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REALISTIC ABIOTIC AND MECHANICAL STRESS FACTORS LIMITING PRE- AND POST-HARVEST QUALITY OF ROSE, CHRYSANTHEMUM, CARNATION, AND GERBERA: A COMPARATIVE PHYSIOLOGICAL ANALYSIS

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ABSTRACT:
Rose (Rosa hybrida L.), chrysanthemum (Chrysanthemum morifolium Ramat.), carnation (Dianthus caryophyllus L.) and gerbera (Gerbera jamesonii Bolus ex Hook. f.) are grown almost exclusively under protected cultivation, where the dominant stress factors are greenhouse heat accumulation, irrigation water salinity, high-relative-humidity-induced stomatal dysfunction and mechanical injury during harvesting, bunching and transport. This review compares the physiological responses of the four species to these production-relevant stress factors, with particular emphasis on species-specific differences that determine cultivar choice and management practice. Rose and chrysanthemum show the strongest antioxidant enzyme induction and osmotic adjustment under salinity and heat, making them comparatively more tolerant of variable greenhouse conditions. Carnation possesses a distinct post-harvest advantage through polyamine-mediated suppression of ethylene biosynthesis, which is directly relevant to its tolerance of handling and transport stress. Gerbera is the most sensitive of the four species, showing pronounced stomatal malfunction under high relative humidity, severe photoinhibition under heat and high light and well-documented susceptibility to stem bending caused by water stress during the post-harvest period. This review concludes that comparative physiological data should guide cultivar selection, greenhouse climate management and handling protocols for these four major cut flower crops.

KEYWORDS: Rosa hybrida, Chrysanthemum morifolium, Dianthus caryophyllus, Gerbera jamesonii, greenhouse stress, mechanical stress, post-harvest physiology, floriculture

1. INTRODUCTION

Rose, chrysanthemum, carnation and gerbera together account for more than 60% of the global cut flower trade, which is valued at over USD 8 billion annually. Their popularity in both domestic and export markets is largely attributed to their wide range of flower forms and colors, good vase-life potential and suitability for year-round production under protected cultivation systems [1, 2]. Unlike many field crops that dominate the abiotic stress physiology literature, these ornamental species are cultivated primarily in protected environments such as polyhouses, naturally ventilated greenhouses and shade-net structures. Such production systems reduce exposure to the severe environmental stresses commonly experienced under open-field conditions, thereby shifting the major production challenges toward greenhouse-specific stress factors [3]. Nevertheless, irrigation water salinity remains a significant constraint across all four species because borewell and recycled water sources often contain elevated levels of dissolved salts and species differ considerably in their ability to tolerate and adapt to these conditions [4]. Although drought stress is generally less severe under protected cultivation, it has emerged as an important area of research because ornamental crops exhibit morphophysiological and biochemical responses to water deficit that differ substantially from those reported in field crops [5, 6].

Among the various environmental constraints affecting commercial floriculture, three categories of stress are particularly relevant. The first is greenhouse heat stress. Even under protected cultivation, temperatures frequently exceed 35°C during the summer months because naturally ventilated structures are often unable to dissipate accumulated solar heat effectively [7]. The second major constraint is irrigation water quality. In many production regions, borewell and recycled water sources exceed the salinity thresholds considered safe for sensitive ornamental crops, resulting in osmotic and ionic stress that can adversely affect plant growth and flower quality [8]. The third and often overlooked, stress factor is mechanical stress associated with harvesting, bunching, grading, packaging and transportation. The resulting quality losses can be comparable to those caused by heat or salinity stress because physical injury triggers wound-induced ethylene production and oxidative responses similar to those observed under abiotic

stress conditions. Despite its practical importance, mechanical stress remains relatively underrepresented in the broader plant stress physiology literature [9, 10].

Another distinctive aspect of cut flower stress physiology is the role of relative humidity (RH). In commercial greenhouse production, growers often maintain high RH levels to reduce transpirational water loss and improve energy-use efficiency. However, prolonged exposure to high humidity can lead to stomatal malfunction in several ornamental species. Sustained RH levels above 85% reduce guard-cell sensitivity to closing stimuli, leaving stomata less responsive when plants are subsequently exposed to lower-humidity environments. As a result, plants grown under high RH frequently fail to close their stomata effectively in response to darkness, ABA application, or desiccation stress because guard-cell signaling pathways become desensitized. This condition can lead to excessive water loss and premature wilting after harvest when cut stems are removed from the humid greenhouse environment [11]. Such a production-specific stress interaction is rarely discussed in general reviews of plant stress physiology.

Accordingly, this review focuses on the stress factors that are demonstrably relevant to the commercial production of rose, chrysanthemum, carnation and gerbera, namely greenhouse heat and humidity stress, irrigation water salinity and mechanical or handling stress. Comparative physiological responses among these four species are examined to identify key differences in stress tolerance and adaptation, providing a basis for practical management recommendations aimed at improving flower quality and reducing production and post-harvest losses.

2. Realistic Stress Factors In Commercial Cut Flower Production

2.1. Greenhouse Heat, Humidity, And Irrigation Water Quality

Among the major cut flower crops, greenhouse rose production has been studied most extensively in relation to irrigation water salinity because roses are commonly grown in soilless or low-buffering substrates where salts can accumulate rapidly when poor-quality irrigation water is used. Cabrera [8] reported that greenhouse-grown roses can tolerate irrigation water with an electrical conductivity (EC) of up to approximately 2.0 dS/m without significant yield reduction. This tolerance is largely due to the ability of the root system to adjust osmotically through the accumulation of compatible solutes, which helps maintain cell turgor under moderate salt stress. However, flower quality and stem length decline progressively once this threshold is exceeded, indicating that the osmotic adjustment capacity of the root system has been surpassed. Such salinity levels are commonly encountered in borewell water used in many commercial production regions. Chrysanthemum exhibits a similar EC threshold, whereas gerbera is considerably more sensitive to root-zone salinity. Its roots are less effective at compensating for increasing substrate EC, resulting in reduced flower size and weaker stems at salinity levels that have relatively little effect on rose or chrysanthemum [12].

