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Effects of Light Intensity on Seedling Emergence and Early Growth of *Liquidambar formosana* Hance

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Abstract: *Liquidambar formosana* Hance is a common deciduous broad-leaved tree known for its fast growth rate and adaptability. However, excessive logging has substantially reduced the area of natural forest patches of *L. formosana*, and seedling regeneration is essential for the long-term continuation of *L. formosana* populations. To explore the effects of light intensity on the seedling emergence and early growth of *L. formosana*, a controlled experiment was conducted under three light-intensity treatments (20%, 60%, and 100% of full sunlight, i.e., the photosynthetic photon flux densities (PPFDs) were 223.93 ± 7.54, 670.94 ± 30.14, and 1119.61 ± 23.19 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively). The seedling emergence percentage, mean germination time, germination synchrony, vitality index, survival percentage, emergence index, morphological characteristics, and biomass allocation under different light intensities were analyzed. The seedling vitality index and survival percentage significantly differed among the treatments and were the lowest under 20% light intensity. With increased light intensity, the seedling mean germination time and germination synchrony increased and then decreased, and the opposite was true for the emergence index. With the increased light intensity, the seedling height, stem diameter, and root length significantly increased. The total, root, stem, and leaf biomasses reached maximum values under full sunlight. With the increased light intensity, the leaf biomass ratio increased, whereas the root biomass, stem biomass, and root–shoot ratios decreased. Our results indicated that the poor light environment under the canopy is not conducive to the survival and growth of *L. formosana* seedlings and may be among the primary reasons for low seedling establishment.

Keywords: biomass allocation; morphological plasticity; natural regeneration; shading

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1. Introduction

Liquidambar formosana Hance (Hamamelidaceae), a common deciduous broad-leaved tree in subtropical broad-leaved evergreen forests, is known as the "pioneer of barren hills" because of its fast growth rate and strong adaptability [1]. *Liquidambar formosana* has a high ornamental value, and, through soil and water conservation, it improves soil quality and contributes to ecological stability. In addition, it is important for the restoration of vegetation and the succession of evergreen broad-leaved forests [2]. Furthermore, its roots, leaves, and fruits are used as medicine, and the relatively hard wood is widely used in the construction of houses and production of furniture [3]. However, over the past few centuries, excessive human logging has substantially reduced the area of the natural forest of *L. formosana* in southeastern Hubei, Guizhou, and northern Guangxi provinces of China [4,5]. *Liquidambar formosana* regeneration occurs through seedling regeneration and budding [6,7]. To adapt to anthropogenic disturbance, *L. formosana* mainly relies on the budding regeneration of felled stakes; however, this strategy does not maintain the genetic diversity and productivity of *L. formosana*. Therefore, natural regeneration from seeds is particularly important for the long-term continuation of *L. formosana* populations.

Previous studies show that adult trees of *L. formosana* can produce a large number of viable seeds [8,9], indicating that seed source restriction is not the primary cause of poor regeneration of *L. formosana* natural populations. The seed-to-seedling transition is generally the key stage determining the survival of plants. This stage is often affected by the microhabitats occupied by seeds after dispersal [10,11]. Seedling regeneration is impacted by many ecological factors such as light, moisture, and temperature [12,13]. Field observations indicate that most of the seedlings are concentrated at the forest edge and almost none in the forest understory. Correspondingly, Wang et al. [14] reported that the mortality rate of *L. formosana* seedlings was as high as 90% at a 3% light transmittance. The seeds of *L. formosana* are generally dispersed into different environments (such as forest understory, forest gap, and forest edge) with different light intensities, which may affect seed emergence and seedling establishment. Previous studies have shown that the seedling emergence percentage of *L. formosana* is at a high level under a variable temperature environment of 10–20 °C and 25% soil moisture. The temperature of spring in the southern region of China is generally within 16–23 °C, and there is sufficient rainfall in the south with few drought conditions [15], so water and temperature may not be limiting factors for the seedling emergence and early growth of *L. formosana* [16–18]. Thus, we hypothesized that poor light in the understory affects the seedling emergence and early growth of *L. formosana* and is one of the important factors leading to poor natural regeneration.

