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EFFECTS OF SHADING ON SOME MORPHOLOGICAL AND PHYSIOLOGICAL CHARACTERISTICS OF *BEGONIA SEMPERFLORENS*

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Abstract

Potted *Begonia semperflorens* were exposed to different levels of shading (25%, 50%, 75%, 87%, and 93%) to investigate the response of the morphological and physiological characteristics of this plant. Results revealed that, as the level of shading increased, the leaf area, water content, superoxide anion ($O_2^{\cdot-}$) production rate, malondialdehyde (MDA) content and plasma membrane permeability exhibited increasing trends when compared with natural light. By contrast, the relative contents of anthocyanin, soluble sugar, starch and the superoxide dismutase (SOD) activity displayed decreasing trends. However, number of flowers per plant, chlorophyll content, nitrate reductase (NR), and peroxidase (POD) activities initially increased but subsequently decreased. Comprehensive analysis indicated that different light intensities exerted different degrees of influence on the morphological characteristics, ornamental quality and physiological characteristics of *B. semperflorens*. This plant can adapt from full illumination to 87% shading, and the number of flowers increased under 25–75% shading, at which the best ornamental quality was also observed.

Key words: Shading, *Begonia semperflorens*, Antioxidant capacity, Morphological characteristics, Physiological characteristics.

Introduction

Light is an important environmental factor that affects plant growth, promotes plant photosynthesis in the form of energy, and regulates morphogenesis in the form of signals (Smith, 2000). The growth environments of plants vary because of different light intensities (Shi *et al.*,2013), which exert varying influences on the shape, structure, photosynthetic characteristics, growth, and development of plants (Xie, 2013; Liu *et al.*, 2015). For example, shading increases plant height but decreases stem diameter, leaf area index, and leaf thickness (Shi *et al.*, 2006). In addition, shading can regulate the carbon and nitrogen metabolism of plants (Evans & Poorter, 2001; Zhi *et al.*, 2001; Song *et al.*, 2010; Zhao & Cai, 2010; Chen *et al.*, 2016). At present, ground cover plants with fast growth, strong resistance, rich color, and high ornamental value have become indispensable parts of modern garden landscaping and greening design. Such plants are typically planted on bare ground, sloping lands, or forest gaps under different lighting conditions. Hence, their growth is affected by varying levels of shading. Therefore, studying the adaptability or shade-tolerance ability of ground cover plants to light intensity is of great theoretical significance and can serve as practical guidance for the scientific configuration of garden plants.

Begonia semperfluorens is a perennial herbaceous groud cover plant and is the most common species of the genus Begonia. It is characterized by a round plant type with flowers that are open for four seasons, and its viewing period is long. Both the flowers and observable leaves of *B.semperfluorens* can be easily planted with other flowerbed plants. It is mainly found in warm environments, and it displays great resistance to heat, moisture, and drought. However, it is not cold-resistant and is sensitive to sunlight. *B. semperfluorens* have become increasingly utilized in southern China. *B. semperfluorens* grow green leaves and red copper leaves, and the latter is considered better in bright summer environments. Anthocyanin synthesis is induced primarily by the accumulation of low-temperature carbohydrates in autumn. Illumination is another indispensable factor in the induction of anthocyanin synthesis (Zhang *et al.,* 2013; Zhang *et al.,* 2016). However, few reports have investigated the effects of different light intensities on the morphological and physiological characteristics of *B. semperfluorens*. Therefore, in our study, potted *B. semperfluorens* plants were treated with different levels of shading, and their morphological characteristics, organic content of small molecules, and antioxidant capacity were assessed to determine the light intensity suitable for their growth. Moreover, the physiological mechanisms of light resistance were studied. The findings of this study provided insights into the physiological mechanism of lightfastness and references for planting ornamental grassland resources with excellent ornamental quality, good growth, and strong resistance to stress in landscaping practices.

Materials and Methods

Cultivation of *B. semperfluorens*: *B. semperfluorens* seedlings were provided by Shanghai Yuanyi Seedling Co., Ltd. On October 2, 2016, the *B. semperfluorens* seedlings were grown under the same condition and transplanted into plastic pots (13 cm high and 8 cm in diameter), which were filled with the same amount of washed fine sand. The experiment consisted of 90 pots containing two plants each. The pots were placed in a shed, watered with tap water for 10 days, and then treated with1/2 concentration of Hoagland nutrient solution. After 20 days, the potted plants were transferred to a greenhouse and treated with Hoagland nutrient solution. The management measures were the same, and the plants were grown until April 10, 2017. Then, the plants were moved under natural light and processed on April 20, 2017.

