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REVIEW ARTICLE

Postharvest physiology of cut flowers

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Abstract

The longevity of cut flowers is limited by their ephemeral nature and by multiple stresses. Impairment in water uptake, depletion of stored carbohydrates, increases in both respiratory activity and ethylene production are signatures of flower senescence. A wide range of techniques is available to extend flower preservation, including the use of flower preservative solutions, ethylene action inhibitors, growth regulators, and control of temperature and flower dehydration. The use of sucrose in pulsing solution, or as a component of vase solution, extends the vase life of flowers by either improving water balance and energy or delaying the senescence via reductions in ethylene biosynthesis. Inhibitors of ethylene production and action affect the longevity by extending the vase life of some ethylene-sensitive flowers. Flowers have intense respiratory activity, which may deplete the limited reserves of carbohydrates in the tissues. Lower temperatures markedly reduce both carbon dioxide concentration and ethylene production as well as its action. However, chilling-sensitive flowers, such as bird-of-paradise, heliconia, orchid, and ginger, cannot be stored below 10 to 13°C due to the intense development of tissue discoloration.

Keywords: ethylene; water relations; respiration; carbohydrates; temperature.

Resumo

Fisiologia pós-colheita de flores de corte

A longevidade das flores de corte é limitada por sua natureza efêmera e por diversos estresses. De forma geral, a diminuição da absorção de água, esgotamento dos carboidratos armazenados, aumento da atividade respiratória e produção de etileno são reflexos senescência floral. Uma ampla gama de técnicas está disponível para estender a preservação de flores, incluindo o uso de conservantes de flores, inibidores da ação do etileno, reguladores de crescimento e controle de temperatura e desidratação das flores. O uso de sacarose em solução pulsante ou como constituinte de solução de vaso pode estender a vida de vaso das flores, melhorando o balanço hídrico, estimulando a abertura das flores ou retardando a senescência devido à menor síntese de etileno. Os inibidores da produção e ação do etileno afetam a longevidade, estendendo a vida de vaso de algumas flores sensíveis ao etileno. As flores têm intensa atividade respiratória, o que pode esgotar as reservas limitadas de carboidratos armazenados nas hastes cortadas. A redução da temperatura reduz tremendamente a produção de CO_2 e etileno, bem como a sua ação. No entanto, em flores sensíveis ao frio como ave-do-paraíso, helicônia, orquídea e gengibre não podem ser armazenadas abaixo de 10 a 13°C devido ao intenso desenvolvimento de descoloração do tecido.

Palavras-chave: etileno; relação hídrica; respiração; carboidratos; temperatura.

Introduction

Cut flowers have limited shelf life due to the depletion of organic reserve compounds by respiration (Finger et al., 2016), bacteria and fungi infection (Muñoz et al., 2019), withering (Elhindi, 2012a), mechanical damage (Fernandes et al., 2020), storage temperature (Menegaes et al., 2019), water quality (Van Doorn, 2012; Costa et al., 2015a), and increase on ethylene sensitivity (Khunmuang et al., 2019). Respiration is inversely related to potential postharvest storage (Tinebra et al., 2021), especially in flowers in which organic respiratory reserves are minimal. Bacteria and fungi infection also decrease the shelf life of cut flowers due to xylem vessel occlusion, hindering the

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transport of water and conservative solutions (Yadeta and Thomma, 2013; Gómez-Merino et al., 2020). Withering occurs due to excessive water loss associated with a higher transpiration rate as a consequence of natural senescence, or due to vascular occlusion by bacteria or fungi (Sun et al., 2001). Mechanical damage caused by improper handling during harvesting, sorting, storage, and transport induces an increase in the respiratory rate and reduces the useful life of flowers (Gómez-Merino et al., 2020). Exposure to unsuitable temperatures for long periods also negatively affects the life span of cut flowers (Çelikel and Reid, 2002). Water quality and presence of contaminants, such as fungi or bacteria, or the high content of salts, especially chlorine, also impair their shelf life (Costa et al., 2015a). Despite the influence of ethylene in reducing the life span of ornamental crops, many cut flowers respond to the application of abscisic acid, gibberellins, and cytokinins (Khunmuang et al., 2019).

