Effects of Shading on Leaf Anatomy and Photosynthetic Characteristics of Alpine Rhododendron (Postprint)

Authors: Song Jie, Li Shufa, Li Shifeng, Cai Yanfei

Date: 2018-10-26T00:00:00+00:00

Abstract

Rhododendron is a world-renowned ornamental horticultural plant, and light has a significant impact on the growth and development of alpine rhododendron. To understand the light energy requirements and adaptability of alpine rhododendron, this study used potted 3-year-old alpine rhododendron cultivar 'Furnivall' s Daughter' as experimental material to investigate the effects of shading on leaf anatomical structure and photosynthetic characteristics. The results showed that light intensity had no significant effect on stomatal density of alpine rhododendron 'Furnivall' s Daughter' leaves, with stomatal density ranging from 299.70 to 327.22 stomata · mm ^{2}, but light had a significant effect on stomatal aperture and individual stoma area, with plants under 100% full light and 30% full light treatments having the smallest and largest leaf stomatal apertures, respectively. Within the range of light intensities tested, as light intensity decreased, leaf thickness, palisade tissue thickness, spongy tissue thickness, and upper and lower epidermal thickness gradually decreased, which is beneficial for improving leaf light use efficiency. Under 100% full light treatment, the light saturation point (LSP), net photosynthetic rate (Pn), saturated photosynthetic rate (Pmax), stomatal conductance (Gs), and transpiration rate (Tr) of alpine rhododendron leaves were all relatively low; shading treatment effectively increased Pn, Pmax, Gs, Tr, and light use efficiency (LUE), and plants under 30% full light treatment had the lowest leaf light compensation point (LCP) and dark respiration rate (Rd), while having the highest LSP, Pn, Pmax, Gs, Tr, and LUE. The above analytical results indicate that the optimal light condition for alpine rhododendron in the Kunming area of Yunnan is approximately 30% full light; in the cultivation and application of alpine rhododendron, appropriate shading measures should be adopted to meet its optimal light conditions for growth.

Full Text

Preamble

DOI: 10.11931/guihaia.gxzw201806031

Title: Effects of Shading on Leaf Anatomy and Photosynthetic Characteristics of Alpine Rhododendron

Authors: SONG Jie[1,2,3], LI Shufa[1,2,3], LI Shifeng[1,2,3], CAI Yanfei[1,2,3]*

Affiliations: 1. National Engineering Research Center for Ornamental Horticulture, Kunming 650205, China 2. Flower Research Institute, Yunnan Academy of Agricultural Sciences, Kunming 650205, China 3. Key Laboratory of Yunnan Flower Breeding, Kunming 650205, China

Abstract: Rhododendron is a world-renowned ornamental garden plant with significant economic and aesthetic value. Light intensity profoundly influences the growth and development of alpine rhododendrons. To understand their light requirements and adaptive capacity, we investigated the effects of shading on leaf anatomical structure and photosynthetic characteristics in three-year-old potted plants of the alpine rhododendron cultivar ‘Furnivall’ s Daughter’ . Our results showed that light intensity had no significant effect on stomatal density, which ranged from 299.70 to 327.22 mm ^{2}. However, light intensity significantly affected stomatal aperture and individual stomatal apparatus area, with plants under 100% full light and 30% full light showing the smallest and largest stomatal apertures, respectively. Across the experimental light gradient, decreasing light intensity progressively reduced leaf thickness, palisade tissue thickness, spongy tissue thickness, and both adaxial and abaxial epidermal thicknesses, thereby enhancing light use efficiency. Under 100% full light, leaves exhibited low light saturation point (LSP), net photosynthetic rate (Pn), light-saturated photosynthetic rate (Pmax), stomatal conductance (Gs), and transpiration rate (Tr). Shading treatments effectively improved Pn, Pmax, Gs, Tr, and light use efficiency (LUE). Notably, plants under 30% full light showed the lowest light compensation point (LCP) and dark respiration rate (Rd), while displaying the highest LSP, Pn, Pmax, Gs, Tr, and LUE. These findings indicate that approximately 30% full light represents the optimal condition for ‘Furnivall’ s Daughter’ rhododendron in Kunming, Yunnan. For cultivation and landscape applications, appropriate shading measures should be implemented to provide optimal light conditions.

