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Research Progress Concerning the Effect of Shading on Plant Morphogenesis

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Abstract This paper systematically reviews the mechanisms by which shading influences the accumulation and distribution of plant biomass, leaf morphology and structure, and plant height growth. Generally, plants adapt to low-light environments by modifying their biomass allocation strategies, for example, by reducing the root-to-shoot ratio. The morphology and anatomical structure of leaves exhibit significant responses to shading, typically characterized by an increase in leaf area and specific leaf area, a reduction in leaf thickness, decreased stomatal density, thinning of the palisade tissue, and a lowered ratio of palisade to spongy tissue. These changes serve to optimize the capture and utilization of light energy. Additionally, shading generally promotes an increase in plant height, but the specific response patterns vary depending on the species and their respective shade tolerance thresholds. The paper ultimately emphasizes that future research should integrate multiple environmental factors for long-term observation to more comprehensively elucidate the mechanisms by which plants adapt to the light environment. This approach will provide a theoretical foundation for the practices of understory planting and urban greening.

Key words Biomass allocation, Leaf morphology, Mesophyll tissue, Plant height, Light adaptation, Ratio of palisade to spongy tissue

0 Introduction

Light serves as the energy source for photosynthesis and is an essential factor for the growth and development of plants. It influences not only photosynthetic processes but also regulates plant growth, development, and morphogenesis[1]. Notably, light intensity exerts a particularly significant effect on the morphological and physiological characteristics of plants[2]. Changes in light intensity influence the photosynthetic characteristics, nutrient accumulation, and distribution in plants, thereby affecting both vegetative and reproductive growth. Additionally, the morphological traits and the physiological and biochemical foundations of plants undergo corresponding modifications[3]. Consequently, light intensity plays a crucial role in the morphogenesis, growth, and development of plants[4]. Conversely, morphological characteristics serve as direct indicators of a plant's adaptability to varying light intensity environments[5].

1 Effect of shading on biomass

An increase in biomass corresponds to greater accumulation of dry matter, enhanced seedling quality, and improved adaptability to adverse stress conditions[6]. Research on the seedlings of *Phoebe zhennan*, *Fagopyrum esculentum*, and *Sarcandra glabra* has demonstrated that moderate shading promotes growth and biomass accumulation, whereas excessive shading inhibits plant development[2,7-8]. Under appropriate shading conditions, the biomass of *P. zhennan* seedlings is greater than that observed in full sunlight[8]. Similarly, the biomass of *F. esculentum* and *S. glabra* seedlings reaches its maximum when subjected to 30% shading[2,7]. However, under severe shading, the biomass of various plant parts decreases significantly, resulting in marked inhibition of seedling growth[9-10].

The localized allocation of biomass in plants can significantly influence variations in plant morphological traits[11-12]. Shading impacts the accumulation and distribution of biomass in both aboveground and belowground plant parts, thereby modifying plant morphology. Under shaded conditions, plants tend to allocate more resources to the growth of aboveground components to maximize light capture and improve light energy absorption and utilization. Concurrently, the investment in belowground parts decreases, resulting in a reduced root-to-shoot ratio as an adaptive response to low light intensity environments[13-14]. For example, shading enhances the growth of the aboveground parts of *Phellodendron amurense* while limiting the accumulation of its belowground biomass[14]. When light intensity decreases, seedlings of mangrove species such as *Sonneratia apetala*, *Kandelia candel*, *Acanthus ilicifolius*, and *Aegiceras corniculatum* allocate a greater proportion of biomass to their aboveground parts. Notably, *K. candel*, *A. ilicifolius*, and *A. corniculatum* increase leaf biomass to improve their capacity for light energy capture[15]. Similar responses have been observed in *Panax notoginseng*[16]. It is posited that in the competition among plants for light resources, a trade-off exists. To acquire greater light resources, plants allocate more biomass to the growth of stems and leaves, resulting in larger initial individuals that sustain a robust capacity for resource acquisition[17]. This allocation strategy reflects an adaptive survival mechanism in plants.

2 Effect of shading on leaf morphology

Leaves represent one of the most sensitive and adaptable or-

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gans in plant evolution in response to environmental changes[18]. As the primary organs responsible for capturing light energy and facilitating photosynthesis, plant leaves can modify their external morphological characteristics through various mechanisms to adapt to diverse light environments. Therefore, in research, changes in leaf morphological characteristics are frequently considered important indicators for assessing a plant's capacity to adapt to light conditions[19-20]. Shading can influence various aspects of leaf morphology, including leaf area, leaf thickness, and leaf anatomical structure.