In this study, a controlled experiment was conducted to investigate the seedling emergence, seedling survival, and seedling growth of *L. formosana* under three light intensities (20%, 60%, and 100% of full sunlight, i.e., the photosynthetic photon flux densities (PPFDs) were 223.93 ± 7.54, 670.94 ± 30.14, and 1119.61 ± 23.19 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively) that simulated natural environmental conditions in *L. formosana* populations. We specifically aimed to (1) determine the optimal light intensity for *L. formosana* seedling emergence and early growth and (2) ascertain whether seedling emergence and growth have different light requirements. Our results would provide a theoretical basis for enhancing the natural regeneration and effective management of *L. formosana* populations.

2. Materials and Methods

2.1. Seed Collection

Fruits of *L. formosana* were collected in October 2019 from Zhangping Wuyi State Forest Farm, Fujian province, China (25°02′ N, 117°29′ E; 900 m a.s.l.). Fruits were randomly collected from at least 15 individual *L. formosana* stands with mature trees. The collected fruits are placed in the sun for 3 to 5 days, during which time they were turned twice with a wooden shovel, and the fruits cracked and seeds came out, and then the impurities of the seeds were removed with a fine sieve [19]. All seeds were manually washed, air-dried, disinfected, and stored at 4 ± 2 °C in the dark until sowing.

2.2. Experimental Design and Shade Treatment

The study was constructed in a flat, open area at Fujian Agriculture and Forestry University (26°15′ N, 119°30′ E; 850 m a.s.l.) in March 2020. Three light gradients (20%, 60%, and 100% of full sunlight) were created using shade houses covered with black nylon shade cloth at increasingly higher mesh gauges. The 20%, 60%, and 100% of full sunlight intensities correspond to the light conditions in forest understory, forest edge, and open space, respectively. The photosynthetic photon flux densities (PPFDs) of 20%, 60%, and 100% were 223.93 ± 7.54, 670.94 ± 30.14, and 1119.61 ± 23.19 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively. A Taiwan Hipoint handheld spectrometer (HP350) was used to measure the light intensity.

Before sowing seeds, pretreatment was required. The seeds of *L. formosana* were washed with deionized water and subsequently soaked with warm water at 20 °C for 12 h. Then, the seeds were disinfected in 1% carbendazim solution for 2 h, rinsed with deionized water, and soaked in warm water at 50 °C until the water naturally cooled down to room temperature [20]. The seeds were soaked in periodical stirring in the same water at room temperature for an additional 12 h to promote emergence. Floating seeds were discarded. Those seeds that immediately sank to the bottom were considered viable. Only viable seeds of a similar size and shape were used. Moreover, a thousand seeds' weight was 4.5 ± 0.13 g in this study. The seeds were sown in 16.5 cm × 17.0 cm plastic pots filled with a mixture of peat soil and vermiculite at a 2:1 ratio. Six replicates were prepared per treatment. Fifty seeds were sown in each pot and then covered with approximately 1 cm substrate [21]. During the experiment, timely watering ensured the growth and development of plants and continuous soil moisture. To ensure an even distribution of light over each pot, the position of the pots was adjusted every two days.

2.3. Investigation of Seedlings of Emergence and Early Growth

The number of emerged seedlings and number of dead seedlings were daily recorded; the counting was terminated if no new seeds emerged after 7 days. Seedling emergence was defined by a seed that emerged with the protrusion of fully expanded cotyledons through the soil surface [20]. Seedling survival was quantified by subtracting the number of dead seedlings from the total number of seedlings that had emerged, whereby a seedling was considered dead upon tissue desiccation following the wilting of the cotyledon when present. Based on the observed data, we calculated the seedling cumulative emergence, emergence percentage, the mean germination time (MGT), germination synchrony, vitality index, survival percentage, and emergence index.

$$\text{Cumulative emergence} = (\text{total number of seedlings emerged on day i/total number of seeds tested}) \times 100\%$$

$$\text{Emergence percentage} = (\text{total number of emerged seedlings/total number of seeds tested}) \times 100\%$$

$$\text{MGT} = \frac{\sum_{i=1}^{k} \text{niti}}{\sum_{i=1}^{k} \text{ni}}$$

where ni is the number of seeds that emerged in the ith time; k is the last day of emergence evaluation; and ti is the time from the beginning of the experiment to the ith observation.

