Effects of Melatonin and AVG on Plant Growth of Three *Pilea* Species in Darkness

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Ornamental foliage plants are valued for their catchy leaves with diverse shapes and colors, but dark-induced plant senescence or deterioration during transport greatly limits the quality of foliage plants. Melatonin is an important signaling molecule that affects pleiotropic developmental progress in plants. Aminoethoxyvinylglycine (AVG) is a potent inhibitor of ethylene biosynthesis and is extensively used to delay plant senescence and fruit ripening. In this study, we compared the effects of melatonin and AVG on alleviating plant deterioration of three *Pilea* species (*P. cadierei* (PC), *P. involucrata* (PI), and *P. mollis* (PM)) through foliar sprays of different concentrations of melatonin or AVG prior to darkness treatment. Our results showed that PC, PI, and PM exhibited distinct responses to melatonin or AVG. PM was the most sensitive species and it exhibited significant increases in stem height, leaf area, chlorophyll, and anthocyanin content in response to 50, 100, and 150 μmol·L⁻¹ of melatonin; similar responses to 150 and 200 μmol·L⁻¹ of melatonin were observed in PI with regard to these plant characteristics. By contrast, much weaker effects of AVG on these plant characteristics were observed in PM and PI, although it increased their Fv/Fm values as did melatonin. Unlike PM and PI, PC is generally not responsive to all melatonin and AVG treatments, although AVG treatments did change its stem elongation. These results may provide growers with science-based information for future practical application of melatonin to improve the post-harvest quality of ornamental plants.

**Key Words:** anthocyanin content, chlorophyll content, dark stress, foliage plants, Fv/Fm.

Introduction

Foliage and evergreen plants are increasingly gaining popularity among consumers due to their striking colors, attractive shapes and the textures of their leaves; they have been extensively used for interior decoration as potted and hanging basket plants. In addition, potted foliage plants have recently been used as phytoremediators to purify indoor air pollution (Irga et al., 2018), and have been recognized as a natural therapy due to their beneficial effects on human health (Song et al., 2016). The wholesale value of foliage plant production in the USA reached $653 million in 2018, and Florida continues to dominate this category, providing 63% of the foliage products for the whole country (USDA, 2019). However, long-distance transportation of these foliage products in closed cargoes across the whole country from the southern tip of the USA is challenging and generally results in plant deterioration and economic loss.

The marketability and supply chain of foliage plants is frequently limited by deteriorating plant quality during transport and retail display (Macnish et al., 2011), during which plants experience a long-period of dark-induced stress. Dark or low light conditions can promote chlorophyll degradation and result in leaf yellowing, premature leaf senescence and abscission, which may substantially affect the aesthetic values of these plants (Ferrante et al., 2015). Currently, it is not practical to equip shipment cargos with light settings, and no other effective measure has been taken to minimize dark-induced plant deterioration; as a result, a
potted foliage plants under dark conditions during long-distance transport.

**Materials and Methods**

**Plant materials and treatments**

Three foliage plant species, *P. mollis* (‘Moon Valley’ (PM)), *P. involucrata* (‘Dark Mystery’ (PI)), and *P. cadieri* (PC) were kindly supplied by Costa Farms (Apopka, FL, USA). All plants were propagated in September 2018 in a greenhouse in Apopka, Florida, United States. One-month-old plants of similar sizes in 4-inch pots were used for this study to minimize the effects of distinct development stages. Each species was treated with four different concentrations (50, 100, 150, and 200 μmol·L⁻¹, distilled water for control) of MEL (Sigma-aldrich, Corp., St. Louis, MO, USA) and AVG (Valent Bio Sciences, LLC, Chicago, IL, USA). Twelve plants were used for each treatment. Whole potted plants were watered well. About 50 mL MEL or AVG solution (or distilled water as control) per plant was exogenously sprayed on both abaxial and adaxial sides of leaves until the leaf surface formed water films and did not drain. After three hours of drying, potted plants for each treatment were randomly assigned to a position in a tray and the whole tray was put into a package box inside a tent (48”×48”×78”; iPOWER, Irwindale, CA, USA) to achieve complete darkness at constant room temperature (22°C). Two additional controls were also included in this experiment. One group of plants was sprayed with distilled water and grown in an artificial environmental room at 22°C with a 14 h light/10 h dark photoperiod (550 μM·m⁻²·s⁻¹) and relative humidity of 60%–70%; this treatment was considered as a light control (0L). The other group of plants treated with distilled water were grown in complete darkness under conditions that were the same as all other treatments; this treatment was considered as a dark control (0D). After 14 days of treatments, the plants were used for various measurements with a minimum of three replications.