2.1 Effect on leaf area As light intensity diminishes, the area of individual leaves progressively enlarges. Plants adapt to low-light environments by increasing leaf area to enhance light capture[21-23]. Under shaded conditions, leaves become larger and thinner, resulting in a rapid increase in specific leaf area (SLA). SLA is defined as the ratio of leaf area to dry mass. A higher SLA corresponds to a greater light-capturing surface and an elevated net photosynthetic rate[24]. Additionally, an increased SLA can reduce the construction cost of leaves[25]. Studies have demonstrated that under low light conditions, the SLA of *Firmiana platanifolia* increases, accompanied by an enhancement in leaf biomass, thereby promoting its healthy growth in such environments[2]. Similarly, *Gardenia jasminoides*, *Quercus liaotungensis*, *Ulmus pumila* 'Jinye', and *Ligustrum robustum* exhibit comparable traits[26-29]. However, the adaptive adjustment of SLA in response to light availability is limited. Under conditions of excessive shading, leaves are unable to perform effective photosynthesis, resulting in a reduction of the plant's total biomass and insufficient nutrient supply for normal growth and development. Consequently, the plant reduces its leaf area to minimize nutrient loss, which further diminishes its capacity to utilize light resources, ultimately impairing normal growth[16,20].

2.2 Effect on leaf thickness Shading can induce alterations in the thickness of plant leaves. Current research indicates that, under shaded conditions, the leaves of most plants become thinner. The primary factor contributing to this leaf thinning is the reduction in the thickness of the palisade tissue[30]. Additionally, as light intensity diminishes, the thickness of the spongy tissue also decreases significantly[20-21,31]. Under shaded conditions, most plants benefit from reducing leaf thickness, as this adaptation enhances the rate of light transmission. This strategy improves the efficiency of light energy capture and utilization in leaves. In certain instances, shading can lead to an increase in leaf thickness. Specifically, when *Bletilla striata* is subjected to 50% and 70% shading, a significant increase in leaf thickness is observed. Concurrently, its apparent quantum efficiency, maximum net photosynthetic rate, light saturation point, and reduced light compensation point also increase[32]. These findings suggest that *B. striata* exhibits enhanced photosynthetic efficiency under low light conditions, which may represent an adaptive strategy employed by shade-tolerant plants to cope with weak light environments.

2.3 Effect on the anatomical structure of leaves

2.3.1 Effect on stomata. Stomata serve as channels for water and gas exchange in plants, influencing both photosynthetic and transpiration rates in leaves. The lower epidermis of leaves contains a high density of stomata. It is widely accepted that stomatal density on the lower epidermis plays a critical role in regulating photosynthesis[33]. Existing research indicates that stomatal density is closely associated with the light environment. Plants exposed to high light conditions exhibit higher stomatal densities, whereas those in low light environments display lower stomatal densities[34]. As the degree of shading increases, the trends in stomatal density vary among different plant species. Specifically, the stomatal density of *Potentilla flagellaris* and *Tilia miqueliana* decreases significantly with increasing shading intensity[21,35]. In contrast, the stomatal density of *Ranunculus ternatus* initially decreases and then increases as shading intensifies, although it remains lower than that of the control (CK)[31].

Shading also influences the degree of stomatal opening. In plants such as *Dioscorea polystachya*[36] and *Cucumis sativus*[37], stomatal apertures decrease under low light intensity, leading to a reduced photosynthetic rate. Conversely, in *Quercus variabilis*, low light intensity results in increased stomatal opening and evapotranspiration, thereby enhancing photosynthetic efficiency[38].

2.3.2 Effect on mesophyll tissue. The mesophyll serves as the primary site of photosynthesis. In dicotyledonous plants, the mesophyll consists of palisade tissue and spongy tissue. Variations in the thickness of these tissues represent significant morphological adaptations to differing light intensity environments[39]. It is widely accepted that plant adaptation to high light intensity is characterized by thicker leaves and well-developed palisade tissue, whereas adaptation to low light intensity is associated with thinner leaves and a more developed spongy tissue[21]. The outermost layer of the palisade tissue exhibits a relatively high chlorophyll content, and its columnar structure serves to increase the depth of direct light penetration[40]. Under conditions of high light intensity, a marked increase in the number of chloroplasts within palisade tissue cells enhances their capacity to capture direct light[41]. Studies on the leaves of *Castanea henryi* and *Quercus dentata* have demonstrated a significant positive correlation between the thickness of the palisade tissue and light intensity[42-43], suggesting that the palisade tissue in these plants is highly responsive to low light stress.