Keywords: alpine rhododendron, anatomical structure, photosynthesis, light intensity

---

Rhododendron is a world-famous ornamental garden plant, with a saying in Europe and America that “no garden is complete without rhododendron.” Alpine rhododendrons represent a major group, generally referring to evergreen rhododendrons in the subgenera *Rhododendron* (scaleless), *Rhododendron* (scaly), and

Azaleastrum, along with their hybrid cultivars (Li et al., 2009). Alpine rhododendrons exhibit brilliant colors, elegant floral forms, and attractive plant architecture, offering exceptionally high economic and ornamental value (Li et al., 2007). However, cultivation and landscape applications have revealed that light intensity critically affects their growth and development. Under strong light, alpine rhododendrons grow slowly, develop yellowing leaves, and suffer from sunscald, whereas excessive shading causes etiolated shoots, disorganized plant form, reduced flower bud numbers, and faded flower color, substantially diminishing both ornamental quality and economic value (Zheng et al., 2010).

Light is a crucial environmental factor that profoundly influences plant morphology and function, playing an essential role in growth, development, and evolution (Aleric & Kirkman, 2005; Sofo et al., 2009; Qiu et al., 2017; Zhao et al., 2017). During long-term adaptation to different light environments, plants modify their leaf morphology and physiological characteristics to maximize photosynthetic capacity and adapt to varying light conditions (Evans, 1989; Cregg et al., 1993; Niinemets & Tenhunen, 1997; Pandey et al., 2009). Plant adaptability to environment is directly or indirectly related to photosynthetic capacity, while environmental factors affect leaf structure and function, thereby influencing whole-plant growth (Chandra, 2003). Recent years have seen growing research interest in the relationship between morphological structure and environmental adaptation in *Rhododendron* species. Wang et al. (2008) examined the structure of overwintering leaves in two rhododendron species (*R. catawbiense* and *R. ponticum*), elucidating the effects of strong light and drought stress on leaf structure and plant adaptation. Wang et al. (2012) investigated leaf anatomical structure and adaptation to alpine environments in three *Rhododendron* species from Changbai Mountain. Rong et al. (2009) analyzed the ecological adaptability of leaf anatomical structures across 13 rhododendron species. Shi and Chen (2005) studied the ecological adaptability of leaf anatomical structures in *Rhododendron* species from Guizhou Province. Cao et al. (2009) examined the ecological adaptability of leaf anatomical structures in five *Rhododendron* species from Taibai Mountain, finding that all five species had palisade-to-spongy tissue ratios far below 1, indicating shade-tolerant characteristics. Among them, species with better strong-light adaptability and lower shade tolerance had well-developed, tightly arranged palisade tissue, whereas species with poor strong-light adaptability but higher shade tolerance showed the highest stomatal density and loosely arranged spongy tissue. These studies reveal that research on light intensity requirements and adaptability of alpine rhododendrons remains limited, focusing primarily on regions with concentrated wild distributions and native germplasm resources, while studies on leaf structure and photosynthetic characteristics of horticultural cultivars widely used in production and landscaping remain scarce.

This study utilized the commercially popular alpine rhododendron cultivar 'Furnivall' s Daughter' to investigate the effects of shading on leaf anatomical structure and photosynthetic characteristics, aiming to understand light energy requirements and adaptability, identify optimal growth light intensity, and provide theoretical foundations and practical guidance for large-scale cultivation and landscape application of alpine rhododendrons.

1. Materials and Methods

1.1 Plant Materials

The experimental material consisted of three-year-old plants of alpine rhododendron ‘Furnivall’ s Daughter’ . All plants were cultivated at the Dachunhe Base of the Flower Research Institute, Yunnan Academy of Agricultural Sciences, under routine water and fertilizer management. The experimental site features a low-latitude plateau monsoon climate with distinct wet (May-October) and dry (November–April) seasons. Shading treatments began in August using black shade nets applied in layers to achieve different intensities: one, two, and three layers of shade net. Light intensity was measured using a DRM-FQ dual radiation sensor, yielding 53%, 30%, and 17% of full sunlight (designated L1, L2, and L3, respectively), with full sunlight as the control (L0). All treated plants were maintained in the same experimental greenhouse, where temperature and humidity variations among treatments were not significant despite marked differences in light intensity. Each treatment comprised 10 pots with three replicates arranged in a randomized block design. Equal water and fertilizer management was maintained throughout the experiment, with pots moved regularly to eliminate edge effects. All measurements were conducted in March of the following year.