Heat stress is another major challenge in protected cultivation systems, particularly in naturally ventilated greenhouses commonly used in India. During peak summer months, temperatures inside these structures frequently exceed 35°C because passive ventilation alone is often insufficient to dissipate accumulated solar heat. Studies have shown that gerbera plants exposed to a day temperature of 38°C exhibit reduced transpiration but increased evapotranspiration compared with plants maintained at 28°C [13]. This response is attributed to heat-induced impairment of guard-cell function, which disrupts the normal relationship between transpiration and evaporative demand. At the molecular level, heat-tolerant and heat-sensitive chrysanthemum cultivars display markedly different gene expression patterns under thermal stress. Heat-tolerant cultivars maintain coordinated expression of photosynthesis- and antioxidant-related genes, enabling better physiological performance under elevated temperatures [14].

To improve growth efficiency and reduce transpirational stress, growers often maintain greenhouse relative humidity (RH) above 85%. However, prolonged exposure to high RH can negatively affect stomatal function. Studies on chrysanthemum, rose and several other ornamental species have shown that plants grown under sustained high humidity develop stomata that respond poorly to closing signals such as darkness, ABA application, or dehydration stress [15]. This reduced responsiveness is attributed to desensitization of guard-cell signaling pathways under prolonged humid conditions. The consequences become particularly evident after harvest. Once flowers are removed from the greenhouse environment, the malfunctioning stomata often fail to close effectively, leading to excessive water loss and rapid wilting [15, 16]. Consequently, pre-harvest environmental conditions, particularly RH management, are now recognized as important determinants of post-harvest flower quality because stomatal characteristics established during cultivation persist after harvest. This area has therefore emerged as an important research priority in cut flower physiology [17].

2.2. Mechanical and Handling Stress

Mechanical stress is one of the most common yet least studied stress factors in commercial cut flower production. Unlike environmental stresses, mechanical stress is unavoidable because harvesting, handling, packaging and transportation are integral parts of the supply chain. Transportation-related vibration, for example, has been directly associated with reduced vase life, impaired water relations, weakened stem strength and increased oxidative damage in carnation [18]. Repeated mechanical movement disrupts vascular continuity and stimulates the production of wound-induced reactive oxygen species, with the severity of injury depending largely on the duration and frequency of vibration exposure. Several mitigation strategies, including nano-silver, melatonin and silicon-based foliar applications, have been shown to reduce vibration-induced senescence by improving water balance, strengthening stem tissues and enhancing antioxidant enzyme activity before mechanical damage progresses into visible senescence symptoms [18, 19].

Mechanical injury also occurs during harvesting and bunching operations. Flower stems are frequently exposed to cutting wounds, compression and abrasion against neighboring stems and packaging materials, particularly because dense bunching is necessary for efficient transport. Floriculture post-harvest handling guidelines recognize disorders such as bent neck in rose, stem breakage in gerbera and calyx splitting in carnation as common consequences of mechanical damage. Accordingly, protective practices such as individual sleeving and corrugated paper wrapping are

recommended because they minimize direct contact between stems and reduce bruising during packaging and transportation [20].

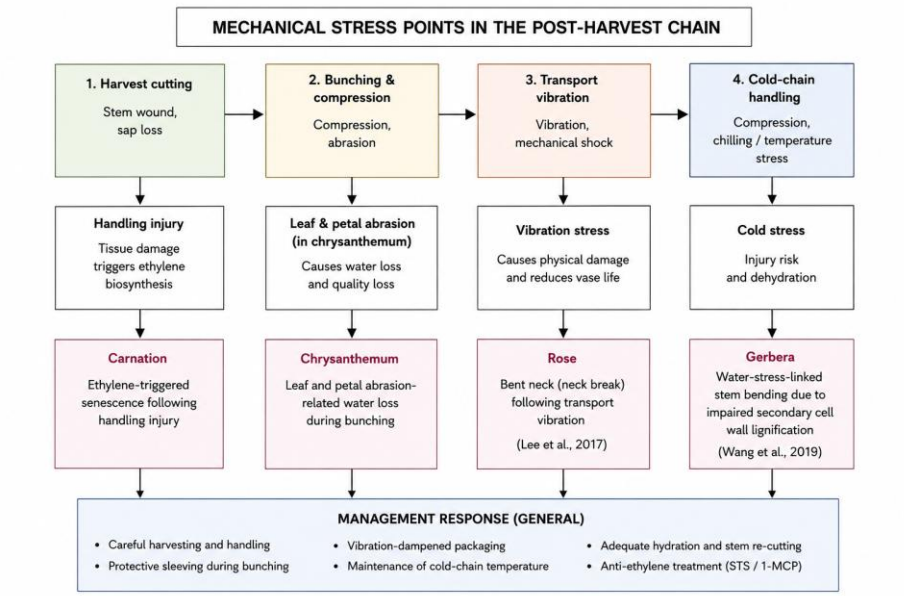

Fig. 5 Mechanical and handling stress factors across the post-harvest chain in cut flower crops. Schematic representation of mechanical stress points encountered during commercial handling -harvest cutting, bunching and compression, transport vibration, and cold-chain handling and their documented physiological consequences in the four species: bent neck in rose following transport vibration, ethylene-triggered senescence in carnation following handling injury, leaf and petal abrasion-related water loss in chrysanthemum during bunching, and water-stress-linked stem bending in gerbera caused by impaired secondary cell wall lignification. Species-specific handling recommendations are summarized in Table 4.

