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Review article

Influence of water deficit on the longevity of ethylene-sensitive and ethylene-insensitive flowers

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ABSTRACT

Water balance significantly influences the longevity, quality, and ornamental value of floricultural products. Inadequate irrigation during cultivation and dry postharvest storage may result in water imbalance, leading to dehydration in ornamental crops and cut flowers. This review focuses on the responses of both ethylene-sensitive and ethylene-insensitive flowers to water deficit and the potential application of exogenous substances to alleviate the harmful effects of dehydration. Alterations in stomatal function and hydraulic conductivity are key changes that drive water loss and hormones like ABA and ethylene play an essential role in determining flower longevity during desiccation events. To overcome the adverse effects of dehydration, mechanisms including osmotic adjustment, antioxidant systems and/or abscission must be tightly regulated in both ethylene-sensitive and ethylene-insensitive flowers. Understanding these processes in ornamental crops and floricultural products will help develop strategies to enhance water stress tolerance and, consequently, flower longevity.

1. Introduction

Floricultural products have become vital elements of commercial horticulture exportation due to their significant demand in the market and cut flower industry moving more than four billion dollars worldwide (BCC, 2023). The high economic value of exported cut flowers, potted flowers, and bedding plants has nowadays led to a substantial increase in their production. Their market value and marketability are particularly susceptible to flower quality, which in turn strongly depend on visual and olfactive characteristics as well as longevity. In this sense, traits such as color and fragrance of the flower corollas or timings in flower opening and petal wilting determine their commercial value and have been subjected to extensive breeding programs. However, environmental factors such as water availability may hinder profits in floriculture trading by affecting quality traits. Water status of plants intended for the ornamental flower market may limit growth and development, as well as alter several other physiological processes, including flower anthesis or shelf-life (Sánchez-Blanco et al., 2009; Moody et al., 2014). Limited irrigation or water deficit, can induce severe water stress and reduce the ornamental value, flower yield, and quality of many potted and cut floricultural products inducing stem bending or bud abscission in species such as carnation (Álvarez et al., 2009), primrose (Caser et al., 2017), canterbury bell (Mao et al., 2014), geraniums (Sánchez-Blanco et al., 2009) and lilies (van Doorn and Han, 2011), among others. The main factors that cause water deficit, dehydration, or water stress in floricultural products are the inadequate environmental conditions and irrigation practices used both during crop management before harvest and during their handling after harvest (Fig. 1).

Water deficit and dehydration (understood here as the stress condition and the consequence of this condition, respectively) in floricultural products before harvesting occur through a variety of factors, the primary being related to the environmental conditions in the cultivation area. High relative humidity, low air velocity, and continuous light have been reported as environmental factors negatively affecting stomatal functionality during cultivation, all of which could induce water stress symptoms and reduce the vase life of flower products (Fanourakis et al., 2015; Schouten et al., 2018). Moreover, an adequate irrigation management is crucial for potted seasonal plants. Poor irrigation, freshwater shortage, and/or insufficient rainfall (depending on the species, cultivar and growth conditions) directly limit soil moisture and result in water stress eventually causing dramatic production losses, most particularly in arid and semi-arid areas of the globe dedicated to horticulture (Akhtar et al., 2022; da Silva et al., 2022). Even when water is available and not

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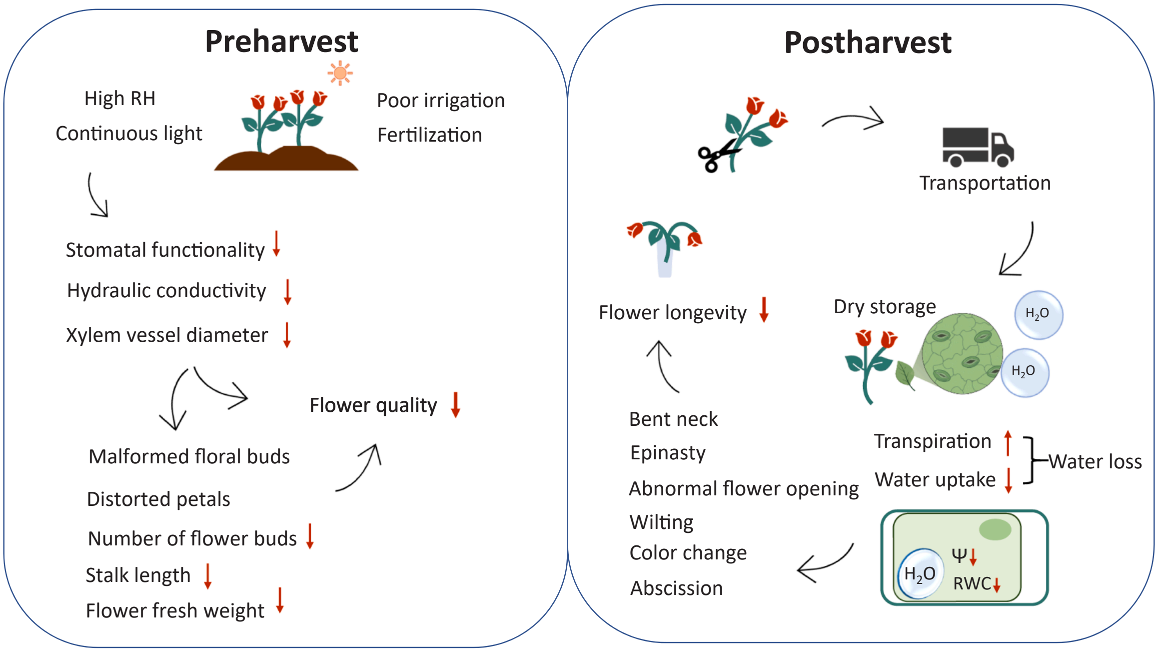


Fig. 1. Preharvest and postharvest factors inducing water deficit in floricultural products and the response of flowers to water deficit. At preharvest, high relative humidity, continuous light, poor irrigation and/or fertilization are the major factors altering water relations, affecting both water status and flower quality. At postharvest, water loss of cut flower can occur during transportation and dry storage due to high transpiration and low water uptake, leading to altered water relations (resulting in low water potentials and low water contents), thus leading to lower quality and reduced vase life. RH, relative humidity; RWC, relative water content.

limiting production in other areas, optimizing irrigation strategies to sustainably produce ornamental plants is essential to reduce the water supply used for flower cultivation and save water for other agricultural application or human consumption in the same or other parts of the world. Although water use efficiency can be improved in some ornamental flowers by training the plants to modulate stomatal closure more efficiently resulting in low transpiration rates and similar plant production under mild water deficit (Cirillo et al., 2014; Caser et al., 2017), this strategy is not always effective and water deprivation is still usually limiting flower production and quality in most species and cultivars. At the same time, potted flowers usually require a high amount of moisture during shipping and distribution (Oh et al., 2021), particularly when they experience unfavorable conditions related to strong variations in temperature, humidity, and wind speeds. These factors affect the water balance in plants, and additionally, the limitation of establishing realistic strategies for irrigation of plants during transportation easily leads to water deficit conditions and dehydration events (Allen and Allen, 2021).

Postharvest in floriculture is dominated by the cut flower market, where water deficit may result from different postharvest management processes including cutting and transporting, as well as postharvest packing. Long-distance transportation without placing cut flowers in water largely contributes to water loss and leads to water deficit stress in some cut flowers (Jin et al., 2006; Jiang et al., 2015). The transpiration rate of cut flowers is usually higher than the rate of water uptake after harvest resulting in severe dehydration events (van Doorn, 2012). Vascular occlusion is one of the major factors limiting water uptake in several cut flowers due to cavitation and high bacterial growth in the stem, a phenomenon that is exacerbated in several cases as a result of inadequate cutting of flower stems (van Doorn et al., 2002; Elibox and Umaharan, 2010). Therefore, water deficit during transportation, storage, and postharvest handling strongly impacts the quality of cut flowers, including their shelf life. It is well known that long periods of dehydration decrease flower vase life and accelerate flower senescence in many cut flowers (van Doorn and Han, 2011; Jiang et al., 2015; Chen and Miller, 2022; Fanourakis et al., 2022).

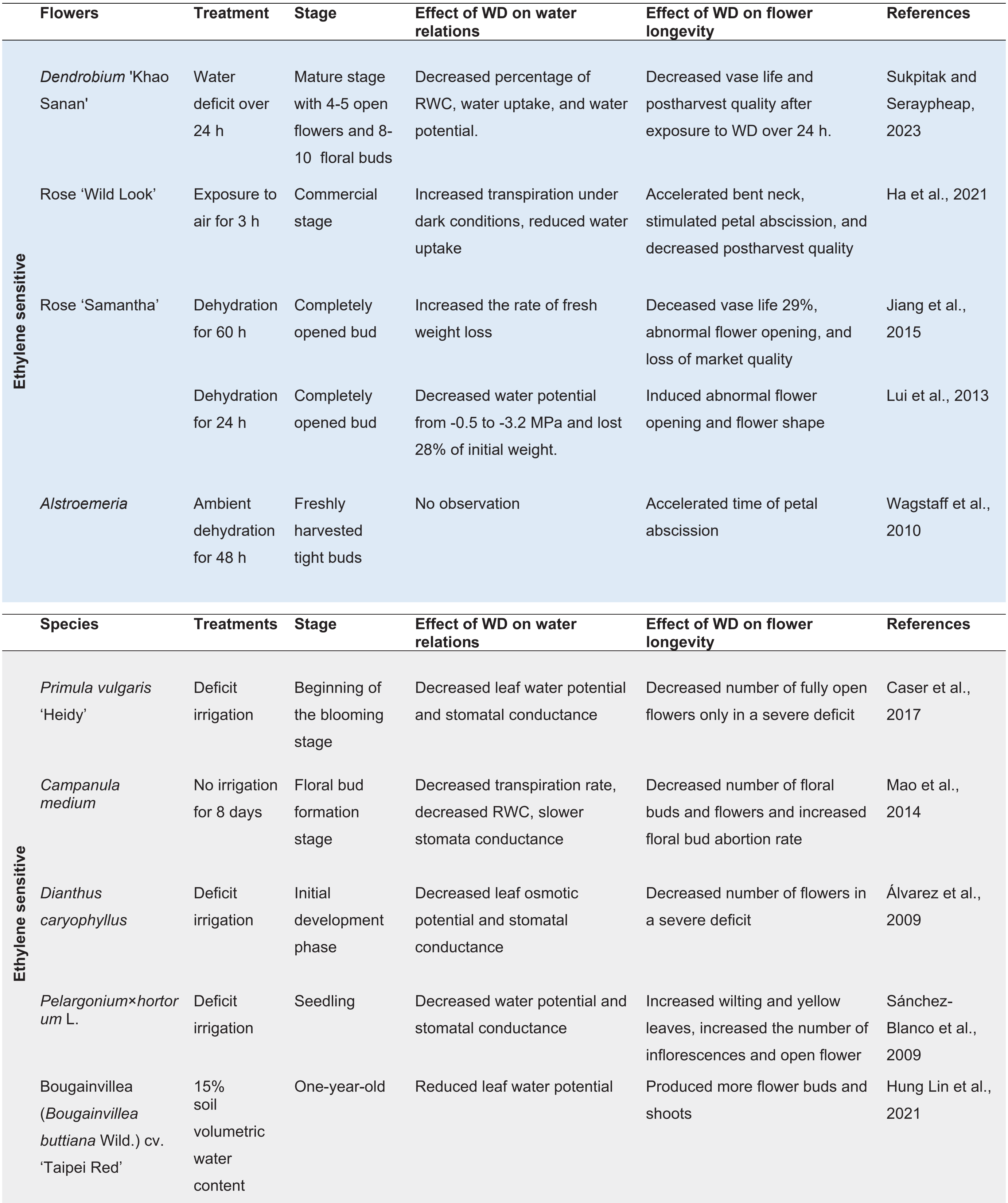
Flowers have been classified into two groups based on their susceptibility to ethylene, a natural plant hormone essential for several plant functions, including senescence. In ethylene-sensitive flowers, senescence processes are triggered by ethylene, whereas there is no rise in ethylene production during the senescence of ethylene-insensitive flowers (Dar et al., 2021). The present review aims at discussing the effects of water deficit in flower longevity as a quality trait in both potted plants and cut flowers, including studies of ethylene-sensitive and ethylene-insensitive flowers. We will particularly focus on discussing the protective responses and role of ethylene modulating senescence processes, longevity and shelf life of potted plants and cut flowers exposed to water deficit, including what occurs during rehydration events. Furthermore, the application of exogenous compounds alleviating the effects of water deficit will also be discussed. This is an essential knowledge that can be applied to enhance dehydration tolerance during both preharvest and postharvest processing of ornamental plants.

