

Article

Plastic Responses in Growth, Morphology and Biomass Allocation of Five Subtropical Tree Species to Different Degrees of Shading

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Abstract: We investigated how different degrees of shading affected growth, morphology, and biomass allocation in seedlings from two coniferous and three broadleaved species. The experiment was conducted in a shade house over a 1-year period. Our results showed that under increasing shade, seedlings from most species exhibited lower total biomass, net assimilation rates, relative growth rates, root mass ratios, and root/shoot ratios. In contrast, the slenderness quotients, leaf area ratios, and specific leaf areas increased with increasing shade. For coniferous species, growth traits were relatively more plastic (responsive to shade) than morphology or biomass allocation traits, whereas for broadleaved species, growth and biomass allocation were the most shade-sensitive traits. When comparing coniferous versus broadleaved species, the former had a higher growth plasticity index and lower allocation plasticity than the latter. Root biomass and stem mass ratio were the most and least plastic traits in response to shading. Our results indicate that shade differentially affects coniferous and broadleaved species in terms of their growth, morphology, and biomass allocation. These findings have important implications for the establishment and maintenance of mixed-species stands.

Keywords: plasticity; light adaptation; shade tolerance; morphology; shade avoidance syndrome

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1. Introduction

China has the largest monoculture plantation area (~69 × 10⁶ ha) worldwide, accounting for 25% of global plantations [1]. The majority of these Chinese plantations are even-aged [2], and in general, even-aged monocultures lead to declines in biodiversity and ecosystem structure and functions [3–6]. A way to resolve this negative outcome is by converting the plantations into complex mixed-species stands [7–9], such as through selecting suitable species for under-planting among the existing monoculture [10–12]. Mixed-species planting not only improves stand structure and forest products but also promotes important ecosystem services [13]. However, a major challenge facing forest managers when choosing the most appropriate silvicultural management strategy is a lack of information on how different species grow in shaded conditions [14]. Therefore, more data regarding interspecific variation in shade tolerance is needed for managing mixed-species understory plantations.

Shade tolerance is related to the ability of a tree species to efficiently capture and use limited light resources [15], achieved through a combination of morphological and physiological adaptations [16]. To mitigate stress and maximize light capture, plants in low-light conditions, such as tree seedlings under closed-canopy forests, survive through adjusting multiple aspects of their growth, morphology, and resource allocation [17–19]. For example, plants usually reduce growth rates in response to increasing shade [1,16]. For most species, height, diameter, and biomass accumulation are negatively correlated with shade levels [1,14,20]. However, because growth strategies differ markedly among plant species, we must better understand subtle interspecific differences in response to shading before we can create an optimal light environment for target trees.

To date, the majority of comparative studies have assessed seedling growth in response to two or three shade levels [14,21]. As a result, the general qualitative responses to shade are well known for many species. However, we know far less about seedling response to shade gradients. For example, Poorter [22] assessed the growth rates of 15 rainforest tree seedlings across five light levels. The results showed that morphology and biomass allocation had the widest variation at poor light levels, while most seedlings reached maximum growth rates at intermediate light levels. In general, the available evidence indicates that growth and morphological characteristics are more sensitive to resource availability than is biomass allocation [23]. This trend is likely because biomass allocation has low phenotypic plasticity, being largely ontogenetic and varying little according to resource availability. Thus, clarifying the plastic responses to shade would allow us to determine the optimal irradiance level for a species to achieve maximal growth.

Plasticity in response to shade may be related to foliage physiognomy (coniferous versus broadleaf), as leaves are considered the most plastic plant organs [24]. Coniferous needles generally have lower photosynthetic rates, leaf N, and specific leaf area (SLA) than broad leaves [25,26]. However, we do not know the extent to which coniferous and broadleaved species exhibit plasticity in morphological and biomass allocation under shaded conditions nor do we understand how these responses vary across species with differing shade tolerance.

In this study, we examined the plastic responses of five tree species, *Cunninghamia lanceolata* (Lamb.) Hook, *Pinus massoniana* Lamb., *Phoebe zhennan* S. Lee, *Schima superba* Gardn. et Champ., and *Liquidambar formosana*. Hence, to different degrees of shading, *C. lanceolata*, the high-yielding, fast-growing conifer, is one of the most important plantation species in China [12]. Similar to other monoculture species, soil degradation, production loss, biodiversity reduction, and a lack of self-regeneration all threaten the sustainability of *C. lanceolata* plantations [1,27–30]. To overcome this problem, *P. zhennan*, *S. superba*, *L. formosana*, and *P. massoniana* have been planted in the understory of various *C. lanceolata* stands [1,28,31,32]. Both *C. lanceolata* and *P. massoniana* are coniferous and considered to be light-demanding [1,33], whereas *S. superba*, *P. zhennan*, and *L. formosana* are shade-tolerant broadleaved trees. However, most of this classification is based on traditional categorization of tree species into shade-tolerance classes according to the silvics of the species rather than empirical research evaluating species-specific responses to different shade levels. Thus, we tested the growth, morphology, and biomass allocation of five widely distributed subtropical tree species (*C. lanceolata*, *P. massoniana*, *S. superba*, *P. zhennan*, and *L. formosana*) under five shade levels. We focused on the seedling stage because it is the stage with the highest selective pressure. Our key objectives were to determine: (1) species-specific patterns in growth, morphology, and biomass allocation under various shaded conditions; (2) whether broadleaved species have higher plasticity than coniferous species in response to shade; (3) whether growth and morphological traits are more sensitive to shade than biomass allocation; and (4) which phenotypic traits have the most plastic response to shade.