**Measurement of chlorophyll fluorescence**

The chlorophyll fluorescence parameters were measured using LICOR-6800 (LI-COR Inc., Lincoln, NE, USA). Nine mature leaves for each treatment were randomly selected for this measurement. A measuring beam (0.5 μmol·m⁻²·s⁻¹) was first used to determine the minimum fluorescence (F₀), and a saturation pulse (8000 μmol·m⁻²·s⁻¹) with a duration of 1000 ms was used to measure the maximum fluorescence (Fm), and the Fv/Fm ratio was calculated for comparison among treatments.

**Measurement of leaf area, stem height, and dry mass**

Ten mature leaves at the third node of each stem were selected from each treatment to determine the leaf area using a LiCOR-3100 area meter (Li-COR Inc.).
Stem heights of 10 plants for each treatment were measured from the base to the tip of each plant. Around 1 g of leaves was collected and weighted to confirm fresh weight prior to being dried in a conventional oven at 65°C for three days after which no further water loss was observed and dry weight was subsequently measured.

**Determination of chlorophyll content**

Leaf tissues from the same mature leaves that were used to measure leaf area and dry mass were used for chlorophyll measurements. These fresh leaf tissues were flash-frozen in liquid nitrogen and stored at −80°C until use. The chlorophyll content was determined according to the method described by Zhang et al. (2013). Briefly, 100 mg of leaf tissues were placed in 10 mL 95% ethanol, and the mixture was incubated at 4°C in the dark for 24 h. The absorbance at OD of 530 nm (A_{530}) and 657 nm (A_{657}) was measured with a spectrophotometer. The anthocyanin content was calculated using the following formula: A = A_{530} − 0.25A_{657}, where A is the relative content of anthocyanin.

**Statistical analysis**

All data were analyzed using SPSS statistical software version 17.0. A one-way ANOVA followed by the Least Significant Difference (LSD) method were used to compare significant differences at P < 0.05 among means. Then, graphs were generated in Microsoft Excel 2010. Data for anthocyanin concentration and chlorophyll fluorescence (Fv/Fm) are presented as mean ± standard error.

**Results**

**Effects of MEL and AVG on stem height of the three Pilea species**

Both MEL and AVG had a significant impact on stem height, but they had different effects on plant growth and these effects greatly varied among the three different species (Fig. 1A, B). Plants of all species were responsive to 50, 100, and 150 μmol·L^{-1} of MEL, and stem height increased 37.15%, 39.33%, and 37.08% for PM, and 14.52%, 14.36%, and 14.19% for PC, compared to their counterparts with treated with water only (Fig. 1A). Additionally, PI did not exhibit any difference in stem height under 100 μmol·L^{-1} MEL treatment, despite significant increases being observed under 50, 150, and 200 μmol·L^{-1}. The stem height under 200 μmol·L^{-1} reached a peak value with an increase of 52.48%.

Under all but 200 μmol·L^{-1} AVG treatment, PC exhibited a significant decrease in stem height compared to plants under the dark control treatment. Conversely, the stem height of PI increased dramatically (P < 0.05) with 50 and 100 μmol·L^{-1} AVG treatments, although no noticeable change was observed with treatments of 150 and 200 μmol·L^{-1} AVG. To our surprise, PM exhibited no responses to any AVG treatments (Fig. 1B), which is very distinct from its strong responses to MEL treatments.