2. Influence of water deficit on flower longevity in potted plants and cut flowers

Water plays a crucial role in plant cells and hence, lack of water induces adverse effects in both potted and cut flowers. The first visible symptom is wilting which is caused by an imbalance between plant water loss and water uptake (van Doorn, 2012). Additionally, water stress promotes ethylene production in a variety of plants, including potted and cut flowers. The sensitivity of flowers to ethylene and its potential effects on vase life depend on the genetic background of flower species and cultivars (Macnish et al., 2010; Fanourakis et al., 2013; Moody et al., 2014). Species with flowers highly sensitive to ethylene usually show drastic physiological and morphological responses to low ethylene concentration as well as to short periods of ethylene exposure that lead to flower senescence (Costa et al., 2021). Although morphological and physiological responses to water deficit of flower crops may strongly differ depending on the species and the sensitivity level to ethylene; an alteration of water relations is common in all types of flowers. Indeed, water deficit has a negative impact on water status that

Table 1

Effects of water deficit on the responses of ethylene-sensitive and ethylene-insensitive flowers (in blue) and in various ornamental plants (in grey).



	Flowers	Treatment	Stage	Effect of WD on water relations	Effect of WD on flower longevity	References
Ethylene sensitive	*Dendrobium* 'Khao Sanan'	Water deficit over 24 h	Mature stage with 4-5 open flowers and 8-10 floral buds	Decreased percentage of RWC, water uptake, and water potential.	Decreased vase life and postharvest quality after exposure to WD over 24 h.	Sukpitak and Seraypheap, 2023
	Rose ‘Wild Look’	Exposure to air for 3 h	Commercial stage	Increased transpiration under dark conditions, reduced water uptake	Accelerated bent neck, stimulated petal abscission, and decreased postharvest quality	Ha et al., 2021
	Rose ‘Samantha’	Dehydration for 60 h	Completely opened bud	Increased the rate of fresh weight loss	Deceased vase life 29%, abnormal flower opening, and loss of market quality	Jiang et al., 2015
		Dehydration for 24 h	Completely opened bud	Decreased water potential from -0.5 to -3.2 MPa and lost 28% of initial weight.	Induced abnormal flower opening and flower shape	Lui et al., 2013
	Alstroemeria	Ambient dehydration for 48 h	Freshly harvested tight buds	No observation	Accelerated time of petal abscission	Wagstaff et al., 2010

	Species	Treatments	Stage	Effect of WD on water relations	Effect of WD on flower longevity	References
Ethylene sensitive	*Primula vulgaris* ‘Heidy’	Deficit irrigation	Beginning of the blooming stage	Decreased leaf water potential and stomatal conductance	Decreased number of fully open flowers only in a severe deficit	Caser et al., 2017
	Campanula medium	No irrigation for 8 days	Floral bud formation stage	Decreased transpiration rate, decreased RWC, slower stomata conductance	Decreased number of floral buds and flowers and increased floral bud abortion rate	Mao et al., 2014
	Dianthus caryophyllus	Deficit irrigation	Initial development phase	Decreased leaf osmotic potential and stomatal conductance	Decreased number of flowers in a severe deficit	Álvarez et al., 2009
	Pelargonium×hortorum L.	Deficit irrigation	Seedling	Decreased water potential and stomatal conductance	Increased wilting and yellow leaves, increased the number of inflorescences and open flower	Sánchez-Blanco et al., 2009
	Bougainvillea (*Bougainvillea buttiana* Wild.) cv. ‘Taipei Red’	15% soil volumetric water content	One-year-old	Reduced leaf water potential	Produced more flower buds and shoots	Hung Lin et al., 2021

(continued on next page)

Table 1 (*continued*)

	Flowers	Treatments	Stage	Effect of WD on water relations	Effect of WD on flower longevity	References
Ethylene insensitive	Zinnia 'Benary Giant Deep Red'	Dry storage for 24 h	Fully open flower	Reduced water potential, water uptake, no rehydration after drying for 24 h	Decreased vase life	Kalinowski et al., 2022
	Lilium	Dehydration over 24 h	Fully open flower	Reduced total water uptake	Reduced life span of flowers.	Chen and Miller, 2022
	Chrysanthemum	Long-term storage under cold conditions	Fully open flower	No effect on stomatal function and water uptake restoration ability	Decreased vase life depending on the storage period	Fanourakis et al., 2022
	Chrysanthemum 'Code Green', 'Fiana'	Desiccation for 6 h	Fully open flower	Increased water loss and failed to decrease transpiration rate	Decrease vase life under 5-10% desiccation	Fanourakis et al., 2021
	Iris (*Iris x hollandica*)	Dry storage for 3 days	Commercial stage	Decreased flower fresh weight	No flower opening at any temperature	van Doorn et al., 2014

can strongly limit flower longevity in both potted and cut flowers, as shown in several previous studies conducted under various water deficit conditions and developmental stages (Table 1).

On the one hand, water relations during preharvest strongly influence ornamental plant performance and results in physiological changes that can affect final flower quality. A decrease in stomatal conductance together with reductions in the relative water content (RWC) have been reported in many potted flowers during exposure to water stress. For instance, severe desiccation markedly reduced leaf osmotic potential and stomatal conductance in potted *Dianthus caryophyllus L.* (Álvarez et al., 2009). Drought stress also significantly decreased RWC and leaf area in *Campanula medium* at bud formation stage (Mao et al., 2014). In the latter, severe water stress during cultivation reduced shoot hydraulic conductivity as a result of smaller xylem vessel diameter that directly affected water transport (Twumasi et al., 2005). Dehydration not only affects water relations but also has a significant impact on morphological and developmental traits. Severe deficit irrigation in geranium (*Pelargonium hortorum* L.) strongly reduced the number of flowers (Sánchez-Blanco et al., 2009). Similarly, drought stress influenced flower development during cultivation, resulting in malformed floral buds with short petal lengths and distorted petals in roses (Shi et al., 2019). In *Eustoma grandiflorum,* flowers grown under severe deficit irrigation showed shorter stalk length, lower number of floral buds, and lower fresh weight, thus decreasing harvestable quality (Chuang and Chang, 2012). Interestingly, in *Zinnia elegans,* although water stress decreased the size of cut flowers (leaf area, stem length, fresh weight), a longer vase life was observed, probably related to leaf morphology modifications by reductions of the leaf area that could ameliorate water loss during vase life (Twumasi et al., 2005).

On the other hand, the consequence of dehydration in floricultural products during postharvest is the abnormal development of flowers, which has been reported for several species. For instance, water deficit in cut roses induced abnormal flower opening and decreased flower size (Jin et al., 2006; Liu et al., 2013; Jiang et al., 2015). Stomatal transpiration is the main cause of water loss in cut flowers, which occurs through the stomata present on leaves, stem, sepals, and/or petals (Huang et al., 2018; Lin et al., 2020). Apart from that, water loss can also occur via cuticular transpiration in some cases, particularly when stomata are non-functional or closed (Cheng et al., 2021). After harvest, petals represent the main source of water loss during drought stress because of their significantly higher cuticle leakiness compared with leaves (Bourbia et al., 2020; Roddy et al., 2023). This is related to the chemical composition of the cuticle wax that provides weaker properties of transpiration barrier on petals than on leaves (Cheng et al., 2019, 2021). Roddy et al. (2019) evaluated hydraulic traits of leaves and flowers and found that flowers had higher hydraulic capacitance and required higher turgor pressure to remain upright. Hence, in the absence of leaves, the petals are likely to be the main route of water loss by cuticle transpiration in cut flowers after harvest. Xylem embolism occurs as well under drought stress in *Magnolia grandiflora*, where it was found that flower peduncles were more vulnerable to cavitation than petioles and stems, supporting the idea that leaves and stems are given priority over flowers during water stress (Zhang et al., 2021). In chrysanthemums, cultivars with higher rates of transpiration exhibited shorter vase life in comparison to cultivars with lower rates of transpiration during dehydration (Fanourakis et al., 2021). Stomatal response under water stress conditions differs between cultivars and stress levels. For instance, changes in stomatal opening and transpiration rates were found in leaves of cut roses exposed to long-term dry storage (28 days) under cold conditions, with different cultivars showing contrasting responses. In this experiment, 'Grand Prix' cultivar was found to maintain the water balance very efficiently in the cut flower through finetuning stomatal closure and transpiration rates depending on stress severity. In contrast, 'Akito' cultivar showed difficulties to maintain water balance after long-term storage due to impaired stomatal functionality under water stress (Woltering and Paillart, 2018). Besides, in another study, exposure of cut rose 'Wild look' to air for 1 to 3 h without placing the stems in water increased the ratio of stomata opening under dark conditions, leading to higher transpiration rates (Ha et al., 2021). Consequently, the regulation of stomatal closure is a key factor for water stress tolerance.

Furthermore, increases in bacterial population at the base of the stem causing vascular occlusion also reduce vase life of cut roses leading to a decrease in water uptake that results in early wilting symptoms and decreased postharvest longevity (Ha et al., 2021). Vulnerability of reproductive organs is usually higher than vegetative organs as also observed in the perennial daisy *Tanacetum cinerariifolium*, where flowering stems were found to be more vulnerable to xylem cavitation than leaves and therefore, died at higher rates (Bourbia et al., 2020). Higher cavitation in the xylem of flower stems can indeed be considered a plant strategy to avoid high rates of water loss in flowers to maintain hydraulic integrity of vegetative organs and survive if rehydration events eventually occur (Bourbia et al., 2020).