2. Materials and Methods

2.1. Experimental Design and Shade Treatments

We established a controlled shading experiment at Fujian Agriculture and Forestry University (Figure 1). We created five shade treatments: 0% shaded (no-shade, 100% full sunlight), 40% shade (60% full sunlight), 60% shaded (40% full sunlight), 85% shaded (15% full sunlight), and 95% shaded (5% full sunlight) conditions. Light conditions were measured with light meters during a clear day, as described previously [1]. Each shade treatment was created through erecting individual shade houses covered with black polypropylene fabric of different mesh sizes. The 0% shaded control did not use a shade fabric. The shade houses were placed parallel to the sun's daily track to minimize spatiotemporal variation in solar radiation [1,34] and ensure consistency in other environment factors. Between-species comparisons of seedling development under uniform light conditions help elucidate important morphological traits for growth and survival while contributing to our understanding of the biodiversity-maintenance mechanisms in forest communities.

In May 2018, seedlings were transplanted into pots containing a mixture of peat soil and vermiculite (2:1 *v/v*) and grown in a glasshouse for 1 month, with one seedling per pot. Subsequently, seedlings with similar height and basal diameter from each species were selected and randomly assigned to one of the five shade treatments. Each shade group consisted of five seedlings per species. Individual seedling pots were randomly positioned to ensure that each plant was exposed to the same light environment with no mutual shading. Pots were rotated weekly to ensure homogeneous conditions. The experiment lasted for 1 year. To guarantee sufficient soil moisture for seedling establishment, all seedlings were watered 2–3 times per week. Shade houses were not waterproofed; more rainfall was blocked as mesh gauges increased, so the water supply amount under different treatments was not consistent. It should be adjusted according to actual situation to ensure that the soil moisture under each treatment is relatively consistent as much as possible.

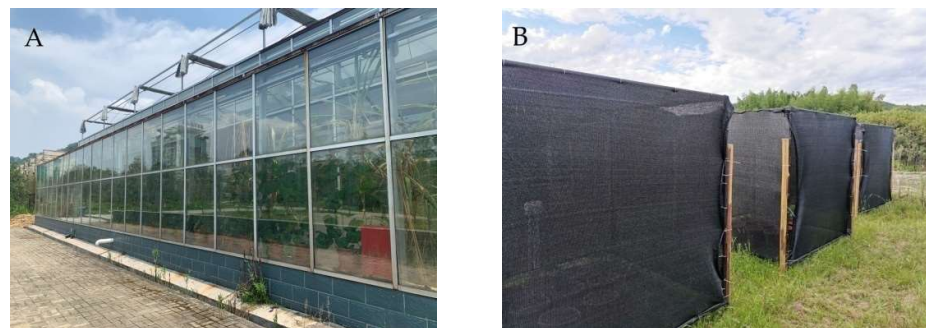


Figure 1. Glasshouse (A) and shade house (B) of the experiment.

2.2. Seedling Functional Traits

Prior to shade treatment, initial growth status (stem basal diameter, height, leaf area, leaf biomass, stem biomass, and root biomass) was determined based on a random selection of 10 seedlings. At the end of the experiment (June 2019), basal diameter and height were measured before seedlings were harvested. The height was measured vertically from the soil surface to the stem apex using a measuring tape. Basal diameter was measured with Vernier calipers to the nearest 0.01 mm. Leaf traits were estimated via randomly sampling 10 healthy leaves (fully expanded and green) from the same seedling. These leaves were scanned using an Expression 10000XL scanner (Epson, Tokyo, Japan), and leaf area was measured from the images in WinRHIZO (version 2003e, Regent Instruments, Québec City, QC, Canada). Seedlings were then divided into leaves, stems, and roots, placed in paper bags, and oven-dried at 80 °C for 24 h until of constant mass. The

following traits were determined: total biomass (W_T , g), leaf biomass (M_L , g), stem biomass (M_S , g), root biomass (M_R , g), leaf mass ratio (LMR, M_L/W_T), stem mass ratio (SMR, M_S/W_T), root mass ratio (RMR, M_R/W_T), root-to-shoot ratio (R:S, $M_R/(M_S+M_L)$), height (H, cm), basal diameter (D, cm), slenderness quotient (SQ, H/D), leaf area (LA, cm^2), specific leaf area (SLA, LA/M_L , $\text{cm}^2\cdot\text{g}^{-1}$), and leaf area ratio (LAR, LA/W_T , $\text{g}\cdot\text{g}^{-1}$) [1].

