Plant Gene and Trait 2025, Vol.16, No.4, 162-172
http://genbreedpublisher.com/index.php/pgt

Feature Review Open Access

Regulation of Light Environment and Growth Response of Understory Crops in Mulberry-Based Vertical Systems

Kaiwen Liang
Agri-Products Application Center, Hainan Institute of Tropical Agricultural Resources, Sanya, 572025, Hainan, China
Corresponding email: kaiwen.liang@hitar.com
Plant Gene and Trait, 2025, Vol.16, No.4 doi: 10.5376/pgt.2025.16.0018
Received: 03 Jul., 2025
Accepted: 10 Aug., 2025
Published: 19 Aug., 2025

Preferred citation for this article:
Liang K.W., 2025, Regulation of light environment and growth response of understory crops in mulberry-based vertical systems, Plant Gene and Trait, 16(4): 162-172 (doi: 10.5376/pgt.2025.16.0018)

Abstract This study collates relevant research on the impact of light regulation on the growth of understory crops in mulberry three-dimensional planting systems. Starting from aspects such as the structural design of mulberry planting and the changing characteristics of light distribution, it examines how understory crops adapt to different light conditions and summarizes some key factors affecting the shade tolerance of crops. Several simple and effective methods to improve the lighting environment under the forest are introduced, such as appropriate pruning of mulberry trees, adjusting the planting orientation, and laying reflective films. The example of “intercropping mulberry trees and soybeans” is also used to illustrate that by improving the lighting conditions, not only can the yield of soybeans be increased, but also their quality can be enhanced. This study aims to provide some theoretical and practical operation suggestions for the efficient planting of lower layer crops in the three-dimensional mulberry planting system.
Keywords Mulberry-based vertical planting; Understory crops; Light environment regulation; Shade response; Resource use efficiency

1 Introduction

The agroforestry system is a planting method that groups different plant species together and arranges them in layers. This can make better use of the land and also enhance ecological benefits. Mulberry (*Morus* spp.) are often selected as upper-layer tree species due to their strong adaptability and high economic value. Its leaves can be used to feed silkworms and can also be grown together with many crops to increase the output rate and resource utilization rate of each plot (Chanotra et al., 2024). In recent years, mulberry has also begun to appear in vertical agriculture and controlled environment planting systems, and are regarded as a good idea for developing sustainable agriculture (Baciu et al., 2023).

However, under the shade of tall crops like mulberry, the crops planted below often do not receive enough sunlight. The shape of the canopy and the seasonal variation of mulberry leaves can directly affect the light conditions under the canopy, which may limit the growth and yield of crops (De Pauw et al., 2021; Kara, 2022). Studies have found that the intensity and variation of light under the forest can affect the growth rate, photosynthetic efficiency and nutrient absorption capacity of crops (Baligar et al., 2020; Modolo et al., 2021; Xu et al., 2023). Therefore, how to adjust the canopy structure or adopt a more reasonable planting method to improve the light conditions below is a key issue that needs to be solved in current three-dimensional planting (Su et al., 2023).

This study reviews the research progress on how to regulate light in the three-dimensional planting system of mulberry and what impact this has on the crops under the forest. We also analyzed the physiological and ecological responses of undergrowth crops under different lighting conditions. This study hopes that these contents can provide some theoretical references and practical suggestions for the design and management of mulberry planting systems.

2 Characteristics of Mulberry-Based Vertical Planting Systems

2.1 Structural configurations of mulberry-based systems

Several common layout methods are often used in the three-dimensional planting system of mulberry, such as pit type, row type and double-row type. The pit type (90×90 cm) is generally used for growing one-year-old mulberry seedlings. The row type (60×90 cm) is suitable for close planting, while the double-row type (90+150×60 cm) is suitable for the middle and later stages or plots with different density requirements. On the vacant land beside the fields, people often grow some vegetables for intercropping, which makes the space utilization rate higher. In addition, new technologies such as hydroponics, aeroponics and aquaponics have also been used to grow mulberry in controlled environments, which can save water and increase yield (Baciu et al., 2023; Chanotra et al., 2024).

2.2 Typical crop combinations and ecosystem services

Mulberry can also be grown in combination with many crops, such as alfalfa, turmeric, potatoes, garlic, onions and fennel. These intercropping patterns not only improve the land utilization rate, but also make the soil healthier, with more microorganisms and smoother nutrient cycling (Zhang et al., 2019; Chanotra et al., 2024). After planting vegetables, farmers can still harvest several crops a year, and their income becomes more stable. This combination can also reduce soil erosion, assist in carbon sequestration, and improve the microclimate (Kaushal et al., 2024).

2.3 Benefits and limitations of vertical agroforestry models

Vertical agroforestry systems have many advantages. It can make full use of land and resources and increase the yield per unit area. The multi-layer structure can also make the soil looser and more nutrient-rich, which is conducive to improving the carbon sink function and regulating the climate (Kaushal et al., 2024). Meanwhile, when there are more types of crops, farmers' income sources become more stable and their ability to withstand market fluctuations or natural disasters is stronger (Chanotra et al., 2024). From an ecological perspective, there are more types of microorganisms in the soil and the system is more stable (Zhang et al., 2019). But there are also some problems. For example, mulberry itself is relatively tall and have a high demand for water and space. If they are planted too densely, they may compete for resources with the crops below (Magadum et al., 2020). Different crops have different requirements for sunlight, water and nutrients. If not managed properly, some crops may not grow well. In addition, this type of system requires a considerable initial investment, is troublesome to manage after cultivation, and has relatively high technical requirements for farmers (Baciu et al., 2023).