Different shading treatment: Shading nets of different specifications were used to implement different levels of shading. The shading nets were set at a height of 1.5 m from the ground. The experiment was set up with six treatments-one for 15 pots. The control was natural light (full light, 100% light transmission, i.e., CK). The different levels of shading consisted of 25% shading (75% transmittance), 50% shading (50% transmittance), 75% shading (25% transmittance), 87% shading (13% light transmittance), and 93% shading (7% transmittance). The light intensity was measured with a YF-172 digital illuminometer at five points for each treatment: 6, 9, 12, 15, and 18. Light transmittance=light intensity of shading treatment/natural light 100%, shading = (1-light transmittance) × 100%. All other management measures were constant during the processing, and measurement was conducted after 25 days.

Measurement method: Photos of the treated plants and their leaves were captured. The number of flowers per plant was counted for 16 plants per treatment. The relevant indicators were measured using the leaves of the same leaf position, and the measurement was repeated thrice for each treatment. The physiological indicators, such as fresh weight, Dry weight, chlorophyll and anthocyanin content, soluble sugar content, starch content, nitrate reductase (NR) activity, SOD activity, POD activity and MDA content were determined according to previous method (Liu & Zhao, 2005a; Liu & Zhao 2005b; Liu *et al.*, 2006).

Data analysis: The results were expressed as the standard deviation of the mean of three replicates, and multiple comparisons were performed using DPS data processing software.

Results

Shading effects on plant growth, number of flowers, leaf area, leaf water content, chlorophyll content, and relative content of anthocyanin: As shown in Fig. 1, the control plants had the lowest plant height and the most compact plant type in all treatments. The control plants displayed the darkest red leaves, the smallest area, and upward symmetry with the midribs. As the level of shading was increased, the plant height increased, the plant type gradually loosened, the leaf area gradually increased, the leaf surface tended to flatten, and the leaf color gradually changed from red to green.

As shown in Table 1, compared with the control group, the number of flowers per plant initially increased and subsequently decreased under 25%–75% shading. The number of flowers per plant was higher than that of the control, showing a reduction from 141.79% to 113.10%. Under the 87%–93% shading rates, the number of flowers per plant was only 65.13% and 50.21% of the control, which indicated a significant difference. As the level of shading was increased, both the leaf area and the leaf water content displayed increasing trends by 46.99%–194.86% and 0.39%–2.27%, respectively, under 25%–93% shading. The differences were significant. Under 25%–87% shading, the chlorophyll content showed an increasing trend by 69.86%–287.51% relative to the control. The chlorophyll content under 93% shading was lower than that under 87% shading but was still greater than the control by 231.95%. The relative content of anthocyanin decreased with increasing level of shading. Under 25%–93% shading, the relative content of anthocyanin decreased by 66.87%–96.00% relative to the control, and the difference was significant.

Effects of shading on soluble sugar content, starch content and NR activity: As shown in Fig. 2, the soluble sugar, and starch contents exhibited a downward trend as the level of shading increased, decreasing by 9.16%–71.50% and 22.27%–77.48%, respectively, relative to the control. The difference in soluble sugar content under 25%–50% shading and the control was insignificant, whereas that under 75%–93% shading significantly differed from the control. The starch content under 25%–93% shading significantly differed from the control. As the level of shading increased, the NR activity initially increased and subsequently decreased. Under 25%–50% shading, NR activity increased from 17.79% to 45.12%. The NR activity under 75%–93% shading was 3.08%–71.46% lower than the control.