Additionally, relative growth rate (RGR, dry biomass increment per unit total seedling biomass per unit time, $\text{g}\cdot\text{g}^{-1}\cdot\text{month}^{-1}$) and net assimilation rate (NAR, biomass growth per unit leaf area, $\text{g}\cdot\text{cm}^{-2}\cdot\text{day}^{-1}$) were calculated using two equations:

$$\text{RGR} = (\ln W_2 - \ln W_1)/t$$

$$\text{NAR} = \frac{W_2 - W_1}{t} \times \left[\frac{\ln A_2 - \ln A_1}{A_2 - A_1} \right]$$

where W_1 (g) is initial total dry mass, W_2 (g) is final total dry mass, A_1 (cm^2) and A_2 (cm^2) are total leaf area, and t is monthly interval between initial and final growth measurements.

Finally, plasticity index (PI) was calculated to observe the sensitivity of each trait to different degrees of shading using the equation from Khan et al. [35]:

$$\text{PI} = \frac{\max T - \min T}{\max T}$$

where T is the mean trait value for each shade group. These values ranged from 0.0 to 1.0, where 0.0 indicates no plasticity and 1.0 indicates maximum plasticity.

2.3. Statistical Analysis

One-way ANOVA and least significant difference (LSD) were used to test differences in species-specific growth, morphology, and biomass allocation across shade treatments. Data are expressed as the mean \pm standard error (SE). Significance was set at $p < 0.05$. All statistical analyses were performed in SPSS for Windows (version 20.0, SPSS Inc., Chicago, IL, USA).

To evaluate plasticity in growth, morphology, and biomass allocation, the mean PI was calculated for all traits. Differences in mean PI between coniferous and broadleaved trees were determined with an independent sample t -test. Finally, the PI values of all five species were averaged across each trait and ranked to determine sensitivity of the traits to shading.

3. Results

3.1. Growth, Morphology, and Biomass Allocation

Seedling biomass (total, leaf, stem, root), RGR, and NAR of the species differed significantly across shade treatments (Table 1). Root biomass decreased with increasing shading level for all species except *P. zhennan*. For *C. lanceolata*, *P. massoniana*, and *L. formosana*, stem biomass decreased with increasing shading level. For *P. zhennan*, stem biomass initially increased from zero to 60–85% shade and then declined significantly at 95% shade. For all species except *P. massoniana*, leaf biomass increased from zero to 60–85% shading levels and then declined at the 95% shading level. For *P. massoniana*, leaf biomass decreased with increasing shading level. Total biomass and RGR decreased with increasing shading, with the largest values observed at the 0–60% shading level for *C. lanceolata*, *S. superba*, and *L. formosana*. For *P. massoniana*, total biomass and RGR were highest in the no-shade treatment. For *P. zhennan*, total biomass and RGR initially increased with more shade, peaking at 40%, but then declined significantly at the 95% shading level. In all species, NAR decreased with increasing shading level.

Table 1. Seedling growth characteristics of five tree species under different shade treatments.

