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Research Article

# Improvement of quality, physiological parameters and antioxidant status of chrysanthemum by priming of seedlings with UV-A radiation

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## Abstract

In conventional chrysanthemum production systems, supplemental lighting is used to induce flowering. Plants perceive radiation in the range of 280 to 750 nm, and UV radiation has been shown to improve plant productivity. Modern technology allows efficient manipulation of these wavelengths, facilitating their direct application to seedlings. This study evaluated the effect of different UV-A exposure times (1, 2, 3 and 4 hours) on chrysanthemum seedlings of the varieties 'Polaris' and 'Codorniz' (*Chrysanthemum × morifolium*). In 'Polaris', priming the seedlings with UV-A increased growth by 8% and flower diameter by 6%, in addition to improving photosynthesis, with increases of up to 38%. The Fv/Fm index, an indicator of the photochemical efficiency of PSII, increased by 5%. In leaves, β-carotene increased by 45%, vitamin C by 8% and total chlorophylls by 56%. In petals, phenolics increased by 12% and 15%, while flavonoids increased by 12%. In contrast, 'Codorniz' showed less sensitivity to UV-A radiation, no change in growth and no change in biochemical compounds, although photosynthesis improved by 20%. UV-A radiation showed great potential for optimizing quality and productivity in chrysanthemums, especially in the 'Polaris' variety. These differences highlight the importance of taking into account the specific characteristics of each variety when implementing management strategies using UV-A light.

***Keywords:*** antioxidant system; chlorophyll fluorescence; flower quality; ornamental crops; photosynthesis; stress memory

## Introduction

The cut flower industry is one of the main industries within the agricultural sector in several developing and underdeveloped countries (Mohiuddin, 2016). Chrysanthemum is considered the third most relevant crop

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in the floricultural sector, in 2022, the largest exporters of chrysanthemums for ornamental purposes were the Netherlands ($411 million), Colombia ($180 million), Malaysia ($83.6 million), Vietnam ($53.9 million) and China ($39.5 million). The main importers were the United Kingdom ($137 million), the United States ($125 million), Russia ($122 million), Japan ($110 million) and Germany ($67.9 million) (Observatory of Economic Complexity, 2022). Floriculture in Mexico has increased in recent decades because it is considered a viable economic activity. The ornamental plant market includes cut flowers, indoor and outdoor plants and flower bulbs (Mohiuddin, 2016). In 2020, the main cut flowers grown in the Mexican market were chrysanthemums, roses, sword lilies and carnations (SIAP, 2021). Chrysanthemum is considered the leading commercial cut and potted flower in the global market, and is extremely popular for its wide range of color and flower structure (Reddy, 2016; Hadizadeh *et al.*, 2022). Chrysanthemums are among the plants that require short days to induce flowering, so they can be programmed to flower throughout the year by manipulating day length (Trolinger *et al.*, 2017; Nissim-Levi *et al.*, 2019). Chrysanthemum flowering is prevented by adding low intensity artificial light (1–2 μmol $m^{-2}$ $s^{-1}$) at the end of the day, extending the light period to up to 16 hours. This uses white, incandescent, or fluorescent light, but incandescent bulbs are no longer being used due to their energy inefficiency, and more efficient sources such as fluorescent and light-emitting diodes (LEDs) are being used instead (Nissim-Levi *et al.*, 2019). The use of lighting systems provides farmers with numerous production benefits, such as planning production in advance, improving plant growth, regulating the color of leaves and flowers, and generally improving the quality of final products (Trivellini *et al.*, 2023).

Plants have a remarkable ability to respond and adapt to changes in their environment. Light stands out as one of the most important environmental elements, through different photoreceptor systems, plants use wavelengths ranging from UV-B (280-315 nm) to the far spectrum (700 nm) to control gene expression, metabolism (biochemical composition) and plant morphology (Zoratti *et al.*, 2014; Escobar-Bravo *et al.*, 2021). The perception of UV radiation is performed by its photoreceptors, which detect light and convert it into an electrical or chemical signal, these are cryptochromes (CRYs) (Ahmad *et al.*, 2002), phototropins (PHOTs) (Christie and Briggs, 2001; Vandenbussche *et al.*, 2014), phytochrome A (PHYA) (Shinomura, 1996), and UVB-RESISTANCE 8 (UVR8) as a specific UV-B sensor (Heijde and Ulm, 2012). The chrysanthemum UV-B-sensing photoreceptor (CmUVR8) plays an important role in UV-B signalling and UV-B-induced accumulation of flavonoids as a counterpart to the Arabidopsis UV-B photoreceptor AtUVR8 (Yang *et al.*, 2018).

Once radiation is perceived by photoreceptors, signalling cascades are activated that control the expression of hundreds of genes (Verdaguer *et al.*, 2017). UV-A (315-400 nm) has been shown to affect growth, photosynthesis, plant secondary metabolites, and plant-insect interactions in important horticultural and agricultural crops (Neugart and Schreiner, 2018). Bornman *et al.* (2019) highlight that UV radiation primarily acts as an environmental regulator, modulating plant growth and developmental processes. Recently, the properties of UV radiation have been exploited for priming seeds, seedlings and developing plants (Brazaitytė *et al.*, 2019; Foroughbakhch *et al.*, 2019; Lee *et al.*, 2019). In particular, UV priming of seedlings during their early growth phase is used for various purposes, and its effects may depend on factors such as radiation dose, specific wavelength, and duration of exposure (Poonia *et al.*, 2022).

Application of UV-A (366 nm) to seeds at three different exposure times (2, 4 and 6 hours). UV-A improved germination rate, specific leaf area, root length and dry weight increase of mung bean (*Vigna radiata*) plants (Hamid and Jawaid, 2011). The use of different UV-A wavelengths (366, 390 and 402 nm) for different durations (10 and 16 h) was not significant for biomass production in microgreens and mustard (*Brassica juncea* L. cv. León Rojo); however, UV-A (402 nm) increased the leaf area of microgreens. UV-A at 366 and 390 nm, on the other hand, increased phenolic compounds and tocopherol, as well as nitrate at both light durations (Brazaitytė *et al.*, 2019). Three different UV-A intensities (5, 10 or 15 W $m^{-2}$) for kale plants at 5 and 10 W $m^{-2}$ UV-A intensities promoted significant growth (35-50%) in shoot fresh weight. Exposure to 10 W $m^{-2}$ significantly improved photosynthesis, water use efficiency and photosystem II quantum efficiency (Sonjaroon *et al.*, 2024).

Furthermore, there is still a lack of information on how UV radiation induces changes in the biomass of ornamental crop species, as this is not the most relevant aspect for these plants (Neugart and Schreiner, 2018). The aim of this study was to evaluate the effects of seedling priming with different doses of UV-A radiation (385 nm) on the production of secondary metabolites, growth and flower quality of two chrysanthemum cultivars ('Polaris' and 'Codorniz').