Among the several techniques available to increase shelf life and storage of cut flowers, the appropriate control of temperature, relative humidity, and atmospheric composition are the most important ones (Fernandes et al., 2020). In addition, treatments with substances that reduce the water stress, delay the senescence event, or extend the shelf life of cut flowers can be highlighted (Van Doorn, 2012; Costa et al., 2015a). The main postharvest substances include sugars, as energy supply, and acidifiers, to reduce pathogenic fungi and bacteria proliferation and to prevent xylem occlusion (Gul et al., 2020; Gómez-Merino et al., 2020). Ascorbic acid (AsA) (Barth et al., 2006; Ghadimian and Danaei, 2020) is probably the most widely-used preservative compound, while solutions based on aluminum (Al) (Gómez-Merino and Trejo-Téllez, 2018), cobalt (Co), lanthanum (La) (Gómez-Merino et al., 2020), and selenium (Se) (Costa et al., 2020) are emerging as novel players on preservation responses in flowers. As flowers continue to have high respiratory activity, thus depleting the organic substrates already limited in the petals, the carbon dioxide production (Finger et al., 2016) can be diminished by lower temperature during storage. However, flowers that originated from tropical and subtropical regions are susceptible to chilling injury, which restricts the period of shipping and storage at low temperatures (Thailand, 2018; Poonsri, 2020).

By nature, flowers are ephemeral organs (Smyth, 2005), and the adequate handling of postharvest practices is essential to maintain their quality, allowing long-term storage and transportation. However, for most species, relatively short-term storage at retail stores may be required (Horibe, 2020). In most cases, particularly in developing countries, the production areas of flowers are close to marketing centers, but even without modern postharvest handling, the final consumer still receives products of standard quality (Mahajan et al., 2014). Nevertheless, for long-distance markets or exports, new techniques of preservation must be incorporated to guarantee quality to the florist and the consumers' satisfaction.

In this review, the different aspects of cut flower physiology and preservation are discussed, specially focusing on the postharvest treatments available to diminish the rate of flower senescence.

Postharvest treatments

The longevity of flower species correlates with the control of senescence, which is a process that varies between species and requires the optimization of water relations, reduction of abscission or wilt, control of microorganism as well as respiratory and ethylene production rates. Thus, in addition to the management of storage temperature, relative humidity, and the composition of gases in the atmosphere surrounding the product, flowers can be treated with several chemical compounds that benefit tissue rehydration (Dias-Tagliacozzo et al., 2005).

Sugars, organic acids, inhibitors of the action or synthesis of ethylene, and antibacterial agents can be applied as solutions of pulsing (conditioning) or vase solutions (conservation). The first case corresponds to a quick treatment of pre-transport or storage, which affects the initial stage of the flower life, which is extended even after being transferred to water or vase solution. The vase solution uses commercial preparations to maintain the quality of the cut flower (Sonego and Brackmann, 1995).

Sucrose is the most used sugar to prolong floral longevity, aiming at replacing the substrates consumed during respiration and improving the absorption capacity, favoring the maintenance of petal turgidity, increasing the shelf life of cut flowers, and promoting the opening of immature buds (Doi and Reid, 1995). Sucrose can be used in vase solution at concentrations between 2%–5%. Among organic acids, citric acid is used in vase solutions, as it reduces its pH and, consequently, the proliferation of bacteria. Such microorganisms block xylem vessels in the cut region and prevent the maintenance of water balance, thereby limiting the flower longevity.

Among the several chemical compounds used for soothing or inhibiting the action of ethylene, aminoethoxyvinylglycine (AVG) and aminooxyacetic acid (AOA) inhibit the synthesis of ethylene by reducing the competitive and irreversible activity of 1-Aminocyclopropane-1-carboxylic acid (ACC) synthase, reducing the amount of substrate for ACC oxidase, and therefore the conversion of ACC to ethylene (Finger and Barbosa, 2006). The silver ion (Ag^+), which binds to the same binding sites as ethylene, is applied as silver thiosulfate (STS) and is considered an efficient inhibitor of ethylene biosynthesis (Reid and Wu, 1992). However, in more recent years, Ag^+ has been replaced in pulsing treatments by the fumigation with 1-methylcyclopropene (1-MCP), also an inhibitor of the ethylene action without harming the environment.

Plant hormones are involved in the regulation of senescence in flowers in a way that such compounds act as signals to regulate or interrupt specific reactions. Studies on the longevity of cut flowers have been conducted with plant hormones or inhibitors in the vase solution, resulting in flowers with delayed senescence (Mansouri, 2012). Salicylic acid (SA) is well-known as a signal molecule that plays a key role in plant growth, development, and protection by inhibiting ethylene production and reducing oxidase activity (Finger and Barbosa, 2006).