1.2 Methods

1.2.1 Leaf Anatomical Structure Observation Mature leaf sections (avoiding veins) were fixed in FAA solution for one week, then dehydrated through an ethanol gradient, cleared in xylene, and infiltrated and embedded in paraffin. Embedded samples were sectioned transversely at 8-10 m thickness using a rotary microtome (MICROM HM315, Germany), stained with hematoxylin, and mounted as permanent slides. For epidermal structure observation, leaf samples were soaked in 50% sodium hypochlorite solution for one week before scraping away mesophyll tissue with a blade to prepare temporary epidermal mounts. Observations were made using a biological microscope (Nikon Eclipse E800, Yokohama, Japan) with images captured by a Nikon-DXM1200 digital microscopy system. Image-Pro Plus 6.0 software was used to measure leaf thickness, cuticle thickness, adaxial and abaxial epidermal thicknesses, palisade and spongy tissue thicknesses, stomatal length and width, stomatal density, stomatal apparatus length and width. Stomatal density (SD) was calculated as the number of stomata per field area. Individual stomatal apparatus area (As) was calculated as × stomatal apparatus length (l) × width (w) / 4, and total stomatal area percentage (At) as As × SD × 100 (James & Bell, 2001). Mean values were obtained from 30 fields per treatment.

1.2.2 Leaf Photosynthetic Parameter Measurement Photosynthetic measurements were performed using a portable photosynthesis system (LI-6400 XT, Li-Cor Inc., Nebraska, USA). A LI-6400-02 LED provided red-blue light sources at various intensities (2,000, 1,600, 1,200, 1,000, 800, 600, 500, 400, 300, 200, 150, 100, 50, 20, and 0 mol • m ^{2} • s ^{1}) with an open airflow pathway for CO . Prior to measurement, leaves were induced at 1,000 mol • m ^{2} • s ^{1} for 15 minutes. During measurement, leaf chamber temperature was maintained at 20°C with relative humidity at 50–60%. At each light intensity, measurements were recorded after approximately 3 minutes of equilibration when ΔH O, ΔCO , net photosynthetic rate (Pn), transpiration rate (Tr), and stomatal conductance (Gs) readings stabilized. A minimum of three leaves were measured per treatment.

Light response curves were fitted using Photosyn Assistant software (V1.1, Dundee Scientific, UK) according to the non-rectangular hyperbola model (Prioul & Chartier, 1977; Rothstein & Zak, 2001). This software calculated photosynthetic parameters including light-saturated photosynthetic rate (Pmax), light saturation point (LSP), light compensation point (LCP), and dark respiration rate (Rd).

1.2.3 Data Analysis All data were analyzed using SPSS 13.0 for Windows (SPSS Inc., Chicago, USA). Treatment comparisons were performed using ANOVA and LSD tests. Statistical graphs were generated using SigmaPlot 9.0 (Systat Software, Inc.). Plasticity index (PI) for relevant variables was calculated according to Valladares et al. (2000) as PI = (maximum mean value - minimum mean value) / maximum mean value. Plasticity index ranges from 0 to 1, with higher values indicating greater plasticity.

2.1 Effects of Shading on Epidermal Characteristics of Rhododendron Leaves

Microscopic observation of treated leaf surfaces revealed no stomata on the adaxial epidermis, while the abaxial epidermis displayed oval or elliptical stomata (Figure 1 [Figure 1: see original paper]A). Stomatal density (SD) across the four treatments ranged from 299.70 to 327.22 mm ^{2}, showing no significant variation with light intensity. However, stomatal length (SL) and width (SW) increased with shading intensity, as did individual stomatal apparatus area (As) and total stomatal area percentage (At). Notably, L2 treatment (30% full light) showed the largest stomatal density and aperture (Table 1).