## Materials and Methods

Two different cultivars of Chrysanthemum (*Chrysanthemum* × *morifolium* Ramat, cv. 'Polaris' and cv. 'Codorniz') were established for the development of the experiment. The cuttings were obtained from a floricultural corridor in the state of Mexico. Four rooted cuttings were transplanted into 1 L black polyethylene bags containing a mixture of perlite and peat moss in a 1:1 ratio as substrate. The distance between plants was 10 cm and between containers 20 cm, with a final density of 60 plants per $m^{-2}$. The apical meristem was pruned to leave 3-4 true leaves per stem. A 16-hour photoperiod was then added for 20 days using a 100 W white LED lamp. Both cultivars were fed with Steiner's solution at a concentration of 10% (Steiner, 1961). The pH of the nutrient solution was adjusted to 6.5 using sulfuric acid, and the electrical conductivity (EC) was maintained between 1.8-2.2 mS $cm^{-1}$ throughout the growing cycle. Both cultures were grown for 120 days after transplanting.

### *Application of UV-A radiation as seedling priming*

The application of UV-A radiation (385 nm) was carried out with LED lamps of 25 W and 2.2 m long (model LILZBAL-S100WFRBPBC, Sola Basic, Mexico City, Mexico). The seedling priming with UV-A radiation was made before transplanting in a single operation; for different times according to the treatments. To prime the seedlings, the lamp was placed 30 cm above the canopy.

The treatments were a control with no application of UV-A radiation (T0), a treatment with a 1-hour application of UV-A radiation (T1), a treatment with a 2-hour application of UV-A radiation (T2), a treatment with a 3-hour application of UV-A radiation (T3), and a treatment with a 4-hour application of UV-A radiation (T4).

### *Agronomic parameters*

At 120 days after transplanting, plant height, flower diameter, stem diameter, shoot fresh biomass, number of leaves and vase life were measured.

### *Physiological parameters*

At 40 days after transplanting, net photosynthetic rate (Pr), intracellular carbon dioxide content (Ci), transpiration (Tr), stomatal conductance (Gs), and water use efficiency (WUE) were determined using a photosynthesis analyzer (3051C, Plant Photolysis Meter, Chincan Trading Co., Hangzhou, China). In addition, the efficiency of photosystem II (PSII) was determined using a chlorophyll a fluorometer (Chlorophyll Fluorescence Analyzer, Yaxin-1162, Beijing Yaxin Li Science and Technology Co., Ltd., Beijing, China). For this, plants were assessed after dark adaptation, so measurements were taken one hour after sunset.

### *Biochemical compounds*

Leaves were collected 60 days after transplanting for determination of biochemical compounds. Samples were collected at noon, fully developed young leaves were collected on ice and stored at -20 °C for two days. They were then lyophilized and ground for biochemical analysis. Petals were collected for biochemical analysis 100 days after transplanting. Petals were collected at noon and when flowers were fully developed, placed on ice and stored at -20 °C for two days. They were then lyophilized and ground for biochemical analysis.

The contents of chlorophylls, β-carotene (Nagata and Yamashita, 1992), yellow carotenoids (β-carotene, β-cryptoxanthin, zeaxanthin) (Hornero-Méndez and Minguez-Mosquera, 2001), Vitamin C (Hung and Yen, 2002), phenolics (Yu and Dahlgren, 2000), and flavonoids (Arvouet-Grand *et al.*, 1994) were determined.

*Statistical analysis*

The experiment used a randomized complete block design with four replications per treatment and ten plants per experimental unit. The normality of the data was checked using the Shapiro-Wilks test. Analysis of variance and Fisher's least significant difference test ($p < 0.05$) were performed using InfoStat software (v2019).

## Results

Application of UV-A radiation to chrysanthemum seedlings promoted increased growth. In 'Polaris', an increase of 7% and 8% was observed in UV1 and UV3, compared to T0. However, in 'Codorniz', growth was reduced by 9% in UV3 compared to T0 (Figure 1A). Flower diameter increased by 6% in 'Polaris' in UV2, UV3 and UV4 treatments, while in 'Codorniz' no significant changes were recorded between treatments (Figure 1B). In stem diameter, there were no differences in any of the cultivars (Figure 1C). Fresh weight in 'Polaris' did not show changes compared to T0, but in 'Codorniz' it was reduced by 16% and 23% in UV1 and UV3 (Figure 1D). Also, the number of leaves was lower in 'Codorniz', in UV1, UV3 and UV4 (Figure 1E). Finally, vase life did not show significant variations between cultivars or vase life (Figure 1F).

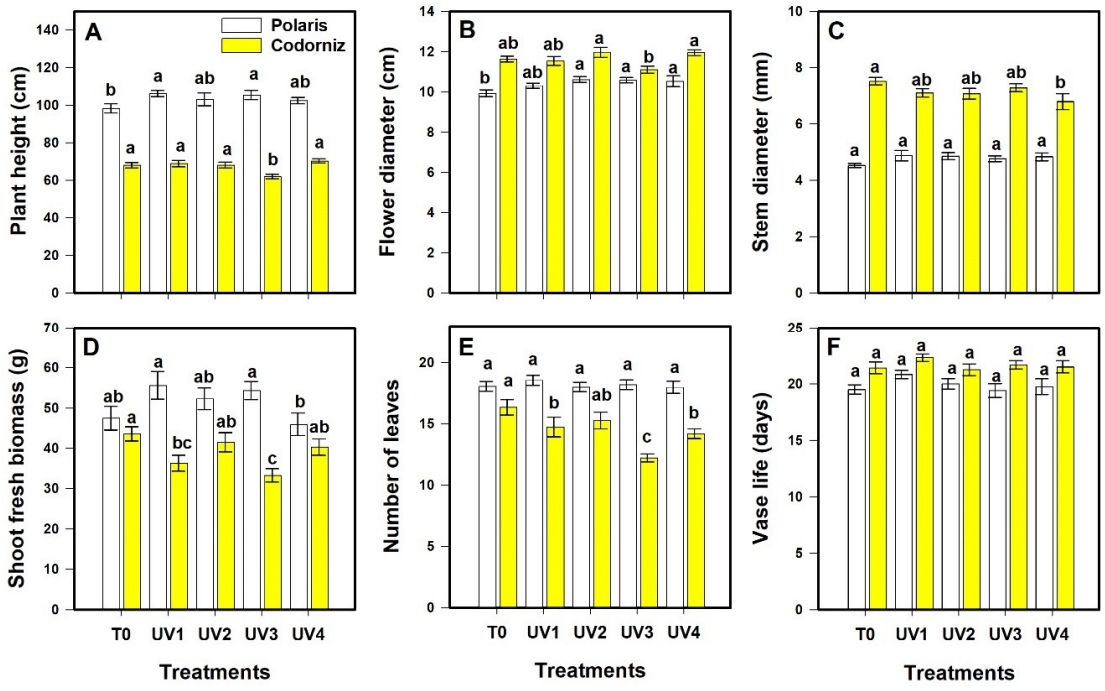


**Figure 1.** Effect of priming seedlings with UV-A radiation on the growth and development of 'Polaris' and 'Codorniz' chrysanthemum plants

T0: control; UV1, UV2, UV3 and UV4 are the treatments with 1, 2, 3 and 4 hours of UV-A irradiation respectively. n = 4 ± standard error. Different letters indicate significant differences between treatments according to the Fisher's least significant difference test ($p < 0.05$)

In the analysis of photochemical activity of photosystem II (PSII), seedling priming did not affect basal fluorescence in any of the evaluated varieties (Figure 2A). In 'Polaris', there were no changes in the reduction of QA, while in 'Codorniz' it showed a 10% increase under UV4 treatment (Figure 2B). Electron transfer from QA to QB did not present alterations in any cultivar (Figure 2C), and no differences were evident in maximum fluorescence (Figure 2D). The Fv/Fm index, which indicates the photochemical efficiency of PSII, increased under all UV conditions, registering an increase of 5% in 'Polaris' but without differences in 'Codorniz' (Figure 2E).