**Fig. 1.** Effect of melatonin and aminoethoxyvinylglycine (AVG) on plant height of three *Pilea* species. The asterisks denote a significant difference at P < 0.05 between melatonin or AVG-treated plants and water (at a concentration of 0)-treated plants. OD is the dark control.
Effects of MEL and AVG on dry matter content of three the Pilea species

Only PM and PI were significantly higher in dry matter content with 150 μmol·L\(^{-1}\) of MEL treatment than their respective controls in the darkness (Fig. 2A). Conversely, PI showed a significant decrease in dry matter content with 50 and 200 μmol·L\(^{-1}\) AVG treatments (Fig. 2B). No marked difference was observed for any of three species under other treatments with both MEL and AVG.

Effects of MEL and AVG on leaf area of three Pilea species

The three different Pilea species exhibited highly distinct responses to MEL treatments with regard to leaf area (Fig. 3A). Under 100 and 150 μmol·L\(^{-1}\) MEL treatments, the leaf area of PM significantly increased compared to the dark control treatments. For example, the leaf area of control plants grown in darkness was 17.33 cm\(^2\), while PM treated with 50, 100, and 150 μmol·L\(^{-1}\) of MEL had average leaf areas of 23.79, 25.37, and 25.25 cm\(^2\), respectively. Average leaf areas of PI treated with 100, 150, and 200 μmol·L\(^{-1}\) of MEL also increased 0.97, 0.75, and 0.89 fold compared to the control plants in darkness. However, there was no difference in leaf area for PC among any MEL treatments. By contrast, no alteration in leaf area was observed in PM or PC in any AVG treatments, despite a sharp rise in leaf area of PI with the treatments of 100, 150, and 200 μmol·L\(^{-1}\) AVG (Fig. 3B).

Effects of MEL and AVG on chlorophyll content of the three Pilea species

Changes in chlorophyll content may indicate plant quality since darkness or low-light conditions can induce chlorophyll degradation (Weaver and Amasino, 2001); therefore, we examined the effect of exogenous MEL and AVG on the chlorophyll content of tested plants. Regarding Chla, Chlb, and total chlorophyll Chl\((a + b)\), compared with the dark control PI was the most sensitive to the majority of MEL (Fig. 4A, B, C) and AVG treatments (Fig. 4D, E, F). Except for no change in Chla under 50 μmol·L\(^{-1}\) MEL treatment, the contents of Chla, Chlb, Chl\((a + b)\) were significantly higher in PI under all other MEL treatments compared to plants treated with water in darkness; a similar trend was observed in PI plants treated with 100, 150, and 200 μmol·L\(^{-1}\) of AVG, despite the fact that there was no change in PI treated with 50 μmol·L\(^{-1}\) AVG. Similar to PI, there were increases in Chla, Chlb, Chl\((a + b)\) in PM treated with 50, 100, and 200 μmol·L\(^{-1}\) of MEL or 100 and 150 μmol·L\(^{-1}\) of AVG. The optimum concentrations for MEL and AVG were 100 μmol·L\(^{-1}\) for PM and 150 μmol·L\(^{-1}\) for PI, at which Chl\((a + b)\) was 1.51 and 1.75 fold higher under the MEL treatment, and 1.42 and 1.50 fold higher under the AVG treatment for PI.
and PM, respectively. In contrast to PM and PI, PC was not responsive to any MEL or AVG treatments, resulting in no obvious change in Chl\textsubscript{a}, Chl\textsubscript{b}, or Chl\textsubscript{(a + b)}. Compared with the light control, marked decreases were observed in Chl\textsubscript{a}, Chl\textsubscript{b}, and Chl\textsubscript{(a + b)} of the dark control PM and PI plants under both MEL and AVG treatments.

**Effects of MEL and AVG on anthocyanin content of the three Pilea species**

The three *Pilea* species contained different levels of anthocyanin as indicated by their leaf colors. PI had the highest level of anthocyanin, which was 10.8 and 50 fold higher than those of PM and PC, respectively (Tables 1 and 2; Figs. 5 and 6). The higher anthocyanin of PI may be correlated with the darker color of its leaves. As for anthocyanin content, the three *Pilea* species also exhibited very distinct responses to MEL treatments. The anthocyanin level was dramatically increased in PM under all MEL treatments (Table 1). Compared to the PM plants treated with water in darkness, the anthocyanin level increased 69.56% and reached the maximum level in PM plants treated with 50 μmol·L\textsuperscript{-1} MEL, despite no observed variation with

![Image](image_url)

**Fig. 4.** The effect of melatonin and AVG on the chlorophyll content of three *Pilea* species. 0D is the dark control and 0L is the light control. The same letter means no significance difference (P < 0.05).