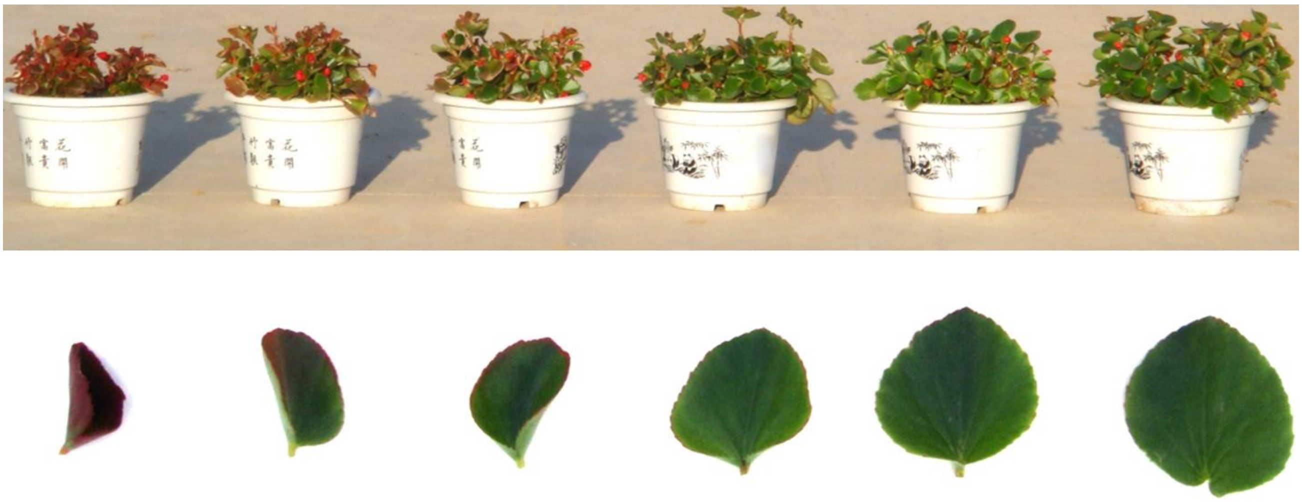

Fig. 1. Growth of *B. semperfluorens* plants and their leaves under full light and shade treatments.

Table 1. Effects of shading on flower number, leaf area, leaf water content, chlorophyll content, and relative content of anthocyanin.

Shading percent	Flower number (number/plant)	Leaf area (cm^2)	Water content of leaf (%)	Chlorophyll content (mg/g)	Relative contents of anthocyanins
0	15.1 ± 0.5b	8.70 ± 0.63f	94.45 ± 0.16c	0.042 ± 0.008c	134.21 ± 6.40a
25%	21.4 ± 2.3a	11.90 ± 0.65e	94.81 ± 0.16c	0.071 ± 0.007c	44.47 ± 3.43b
50%	20.7 ± 2.8a	15.78 ± 1.01d	95.64 ± 0.69b	0.115 ± 0.015b	19.85 ± 2.61c
75%	17.1 ± 1.9b	18.69 ± 1.02c	96.20 ± 0.26ab	0.123 ± 0.034b	11.54 ± 1.99d
87%	9.8 ± 0.9c	21.75 ± 0.99b	96.58 ± 0.11a	0.161 ± 0.009a	8.34 ± 1.96d
93%	7.6 ± 0.6c	23.87 ± 1.43a	96.59 ± 0.21a	0.138 ± 0.028ab	5.38 ± 0.41d