In chrysanthemum, silver and zinc nanoparticle treatments have been reported to extend vase life by reducing microbial-induced vascular blockage, demonstrating that chemical interventions can complement improvements in physical handling practices [21].

Transport vibration represents another important form of mechanical stress. Simulated transportation at vibration frequencies between 7.5 and 10 Hz has been shown to significantly reduce vase life and relative fresh weight while accelerating flower opening in cut rose [22]. The observed effects are attributed to disruption of xylem water transport and accelerated ethylene-mediated senescence. The extent of damage varies among cultivars and can also depend on the position of flowers within the shipping container. To mitigate these effects, pre-harvest applications of γ-aminobutyric acid (GABA) and calcium chloride have been shown to improve vase life and post-harvest quality by strengthening cell walls and enhancing antioxidant defenses before transportation begins [23].

Gerbera is particularly vulnerable to mechanical failure in the form of stem bending, a disorder in which the flowering stem loses rigidity and bends below the flower head during the post-harvest period. Transcriptomic studies have demonstrated that stem bending is closely associated with water stress and ABA-mediated regulation of secondary cell wall lignification [24]. Reduced lignin deposition and inadequate cell wall thickening weaken stem tissues, preventing them from supporting the weight of the flower head. Since lignin is the primary structural polymer responsible for stem rigidity, any reduction in its accumulation directly compromises mechanical strength.

Several treatments have been developed to address this problem. Melatonin application has been shown to reduce stem bending and extend vase life by promoting nitric oxide production, salicylic acid accumulation and lignin biosynthesis within stem tissues [25]. More recently, foliar application of melatonin-capped copper nanoparticles has been reported to further enhance stem strength because the nanoparticle formulation stimulates lignin biosynthesis genes more effectively than melatonin alone [26]. These findings highlight the potential of targeted physiological interventions for improving post-harvest quality and reducing mechanical losses in gerbera.

3. Species-Specific Physiological Responses To Production-Relevant Stress

3.1. Antioxidant Defense And Osmotic Adjustment

Under salinity and heat stress conditions commonly encountered in greenhouse production, plants activate enzymatic antioxidants such as SOD, CAT, APX and POD, while simultaneously accumulating osmolytes including proline and glycine betaine. These responses help counteract the reactive oxygen species and osmotic imbalances generated under combined stress conditions, thereby protecting cellular structures and maintaining water balance within plant tissues [27, 28].

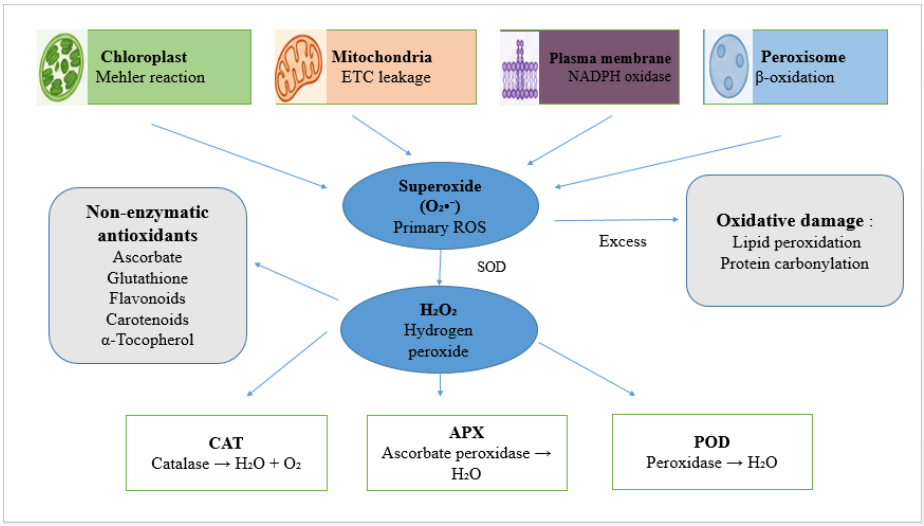

Fig. 1 ROS generation and antioxidant defense network in cut flower crops. The diagram illustrates the primary intracellular compartments (chloroplast, mitochondria, peroxisome, apoplast) from which ROS ($O_2^{\bullet-}$, H_2O_2, •OH, $^1O_2$) originate under abiotic stress, and the enzymatic (SOD, CAT, APX, POD, GR) and non-enzymatic (ascorbate, glutathione, flavonoids, carotenoids, tocopherols) antioxidant defense components operating through the ascorbate–glutathione (Halliwell–Asada) cycle that protect Rosa hybrida, Chrysanthemum morifolium, Dianthus caryophyllus, and Gerbera jamesonii from oxidative damage.