**Table 1.** The anthocyanin content in leaves of three *Pilea* species treated with melatonin.

| Melatonin concentration (μmol·L\textsuperscript{-1}) | PM          | PI          | PC          |
|-----------------------------------------------------|-------------|-------------|-------------|
| Dark control                                        | 0.023 ± 0.002 b | 0.257 ± 0.001 bc | 0.005 ± 0.001 a |
| 50                                                  | 0.039 ± 0.002 a | 0.297 ± 0.022 bc | 0.005 ± 0.002 a |
| 100                                                 | 0.035 ± 0.001 a | 0.317 ± 0.043 ab | 0.003 ± 0.002 a |
| 150                                                 | 0.030 ± 0.002 a | 0.395 ± 0.007 a  | 0.004 ± 0.001 a |
| 200                                                 | 0.036 ± 0.007 a | 0.362 ± 0.024 a  | 0.002 ± 0.000 a |

Values expressed as means ± standard error.
The same letter means no significance difference (P<0.05).
other MEL treatments. Similarly, a significantly higher level of anthocyanin was observed in PI plants treated with 150 and 200 μmol·L\(^{-1}\) of MEL, with a peak value of 0.395 with 150 μmol·L\(^{-1}\) MEL treatment. However, the 50 and 100 μmol·L\(^{-1}\) MEL treatments did not cause any change in the anthocyanin content of PI plants. Un-

**Table 2.** The anthocyanin content in leaves of three *Pilea* species treated with AVG.

| AVG concentration (μmol·L\(^{-1}\)) | PM     | PI       | PC       |
|-------------------------------------|--------|----------|----------|
| Dark control                        | 0.023 ± 0.002 c | 0.257 ± 0.001 ab | 0.005 ± 0.001 a |
| 50                                  | 0.036 ± 0.002 ab | 0.200 ± 0.030 b  | 0.005 ± 0.003 a |
| 100                                 | 0.035 ± 0.004 ab | 0.334 ± 0.050 a  | 0.005 ± 0.001 a |
| 150                                 | 0.029 ± 0.002 bc | 0.327 ± 0.035 ab | 0.005 ± 0.000 a |
| 200                                 | 0.040 ± 0.001 a  | 0.259 ± 0.040 ab | 0.006 ± 0.001 a |

Values expressed as means ± standard error.
The same letter means no significance difference (\(P > 0.05\)).
like PM and PI, PC was unaffected by all MEL treatments, and there was no difference in anthocyanin content between the MEL-treated and water treated PC plants in darkness.

Similar to MEL treatments, applications of AVG caused alterations in the anthocyanin content of PM and PI leaves, but not in PC (Table 2). For example, the anthocyanin content reached its highest level in leaves of PM plants treated with 200 μmol·L⁻¹ AVG, which was 73.9% higher than that of control plants in darkness (Table 2). The anthocyanin content also significantly increased in leaves of PM plants treated with 50 and 100 μmol·L⁻¹ AVG, but not with 150 μmol·L⁻¹ AVG. The response of PI to AVG was exactly the same as its response to MEL. Compared with the control plants in darkness, significantly higher levels of anthocyanin were observed in PI plants treated with 100, 150, and 200 μmol·L⁻¹ of AVG, but no significant change in anthocyanin occurred in PI plants treated with 50 μmol·L⁻¹ AVG.

**Effects of MEL and AVG on Fv/Fm of the three Pilea species**

The ratio of Fv/Fm indicates the quantum efficiency of photosystem II, and is an important parameter for measuring whether stresses affect photosystem II in a dark-adapted state (Kalaji et al., 2016). We next examined if foliar applications of MEL and AVG had any effect on the Fv/Fm of the three Pilea species. Under the control conditions, PM had the highest Fv/Fm (0.814), while the Fv/Fm ratios of PI (0.783) and PC (0.799) were comparable (Table 3). Our results showed that MEL exhibited a large effect on the Fv/Fm ratios of PM and PI plants under dark conditions (Table 3). Significant increases in the Fv/Fm ratio were observed in PM and PI plants treated with different concentrations of MEL when compared to control counterparts treated with water only in darkness (Table 3), even though there was no dose effect of MEL on Fv/Fm. However, PC was not responsive to any MEL treatment, and its Fv/Fm ratio remained unchanged with all treatments (Table 3).