In response to desiccation, the flowers of some species produce more ethylene than others and the responsiveness to ethylene is also highly dependent on cultivars. It has been demonstrated that in cut roses, there are both ethylene-sensitive and insensitive cultivars with the sensitivity level to ethylene strongly varying among cultivars (In et al., 2017). Ethylene-sensitive rose cultivars typically induce the expression of the genes encoding for the ethylene biosynthesis enzyme, 1-aminocyclopropane-1-carboxylate synthase (*RhACS1* and *RhACS2*) under water deficit, causing a general boost in ethylene production throughout the flower, particularly incremented in the flower sepals (Liu et al., 2013). This study also showed that enhanced ethylene contents paralleled an increased expression of the ethylene receptor gene, *RhETR3*, in rose petals during dehydration (Liu et al., 2013). Similarly, dehydration induced a higher accumulation of the ethylene precursor 1-aminocyclopropane-1-carboxylic acid (ACC) in cut carnation (Borochov et al., 1982). In carnation and *Dendrobium* orchid, exposure to water deficit induced an earlier peak of ethylene (Drory et al., 1995; Sukpitak and Seraypheap, 2023). In addition, different flower parts showed different levels of ethylene: ovaries and styles of cut carnation produced the highest ethylene concentrations, whereas leaves and petals did not show remarkable changes in ethylene production (Yakimova and Woltering, 1997). At the same time, rehydration events also exacerbate ethylene production as seen in cut roses (Liu et al., 2013) or *Dendrobium* orchids (Sukpitak and Seraypheap, 2023). Although increases in ethylene content could stimulate flower opening, it might also cause negative effects on this physiological process such as abnormal flower opening and reductions on flower size. Therefore, water deficit in ethylene-sensitive flowers may trigger an ethylene autocatalytic production and affect flower development, including flower longevity (Fig. 2).

Water stress also affects ethylene-insensitive flowers such as *Lilium* (Arrom and Munné-Bosch, 2012) or *Gladiolus grandiflora* (Kumar et al., 2014). In this type of flowers, abscisic acid (ABA) plays a crucial role in the response of potted plants and cut flowers to abiotic stresses, including water deficit. When plants are exposed to water stress conditions, ABA production is induced and accumulates in plant leaves, resulting in stomatal closure to prevent water loss (van Iersel et al., 2009). Besides stress responses, ABA is involved in senescence processes, especially of ethylene-insensitive flowers. Water deficit increased endogenous ABA levels and induced the onset of early senescence in daylily petals (Panavas et al., 1998). Likewise, transcriptome analysis in *Gerbera hybrida* revealed that the genes encoding ABA biosynthesis enzymes such as 9-cis-epoxycarotenoid dioxygenase (*NCED*), ABA oxidase (*AAO*), and short-chain alcohol dehydrogenase/reductase (*SDR*) increased during stem bending caused by water stress (Fig. 2). Moreover, protein phosphatase 2 C (*PP2C*) and serine/threonine-protein kinase (*SAPK*), key genes related to ABA signal transduction, were remarkably up-regulated. An increase in ABA contents during water stress may be attributed to higher tolerance to oxidative stress, as it has been described in gerbera (Ge et al., 2019). However, further research is needed to examine the interaction of ABA, ethylene, and other hormones, in conferring water stress tolerance in floricultural commodities.

3. Protective responses against water stress in potted and cut flowers

Water stress in ornamental plants induces the accumulation of reactive oxygen species (ROS) in plant cells, particularly in leaves, leaves of flower stems or other photosynthetic tissues that contain chloroplasts (such as sepals, or some petals [or tepals such as those of *Lilium*] at early stages of development, Arrom and Munné-Bosch (2010)], where water stress leads to energy excess in the reaction centers of the chloroplastic electron transport chain and prompts the production of singlet oxygen ($^1O_2$), which may lead to photoinhibitory events (Chang et al., 2015; Muñoz and Munné-Bosch, 2018). Chloroplasts are also a source of other ROS, such as superoxide anion ($O_2^{\bullet-}$) and hydrogen peroxide (H_2O_2), which can also be produced at high rates in mitochondria due to increased respiration demands (Sun et al., 2005; Li et al., 2020). In general, low levels of ROS increasing transiently would serve as signaling molecules that regulate various processes of plant growth and development while sustained production of ROS at high levels cause oxidative damage to plant tissue (Muñoz and Munné-Bosch, 2018). Thus, the role of ROS in plant cells strongly depends on the balance between the spatiotemporal variations in ROS generation and scavenging. Under water stress, ROS can induce protective signaling responses, but if produced continuously in time and at high levels, the associated oxidative stress (redox unbalance) will lead to cell damage. It has been reported that long periods of water stress increased ROS production in flowers of various plants species causing membrane lipid peroxidation, as reflected by enhanced malondialdehyde (MDA) contents, leading to electrolyte leakage from cell membranes, thereby indicating damage (Jiang et al., 2015; Hemmati et al., 2018; Fanourakis et al., 2022). Therefore, to minimize the adverse effects of water deficit, both ethylene-sensitive and ethylene-insensitive species have developed protective mechanisms such as antioxidant systems and accumulation of protective osmolytes to tolerate water stress conditions better and prevent oxidative stress events that can lead to a reduction in flower longevity. However, once pollination has occurred and double fertilization is achieved, petals are no longer necessary (since they have already accomplished their role of pollinators attraction) and senescence is rapidly induced. Thus, protective mechanisms serve a role during early stages of flower development, flower anthesis and pollination, always before double fertilization occurs.

Antioxidant protective mechanisms are constituted by enzymatic and non-enzymatic systems with the ability to scavenge ROS or minimize lipid peroxidation. Under severe water stress, the production of ethylene and ROS significantly increased in ethylene-sensitive species (e.g., *Dendrobium* orchid, *Impatiens walleriana*). We hypothesize that ethylene might play a role in excess ROS production causing lipid peroxidation and cell damage as some ethylene response factors (ERFs) have been reported to play a role in antioxidant regulation (Sewelam et al., 2013; Zhang et al., 2016). However, there is currently no report on that mechanism at the molecular level in ethylene-sensitive flowers under water stress. One of the antioxidant enzymes responsible for the initial detoxification in the ROS scavenging mechanisms is superoxide dismutase (SODs). The studies in both cut flower and potted flower species revealed that SODs enzymes particularly Cu/Zn SODs isoform were shown to be the most abundant form in response to dehydration, which could play a pivotal role in strengthening and water deficit tolerance of flower species (Jiang et al., 2015; Antonić et al., 2020). Likewise, catalase (CAT), ascorbate peroxidase (APX), and peroxidase (POD) activity increased in flowers during desiccation and decreased to control levels after rehydration, suggesting that some ROS may be reduced for preventing cell damage (Jin et al., 2006; Jinfen and Bowen, 2022; Sukpitak and Seraypheap, 2023).

The same protective responses of antioxidant systems were also reported in ethylene-insensitive species. In *Tagetes erecta* and *Tagetes patula* extreme water deficiencies increased SOD and CAT activity, while total antioxidant potential was also enhanced (Yashewar et al., 2017). In a study evaluating the production of non-enzymatic antioxidants in *Lilium* tepals of soil-grown and cut flowers, it was shown that the production of tocopherols (vitamin E) considerably increased in stem-cut flowers. The oxidative cellular status was also increased at the latest developmental stages of cut flowers (Arrom and Munné-Bosch, 2010), suggesting that tocopherols might be induced to balance the redox systems under water stress conditions.

Oxylipin production results from oxidation of polyunsaturated fatty acids of cell membranes, either resulting from enzymatic processes initially triggered by lipoxygenases or by non-enzymatic processes, in which ROS play a key role (Farmer and Müller, 2013; Muñoz and Munné-Bosch, 2020). It has been found that dehydration tolerance in cut rose was regulated by the biosynthesis of jasmonic acid level mediated by an *RhHB1*/*RhLOX4* regulatory module (Fan et al., 2020) even though it was not evaluated the direct influence of ROS production to mediate these signaling mechanisms. Production of ROS in stress-induced precocious senescence is also enhanced by apoplastic NADPH oxidase (Rboh). A recent study in *Rosa hybrida* showed that the module of RhWRKY33a and RhPLATZ9, an age- and dehydration-induced PLATZ (plant AT-rich sequence and zinc-binding) protein could regulate *RhRbohs* in dehydration conditions by which *RhPLATZ9*-silenced flowers showed higher ROS accumulation and accelerated senescence in rose flowers. Therefore, cutting flowers and their water stress-associated effects may considerably influence redox balance and trigger early senesce symptoms in the flower. However, the redox signaling mechanisms associated to precocious flower deterioration by dehydration are far from being fully elucidated.

Much more work has been performed to describe endogenous signals to promote osmotic adjustments. Dehydration increased the expression of *RhNAC3* in rose petals, which could influence the expression of osmotic adjustment-related genes, enhancing water deficit stress resistance (Jiang et al., 2014). In *Rosa hybrida* (cv. 'Samantha'), the regulatory interaction of *RhNAP*, which is involved in ABA responses, and *RhCKX6*, a gene encoding for cytokinin oxidase/dehydrogenase leading to cytokinin degradation, enhanced dehydration tolerance in young flowers but accelerated petal senescence in mature flowers. During dehydration, ABA induced the expression of *RhABF2*, an ARE-B/ABF transcription factor involved in the ABA signaling pathway that directly activated the ferritin gene *RhFer1*, which could at the same time regulate Fe homeostasis during dehydration and the RhABF2/RhFer1 to improve dehydration resistance by ensuring flower opening following rehydration (Liu et al., 2017). Moreover, drought stress enhanced the expression of *pyrroline-5-carboxylate synthetase* (*P5CS*), a gene encoding the key enzyme for proline biosynthesis (Adamipour et al., 2020). Likewise, impatiens and cut orchids showed higher content of proline and soluble sugar when cut stems were subjected to dehydration (Hemmati et al., 2018; Shakarami et al., 2019; Antonić et al., 2020). Therefore, accumulation of osmolytes or compatible solutes such as proline under drought stress could lower water potential and maintain water balance in plant cells of floricultural products.

The studies in potted chrysanthemums, which could serve as a model of species with ethylene-insensitive flowers, reveal that drought stress tolerance involved the regulation of ABA-responsive genes such as *ABI3* and *ABI4* through the synergistic function of the GRAS protein, *CmSCL4,* and the MYB transcription factor, *CmR1MYB1* (Zhang et al., 2022). Moreover, water stress induced the expression of *CmWRKY10*, another transcription factor gene involved in drought stress tolerance, which regulated ABA-biosynthesis genes (*NCED*) and antioxidant enzyme gene (*ZnSOD*) expression, as well as an increase in the levels and activities of some antioxidant enzymes, such as SOD, POD, and CAT activities (Jaffar et al., 2016). Overall, accumulation of osmolytes or compatible solutes such as proline under drought stress could lower water potential and maintain water balance in plant cells of floricultural products, including both ethylene-sensitive and ethylene-insensitive flowers.