2.2 Effects of Shading on Mesophyll Characteristics of Rhododendron Leaves

Leaf anatomical structure of ‘Furnivall’ s Daughter’ is shown in Figure 1B. Light intensity significantly affected leaf thickness, with L0 (100% full light) plants showing the thickest leaves—13.9%, 22.1%, and 22.7% thicker than L1, L2, and L3 treatments, respectively. The adaxial epidermis consisted of two cell layers, while the abaxial epidermis comprised a single layer. Adaxial epidermal cells were relatively large and covered by a thin cuticle layer. Both adaxial and abaxial epidermal thicknesses decreased progressively with reduced light intensity, though cuticle thickness showed no significant differences. Palisade and spongy tissue thicknesses declined significantly with decreasing light intensity, demonstrating high sensitivity to light reduction. Palisade tissue thickness in L0 plants was 9.39%, 16.73%, and 19.63% greater than in L1, L2, and L3 treatments, respectively, while spongy tissue thickness was 19.27%, 29.22%, and 26.43% greater (Table 2).

2.3 Plasticity Index Analysis of Leaf Structural Characteristics

Plasticity analysis across the four treatments revealed that leaf thickness, abaxial epidermal thickness, palisade tissue thickness, and spongy tissue thickness had plasticity indices exceeding 0.15. Cuticle thickness, adaxial epidermal thickness, and stomatal length showed intermediate plasticity indices between 0.10 and 0.15, while all other parameters had plasticity indices below 0.10 (Table 3).

2.4 Effects of Shading on Light Response Curves of Rhododendron

Light response curves represent critical indicators for studying plant photosynthetic characteristics. All four treatments showed similar Pn trends with increasing photosynthetically active radiation (PAR): rapid increase below 200 mol · m^{2} · s^{1}, followed by slower increase at higher PAR, stabilizing after reaching LSP (Figure 2 [Figure 2: see original paper]A). Significant differences in Pn were observed among treatments, following the pattern L2 > L3 > L1 > L0.

Stomatal conductance (Gs) and transpiration rate (Tr) exhibited similar trends to Pn. At low light intensities, Gs and Tr increased rapidly with PAR; at higher intensities, they increased slowly and stabilized after reaching LSP. Among treatments, Gs followed the pattern L2 > L3 > L0 > L1 (Figure 2B), while Tr showed L3 > L2 > L0 > L1 (Figure 2C), with L2 and L3 treatments demonstrating significantly higher Gs and Tr than L0 and L1.

Light use efficiency (LUE) increased rapidly at low PAR (<50 mol · m^{2} · s^{1}), then gradually decreased with further PAR increases. L2 treatment exhibited the highest LUE, followed by L3, while L0 and L1 showed similar LUE values. Both L2 and L3 treatments had significantly higher LUE than L0 and L1 (Figure 2D), indicating that appropriate shading effectively improved LUE. Water use efficiency (WUE) and intrinsic water use efficiency (WUEi) also differed significantly among treatments, with L1 showing the highest values, followed by L0. After reaching LSP, WUE and WUEi in all treatments decreased with increasing PAR, but L0 and L1 maintained significantly higher WUE and WUEi than L2 and L3 (Figure 2E, F).

2.5 Effects of Shading on Photosynthetic Parameters of Rhododendron Leaves

As shown in Figure 3 [Figure 3: see original paper], L2 and L1 treatments exhibited the lowest and highest LCP, respectively. L0 treatment had the lowest LSP, significantly lower than L1, L2, and L3 by 67.1%, 69.6%, and 63.5%, respectively. L2 treatment showed both the lowest LCP and highest LSP, indicating the broadest range for light energy utilization. Pmax in L0 and L1 treatments was significantly lower than in L2 and L3, with L2 achieving the highest Pmax among all treatments. L0 treatment showed the highest dark respiration rate, significantly exceeding the other three treatments, while L2 had the lowest Rd.

3.1 Effects of Shading on Leaf Anatomical Structure of Rhododendron

Leaves are evolutionarily sensitive organs with high plasticity that develop various adaptive types under different selective pressures, with structural features that best reflect environmental influences or plant adaptations (Aasamaa et al., 2001). Generally, thick leaves with well-developed palisade tissue characterize plants adapted to high-light, xeric habitats, whereas thin leaves with developed spongy tissue represent adaptations to low-light, well-watered environments (Li & Bao, 2005). In this study, increasing shade intensity progressively reduced leaf thickness and mesophyll tissue thickness in alpine rhododendron. L0 plants under the strongest light exhibited thicker mesophyll tissue, which not only conserved internal water but also provided strong light refraction to prevent damage from excessive illumination. Increased mesophyll thickness and expanded mesophyll cell area with more chloroplasts help maintain high photosynthetic capacity, but the thick mesophyll tissue in L0 plants increased CO diffusion resistance from the substomatal cavity to photosynthetic sites, limiting photosynthate accumulation and reducing photosynthetic rate (Niinemets, 1999; Ma & Lü, 2014). L2 and L3 plants showed significantly thinner palisade and spongy tissues than L0 plants, shortening water and CO diffusion pathways and facilitating gas exchange, thereby enabling higher photosynthetic rates.