The effect of AVG on the Fv/Fm ratio of the three foliage species under dark conditions is shown in Table 4. Unlike MEL treatments, the Fv/Fm ratios of PM and PI varied in an AVG-dose-dependent manner. For example, the Fv/Fm ratios of PM and PI plants treated with 50 and 100 μmol·L⁻¹ of AVG reached the highest levels, followed by a slight decline with 150 and 200 μmol·L⁻¹ of AVG treatments (Table 4). In contrast to PI and PM, AVG treatments generally caused no change or a decrease in the Fv/Fm ratios of PC plants.

**Discussion**

The increasing interest in interior plantscaping has led to the development of international markets for tropical foliage plants, which generally require long-distance transportation from producers to wholesalers in an enclosed environment. However, the deterioration of potted plants during long-distance shipment has become a great challenge to the marketing and production of foliage plants. In this study, we examined the effects of MEL and AVG on three potted foliage species under dark conditions that simulated a long-distance transport environment.

We observed that darkness can accelerate plant deterioration, particularly degradation of chlorophyll (Fig. 4), which is typically associated with decreased
photosynthetic efficiency of photosystem II (PS II) (De Ell and Toivonen, 1999). Photosynthetic performance and stress-induced perturbations in the photosynthetic apparatus can be monitored by measuring the Fv/Fm ratio (Adams and Demmig-Adams, 2004; Baker and Rosenqvist, 2004). Interestingly, the Fv/Fm ratios were maintained at a high level in MEL-treated PM and PI plants, indicating that the dark-stress-induced perturbation in the photosynthetic apparatus and degradation of chlorophyll could be alleviated by the application of exogenous MEL. Several studies have demonstrated that MEL can act together with other antioxidant molecules to effectively scavenge reactive oxygen species (ROS) to prevent chloroplasts from ROS-triggered damage and maintain a high level of chlorophyll (Lee and Back, 2018). The application of exogenous MEL suppressed dark-induced leaf senescence by increasing ROS scavenging capacity and maintaining a higher activity of antioxidases in perennial ryegrass (Zhang et al., 2016a). It has been demonstrated that MEL acted as a growth regulator in a similar way to indoleacetic acid (IAA), and was able to induce growth in shoots and leaves (Pelagio-Flores et al., 2012). This was also supported by our observation of the effect of MEL on promoting the growth of stems and leaves in PM and PI.

Different plant species exhibited different sensitivities to MEL in relieving dark-induced leaf senescence. For example, 20 μM of MEL was sufficient to mitigate leaf senescence of perennial ryegrass treated with darkness (Zhang et al., 2016a), and 1 mM of MEL was applied to effectively delay leaf senescence in barley (Arnao and Hernandez-Ruiz, 2009) and Gardenia (Zhao et al., 2017), whereas 10 mM of MEL was required to have similar effects in alleviating apple leaf senescence (Malus domestica) (Wang et al., 2012). The present study also demonstrated that three plant species of the Pilea genus responded distinctly to MEL. Although marked effects were observed in PM and PI plants treated with different concentrations of MEL, the optimum concentrations of MEL were 100–150 μM for PM and 150 μM for PI, respectively. However, no noticeable morphological change except stem height was observed in PC treated with 50, 100, and 150 μM of MEL, suggesting the distinct responses of the three plant species to MEL treatments. This distinction could be attributed to the varied absorption ability of exogenous MEL due to different leaf textures. PM leaves are softer compared to the waxy leaves of PI and PC, which may enable PM to absorb melatonin more efficiently and cause significant morphological and physiological changes.