3 Light Environment in Multilayer Planting Systems

3.1 Vertical light distribution and shading patterns

In a multi-layer planting system, the distribution of light in the up and down directions is very uneven. The upper crops or trees will block the sunlight, greatly reducing the light that the lower crops receive. For instance, in the sloping forest where multiple plants are mixed, the relative photosynthetic photon flux density (rPPFD) at different heights varies significantly. The rPPFD under the forest is much lower than that on single-story slopes, and the light variation is significant whether in the up-down or left-right direction. In artificial cultivation factories, when planting in the traditional vertical I-shaped method, the lower down, the weaker the light becomes, and the photosynthesis of the lower layer crops will be affected. However, if S-shaped lateral layering planting is adopted and side supplementary lighting is added, the light distribution can be more uniform, and the crop quality and light utilization rate will also be higher. In addition, reasonable arrangement of planting structure and crop types can also reduce shadow coverage and enable the lower layer crops to grow better (Feng et al., 2019; Solanki et al., 2024).

3.2 Temporal and seasonal light dynamics

The light in a multi-layer system is not only unevenly distributed but also varies greatly over time. The intensity of light under the forest or in multi-story structures fluctuates constantly with the position of the sun throughout the day and the change of seasons. Especially in places where there are gaps in the forest canopy, the changes in sunlight are even more obvious. Artificial light sources (such as leds) can adjust the duration and intensity of illumination, which can alleviate the influence of seasonal changes in natural light to a certain extent and maintain relatively stable illumination throughout the year (Gerovac et al., 2016). Nowadays, there are also lighting devices that can move along with the sun, which can guide natural light as much as possible to the lower layers of the structure. This not only enhances the lighting of the lower layers but also saves electricity.

3.3 Key metrics for light environment assessment

It is very important to scientifically assess the light environment of multi-layer systems. Common light assessment indicators include: rPPFD (relative value of photosynthetic photon flux density), daylight integral (DLI), total photon flux (TPF), uniformity of light distribution, and light quality (that is, the color composition of light). Among them, rPPFD is the most core indicator, used to see how much effective light can be received at each layer height (Zhu et al., 2020). DLI and TPF represent the total amount of light absorbed by crops over a period of time, which is directly related to the growth rate and yield of crops. If one wants to understand whether the light distribution is uniform, three-dimensional modeling or radiation models can be used for analysis. The influence of different planting methods on the light distribution can be clearly seen at a glance. In addition, the quality of light is also very important. For instance, red light, blue light and far-red light all have regulatory effects on the growth of leaves, flowering and fruiting of crops. Nowadays, LED lights can adjust these spectra to help crops grow better and have higher yields (Gerovac et al., 2016).

4 Physiological Responses of Understory Crops to Shading

4.1 Photosynthetic adaptation under low light

In the shaded environment under the forest, the photosynthesis of crops will undergo obvious changes. Generally speaking, shading can reduce the net photosynthetic rate, stomatal conductance and transpiration rate of leaves, while increasing the CO_2 concentration between cells. This indicates that the decline in photosynthesis is mainly not caused by stomatal limitation, but by non-stomatal factors (Raai et al., 2020; Wang et al., 2021; Zhang et al., 2024). To adapt to weak light, crops usually increase chlorophyll, especially chlorophyll b, which can better absorb blue light (Gong et al., 2022; Sun et al., 2023). Some varieties also enhance the expression of some genes related to photosynthesis, such as the Lhcb1 protein, which helps to better capture light energy under weak light. Meanwhile, shading also activates the antioxidant enzyme system, enhancing the resistance of crops to photosuppression and oxidative stress (Ren et al., 2022).

4.2 Morphological plasticity

In an environment with insufficient light, the appearance of crops under the forest will also undergo many changes. For example, the stems become longer, the leaves thinner, the leaf area larger, and the petioles elongated. This enables them to receive sunlight more easily (Gong et al., 2022; Gatti et al., 2023). Like the vine plant *Mikania micrantha*, the stem nodes grow longer and the epidermal cells stretch under weak light, which is conducive to rapid growth. The internal structure of the leaves will also change. For example, the palisade tissue and spongy tissue become loose, which is more conducive to absorbing scattered light. In addition, shading can also affect the hormone levels within plants. For example, changes in auxin, gibberellin and brassinolide can promote the growth of leaves and stems (Jiang et al., 2020).

4.3 Impact on reproductive development and crop quality

Shading can also affect the flowering and yield of crops. Very often, shading can prolong the entire growth cycle of crops and postpone the flowering and maturation time. In terms of yield, shading usually leads to a reduction in the dry matter of crops, and the number and weight of grains also decrease, resulting in a decline in total yield (Liang et al., 2020). However, there are also some crops that do not reduce yield under moderate shading conditions (such as 30% shading), and sometimes the protein content even increases (Raai et al., 2020). In addition, shading can also affect some nutritional indicators and stress resistance. For example, starch content, protein content and antioxidant capacity may also be affected (Laub et al., 2021; Wang et al., 2021).