Trait	Shade	Species				
		<i>C. lanceolata</i>	<i>P. massoniana</i>	<i>S. superba</i>	<i>P. zhenan</i>	<i>L. formosana</i>
Root biomass (g)	0%	10.6 ± 1.5 a	4.8 ± 1.0 a	14.5 ± 2.1 a	7.0 ± 0.2 b	14.5 ± 1.6 a
	40%	10.1 ± 1.4 a	1.7 ± 0.3 b	11.7 ± 0.8 a	9.9 ± 1.0 a	13.6 ± 0.1 ab
	60%	8.2 ± 0.8 a	0.8 ± 0.1bc	7.8 ± 1.1 b	6.3 ± 0.1 b	9.7 ± 2.3bc
	85%	4.2 ± 1.0 b	0.3 ± 0.1bc	4.4 ± 0.3 bc	5.6 ± 1.4 b	6.7 ± 0.6 c
	95%	1.2 ± 0.1 b	0.2 ± 0.0 c	1.7 ± 0.1 c	1.9 ± 0.1 c	1.8 ± 0.3 d
Stem biomass (g)	0%	7.3 ± 0.7 a	6.4 ± 1.3 a	5.8 ± 1.0a	3.3 ± 0.2bc	11.7 ± 2.7 a
	40%	5.4 ± 0.7 b	4.6 ± 1.3 a	6.8 ± 0.4 a	5.3 ± 0.3 ab	11.1 ± 2.1 a
	60%	6.2 ± 0.3 ab	1.8 ± 0.3 b	7.5 ± 0.7 a	6.2 ± 0.4 a	12.1 ± 2.6 a
	85%	5.6 ± 0.8 ab	1.0 ± 0.1 b	5.6 ± 0.2 a	6.7 ± 1.7 a	9.9 ± 1.2 ab
	95%	2.0 ± 0.0 c	0.7 ± 0.1 b	2.6 ± 0.3 b	2.6 ± 0.3 c	4.2 ± 0.3 b
Leaf biomass (g)	0%	10.2 ± 1.5 a	10.8 ± 1.8 a	5.7 ± 0.2 b	2.7 ± 0.1 c	4.3 ± 0.9 a
	40%	11.3 ± 1.1 a	6.1 ± 1.6 b	7.8 ± 0.6 a	5.5 ± 0.3 ab	6.5 ± 0.7 a
	60%	12.2 ± 0.6 a	2.5 ± 0.3 c	9.0 ± 0.4 a	6.5 ± 0.8 ab	6.3 ± 1.6 a
	85%	9.7 ± 1.2 a	1.1 ± 0.2 c	7.9 ± 0.7 a	7.6 ± 1.6 a	4.0 ± 0.6 a
	95%	3.5 ± 0.3 b	0.8 ± 0.1 c	6.2 ± 0.3 b	4.5 ± 0.2 bc	3.0 ± 0.5 b
Total biomass (g)	0%	28.0 ± 3.5 a	22.0 ± 3.9 a	26.0 ± 2.9 a	13.0 ± 0.4 ab	30.4 ± 5.0 a
	40%	26.7 ± 3.3 ab	12.4 ± 3.1 b	26.3 ± 0.4 a	20.7 ± 1.5 a	25.4 ± 2.6 a
	60%	26.6 ± 0.9 ab	5.1 ± 0.7 c	24.4 ± 1.4 a	19.0 ± 1.0 a	34.2 ± 6.4 a
	85%	19.4 ± 3.0 b	2.4 ± 0.3 c	17.9 ± 1.0 b	19.8 ± 4.6 a	17.9 ± 1.8 ab
	95%	6.7 ± 0.3 c	1.7 ± 0.1 c	10.6 ± 0.5 c	9.0 ± 0.5 b	10.5 ± 0.6 b
Relative growth rate (RGR, g·g ⁻¹ ·month ⁻¹)	0%	0.19 ± 0.01 a	0.24 ± 0.02 a	0.21 ± 0.01 a	0.12 ± 0.00 b	0.20 ± 0.01 a
	40%	0.19 ± 0.01 a	0.19 ± 0.02 b	0.21 ± 0.00 a	0.15 ± 0.01 a	0.18 ± 0.01 ab
	60%	0.19 ± 0.00 a	0.12 ± 0.01 c	0.20 ± 0.00 a	0.15 ± 0.00 a	0.21 ± 0.01 a
	85%	0.16 ± 0.01 b	0.05 ± 0.01 d	0.18 ± 0.00 b	0.15 ± 0.02 a	0.15 ± 0.02 bc
	95%	0.07 ± 0.00 c	0.03 ± 0.01 d	0.13 ± 0.00 c	0.08 ± 0.00 c	0.11 ± 0.02 c
Net assimilation rate (NAR, g·cm ⁻² ·day ⁻¹)	0%	1.94 ± 0.11 a	2.06 ± 0.18 a	2.44 ± 0.28 a	1.47 ± 0.03 a	3.19 ± 0.21 a
	40%	1.39 ± 0.10 b	1.58 ± 0.18 b	1.66 ± 0.08 b	1.48 ± 0.09 a	2.74 ± 0.40 a
	60%	1.26 ± 0.03 b	0.83 ± 0.08 c	1.29 ± 0.11 bc	1.21 ± 0.05 b	1.57 ± 0.42 b
	85%	0.84 ± 0.08 c	0.34 ± 0.07 d	0.92 ± 0.03 cd	1.01 ± 0.14 b	1.33 ± 0.11 b
	95%	0.33 ± 0.02 d	0.21 ± 0.05 d	0.50 ± 0.02 d	0.44 ± 0.02 c	0.70 ± 0.22 b

Note: Data are presented as the means ± standard error (SE); the different lowercase letters indicate significant differences among shade treatments at 0.05 level; 0%: no-shade; 40%: 40% shaded; 60%: 60% shaded; 85%: 85% shaded; 95%: 95% shaded.

Seedling height, basal diameter, SQ, SLA, LAR, and LA of the species differed significantly across shade treatments (Table 2). Seedling height for species other than *P. massoniana* rose with increasing shade, up to 85%, but then declined at 95% shade. Broad-leaved species (*S. superba*, *P. zhenan*, and *L. formosana*) were taller overall than the conifers (*C. lanceolata* and *P. massoniana*). Basal diameter decreased with increasing shade for *C. lanceolata*, *P. massoniana*, and *L. formosana*, and was significantly lower in 95% shade than in 0–85% shade for *S. superba* and *P. zhenan*. All species exhibited the lowest basal diameter at 95% shade. In all species except *P. zhenan* (no significant change), SQ increased with increasing shade. Both SLA and LAR increased with more shade in all five species. Additionally, LA rose significantly under more shade at first and then declined for all species except *P. massoniana*, where LA decreased with increasing shade.

Table 2. Seedling morphology characteristics of five tree species under different shade treatments.