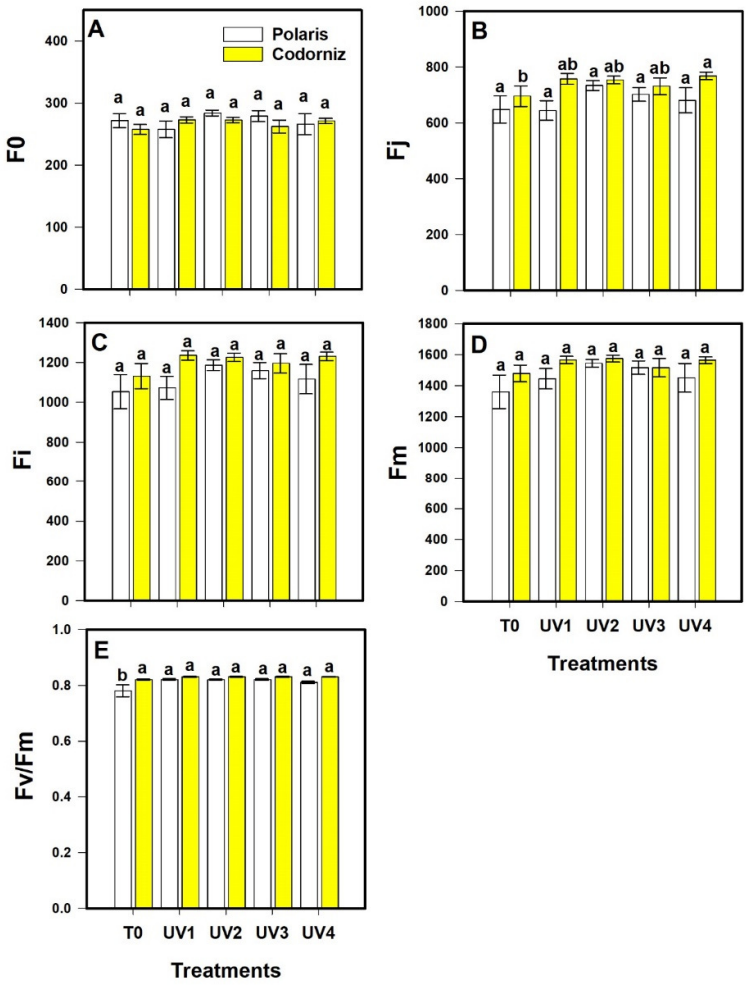


**Figure 2.** Effect of priming seedlings with UV-A radiation on chlorophyll a fluorescence of 'Polaris' and 'Codorniz' chrysanthemum plants

T0: control; UV1, UV2, UV3 and UV4 are the treatments with 1, 2, 3 and 4 hours of UV-A irradiation respectively. n = 4 ± standard error. Different letters indicate significant differences between treatments according to the Fisher's least significant difference test ($p < 0.05$)

Seedling priming significantly optimized photosynthesis in both cultivars; in 'Polaris' the UV4 and UV1 treatments were 38% and 29% higher, respectively, and in 'Codorniz' the UV2 and UV4 treatments were 20% and 19.5% higher, respectively; there were no differences in the other treatments (Figure 3A). Transpiration in 'Polaris' increased by 20.5% with the UV1 treatment, while in 'Codorniz' there were no differences compared to T0 (Figure 3B). The intracellular $CO_2$ concentration was reduced in both cultivars; in 'Polaris' the UV1 and UV2 treatments were -5% and -5.5% respectively, and in 'Codorniz', the UV2 treatment was -

6.2% (Figure 3C). Stomatal conductance in 'Polaris' increased by 16.4% and 15.1% with the UV1 and UV3 treatments. While in 'Codorniz' there was no change (Figure 3D). Regarding the efficient use of water (WUE), in 'Polaris', the UV4 treatment increased by 33%, and in 'Codorniz' the UV1 and UV2 treatments increased it by 19% and 22.7% respectively (Figure 3E).

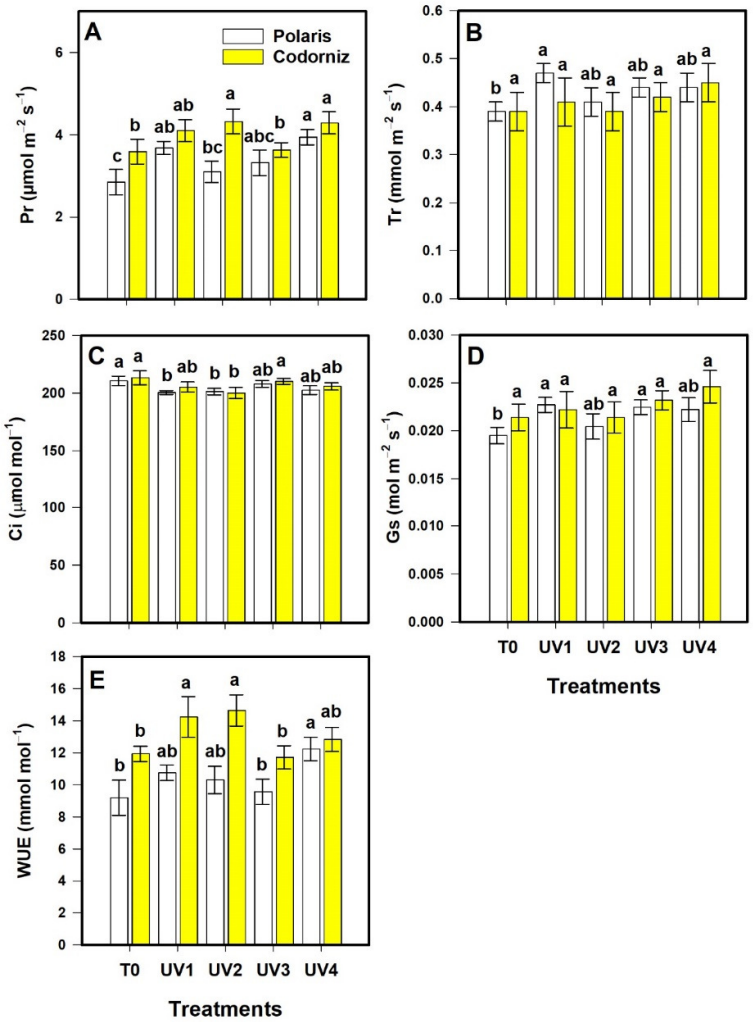


**Figure 3.** Effect of priming seedlings with UV-A radiation on the photosynthetic rate (Pr), transpiration (Tr), intracellular $CO_2$ concentration (Ci), stomatal conductance (Gs) and water use efficiency (WUE) of 'Polaris' and 'Codorniz' chrysanthemum plants