Leaf stomata and epidermis constitute the primary sites for water transpiration, with stomatal size and density closely related to photosynthesis and water use efficiency (Dai et al., 2008; Shi & Cai, 2006). Generally, plants under high light exhibit higher stomatal density than those under low light, with shaded leaves showing reduced stomatal density, looser arrangement, and significantly decreased stomatal aperture and resistance (Luo et al., 2006; He et al., 2012). Our results did not fully support this pattern; while light intensity did not significantly affect stomatal density, it markedly influenced stomatal size and individual stomatal apparatus area. L2 and L3 treatments under lower light showed larger stomatal apertures, consistent with findings in pepper seedlings (Sui et al., 2009). Larger stomatal apertures facilitated water and CO exchange, resulting in significantly higher Gs and Tr than in L0 and L1 treatments, effectively increasing the rate of water and CO entry into photosynthetic organs and manifested as higher Pmax and Pn values, favoring net carbon accumulation. L0 plants under the strongest light showed the smallest stomata and stomatal apparatus, enabling rapid stomatal regulation—partial closure under excessive light intensity quickly reduced Gs, effectively preventing severe transpirational water loss, representing another adaptation to high-light environments. After stomatal closure, the leaf epidermis becomes the main channel for water loss, with the cuticular layer preventing excessive water evaporation. In this study, cuticle thickness did not differ significantly among the four treatments with decreasing light intensity, while adaxial and abaxial epidermal thicknesses gradually decreased, effectively increasing internal leaf light intensity and enhancing the capacity to capture diffuse and scattered light, thereby improving light use efficiency as an adaptation to low-light environments (Qin et al., 2012).

To evaluate the role of leaf anatomical parameters in adapting to different light environments, we conducted plasticity analysis of rhododendron leaf structural characteristics. Results showed that mesophyll-related parameters such as leaf thickness, abaxial epidermal thickness, palisade tissue thickness, and spongy tissue thickness had relatively high plasticity indices, whereas stomatal-related parameters including stomatal density, stomatal length, and stomatal width showed lower plasticity indices. This indicates that mesophyll tissue plays a more important role than stomatal characteristics in the adaptation of alpine rhododendron to varying light intensities.

3.2 Effects of Shading on Photosynthetic Characteristics of Rhododendron

Light saturation point and light compensation point serve as physiological indicators of plant light requirements, representing the upper and lower limits of light intensity tolerance, respectively, with their range reflecting light energy utilization capacity (Shang et al., 2008). In this study, shading treatments substantially affected both parameters in alpine rhododendron. L2 treatment showed the lowest LCP and highest LSP, indicating the broadest light utilization range, which contributed significantly to its maximum net photosynthetic rate. Additionally, L2 treatment exhibited significantly lower Rd than the other three treatments, suggesting that it maintained carbon balance with lower net photosynthetic consumption, which is crucial for organic matter accumulation and carbon equilibrium (Cai et al., 2011). In practice, L2-treated plants showed the best growth with tender green leaves. The light response curves demonstrated that after exceeding LSP, photosynthetic rates stabilized without significant decline, indicating that short-term strong light did not damage photosynthetic organs. However, prolonged strong light can cause severe damage and photoinhibition (Hanba et al., 2002; Raven, 2011; Li et al., 2008). In this study, under 100% full light, midday photosynthetic photon flux density reached approximately 2,000 mol • m ^{2} • s ^{1}, substantially exceeding the LSP (447.41 mol • m ^{2} • s ^{1}) for extended periods. Under such conditions, leaves could not dissipate excess light energy, leading to photosynthetic apparatus damage and photoinhibition, manifested as poor growth, yellowing leaves, and numerous withered leaves, with photosynthetic rates only 39.18% of those under the more suitable L2 treatment, demonstrating that prolonged strong light created stressful conditions.