Cut flowers of pink *Antigonon leptopus* treated with AS and sucrose showed an increase in shelf life, with higher water uptake and reduced flower abscission (Seman and Rafdi, 2019). The gibberellic acid (GA_3) and spermine (SPM) have been described to extend the postharvest life of flowers. The application of these growth regulators improved the commercial quality of inflorescences of *Anthurium* cv. Arizona (Simões et al., 2018).

Several options of floral preservatives are commercially available, which may contain a mixture of compounds, including the bactericide 8-Hydroxyquinoline (8-HQ) or its sulfate (8-HQS) and citrate (8-HQC), which may reduce bacteria population growth in the vase solution. Solutions containing 8-HQS showed better water consumption by preventing microorganism growth in the xylem vessels, reducing weight loss, extending the vase life of Alstroemeria and Hydrangea flowers (Kabari and Solimandarabi, 2019; Kazaz et al., 2019). The use of 8-HQC and sucrose also improved the storage life of *Gladiolus grandiflorus* (Belwal Sheeba et al., 2019).

The sodium hypochlorite (NaClO) may prevent bactericidal contamination. The mechanism of action of chlorine is nonspecific and involves the oxidation of the cellular components of microbial agents. The application of sodium hypochlorite improved the vase life of several cut flowers (Bastos et al., 2016). Similarly, aluminum sulfate ($Al_2(SO_4)_3$) has been recommended to enhance the vase life of gladiolus and calla lily flowers (Gupta et al., 2020; Sales et al., 2021), as it acidifies the storage solution, limiting bacterial growth and consequently improving water uptake.

Nowadays, finding new compounds as alternatives to common chemicals is a trending objective concerning the postharvest quality of cut flowers. The synthesis and application of green silver nanoparticles and chitosan – a natural biopolymer safe for the environment – are receiving growing attention due to their antimicrobial and antioxidant properties. Recent studies have observed that the life of cloves has been extended by the addition of either chitosan or green silver nanoparticles (Solgi, 2018).

Water relations

In many flower species, wilting and senescence of petals are closely related to water deficit, which is mainly caused by continuous reductions in water uptake. Several events may hinder water absorption by the flowers such as xylem occlusion by microorganisms, deposition of pectin and phenols, or air embolism (Jędrzejuk et al., 2012).

In carnation and roses, longevity reduction was also strongly associated with the capacity of water uptake by the cut flower. Van Doorn et al. (1995), for instance, found the presence of *Pseudomonas* spp., *Acinetobacter calcoaceticus,* and *Alcaligenes* sp. bacteria in the xylem of these flowers after ten days at room temperature, which hindered water uptake and inversely reduced their longevity as a function of bacterial population increases. However, regardless of the vase blockage causes, the hydraulic conductance is diminished over the flower vase life, provoking an imbalance between water uptake and transpiration. In roses, the vascular occlusion in the xylem was primarily associated with the presence of bacteria in both stem and vase solution, thus blocking the water flow. It can also get worse due to the presence of extracellular polysaccharides and other degradation products that originated from dead bacteria (Van Doorn, 1997). In such conditions, the roses develop several symptoms of water deficiency, including abnormal flower opening, bend neck, and leaf wilting (Bleeksma and Van Doorn, 2003).

In *Zinnia elegans*, Carneiro et al. (2002) observed that the reduction in water uptake of the flowers negatively affects their fresh weight, in such a way that decreases started at the first 24 h after harvesting. However, when the base of the stem was recut every 12 h, the weight loss decreased compared with the uncut flowers, thereby improving the flower water balance. In bird-of-paradise (*Strelitzia reginae*), the flower water content may also be maintained by recutting 2-cm stem base every 48 h (Karsten et al., 2015; Folha et al., 2016). Such procedure led to increases in the longevity of this species by two days. The magnitude of the response was also associated with stem diameters (Figure 1). Similarly, the same life extension was observed in *Heliconia wagneriana* by cutting every two days (Costa et al., 2015b). In chrysanthemum, the xylem occlusion in the base of the stem occurs due to the joint activity of peroxidase and phenoloxidase, lignin, and suberin biosynthesis-related enzymes (Van Doorn and Vaslier, 2002). However, when inhibitors for such enzymes were applied to the vase solution, a delayed xylem vessel occlusion was observed, resulting in a delayed leaf wilting. Recently, considerable evidence demonstrated that aquaporin expression would benefit flower quality and water balance in *Paeonia lactiflora* Pall. (Xue et al., 2020).