5 Species-Specific Shade Tolerance in Understory Crops

5.1 Classification of crops by shade tolerance

The shade tolerance of under-forest crops can be judged by many indicators. Some are classified based on expert experience, while others use the growth conditions in the field as a reference. The commonly used approach nowadays is to examine the physiological characteristics of crops, such as photosynthetic efficiency and leaf features. Studies in North America and Europe have classified plants into several categories: those that are particularly shade-tolerant (such as some ferns and mosses), those that are moderately shade-tolerant (some herbaceous and shrub species), and those that are less shade-tolerant (mostly sun-loving tree species). The degree of shade tolerance is generally indicated by numbers from 1 to 9, where 1 is the most shade-tolerant and 9 is the most shade-afraid (Feng et al., 2018). The study also found that the "low light abundance index" is a relatively practical method for evaluating the shade tolerance of undergrowth plants. In addition, factors such as seed size, leaf shape (coniferous or broad-leaved), and growth rate are also related to shade tolerance.

5.2 Mechanisms of shade avoidance and acclimation

The responses of undergrowth crops to shade are usually divided into two categories. One type is the "shade-avoiding type". Crops of this type will rapidly elongate their stems and leaves under weak light, striving to obtain as much sunlight as possible. Another type is the "shade-tolerant type", which can adapt to weak light by improving photosynthetic efficiency, increasing chlorophyll, and enhancing water use efficiency (Figure 1) (Martinez-Garcia and Rodriguez-Concepcion, 2023). Shade-tolerant crops usually do not grow taller blindly but maintain a high carbon utilization efficiency and survival rate (Schmiege et al., 2020; Cifuentes and Moreno, 2022). This type of crop also shows particular performance in terms of root distribution, leaf size and lifespan. Some crops can also better adapt to low light by increasing the nitrogen content in leaves and raising the ratio of chlorophyll to nitrogen (Kang et al., 2022).

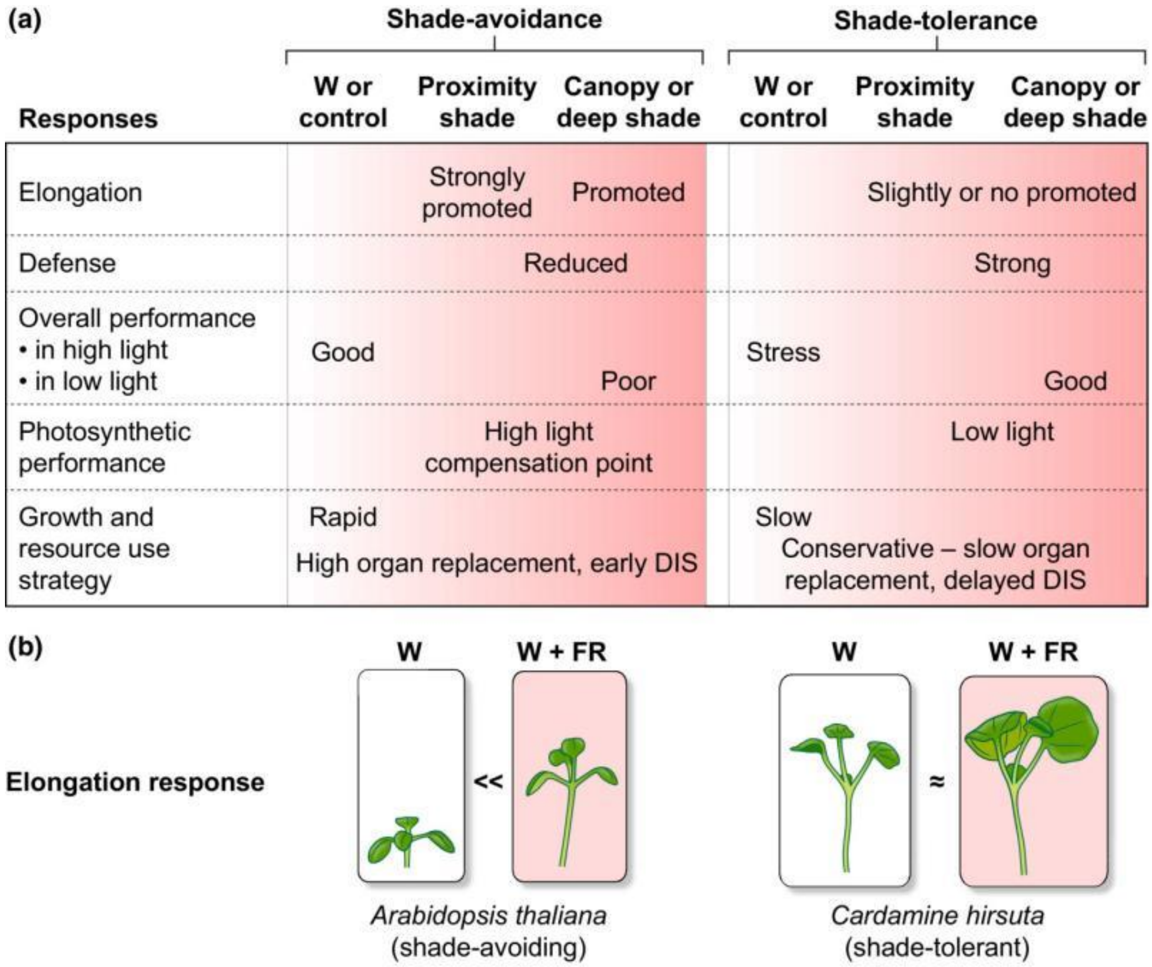

Figure 1 Summary of some differential responses associated with either shade avoidance or shade tolerance strategies (Adopted from Martinez-Garcia and Rodriguez-Concepcion, 2023)

Image caption: (a) Plant responses known to differ between strategies are described in the various laboratory conditions used: white (W) or control, proximity shade and canopy or deep shade. (b) Aspect of seedlings of *Arabidopsis thaliana* and *Cardamine hirsuta* grown under W (control or unshaded) or W enriched with FR (W + FR, proximity of canopy shade) illustrating the differences in their hypocotyl length. FR, far-red light (Adopted from Martinez-Garcia and Rodriguez-Concepcion, 2023)