Light use efficiency is a key indicator of plant light utilization capacity. Among the four treatments, L2 showed the highest LUE, with both L2 and L3 treatments having significantly higher LUE than L0 and L1. This may relate to increased red-to-blue light ratio under low light intensity stimulating photochemical reactions and stomatal opening, thereby enhancing photosynthetic rate (Zhang et al., 1993). Furthermore, L2 and L3 plants had significantly thinner adaxial and abaxial epidermal layers and leaf thickness than L0 and L1 plants, with thinner leaves facilitating diffuse and scattered light transmission within mesophyll cells and effectively improving light use efficiency under low-light conditions. Water use efficiency is a stable indicator of the ratio between carbon fixation and water consumption. Although L2 and L3 treatments showed lower WUE and WUEi than L0 and L1 treatments, their Pn was substantially higher at any light intensity, indicating that L2 and L3 plants maintained high photosynthetic efficiency through greater water consumption, closely related to their larger stomatal density and aperture. Additionally, while L2 and L3 treatments had significantly higher Gs and Tr than L0 and L1, their WUE was markedly lower, demonstrating that stomatal conductance plays a significant regulatory role in gas exchange and water use in rhododendron leaves.

In summary, the optimal spring light environment for alpine rhododendron in Kunming, Yunnan is approximately 30% full light. Under this condition, rhododendron leaves exhibit larger stomatal apertures and appropriate leaf thickness, facilitating CO and water exchange. This light intensity also provides the highest photosynthetic capacity, lowest LCP and Rd, and highest LSP, Gs, and Tr. Therefore, appropriate shading measures should be implemented during cultivation and application to create optimal light conditions for rhododendron growth.

References

AASAMAA K, SOBER A, RAHI M, 2001. Leaf anatomical characteristics associated with shoot hydraulic conductance, stomatal conductance and stomatal sensitivity to changes of leaf water status in temperate deciduous trees [J]. Aust J Plant Physiol, 28(8): 765-774.

ALERIC KM, KIRKMAN LK, 2005. Growth and photosynthetic responses of the federally endangered shrub, *Lindera melissifolia*, to varied light environments [J]. Amer J Bot, 92(4): 682-689.

CAI YF, LI SHF, XIE WJ, et al, 2011. Influences of growth environments on photosynthetic characteristics and leaf traits of *Clematis* variety ‘Vyryan Pennell’ [J]. Acta Hortic Sin, 3(7): 1377-1384. [蔡艳飞，李世峰，解玮佳，等，2011. 不同光照环境对‘薇安’铁线莲光合特性的影响 [J]. 园艺学报，3（7）：1377-1384.]

CAO XJ, LIU JJ, YANG M, 2009. Photosynthetic characteristics and anatomical structure of five species of *Rhododendron* in the Taibai Mountain [J]. Acta Bot Boreal-Occident Sin, 29(12): 2483-2491. [曹晓娟，刘建军，杨梅，2009. 太白山 5 种杜鹃属植物叶片光合特性及解剖结构的生态适应性研究 [J]. 西北植物学报，29（12）：2483-2491.]

CHANDRA S, 2003. Effects of leaf age on transpiration and energy exchange of *Ficus glomerata*, a multipurpose tree species of central Himalayas [J]. Physiol Mol Biol Plants, 9(5): 255-260.

DAI L F, CUI L J, ZHANG ZHX, 2008. Influence of shading treatment on growth of *Jatropha curcas* seedling [J]. J Anhui Agric Sci, 36(14): 5729-5731. [戴凌峰，崔令军，张志翔，2008. 遮阴处理对小桐子幼苗生长的影响 [J]. 安徽农业科学，36（14）：5729-5731.]

EVANS JR, 1989. Photosynthesis and nitrogen relationships in leaves of C3 plants [J]. Oecologia, 78(1): 9-19.

HANBA YT, KOGAMI H, TERASHIMA I, 2002. The effect of growth irradiance on leaf anatomy and photosynthesis in *Acer* species differing in light demand [J]. Plant Cell Environ, 25(8): 1021-1030.

HE AN, OU LJ, LI SHH, et al, 2012. Effect of shading on the photosynthetic characteristics of *Saxifrage stolonifera* Curt [J]. Bull Bot Res, 32(6): 657-661. [贺安娜，欧立军，李胜华，等，2012. 虎耳草不同光温条件下光合特性及有效成分含量的相关性分析 [J]. 植物研究，33（5）：587-592.]