The anthocyanin content in plants can be influenced by a variety of factors including light, temperature, sucrose, riboflavin and so on (Chalker-Scott, 1999; Matsumoto et al., 2014). Dark or low light was reported to inhibit the synthesis of anthocyanin (Mol et al., 1996). However, in the present study, higher concentrations of anthocyanin accumulation than the control plants in darkness were found in PM plants with all MEL treatments and in PI plants treated with 150 and 200 μM of MEL. The possible reason is that MEL may compensate for the deprived light effect to sustain normal developmental processes, which in turn leads to normal anthocyanin production even under dark conditions. This beneficial effect of MEL on anthocyanin accumulation was also reported in cabbage (Zhang et al., 2016b). MEL and anthocyanin both act as scavengers of excess ROS; therefore, the application of exogenous MEL and the enhanced anthocyanin accumulation due to MEL treatment may synergistically act together to further mitigate the adverse effects of free radicals on plant growth, thus resulting in the better plant quality compared to the dark control without the MEL application. In addition, transient anthocyanin accumulation due to the application of exogenous MEL may also trigger plants to adjust themselves with quick responses to environmental variability (Chalker-Scott, 1999).

Ethylene can accelerate leaf abscission and senescence in foliage plant species (Blessington and Collins, 1993). Different measures have been taken to combat ethylene production and to alleviate its perceived stress-induced damage to ornamental plants (Macnish et al., 2011; Ferrante et al., 2015). The ethylene production inhibitor, AVG, has been extensively used to reduce pre-harvest fruit drop and improve post-harvest fruit quality (Torrigiani et al., 2004); however, few studies have reported on the effect of AVG on ornamental potted plants under dark stress. In this study, we found that AVG promoted stem growth of PI plants compared to the untreated control plants in darkness, and the effect of AVG on promoting apical shooting was also observed in in-vitro-cultured roses (Park et al., 2016). However, slight inhibition or no marked change in stem growth were observed in PC and PM plants treated with AVG, respectively, suggesting that different plant species exhibit different responses to AVG treatments.

Although MEL was able to counteract the detrimental effects of dark stress on PM and PI, MEL and AVG treatments also promoted stem growth. Stem elongation may negatively affect aesthetic value and has been considered a non-desirable trait for foliage plants because plants with compact architecture are preferentially favored by consumers. In addition, the current prohibitive price of MEL may impose challenges for its extensive application in nursery plant production. However, these challenges could be resolved in the future by the advent of new manufacturing technology for cheaper MEL production. Alternatively, this cost issue can be mitigated if a low dose MEL is applied in combination with other less expensive hormones like AVG, which could also generate a better beneficial effect. Therefore, how the combination of MEL with different plant hormones affects post-harvest plant quality remains to be examined in the future. In cases where dark-induced stresses...
highly affect plant quality, the benefit of MEL may outweigh its cost. In addition, strong demand for high value indoor plants in luxury resorts may also expedite its application of these chemicals to improve post-harvest plant quality.

Conclusion

Morphological and physiological characteristics of three Pilea species plants were evaluated following the application of melatonin or aminoethoxyvinylglycine under simulated post-harvest transport conditions. The application of 50 or 150 μM of exogenous MEL exhibited the best beneficial effect on mitigating dark stress to improve the quality of PM and PI plants, respectively. The AVG treatments were able to alleviate chlorophyll degradation and maintain a high Fv/Fm ratio in PM and PI plants, but AVG had no obvious effect on other plant characteristics of these two plants species. Additionally, PC was not responsive to either MEL or AVG treatments and exhibited no change after both treatments. In summary, melatonin was better than AVG at alleviating the dark stress of three Pilea species.

Literature Cited

Adams, W. W. and B. Demmig-Adams. 2004. Chlorophyll fluorescence as a tool to monitor plant response to the environment. p. 584–598. In: G. C. Papageorgiou and Govindjee (eds.). Chlorophyll a fluorescence. Advances in photosynthesis and respiration. Springer, Dordrecht.

Ahammed, G. J., W. Xu, A. Liu and S. Chen. 2019. Endogenous melatonin deficiency aggravates high temperature-induced oxidative stress in Solanum lycopersicum L. Environ. Exp. Bot. 161: 303–311.

Arnao, M. B. and J. Hernandez-Ruiz. 2009. Protective effect of melatonin against chlorophyll degradation during the senescence of barley leaves. J. Pineal Res. 46: 58–63.