5.3 Screening and breeding of shade-compatible cultivars

To ensure that the under-forest crops in the mulber-based three-dimensional planting system grow better, it is crucial to select and breed varieties suitable for shady environments. Studies have found that different crop varieties perform differently under different shading conditions. For example, cocoa and some coniferous trees have significant differences in physiological responses when the light is different (Ávila-Lovera et al., 2020; Schmiege et al., 2020; García-Pérez et al., 2021). Nowadays, molecular biology and genetics studies have also identified many genes and pathways related to shade tolerance, providing a basis for future molecular breeding (Martinez-Garcia and Rodriguez-Concepcion, 2023). In addition, the use of quantitative indicators such as "low light abundance index" can more accurately select varieties suitable for weak light (Feng et al., 2018).

6 Regulation of the Light Environment for Optimized Growth

6.1 Pruning and canopy management of mulberry

The canopy of a mulberry can affect whether the crops beneath it can be exposed to sunlight. Pruning, rotation and shaping can help us control the tree canopy, allowing more sunlight to reach the understory of the forest and enhancing the photosynthesis and growth of crops. For instance, rotational cutting, top pruning or cutting off some branches can not only reduce soil erosion and improve the soil, but also open the tree canopy, allowing sunlight to penetrate more easily, resulting in better crop growth and increased yield and quality (Kaushal et al., 2024). In some places, mixed forests or multi-layer planting systems are used. Under such structures, sunlight varies greatly, especially during seasonal changes. Regular pruning is very useful as it can increase light gaps and help the crops below grow better (Kara, 2022).

6.2 Use of reflective materials and row orientation

In addition to pruning, we can also use some simple tools to enhance sunlight, such as laying reflective film, white ground film, etc. These things can reflect sunlight to the understory of the forest, especially scattered light, which enables the lower leaves to absorb more light and enhance photosynthesis. In addition, when planting mulberry, if the rows face north and south, the sunlight will be more evenly distributed and it is less likely that there will be too much shadow covering the crops below. Studies have found that using LED for supplementary lighting, adjusting the intensity or color of the light (such as supplementing blue or white light) can also make undergrowth crops grow better and accumulate more nutrients (Win et al., 2022; Paponov, 2025).

6.3 Controlled intercropping and spacing adjustments

The planting layout is also very important. By changing the types, densities or arrangements of intercropping crops, they can be made to compete for less light and cooperate more. For instance, when mulberry is planted together with turmeric and vegetables, if the row spacing and plant spacing are designed reasonably, sunlight can be distributed better, the yield and quality of under-forest crops can be improved, and the land can be used more efficiently (Kaushal et al., 2024). Moreover, different planting methods, such as pit planting, single-row planting, and double-row planting, will cause the crops below to receive different amounts of light. The appropriate approach should be selected based on the actual situation (Chanotra et al., 2024).

7 Interactions Between Light, Microclimate, and Soil Factors

7.1 Light-mediated effects on temperature and humidity

In vertical planting systems, light not only has a direct effect on the photosynthesis of crops but also indirectly affects their growth conditions. For instance, after the lights are turned on, the LED lights will make the surrounding area warmer, which will change the air humidity and also accelerate the evaporation rate of soil moisture (Kamenchuk et al., 2023). Moreover, different combinations of light intensity and spectra can also cause changes in temperature and humidity. Therefore, when designing vertical systems, one cannot only consider whether the light intensity is strong or not, but also find ways to make the microclimate suitable for crop growth.

7.2 Effects on soil moisture retention and microbial activity

In mulber-based composite systems, soil moisture can be maintained, rainwater erosion can be reduced, soil loss can be decreased, and the organic carbon and moisture content in the soil can also be increased by managing the tree canopy and reasonable intercropping (Kaushal et al., 2024). If planting is reasonable and fertilization is scientific (especially nitrogen fertilizer), it can also improve the soil structure, make the microorganisms in the soil more diverse and vigorous, and enhance the activity of enzymes, which is conducive to the cycling and utilization of nutrients (Zhang et al., 2021). In addition, changes in soil temperature and moisture can also affect the types and activities of microorganisms, which have a significant impact on the environment around plant roots and nutrient absorption (Zhang et al., 2019; Li et al., 2023).

7.3 Integrated microenvironment management strategies

To make crops grow better, some comprehensive management methods can be adopted, such as pruning the tree canopy, reasonable intercropping, application of biochar, and zonal watering, etc. (Wang et al., 2020; Wang et al., 2022a). For instance, when mulberry and crops are planted together and combined with pruning methods, not only can soil erosion be reduced and soil fertility be enhanced, but also water can be retained, the number and variety of microorganisms in the soil can be increased, making the entire system more stable and environmentally friendly (Kaushal et al., 2024). In addition, by adjusting the pH value and carbon-nitrogen ratio of the soil, it can also help establish a more crop friendly microbial community (Wang et al., 2022b; Li et al., 2023).

8 Productivity and Resource Use Efficiency in Mulberry-Based Systems

8.1 Biomass partitioning and yield components

Mulberry adjusts their growth patterns in different environments. For instance, when encountering drought or heavy metals in the soil, mulberry will devote more energy to root growth and increase the ratio of roots to stems (R/S), which can better resist environmental stress (Wang et al., 2022a; Zhang et al., 2023). When grown together with other crops (such as intercropping with alfalfa), the leaf, stem and crude protein content of mulberry can increase by 36.4%, 61.1% and 12.7% respectively, indicating a significant increase in yield. Furthermore, when mulberry is planted on hillsides or in marginal plots, the branches pruned each year can contain 17.0 to 22.5 tons of dry matter, which is more than that of many fast-growing trees or perennial grass crops (Lu et al., 2009).