JAMES SA, BELL DT, 2011. Leaf morphological and anatomical characteristics of heteroblastic *Eucalyptus globulus* ssp. *globulus* (Myrtaceae) [J]. Aust J Bot, 49(2): 259-269.

LI FL, BAO WK, 2005. Responses of the morphological and anatomical structure of the plant leaf to environmental change[J]. Chin Bull Bot, 22(Z1): 118-127. [李芳兰，包维楷，2005. 植物叶片形态解剖结构对环境变化的响应与适应 [J]. 植物学通报，22（增刊）：118-127.]

LI Q, XIAO JZH, LI ZHIB, et al, 2009. Physiological and biochemical research on critical period of floral initiation in *Rhododendron* hybrids [J]. J Agric Univ Hebei, 32(1): 47-50. [李倩，肖建忠，李志斌，等，2009. 高山杜鹃花芽分化临界期生理生化研究 [J]. 河北农业大学学报，32（1）：47-50.]

LI ZHB, BAI XX, LI P, 2007. The alpine rose will become our country top grade landscaping new favorite—the past, now, future of alpine rose studies [J]. Agric Sci Inform, 7(1): 82-85. [李志斌，白霄霞，李萍，2007. 高山杜鹃将成为我国高档园林绿化的新秀——高山杜鹃研究的过去・现在・未来 [J]. 农业科技与信息（现代园林），7（1）：82-85.]

LI ZR, ZHANG SHB, HU H, et al, 2008. Photosynthetic performance along a light gradient as related to leaf characteristics of a naturally occurring *Cypripedium flavum* [J]. J Plant Res, 121(6): 559-569.

LUO J, ZHANG H, CHEN Y Q, et al, 2006. Relationship of energy sugarcane leaf forms and gas exchange with its yield [J]. Chin J Appl Environ Biol, 12(6): 754-760. [罗俊，张华，陈由强，等，2006. 能源甘蔗不同叶位叶片形态、光合气体交换及其与产量关系 [J]. 应用与环境生物学报，12（6）：754-760.]

MA HL, LÜ DG, 2014. Effects of light condition on structure and photosynthetic characteristics of leaves in ‘Hanfu’ apple [J]. Chin J Appl Ecol, 25(7): 1927-1932. [马慧丽，吕德国，2014. 光照条件对‘寒富’苹果叶片结构和光合特性的影响 [J]. 应用生态学报，25（7）：1927-1932.]

NIINEMETS Ü, 1999. Components of leaf dry mass per area-thickness and density-alter photosynthetic capacity in reverse directions in woody plants [J]. New Phytol, 144(1): 35-47.

NIINEMETS Ü, TENHUNEN JD, 1997. A model separating leaf structural and physiological effects on carbon gain along light gradients for the shade-tolerant species *Acer saccharum* [J]. Plant Cell Environ, 20(7): 845-866.

PANDEY SK, SINGH H, SINGH JS, 2009. Species and site effects on leaf traits of woody vegetation in a dry tropical environment [J]. Curr Sci, 96(8): 1109-1114.

PRIOUL JL, CHARTIER P, 1977. Partitioning of transfer and carboxylation components of intercellular resistance to photosynthetic CO fixation: a critical analysis of the methods used [J]. Ann Bot, 41(4): 789-800.

QIN FF, LIQ, CUI ZHM, et al, 2012. Leaf anatomical structures and ecological adaptabilities to light of three alfalfa cultivars with different fall dormancies under shading during overwintering [J]. Chin J Plant Ecol, 36(4):333-345. [覃凤飞，李强，崔棹茗，等，2012. 越冬期遮阴条件下 3 个不同秋眠型紫花苜蓿品种叶片解剖结构与其光生态适应性 [J]. 植物生态学报，36（4）：333-345.]

QIU ZF, ZENG BS,GUO GS, et al, 2017. Effects of various LED lights on growth and development of *Tectona grandis* plantlets in vitro [J]. Guihaia, 37(5): 592-598.[裘珍飞，曾炳山，郭光生，等，2017. 不同光源对柚木组培苗生长发育的影响 [J]. 广西植物，37（5）：592-598.]

RAVEN JA, 2011. The cost of photoinhibition [J]. Physiol Plant, 142(1): 87-104.