It may therefore be inferred that plants with both ethylene-sensitive and ethylene-insensitive flowers have developed several protective mechanisms to tolerate water deficit which might improve the longevity and quality of flowers. However, once pollination trigger double fertilization, senescence processes are triggered naturally. Thus, it is necessary to study the effects of water stress taking into account the developmental stage of flowers and identify putative signals that regulate in a spatiotemporal manner early flower senescence under water deficit to fulfill our understanding of flower responses to dehydration, which may have a significant impact for plant breeding and the development of innovative preservation strategies and products to ameliorate water stress symptoms.

4. Ethylene modulates flower longevity under water stress

Exposure to ethylene can accelerate petal senescence and flower abscission, resulting in a shortened vase life in many ethylene-sensitive cut flowers such as carnation (Liu et al., 2018; Kondo et al., 2020), peony (Wu et al., 2017), dahlia (Azuma et al., 2020), *Dendrobium* orchid (Uthaichay et al., 2007), *Mokara* orchid (Wongjunta et al., 2021), *Delphinium* (Okamoto et al., 2022) and some cultivars of roses (Daneshi Nergi and Ahmadi, 2014; Ha et al., 2019; Ha et al., 2020) as well as in potted flowers including *Phalaenopsis* orchid (Favero et al., 2016), *Begonia* (Kim and Kim, 2012) and *Plectranthus* (Rice et al., 2013). The onset of flowering, pollination, and senescence is often accompanied by an increase in ethylene production (Luangsuwalai et al., 2011; Shibuya et al., 2013), but biotic and abiotic stress conditions can also trigger ethylene biosynthesis and induce early senescence in flowers.

Moderate water stress from simulated transportation like darkness, water deficit, and vibration could induce ethylene production in potted miniature roses (Müller et al., 2000). Moreover, in cut *Dendrobium* orchid, long dehydration periods after cutting can induce higher ethylene production by the inflorescences (Sukpitak and Seraypheap, 2023). It has been well established that ethylene is perceived by its specific receptors in plant cells, and the signal is sent through signal transduction cascade events to stimulate the expression of ethylene-responsive genes. Ethylene receptor genes *ERS1*, *ERS2* and *ETR*1 identified in carnation (*Dianthus caryophyllus* L.) were hypothesized to participate in flower senescence, and it was found that the expression of these receptors is increased in flower opening in a tissue-specific manner, independently of ethylene production during senescence (Shibuya et al., 2002). Likewise, bending of the peduncle induced by vascular occlusion resulted in the upregulation of some ethylene response factors (ERFs) in *Rosa chinensis*, a highly sensitive ethylene flower (Lear et al., 2022).

In flowering plants, petal senescence is a highly regulated process of programmed cell death (PCD). Although this is a developmental process tightly regulated by massive changes in gene expression and linked to age-related plant development, abiotic stress can also trigger PCD in flower corollas. Senescing corollas of Japanese morning glory (*Ipomoea nil*) showed that PCD was positively regulated by the NAC transcription factor EPHEMERAL1 (EPH1), which triggers ethylene production in these flowers (Shibuya et al., 2014). Moreover, in senescing corollas, PCD is initiated by cellular autophagy, a process modulated by ethylene. As a central component of the autophagy pathway, *Autophagy Gene 6* (*ATG6*) was characterized by the study of CRISP/Cas9 knockout lines in *Petunia* × *hybrida* 'Mitchell Diploid' (Lin and Jones, 2022). *PhATG6*-KO lines showed an earlier induction of ethylene production and an upregulated expression of ethylene biosynthesis genes and accelerated petal senescence. Although the study did not evaluate the effects of dehydration-triggered senescence, enhanced ethylene biosynthesis in mutant flowers indicates that autophagy affects flower longevity through ethylene production, which is also triggered by abiotic stresses such as drought events.

In plant species showing ethylene-insensitive petal senescence, ethylene could affect some developmental processes, such as flower opening, ovary development, and pedicel elongation (Çelikel and van Doorn, 2012), as well as flower bud abscission and flower abscission

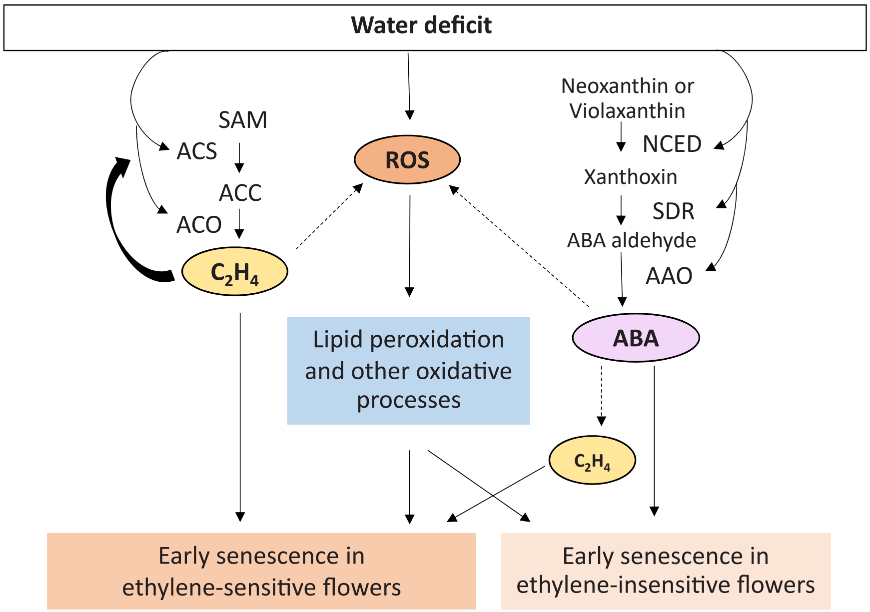


Fig. 2. Simplified model of senescence regulation in ethylene-sensitive and ethylene-insensitive flowers in response to water deficit. Water deficit induces ethylene and ABA biosynthesis in ethylene-sensitive and ethylene-insensitive flowers, respectively, and also induces ROS in both of them. Elevated levels of ethylene and ABA might induce ROS generation as well, causing oxidative processes and resulting in early senescence in both ethylene-sensitive and ethylene-insensitive flowers. ABA can also promote ethylene production in ethylene-sensitive flowers, leading to an acceleration of senescence under water deficit conditions. AAO, ABA aldehyde oxidase; ACC, 1-aminocyclopropane-1-carboxylic acid; ACO, ACC oxidase; ACS, ACC synthase; NCED, 9-*cis*-epoxycarotenoid dioxygenase; SAM, S-adenosyl methionine; SDR, short-chain alcohol dehydrogenase/reductase.

(van Doorn and Han, 2011) of the flower stems. Consequently, although not triggering petal senescence in these flowers, developmental processes related to flowering and the vase life of flower stems can be significantly affected by ethylene. Since jasmonates and ethylene share some common signaling cascades (e.g. ERFs, Müller and Munné-Bosch, 2015) and cutting the flowers can significantly exacerbate the wounding response mediated by ROS, jasmonates and ethylene (Jing et al., 2021), it is very likely that ROS and ethylene interact under severe water deficit to reduce flower longevity not only in ethylene-sensitive flowers but also in ethylene-insensitive ones. However, the exact molecular events associated to the intertwined processes mediating redox and ethylene signaling mechanisms associated to precocious flower deterioration by dehydration, most particularly in ethylene-insensitive flowers, are far from being fully elucidated.

5. The importance of rehydration following dehydration events

The ability to rehydrate after a dehydration event of cut flowers depends on their species including cultivars and it could be assumed as an indicator of water transport restoration in plants. For example, some cultivars of cut roses showed a positive correlation between rehydration ability and vase life, whereas another study showed no contribution of water recovery following water deficit to flower longevity (Fanourakis et al., 2016). It has been revealed that rehydration following a desiccation event could induce ethylene biosynthesis which might affect the vase life of ethylene-sensitive flower species. Interestingly, the molecular evidence in cut roses suggested that the expression of *RhMKK*, a rose MAP KINASE KINASE gene has been shown to be the upstream component of the *RhMKK9-RhMPK6-RhACS1* cascade which triggered the induction of ethylene biosynthesis in gynoecia during water recovery (Chen et al., 2017). Furthermore, the enhancement of ethylene production during rehydration could increase the number of floral bud openings and hasten flower senescence (Ma et al., 2008; Sukpitak and Seraypheap, 2023).

6. Application of exogenous compounds for alleviating water deficit

In order to mitigate the negative impacts and enhance the ability of floricultural products to cope with water stress, chemical treatments such as ethylene inhibitors, some plant hormones, and natural substances were applied in several studies (Table 2). In ethylene-sensitive flowers, the application of 1-methylcyclopropene (1-MCP), aminoethoxyvinylglycine (AGV), and silver thiosulfate (STS), which are ethylene inhibitor compounds can improve the quality of flowers under water deficit. Pretreatment of cut roses with 1-MCP (ethylene action inhibitor) before exposure to dehydration could prevent the negative effects on flower opening and cell expansion in petals. Application of STS, by pulsing to *Iris x hollandica* before dehydration could prevent an increase in ACC level and ethylene production resulting in the improvement of flower opening (Çelikel and van Doorn, 2012). Therefore, applying ethylene inhibitors before being subjected to water stress could prevent the negative effects of dehydration on flower longevity.

The application of ABA has been used for alleviating water loss. Exogenous application of s-ABA rapidly triggered stomatal closure under drought in chrysanthemums flowers, leading to the reduction of transpiration water loss. Moreover, it was found that ABA treatment could maintain marketable quality after rehydration under severe stress (Waterland et al., 2010). Similarly, ABA spraying on sepals and leaves of potted hydrangea (Oh et al., 2021) and cut roses (Woltering and Paillart, 2018) reduced the transpiration rate by inducing stomatal closure. Both ethylene-sensitive and ethylene-insensitive flowers showed a similar response to exogenous ABA under a desiccation event. According to favorable results in many plant species, we suggest that ABA application is a good treatment to reduce the adverse effects of drought stress.

Apart from ABA, the roles of brassinosteroids (BRs) have been reported to be associated with physiological responses to abiotic stress by improving stress tolerance in many plant species. It was found that the exogenous application of 24-epibrassinolide (EBL), which is one of the BRs forms, could alleviate the negative effects of water deficit. Yao et al. (2017) reported that EBL application on fresh daylily flower buds during

Table 2
Effect of compounds application on ethylene-sensitive and ethylene-insensitive flowers and various ornamental plants under water deficit.