Among the four species examined, rose and chrysanthemum exhibit the strongest and most consistent activation of these defense mechanisms. In rose, irrigation water salinity equivalent to 100–150 mM NaCl significantly increases the activity of SOD, CAT and APX enzymes [29] Table 1. Antioxidant enzyme activities in four cut flower crops under production-relevant abiotic stress conditions

Table 1. Antioxidant enzyme activities in four cut flower crops under production-relevant abiotic stress conditions

Species and stress condition	SOD (U mg^{-1} FW)	CAT (U mg^{-1} FW)	APX (U mg^{-1} FW)	POD (U mg^{-1} FW)	Reference
Rosa hybrida – Salinity (150 mM NaCl)	58.4	31.6	22.1	44.8	[29]
Rosa hybrida – Heat (38°C, 72 h)	72.3	28.9	18.6	39.2	[29]
Chrysanthemum morifolium – Drought (−0.5 MPa)	65.7	42.3	30.4	56.1	[30]
Chrysanthemum morifolium – Cold (4°C, 48 h)	48.2	38.6	26.9	49.5	[46]
Dianthus caryophyllus – Water deficit (50% FC)	53.9	26.7	19.3	37.4	[33]
Dianthus caryophyllus – Salinity (100 mM NaCl)	61.8	33.4	24.7	43.6	[33]
Gerbera jamesonii – Salinity (100 mM NaCl)	48.3	16.4	12.1	24.8	[12]
Gerbera jamesonii – Heat (36°C, 20 d)	42.7	10.8	8.3	20.4	[13]

SOD- superoxide dismutase, CAT- catalase, APX- ascorbate peroxidase, POD- peroxidase,FW- fresh weight.

Chrysanthemum, meanwhile, accumulates the highest concentration of proline under both drought and salinity stress, reaching 68.3 µmol g−1 FW, which is nearly three times higher than the level recorded in gerbera (24.8 µmol g−1 FW) [30, 31].

Table 2. Osmolyte concentrations in four cut flower crops under production-relevant abiotic stress conditions

Species and stress condition	Proline (µmol g^{-1} FW)	Glycine betaine (µmol g^{-1} DW)	Soluble sugars (mg g^{-1} FW)	Reference
Rosa hybrida – Salinity (150 mM NaCl)	32.4	12.8	28.5	[29]
Rosa hybrida – Drought (40% FC)	41.7	15.6	35.8	[29]
Chrysanthemum morifolium – Drought	68.3	18.2	44.6	[30]
Chrysanthemum morifolium – Salinity (100 mM NaCl)	55.1	14.9	38.2	[30]
Dianthus caryophyllus – Water deficit	27.6	9.3	22.4	[33]
Dianthus caryophyllus – Cold stress	43.8	11.7	51.3	[33]
Gerbera jamesonii – Heat stress	19.2	7.4	18.9	[13]
Gerbera jamesonii – Salinity stress	24.8	8.8	21.3	[12]

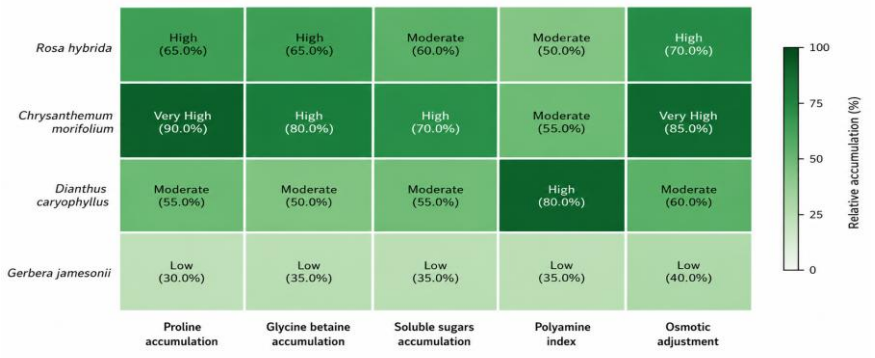

Fig. 2 Comparative osmolyte accumulation profiles in four cut flower crops under primary abiotic stress conditions. Chrysanthemum morifolium shows the highest accumulation of proline (68.3 µmol g^{-1} FW) and glycine betaine (18.2 µmol g^{-1} DW) under drought stress, indicating superior osmotic adjustment capacity, while Gerbera jamesonii consistently shows the lowest osmolyte concentrations across all stress types examined.

As a compatible solute, proline lowers cellular osmotic potential without interfering with enzyme activity, helping cells maintain turgor under water-deficit conditions. Heterografted chrysanthemum plants demonstrate an additional advantage, showing enhanced salt tolerance through the combined effects of ROS scavenging, soluble sugar accumulation and increased proline content across both rootstock and scion tissues [32].

In comparison, carnation displays moderate antioxidant and osmolyte responses and relies more heavily on efficient stomatal regulation. By limiting water loss through stomatal control, the plant reduces its dependence on extensive osmotic adjustment mechanisms [33]. Gerbera consistently exhibits the weakest antioxidant and osmolyte responses among the four species. Its roots and leaves show a comparatively limited biochemical response to ionic stress, which corresponds with its greater sensitivity to root-zone salinity [12, 31].

Several treatments have been shown to partially improve stress tolerance in gerbera. Exogenous spermidine application alleviates salinity stress by enhancing antioxidant enzyme activity and stabilizing chlorophyll–protein complexes, thereby improving chlorophyll stability [34]. Salicylic acid treatment similarly enhances salt tolerance through simultaneous osmotic and oxidative adjustment mechanisms [35]. In addition, the combined application of proline, IAA and PGPR under salinity stress improves physiological resilience by targeting complementary osmotic and antioxidant pathways across different cultivars [36].

From a post-harvest perspective, carnation possesses a unique osmolyte-related advantage. Exogenous spermine application at concentrations of 0.5–1.0 mM suppresses ethylene production by competing with ethylene biosynthesis for the common precursor S-adenosylmethionine. This mechanism has been shown to extend vase life by 30–50% under mild water-deficit and handling stress conditions [33, 37]. The polyamine–ethylene interaction is particularly important because carnation's primary post-harvest limitation is ethylene-induced senescence resulting from mechanical handling. Similar antioxidant and osmotic adjustment pathways have also been reported in drought-stressed rose plants. However, morphophysiological and molecular responses differ between drought and salinity stress, indicating that these stresses activate only partially overlapping signaling pathways even within the same species [5].