Germination synchrony is the quotient between the sum of the partial combinations of the number of seeds that emerged in each ti, two by two and the two by two combination of the total number of seeds that emerged at the end of the experiment, assuming that all seeds that emerged simultaneously did so.

$$\text{Germination synchrony} = \frac{\sum_{i=1}^{k} C_{ni,2}}{C_{\sum ni,2}}, \text{ being } C_{ni,2} = \text{ni}\,(\text{ni} - 1)/2$$

where $C_{ni,2}$ is the combination of seeds that emerged in the ith time, two by two; ni is the number of seeds that emerged in the ith time; and k is the last day of emergence evaluation.

$$\text{Emergence index} = \Sigma\text{Gi/Di}$$

where Gi is the number of emerged seeds in the ith time, and Di is the corresponding number of emergence days.

$$\text{Vitality index} = \text{emergence index} \times \text{seedling root length}$$

Survival percentage = (total number of surviving seedlings/total number of seeds tested) × 100%

In the middle of June 2020, all seedlings were measured to determine heights and stem diameters. The height from the soil surface to highest point of the live crown was obtained with a measuring tape. The stem diameter was measured at 1 cm from the ground with Vernier calipers. Then all seedlings were divided into roots, stems, and leaves. Roots were carefully washed using distilled water. All plant tissues were placed in separate envelopes and oven-dried first at 105 °C for 2 h and then at 85 °C for 48 h to a constant weight. Dry weight of leaves, roots, and stems were separately measured. The total biomass, root biomass ratio, stem biomass ratio, leaf biomass ratio, and root–shoot ratio of the seedlings were calculated as follows:

$$\text{Total biomass} = \text{root biomass} + \text{stem biomass} + \text{leaf biomass}$$

$$\text{Root biomass ratio} = \text{root biomass}/\text{total biomass}$$

$$\text{Stem biomass ratio} = \text{stem biomass}/\text{total biomass}$$

$$\text{Leaf biomass ratio} = \text{leaf biomass}/\text{total biomass}$$

$$\text{Root-shoot ratio} = \text{root biomass}/\text{stem and leaf biomass}$$

2.4. Data Analysis

Data were recorded and plotted in Microsoft Excel 2010 and analyzed using SPSS 20.0 software (IBM Corp., Armonk, NY, USA). The differences between treatments were assessed using a one-way analysis of variance and least significant difference (LSD) tests, with a significance level of 0.05. Data were presented as average ± standard error. Graphs were drawn using Origin2018 (OriginLab, Northampton, MA, USA) and Excel software.

3. Results

3.1. Effects of Light Intensity on Seedling Emergence

The emergence experiment lasted 43 days. The first cotyledon through the soil surface appeared on the 10th day after sowing and quickly entered the peak period of seedling emergence under all light intensities. Under 20% light intensity, the seedling emergence percentage reached a maximum in the first 5 days after emergence, closely followed by the maximum cumulative emergence (66%; Figure 1). Under 60% and 100% light intensities, the maximum seedling emergence percentage was observed on days 37 (67%) and 22 (74%) after sowing, respectively. In the first 5 days of seedling emergence, under 20% light intensity, the seedling emergence percentage was significantly higher than those under 60% and 100% light intensities, but the emergence lasted just 7 days. In contrast, the emergence period under the other two treatments lasted longer, and the cumulative emergence was the highest under 100% light intensity.