	Flower	Compound	Concentration	Stage	Method	Effect on water relations	Effect on flower longevity	Reference	Remarks
Ethylene sensitive	Rose 'Samantha'	1-MCP	2 ppm	Completely opened bud	Fumigation 12 h	No observation	Decreased negative effect on flower opening and flower quality	Lui et al., 2013	Dehydration
		AsA	6 mM	Completely opened bud	Pulsing for 12 h	Alleviated water potential after recovery for 2 h	Alleviated vase life, flower growth, and opening rate	Jin et al., 2006	Water deficit for 24 h
	Rose 'Sonia' and *Bouvardia* flowers	Alkylethoxylates	8 or 14 C atoms with 5 or 8 ethoxy units	Commercial maturity	Pulsing for 24 h	Increased water uptake	Increased vase life	Van Doorn et al., 2002	Dry storage for 24 h
	Chrysantemum	ABA	500 mg/L	Half opened flower	Spraying or drenching	Reduced transpiration by closing stomata	Delayed wilting and extended shelf life	Waterland et al., 2010	Drought stress
		Tropolone	1.5 mM	Commercial maturity	Pulsing for 5 h	Recovered hydraulic capacity	No observation	van Meeteren et al., 2006	Dehydration
	Iris x *hollandica*	AVG or STS	0.125 mM	Bud stage	Pulsing for 4 h	No clear negative effect on water balance	Improved flower opening	Çelikel and van Doorn, 2012	Dehydration 48 h

	Species	Compound	Concentration	Stage	Method	Effect on water relations	Effect on flower longevity	Reference
Ethylene sensitive	*Tropaeolum majus*	Spermine	1 mM	Seedling	Spraying	Improved RWC	Increased number of flowers	da Silva et al., 2022
	Begonia × hybrida	Acetic acid	10 mM	Commercial stage		Reduced water use	Increased survival under drought	Allen and Allen, 2021
	Impatiens walleriana	Salicylic acid	2 mM	8 week-old plant	Spraying	Maintained RWC and prevented wilting	No effects on flower preservation	Antonic et al., 2020
	Hydrangea	ABA	2000 mg/L	Commercial stage	Spraying	Reduced transpiration	Extended shelf-life for 2 days	Oh et al., 2021
	Catharanthus roseus	TiO_2 NPs NaSH SA	0.5 mM 1 mM	Seedling to flowering	Foliar spraying	Improved gas exchange	Improved ornamental quality and longevity	Zomorrodi et al., 2022

	Flower	Compound	Concentration	Stage	Method	Effect on water relations	Effect on flower longevity	Reference	Remarks
Ethylene insensitive	Lilium	EBR	10^{-7} M	Fully open flower	Soaking	No observation	Delayed senescence	Jinfen et al,2022	Dry storage
	Daylily	EBR	0.5 mg/L	Floral bud	Spraying	Reduced weight loss	Delayed senescence	Yao et al.,2017	Stored at 4±1 °C for 24 days
	Rose 'Akito'	ABA	0.1 mM	Commercial stage	Soaking	Improved stomatal function	No clear effect	Woltering and Pallart, 2018	Cold storage
	Roses 'Bordeaux', 'Lenny' and 'Testarossa'	SNP, Salicylic acid	15 uM	Floral bud	Soaking	Decreased transpiration rate	Improved vase life under desiccation	Fanourakis et al., 2016	Mild desiccation (12% weight loss)

(continued on next page)

Table 2 (*continued*)

	Species	Compound	Concentration	Stage	Method	Effect on water relations	Effect on flower longevity	Reference
Ethylene insensitive	Marigold	AsA and EBR	10 mM AsA and 10^{-7} M EBR	Flowering stage	Foliar spraying	Improved RWC	No observation, but improved essential oil percentage	Hemmati et al., 2018
		Chitosan	7.5 mg/L	6 leaf stage	Foliar spraying	Increased transpiration, stomatal conductance, and water use efficiency	No observation	Akhtar et al., 2022
	Lilium "Fangio"	EBR	1.5 uM	Bulb sprouting	Foliar spraying	Improved water use efficiency under moderate deficit	No observation	Omidian et al., 2022

*Blue color = cut flower, grey color = potted plant

storage could maintain membrane integrity and increase antioxidant enzyme activities including SOD, CAT, POD, and APX. Moreover, EBL treatment improved hormonal balance during storage by enhancing gibberellins and cytokinins, and by decreasing ABA content. Similarly, exogenous EBL in cut lilies under drought stress led to a higher expression of antioxidant-related genes resulting in an improvement of antioxidant contents and activities (Jinfen and Bowen, 2022). In addition, foliar applications of EBL in the lily plant could alleviate the adverse effects of deficit irrigation and improve water use efficiency (Omidian et al., 2022). Besides, under non-stress condition, low concentration of EBL decreased ethylene synthesis resulting in prolonged flower vase life (Darvish et al., 2021). According to these studies, the use of BRs has the potential to improve postharvest quality and longevity, as well as water use efficiency in floricultural products.

The use of salicylic acid (SA), a phytohormone that functions in several developmental processes including responses to biotic and abiotic stresses, ameliorated the negative effects of drought stress in potted *Impatiens walleriana* by maintaining water balance and preventing plant wilting, inducing the accumulation of osmolytes and regulating antioxidant activities by decreasing lipid peroxidation (Antonić et al., 2020). Likewise, Zomorrodi et al. (2022) found that SA application could improve ornamental quality and longevity under water deficit. Apart from SA, these authors also reported that the optimal concentration of sodium hydrosulfide and titanium dioxide nanoparticles (TiO_2NPs) also mitigated the negative effects of water stress. The application of acetylsalicylic acid (which is quickly converted to salicylic acid in plants) induced stomatal closure resulting in a lower transpiration rate, and consequently improved postharvest vase life of some cultivars of cut roses exposed to mild desiccation (Fanourakis et al., 2016). Moreover, acetic acid could function as an antitranspirant compound. Application of acetic acid at low concentrations decreased water use without reducing flowering under drought stress in begonias (Allen and Allen, 2021).

Polyamines have also been applied to ornamental plants for ameliorating water stress effects. Under drought stress, application of spermine (the major polyamine found in several species) by spraying increased water deficit tolerance in *Tropaeolum majus* by enhancing water contents, the levels of amino acids and non-reducing sugars, antioxidant enzymes activities, and by decreasing lipid peroxidation. Moreover, spermine treatment improved the number of flowers under moderate water stress (da Silva et al., 2022).

Ascorbic acid is a water-soluble antioxidant present at high concentration in plant cells and an electron-specific donor of APX to reduce H_2O_2 to water. Among other effects, an application of ascorbic acid may serve to boost antioxidant protection in plant cells and enhance the activity of APX which is one of the major antioxidant enzymes playing a

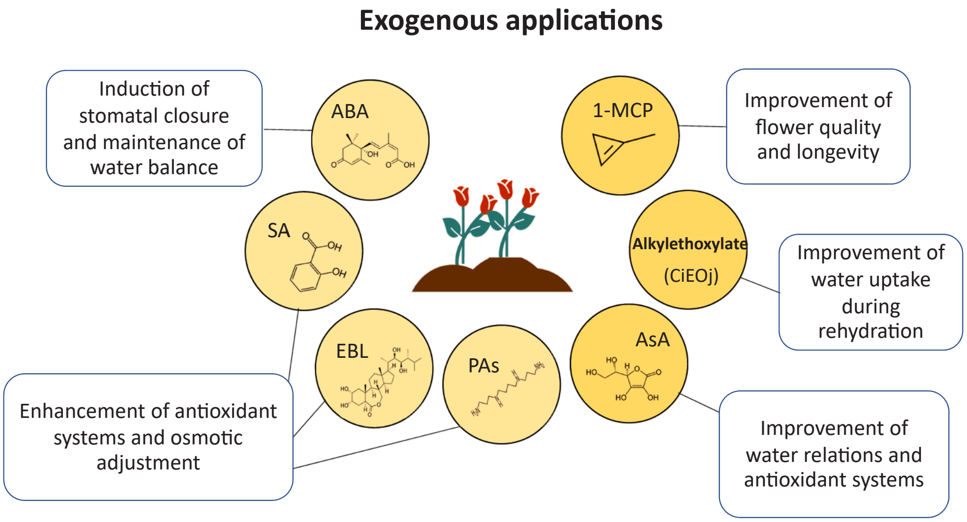


Fig. 3. Effects of exogenous applications of non-phytohormones (1-MCP, alkylethoxylate, and AsA) and phytohormones (ABA, SA, EBL, and PA) on the floricultural products under water stress conditions.

key role in redox balance. Consequently, ascorbic acid reduced the adverse effect of water deficit during dry storage, increased APX activity and led to a reduction in the extent of lipid peroxidation (Jin et al., 2006), leading to a reduction in the extent of lipid peroxidation, probably through its effects on tocopherol recycling (Munné-Bosch and Alegre, 2002). Likewise, the use of ascorbic acid in potted marigolds induced water stress tolerance by reducing ROS, increasing antioxidant enzyme activity and leading to osmotic adjustment (Hemmati et al., 2018).

Finally, the application of other compounds can also improve water uptake in cut flowers prior to exposure to dry storage. It has been reported that some mixtures of alkylethoxylates significantly increased water uptake and prolonged the vase life of cut roses and *Bouvadia* flowers (van Doorn et al., 2002). As a long-term dry period reduced hydraulic conductivity, which cannot be reversed after rehydration due to the stem blockage from wound-induced enzymes, there has been shown that pulsing with tropolone (a metal chelator) could prevent enzymatic reactions in cut stems (van Meeteren et al., 2006). Moreover, chitosan also improved water relations in potted flowers under water stress (Akhtar et al., 2022).

In summary, exogenous applications of chemical treatments such as ethylene inhibitors, plant hormones, and other compounds can be used to improve water stress tolerance in floricultural products (Fig. 3). The primary approaches that can be considered to alleviate the negative consequences of dehydration are improving the water status in plant cells and minimizing the production of ethylene, especially in ethylene-sensitive flowers. However, to select the optimal treatments, factors such as ethylene responses, water stress tolerance and the rehydration ability of flowers in different cultivars are very important points to consider. For example, in cut flowers that recover well after rehydration but are sensitive to ethylene, the use of ethylene inhibitors is usually the best choice. Furthermore, a detailed screening trait study, including the most adequate mechanistic approach that the application is seeking to achieve, together with an adequate preliminary study of the potential range of concentrations to be used, is strongly recommended.

7. Conclusions and prospects

Water deficit is a major issue in ornamental crops and cut flower industry that affects the quality and longevity of flowers leading to lower economic value. By compiling available studies published thus far, we have shown here that ethylene-sensitive and ethylene-insensitive flowers have a similar response to water stress in terms of water relations, stomatal function regulation, osmotic adjustment, and antioxidant protection systems. The investigation of the mechanisms underlying plant responses to water stress, especially hormonal changes (including ABA and ethylene) are essential for finding suitable treatments to alleviate the harmful effects of water deficit. Although the application of many compounds has been used for enhancing water stress tolerance of floricultural products, the use of plant hormones or compounds affecting their physiological action seems to be the most suitable method to overcome the adverse effects of water deficit. However, there are still several gaps on the mechanistic aspects underlying hormonal actions and more studies in this respect using cut flowers and potted flowers exposed to desiccation events are needed. Also, we suggest that future research studies should focus more on physiological responses during rehydration, which would provide beneficial information to develop suitable treatments for improving water stress resistance in floricultural products.