8.2 Light-use efficiency and land equivalent ratio (LER)

In the intercropping system, mulberry can also make better use of sunlight. Compared with monoculture, the light saturation point, light compensation point and maximum photosynthetic rate of mulberry under intercropping conditions have increased by 15.0%, 39.3% and 20.7% respectively. That is to say, it has a stronger ability to absorb and utilize sunlight. Meanwhile, the land equivalent ratio (LER) of the intercropping system reached 1.29, which indicates that more can be produced per unit of land. Under the condition of increased carbon dioxide concentration, the efficiency of photosynthesis and PSII light system of mulberry is also higher, which helps it grow faster and accumulate more dry matter (Shi et al., 2025).

8.3 Nutrient and water use efficiency under shade conditions

Under conditions of weak sunlight or limited resources, the mulberry composite system can also perform well. For instance, by using a low-cost drip irrigation plus fertilization (LCDF) method, the water utilization efficiency can be increased by 61%, the fertilizer utilization efficiency by 63%, and 24% of water can be saved (Mahesh et al., 2020). During droughts, the water use efficiency of mulberry can even increase by 104% to 163%. Its roots can also better absorb nutrients such as nitrogen, phosphorus and potassium, improving the drought resistance and yield of the entire system (Ren et al., 2025; Shi et al., 2025). In addition, planting mulberry together with other crops can also reduce soil erosion, prevent nutrients from being washed away, and at the same time increase the nitrogen, phosphorus content and enzyme activity in the soil, making the soil healthier (Piao et al., 2020; Kaushal et al., 2024).

9 Case Study: Light Regulation and Crop Response in a Mulberry-Soybean Intercropping System

9.1 Site description and system configuration

In northern China, farmers often intercrop mulberry and soybeans to make better use of the land. This method is called the mulberry - soybean intercropping system. Generally, their positions are arranged in a band-like pattern or by alternating wide and narrow rows. Mulberry (*Morus alba* L.) grows tall and is perennial, while soybeans are harvested in the same year they are planted and are relatively short. When the two are staggered and planted together, a two-layer structure can be formed. In this way, sunlight can be utilized more effectively and the land use efficiency is also higher (Figure 2) (Feng et al., 2025).

Figure 2 Intercropping of forage mulberry and soybean (Adopted from Feng et al., 2025)

Image caption: (A) Diagram of the row configuration of forage mulberry and soybean. (B) Forage mulberry starting to grow leaves during the soybean seedling stage in the field. (C) Soybean seedlings when the forage mulberry begins leaf-sprouting in the field. (D) Before the forage mulberry is mowed, soybeans and forage mulberries are nearly of equal height. (E) Before the forage mulberries are mowed, soybeans are at the R1 stage. Notes: SN indicates sole cropping of soybeans; IN indicates intercropped with forage mulberry (Adopted from Feng et al., 2025)

9.2 Light environment monitoring and management interventions

To understand the utilization of sunlight, researchers measure some light indicators, such as photosynthetically active radiation (PAR), light saturation point, light compensation point, and the ratio of red light to far-red light (R:FR). Research has found that in this intercropping system, mulberry can utilize the strong light in the upper layer, while soybeans are more suitable for the weak light in the lower layer. The apparent quantum efficiency of soybeans is also quite high. By adjusting the row spacing, bandwidth, or pruning mulberry, the light exposure of soybeans can be improved to make them grow better (Jin et al., 2024; Wu et al., 2025). However, the light received by soybeans in different positions varies. For instance, the rows on the edge receive more light, while the rows in the inner part may appear to have insufficient light due to being blocked by mulberry.

9.3 Crop performance and system productivity outcomes

Under such a planting model, soybeans also perform better. Its chlorophyll content, photosynthetic rate, leaf area and yield have all increased, and the number of root nodules has also increased, indicating better nutrient absorption (Feng et al., 2025). Moreover, the mulberry itself has grown better, with an increase in height, more chlorophyll, and an increase in the biomass of their roots and above-ground parts. Soybeans are also well adapted to weak light. Its leaf area index, photosynthesis and yield are basically positively correlated with the amount of light it can receive (Jin et al., 2024; Wu et al., 2025). If the row spacing and bandwidth are reasonably arranged, mulberry and soybeans can work together to increase production, making the land use efficiency higher and the output of the entire system more considerable.

10 Concluding Remarks

Research has found that crops under the forest are highly sensitive to changes in light and are also prone to changes. Take *Camellia oleifera* and perennial leguminous plants as examples. If the light is appropriate, for instance, reaching 75% of full sunlight, it can significantly increase their leaf size, enhance photosynthesis, and accelerate nutrient absorption. Eventually, the plants will grow stronger and bear more fruits. The mulberry itself is no different. The growth of its leaves and the amount of its biomass are both directly related to the light it receives. Different forest land structures, such as mixed forests or intercropping methods, combined with reasonable thinning, can also help the crops under the forest obtain a better light environment. In this way, light can be utilized better and the output can also increase accordingly. This indicates that when designing a system where multiple plants are grown together, it is necessary to consider the light requirements of each crop and appropriately adjust the shape of the tree canopy and the distribution of light, so that different crops can coexist and grow better.