Trait	Shade	Species				
		<i>C. lanceolata</i>	<i>P. massoniana</i>	<i>S. superba</i>	<i>P. zhennan</i>	<i>L. formosana</i>
Height (cm)	0%	33.1 ± 1.3 c	39.1 ± 0.9 a	45.1 ± 1.5 c	40.2 ± 1.8 bc	64.5 ± 2.4 b
	40%	32.5 ± 0.9 c	43.0 ± 2.2 a	55.5 ± 5.2 bc	51.1 ± 3.3 ab	68.4 ± 3.5 b
	60%	36.4 ± 0.9 b	39.9 ± 1.1 a	57.6 ± 1.3 b	56.0 ± 5.3 a	83.6 ± 4.1 a
	85%	42.4 ± 1.4 a	33.7 ± 1.5 b	70.3 ± 6.2 a	56.4 ± 5.7 a	84.7 ± 1.8 a
	95%	33.8 ± 0.6bc	28.5 ± 0.9 c	50.9 ± 4.4bc	38.5 ± 1.8 c	63.8 ± 3.0 b
Basal diameter (cm)	0%	0.55 ± 0.05 a	0.66 ± 0.05 a	0.63 ± 0.02 a	0.59 ± 0.04 b	0.88 ± 0.05 a
	40%	0.52 ± 0.04 ab	0.53 ± 0.04 b	0.68 ± 0.03 a	0.67 ± 0.01 a	0.74 ± 0.03 ab
	60%	0.54 ± 0.02 ab	0.42 ± 0.03 c	0.62 ± 0.02 a	0.64 ± 0.02 ab	0.74 ± 0.09 ab
	85%	0.45 ± 0.02 bc	0.33 ± 0.01 cd	0.60 ± 0.03 a	0.67 ± 0.02 a	0.66 ± 0.04 b
	95%	0.36 ± 0.01 c	0.28 ± 0.01 d	0.39 ± 0.02 b	0.45 ± 0.02 c	0.39 ± 0.02 c
Slenderness quotient (SQ)	0%	61 ± 3 b	61 ± 7 c	72 ± 4 c	70 ± 5 a	74 ± 6 c
	40%	63 ± 5 b	82 ± 3 b	83 ± 9bc	76 ± 4 a	93 ± 7 c
	60%	68 ± 4 b	96 ± 6 ab	94 ± 4 b	87 ± 9 a	119 ± 12 b
	85%	94 ± 4 a	102 ± 4 a	118 ± 10 a	85 ± 9 a	130 ± 5 b
	95%	94 ± 3 a	103 ± 6 a	130 ± 7 a	88 ± 8 a	165 ± 5 a
Specific leaf area (SLA, cm ² ·g ^{−1})	0%	74 ± 8 d	71 ± 1 c	99 ± 7 d	95 ± 2 d	126 ± 3 c
	40%	100 ± 2 c	73 ± 2 c	134 ± 5 c	122 ± 6 c	135 ± 4 c
	60%	109 ± 2 c	96 ± 3 b	148 ± 5 c	122 ± 5 c	164 ± 7 c
	85%	144 ± 4 b	127 ± 8 a	167 ± 4 b	141 ± 4 b	278 ± 17 b
	95%	174 ± 7 a	127 ± 8 a	208 ± 8 a	171 ± 3 a	341 ± 28 a
Leaf area ratio (LAR, g·g ^{−1})	0%	25 ± 1 e	35 ± 1 c	22 ± 2 e	20 ± 0 e	18 ± 1 b
	40%	43 ± 1 d	36 ± 1 c	40 ± 3 d	33 ± 2 d	29 ± 3 ab
	60%	50 ± 1 c	50 ± 1 ab	55 ± 4 c	42 ± 4 c	38 ± 2 ab
	85%	73 ± 2 b	56 ± 5 a	73 ± 4 b	55 ± 4 b	66 ± 19 ab
	95%	93 ± 4 a	47 ± 3 b	123 ± 4 a	86 ± 0 a	79 ± 31 a
Leaf area (LA, cm ²)	0%	655 ± 66b	765 ± 124 a	566 ± 19 c	259 ± 13 c	541 ± 111 c
	40%	1134 ± 114 a	444 ± 118 b	1044 ± 81 b	672 ± 36 b	726 ± 61bc
	60%	1325 ± 63 a	273 ± 21 bc	1336 ± 52 a	796 ± 99 ab	1281 ± 59 a
	85%	1392 ± 165 a	134 ± 22 c	1313 ± 119 a	1070 ± 225 a	1042 ± 135 ab
	95%	603 ± 50 b	81 ± 1 c	1300 ± 51 a	776 ± 40 ab	714 ± 212bc

Note: Data are presented as the means ± standard error (SE); the different lowercase letters indicate significant differences among shade treatments at 0.05 level; 0%: no-shade; 40%: 40% shaded; 60%: 60% shaded; 85%: 85% shaded; 95%: 95% shaded.

For all species, RMR and R:S ratio decreased continuously with increasing shade (Table 3). SMR increased with increasing shade for *P. massoniana* and *L. formosana*. For *S. superba* and *P. zhennan*, SMR declined significantly at 95% shade. Lastly, LMR increased with increasing shading levels in *C. lanceolata*, *S. superba*, *P. zhennan*, and *L. formosana* but exhibited no significant difference across shade treatments in *P. massoniana*.

Table 3. Seedling biomass allocation characteristics of five tree species under different shade treatments.