CRediT authorship contribution statement

Sukpitak Chawisa: Conceptualization, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **Muñoz Paula:** Formal analysis, Visualization, Writing – original draft. **Seraypheap Kanogwan:** Supervision, Writing – original draft, Writing – review & editing. **Munné-Bosch Sergi:** Conceptualization, Formal analysis, Project administration, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

All the authors declare that they have no conflict of interest

Data Availability

No data was used for the research described in the article.

References

Adamipour, N., Khosh-Khui, M., Salehi, H., Razi, H., Karami, A., Moghadam, A., 2020. Metabolic and genes expression analyses involved in proline metabolism of two rose species under drought stress. Plant Physiol. Biochem. 155, 105–113. https://doi.org/10.1016/j.plaphy.2020.07.028.

Akhtar, G., Faried, H.N., Razzaq, K., Ullah, S., Wattoo, F.M., Shehzad, M.A., Sajjad, Y., Ahsan, M., Javed, T., Dessoky, E.S., Abdelsalam, N.R., Chattha, M.S., 2022. Chitosan-induced physiological and biochemical regulations confer drought tolerance in pot marigold (*Calendula officinalis* L.). Agronomy 12, 474. https://doi.org/10.3390/agronomy12020474.

Allen, M.M., Allen, D.J., 2021. Acetic acid is a low cost antitranspirant that increases begonia survival under drought stress. Sci. Hortic. 287, 110257 https://doi.org/10.1016/j.scienta.2021.110257.

Álvarez, S., Navarro, A., Bañón, S., Sánchez-Blanco, M.J., 2009. Regulated deficit irrigation in potted *Dianthus* plants: effects of severe and moderate water stress on growth and physiological responses. Sci. Hortic. 122, 579–585. https://doi.org/10.1016/j.scienta.2009.06.030.

Antonić, D.D., Subotić, A.R., Dragićević, M.B., Pantelić, D., Milošević, S.M., Simonović, A.D., Momčilović, I., 2020. Effects of exogenous salicylic acid on drought response and characterization of dehydrins in *Impatiens walleriana*. Plants 9, 2589. https://doi.org/10.3390/plants9111589.

Arrom, L., Munné-Bosch, S., 2010. Tocopherol composition in flower organs of *Lilium* and its variations during natural and artificial senescence. Plant Sci. 179, 289–295 https://doi-org.sire.ub.edu/10.1016/j.plantsci.2010.05.002.

Arrom, L., Munné-Bosch, S., 2012. Hormonal regulation of leaf senescence in *Lilium*. J. Plant Physiol. 169, 1542–1550. https://doi.org/10.1016/j.jplph.2012.06.012.

Azuma, M., Onozaki, T., Ichimura, K., 2020. Difference of ethylene production and response to ethylene in cut flowers of dahlia (*Dahlia variabilis*) cultivars. Sci. Hortic. 273, 109635 https://doi.org/10.1016/j.scienta.2020.109635.

BCC (Business Communications Company), 2023. Global Flower and Ornamental Plants Market 2023–2027. Academy Association, Inc., Durham, NC, United States.

Borochov, A., Mayak, S., Broun, R., 1982. The involvement of water stress and ethylene in senescence of cut carnation flowers. J. Exp. Bot. 33, 1202–1209.

Bourbia, I., Carins-Murphy, M.R., Gracie, A., Brodribb, T.J., 2020. Xylem cavitation isolates leaky flowers during water stress in pyrethrum. N. Phytol. 227, 146–155 https://doi-org.sire.ub.edu/10.1111/nph.16516.

Caser, M., Lovisolo, C., Scariot, V., 2017. The influence of water stress on growth, ecophysiology and ornamental quality of potted *Primula vulgaris* 'Heidy' plants. New insights to increase water use efficiency in plant production. Plant Growth Regul. 83, 361–373. https://doi.org/10.1007/s10725-017-0301-4.

Çelikel, F.G., van Doorn, W.G., 2012. Endogenous ethylene does not regulate opening of unstressed *Iris* flowers but strongly inhibits it in water-stressed flowers. J. Plant Physiol. 169, 1425–1429. https://doi.org/10.1016/j.jplph.2012.05.012.

Chang, Y.-C., Chaang, Y.-S., Lin, L.-H., 2015. Response of shoot growth, photosynthetic capacity, flowering, and fruiting of potted 'Nagami' kumquat to different regulated deficit irrigation. Hortic. Environ. Biotechnol. 56, 444–454 https://doi.org/10.1007/s13580-015-0012-6.

Chen, J., Zhang, Q., Wang, Q., Feng, M., Li, Y., Meng, Y., Zhang, Y., Liu, G., Ma, Z., Wu, H., Gao, J., Ma, N., 2017. *RhMKK9*, a rose MAP KINASE KINASE gene, is involved in rehydration-triggered ethylene production in rose gynoecia. BMC Plant Biol. 17, 51 https://doi.org/10.1186/s12870-017-0999-1.

Chen, Y.-H., Miller, W.B., 2022. Nonrefrigerated dry storage can have negative effects on postharvest quality of cut *Lilium*. HortScience 57, 1475–1479. https://doi.org/10.21273/HORTSCI16766-22.

Cheng, G., Huang, H., Zhou, L., He, S., Zhang, Y., Cheng, X.A., 2019. Chemical composition and water permeability of the cuticular wax barrier in rose leaf and petal: A comparative investigation. Plant Physiol. Biochem. 135, 404–410. https://doi.org/10.1016/j.plaphy.2019.01.006.

Cheng, G., Wang, L., Wu, H., Yu, X., Zhang, N., Wan, X., He, L., Huang, H., 2021. Variation in petal and leaf wax deposition affects cuticular transpiration in cut lily flowers. Front. Plant. Sci. 12 https://doi.org/10.3389/fpls.2021.781987.

Chuang, Y.C., Chang, A., 2012. Effect of pre-harvest deficit irrigation on cut flower quality of *Eustoma grandiflorum*. Acta Hortic. (937), 475–481. https://doi.org/10.17660/ActaHortic.2012.937.58.

Cirillo, C., Rouphael, Y., Caputo, R., Raimondi, G., De Pascale, S., 2014. The influence of deficit irrigation on growth, ornamental quality, and water use efficiency of three potted *Bougainvillea* genotypes grown in two shapes. HortScience 49, 1284–1291. https://doi.org/10.21273/HORTSCI.49.10.1284.

Costa, L., Araújo, F., Souto Ribeiro, W., Santos, M., Finger, F., 2021. Postharvest physiology of cut flowers. Ornam. Hortic. 27, 374–385. https://doi.org/10.1590/2447-536x.v27i3.2372.

da Silva, T.I., Dias, M.G., de Araújo, N.O., Santos, M.N.D.S., Ribeiro, W.S., dos Santos Filho, F.B., Dias, T.J., Barbosa, J.G., Grossi, J.A.S., 2022. Spermine reduces the harmful effects of drought stress in *Tropaeolum majus*. Sci. Hortic. 304, 111339 https://doi.org/10.1016/j.scienta.2022.111339.

Daneshi Nergi, M.A., Ahmadi, N., 2014. Effects of 1-MCP and ethylene on postharvest quality and expression of senescence-associated genes in cut rose cv. Sparkle. Sci. Hortic. 166 78–83. https://doi.org/10.1016/j.scienta.2013.12.015.

Dar, R.A., Nisar, S., Tahir, I., 2021. Ethylene: a key player in ethylene sensitive flower senescence: a review. Sci. Hortic. 290, 110491 https://doi.org/10.1016/j.scienta.2021.110491.

Darvish, M., Shirzad, H., Asghari, M., Noruzi, P., Alirezalu, A., Pateiro, M., Takshe, A., Lorenzo, J.M., 2021. 24-epibrasinolide modulates the vase life of lisianthus cut flowers by modulating ACC oxidase enzyme activity and physiological responses (basel). plants 10. https://doi.org/10.3390/plants10050995.

Drory, A., Beja-Tal, S., Borochov, A., Gindin, E., Mayak, S., 1995. Transient water stress in cut carnation flowers: effects of cycloheximide. Sci. Hortic. 64, 167–175. https://doi.org/10.1016/0304-4238(95)00840-3.

Elibox, W., Umaharan, P., 2010. Cultivar differences in the deterioration of vase-life in cut-flowers of *Anthurium andraeanum* is determined by mechanisms that regulate water uptake. Sci. Hortic. 124, 102–108. https://doi.org/10.1016/j.scienta.2009.12.005.

Fan, Y., Liu, J., Zou, J., Zhang, X., Jiang, L., Liu, K., Lü, P., Gao, J., Zhang, C., 2020. The *RhHB1/RhLOX4* module affects the dehydration tolerance of rose flowers (*Rosa hybrida*) by fine-tuning jasmonic acid levels. Hortic. Res. 7, 74 https://doi.org/10.1038/s41438-020-0299-z.

Fanourakis, D., Pieruschka, R., Savvides, A., Macnish, A.J., Sarlikioti, V., Woltering, E.J., 2013. Sources of vase life variation in cut roses: a review. Postharvest Biol. Technol. 78, 1–15. https://doi.org/10.1016/j.postharvbio.2012.12.001.

Fanourakis, D., Vélez-Ramírez, A.I., In, B.C., Barendse, H., van Meeteren, U., Woltering, E.J., 2015. A survey of preharvest conditions affecting the regulation of water loss during vase life. Acta Hortic. (1064), 195–204. https://doi.org/10.17660/ActaHortic.2015.1064.22.

Fanourakis, D., Giday, H., Li, T., Kambourakis, E., Ligoxigakis, E.K., Papadimitriou, M., Strataridaki, A., Bouranis, D., Fiorani, F., Heuvelink, E., Ottosen, C.-O., 2016. Antitranspirant compounds alleviate the mild-desiccation-induced reduction of vase life in cut roses. Postharvest Biol. Technol. 117, 110–117. https://doi.org/10.1016/j.postharvbio.2016.02.007.

Fanourakis, D., Papadopoulou, E., Valla, A., Tzanakakis, V.A., Nektarios, P.A., 2021. Partitioning of transpiration to cut flower organs and its mediating role on vase life response to dry handling: a case study in chrysanthemum. Postharvest Biol. Technol. 181, 111636 https://doi.org/10.1016/j.postharvbio.2021.111636.

Fanourakis, D., Papadakis, V.M., Psyllakis, E., Tzanakakis, V.A., Nektarios, P.A., 2022. The role of water relations and oxidative stress in the vase life response to prolonged storage: a case study in chrysanthemum. Agriculture 12, 185. https://doi.org/10.3390/agriculture12020185.

Farmer, E.E., Müller, M.J., 2013. ROS-mediated lipid leroxidation and RES-activated signaling. Annu. Rev. Plant Biol. 64, 429–450. https://doi.org/10.1146/annurev-arplant-050312-120132.