3.2. Photosynthetic Efficiency and Stomatal Behavior

The maximum quantum efficiency of photosystem II (Fv/Fm) is widely used as a sensitive indicator of stress-induced photoinhibition, with values below 0.75 generally indicating sustained damage to the photosynthetic apparatus [38].

Among the four species, gerbera exhibits the greatest decline in Fv/Fm under heat and high-light stress, reflecting its relatively limited photoprotective capacity. In contrast, carnation maintains the highest Fv/Fm values under water-deficit conditions because efficient stomatal regulation reduces the secondary photoinhibitory effects that often accompany drought stress [33].

Rose displays an intermediate level of sensitivity. Heat stress causes more severe photosystem damage than salinity stress because the oxygen-evolving complex of PSII is particularly susceptible to high temperatures. As a result, electron transport is disrupted before photoprotective mechanisms can fully compensate. This pattern is supported by transcriptomic studies that have identified heat-responsive genes associated with photosystem subunits [39, 40].

Table 3. Photosynthetic efficiency parameters in four cut flower crops under production-relevant abiotic stress conditions

Species and stress condition	Fv/Fm	Net A (µmol m^{-2} s^{-1})	gs (mol m^{-2} s^{-1})	Reference
Rosa hybrida – Salinity	0.71	8.4	0.18	[29]
Rosa hybrida – Heat	0.68	6.9	0.14	[39]
Chrysanthemum morifolium – Drought	0.65	7.1	0.12	[30]
Chrysanthemum morifolium – Cold	0.72	9.3	0.21	[46]
Dianthus caryophyllus – Water deficit	0.74	10.2	0.23	[33]
Dianthus caryophyllus – Salinity	0.69	7.6	0.16	[33]
Gerbera jamesonii – Heat	0.62	6.1	0.11	[13]
Gerbera jamesonii – Salinity	0.59	5.4	0.10	[12]

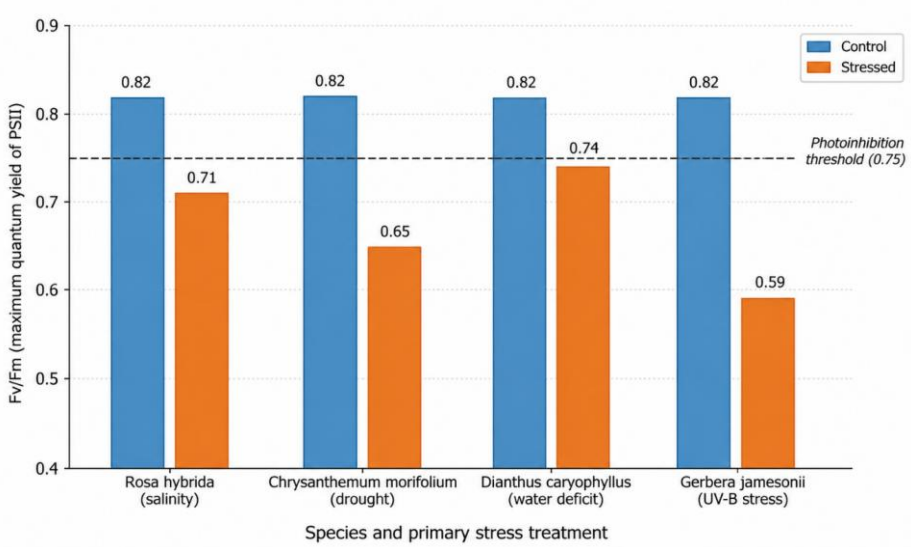

Fig. 3 Photosynthetic efficiency parameters (Fv/Fm) in four cut flower crops under normal and primary abiotic stress conditions. Dianthus caryophyllus maintains the highest photosynthetic efficiency under water deficit (Fv/Fm = 0.74), while Gerbera jamesonii shows the greatest PSII impairment under salinity stress (Fv/Fm = 0.59), below the photoinhibition threshold of 0.75 reported for unstressed C3 plants.

In chrysanthemum, elevated temperature has a more pronounced negative effect on photosynthesis than equivalent increases in relative humidity. Heat stress directly affects photosynthetic enzymes, whereas humidity primarily influences photosynthesis indirectly through changes in stomatal behavior. Consequently, stomatal conductance and PSII efficiency respond differently to thermal and humidity stress [41]. Under drought conditions, chrysanthemum experiences a 66% reduction in stomatal conductance accompanied by an 80% reduction in net CO2 assimilation [30]. Exogenous melatonin application further enhances drought tolerance by reducing membrane lipid peroxidation and strengthening antioxidant defenses, thereby minimizing cumulative oxidative damage [42].

A similar protective role of melatonin has been reported in carnation under heat stress. Melatonin improves growth, maintains photosynthetic efficiency and preserves leaf ultrastructure while enhancing antioxidant activity [43]. Furthermore, melatonin treatment induces both physiological and molecular responses in carnation, suggesting that its effects extend beyond simple antioxidant scavenging and involve broader signaling functions [44].

In contrast to drought-induced stomatal closure, high-relative-humidity greenhouse conditions can lead to stomatal malfunction due to an inability of stomata to close effectively when water conservation becomes necessary. This phenomenon results from guard-cell desensitization, which operates in the opposite manner to drought-induced responses. Understanding this distinction is important because it helps explain why gerbera and chrysanthemum grown under similar greenhouse environments may exhibit markedly different post-harvest water relations depending on their humidity conditions during cultivation [15, 16].

