube development (Kwon *et al*., 2015) [35].
It is also used to break bud dormancy and seed dormancy.
Cytokinin and gibberellins have a potential to decline the weight loss and improved the quality of cut gerbera flowers. GA_3 treated samples resulted in increased solution uptake and also decreased transpiration thereby, decreases the rate of senescence. GA_3 had a favorable changes like stimulated antioxidant activity, declined degradation and alleviated senescence. It regulates DNA and RNA levels, increased intensity of cell division, biosynthesis of enzymes, proteins, carbohydrates and photosynthetic pigments (Pogroszewska *et al*., 2014) [54].

e) Cytokinin

Cytokinin influences various processes in growth and development of plants, including the promotion of cell division, the counteraction of senescence, the regulation of apical dominance and the transmission of nutritional signals. Kinetin was the first substance to be identified and it is not naturally produced. The naturally occurring cytokinin
trans-zeatin was first isolated from immature maize endosperm in the early 1960s (Letham, 1963) [39]. Cytokinins delays leaf senescence due to their inhibitory effect on the Chl-breakdown and protein degradation (Thimann, 1985) [73]. Cytokinins application has been shown to slow down the aging process in rose and carnation petals (van Staden *et al*., 1990) [85]. It has been well known growth regulator which markedly delay or reverse leaf yellowing and senescence in various species. Cytokinin (BA) increased the vase life of anthurium, heliconia and red ginger. It slows down the process of senescence by their ability to promote the transport, accumulation and retention of metabolites in tissues and organs besides it protects the membranes against degradation. It interacts with other plant hormones in delaying senescence and extending plant organs longevity. Cytokinin application improved postharvest quality of rose cut flowers by reducing petal senescence, because cytokinin plays an anti-ethylene role and prevents fresh tissues from chlorophyll degradation (van Doorn and Cruz, 2000) [81].
Anthurium cultivar 'Leilani' and 'Marian See furth' consistently showed response to benzyl adenine with increased vase life. The vase life and degree of response to BA varied from harvest to harvest and BA always increased the vase life of responsive cultivars. Response to cytokinin would be probably a concentration-dependent reaction or tissue sensitivity. It could delay senescence process either by suppressing ethylene production or by alleviating the sensitivity of tissues to ethylene. BA treatments extend the vase life of many flowers such as Eustoma, Lilium (Asil and Karimi. 2010) [4].
Cytokinin enhances the cell division and accumulates carbohydrates on cell wall of tender cells of rose cut flowers, decreased electrolyte leakage from these cells. Cytokinin increased total protein content by inducing the accumulation

of amino acids and proteins in treated tissue. It also increased the longevity and retarded the senescence of rose cut flowers by enhancing the peroxidase and catalase activity (Mortazavi *et al*., 2007) [49].

BA delayed senescence by lowering the ABA content, which is known to increase during flower development and senescence in both ethylene sensitive and insensitive species (Trivellini *et al*., 2011) [76] and BA also down regulates the ethylene receptor expression.

In cut lotus flowers (*Nelumbo nucifera*), BA and thidiazuron were observed to prevent petal blackening. BA induces genes which affect ABA biosynthesis, catabolism and signaling pathways (Trivellini *et al*., 2015) [75].

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