Favero, T.B., Poimenopoulou, E., Himmelboe, M., Stergiou, T., Müller, R., Lütken, H., 2016. Efficiency of 1-methylcyclopropene (1-MCP) treatment after ethylene exposure of mini-*Phalaenopsis*. Sci. Hortic. 211, 53–59. https://doi.org/10.1016/j.scienta.2016.08.010.

Ge, Y., Lai, Q., Luo, P., Liu, X., Chen, W., 2019. Transcriptome profiling of *Gerbera hybrida* reveals that stem bending is caused by water stress and regulation of abscisic acid. BMC Genom. 20 (1), 22. https://doi.org/10.1186/s12864-019-5961-1.

Ha, S.T.T., Lim, J.-H., In, B.-C., 2019. Extension of the vase life of cut roses by both improving water relations and repressing ethylene responses. Hortic. Sci. Technol. 37, 65–77. https://doi.org/10.12972/kjhst.20190007.

Ha, S.T.T., Lim, J.-H., In, B.-C., 2020. Simultaneous inhibition of ethylene biosynthesis and binding using AVG and 1-MCP in two rose cultivars with different sensitivities to ethylene. J. Plant Growth Regul. 39, 553–563. https://doi.org/10.1007/s00344-019-09999-6.

Ha, S.T.T., Nguyen, T.K., Lim, J.H., 2021. Effects of air-exposure time on water relations, longevity, and aquaporin-related gene expression of cut roses. Hortic. Environ. Biotechnol. 62, 63–75. https://doi.org/10.1007/s13580-020-00302-1.

Hemmati, K., Ebadi, A., Khomari, S., Sedghi, M., 2018. Influence of ascorbic acid and 24-epibrassinolide on physiological characteristics of pot marigold under water-stress condition. J. Plant Interact. 13, 364–372. https://doi.org/10.1080/17429145.2018.1483033.

Huang, X., Lin, S., He, S., Lin, X., Liu, J., Chen, R., Li, H., 2018. Characterization of stomata on floral organs and scapes of cut ‘Real’ gerberas and their involvement in postharvest water loss. Postharvest Biol. Technol. 142, 39–45. https://doi.org/10.1016/j.postharvbio.2018.04.001.

In, B.-C., Ha, S.T.T., Lee, Y.S., Lim, J.H., 2017. Relationships between the longevity, water relations, ethylene sensitivity, and gene expression of cut roses. Postharvest Biol. Technol. 131, 74–83. https://doi.org/10.1016/j.postharvbio.2017.05.003.

Jaffar, M.A., Song, A., Faheem, M., Chen, S., Jiang, J., Liu, C., Fan, Q., Chen, F., 2016. Involvement of *CmWRKY10* in drought tolerance of chrysanthemum through the ABA-signaling pathway. Int. J. Mol. Sci. 17, 693. https://doi.org/10.3390/ijms17050693.

Jiang, X., Zhang, C., Lü, P., Jiang, G., Liu, X., Dai, F., Gao, J., 2014. RhNAC3, a stress-associated NAC transcription factor, has a role in dehydration tolerance through regulating osmotic stress-related genes in rose petals. Plant Biotechnol. J. 12, 38–48. https://doi.org/10.1111/pbi.12114.

Jiang, Y., Khan, M.A., Wang, Z., Liu, J., Xue, J., Gao, J., Zhang, C., 2015. Cu/ZnSOD involved in tolerance to dehydration in cut rose (*Rosa hybrida*). Postharvest Biol. Technol. 100, 187–195. https://doi.org/10.1016/j.postharvbio.2014.10.005.

Jin, J., Shan, N., Ma, N., Bai, J., Gao, J., 2006. Regulation of ascorbate peroxidase at the transcript level is involved in tolerance to postharvest water deficit stress in the cut rose (*Rosa hybrida* L.) cv. Samantha. Postharvest Biol. Technol. 40, 236–243. https://doi.org/10.1016/j.postharvbio.2006.01.014.

Jinfen, W., Bowen, C., 2022. 2,4-epibrassinolide relieves the damage of drought stress on freshcut lilies by increasing antioxidant enzyme activities. Pak. J. Bot. 54, 2043–2049.

Jing, W., Zhao, Q., Zhang, S., Zeng, D., Xu, J., Zhou, H., Wang, F., Liu, Y., Li, Y., 2021. *RhWRKY33* positively regulates onset of floral senescence by responding to wounding- and ethylene-signaling in rose plants. Front Plant Sci. 12, 726797 https://doi.org/10.3389/fpls.2021.726797.

Kim, Y.J., Kim, K.S., 2012. 1-MCP Improves display life in *Begonia* × *hiemalis* ’Blitz’ and ’Carnival. Korean J. Hortic. Sci. Technol. 30, 152–157. https://doi.org/10.7235/hort.2012.11120.

Kondo, M., Nakajima, T., Shibuya, K., Ichimura, K., 2020. Comparison of petal senescence between cut and intact carnation flowers using potted plants. Sci. Hortic. 272, 109564 https://doi.org/10.1016/j.scienta.2020.109564.

Kumar, M., Singh, V.P., Arora, A., Singh, N., 2014. The role of abscisic acid (ABA) in ethylene insensitive gladiolus (*Gladiolus grandiflora* Hort.) flower senescence. Acta Physiol. Plant 36, 151–159. https://doi.org/10.1007/s11738-013-1395-6.

Lear, B., Casey, M., Stead, A.D., Rogers, H.J., 2022. Peduncle necking in *Rosa hybrida* induces stress-related transcription factors, upregulates galactose metabolism, and downregulates phenylpropanoid biosynthesis genes. Front. Plant Sci. 13, 874590 https://doi.org/10.3389/fpls.2022.874590.

Li, T., Wang, R., Zhao, D., Tao, J., 2020. Effects of drought stress on physiological responses and gene expression changes in herbaceous peony (*Paeonia lactiflora* Pall.). Plant Signal. Behav. 15, 1746034. https://doi.org/10.1080/15592324.2020.1746034.

Lin, X., Li, H., He, S., Pang, Z., Lin, S., Li, H., 2020. Investigation of stomata in cut ‘Master’ carnations: organographic distribution, morphology, and contribution to water loss. HortScience 55, 1144–1147. https://doi.org/10.21273/HORTSCI14945-20.

Lin, Y., Jones, M.L., 2022. CRISPR/Cas9-Mediated editing of *autophagy gene 6* in petunia decreases flower longevity, seed yield, and phosphorus remobilization by accelerating ethylene production and senescence-related gene expression. Front. Plant Sci. 13, 840218 https://doi.org/10.3389/fpls.2022.840218.

Liu, D., Liu, X., Meng, Y., Sun, C., Tang, H., Jiang, Y., Khan, M.A., Xue, J., Ma, N., Gao, J., 2013. An organ-specific role for ethylene in rose petal expansion during dehydration and rehydration. J. Exp. Bot. 64, 2333–2344. https://doi.org/10.1093/jxb/ert092.

Liu, J., Fan, Y., Zou, J., Fang, Y., Wang, L., Wang, M., Jiang, X., Liu, Y., Gao, J., Zhang, C., 2017. A RhABF2/Ferritin module affects rose (*Rosa hybrida*) petal dehydration tolerance and senescence by modulating iron levels. Plant J. 92, 1157–1169. https://doi.org/10.1111/tpj.13751.

Liu, J., Zhang, Z., Li, H., Lin, X., Lin, S., Joyce, D.C., He, S., 2018. Alleviation of effects of exogenous ethylene on cut ‘Master’ carnation flowers with nano-silver and silver thiosulfate. Postharvest Biol. Technol. 143, 86–91. https://doi.org/10.1016/j.postharvbio.2018.04.017.

Luangsuwalai, K., Ketsa, S., van Doorn, W.G., 2011. Ethylene-regulated hastening of perianth senescence after pollination in *Dendrobium* flowers is not due to an increase in perianth ethylene production. Postharvest Biol. Technol. 62, 338–341. https://doi.org/10.1016/j.postharvbio.2011.07.011.

Ma, N., Xue, J., Li, Y., Liu, X., Dai, F., Jia, W., Luo, Y., Gao, J., 2008. *Rh-PIP2;1*, a rose aquaporin gene, is involved in ethylene-regulated petal expansion. Plant Physiol. 148, 894–907. https://doi.org/10.1104/pp.108.120154.

Macnish, A.J., Leonard, R.T., Borda, A.M., Nell, T.A., 2010. Genotypic variation in the postharvest performance and ethylene sensitivity of cut rose flowers. HortScience 45, 790–796. https://doi.org/10.21273/HORTSCI.45.5.790.

Mao, H., Sun, Y., Müller, R., Liu, F., 2014. Effects of soil water deficits on three genotypes of potted *Campanula* medium plants during bud formation stage. Sci. Hortic. 166, 91–96. https://doi.org/10.1016/j.scienta.2013.12.017.

Moody, E.P., Dole, J.M., Barnes, J., 2014. Refining postharvest handling procedures increased cut rose vase life. HortTechnology 24, 676–685. https://doi.org/10.21273/horttech.24.6.676.

Müller, M., Munné-Bosch, S., 2015. Ethylene response factors: A key regulatory hub in hormone and stress signaling. Plant Physiol. 169, 32–41. https://doi.org/10.1104/pp.15.00677.

Müller, R., Sisler, E.C., Serek, M., 2000. Stress induced ethylene production, ethylene binding, and the response to the ethylene action inhibitor 1-MCP in miniature roses. Sci. Hortic. 83, 51–59. https://doi.org/10.1016/S0304-4238(99)00099-0.

Munné-Bosch, S., Alegre, L., 2002. Interplay between ascorbic acid and lipophilic antioxidant defences in chloroplasts of water-stressed *Arabidopsis* plants. FEBS Lett. 524, 145–148. https://doi.org/10.1016/s0014-5793(02)03041-7.

Muñoz, P., Munné-Bosch, S., 2018. Photo-oxidative stress during leaf, flower and fruit development. Plant Physiol. 176, 1004–1014. https://doi.org/10.1104/pp.17.01127.

Muñoz, P., Munné-Bosch, S., 2020. Oxylipins in plastidial retrograde signaling. Redox Biol. 37, 101717 https://doi.org/10.1016/j.redox.2020.101717.

Oh, S.I., Kim, J., Lee, A.K., 2021. Comparison of shelf life and quality of potted hydrangea ‘Speedy Red’ under different abscisic acid spray concentrations. Hortic. Sci. Technol. 39 615–624. https://doi.org/10.7235/HORT.20210055.

Okamoto, M., Niki, T., Azuma, M., Shibuya, K., Ichimura, K., 2022. Expression of ethylene biosynthesis genes in the gynoecium and receptacle associated with sepal abscission during senescence in *Delphinium grandiflorum*. Plant Growth Regul. 97, 593–609. https://doi.org/10.1007/s10725-022-00822-z.

Omidian, M., Roein, Z., Shiri, M.A., 2022. Effect of foliar application of 24-epibrassinolide on water use efficiency and morpho-physiological characteristics of *Lilium* LA hybrid under deficit irrigation. J. Plant Growth Regul. 41, 1547–1560. https://doi.org/10.1007/s00344-021-10400-8.