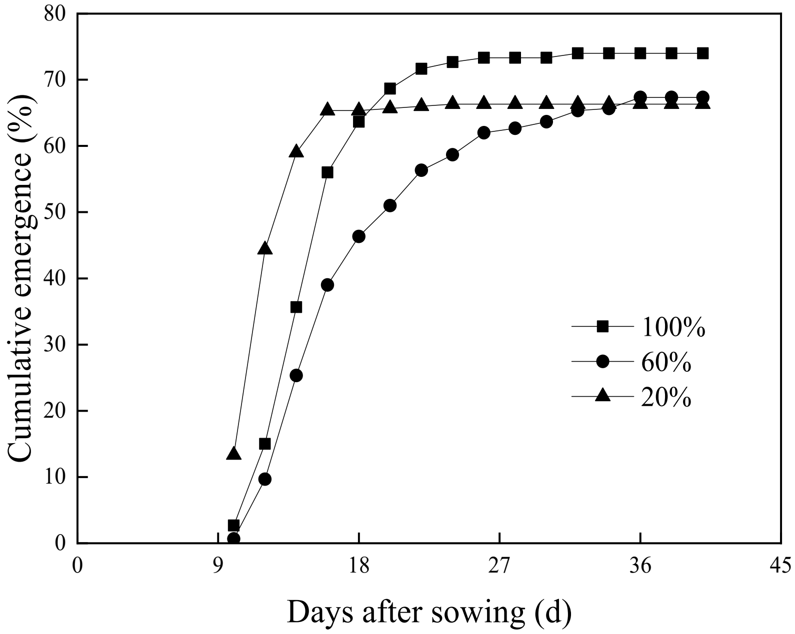

Figure 1. Cumulative emergence of *Liquidambar formosana* seedlings under different light intensities.

There was no significant difference in the seedling emergence percentage among three light-intensity treatments. The mean germination time and germination synchrony were significantly higher under 60% light intensity than under 20% and 100% light intensities. The seedling vitality index and survival percentage decreased with decreasing light intensity, reaching the lowest levels under 20% light intensity. The emergence index under 60% light intensity was significantly lower than that under the other two treatments (Figure 2).

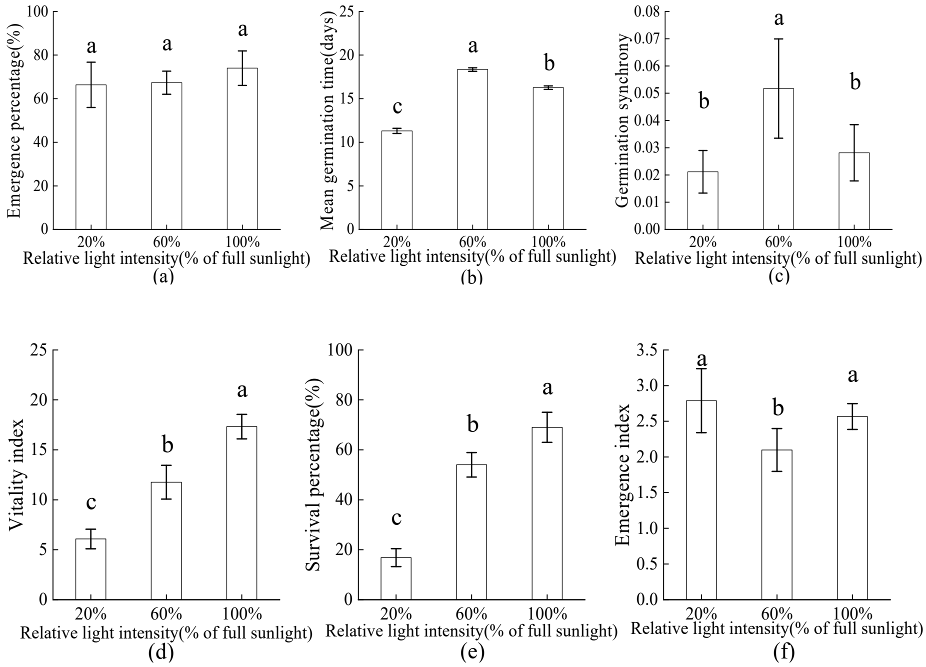

Figure 2. (**a**) Emergence percentage; (**b**) mean germination time; (**c**) germination synchrony; (**d**) vitality index; (**e**) survival percentage; and (**f**) emergence index. They are all measured indicators of *Liquidambar formosana* seedlings under different light intensities. Different letters denote significant differences among average values of treatments at the 0.05 level, and the error bars denote standard deviation.

3.2. Effects of Light Intensity on Growth and Morphological Characteristics of L. formosana Seedlings

The seedling height, stem diameter, and root length increased with increasing light intensity (Figure 3). Under 20%, 60%, and 100% light intensities, the seedling height was in the range of 4.95–5.90, 6.40–7.17, and 9.18–9.92 cm, respectively; the stem diameter was in the range of 0.65–0.74, 0.78–0.91, and 1.07–1.19 cm, respectively; and the root length was in the range of 1.70–2.32, 4.68–5.77, and 6.34–8.11 cm, respectively. The distribution trend was concentrated, with no outliers.