3.3. Transcription Factors and Hormone Signaling

Stress-responsive transcription factors play a central role in regulating antioxidant- and osmolyte-related gene expression in ornamental crops. Among these, members of the DREB/CBF and WRKY families are particularly important in rose and chrysanthemum under drought and cold stress conditions because they bind directly to stress-responsive promoter regions and regulate downstream defense pathways [45, 46].

Comparative transcriptomic analyses of heat-tolerant and heat-sensitive chrysanthemum cultivars have demonstrated that differences in stress tolerance are associated with the regulation of heat shock factors, WRKY transcription factors and genes involved in secondary metabolite biosynthesis. Tolerant cultivars maintain coordinated expression of these gene groups, enabling more effective stress adaptation [14].

In rose, drought tolerance is further enhanced by silicon-mediated improvements in membrane stability and osmolyte accumulation. Silicon deposition strengthens cell-wall and membrane integrity under water-deficit conditions, suggesting that substrate amendments may influence the drought tolerance threshold of commercial cultivars [47]. Comparable transcription factor networks in carnation and gerbera remain relatively unexplored, representing an important knowledge gap that may help explain their differing levels of stress tolerance [48].

Among phytohormones, ethylene is particularly important for post-harvest flower quality because its production is rapidly induced by mechanical injury and handling. Consequently, suppression of ethylene action through silver thiosulfate (STS) or 1-methylcyclopropene (1-MCP) treatment remains one of the most widely adopted commercial approaches for extending vase life, especially in carnation [20, 33].

At the molecular level, the transcription factor DcWRKY33 directly binds to the promoters of genes involved in ethylene biosynthesis, ABA signaling and reactive oxygen species generation. Through this regulatory function, it promotes the senescence cascade during carnation petal ageing and therefore represents a potential target for improving vase life [49].

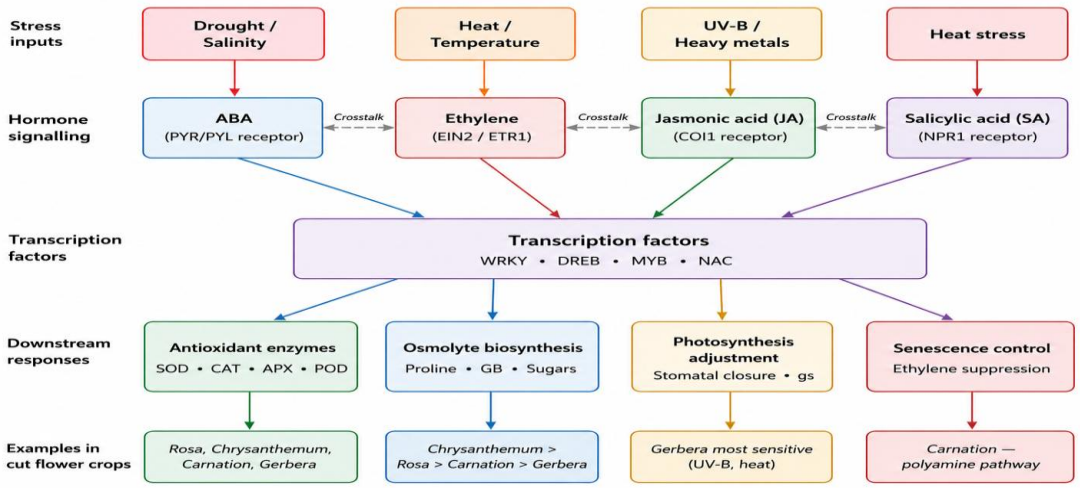

Fig. 4 Phytohormone signaling crosstalk under abiotic stress in cut flower crops. Stress signals perceived through hormone receptors (PYR/PYL for ABA; ETR1/EIN2 for ethylene; COI1 for JA; NPR1 for SA) activate transcription factors (WRKY, DREB, MYB, NAC) that coordinate stress-adaptive responses, including antioxidant enzyme induction, osmolyte accumulation, photosynthetic adjustment, and senescence regulation, in the four cut flower species.

In addition to transcription factor regulation, DNA methylation has been identified as another important component of ethylene-induced petal senescence. Epigenetic modification of ethylene-responsive genes provides an additional layer of regulation that contributes to the progression of senescence in ornamental flowers [50].
Post-harvest melatonin treatment has also been shown to extend vase life in rose by strengthening antioxidant defense systems in a manner similar to that reported in carnation and chrysanthemum [51]. These findings suggest that hormonal regulation and antioxidant priming strategies may have broader applicability across multiple cut flower species.

4. Comparative Analysis And Production Management Strategies

As discussed in the preceding sections, rose, chrysanthemum, carnation and gerbera differ considerably in their physiological responses to the major stress factors encountered under commercial production conditions. This section integrates those differences into a comparative framework that can assist growers in cultivar selection, greenhouse climate management and post-harvest handling decisions.