T0: control; UV1, UV2, UV3 and UV4 are the treatments with 1, 2, 3 and 4 hours of UV-A irradiation respectively. n = 4 ± standard error. Different letters indicate significant differences between treatments according to the Fisher's least significant difference test ($p < 0.05$)

UV-A radiation caused notable changes in some biochemical variables in the leaves of Chrysanthemum 'Polaris'. The phenol content did not show significant modifications (Figure 4A), while flavonoids decreased by 12% and 10% in the UV1, UV2, UV3, UV4 compared to T0 (Figure 4B). Vitamin C increased by 8% in UV4 treatment (Figure 4C), and β-carotene increased significantly in UV1 and UV3 treatments, with increases of 32% and 45% respectively compared to T0 (Figure 4D). In addition, UV-A altered the pigments, highlighting UV3 with an increase in chlorophylls a and b of 60% and 50% and total by 56%, the other treatments had lower values, but higher than T0 (Figure 4E). In the 'Codorniz', phenol content was reduced

by 30% with UV3 treatment compared to T0 (Figure 4F), while flavonoids did not show significant changes (Figure 4G). Vitamin C content decreased by 5.4% and 7.4% in UV2 and UV4 treatments, relative to T0 (Figure 4H). β-carotene was reduced in all irradiated treatments, with UV3 and UV4 treatments standing out with decreases of 44% and 39% (Figure 4I). UV-A did not induce modifications in leaf chlorophylls (Figure 4J).

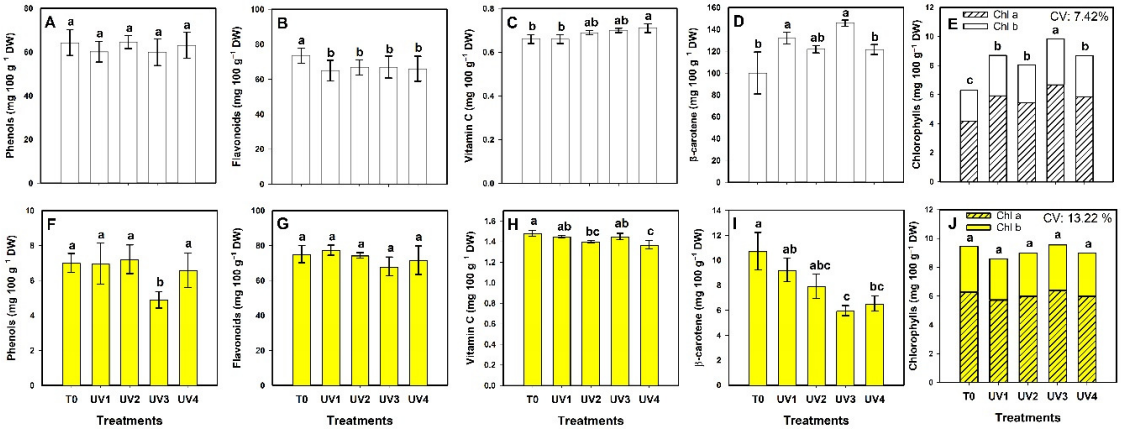


**Figure 4.** Effect of priming seedlings with UV-A radiation on the antioxidants and chlorophylls on leaves of 'Polaris' (A-E) and 'Codorniz' (F-J) chrysanthemum plants

T0: control; UV1, UV2, UV3 and UV4 are the treatments with 1, 2, 3 and 4 hours of UV-A irradiation respectively. CV: coefficient of variation. n = 4 ± standard error. Different letters indicate significant differences between treatments according to the Fisher's least significant difference test at $p < 0.05$

Seedling priming modified flower quality attributes of chrysanthemum 'Polaris'. Phenol content in chrysanthemum petals was improved by UV3 and UV4 treatments by 12% and 15% relative to T0 (Figure 5A). While flavonoids increased by UV1 and UV2 treatments by 12% relative to T0 (Figure 5B). In contrast, in β-carotene content no differences were detected between treatments (Figure 5C). In chrysanthemum 'Codorniz', the amount of phenols in petals decreased by 13% with the UV1 treatment, while the other treatments showed no significant difference compared to T0 (Figure 5D). While in flavonoid content no modifications were observed in any of the treatment conditions (Figure 5E). In contrast, petal yellow pigments increased with UV2 treatment, and decreased in UV4, however were not different from T0 (Figure 5F).

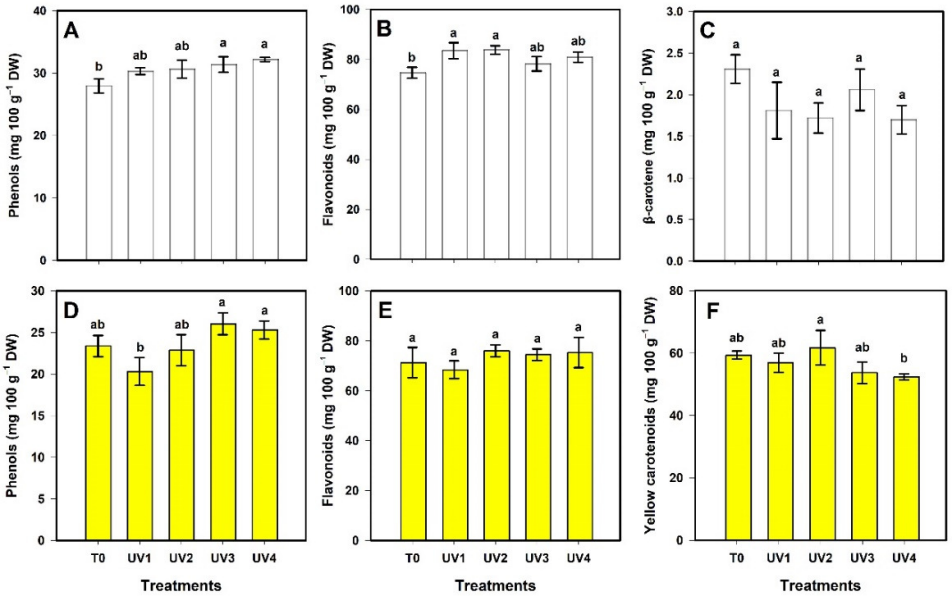


**Figure 5.** Effect of priming seedlings with UV-A radiation on the antioxidants and carotenoids on flowers of 'Polaris' chrysanthemum plants.

T0: control; UV1, UV2, UV3 and UV4 are the treatments with 1, 2, 3 and 4 hours of UV-A irradiation respectively. n = 4 ± standard error. Different letters indicate significant differences between treatments according to the Fisher's least significant difference test ($p < 0.05$).