Trait	Shade	Species				
		<i>C. lanceolata</i>	<i>P. massoniana</i>	<i>S. superba</i>	<i>P. zhennan</i>	<i>L. formosana</i>
Root mass ratio (RMR)	0%	0.38 ± 0.01 a	0.22 ± 0.01 a	0.55 ± 0.03 a	0.54 ± 0.01 a	0.48 ± 0.03 a
	40%	0.37 ± 0.01 a	0.15 ± 0.01 b	0.44 ± 0.03 b	0.48 ± 0.02 b	0.44 ± 0.04 a
	60%	0.31 ± 0.02 b	0.15 ± 0.01 b	0.32 ± 0.03 c	0.33 ± 0.01 c	0.35 ± 0.00 b

Stem mass ratio (SMR)	85%	0.21 ± 0.02 c	0.13 ± 0.02 b	0.25 ± 0.01 d	0.28 ± 0.02 d	0.33 ± 0.00 b
	95%	0.19 ± 0.01 c	0.13 ± 0.01 b	0.16 ± 0.01 e	0.21 ± 0.02 e	0.19 ± 0.02 c
	0%	0.26 ± 0.01 ab	0.29 ± 0.02 b	0.22 ± 0.02 b	0.25 ± 0.01 c	0.38 ± 0.02 ab
	40%	0.20 ± 0.00 c	0.37 ± 0.02 ab	0.26 ± 0.02 ab	0.26 ± 0.01 c	0.35 ± 0.04 b
	60%	0.23 ± 0.02 bc	0.36 ± 0.01 ab	0.31 ± 0.02 a	0.33 ± 0.02 ab	0.43 ± 0.02 ab
	85%	0.29 ± 0.01 a	0.43 ± 0.04 a	0.31 ± 0.01 a	0.33 ± 0.01 a	0.48 ± 0.03 a
	95%	0.30 ± 0.01 a	0.43 ± 0.03 a	0.25 ± 0.02 b	0.29 ± 0.02 bc	0.47 ± 0.05 c
Leaf mass ratio (LMR)	0%	0.36 ± 0.02 d	0.49 ± 0.02 a	0.22 ± 0.02 c	0.21 ± 0.01 c	0.14 ± 0.01 b
	40%	0.42 ± 0.01 c	0.49 ± 0.01 a	0.30 ± 0.02 c	0.27 ± 0.01 c	0.21 ± 0.01 b
	60%	0.46 ± 0.01 bc	0.49 ± 0.01 a	0.37 ± 0.03 b	0.34 ± 0.03 b	0.22 ± 0.02 b
	85%	0.50 ± 0.02 ab	0.44 ± 0.04 a	0.44 ± 0.02 b	0.39 ± 0.03 b	0.19 ± 0.03 b
	95%	0.52 ± 0.02 a	0.44 ± 0.03 a	0.59 ± 0.02 a	0.50 ± 0.00 a	0.33 ± 0.05 a
Root-to-shoot ratio (R:S)	0%	0.61 ± 0.03 a	0.28 ± 0.01 a	1.26 ± 0.14 a	1.16 ± 0.05 a	0.95 ± 0.11 a
	40%	0.60 ± 0.02 a	0.17 ± 0.02 b	0.81 ± 0.10 b	0.91 ± 0.06 b	0.81 ± 0.12 a
	60%	0.45 ± 0.05 b	0.18 ± 0.02 b	0.47 ± 0.06 c	0.50 ± 0.03 c	0.53 ± 0.01 b
	85%	0.27 ± 0.03 c	0.15 ± 0.02 b	0.33 ± 0.03 cd	0.39 ± 0.05 cd	0.48 ± 0.01 bc
	95%	0.23 ± 0.02 c	0.15 ± 0.01 b	0.19 ± 0.01 d	0.26 ± 0.03 d	0.24 ± 0.03 c

Note: Data are presented as the means ± standard error (SE); the different lowercase letters indicate significant differences among shade treatments at 0.05 level; 0%: no-shade; 40%: 40% shaded; 60%: 60% shaded; 85%: 85% shaded; 95%: 95% shaded.

3.2. Plasticity of Traits

Mean PI for species across all five shade treatments ranged from 0.11 to 0.95. For *C. lanceolata*, the most plastic traits were root mass, NAR, total biomass, stem biomass, LAR, and leaf mass, while the least plastic traits were height, LMR, SMR, basal diameter, SQ, and RMR (Table 4). For *P. massoniana*, root mass, leaf mass, total biomass, NAR, LA, and stem mass were the most plastic, whereas LMR, SMR, height, LAR, RMR, and SQ were the least plastic traits. For *S. superba*, *P. zhennan*, and *L. formosana*, the most plastic traits were root mass, R:S, LAR, NAR, and LA, while the least plastic traits were SMR, height, SQ, basal diameter, RGR, leaf biomass, and SLA. Across all species, the three most plastic traits were root mass, NAR, and total biomass, while the three least plastic traits were SMR, height, and SQ.

Table 4. Phenotypic plasticity index of traits in five tree species under different shade treatments.

Group	Trait	Phenotypic Plasticity Index (PI)				
		<i>C. lanceolata</i>	<i>P. massoniana</i>	<i>S. superba</i>	<i>P. zhennan</i>	<i>L. formosana</i>
Growth	Root biomass	0.88	0.95	0.88	0.81	0.88
	Stem biomass	0.73	0.89	0.65	0.61	0.65
	Leaf biomass	0.71	0.93	0.37	0.64	0.53
	Total biomass	0.76	0.92	0.60	0.56	0.69
	RGR	0.62	0.88	0.36	0.45	0.48
	NAR	0.83	0.90	0.80	0.70	0.78
Morphology	Height	0.23	0.34	0.36	0.32	0.25
	Basal diameter	0.35	0.58	0.42	0.33	0.56
	SQ	0.35	0.41	0.44	0.21	0.55
	SLA	0.57	0.44	0.52	0.44	0.63
	LAR	0.73	0.37	0.82	0.77	0.78
	LA	0.57	0.89	0.58	0.76	0.58
Biomass allocation	SMR	0.32	0.33	0.29	0.23	0.27
	LMR	0.30	0.11	0.62	0.59	0.58