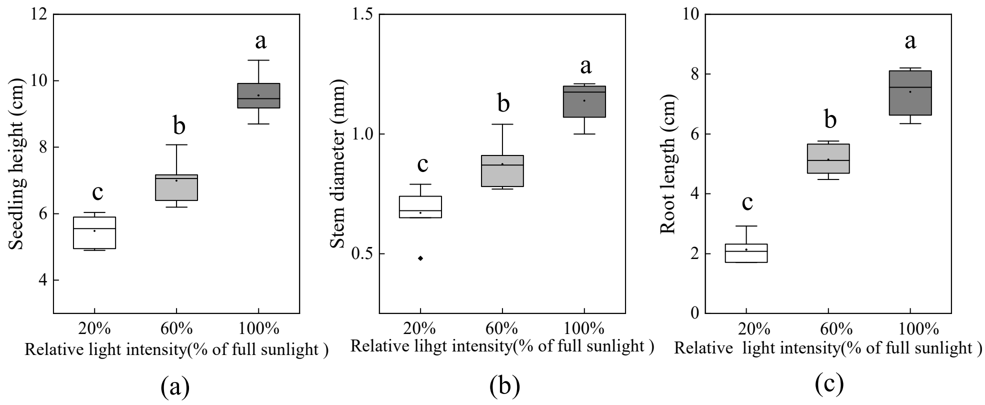

Figure 3. (**a**) Seedling height; (**b**) stem diameter; and (**c**) root length. They are all measured indicators of *Liquidambar formosana* seedlings under different light intensities. Different letters denote significant differences among average values of treatments at the 0.05 level, and the error bars denote confidence interval.

3.3. Effects of Light Intensity on Biomass Accumulation and Allocation

The changes in the root, stem, leaf, and total biomasses of *L. formosana* seedlings followed the same trend, reaching maximum values under 100% light intensity and minimum values under 20% light intensity (Figure 4).

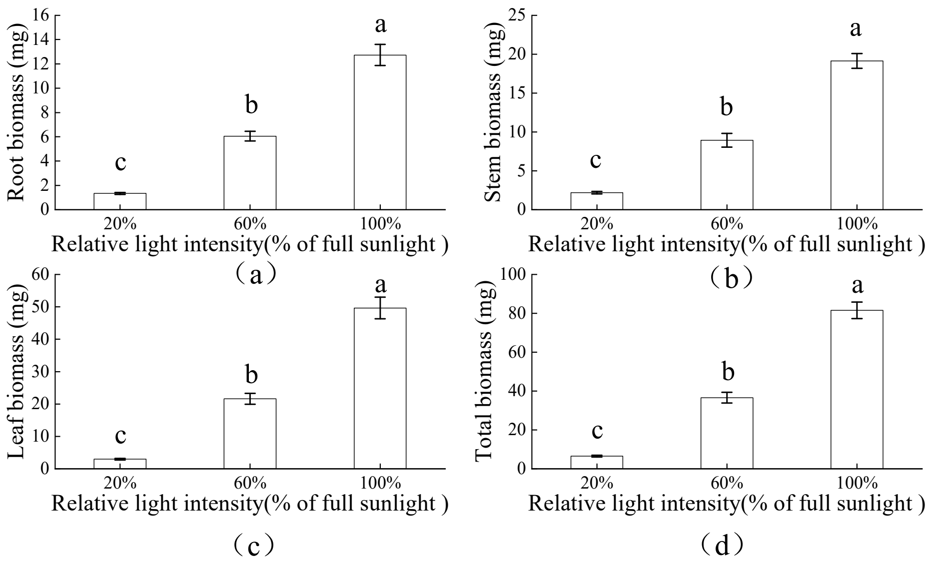

Figure 4. (**a**) Root biomass; (**b**) stem biomass; (**c**) leaf biomass; and (**d**) total biomass. They are all measured indicators of *Liquidambar formosana* seedlings under different light intensities. Different letters denote significant differences among average values of treatments at the 0.05 level, and error bars denote standard deviation.