## Discussion

*Impact of UV-A seedling priming on growth and development*

Photomorphogenic responses to UV-A radiation are mediated by photoreceptors such as cryptochromes and phototropins, and recent evidence indicates that UVR8 may also play an important role in the perception of UV-A radiation, in addition to UV-B, either acting independently or in conjunction with cryptochromes through various interactions to regulate gene expression (Rai *et al.*, 2020). Therefore, some morphological parameters of chrysanthemum plants could be modified by priming seedlings. In addition, UV radiation is also relevant in triggering various stress responses and can be used as a stressor in plants to induce prolonged acclimation (Loconsole and Santamaria, 2021; Jansen *et al.*, 2022). High doses of UV-A activate the production of abscisic acid (ABA), salicylic acid (SA) and jasmonic acid (JA), which are mainly involved in stress responses and growth inhibition, as a symptom of toxicity (Mannucci *et al.*, 2020). While low doses are likely to induce hormone synthesis, such as the induction of auxin synthesis, which is involved in the blue light signaling pathway (Esmon *et al.*, 2006). UV-A radiation shares mechanisms with blue light, as both wavelengths are detected by photoreceptors such as phototropins, cryptochromes (cry1 and cry2), and Zeitlupe proteins (ZTL) (Christie *et al.*, 2015). Recent evidence confirms that the UVR8 photoreceptor may play an important role in both UV-A (315-350 nm) and UV-B detection, activating gene expression in coordination with cryptochromes (Rai *et al.*, 2020). Previously, it was speculated that the action spectrum of HY5 (HYPOCOTYL 5 ELONGATED) was related to UVR8, since transcript accumulation levels were detected at 310 nm in leaves of *Arabidopsis thaliana* (Brown *et al.*, 2009). Some key elements in light signaling, such as PIFs and HY5, link light signaling to hormonal pathways such as ethylene, gibberellin (GA), and cytokinin (CK) (Liu *et al.*, 2017). This could be demonstrated by the results obtained in 'Polaris', which showed improvements in morphology (Figure 1). In contrast, 'Codorniz' showed no relevant changes, with a reduction in agronomic parameters, possibly due to the exposure time to UV3 (Figure 1). UV-A (370 nm) increased

tomato growth by adapting its morphology to capture more light (Zhang *et al.*, 2020). Song *et al.* (2023) indicate that UV-A radiation (397 nm) was not beneficial for biomass accumulation in Chrysanthemum morifolium. On the other hand, in sweet basil (*Ocimum basilicum* L.), a low dose of UV-A (385 nm at 10 W $m^{-2}$) resulted in increased biomass production and phenolic content without reducing photosynthetic capacity (Fv/Fm) (Kang *et al.*, 2022).

UV radiation can have diverse effects, both beneficial and detrimental, on plant growth and development, depending on the genotype (Yadav *et al.*, 2020), as seen in the two cultivars in Figure 1. This has also been demonstrated in Arabidopsis, with stimulatory effects on growth (Biswas and Jansen, 2012), as well as in species of commercial interest. For example, UV-A light (315-400 nm) regulated the growth of cucumber, where a supplement of 3.6 W $m^{-2}$ resulted in shorter and more robust plants, positive traits from a horticultural perspective, without affecting yield (Qian *et al.*, 2020). Supplemental UV-A (315–400 nm) doses of 71.67 kJ $m^2$ $d^{-1}$ reduced stem height in pepper (*Capsicum annuum* cv. California Wonder), although it did not affect the architecture of eggplant (*Solanum melongena* cv. Black Beauty) (Dáder *et al.*, 2014). However, how plant architecture is modified by UV-A radiation and the precise effects on plant growth are not fully understood (Zhang *et al.*, 2020).

*Impact of UV-A seedling priming on physiological processes*

Seedling priming with UV-A radiation can improve photosynthetic rate by enhancing the ability to capture light and convert it into chemical energy, thus optimizing its physiological performance against stress (Štroch *et al.*, 2015; Jansen *et al.*, 2022). Stimulation of photoreceptors such as UVR8, cryptochromes and phototropins by UV-A radiation these photoreceptors could also influence the enhancement of PSII and photoprotective activities (Brelsford *et al.*, 2019). With regard to fluorescence, the Fv/Fm ratio is a key indicator of the photochemical efficiency of photosystem II and its relationship to stress (Gartia *et al.*, 2003). In the results obtained, the improvement of the Fv/Fm ratio in 'Polaris' (Figure 2E). It suggests a higher efficiency in photosynthetic capacity, indicating that the seedlings responded favorably to priming with UV-A. Furthermore, the fact that there is no significant difference in the Fv/Fm index between treatments indicates that the plants were not subjected to photoinhibitory stress, which means that UV-A exposure was not harmful but beneficial in terms of photosynthetic efficiency under the conditions studied. UV-A (397 nm) caused a reduction in the activity of the PSI reaction center in leaves of *S. floribundum* and *C. morifolium*, but the maximum photochemical efficiency of the PSII reaction center showed no significant difference between the light treatments. This suggests that the PSI reaction center of *S. floribundum* and *C. morifolium* leaves is more sensitive to UV radiation than the PSII reaction center (Song *et al.*, 2023). In contrast, there are species that tend to recover from light stress after UV stress; *Silene littorea* did not show symptoms of chronic photoinhibition, as its Fv/Fm values after photoinactivation were within the range of healthy plants (0.74–0.85) (Del Valle *et al.*, 2020).

*Impact of UV-A seedling priming on photosynthetic pigments*

Very little is known about UV-induced production of metabolites such as carotenoids (Badmus *et al.*, 2022). Interestingly, β-carotenes increased in leaves of 'Polaris' (Figure 4D), but decreased in a time-dependent manner in 'Codorniz' (Figure 4I). The physiological processes involving carotenoids are photoprotection of the photosynthetic machinery (Biswas and Jansen, 2012). Prolonged exposure to intense light increases the ratio of carotenoids to chlorophyll, reflecting an increased need for protection. However, it has been suggested that UV-induced changes in carotenoids are not only aimed at protecting against UV radiation, but also at protecting the plant from other stressors, such as high irradiance and high light intensity (Inostroza-blancheteau *et al.*, 2014; Badmus *et al.*, 2022). On the other hand, photosynthetic pigments increased in 'Polaris' (Figure 4E), but did not show significant changes in 'Codorniz' (Figure 4J). UV-A exposure improves plant growth by increasing photosynthetic efficiency, probably due to the increase in photosynthetic pigment content (Verdaguer *et al.*, 2017). Previous studies have shown that UV-A increases chlorophyll content in

species such as lettuce (Chen *et al.*, 2019) and radish (Tohidi-moghadam *et al.*, 2012). Lee *et al.* (2019) suggest that the most positive responses in kale are due to 385 nm wavelength, compared to 370 nm, in inducing improvements in growth parameters. In some species, increased biomass accumulation in response to UV-A radiation associated with increased leaf chlorophyll content and enhanced photosynthetic activity.