RMR	0.51	0.40	0.71	0.61	0.60
R:S	0.62	0.46	0.85	0.77	0.74

In general, growth and biomass allocation traits had relatively higher mean PI than morphological traits (Figure 2). Additionally, we found significant interspecific differences in mean PI for growth, morphology, and biomass allocation. Both *C. lanceolata* and *P. massoniana* exhibited higher growth plasticity and lower allocation plasticity than *S. superba*, *P. zhennan*, and *L. formosana*. However, mean PI for morphology and all variables combined did not significantly differ between coniferous and broadleaved trees.

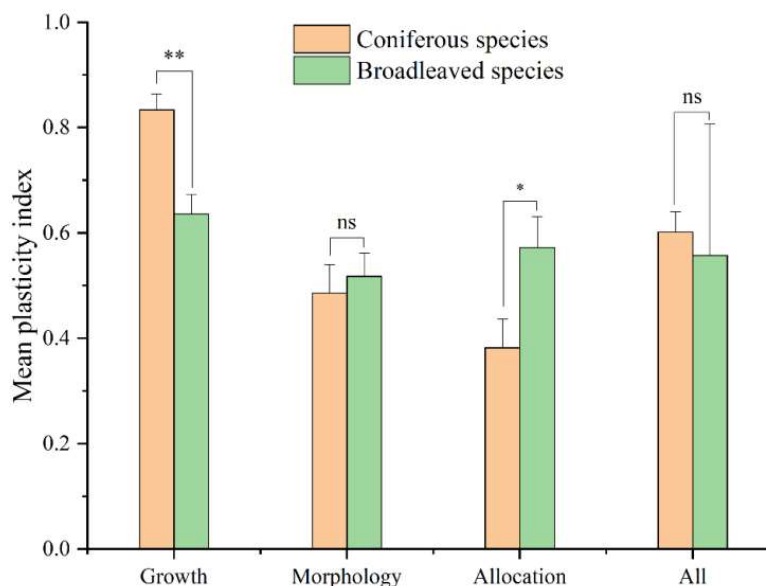


Figure 2. Mean phenotypic plasticity indices of growth, morphology, biomass allocation, and all variables combined for five species. * $p < 0.05$, ** $p < 0.01$, ns = not significant.

4. Discussion

4.1. Effects of Shading on Growth

Here, we found that total biomass, RGR, and NAR decreased significantly with increasing shade for all species except *P. zhennan*. This outcome is in line with previous research showing that seedlings under shaded conditions have lower total biomass than seedlings under high light [36]. Our study also found that 95% shade severely inhibited growth and biomass accumulation in all five species, suggesting that seedlings cannot maintain photosynthesis under extremely low-light conditions [37]. Moreover, the growth variables of the five species differed significantly across shade treatments. Previous research suggests that growth rates of shade-tolerant seedlings are highest under intermediate light intensities (16–50% sunlight) [38], while optimal conditions for light-demanding species are between 26% and 100% sunlight [39]. Consistent with our results, many other studies have shown that seedling RGR increases with decreasing shade [20,40].

Seedling heights of *C. lanceolata*, *S. superba*, *P. zhennan*, and *L. formosana* increased with increasing shade but declined at 95% shade. Among these four species, seedlings were tallest under intermediate light intensities (15–40% sunlight), consistent with other studies [14,38]. Our results partially confirm the hypothesis that seedlings maximize height for light capture when grown in a low-light environment. However, the significant height decline at 95% shade suggests that their growth would be inhibited under a closed canopy. On the contrary, *P. massoniana* was taller than the other four species at lower shade levels, with height tending to decrease with more shade. Consistent with previous

studies, the basal diameter growth of trees declines as shade increases [20,41]. Similar to our findings, both conifers [42] and broadleaved species such as beech and oak [20] experienced a decline in stem diameter as shade increased. However, height and diameter growth in response to shade were greater for broadleaved trees than for conifers, consistent with research demonstrating that shade-tolerant species grow higher and wider than shade-intolerant species under low light. This strategy may facilitate escape from darker areas in natural ecosystems [20]. The slenderness quotient (SQ) generally rose with increasing shade for all species, although this difference was not significant in *P. massoniana*. A previous study [14] showed that shade influenced SQ, depending on the species. For instance, SQ increased significantly with increasing shade in *Elaeocarpus sylvestris* and *Gardenia jasminoides*, whereas shade did not influence SQ in *Quercus phillyraeoides*. On the whole, this result suggests that seedlings growing in low light prioritize biomass allocation to height over diameter [20,41].

4.2. Effects of Shading on Morphology

Morphological traits showed significant variation among different degrees of shading. Leaves require considerable acclimation capacity to efficiently capture limited resources under different environmental conditions. Thus, leaf area is an important trait for light interception [1,43], and shade-adapted plants have larger and/or thinner leaves [20,44,45]. Seedlings grown in low-light environments often have increased SLA and LAR [46,47]. In our study, SLA showed a linear increase with increasing shade across all species, in line with other studies [14,20,48–50]. Higher SLA and LAR in low-light environments allow seedlings to have greater surface area for optimizing light interception and photosynthetic efficiency [48,51].