However, in actual operation, it is still quite difficult to achieve a reasonable distribution of light. Because each crop has different light requirements, some prefer strong light while others are suitable for weak light. If the light is too strong or too weak, it may cause crops to grow poorly, and even fruits may not grow at all. Moreover, if a large number of trees or grass are planted in the forest, the structure of the tree crowns, the combination of species and the intensity of tree cutting all need to be carefully considered. Otherwise, the light may be unevenly distributed, and the crops may compete with each other instead. Especially for some herbaceous plants and saplings under the forest, they may also have the problem of "grabbing territory" due to changes in light and temperature. Therefore, these situations should be taken into account when managing forest land.

Future research can start from several directions. First, it is necessary to further clarify exactly how strong the light and which color of light different forest floor crops prefer, and to understand their responses to light from a physiological perspective. Secondly, we can develop light regulation models suitable for growing multiple crops together to help us better plan the structure and management methods of the forest. Thirdly, in the context of increasingly severe climate change, it is also necessary to study how factors such as light, temperature, and soil moisture jointly affect crops, and find ways to make the system as a whole more adaptable to the environment. Finally, it would be best to combine some new sensors and models to monitor and adjust light in real time, so that the forest farmers' system can be both efficient and sustainable.

Acknowledgments
GenBreed Publisher appreciates the modification suggestions from Dr. Qin on the manuscript of this study.

Conflict of Interest Disclosure
The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

References
Ávila-Lovera E., Blanco H., Móvil O., Santiago L., and Tezara W., 2020, Shade tree species affect gas exchange and hydraulic conductivity of cacao cultivars in an agroforestry system, Tree Physiology, 41(2): 240-253.
https://doi.org/10.1093/treephys/tpaa119

Baciu E., Baci G., Moise A., and Dezmirean D., 2023, A status review on the importance of mulberry (*Morus* spp.) and prospects towards its cultivation in a controlled environment, Horticulturae, 9(4): 444.
https://doi.org/10.3390/horticulturae9040444

Baligar V., Elson M., He Z., Li Y., Paiva A., Almeida A., and Ahnert D., 2020, Light intensity effects on the growth, physiological and nutritional parameters of tropical perennial legume cover crops, Agronomy, 10(10): 1515.
https://doi.org/10.3390/agronomy10101515

Chanotra S., Bhat M., Attri M., and Kapoor S., 2024, Mulberry based integrated cropping system: an ideal approach for effective utilization of land resources in Sericulture, International Journal of Agriculture Extension and Social Development, 7: 36-39.
https://doi.org/10.33545/26180723.2024.v7.i4sa.523

Cifuentes L., and Moreno F., 2022, Trait coordination at leaf level explains the resistance to excess light stress in shade-tolerant tropical tree species, Tree Physiology, 42(7): 1325-1336.
https://doi.org/10.1093/treephys/tpac014

De Pauw K., Sanczuk P., Meeussen C., Depauw L., De Lombaerde E., Govaert S., Vanneste T., Brunet J., Cousins S., Gasperini C., Hedwall P., Iacopetti G., Lenoir J., Plue J., Selvi F., Spicher F., Uria-Diez J., Verheyen K., Vangansbeke P., and De Frenne P., 2021, Forest understorey communities respond strongly to light in interaction with forest structure, but not to microclimate warming, The New Phytologist, 233(1): 219-235.
https://doi.org/10.1111/nph.17803

Feng J., Zhao K., He D., Fang S., Lee T., Chu C., and He F., 2018, Comparing shade tolerance measures of woody forest species, PeerJ, 6: e5736.
https://doi.org/10.7717/peerj.5736

Feng L., Raza M., Chen Y., Khalid M., Meraj T., Ahsan F., Fan Y., Du J., Wu X., Song C., Liu C., Bawa G., Zhang Z., Yuan S., Yang F., and Yang W., 2019, Narrow-wide row planting pattern improves the light environment and seed yields of intercrop species in relay intercropping system, PLoS One, 14(2): e0212885.
https://doi.org/10.1371/journal.pone.0212885

Feng X., Zhong M., Zhao X., Zhang X., Hu Y., and Zhang H., 2025, Intercropping forage mulberry benefits nodulation and growth of soybeans, Agriculture, 15(8): 902.
https://doi.org/10.3390/agriculture15080902

García-Pérez J., Oliet J., Villar-Salvador P., and Guzmán J., 2021, Root growth dynamics and structure in seedlings of four shade tolerant Mediterranean species grown under moderate and low light, Forests, 12(11): 1540.
https://doi.org/10.3390/f12111540

Gatti M., Cornaglia P., and Golluscio R., 2023, Morphogenetic and structural responses to tree-shading in three temperate perennial grasses: implications for growth, persistence and defoliation practices, Agroforestry Systems, 97: 549-559.
https://doi.org/10.1007/s10457-023-00809-3

Gerovac J., Craver J., Boldt J., and Lopez R., 2016, Light intensity and quality from sole-source light-emitting diodes impact growth, morphology, and nutrient content of *Brassica* microgreens, Hortscience, 51(5): 497-503.
https://doi.org/10.21273/HORTSCI.51.5.497

Gong X., Liu C., Dang K., Wang H., Du W., Qi H., Jiang Y., and Feng B., 2022, Mung bean (*Vigna radiata* L.) source leaf adaptation to shading stress affects not only photosynthetic physiology metabolism but also control of key gene expression, Frontiers in Plant Science, 13: 753264.
https://doi.org/10.3389/fpls.2022.753264