As light intensity increased, the root biomass, stem biomass, and root–shoot ratios decreased, and they were significantly higher under 20% than under 100% and 60% light intensities. Conversely, the leaf biomass ratio increased with increasing light intensity, and it was significantly lower under 20% light intensity than under the other two treatments. In addition, there was no significant difference in biomass allocation to the roots, stems, leaves, and root–shoot ratio under 60% and 100% light intensities (Figure 5).

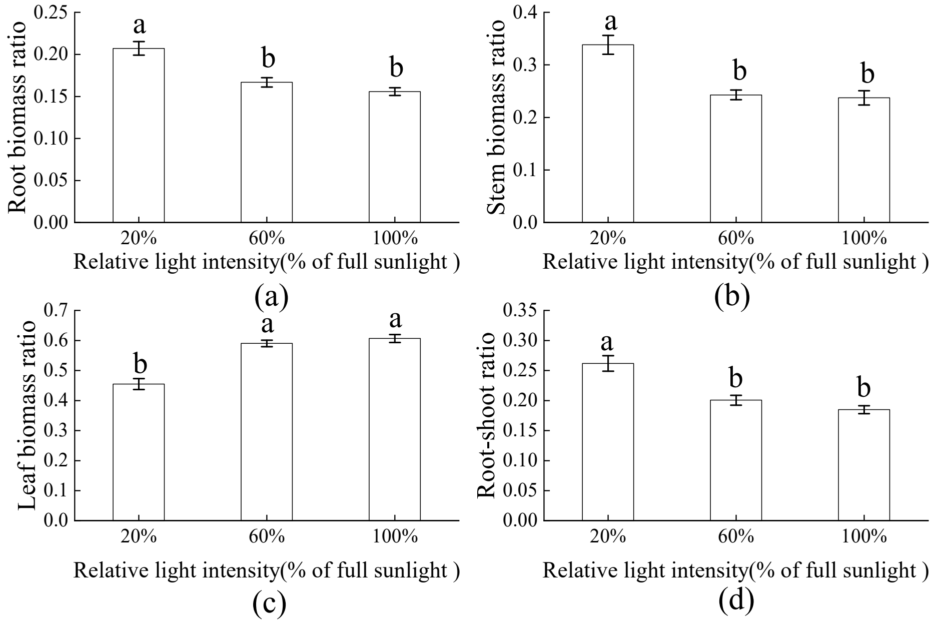

Figure 5. (**a**) Root biomass ratio; (**b**) stem biomass ratio; (**c**) leaf biomass ratio; and (**d**) root–shoot ratio. They are all measured indicators of *Liquidambar formosana* seedlings under different light intensities. Different letters denote significant differences among average values of treatments at the 0.05 level, and the error bars denote standard deviation.