4.3. Effects of Shading on Allocation

Under the functional equilibrium theory [52], seedlings preferentially allocate more biomass to components facing resource limitations, including limited light [53,54]. Generally (although there is interspecific variation), as shade increases, plants allocate more biomass to light-trapping tissues (leaves and stems) while reducing RMR and R:S ratios [51,55,56]. Our findings and multiple other studies [20,50] are consistent with the functional equilibrium theory. We also observed clear interspecific variation in response to light such that LMR increased with shade in *C. lanceolata*, *S. superba*, *P. zhenan*, and *L. formosana*, while it decreased in *P. massoniana*. These results support the hypothesis by Poorter [57], who suggested that investment in a large leaf area per unit leaf biomass can compensate for low LMR. Irrespective of light availability, almost all R:S ratios were less than 1, indicating that seedlings generally allocate more biomass to shoots than to roots. This strategy is useful for increasing photosynthesis to help seedlings meet their growth and developmental needs.

4.4. Interspecific Variation in Plasticity

Interspecific variation in plasticity to shade is well-established [50,58,59]. Because shade-intolerant species usually occupy habitats with heterogeneous resources, they often exhibit higher plasticity in response to shade than shade-tolerant species [50]. Our data demonstrate that conifer species (*C. lanceolata* and *P. massoniana*) have greater growth plasticity and lower allocation plasticity than broadleaved species (*L. formosana*, *S. superba*, and *P. zhenan*). Thus, the two functional groups differed in strategies across shade treatments, acclimating to various light conditions through regulating growth and biomass allocation. However, we did not find significant differences in mean morphological plasticity index or mean total plasticity index between conifers and broadleaved trees. This lack of significant interspecific differences in overall mean plasticity across traits may be because each species possesses different shade-sensitive traits. In other words, while overall plasticity may be similar, the specific individual traits that are plastic vary from species to species [60].

4.5. Differences in Plasticity across Traits

Plants modify their growth, morphology, and biomass allocation in response to shade [23,50,61,62], with growth and morphological traits exhibiting higher plasticity than biomass allocation traits [50]. Here, we found that conifer species had less morphological and biomass allocation plasticity than growth plasticity, while broadleaved species had higher growth and biomass allocation plasticity than morphological plasticity. Seedlings tend to invest the majority of their biomass in organs that capture the largest limiting environmental resource [54], meaning that organs responsible for obtaining highly variable resources should have the greatest flexibility in biomass investment. Because they adjust growth traits in response to abiotic stress, conifers employ a more conservative strategy of biomass allocation than broadleaved trees. Our findings also indicated that growth and allocation traits were more sensitive to shade than morphological traits in shade-tolerant species.

Root biomass was the most plastic trait for both coniferous and broadleaved species. Under high-light conditions, seedlings allocated more biomass to roots for better water and nutrient absorption. In low-light conditions, allocation to roots decreased and allocation to shoots increased, allowing greater light capture. We also found that SMR and height were the least plastic traits for all five species. Height is particularly important when light competition is high, but in general, it is a phylogenetically restrained trait, and previous research has demonstrated that current light conditions do not affect height increases [20]. Low SMR plasticity contrasts with findings from previous research [50,60] and suggests that investment in stem biomass is only weakly dependent on light conditions [50]. The key role of stems in water conductance and leaf positioning may explain why stem biomass allocation was maintained across shade treatments in this study and in others [50]. The observation of high root biomass plasticity and low SMR plasticity indicated that seedling biomass allocation to roots was more shade-sensitive than allocation to stems, again inconsistent with previous findings [63].

5. Conclusions

We examined the growth, morphology, and biomass allocation of five tree seedling species across different degrees of shading. We found that shade induced changes in growth, morphology, and allocation across all species. To improve individual fitness, seedling capacity to absorb light increased with more shade, although this compensation was insufficient under the darkest condition (5% sunlight), which inhibited growth in all seedlings. For most of the tested species, SQ, SLA, LAR, and mass of light-trapping tissues (leaves and stems) increased with more shade, while the R:S ratio and RMR decreased. In shade-intolerant conifers, growth traits were more sensitive to shade than morphological and biomass allocation traits, leading to a higher plasticity in growth but a lower plasticity in biomass allocation, while both growth and biomass allocation traits were sensitive to shade for shade-tolerant broadleaved species. Our findings have important implications for the sustainable management of multi-species stands. Broadleaved species should be planted during the later stages of succession after a canopy of coniferous species such as *C. lanceolata* and *P. massoniana* are well developed but before full canopy closure, as they are better adapted to a wide range of light intensities. In already established high-density plantations of *C. lanceolata* or *P. massoniana*, thinning should be performed first to allow sufficient light to reach the understory. When coupled with a thinning strategy, under planting broadleaved species within established coniferous plantations is a viable option to easily establish mixed-species stands that enhance biodiversity and ecosystem services. On the whole, our results clearly demonstrate the importance of functional traits when determining interspecific differences in plant response to shade.

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