Arnao, M. B. and J. Hernandez-Ruiz. 2015. Functions of melatonin in plants: a review. J. Pineal Res. 59: 133–150.

Baker, N. R. and E. Rosenqvist. 2004. Applications of chlorophyll fluorescence as a tool to monitor physiological status of plants under abiotic stress conditions. Acta Physiol. Plant. 38: 102.

Ke, Q. B., J. Ye, B. M. Wang, J. H. Ren, L. N. Yin, X. P. Deng and S. W. Wang. 2018. Melatonin mitigates salt stress in wheat seedlings by modulating polyamine metabolism. Front. Plant Sci. 9: 914.

Lee, H. Y. and K. Back. 2018. Melatonin induction and its role in high light stress tolerance in Arabidopsis thaliana. J. Pineal Res. 65: e12504.

Lee, H. Y., Y. Byeon, D. X. Tan, R. J. Reiter and K. Back. 2015. Arabidopsis serotonin N-acetyltransferase knockout mutant plants exhibit decreased melatonin and salicylic acid levels resulting in susceptibility to an avirulent pathogen. J. Pineal Res. 58: 291–299.

Lee, K. and K. Back. 2017. Overexpression of rice serotonin N-acetyltransferase 1 in transgenic rice plants confers resistance to cadmium and senescence and increases grain yield. J. Pineal Res. 62. DOI: 10.1111/jpi.12392.

Liang, D., Y. Shen, Z. Ni, Q. Wang, Z. Lei, N. Xu, Q. Deng, L. Lin, J. Wang, X. Lv and H. Xia. 2018. Exogenous melatonin application delays senescence of kiwifruit leaves by regulating the antioxidant capacity and biosynthesis of flavonoids. Front. Plant Sci. 9: 426.

Macnish, A. J., R. T. Leonard and T. A. Nell. 2011. Sensitivity of potted foliage plant genotypes to ethylene and 1-methylcyclopropene. HortScience 46: 1127–1131.

Mandal, M. K., H. Suren, B. Ward, A. Boroujerdi and C. Kousik. 2018. Differential roles of melatonin in plant-host resistance and pathogen suppression in cucurbits. J. Pineal Res. 65: e12505.

Matsumoto, T., K. Nishida, M. Noguchi and E. Tamaki. 2014. Some factors affecting the anthocyanin formation by populations in suspension culture. Agric. Biol. Chem. 37: 561–567.

Mcfadyen, L., D. Robertson, M. Sedgley, P. Kristiansen and T. Olesen. 2012. Effects of the ethylene inhibitor aminoethoxyvinylglycine (AVG) on fruit abscission and yield on pruned and unpruned macadamia trees. Sci. Hortic. 137: 125–130.

Mita, Y. S., N. Murano, M. Akaike and K. Nakamura. 1997. Mutants of Arabidopsis thaliana with pleiotropic effects on the expression of the gene for β-amylase and on the accumulation of anthocyanin that are inducible by sugars. Plant J. 11: 841–851.

Mol, J., G. Jenkins, E. Schafer and D. Weiss. 1996. Signal perception, transduction, and gene expression involved in anthocyanin biosynthesis. Crit. Rev. Plant Sci. 15: 525–557.

Mukherjeea, S., A. Davida, S. Yadava, F. Baluška and S. C. Bhattacharya. 2018. Salt-stress-induced seedling growth inhibition coincides with differential distribution of serotonin and melatonin in sunflower seedling roots and cotyledons. Physiol. Plant. 152: 714–728.

Nawaz, M. A., Y. Huang, Z. L. Bie, W. Ahmed, R. J. Reiter, M. L. Niu and S. Hamed. 2016. Melatonin: current status and future perspectives in plant science. Front. Plant Sci. 6:
1230.

Park, J. S., A. H. Naing and C. K. Kim. 2016. Effects of ethylene on shoot initiation, leaf yellowing, and shoot tip necrosis in roses. Plant Cell Tissue Organ Cult. 127: 425–431.

Pelagio-Flores, R., E. Munoz-Parra, R. Ortiz-Castro and J. Lopez-Bucio. 2012. Melatonin regulates arabidopsis root system architecture likely acting independently of auxin signaling. J. Pineal Res. 53: 279–288.