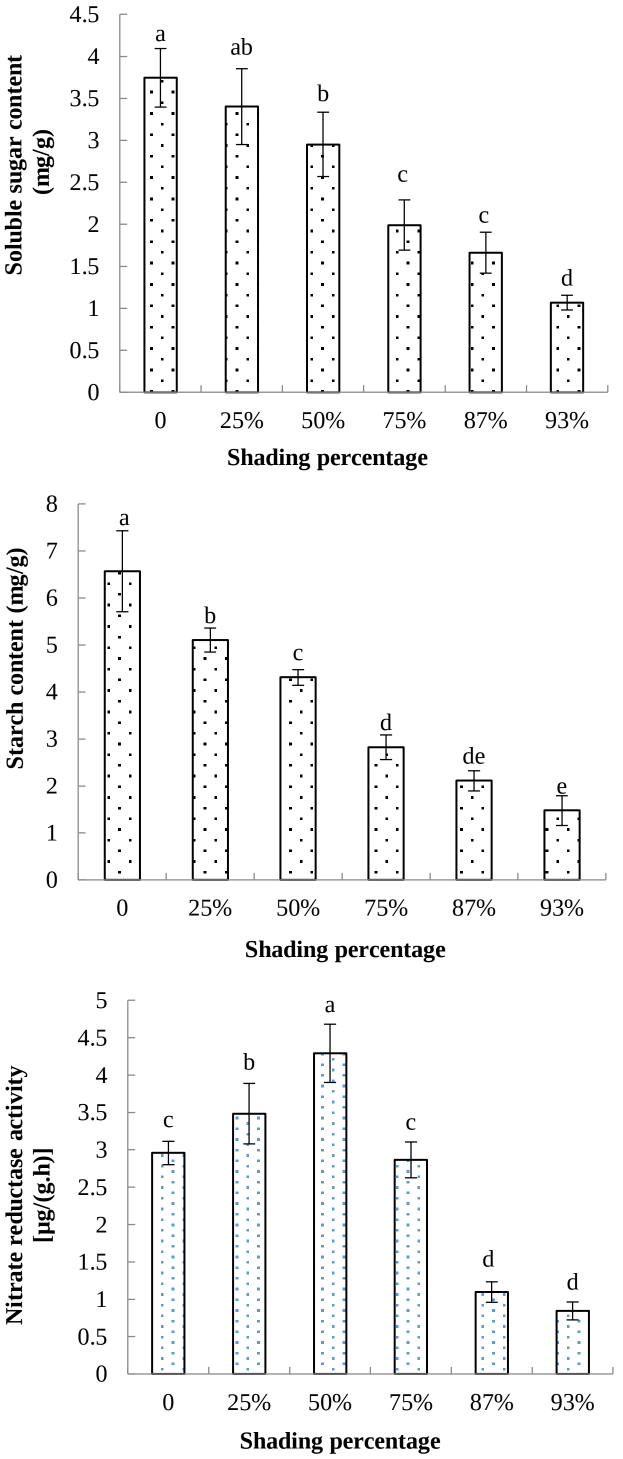

Fig. 2. Effects of shading on nitrate reductase activity, soluble sugar, and starch contents.

Shading effects on SOD and POD activities, $O_2^{\cdot-}$ production rate, MDA content, and plasma membrane permeability: Compared with the control, the SOD activity was reduced by 18.13%–89.38% under 25%–93% shading, and the difference was significant (Fig. 3). As the level of shading was increased, the POD activity initially increased and subsequently decreased, and it was higher than the control. The POD activity was strongest under 75% shading, reaching 309.47 U/(g·min), which was 88.38% higher than that of the control, and the difference was significant. The POD activity under 93% shading reached only 216.53 U/(g·min) but was 31.82% higher than that of the control, and the difference was significant. Compared with the corresponding control, $O_2^{\cdot-}$ production rate, MDA content, and plasma membrane permeability increased by 59.83%–256.75%, 22.11%–139.62%, and 11.91%–82.13%, respectively, under 25%–93% shading. The $O_2^{\cdot-}$production rate under 25%–93% shading was significantly higher than that of the control. MDA content and plasma membrane permeability under 25% shading were not significantly different from those of the corresponding control, whereas those under 50%–93% shading significantly differed from the control.

Discussion

After 25 days of treatment, the *B. semperfluorens* plants became compact and short under full light, displaying small leaves and symmetrical sinusoidal upturns in the midrib. Thus, the vertical projection area was reduced, and the leaf color changed from green to red to reduce the radiant energy of full illumination and avoid the self-protection against the damage caused by strong light. This phenomenon is a morphological adaptive change. As the level of shading, the plant height increased, the crown width increased, the plant type loosened, the leaves expanded and flattened, and the leaf color changed from red to green. Then, the light intensity gradually weakened. This phenomenon serves as a means to capture more solar radiation energy to adapt to the morphological response of the shading environment. Therefore, this change affected the morphological characteristics. Plant type, crown width, plant height, leaf area, leaf color, and leaf extension were sensitive to different light intensities. Related studies suggested that under shading conditions, plants increased their height and crown width to expand the area of light reception in the vertical and horizontal directions and thus obtain more light. Moreover, such response enhances the plant's ability to receive diffused and scattered light. The present study is consistent with the literature(Molas, 1998; Peralta *et al.*, 2002).