In certain shade-tolerant plants, it has been observed that an increase in the thickness of the palisade tissue can enhance the leaves' capacity to absorb light, thereby improving the efficiency of light energy utilization. For example, under 40% shading conditions, the thickness of the palisade tissue in *L. robustum* increases, resulting in an overall increase in leaf thickness. Similarly, under 20% and 30% shading conditions, both the palisade and spongy tissues of *Camellia hirsuta* exhibit increased thickness[44]. Given the high photosynthetic efficiency of the palisade tissue, its augmented thickness enhances the plant's ability to adapt to shaded environments.

The ratio of palisade to spongy tissue is defined as the ratio of the thickness of the palisade tissue to that of the spongy tissue, serving as an indicator of the development level of the palisade tissue. Generally, the photosynthetic capacity of palisade tissue exceeds that of spongy tissue[45], and this ratio is positively correlated with photosynthetic efficiency[46]. Numerous studies have demonstrated that the ratio of palisade to spongy tissue is significantly higher under full light conditions compared to shading treatments[35]. Shading induces a more pronounced reduction in the thickness of the palisade tissue relative to the spongy tissue, leading to a decreased ratio of palisade to spongy tissue[21,31,43,47-48]. The presence of thinner palisade tissue alongside loosely arranged spongy tissue with large intercellular spaces facilitates the reduction of light quantum loss, enhances light transmittance, and improves the efficiency of light energy utilization in plants subjected to low light conditions[38,49-50].

Several studies have reported that low light intensity promotes an increase in the ratio of palisade to spongy tissue in certain plant species, indicating that the thickening rate of palisade tissue exceeds that of spongy tissue. Examples include *L. robustum*[27], *Glycine max*[5], *Arctium lappa* seedlings[23], and *Sphagneticola* sp.[33]. These plants exhibit strong adaptability to shaded environments and are classified as shade-tolerant species.

Light influences the morphology and arrangement of mesophyll cells. As the degree of shading increases, the cells of the palisade tissue progressively change from elongated columnar shapes to oval and short strip-like forms. Concurrently, the intercellular spaces widen, and the cellular arrangement becomes irregular, with the palisade tissue exhibiting a tendency to transform into spongy tissue. The spongy tissue displays a loose organization, rendering its structural features difficult to discern and indicating damage[3,20,31,49]. The formation of palisade tissue necessitates adequate light to stimulate cell wall extension and cell division. Under shading conditions, the photon supply diminishes, weakening the photosynthetic signal. This attenuation impedes the elongation of palisade cells, reduces the number of cell layers, and decreases tissue thickness[51], consequently altering the morphology and arrangement of mesophyll cells.

3 Effect of shading on plant height

Plant height is a critical indicator trait that reflects the survival strategies of plants[52]. Under shaded conditions, plants tend to increase their height to optimize light capture. In some species, plant height increases with the degree of shading, resulting in a more "slender" morphology, with the rate of height growth exceeding that of stem thickness[53]. This phenomenon has been observed in the seedlings of *F. platanifolia* and *Keteleeria fortune* var. *cyclolepis*, *etc.*[54-55]. Certain plant species exhibit an initial increase in height followed by a decrease as shading intensity increases. For instance, *B. striata* and seedlings of *P. zhennan* attain their maximum heights under 50% shading conditions[8]. Similarly, tobacco leaves reach their greatest height under shading treatments ranging from 25% to 35%[56]. These observations highlight the varying tolerance levels of different plant species to shaded environments. However, some plant species exhibit a significant reduction in both plant height and stem thickness as shading increases[16,31]. This phenomenon occurs because the available light energy becomes insufficient to sustain normal photosynthetic activity, leading to decreased production and accumulation of organic matter. Consequently, vegetative growth is inhibited, resulting in reduced plant height, which serves to minimize organic matter consumption and align with the diminished photosynthetic capacity[16].

4 Prospects

Plants possess a specific threshold range within which they can adapt to low light conditions. In the absence of genetic variation, plants respond to changes in light environments by modifying morphogenesis, growth characteristics, and physiological functions. However, when light intensity deviates beyond the tolerable range, plant growth is likely to decline. Therefore, this range of light intensity may serve as a reference indicator for assessing the shade tolerance of plants. However, this indicator should not be used in isolation, and must be considered in conjunction with other factors, including temperature, humidity, seasonality, plant age, soil conditions, *etc.* Moreover, existing shading experiments predominantly rely on short-term observations, typically spanning only a few months, and lack long-term, systematic observational data. A systematic understanding of plant adaptation to low-light environments facilitates the optimal utilization of understory spaces in forests, thereby enhancing plant productivity and ecological benefits. This knowledge is particularly valuable for applications such as understory cultivation and the selection of groundcover species in urban green spaces.

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