Jiang Z., Wang Y., Zheng Y., Cai M., Peng C., and Li W., 2020, Physiological and transcriptomic responses of *Mikania micrantha* stem to shading yield novel insights into its invasiveness, Biological Invasions, 23: 2927-2943.
https://doi.org/10.1007/s10530-021-02546-z

Jin F., Wang Z., Zhang H., Huang S., Chen M., Kwame T., Yong T., Wang X., Yang F., Liu J., Yu L., Pu T., Fatima A., Rahman R., Yan Y., Yang W., and Wu Y., 2024, Quantification of spatial-temporal light interception of crops in different configurations of soybean-maize strip intercropping, Frontiers in Plant Science, 15: 1376687.
https://doi.org/10.3389/fpls.2024.1376687

Kamenchuk V., Rumiantsev B., Dzhatdoeva S., Sadykhov E., and Kochkarov A., 2023, Analysis of cross-influence of microclimate, lighting, and soil parameters in the vertical farm, Agronomy, 13(8): 2174.
https://doi.org/10.3390/agronomy13082174

Kang H., Tomimatsu H., Zhu T., Ma Y., Wang X., Zhang Y., and Tang Y., 2022, Contributions of species shade tolerance and individual light environment to photosynthetic induction in tropical tree seedlings, Tree Physiology, 42(10): 1975-1987.
https://doi.org/10.1093/treephys/tpac056

Kara F., 2022, Effects of light transmittance on growth and biomass of understory seedlings in mixed pine-beech forests, European Journal of Forest Research, 141: 1189-1200.
https://doi.org/10.1007/s10342-022-01501-4

Kaushal R., Kumar A., Mandal D., Tomar J., Jinger D., Islam S., Panwar P., Jayaprakash J., Uthappa A., Singhal V., Barh A., and Madhu M., 2024, Mulberry based agroforestry system and canopy management practices to combat soil erosion and enhancing carbon sequestration in degraded lands of Himalayan foothills, Environmental and Sustainability Indicators, 24: 100467.
https://doi.org/10.1016/j.indic.2024.100467

Laub M., Pataczek L., Feuerbacher A., Zikeli S., and Högy P., 2021, Contrasting yield responses at varying levels of shade suggest different suitability of crops for dual land-use systems: a meta-analysis, Agronomy for Sustainable Development, 42: 51.
https://doi.org/10.1007/s13593-022-00783-7

Li M., Wei Y., Yin Y., Zhu W., Bai X., and Zhou Y., 2023, Characteristics of soil physicochemical properties and microbial community of mulberry (*Morus alba* L.) and alfalfa (*Medicago sativa* L.) intercropping system in northwest Liaoning, Microorganisms, 11(1): 114.
https://doi.org/10.3390/microorganisms11010114

Liang X., Gao Z., Shen S., Paul M., Zhang L., Zhao X., Lin S., Wu G., Chen X., and Zhou S., 2020, Differential ear growth of two maize varieties to shading in the field environment: effects on whole plant carbon allocation and sugar starvation response, Journal of Plant Physiology, 251: 153194.
https://doi.org/10.1016/j.jplph.2020.153194

Lu L., Tang Y., Xie J., and Yuan Y., 2009, The role of marginal agricultural land-based mulberry planting in biomass energy production, Renewable Energy, 34: 1789-1794.
https://doi.org/10.1016/j.renene.2008.12.017

Magadum S., Sharma P., Bala M., Kouser R., Sharma A., Deskit L., Aziz F., Lal J., and Singh S., 2020, Evaluation of different mulberry plantation systems for leaf yield and yield contributing characters, International Journal of Current Microbiology and Applied Sciences, 9: 3222-3229.
https://doi.org/10.20546/ijcmas.2020.912.383

Mahesh R., Anil P., Debashish C., and Sivaprasad V., 2020, Improved mulberry productivity and resource efficiency through low-cost drip fertigation, Archives of Agronomy and Soil Science, 68: 749-763.
https://doi.org/10.1080/03650340.2020.1852552

Martinez-Garcia J., and Rodriguez-Concepcion M., 2023, Molecular mechanisms of shade tolerance in plants, The New Phytologist, 239(4): 1190-1202. https://doi.org/10.1111/nph.19047

Modolo G., Santos V., and Ferreira M., 2021, Testing for functional significance of traits: effect of the light environment in tropical tree saplings, Ecology and Evolution, 11: 6480-6492. https://doi.org/10.1002/ece3.7499

Paponov I., and Paponov M., 2025, Supplemental lighting in controlled environment agriculture: enhancing photosynthesis, growth, and sink activity, CABI Reviews, 20: 1. https://doi.org/10.1079/cabireviews.2025.0008

Piao H., Li S., Yan Z., and Li C., 2020, Understanding nutrient allocation based on leaf nitrogen isotopes and elemental ratios in the karst region of southwest China, Agriculture, Ecosystems and Environment, 294: 106864. https://doi.org/10.1016/j.agee.2020.106864

Raai M., Zain N., Osman N., Rejab N., Sahruzaini N., and Cheng A., 2020, Effects of shading on the growth, development and yield of winged bean (*Psophocarpus tetragonolobus*), Ciência Rural, 50(2): e20190570. https://doi.org/10.1590/0103-8478cr20190570

Ren B., Yu W., Liu P., Zhao B., and Zhang J., 2022, Responses of photosynthetic characteristics and leaf senescence in summer maize to simultaneous stresses of waterlogging and shading, The Crop Journal, 11(1): 269-277. https://doi.org/10.1016/j.cj.2022.06.003