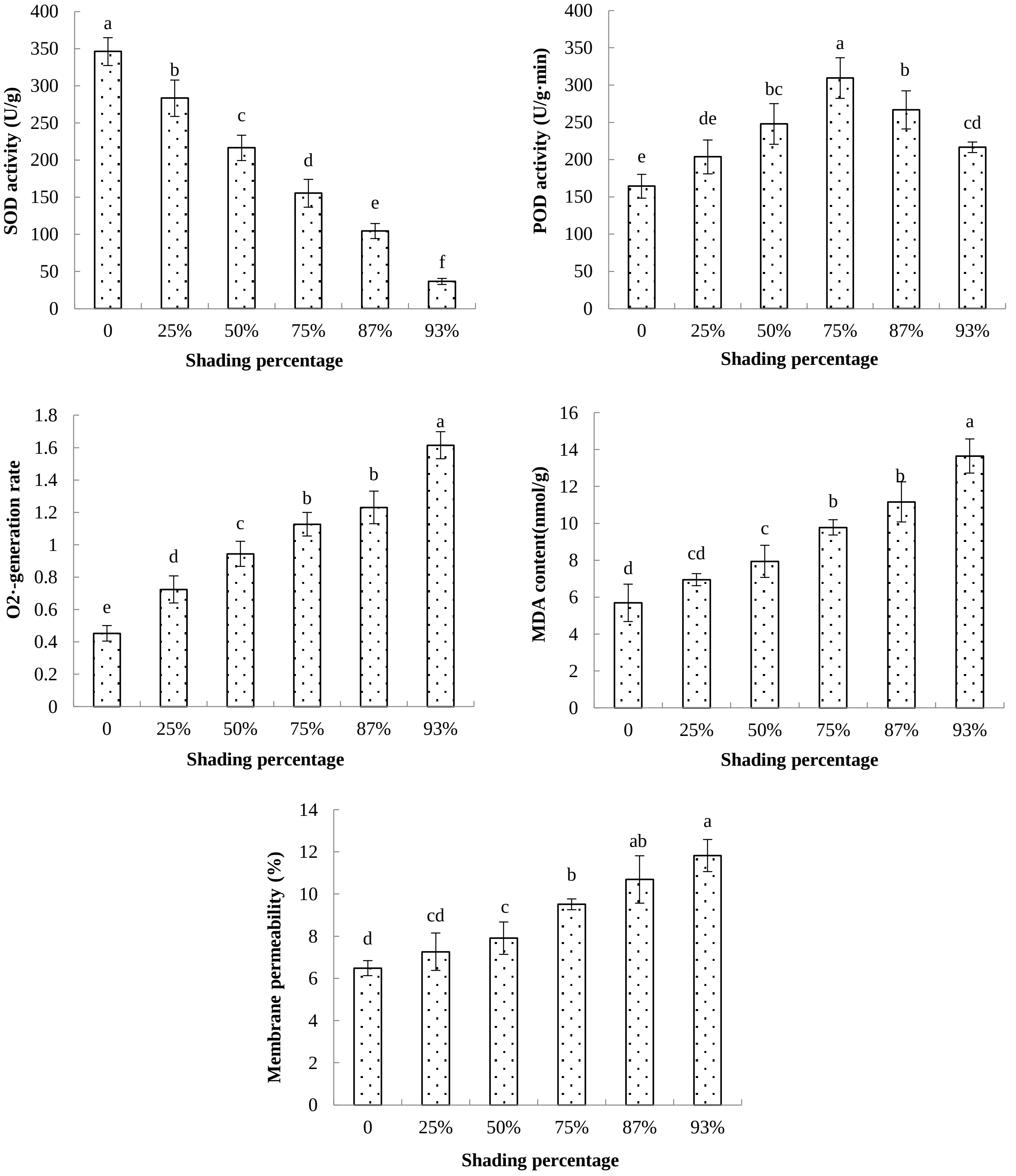

Fig. 3. Effects of shading on SOD and POD activities, $O_2^{\cdot -}$ production rate, MDA content, and plasma membrane permeability.