*Impact of UV-A seedling priming on the antioxidant system*

UV induces the generation of reactive oxygen species (ROS), mainly in chloroplasts, mitochondria and peroxisomes, causing oxidative damage to lipids, proteins and DNA. To prevent damage, cells activate their antioxidant system (Tan *et al.*, 2023). In addition, UV regulates genes responsible for activating secondary metabolism by producing various organic compounds (alkaloids, terpenoids, flavonoids, phenols, among others). These compounds counteract the negative effects of UV stress (Neugart and Schreiner, 2018; Salam *et al.*, 2023; Thakur *et al.*, 2023). Low UV doses reset the antioxidant system and activate pathways such as glutathione, phenylpropanoids, cinnamates, flavonoids and pyridoxine synthesis. This highlights the role of UV radiation as a signaling agent by activating specific signal transduction pathways in plant cells (Wargent, 2016), and affecting plant metabolism and development (Czégény *et al.*, 2016). These enzymes help neutralize ROS and protect plant cells from oxidative damage (Köhler *et al.*, 2017). This study revealed an increase in flavonoid and phenolic compounds in chrysanthemum petals, which may contribute to the aroma and color of the flowers, making them more attractive for marketing (Figure 5). Mariz-Ponte *et al.* (2018) irradiated tomato plants with UV-A radiation (368 nm) for 1 hour per day at a dose of 0.8 J $m^{-2}$. They observed that the antioxidant pathways SOD, CAT, APX and GPX were not increased. Their results suggest that the main antioxidant pathways protecting against UV radiation involve phenylpropanoid compounds by increasing their biosynthesis. This hypothesis was confirmed by the increase in phenolic compounds and the regulation of the *chs* and *fls* genes, which encode the CHS and FLS enzymes. On the other hand, it is possible to control the production of secondary metabolites and plant yield by manipulating the UV radiation dose. Plants are grown under ideal conditions to a certain stage of development and then exposed to UV radiation to induce the desired compounds. This minimizes negative effects on their morphology (Lima *et al.*, 2023). Flavonoid content in C. morifolium gradually increased during the flowering and then decreased (Wang *et al.*, 2014). Doan *et al.* (2024) quantified phenolic compounds in leaves and flowers of different cultivars of *C. morifolium* and found that 3 out of 6 cultivars contained high levels of phenolic compounds and exhibited strong antioxidant capacities.

## Conclusions

The application of UV-A irradiation to chrysanthemum seedlings is a promising strategy for influencing growth, photosynthesis and flower quality. Its effectiveness varies among cultivars, suggesting the need for specific adjustments in the timing of UV-A irradiation according to the characteristics of each cultivar. In general, seedling priming with UV-A can improve physiological performance without causing significant plant stress, making it a useful tool in floricultural production to improve both plant development and the aesthetic and aromatic quality of flowers.

## Authors' Contributions

Conceptualization: A.J.-M. and A.B.-M.; Methodology: D.I.E.-H. and Y.G.-G.; Project administration and Supervision: E.O.-S., A.B.-M. and A.J.-M.; Writing - original draft: D.I.E.-H. and Y.G.-G. All authors read and approved the final manuscript.

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## Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

## References

Ahmad M, Grancher N, Heil M, Black RC, Giovani B, Galland P, Lardemer D (2002). Action spectrum for cryptochrome-dependent hypocotyl growth inhibition in *Arabidopsis*. Plant Physiology 129(2):774-785. https://doi.org/10.1104/pp.010969

Arvouet-Grand A, Vennat B, Pourrat A, Legret P (1994). Standardization of a propolis extract and identification of the main constituents. Journal de Pharmacie de Belgique 49(6):462-468.

Badmus UO, Crestani G, Cunningham N, Havaux M, Urban O, Jansen MAK (2022). UV radiation induces specific changes in the carotenoid profile of *Arabidopsis thaliana*. Biomolecules 12:1879. https://doi.org/10.3390/biom12121879

Biswas DK, Jansen MAK (2012). Natural variation in UV-B protection amongst *Arabidopsis thaliana* accessions. Emirates Journal of Food and Agriculture 24(6):621-631. https://doi.org/10.9755/ejfa.v24i6.14681

Bornman JF, Barnes PW, Robson TM, Robinson SA, Jansen MAK, Ballare CL, Flint SD (2019). Linkages between stratospheric ozone, UV radiation and climate change and their implications for terrestrial ecosystems. Photochemical & Photobiological Sciences 18:681-716. https://doi.org/10.1039/C8PP90061B

Brazaitytė A, Viršilė A, Samuolienė G, Vaštakaitė-Kairienė V, Jankauskienė J, Miliauskienė J, ... Duchovskis P (2019). Response of mustard microgreens to different wavelengths and durations of UV-A LEDs. Frontiers in Plant Science 10:1-14. https://doi.org/10.3389/fpls.2019.01153

Brelsford CC, Morales LO, Nezval J, Kotilainen TK, Hartikainen SM, Aphalo PJ, Robson TM (2019). Do UV-A radiation and blue light during growth prime leaves to cope with acute high light in photoreceptor mutants of *Arabidopsis thaliana*? Physiologia Plantarum 165:537-554. https://doi.org/10.1111/ppl.12749

Brown BA, Headland LR, Jenkins GI (2009). UV-B action spectrum for UVR8-mediated HY5 transcript accumulation in *Arabidopsis*. Photochemistry and Photobiology 85:1147-1155. https://doi.org/10.1111/j.1751-1097.2009.00579.x

Chen Y, Li T, Yang Q, Zhang Y, Zou J, Bian Z, Wen X (2019). UVA radiation is beneficial for yield and quality of indoor cultivated lettuce. Frontiers in Plant Science 10:1-10. https://doi.org/10.3389/fpls.2019.01563

Christie JM, Blackwood L, Petersen J, Sullivan S (2015). Plant flavoprotein photoreceptors. Plant Cell Physiology 56:401-413. https://doi.org/10.1093/pcp/pcu196

Christie JM, Briggs WR (2001). Blue light sensing in higher plants. Journal of Biological Chemistry 276:11457-11460. https://doi.org/10.1074/jbc.R100004200

Czégény G, Mátai A, Hideg É (2016). UV-B effects on leaves: oxidative stress and acclimation in controlled environments. Plant Science 248:57-63. https://doi.org/10.1016/j.plantsci.2016.04.013

Dáder B, Gwynn-Jones D, Moreno A, Winters A, Fereres A (2014). Impact of UV-A radiation on the performance of aphids and whiteflies and on the leaf chemistry of their host plants. Journal of Photochemistry and Photobiology B: Biology 138:307-316. https://doi.org/10.1016/j.jphotobiol.2014.06.009

Del Valle JC, Buide ML, Whittall JB, Valladares F, Narbona E (2020). UV radiation increases phenolic compound protection but decreases reproduction in *Silene littorea*. PLoS One 15(6):e0231611. https://doi.org/10.1371/journal.pone.0231611