4. Discussion

4.1. Seedling Emergence of L. formosana under Different Light Intensities

Studies have shown that the light intensity necessary for seedling emergence is determined by environmental and genetic factors [12,22]; therefore, the light requirements of seedling emergence from different tree species also differ. Notably, light directly affects seedling emergence not as an energy source but as a signal that stimulates seedling emergence [23]. In the present study, although the seedling emergence percentage of *L. formosana* was the highest under 100% light intensity, there was no significant difference in the seedling emergence percentage among different light-intensity treatments; the result indicated that the effect of light intensity on the emergence of *L. formosana* seedlings was not evident, similar to the results of previous studies on the seedling emergence of *Keteleeria fortunei* (A. Murray) var. *cyclolepis* (Flous) Silba (Pinaceae), *Betula halophila* Ching ex P.C. Li (Betulaceae), *Incarvillea sinensis* Lam (Bignoniaceae), and *Hypochaeris grandiflora* F.Phil (Asteraceae) [24–26]. In this study, MGT was negatively correlated with the seedling emergence index, and MTG was the highest and the seedling emergence index was the lowest at 60% light intensity. The result indicated that MGT successfully revealed the differences in seed vigor under different light-intensity conditions, as shown by their seedling emergence index in the experiment, similar to the results of previous studies on the seedling emergence of *Astragalus sinicus* L., *Abelmoschus esculentus* L. Moench, and *Gleditsia triacanthos* L. Fabaceae; the seed lots with longer MGT are lots with slow and lower emergence, and vice versa [27–29]. Plants can have synchronous seed germination (i.e., the germination of all seeds occurs at the same time), with the benefit that any suitable conditions can benefit all seeds in the seed bank. Similarly, faster germination may bring benefits in terms of early access to resources (or space) and can lead to less competition in the initial stages of establishment [30]. Germination synchrony in this study was significantly higher under 60% light intensity than under other light-intensity conditions. However, the mean germination time and seedling emergence index were significantly lower under 60% light-intensity conditions than under 20% and full sunlight conditions. The study suggested that in natural environments, increased seed germination synchrony may have a negative impact on the species if unsuitable conditions after germination result in high seedling mortality. In contrast, asynchronous germination may ensure that seeds appear in the soil seed bank at different times of the year, promoting the persistence of the species [31,32]. Simultaneously, the seedling vitality index and survival percentage significantly increased with increasing light intensity, similar to the results of a study on the survival rate of *Pinus yunnanensis* (Franch) var. *tenuifolia* Cheng & Law (Pinacese) [33], indicating that light is the key factor affecting the survival of *L. formosana* seedlings and proving that the growth of *L. formosana* improves under strong light conditions. In the closed evergreen broad-leaved forest, the lack of light in the forest understory has little effect on the emergence process of *L. formosana* seedlings. However, the survival percentage of seedlings after seedling emergence will be low, and growth will be seriously inhibited, severely hindering the natural regeneration of *L. formosana*. This result is consistent with the findings of a study on a *L. formosana* forest in southeastern Hubei province [34]. Therefore, light intensity has little effect on the seedling emergence percentage but has a significant effect on the seedling survival percentage. This may be an important limiting factor of *L. formosana* regeneration in the forest understory.

4.2. Morphological Characteristics of L. formosana Seedlings under Different Light Intensities

Plants in different light-intensity environments improve the population's fitness and ability to obtain resources through morphological regulation [35]. Under the growth environment of the artificial setting of different light treatments, the different response of the seedling morphology of tree species to light treatment reflects the different adaptability and ecological countermeasures of the tree species. In our study, the seedling height, root length, and stem diameter of *L. formosana* seedlings significantly increased with increasing light intensity. Several studies have shown that enhanced light within a specific range promotes the growth of seedlings [36–38]. The results of the present study were similar to the morphological characteristics observed in the seedlings of *Quercus mongolica* Fisch. ex Ledeb. (Fagaceae) and *Pinus massoniana* Lamb. (Pinaceae) under different light intensities [39,40].

As an important environmental factor, light directly affects the growth and developmental processes of the aboveground plant parts and indirectly affects the underground roots [39]. Typically, at high light intensities, plants exhibit more developed root systems that adapt to strong light conditions by expanding their underground parts to absorb more water and nutrients [41]. To improve light interception in a closed forest environment, plants usually invest more resources in the growth and elongation of seedlings and thickening of the stem diameter, resulting in the increased seedling height and stem diameter, as well as decreased root length [42]. In the present study, the decrease in light intensity resulted in a significant decrease in the seedling height, stem diameter, and root length of *L. formosana* seedlings. Under shade conditions, the lack of light inhibits photosynthesis in the aboveground parts, which affects the transport of photosynthetic products to the root system, and, therefore, root growth is inhibited [39]. As a result, an insufficient amount of energy is invested on the root length, seedling height, and stem diameter received, inhibiting plant growth.

4.3. Biomass Accumulation and Allocation Pattern in L. formosana Seedlings under Different Light Intensities

The differences in biomass accumulation and biomass allocation of different organs under different light intensities are a comprehensive expression of the effective utilization of resources and the supply of environmental resources, reflecting the adaptation characteristics of plants under different light intensities. Studies have shown that there may be two kinds of effects of light on plant biomass allocation: the optimal light intensity for biomass accumulation of different species is different. For example, Zhang Lan et al. [35] studied *Quercus wutaishanica* Mayr. growing under different light intensities. The results showed that biomass accumulation peaked under medium shading, whereas the total biomass of *Bretschneidera sinensis* Hemsl. seedlings peaked under heavy shading [43]. Under different light intensities, the distributions of the biomass of the same plant in different organs are different. In general, plants growing under higher light intensities allocate more biomass to the underground part for root growth, which facilitates mineral and water absorption and reduces leaf temperature to meet plant growth needs [44]. Plants growing in a poor-light environment will allocate more biomass to the aboveground part for leaf growth in order to fully absorb limited light energy and meet the photosynthetic needs of plants [45]. The optimal allocation of plant biomass is based on the fact that plants can obtain sufficient light energy for photosynthesis to meet the needs of plant growth, and, therefore, there is a tradeoff mechanism in biomass allocation [46].