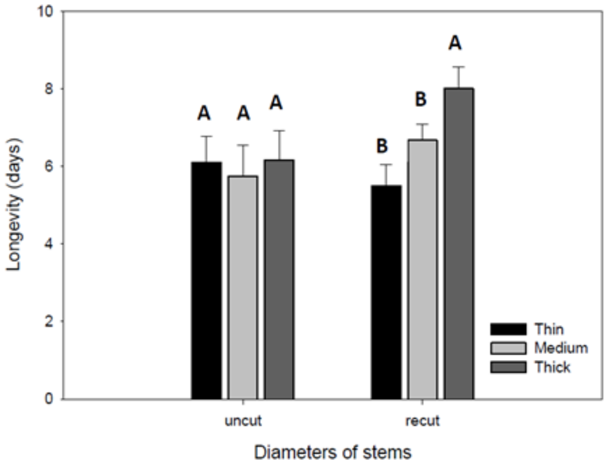


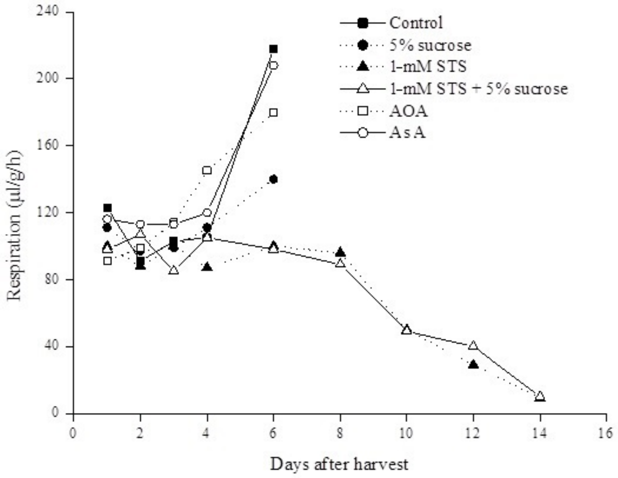
Figure 1. Longevity (days) of *Strelitzia reginae* stems harvested at three different diameters (thin, medium, and thick) submitted to base cutting every 48 h. The vertical bars represent the standard error of the mean and the same letters in each treatment did not differ according to the Scott-Knott test at 5% probability (Karsten et al., 2015).

Nevertheless, the mechanism that may provide a theoretical foundation for the development of technologies to improve the efficiency in the flower water uptake is still unknown.

Respiration

In general, flowers have high respiration rates compared with other horticultural products, which might lead to carbohydrate depletion, as they do not hold long-term storage organs. In addition, other deleterious effects are present, including higher transpiration rates and ethylene production and action. The temperature coefficient (Q_{10}) for most of the vegetables and fruits is close to two, but in flowers it might reach values up to eight (Wills et al., 1998). In cut *Narcissus* flowers, the respiration rate in two cultivars was exponentially increased over the temperature range of 0 and 12.5°C, given a Q_{10} close to 3.5, showing a negative linear relationship between the respiration and the vase life (Cevallos and Reid, 2000). Similar respiration and vase life behavior were observed in cut flowers of gerbera and sunflower when kept in temperatures ranging from 0 to 20°C (Çelikel and Reid, 2002). Thus, for these flowers, respiration can be used as an excellent index to predict the longevity of the vase life in a range of temperature conditions

The respiration of ethylene-sensitive flowers can be reduced by applying inhibitors of its action, in particular the silver thiosulfate (STS), which acts as a persistent inhibitor of the ethylene action. Altman and Solomos (1995) found that carnation flowers had no response to exogenous ethylene regarding the development of petal wilting or increase in respiration behavior when the vase solution contained 0.2-mM STS. The senescence of the flowers in *Consolida ajacis* is associated with the increase in ethylene production and respiration (Finger et al., 2004). When cut flowers of *Consolida ajacis* were pulsed with 1-mM STS or 1-mM STS+5% sucrose, it partially inhibited respiration activity, thereby prolonging the flower vase life (Figure 2). However, by loading the flowers with sucrose, no influence on the longevity was detected, probably due to the weak effect of the carbohydrate in attenuating the respiration compared with STS (Finger et al., 2004). Similar to sucrose pulsing, spraying the flowers with 2-mM AOA or 20-mM AsA had no effect on respiration and, consequently, on the flower longevity (Figure 2).