RONG L,CHEN X, WANG XCH, 2009. Leaf anatomical characters and its ecological adaptation of 13 species of *Rhododendron* in Baili azalea area [J]. J Anhui Agric Sci, 37(3): 1084-1088. [容丽，陈训，汪小春，2009. 百里杜鹃杜鹃属 13 种植物叶片解剖结构的生态适应性 [J]. 安徽农业科学，37（3）：1084-1088.]

ROTHSTEIN DE, ZAK DR, 2001. Photosynthetic adaptation and acclimation to exploit seasonal periods of direct irradiance in three temperate, deciduous-forest herbs [J]. Funct Ecol, 15(6): 722-731.

SHANG HL, LI FM, LIN Y, et al, 2008. Photosynthetic characteristics of *Sinopodophllum hexandrum* from different distribution areas in China [J]. Acta Bot Boreal-Occident Sin, 28(7): 1440-1447. [尚海琳，李方民，林玥，等，2008. 桃儿七光合生理特性的地理差异研究 [J]. 西北植物学报，28（7）：1440-1447.]

SHI DH, CHEN X, 2005. Study on the leaf blade structure of six species of *Rhododendron* [J]. Guizhou Sci, 23(3): 39-45. [石登红，陈训，2005. 6 种杜鹃花属(Rhododendron）植物叶片结构的研究 [J]. 贵州科学，23（3）：39-45.]

SHI GR, CAI QSH, 2006. Leaf anatomic plasticity of white clover and its response to different light intensities [J]. Acta Agrect Sin, 14(4): 301-305. [史刚荣，蔡庆生，2006. 白三叶叶片解剖可塑性及其对光强的响应 [J]. 草地学报，14（4）：31-305.]

SOFO A, DICHIO B, MONTANARO G, et al, 2009. Shade effect on photosynthesis and photoinhibition in olive during drought and rewatering [J]. Agric Water Manage, 96(8): 1201-1206.

SUI SL, MAO SHL, WANG LH, et al, 2009. Response of anatomical structure and photosynthetic characteristics to low light in leaves of capsicum seedlings [J]. Acta Hortic Sin, 36(2): 195-208. [眭晓蕾，毛胜利，王立浩，等，2009. 辣椒幼苗叶片解剖特征及光合特性对弱光的响应 [J]. 园艺学报，36（2）：195-208.]

VALLADARES F, WRIGHT SJ, LASSO E, 2008. Plastic phenotypic response to light of 16 congeneric shrubs from a panamanian rainforest [J]. Ecology, 81(7): 1925-1936.

WANG YP, LIU SHL, CHEN YZH, et al, 2012. Leaf structural characteristics of three wild *Rhododendron* plants and their adaptability to Changbai Mountains' northeastern China [J]. J Beijing For Univ, 34(4): 18-25. [王艳萍，刘胜利，陈玉珍，等，2012. 3 种长白山高山杜鹃叶片结构及其对环境的适应性 [J]. 北京林业大学学报，34（04）：18-25.]

WANG X, ARORA R, HORNER TH, et al, 2008. Structural adaptations in overwintering leave of thermonastic and nonthermonastic *Rhododendron* species [J]. J Am Soc Hortic Sci, 133(6): 768-776.

ZHANG CHQ, ZHANG H, ZHANG NY, et al, 1993. The effect of light of different colour on growth and photosynthesis on *Rhododendron irroratum* [J]. Acta Bot Yunnan, 15(4): 392-394. [张长芹，张禾，张能义，等，1993. 不同光质对露珠杜鹃生长发育和光合作用的影响 [J]. 云南植物研究，15（4）：392-394.]

ZHAO B, FU NF, XIANG YC, et al, 2017. Effects of light intensity and planting substrates on the growth of *Begonia ningmingensis* 'Ningming Silver', a new begonia cultivar [J]. Guihaia, 37(9): 1153-1160. [赵斌，付乃峰，向言词，等，2017. 光照强度及栽培基质对秋海棠新品种‘宁明银’生长的影响 [J]. 广西植物，37（9）：1153-1160.]

ZHEN BQ, WANG Y, FENG YJ, 2010. Flower regulation of *Rhododendron* in Beijing area [J]. Chin Flowers Hort, 10(1): 34-36. [郑宝强，王雁，冯艺佳，2010. 北

京地区高山杜鹃花期调控 [J]. 中国花卉园艺，10 (1)：34-36.]

Note: Figure translations are in progress. See original paper for figures.

Source: ChinaXiv —Machine translation. Verify with original.