Resources in plant habitats can directly determine the biomass accumulation of plants. Light directly affects the photosynthetic efficiency of plants, production of organic matter, and accumulation biomass [47]. Our results indicated that the growth characteristics of *L. formosana* seedlings were significantly better under full light than under shade, and the root, stem, leaf, and total biomasses were significantly higher under full sunlight than under shade conditions. The growth characteristics of *L. formosana* seedlings were the highest under full light and the lowest under 20% light intensity, which may be related to the ecological characteristics of *L. formosana*. Because *Liquidambar formosana* is a light-loving tree species, full sunlight provides sufficient energy for its growth and development, while a large amount of biomass is accumulated. Under shade conditions, seedlings will adopt conservative strategies to reduce resource acquisition and energy consumption; thus, the biomass of each organ will decrease. The decrease in the root biomass results in the weakening of the plant's ability to absorb underground water and nutrients, causing a reduction in the photosynthetic rate. The decrease in the stem biomass leads to a decrease in the transport capacity of plants, while a decrease in the leaf biomass leads to a decrease in the plant's ability to capture light, resulting in reduced photosynthesis. Finally, the overall biomass of the plant decreases [2].

Changes in the root–shoot ratio of trees are an adaptation strategy for distributing photosynthates to better meet the needs for growth and development under a changing environment [48]. Generally, in poor-light environments, plants will allocate more biomass to aboveground parts, increasing the biomass of stems and leaves, and thus will capture more solar radiation energy. In full-light environments, the restriction in plant growth mainly originates from the root system; thus, plants will allocate more biomass to the belowground parts [49]. On the contrary, in the present study, the root–shoot ratio of *L. formosana* seedlings decreased with a decrease in light intensity, which may be related to the species characteristics of *L. formosana*. Owing to its propensity for light, in a sufficient light environment, more biomass was allocated to the leaves to ensure increased photosynthesis and the accumulation of more matter and energy. In a poor-light environment, the biomass distribution pattern of *L. formosana* may be explained by the stress tolerance hypothesis, which suggests that shade-tolerant plants will invest more biomass in the stem and propels the roots and stems to store more material to improve their tolerance to the poor-light environment.

5. Conclusions

The seedling emergence percentage of *L. formosana* was not significantly affected by light intensity but slightly increased under full-light conditions. The survival percentage of *L. formosana* seedlings was the lowest under 20% light intensity. The mean germination time and germination synchrony were the highest, and the emergence index was the lowest under 60% light intensity. The biomass of each plant part significantly decreased with decreasing light intensity. Our findings suggested that poor-light conditions under the canopy at least partially explain the low numbers of *L. formosana* seedlings found under forest canopy. Furthermore, under poor-light conditions, *L. formosana* seedlings allocated more biomass to the roots and less biomass to the shoots, supporting the functional equilibrium theory that balances tradeoffs between aboveground part growth (for light interception) and root growth (for nutrient and water acquisition). Therefore, silvicultural measures such as thinning or gap openings are recommended to increase light irradiance in the forest understory with the aim of improving the natural regeneration of *L. formosana.* Based on the results of this study, it is suggested that the gap should be at least twice the average tree height of *L. formosana* to ensure adequate illumination under the forest.

Author Contributions: The authors confirm contribution to the paper as follows: study conception and design: B.L., S.G., L.W., Z.T. and X.T.; data collection: S.G., H.C. and M.L.; analysis and interpretation of results: H.C., B.H. and B.L.; draft manuscript preparation: H.C., B.L., X.T. and Z.T. All authors have read and agreed to the published version of the manuscript.

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