Source: Finger et al. (2004).

Figure 2. Influence of pulsing with sucrose and/or silver thiosulfate (STS), spray with aminooxyacetic acid (AOA) or ascorbid acid (AsA) on respiration of *Consolida ajacis* flowers.

Growth regulators

Ethylene

Ethylene produced by horticultural products may affect cut flowers during transport or storage, reducing their longevity or inducing physiological disorders, including petal wilting, senescence, abscission, epinasty, and chlorophyll depletion in leaves (De Martinis et al., 2015). The magnitude of such responses is related to the degree of sensitivity of the flower, which varies among species and cultivars (Scariot et al., 2014; Costa and Finger, 2016). Species of flowers with high sensitivity to ethylene show physiological responses at a lower concentration, usually between 0.1–1 µl L^{-1} of air for 6 to 12 h of exposure (Table 1).

The vase life of cut flowers, especially those that are sensitive to ethylene, is extended by substances that can either block the ethylene action or reduce the hormone production. Ethylene is synthesized as follows: L-methionine → *S*-adenosyl methionine (SAM) → ACC → ethylene. The two last steps, formation of ACC and oxidation of ACC, are catalyzed by the ACC synthase and ACC oxidase, which are considered the two major key enzymes on ethylene production (Yang and Hoffman, 1984; Pattyn et al., 2021). The ACC synthase activity can be reduced by rhizobitoxin analogs as AVG or AOA; however, neither can completely reduce the ethylene production.

In *Epidendrum ibaguense*, considered another high ethylene-sensitive orchid, the use of AVG prolonged the longevity of the flowers when compared with treatment with no anti-ethylene substances (Mapeli et al., 2009). On the other hand, roses kept in vase solution containing 5% sucrose plus 0.5, 1, 1.5, and 2-mM AOA significantly improved their longevity compared with 5% sucrose alone or control (distilled water), regardless of the applied AOA concentration (Ketsa and Narkbua, 2001). Another inhibitor of ethylene production is the salicylic acid (SA), which inhibits the ACC oxidase enzyme activity. Cut flowers of *Consolida ajacis* sprayed with 2-mM AOA or 20-mM SA showed no difference in the vase life compared with untreated flowers. Nonetheless, AOA and SA presented some slight effects by diminishing the initial rate of flower abscission, which was not enough to extend the flower longevity (Finger et al., 2004). Finally, considerable evidence suggests that Se may partially diminish ethylene biosynthesis. However, further studies are necessary to clarify practical aspects related to the use of Se in conservative solutions for cut flowers (Costa et al., 2020; Lu et al., 2020).

Conversely, the action of ethylene can be blocked by several inhibitors, including Ag^{+}, 1-MCP, 2,5-norbornadiene,

Table 1. Sensitivity of different flower species to ethylene.

High	Low	Insensitive
Alstroemeria[f]	*Anthurium*	*Strelitzia reginae*[b]
Consolida ajacis (*Dephinium*)[j]	Asparagus	Rose
Iris	Gerbera	Gladiolus[d]
Gypsophila paniculata[c]	*Tulipa hybrids*[l]	*Sandersonia aurantiaca*[e]
Narcissus pseudonarcissus[g]	Waxflower	Orchid (*Cymbidium*)[a]
Orchid (*Phalaenopsis*[i], *Dendrobium*[i], *Epidendrum*)	*Chrysanthemum*[i]	*Buddleia davidii*
Petunia hybrida[h]		*Cosmos bipinnatus*
Carnation		*Cercis canadensis*
Snapdragon		*Echinacea purpurea*
Lily[m]		
Lathyrus odoratus[a]		
Portulaca oleracea		
Hibiscus rosa-sinensis[k]		

[a]Van Doorn (2002); [b]Finger et al. (1999); [c]Newman et al. (1998); [d]Costa and Finger (2016); [e]Eason and De Vré (1995); [f]Wagstaff et al. (2005); [g]Hunter et al. (2004); [h]Knee (1995); [i]Woltering and Van Doorn (1988); [j]Santos et al. (2005); [k]Høyer (1996); [l]Sexton et al. (2000); [m]Song and Peng (2004).

and nitrous oxide. Among these inhibitors, 1-MCP is the most promising compound used to hinder ethylene action, mainly due to the high affinity with the ethylene receptor, which is effective at low concentrations (from 0.2 µl L^{-1} to 1 µl L^{-1}). 1-MCP is registered as EthylBloc®, a nontoxic growth plant regulator for use in ornamental plants, being commercialized by AgroFresh, Inc. (Blankenship and Dole, 2003; Prange and DeLong, 2003). Hence, several studies have been done by fumigating both ethylene-sensitive and insensitive flowers. However, the results are controversial because it depends on several endogenous and exogenous factors, including time between harvest and treatment, flower development stage, concentration, temperature, and time of exposure to the 1-MCP.