Doan TTM, Tran GH, Nguyen TK, Lim JH, Lee S (2024). Antioxidant activity of different cultivars of *Chrysanthemum morifolium* and quantitative analysis of phenolic compounds by HPLC/UV. Applied Biological Chemistry 67:17. https://doi.org/10.1186/s13765-024-00875-w

Escobar-Bravo R, Nederpel C, Naranjo S, Kim HK, Rodríguez-López MJ, Chen G, ... Klinkhamer PGL (2021). Ultraviolet radiation modulates both constitutive and inducible plant defenses against thrips but is dose and plant genotype dependent. Journal of Pest Science 94:69-81. *https://doi.org/10.1007/s10340-019-01166-w*

Esmon CA, Tinsley AG, Ljung K, Sandberg G, Hearne LB, Liscum E (2006). A gradient of auxin and auxin-dependent transcription precedes tropic growth responses. Proceedings of the National Academy of Sciences of the United States of America 103:236-241. *https://doi.org/10.1073/pnas.0507127103*

Foroughbakhch PR, Bacópulos ME, Benavides MA, Salas CL, Ngangyo HM (2019). Ultraviolet radiation effect on seed germination and seedling growth of common species from northeastern Mexico. Agronomy 9(6):269. *https://doi.org/10.3390/agronomy9060269*

Gartia S, Pradhan MK, Joshi PN, Biswal UC, Biswal B (2003). UV-A irradiation guards the photosynthetic apparatus against UV-B-induced damage. Photosynthetica 41:545-549. *https://doi.org/10.1023/B:PHOT.0000027518.95032.c1*

Hadizadeh H, Samiei L, Shakeri A (2022). Chrysanthemum, an ornamental genus with considerable medicinal value: A comprehensive review. South African Journal of Botany 144:23-43. *https://doi.org/10.1016/j.sajb.2021.09.007*

Hamid N, Jawaid F (2011). Influence of seed pre-treatment by UV-A and UV-C radiation on germination and growth of mung beans. Pakistan Journal of Chemistry 1(4):164-167. *https://chempublishers.com/pjc/wp-content/uploads/sites/2/2024/10/186_1.pdf*

Heijde M, Ulm R (2012). UV-B photoreceptor-mediated signalling in plants. Trends in Plant Science 17:230-237. *https://doi.org/10.1016/j.tplants.2012.01.007*

Hornero MD, Minguez MMI (2001). Rapid spectrophotometric determination of red and yellow isochromic carotenoid fractions in paprika and red pepper oleoresins. Journal of Agricultural and Food Chemistry 49(8):3584-3588. *https://doi.org/10.1021/jf010400l*

Hung CY, Yen GC (2002). Antioxidant activity of phenolic compounds isolated from *Mesona procumbens* Hemsl. Journal of Agricultural and Food Chemistry 50(10):2993-2997. *https://doi.org/10.1021/jf011454y*

Inostroza BC, Reyes DM, Arellano A, Latsague M, Acevedo P, Loyola R, ... Alberdi M (2014). Effects of UV-B radiation on anatomical characteristics, phenolic compounds and gene expression of the phenylpropanoid pathway in highbush blueberry leaves. Plant Physiology and Biochemistry 85:85-95. *https://doi.org/10.1016/j.plaphy.2014.10.015*

Jansen MAK, Ač A, Klem K, Urban O (2022). A meta-analysis of the interactive effects of UV and drought on plants. Plant, Cell & Environment 45:41-54. *https://doi.org/10.1111/pce.14221*

Kang S, Kim JE, Zhen S, Kim J (2022). Mild-intensity UV-A radiation applied over a long duration can improve the growth and phenolic contents of sweet basil. Frontiers in Plant Science 13:858433. *https://doi.org/10.3389/fpls.2022.858433*

Köhler H, Contreras RA, Pizarro M, Cortés-Antíquera R, Zúñiga GE (2017). Antioxidant responses induced by UV-B radiation in *Deschampsia antarctica* Desv. Frontiers in Plant Science 8:921. *https://doi.org/10.3389/fpls.2017.00921*

Lee JH, Oh MM, Son KH (2019). Short-term ultraviolet (UV)-A light-emitting diode (LED) radiation improves biomass and bioactive compounds of kale. Frontiers in Plant Science 10:1042. *https://doi.org/10.3389/fpls.2019.01042*

Lima IHA, Rodrigues AA, Resende EC, da Silva FB, Farnese FS, Silva LJ, ... Silva FG (2023). Light means power: harnessing light spectrum and UV-B to enhance photosynthesis and rutin levels in microtomato plants. Frontiers in Plant Science 14:1261174. *https://doi.org/10.3389/fpls.2023.1261174*

Liu X, Li Y, Zhong S (2017). Interplay between light and plant hormones in the control of *Arabidopsis* seedling chlorophyll biosynthesis. Frontiers in Plant Science 8:1433. *https://doi.org/10.3389/fpls.2017.01433*

Loconsole D, Santamaria P (2021). UV lighting in horticulture: A sustainable tool for improving production quality and food safety. Horticulturae 7(1):9. *https://doi.org/10.3390/horticulturae7010009*

Mannucci A, Mariotti L, Castagna A, Santin M, Trivellini A, Reyes TH, ... Quartacci MF (2020). Hormone profile changes occur in roots and leaves of Micro-Tom tomato plants when exposing the aerial part to low doses of UV-B radiation. Plant Physiology and Biochemistry 148:291-301. *https://doi.org/10.1016/j.plaphy.2020.01.030*

Mariz-Ponte N, Mendes RJ, Sario S, Ferreira de Oliveira JMP, Melo P, Santos C (2018). Tomato plants use non-enzymatic antioxidant pathways to cope with moderate UV-A/B irradiation: A contribution to the use of UV-A/B in horticulture. Journal of Plant Physiology 221:32-42. *https://doi.org/10.1016/j.jplph.2017.11.013*

Mohiuddin M (2016). Flower business flourish floriculture: A study on Bangladesh. International Journal of Business Management and Invention 5(10):9-13.

Nagata M, Yamashita I (1992). Simple method for simultaneous determination of chlorophyll and carotenoids in tomato fruit. Nippon Shokuhin Kagaku Kogyo Gakkaishi 39(10):925-928. *https://doi.org/10.3136/nskkk1962.39.925*

Neugart S, Schreiner M (2018). UVB and UVA as eustressors in horticultural and agricultural crops. Scientia Horticulturae 234:370-381. *https://doi.org/10.1016/j.scienta.2018.02.021*

Nissim-Levi A, Kitron M, Nishri Y, Ovadia R, Forer I, Oren-Shamir M (2019). Effects of blue and red LED lights on growth and flowering of *Chrysanthemum morifolium*. Scientia Horticulturae 254:77-83. *https://doi.org/10.1016/j.scienta.2019.04.080*

Observatory of Economic Complexity (2022). Chrysanthemums. OEC World. Retrieved 2024 October *https://oec.world/es/profile/hs/chrysanthemums*

Poonia A, Pandey S, Vasundhara (2022). Application of light emitting diodes (LEDs) for food preservation, post-harvest losses and production of bioactive compounds: A review. Food Production, Processing and Nutrition 4:8. *https://doi.org/10.1186/s43014-022-00086-0*