Table 4. Comparative stress vulnerability profile and production management recommendations for four cut flower crops

Crop	Primary production-relevant vulnerability	Key physiological response	Recommended management strategy	References
Rosa hybrida	Heat-induced photosystem damage, moderate transport vibration sensitivity (cultivar-dependent)	Strong SOD/CAT/APX induction under salinity, EC tolerance up to ~2.0 dS/m; greater thermal sensitivity of oxygen-evolving complex	Shade/ventilation management during peak heat vibration-dampened packaging for export GABA/$CaCl_2$ pre-harvest treatment	(29,39)
Chrysanthemum morifolium	High-RH-induced stomatal malfunction affecting post-harvest water relations	Broadest overall stress tolerance, strong osmotic adjustment and DREB-mediated regulation, cultivar differences in salt tolerance mechanisms	Balance greenhouse RH for energy efficiency against post-harvest stomatal function, default cultivar where climate control is limited	(30, 45)
Dianthus caryophyllus	Ethylene-triggered senescence following mechanical handling (harvesting, bunching, transport)	Polyamine-mediated suppression of ethylene biosynthesis efficient stomatal regulation under water deficit DcWRKY33-mediated senescence regulation	STS or 1-MCP post-harvest treatment to block ethylene perception, pre-harvest melatonin priming for combined heat and handling stress	(33,37)
Gerbera jamesonii	Highest sensitivity to root-zone salinity mechanical stem bending caused by water stress and impaired lignification	Weakest antioxidant/osmolyte response of the four species greatest photoinhibition under heat and high light salicylic acid and spermidine	Strict irrigation water EC standards; tighter greenhouse temperature/humidity control individual sleeving pre-harvest melatonin-Cu NP	(12, 24)

		partially alleviate salinity stress	or nanochitosan-melatonin treatments to promote stem lignification	

4.1. Rosa hybrida

Rose exhibits strong antioxidant enzyme induction under salinity and heat stress, provided the electrical conductivity (EC) of irrigation water remains below approximately 2.0 dS/m. This tolerance is largely attributed to the rapid activation of antioxidant systems such as SOD, CAT and APX, which help mitigate ionic and oxidative stress. Consequently, rose is relatively resilient to fluctuations in irrigation water quality commonly observed in commercial production systems [47, 29].

Its primary vulnerability lies in heat-induced damage to the photosynthetic apparatus. The oxygen-evolving complex in rose is more thermally sensitive than that of chrysanthemum or carnation and transcriptomic and metabolomic studies have revealed distinct heat-response pathways involving photosystem subunit genes and secondary metabolite accumulation [39, 40]. From a production perspective, growers should therefore prioritize effective shading and ventilation during periods of high summer temperature, as heat stress poses a greater threat than salinity under most greenhouse conditions.

During the post-harvest stage, rose is moderately susceptible to transport-related vibration stress, although the extent of damage varies among cultivars [22]. For long-distance export markets, selecting vibration-tolerant cultivars and applying pre-harvest treatments such as GABA or calcium chloride may be beneficial, as these approaches help strengthen cell-wall integrity and antioxidant defense systems that are compromised during transport stress [23].

4.2. Chrysanthemum morifolium

Among the four species reviewed, chrysanthemum demonstrates the broadest overall stress tolerance. This resilience results from the combined action of efficient osmotic adjustment, strong antioxidant enzyme activity and effective DREB-mediated transcriptional regulation, which collectively protect the plant against osmotic, oxidative and transcriptional disturbances caused by environmental stress [30, 45].

Nevertheless, salt tolerance in chrysanthemum varies considerably among cultivars. Genotype-specific differences in antioxidant activity, osmolyte accumulation and ion compartmentalization contribute to variations in stress tolerance, indicating that salt tolerance is a complex trait rather than a uniform characteristic across all chrysanthemum cultivars [52].

Because of this broad adaptive capacity, chrysanthemum is generally more forgiving of fluctuations in greenhouse temperature and irrigation water quality, making it a suitable choice where environmental control is limited. However, it remains susceptible to the high-relative-humidity-induced stomatal dysfunction discussed in Section 2.1. The same guard-cell desensitization mechanisms reported in other species can occur in chrysanthemum, potentially reducing post-harvest water relations and vase life when greenhouse humidity is maintained at excessively high levels [15].

4.3. Dianthus caryophyllus

Carnation is distinguished by its ability to suppress ethylene biosynthesis through polyamine-mediated regulation, a mechanism that directly addresses its major commercial limitation—ethylene-induced senescence following harvesting, bunching, handling and transport [33, 37]. Elevated polyamine levels compete with ethylene biosynthesis for common metabolic precursors, thereby delaying senescence and extending flower longevity.

At the molecular level, the transcription factor DcWRKY33 plays a central regulatory role by activating genes associated with ethylene production, ABA signaling and reactive oxygen species generation during petal senescence [49]. This understanding provides a potential target for future genetic and physiological interventions.

As a result of its ethylene-management capacity, carnation is particularly well suited for long-distance transportation and extended retail distribution, provided that post-harvest ethylene exposure is effectively controlled using treatments such as STS or 1-MCP. In addition, exogenous melatonin has been shown to reduce heat-induced damage by improving photosynthetic performance, maintaining leaf ultrastructure and enhancing antioxidant activity [43, 44]. These findings suggest that pre-harvest melatonin priming could complement conventional ethylene-management strategies and improve post-harvest performance under combined heat and handling stress conditions.

4.4. Gerbera jamesonii

Gerbera is consistently the most stress-sensitive species among the four crops evaluated in this review. It exhibits weaker antioxidant and osmolyte responses, greater sensitivity to root-zone salinity and less effective biochemical defense mechanisms compared with rose, chrysanthemum and carnation [12, 31]. Gerbera also experiences a greater reduction in photosynthetic efficiency under conditions of heat and high light intensity.

A distinctive feature of gerbera is stem bending, a well-documented mechanical disorder closely associated with water stress and reduced lignification. Insufficient lignin deposition weakens stem structural integrity, ultimately resulting in post-harvest stem collapse [24].

Several treatments have shown potential for improving stress tolerance in gerbera. Exogenous application of spermidine enhances antioxidant enzyme activity and chlorophyll stability, thereby partially alleviating salinity stress [34]. Similarly, salicylic acid improves salt tolerance through osmotic and oxidative adjustment mechanisms [35]. Combined application of proline, IAA and PGPR further enhances physiological resilience by simultaneously targeting osmotic and oxidative stress responses across different cultivars [36].