Panavas, T., Walker, E.L., Rubinstein, B., 1998. Possible involvement of abscisic acid in senescence of daylily petals. J. Exp. Bot. 49, 1987–1997. https://doi.org/10.1093/jxb/49.329.1987.

Rice, L.J., Soós, V., Ascough, G.D., Balázs, E., Ördög, V., Whitehead, C.S., Finnie, J.F., Van Staden, J., 2013. Ethylene- and dark-induced flower abscission in potted *Plectranthus*: sensitivity, prevention by 1-MCP, and expression of ethylene biosynthetic genes. S. Afr. J. Bot. 87, 39–47. https://doi.org/10.1016/j.sajb.2013.03.011.

Roddy, A.B., Jiang, G.-F., Cao, K., Simonin, K.A., Brodersen, C.R., 2019. Hydraulic traits are more diverse in flowers than in leaves. N. Phytol. 223, 193–203 https://doi-org.sire.ub.edu/10.1111/nph.15749.

Roddy, A.B., Guilliams, C.M., Fine, P.V.A., Mambelli, S., Dawson, T.E., Simonin, K.A., 2023. Flowers are leakier than leaves but cheaper to build. N. Phytol. 239, 2076–2082 https://doi-org.sire.ub.edu/10.1111/nph.19104.

Sánchez-Blanco, M.J., Alvarez, S., Navarro, A., Bañón, S., 2009. Changes in leaf water relations, gas exchange, growth and flowering quality in potted *Geranium* plants irrigated with different water regimes. J. Plant Physiol. 166, 467–476. https://doi.org/10.1016/j.jplph.2008.06.015.

Schouten, R.E., van Dien, L., Shahin, A., Heimovaara, S., van Meeteren, U., Verdonk, J.C., 2018. Combined preharvest and postharvest treatments affect rapid leaf wilting in *Bouvardia* cut flowers. Sci. Hortic. 227, 75–78. https://doi.org/10.1016/j.scienta.2017.09.014.

Sewelam, N., Kazan, K., Thomas-Hall, S.R., Kidd, B.N., Manners, J.M., Schenk, P.M., 2013. Ethylene response factor 6 is a regulator of reactive oxygen species signaling in Arabidopsis. PLoS One 8, e70289. https://doi.org/10.1371/journal.pone.0070289.

Shakarami, K., Zahedi, B., Nejad, A.R., Fard, S.M., 2019. Evaluation of physiological responses of tuberose (Polianthes tuberosa L.) to water deficit stress. J. Ornam. Plants 9, 259–273.

Shi, L., Wang, Z., Kim, W.S., 2019. Effect of drought stress on shoot growth and physiological response in the cut rose 'charming black' at different developmental stages. Hortic. Environ. Biotechnol. 60, 1–8. https://doi.org/10.1007/s13580-018-0098-8.

Shibuya, K., Nagata, M., Tanikawa, N., Yoshioka, T., Hashiba, T., Satoh, S., 2002. Comparison of mRNA levels of three ethylene receptors in senescing flowers of carnation (*Dianthus caryophyllus* L.). J. Exp. Bot. 53, 399–406. https://doi.org/10.1093/jexbot/53.368.399.

Shibuya, K., Niki, T., Ichimura, K., 2013. Pollination induces autophagy in petunia petals via ethylene. J. Exp. Bot. 64, 1111–1120. https://doi.org/10.1093/jxb/ers395.

Shibuya, K., Shimizu, K., Niki, T., Ichimura, K., 2014. Identification of a NAC transcription factor, EPHEMERAL1, that controls petal senescence in Japanese morning glory. Plant J. 79, 1044–1051 https://doi-org.sire.ub.edu/10.1111/tpj.12605.

Sukpitak, C., Seraypheap, K., 2023. Postharvest transient water deficit limits longevity of cut *Dendrobium* 'Khao Sanan' orchid. Sci. Hortic. 309, 111637 https://doi.org/10.1016/j.scienta.2022.111637.

Sun, K., Cui, Y., Hauser, B.A., 2005. Environmental stress alters genes expression and induces ovule abortion: reactive oxygen species appear as ovules commit to abort. Planta 222, 632–642. https://doi.org/10.1007/s00425-005-0010-5.

Twumasi, P., van Ieperen, W., Woltering, E.J., Emons, A.M.C., Schel, J.H.N., Snel, J.F.H., van Meeteren, U., van Marwijk, D., 2005. Effects of water stress during growth on xylem anatomy, xylem functioning and vase life in three *Zinnia elegans* cultivars. Acta Hortic. (669), 303–312. https://doi.org/10.17660/ActaHortic.2005.669.40.

Uthaichay, N., Ketsa, S., van Doorn, W.G., 2007. 1-MCP pretreatment prevents bud and flower abscission in *Dendrobium* orchids. Postharvest Biol. Technol. 43, 374–380. https://doi.org/10.1016/j.postharvbio.2006.09.015.

van Doorn, W.G., 2012. Water relations of cut flowers: an update. In: Janick, J. (Ed.), Horticultural Reviews 40, pp. 55–106. https://doi.org/10.1002/9781118351871.ch2.

van Doorn, W.G., Han, S.S., 2011. Postharvest quality of cut lily flowers. Postharvest Biol. Technol. 62, 1–6. https://doi.org/10.1016/j.postharvbio.2011.04.013.

van Doorn, W.G., Abadie, P., Belde, P.J.M., 2002. Alkylethoxylate surfactants for rehydration of roses and *Bouvardia* flowers. Postharvest Biol. Technol. 24, 327–333. https://doi.org/10.1016/S0925-5214(01)00152-1.

van Iersel, M., Seader, K., Dove, S., 2009. Exogenous abscisic acid application effects on stomatal closure, water use, and shelf life of hydrangea (*Hydrangea macrophylla*). J. Environ. Hort. 27, 234–238. https://doi.org/10.24266/0738-2898-27.4.234.

van Meeteren, U., Arévalo-Galarza, L., van Doorn, W.G., 2006. Inhibition of water uptake after dry storage of cut flowers: role of aspired air and wound-induced processes in chrysanthemum. Postharvest Biol. Technol. 41, 70–77. https://doi.org/10.1016/j.postharvbio.2006.03.005.

Waterland, N.L., Finer, J.J., Jones, M.L., 2010. Abscisic acid applications decrease stomatal conductance and delay wilting in drought-stressed chrysanthemums. HortTechnology 20, 896–901. https://doi.org/10.21273/HORTTECH.20.5.896.

Woltering, E.J., Paillart, M.J.M., 2018. Effect of cold storage on stomatal functionality, water relations and flower performance in cut roses. Postharvest Biol. Technol. 136, 66–73. https://doi.org/10.1016/j.postharvbio.2017.10.009.

Wongjunta, M., Wongs-Aree, C., Salim, S., Meir, S., Philosoph-Hadas, S., Buanong, M., 2021. Involvement of ethylene in physiological processes determining the vase life of various hybrids of *Mokara* orchid cut flowers. Agronomy 11, 160. https://doi.org/10.3390/agronomy11010160.

Wu, F., Zhang, C., Wang, X., Guo, J., Dong, L., 2017. Ethylene-influenced development of tree peony cut flowers and characterization of genes involved in ethylene biosynthesis and perception. Postharvest Biol. Technol. 125, 150–160. https://doi.org/10.1016/j.postharvbio.2016.11.014.

Yakimova, E., Woltering, E., 1997. Stress-induced ethylene production in flower parts of cut carnation flowers cv. Light Pink Tasman. Bulg. J. Plant Physiol. 23, 43–56. Bulg. J. Plant Physiol. 23, 43–56.

Yao, Y., Zhao, N., Xian, T., Tu, S., Pan, L., Tu, K., 2017. Effect of 2,4-epibrassinolide treatment on the postharvest quality and physiological metabolism of fresh daylily flower buds during storage. Sci. Hortic. 226, 110–116. https://doi.org/10.1016/j.scienta.2017.08.039.

Yashewar, A., Umar, S., Sharma, M.P., Khan, W., Ahmad, S., 2017. Variation in ornamental traits, physiological responses of *Tagetes erecta* L. and *T. patula* L. in relation to antioxidant and metabolic profile under deficit irrigation strategies. Sci. Hortic. 214, 200–208 https://doi-org.sire.ub.edu/10.1016/j.scienta.2016.11.037.

Zhang, F.-P., Zhang, J.-L., Brodribb, T.J., Hu, H., 2021. Cavitation resistance of peduncle, petiole and stem is correlated with bordered pit dimensions in *Magnolia grandiflora*. Plant Divers. 43, 324–330 https://doi-org.sire.ub.edu/10.1016/j.pld.2020.11.007.

Zhang, H., Li, A., Zhang, Z., Huang, Z., Lu, P., Zhang, D., Liu, X., Zhang, Z.-F., Huang, R., 2016. Ethylene response factor TERF1, regulated by ETHYLENE-INSENSITIVE3-like factors, functions in reactive oxygen species (ROS) scavenging in tobacco (*Nicotiana tabacum* L.). Sci. Rep. 6, 29948 https://doi.org/10.1038/srep29948.

Zhang, T., Qu, Y., Wang, H., Wang, Z., Jiang, J., Chen, S., Fang, W., Guan, Z., Liao, Y., Chen, F., 2022. *CmSCL4* and *CmR1MYB1* synergistically enhance the drought tolerance by regulation of ABA signaling in chrysanthemum. Environ. Exp. Bot. 199, 104886 https://doi.org/10.1016/j.envexpbot.2022.104886.

Zomorrodi, N., Rezaei Nejad, A., Mousavi-Fard, S., Feizi, H., Tsaniklidis, G., Fanourakis, D., 2022. Potency of titanium dioxide nanoparticles, sodium hydrogen sulfide and salicylic acid in ameliorating the depressive effects of water deficit on Periwinkle ornamental quality. Horticulturae 8, 675. https://doi.org/10.3390/horticulturae8080675.

Further reading

Kalinowski, J., Moody, E.P., Dole, J.M., 2022. Improving hydration and vase life of cut *Zinnia*. Sci. Hortic. 293, 110661 https://doi.org/10.1016/j.scienta.2021.110661.

van Doorn, W.G., Dole, I., Çelikel, F.G., Harkema, H., 2014. Opening of cut *Iris x hollandica* flowers as affected by temperature, dry storage, and light. Postharvest Biol. Technol. 89, 40–43. https://doi.org/10.1016/j.postharvbio.2013.10.006.

Wagstaff, C., Bramke, I., Breeze, E., Thornber, S., Harrison, E., Thomas, B., Buchanan-Wollaston, V., Stead, T., Rogers, H., 2010. A specific group of genes respond to cold dehydration stress in cut *Alstroemeria* flowers whereas ambient dehydration stress accelerates developmental senescence expression patterns. J. Exp. Bot.. 61, 2905–2921. https://doi.org/10.1093/jxb/erq113.