Consolida ajacis flowers treated with 1-MCP showed extended longevity even when exposed to 100-mg L^{-1} ethephon after fumigation with 0.5-g m^{-3} SmartFresh® for six hours at room temperature (Table 2). On the other hand, Cameron and Reid (2001) demonstrated that 1-MCP present a transitory effect in blocking petal abscission in *Pelargonium peltatum* caused by ethylene, in which a second application was needed. Altogether, such results demonstrate that binding sites for ethylene were not completely occupied by 1-MCP, or new receptor sites were induced by the presence of exogenous ethylene. Ag^+ acts as an ethylene inhibitor and has been used in pulsing or vase solution to block the deleterious effects of ethylene, especially in ethylene-sensitive flowers. It can be applied as STS or silver nitrate ($AgNO_3$). STS is more stable and presents higher mobility through plant tissues than $AgNO_3$; therefore, STS is considered less phytotoxic and more effective at lower concentrations.

Table 2. Effect of ethephon and 1-methylcyclopropene on the longevity of *Consolida ajacis* flowers.

Treatments	Longevity (days)*
Control	4.5 c
Ethephon	1.4 d
1-methylcyclopropene	6.0 a
Ethephon + 1-methylcyclopropene	5.2 b
1-methylcyclopropene + Ethephon	6.0 a

*Days for 50% of flower abscission or wilting. Means with the same letter are similar according to the Tukey's test at 5% probability (Santos et al., 2005).

Gibberellins

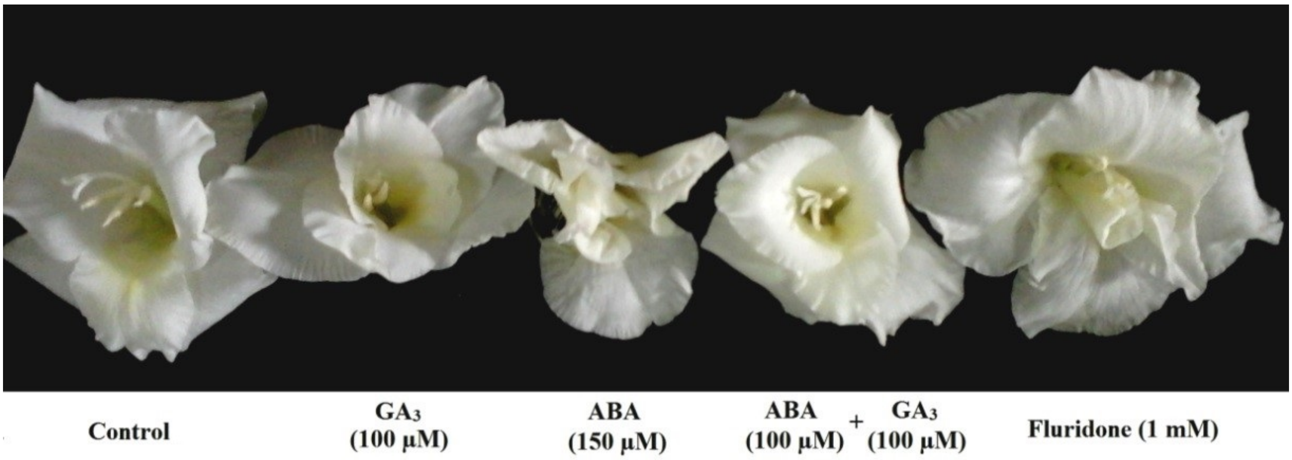
GA_3 has been widely used as an antagonist to the ethylene action in ornamental plants, but the use of this compound has led to other effects rather than the reduction of flower senescence rates. Roses sprayed with 1-mM GA_3 suppressed the development of postharvest diseases caused by *Botrytis cinerea* by inhibiting the senescence-related changes in cell membrane permeability and protein degradation (Shaul et al., 1995). Other studies demonstrated that GA_3 regulates the action of abscisic acid (ABA) in the maintenance of cell membrane and flower opening in gladiolus (Kumar et al., 2014; Costa et al., 2016).