Qian M, Rosenqvist E, Flygare AM, Kalbina I, Teng Y, Jansen MAK, Strid Å (2020). UV-A light induces a robust and dwarfed phenotype in cucumber plants (*Cucumis sativus* L.) without affecting fruit yield. Scientia Horticulturae 263:109110. *https://doi.org/10.1016/j.scienta.2019.109110*

Rai N, O'Hara A, Farkas D, Safronov O, Ratanasopa K, Wang F, ... Morales LO (2020). The photoreceptor UVR8 mediates the perception of both UV-B and UV-A wavelengths up to 350 nm of sunlight with responsivity moderated by cryptochromes. Plant, Cell & Environment 43(6):1513-1527. *https://doi.org/10.1111/pce.13752*

Reddy PP (2016). Protected Cultivation. In: Sustainable Crop Protection under Protected Cultivation. *https://doi.org/10.1007/978-981-287-952-3_1*

Salam U, Ullah S, Tang ZH, Elateeq AA, Khan Y, Khan J, ... Ali S (2023). Plant metabolomics: An overview of the role of primary and secondary metabolites against different environmental stress factors. Life 13(3):706. *https://doi.org/10.3390/life13030706*

Shinomura T, Nagatani A, Hanzawa H, Kubota M, Watanabe M, Furuya M (1996). Action spectra for phytochrome A- and B-specific photoinduction of seed germination in *Arabidopsis thaliana.* Plant Biology 93(15):8129-8133. *https://doi.org/10.1073/pnas.93.15.8129*

SIAP (2021). Anuario Estadístico de la Producción Agrícola. Servicio de Información Agroalimentaria y Pesquera. Retrieved 2024 October 12 *https://nube.siap.gob.mx/cierreagricola/*

Song Y, Liu W, Wang Z, He S, Jia W, Shen Y, ... Shang W (2023). Effect of different monochromatic LEDs on the environmental adaptability of *Spathiphyllum floribundum and Chrysanthemum morifolium.* Plants 12(16):2964. *https://doi.org/10.3390/plants12162964*

Sonjaroon W, Tepkaew T, Kupia M, Tongkok P, Boonkorkaew P, Thussagunpanit J (2024). Pre-harvest UV-A supplementation in plant factory with artificial lighting improves growth, photosynthesis, and phytonutrients in kale. Horticulturae 10(7):701. *https://doi.org/10.3390/horticulturae10070701*

Steiner AA (1961). A universal method for preparing nutrient solutions of a certain desired composition. Plant Soil 15:134-154. *https://doi.org/10.1007/BF01347224*

Štroch M, Materová Z, Vrábl D, Karlický V, Šigut L, Nezval J, Špunda V (2015). Protective effect of UV-A radiation during acclimation of the photosynthetic apparatus to UV-B treatment. Plant Physiology and Biochemistry 96:90-96. *https://doi.org/10.1016/j.plaphy.2015.07.017*

Tan Y, Duan Y, Chi Q, Wang R, Yin Y, Cui D, ... Sun H (2023). The role of reactive oxygen species in plant response to radiation. International Journal of Molecular Sciences 24(4):3346. *https://doi.org/10.3390/ijms24043346*

Thakur K, Kumari C, Zadokar A, Sharma P, Sharma R (2023). Physiological and omics-based insights for underpinning the molecular regulation of secondary metabolite production in medicinal plants: UV stress resilience. Plant Physiology and Biochemistry 204:108060. *https://doi.org/10.1016/j.plaphy.2023.108060*

Tohidi-Moghadam HR, Ghooshchi F, Jamshidpour F, Zahedi H (2012). Effect of UV radiation and elevated $CO_2$ on physiological attributes of canola (*Brassica napus* L.) grown under water deficit stress. Polish Journal of Environmental Studies 21(5):1417-1427. *https://www.pjoes.com/pdf-88886-22745?filename=22745.pdf*

Trivellini A, Toscano S, Romano D, Ferrante A (2023). LED lighting to produce high-quality ornamental plants. Plants 12(8):1667. *https://doi.org/10.3390/plants12081667*

Trolinger JC, McGovern RJ, Elmer WH, Rechcigl NA, Shoemaker CM (2017). Diseases of *Chrysanthemum*. In: McGovern, R., Elmer, W. (eds) Handbook of Florists' Crops Diseases. Handbook of Plant Disease Management. Springer, Cham. *https://doi.org/10.1007/978-3-319-32374-9_16-1*

Vandenbussche F, Tilbrook K, Fierro AC, Marchal K, Poelman D, Van Der Straeten D, Ulm R (2014). Photoreceptor-mediated bending towards UV-B in *Arabidopsis*. Molecular Plant 7(6):1041–1052. *https://doi.org/10.1093/mp/ssu039*

Verdaguer D, Jansen MAK, Llorens L, Morales LO, Neugart S (2017). UV-A radiation effects on higher plants: Exploring the known unknown. Plant Science 255:72-81. *https://doi.org/10.1016/j.plantsci.2016.11.014*

Wang S, Hao LJ, Zhu JJ, Zhang QW, Wang ZM, Zhang X, Song XM (2014). Study on the effects of sulfur fumigation on chemical constituents and antioxidant activity of *Chrysanthemum morifolium* cv. Hang-ju. Phytomedicine 21(5):773-779. *https://doi.org/10.1016/j.phymed.2013.10.019*

Wargent JJ (2016). UV LEDs in horticulture: From biology to application. Acta Horticulturae 1134:25-32. *https://doi.org/10.17660/ActaHortic.2016.1134.4*

Yadav A, Singh D, Lingwan M, Yadukrishnan P, Masakapalli SK, Datta S (2020). Light signaling and UV-B-mediated plant growth regulation. Journal of Integrative Plant Biology 62(9):1270-1292. *https://doi.org/10.1111/jipb.12932*

Yang Y, Yang X, Jang Z, Chen Z, Ruo X, Jin W, ... Xu M (2018). UV RESISTANCE LOCUS 8 from *Chrysanthemum morifolium* Ramat (CmUVR8) plays important roles in UV-B signal transduction and UV-B-induced accumulation of flavonoids. Frontiers in Plant Science 9:955. *https://doi.org/10.3389/fpls.2018.00955*

Yu Z, Dahlgren RA (2000). Evaluation of methods for measuring polyphenols in conifer foliage. Journal of Chemical Ecology 26:2119-2140. *https://doi.org/10.1023/A:1005568416040*

Zhang Y, Kaiser E, Zhang Y, Zou J, Bian Z, Yang Q, Li T (2020). UVA radiation promotes tomato growth through morphological adaptation leading to increased light interception. Environmental and Experimental Botany 176:104073. *https://doi.org/10.1016/j.envexpbot.2020.104073*

Zoratti L, Karppinen K, Escobar AL, Häggman H, Jaakola L (2014). Light-controlled flavonoid biosynthesis in fruits. Frontiers in Plant Science 5:534. *https://doi.org/10.3389/fpls.2014.00534*