Because of its relatively narrow physiological tolerance, gerbera requires more precise greenhouse climate management than the other species. Maintaining strict control over temperature, humidity and irrigation water quality is essential to minimize stress-related losses. Individual sleeving during bunching and careful handling during transportation are widely adopted industry practices because of the crop's susceptibility to mechanical damage and stem bending [20].

Pre-harvest treatments aimed at improving stem lignification offer promising opportunities for reducing post-harvest losses. Melatonin-capped copper nanoparticles have been reported to enhance stem strength by upregulating genes involved in lignin biosynthesis [26]. Likewise, nanochitosan-encapsulated melatonin delays petal senescence by improving membrane stability and antioxidant activity in cut gerbera flowers [53]. These approaches may provide effective strategies for improving both post-harvest quality and marketability.

4.5. Integrated Management Recommendations

Based on the comparative physiological responses observed across the four cut flower species, three key management priorities can be identified. First, irrigation water should be monitored regularly for electrical conductivity, particularly in gerbera, as it has a lower salinity tolerance compared with rose and chrysanthemum [47, 12]. Regular assessment of water quality can therefore help minimize salinity-related stress and maintain flower quality.

Second, greenhouse relative humidity (RH) should be managed carefully to achieve a balance between production efficiency and post-harvest performance. Although high RH conditions can promote growth and improve energy-use efficiency, prolonged exposure may impair stomatal functioning and reduce vase life, especially in gerbera and chrysanthemum [15, 16]. Maintaining optimal RH levels is therefore essential for sustaining both crop growth and post-harvest quality.

Third, handling and packaging practices should be tailored to the specific vulnerabilities of each species. Gerbera requires individual sleeving and adequate stem support during handling and transport to reduce the risk of stem bending [20]. In carnation, ethylene management through treatments such as STS or 1-MCP is more important than mechanical protection, since its major limitation is hormonally regulated senescence rather than physical damage [33]. Rose, on the other hand, benefits from vibration-dampening packaging and pre-harvest antioxidant priming during long-distance transport because vibration stress is a more significant concern than ethylene exposure during the transport stage [22].

5. Knowledge Gaps Specific To Cut Flower Stress Physiology

The comparative analysis presented in this review highlights three important knowledge gaps that are particularly relevant to commercial cut flower production.

First, the molecular mechanisms underlying mechanical stress responses in cut flowers remain largely unexplored at the transcriptomic level. Compared with heat and salinity stress, mechanical stress has received considerably less attention in molecular studies. The transcriptomic investigation of stem bending in gerbera [24] is one of the few studies that has linked mechanical failure with specific changes in gene expression. Considering that mechanical and handling stress can cause quality losses comparable to those resulting from abiotic stress under commercial conditions, this area represents an important opportunity for future research.

Second, the effects of prolonged high-RH greenhouse cultivation on post-harvest stomatal function have been examined in only a limited number of ornamental crops. Most studies on stomatal regulation focus on drought stress rather than excess humidity and species-specific thresholds for RH-induced stomatal dysfunction in rose, carnation and gerbera under tropical greenhouse conditions in India remain poorly defined [15, 17]. Addressing this gap would provide growers with evidence-based RH recommendations that optimize both crop growth and post-harvest quality.

Third, the relationship between pre-harvest stress history and post-harvest performance remains insufficiently understood. Factors such as irrigation water salinity, greenhouse heat exposure and RH management are rarely evaluated together with post-harvest traits such as vase life, stem bending and vibration tolerance within the same study. Most investigations focus on individual stress factors in isolation rather than following the crop from greenhouse production through the post-harvest phase. Future research integrating pre-harvest physiological assessments with post-harvest quality evaluation under realistic commercial conditions would greatly enhance the practical relevance of stress physiology studies in rose, chrysanthemum, carnation and gerbera [17].

6. CONCLUSIONS

Rather than focusing on the wide range of abiotic stresses affecting field crops, this review specifically compares the physiological responses of rose, chrysanthemum, carnation and gerbera to the major stress factors commonly encountered in commercial protected cultivation, namely greenhouse heat and humidity, irrigation water salinity and mechanical or handling stress. The available evidence highlights distinct, production-relevant differences among these four cut flower species. Rose and chrysanthemum exhibit stronger antioxidant activity and osmotic adjustment capacity, enabling them to develop rapid and coordinated biochemical responses under salinity and heat stress. As a result, these species are generally more tolerant of fluctuating greenhouse conditions, although rose remains susceptible to heat-

induced damage to the photosynthetic apparatus [29, 30]. In carnation, polyamine-mediated suppression of ethylene production represents a key adaptive mechanism, as it helps minimize handling-induced senescence, which is one of the major causes of post-harvest quality deterioration [33, 37]. Gerbera was found to be the most sensitive species across most of the parameters evaluated. A notable characteristic of gerbera is stem bending, a well-documented mechanical disorder in which water stress impairs lignification, reducing stem strength and ultimately leading to post-harvest structural failure [24].

As summarized in the comparative analysis presented in Section 4, these species-specific responses provide practical insights for cultivar selection, greenhouse environmental management and the development of appropriate handling protocols. Compared with general descriptions of plant stress physiology, such information offers a more applicable framework for improving cut flower production and quality. Future studies integrating mechanical stress physiology, relative-humidity-dependent stomatal regulation and the relationship between pre-harvest and post-harvest stress responses under commercial production conditions will further enhance our understanding and support strategies aimed at reducing losses and maintaining quality in these important cut flower crops..

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