Qi, Z. Y., K. X. Wang, M. Y. Yan, M. K. Kanwar, D. Y. Li, L. Wijaya, M. N. Alyemeni, P. Ahmad and J. Zhou. 2018. Melatonin alleviates high temperature-induced pollen abortion in Solanum lycopersicum. Molecules 23: 386.

Rath, A. C., I. K. Kang, C. H. Park, W. J. Yoo and J. K. Byun. 2006. Foliar application of aminoethoxyvinylglycine (AVG) delays fruit ripening and reduces pre-harvest fruit drop and ethylene production of bagged “Kogetsu” apples. Plant Growth Regul. 50: 91–100.

Song, C. R., H. Ikei and Y. Miyazaki. 2016. Physiological effects of nature therapy: a review of the research in Japan. Int. J. Env. Res. Pub. He. 13: 781.

Torrigiani, P., A. M. Bregoli, V. Ziosi, S. Scaramaghi, T. Ciriaci, A. Rasori, S. Biondi and G. Costa. 2004. Pre-harvest polyamine and aminoethoxyvinylglycine (AVG) applications modulate fruit ripening in Stark Red Gold Nectarines (Prunus persica L. Batsch). Postharvest Biol. Technol. 33: 293–308.

USDA. 2019. Floriculture Crops-2018 summary. United States Department of Agriculture and National Agricultural Statistics Service. 10.

Wang, L., C. Feng, X. Zheng, Y. Guo, F. Zhou, D. Shan, X. Liu and J. Kong. 2017. Plant mitochondria synthesize melatonin and enhance the tolerance of plants to drought stress. J. Pineal Res. 63: e12429.

Wang, P., L. Yin, D. Liang, C. Li, F. Ma and Z. Yue. 2012. Delayed senescence of apple leaves by exogenous melatonin treatment: toward regulating the ascorbate-glutathione cycle. J. Pineal Res. 53: 11–20.

Weaver, L. M. and R. M. Amasino. 2001. Senescence is induced in individually darkened arabidopsis leaves, but inhibited in whole darkened plants. Plant Physiol. 127: 876–886.

Zhang, J., D. Li, J. Wei, W. Ma, X. Kong, Z. Rengel and Q. Chen. 2019. Melatonin alleviates aluminum-induced root growth inhibition by interfering with nitric oxide production in Arabidopsis. Environ. Exp. Bot. 161: 157–165.

Zhang, J., H. Li, B. Xu, J. Li and B. Huang. 2016a. Exogenous melatonin suppresses dark-induced leaf senescence by activating the superoxide dismutase-catalase antioxidant pathway and down-regulating chlorophyll degradation in excised leaves of Perennial Ryegrass (Lolium perenne L.). Front. Plant Sci. 7: 1500.

Zhang, N., Q. Sun, H. Li, X. Li, Y. Cao, H. Zhang, S. Li, L. Zhang, Y. Qi, S. Ren, B. Zhao and Y. D. Guo. 2016b. Melatonin improved anthocyanin accumulation by regulating gene expressions and resulted in high reactive oxygen species scavenging capacity in cabbage. Front. Plant Sci. 7: 197.

Zhang, X. Q., K. C. Wang, Y. N. Zhang, Q. Wang and Z. W. Cui. 2013. Effects of exogenous nitric oxide on physiology of seed germination and seedling growth of silybum marianum under NaCl stress. Chinese Traditional and Herbal Drugs 44: 3216–3222.

Zhao, D., R. Wang, J. Meng, Z. Li, Y. Wu and J. Tao. 2017. Ameliorative effects of melatonin on dark-induced leaf senescence in Gardenia (Gardenia jasminoides Ellis): leaf morphology, anatomy, physiology and transcriptome. Sci. Rep. 7: 10423.

Ziosi, V., A. M. Bregoli, C. Bonghi, T. Fossati, S. Biondi, G. Costa and P. Torrigiani. 2006. Transcription of ethylene perception and biosynthesis genes is altered by putrescine, spermidine and aminoethoxyvinylglycine (AVG) during ripening in peach fruit (Prunus persica). New Phytol. 172: 229–238.