Abscisic acid

ABA has been pointed out as a signal molecule to trigger leaf and flower senescence, as observed in carnation (Rubinstein, 2000). The authors suggest that ABA plays an important role in signal transduction events, underlying programmed cell death in daylily petals. In roses, Pompodakis et al. (2004) observed that the effect of ABA on flower longevity was pH-dependent. In this study, the addition of 10^{-5} M ABA at pH 6 increased the vase life by inducing stomatal closure in the presence or absence of 1 mg L^{-1} $AgNO_3$. It was also demonstrated that ABA is involved in the induction of senescence-related events in gladiolus flowers such as high loss of membrane stability and abnormal flower opening (Figure 3) (Kumar et al., 2014; Costa et al., 2016).

Cytokinin

Cytokinin is another hormone that has been used as a component of conservative solutions in cut flowers. For instance, benzyl adenine (BA), a generation synthetic cytokinin, has demonstrated different effects on postharvest of cut flowers, mainly depending on the studied species or



Source: Costa et al. (2016).

Figure 3. Visual aspects of gladiolus florets submitted to treatments with abscisic acid (ABA), gibberellic acid (GA_3), and fluridone (an abscisic acid inhibitor).

cultivar. BA also improved the vase life from 1.5 to 2.5-fold of *Anthurium andraeanum*, *Heliconia psittacorum*, *Heliconia chartacea,* and *Alpinia purpurata* flowers. In a similar study, Moraes et al. (2005) evidenced that the response of *Heliconia latispatha* to spraying with BA depended on the concentration. The vase life linearly increased when the flowers were sprayed with 100, 200, or 300-mg L^{-1} BA, in which the gain in longevity reached 1.85-fold, when compared with the untreated flowers.

Carbohydrates

When flowers are cut, the supply of water and nutrients essential to metabolic processes is interrupted, resulting in a fast decrease in the durability of flowers when kept at room temperature (Sonego and Brackmann, 1995). Most losses are caused by the increased plant metabolism, which is closely linked to the intake of organic compounds, such as carbohydrates, which regulate cell osmotic potential and act as messengers in signal transduction and gene expression (Doi and Reid, 1995).

Carbohydrates are an important source of energy and structural components, which can be divided into two groups: the structural, such as cell wall components (cellulose and hemicellulose), and the nonstructural, such as starch and sucrose, which are important players in plant biomass partitioning. Sucrose and starch are the main photosynthetic products (Hewitt et al., 1985). Sucrose is translocated in the plant to support its growth, while starch is carbohydrate reserve, playing an important role in the floral opening. The reserve of polysaccharides is gradually accumulated during the development of the petals, but is quickly degraded at the beginning of anthesis – to generate the osmotic potential that leads to the influx of cellular water and, finally, to bud opening (Van Doorn and Kamdee, 2014). Moreover, considering that the petal cells use carbohydrates as a respiratory substrate, the decrease in carbohydrate content during the storage period triggers events of senescence, which reduces the flower vase life.

Studies on changes in carbohydrate compounds in cut flowers demonstrated strong regulation of sucrose and starch metabolism during floral development. Santos et al. (2016) and Alves et al. (2017) observed variations in the metabolism of nonstructural carbohydrates during floral opening and senescence of *Lilium pumilum* and *Gerbera jamesonii*, exhibiting great mobilization of compounds, which are used in the production of energy demanded by the floral development.

Due to the high perishability of the flowers, it is necessary to develop and use techniques that promote their durability, maintaining the characteristics of the product and reducing postharvest losses. The alternative to overcome such consequences is the use of preservative solutions, and most of them present carbohydrates in their composition, usually sucrose. The exogenous supply of sucrose provides cut flowers with much-needed substrates for respiration. In addition, it enables cut flowers harvested at the bud stage to open, which could not naturally occur otherwise (Pun and Ichimura, 2003). The sucrose absorbed in the solution is reduced by the action of invertases and sucrose synthase, releasing glucose and fructose, suppressing the metabolism of the floral stem, and promoting an increase in the concentration of solutes in the flowers.

Sugars are usually supplied by pulsing treatment or as components of vase solutions, and the main difference between them relies on the concentration of carbohydrates applied to each solution. The cut inflorescences pink *Antigonon leptopus* treatment containing 200-mg/L SA+2% sucrose and 300-mg/L+2% sucrose had 1.6-fold longer vase life than the control, showing a higher water uptake and reduced flower drop by 28% (Seman and Rafdi, 2019). The combination of SA and sucrose also led to a significant reduction in respiration rate and alleviated the moisture stress of cut roses to improve the vase life (Bayat and Aminifard, 2017).