Anthocyanins are flavonoids, and their synthesis requires phenylalanine ammonia-lyase (PAL) to be triggered. PAL is a light-induced enzyme, and its activity is positively correlated to light, suggesting that light promotes the synthesis of anthocyanins (Ju *et al.*, 1995). Previous studies suggested that strong light significantly induced the expression of anthocyanin-synthesis-related genes and increased the accumulation of anthocyanin in leaves. Low light or darkness inhibits the synthesis and accumulation of anthocyanins (Mol *et al.,* 1996). The biosynthesis of chlorophyll requires light, and the extent of a plant's chlorophyll content reflects the strength of its photosynthetic capacity (Hassanein *et al.*, 2013). This experiment was performed to examine the changes in the number of flowers, leaf area, leaf water content, relative anthocyanin content, and chlorophyll content of *B. semperfluorens* under each treatment. Briefly, anthocyanin synthesis was promoted under full light. However, the inhibition of chlorophyll synthesis resulted in the weakest photosynthetic ability. The consumption of more photosynthetic products by the anthocyanin synthesis led to the reduction of the photosynthetic products required for flower organ growth. Consequently, the number of flowers per plant was reduced, and the plant growth was weakened. The low water content in the leaves was due to the high temperature of the surface layer under strong light and strong transpiration effect. Moderate light attenuation (25%–75% shading) inhibited anthocyanin synthesis and promoted chlorophyll synthesis, thereby enhancing the photosynthetic capacity. Given that the amount of photosynthetic products used for anthocyanin synthesis was significantly reduced, the number of flowers was increased and was even greater than that under full light. In addition, the plant growth was enhanced, and the water content was increased due to the reduced surface temperature and the weakened transpiration. Under 87%–93%, although the chlorophyll content was high, less photosynthetic products were accumulated because the light intensity was too weak. Consequently, the number of flowers was markedly decreased, and the overshadowing significantly reduced the surface temperature, further weakening the transpiration and increasing the water content in the plant.

Strong light promotes anthocyanin synthesis and inhibits chlorophyll synthesis, whereas weak light has the opposite effect (Mancinelli *et al.,* 1975). The observed changes in the relative contents of anthocyanin and chlorophyll in this experiment were consistent with the findings of previous studies. In addition, this experiment showed that severely deficient light (93% shading) exerted an inhibitory effect on chlorophyll biosynthesis. Another study suggested that low temperatures favored anthocyanin synthesis (Zhang *et al.,* 2010), whereas high temperatures suppressed the gene expression and reduced the content of anthocyanins (Islam *et al.,* 2005). In our study, compared with full light, the temperature decreased and anthocyanin synthesis was inhibited as the level of shading was decreased. These results were inconsistent with previous studies, suggesting that the anthocyanin synthesis in *B. semperflorens* is more sensitive to strong light than low temperature. At present, anthocyanin accumulation is believed to display these three aspects: anthocyanins can defend against photo-destructive effects, such as absorbing visible light to attenuate incident light energy and absorbing ultraviolet light to reduce its damage (Zhang *et al.*, 2010); they act as antioxidants to effectively scavenge reactive oxygen species (ROS); and they act as soluble osmoregulatorsin vacuoles (Zhang *et al.,* 2010). The large accumulation of anthocyanins under full light may also present these physiological attributes. Therefore, the light energy absorbed by the *B. semperflorens* leaves exceeds the range in which photosynthesis can be utilized. To avoid the damage induced by excess light energy, a large amount of anthocyanins is synthesized and accumulated. This response is a physiologically adaptive change to full light stress.

Soluble sugars and starch are key indicators of carbon metabolism in plants. Sugar can promote the biosynthesis of anthocyanins (Zhang *et al.,* 2013). In this study, soluble sugar, starch, and anthocyanin were accumulated under full light, and shading reduced the soluble sugar and starch contents. These results were consistent with previous studies (Wang & Feng, 2004). However, the chlorophyll content was the lowest under full light conditions, indicating that the photosynthetic capacity weak. Thus, the mechanisms by which the soluble sugar and starch accumulate are unclear. Several studies have investigated the special physiological responses of plants under stress conditions (Zhang & Xu, 2003). Plant growth is relatively slow under adverse conditions, thereby reducing the need for photosynthetic products, such that large amounts of soluble sugar and starch are accumulated in the leaves (Munns, 1993). This result may also be the combined effect of the above mentioned two factors, and it is a physiological response to total light stress. Moderately reduced light (25%–75% shading) may lead to increased plant growth and increased number of flowers, which consume more nutrients, resulting in decreased soluble sugar and starch contents. As illumination was further weakened (87%–93% shading), the soluble sugar and starch contents were markedly reduced probably due to the severe lack of light.