Ren Y., Guo G., Wang Z., Zhu L., and Geng B., 2025, Response of yield and protein content of forage mulberry to irrigation in north China plain, Agronomy, 15(5): 1016. https://doi.org/10.3390/agronomy15051016

Schmiege S., Buckley B., Stevenson D., Cuong T., Nam L., and Griffin K., 2020, Contrasting physiological traits of shade tolerance in *Pinus* and Podocarpaceae native to a tropical Vietnamese forest: insight from an aberrant flat-leaved pine, Tree Physiology, 41(2): 223-239. https://doi.org/10.1093/treephys/tpaa123

Shi S., Li H., Wang X., Wang Z., Xu J., He X., and Yang Z., 2025, Greater biomass production under elevated CO_2 is attributed to physiological optimality, trade-offs in nutrient allocation, and oxidative defense in drought-stressed mulberry, Antioxidants, 14(4): 383. https://doi.org/10.3390/antiox14040383

Solanki B., Choudhary R., Ninama A., Ram K., and Jaiswal J., 2024, Review on multilayer farming: a way towards farmer prosperity, International Journal of Environment and Climate Change, 14(1): 150-154. https://doi.org/10.9734/ijecc/2024/v14i13818

Su S., Jin N., and Wei X., 2023, Effects of thinning on the understory light environment of different stands and the photosynthetic performance and growth of the reforestation species *Phoebe bournei*, Journal of Forestry Research, 35: 6. https://doi.org/10.1007/s11676-023-01651-0

Sun Z., Geng W., Ren B., Zhao B., Liu P., and Zhang J., 2023, Responses of the photosynthetic characteristics of summer maize to shading stress, Journal of Agronomy and Crop Science, 209(3): 330-344. https://doi.org/10.1111/jac.12630

Wang L., Dang Q., and Tedla B., 2020, Biochar and alternate partial root-zone irrigation greatly enhance the effectiveness of mulberry in remediating lead-contaminated soils, Journal of Plant Ecology, 13: 757-764. https://doi.org/10.1093/jpe/rtaa063

Wang L., Wang N., and Ji G., 2022a, Responses of biomass allocation and photosynthesis in mulberry to Pb-contaminated soil, Acta Physiologiae Plantarum, 44: 43. https://doi.org/10.1007/s11738-022-03370-1

Wang X., Hu Y., Guo H., Zhang J., Tang T., and Zeng Q., 2022b, Spatial differentiation of the coupling characteristics of soil carbon and nitrogen on mulberry plantations in China, Journal of Resources and Ecology, 14: 84-91. https://doi.org/10.5814/j.issn.1674-764x.2023.01.008

Wang Y., Huang R., and Zhou Y., 2021, Effects of shading stress during the reproductive stages on photosynthetic physiology and yield characteristics of peanut (*Arachis hypogaea* Linn.), Journal of Integrative Agriculture, 20: 1250-1265. https://doi.org/10.1016/S2095-3119(20)63442-6

Win A., Sankhuan D., Chintakovid W., and Supaibulwatana K., 2022, Bioactive compounds produced in leaves of mulberry (*Morus alba* L.) transplants under modified environments of root and aerial zones, Plants, 11(21): 2850. https://doi.org/10.3390/plants11212850

Wu Y., Chen M., Huang S., Li Y., Li M., He D., Hu P., Duan T., Gong W., Yan Y., Kwame T., Raza M., and Yang W., 2025, Combining modelling and experiment to quantify light interception and inter row variability on intercropped soybean in strip intercropping, European Journal of Agronomy, 164: 127508. https://doi.org/10.1016/j.eja.2025.127508

Xu C., De Frenne P., Blondeel H., De Pauw K., Landuyt D., Lorer E., Sanczuk P., Verheyen K., and De Lombaerde E., 2023, Light more than warming impacts understory tree seedling growth in a temperate deciduous forest, Forest Ecology and Management, 549: 121496. https://doi.org/10.1016/j.foreco.2023.121496

Zhang C., Zhu Q., Li J., Zhang H., Lee D.S., and Chen L.J., 2024, Regulatory mechanisms of temperature, light, and water on the expression of male sterility genes in rice, Molecular Plant Breeding, 15(6): 429-441.
https://doi.org/10.5376/mpb.2024.15.0040

Zhang M., Wang N., Zhang J., Hu Y., Cai D., Guo J., Wu D., and Sun G., 2019, Soil physicochemical properties and the rhizosphere soil fungal community in a mulberry (*Morus alba* L.)/alfalfa (*Medicago sativa* L.) intercropping system, Forests, 10(2): 167.
https://doi.org/10.3390/f10020167

Zhang T., Dong G., Tian Y., Zhou Y., Li Y., Zhang S., and Li H., 2023, Effects of drought stress and Ca supply on the biomass allocation strategies of poplar and mulberry, Forests, 14(3): 505.
https://doi.org/10.3390/f14030505

Zhang X., Teng Z., Zhang H., Cai D., Zhang J., Meng F., and Sun G., 2021, Nitrogen application and intercropping change microbial community diversity and physicochemical characteristics in mulberry and alfalfa rhizosphere soil, Journal of Forestry Research, 32: 2121-2133.
https://doi.org/10.1007/s11676-020-01271-y

Zhu B., Liu F., Xie Z., Guo Y., Li B., and Ma Y., 2020, Quantification of light interception within image-based 3D reconstruction of sole and intercropped canopies over the entire growth season, Annals of Botany, 126(4): 701-712.
https://doi.org/10.1093/aob/mcaa046