In addition to vase solution, sucrose treatment with pulsing also causes increased pot life for many cut flower species. Sweet pea cut flowers had a reduction in senescence when treated in pulsing with 1.38-mM 8-HQS+58.43-mM sucrose for 12 h. This is evidenced by the delayed fresh weight loss in 55.25% compared with 29.28% of the control, due to better hydraulic conductance in the floral stem (Elhindi, 2012a). Similarly, orchids (Cymbidium hybrid 'Red Princess') treated with 5% sucrose pulsing had a longer vase life of 56 days (De et al., 2014).

In addition, Horibe et al. (2014) also showed the importance of leaves in the translocation of sugar. Flowers cut from roses with leaves had a higher soluble sugar content in the petals compared with cut flowers without leaves. This demonstrates that leaves play an important role in the metabolism and transport of soluble carbohydrates. Translocation of sugar from the leaves to the petals improved the quality of the cut flowers. Without leaves, the cut flower cannot abundantly accumulate soluble carbohydrates in the petals, even if treated with glucose. However, more studies are necessary to further understand the functions of leaves in the sugar metabolism and sucrose translocation of cut flowers.

Temperature

Temperature is the most important postharvest factor influencing the quality and longevity of cut flowers. Similar to any fresh horticultural product, ornamental plants maintain high respiratory and transpiratory activities to maintain their vital cell reactions. The intermediate organic molecules are used for the synthesis of new compounds and to generate energy in the form of adenosine triphosphate (ATP). But respiration also produces heat as a by-product, which increases when temperature rises and accelerates the aging process. The rate of senescence is dramatically reduced by cooling the ornamental plants immediately after harvest (Brosnan and Sun, 2001).

To date, the storage of cut flowers at low temperatures has been used as the most adequate technique for long-distance transport and, in many instances, for short-term storage by retail. The major effects of temperature on ornamental plant storability and their posterior display are determined by the rate of respiratory substrate depletion and by the intensity of the transpiration rate and the production and action of ethylene (Finger et al., 2016).

Tropical and subtropical flowers are sensitive to chilling temperatures; such species cannot be stored below a critical temperature ranging from 0 to 13°C. The development of chilling symptoms depends on the species or variety sensitivity, stage of development, period of storage under chilling-inducing temperatures, and temperature itself. For most of the horticultural products, temperatures near 5°C are usually more effective in developing chilling symptoms. In *Alpinia* sp., *Strelitzia* sp., and *Heliconia* sp., the recommended temperature without developing chilling-related injuries ranges between 10 and 13°C (Finger et al., 2003; Jaroenkit and Paull, 2003; Costa et al., 2010). According to Cevallos and Reid (2001), the vase life of cut gillyflowers, narcissuses, irises, chrysanthemums, roses, and tulips does not change when the plant is conditioned in water or dry, provided that the storage temperature is between 0 and 10°C.

The cold storage of flowers can be carried out by dry or wet (in a vase or small tubes) processes, depending on the destination of the product and length of storage. For most flowers, dry storage is performed by wrapping the flowers in bunches and placing them in cardboard boxes. In bird-of-paradise, the flowers are wrapped in bunches with strong paper and perforated polyethylene bag to avoid excessive dehydration (Finger et al., 2003). Roses are usually kept for a longer storage term at 2°C with the stem base in water, as fewer dehydration symptoms are developed.

Conclusions

Cut flowers are horticultural sector products recognized as ornamental worldwide. The cut flower quality depends on its morphological characteristics and longevity, which is determined by the duration of such characteristics. Therefore, shelf life is a critical factor in determining the market value of cut flowers. The cut flowers quality and postharvest longevity depend on senescence delaying factors. Handling conditions, the environment, performance of plant hormones, carbohydrate content, and water relations are the main factors that play a critical role in the senescence regulation of cut flowers. Postharvest techniques and technologies make continuous efforts to regulate senescence factors, improve the quality of cut flowers, and prolong their shelf life.

Author contributions

LC, FA, WS, and MN: literature survey and writing – original draft. FF: conceptualization and writing – review and editing. All authors equally contributed to the development of the theoretical framework of the article and approved the submitted version.

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