NR is the first key enzyme that catalyzes NO_3^- reduction. It is a light-induced enzyme that is closely related to the use of nitrate nitrogen by plants. Illumination not only regulates NR activity but also influences the nitrogen metabolism by inducing its synthesis (Magalhaes & Huber, 1991). In this experiment, the shaded NR activity initially increased and subsequently decreased, which was inconsistent with the decreased NR activity in shaded soybean, cotton, and Manchurian ash leaves (Huo, 2009; Yu *et al.,* 2011), indicating that the NR activity of different plants responds differently to the physiological responses to different light intensities. Therefore, with regard to the use of nitrate nitrogen in *B. semperflorens,* the light may be moderately weakened (i.e., 25%–50% shading), which was favorable to NR activation or the increase in the expression amount. Thus, the NO_3^- reducing ability was strong, and the N supply was high, thereby increasing the number of flowers per plant. When the total illumination and shading were 75%, the NR activation was inhibited or the expression was reduced. The ability to reduce NO_3^- was reduced, and the N supply was relatively weakened, thereby decreasing the number of flowers per plant. Under 87%–93% shading, the NR activity was sharply weakened, the N supply was drastically reduced, and the number of flowers per plant was also sharply reduced.

In view of the disturbance of the balance system of the production and removal of ROS in plants under adversity stress, a large amount of ROS accumulated, causing or exacerbating membrane lipid peroxidation and resulting in membrane damage. SOD and POD are antioxidant enzymes in plants. SOD is disproportionate $O_2^{\cdot-}$ to H_2O_2, and O_2, POD can oxidize H_2O_2 into water. These enzymes work together to remove ROS from cells, reduce the toxic effects of ROS on plants (Lópezbucio *et al.,* 2001), and protect cell structures against damage (Blokhina *et al.*, 2003). Therefore, they are often used as effective indicators of plant antioxidant stress. Previous studies indicated that anthocyanins can reduce light energy capture and quench oxygen free radicals (Wang *et al.,* 1997). In this experiment, the SOD activity was the strongest and the relative content of anthocyanins was highest under full light. Although the POD activity was the lowest, the production rate and MDA content of $O_2^{\cdot -}$ were the lowest, and the permeability of the plasma membrane was the smallest. These results were presumed mainly due to the removal of ROS (such as $O_2^{\cdot -}$and H_2O_2) by SOD and anthocyanins. Therefore, the membrane lipid peroxidation was the lightest, and the damage to the plasma membrane was minimal. Under 25%–75% shading, the SOD activity and relative content of anthocyanin decreased, and the POD activity increased. However, the $O_2^{\cdot -}$production rate, MDA content, and plasma membrane permeability increased, indicating that the ability to clear $O_2^{\cdot -}$was reduced. Given that only a strong POD activity can remove H_2O_2, $O_2^{\cdot -}$ still accumulated. Membrane lipid peroxidation and plasma membrane damage were also increased. Under 87%–93% shading, the SOD activity and the relative content of anthocyanin decreased sharply, whereas POD maintained a high activity. The $O_2^{\cdot -}$ production rate, MDA content, and plasma membrane permeability markedly increased, indicating that ROS (particularly $O_2^{\cdot -}$) was difficult to remove by a single POD, which is strongly dependent on activity. Thus, membrane lipid peroxidation and plasma membrane injury were gradually increased.

Conclusion

In summary, under full light, *B. semperflorens* exhibited a red leaf color, a large number of flowers, upward leaf curling (above the top), a compact plant type, moderate reduction nitrate capacity, and a strong antioxidant capacity. However, the plant growth was weak due to the low chlorophyll content. Under 25%–50% shading, the leaf color changed from red to green, and the upper leaf response decreased. In view of the strong reduction nitrate capacity, the antioxidant capacity was strong, and the number of flowers was the greatest under treatment. Moreover, the plant type and the ornamental quality were the best. Under 75%–93% shading, the leaves were green and flat. The reduction nitrate capacity was significantly weakened, the membrane lipid peroxidation gradually increased, the number of flowers was gradually decreased, and the plant type tended to be loose.

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