Responses of Chinese fir and *Schima superba* seedlings to light gradients: implications for the restoration of mixed broadleaf-conifer forests from Chinese fir monocultures

Bo Liu[a], Qingqing Liu[a], Stefani Daryanto[c], Si Guo[a], Zhijun Huang[a], Zhengning Wang[a], Lixin Wang[b,*], Xiangqing Ma[a,*]

[a]*College of Forestry, Fujian Agriculture and Forestry University, Fuzhou, 350002, China*

[b]*Department of Earth Sciences, Indiana University-Purdue University, Indianapolis (IUPUI), Indianapolis, IN 46202, USA*

[c]*State Key Laboratory of Earth Surface Processes and Resource Ecology, Faculty of Geographical Science, Beijing Normal University, No. 19, XinJieKouWai St., HaiDian District, Beijing 100875, China*

* Corresponding author emails: lxwang@iupui.edu; lxymxq@126.com

Author e-mail addresses: liubo@fafu.edu.cn; (B. Liu), liuqqing222@126.com (Q. Liu); stdaryan@iupui.edu (S. Daryanto*); fafugs2017@163.com (S. Guo); wangzn@fafu.edu.cn (Z. Wang); fjhuangzj@126.com (Z. Huang); lxwang@iupui.edu (L.Wang)* **; lxymxq@126.com (X. Ma)**

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ABSTRACT

Although Chinese fir (*Cunninghamia lanceolata* (Lamb.) Hook) plantations are widely grown for timber production in southern China, they have low biodiversity and provide limited ecosystem services. To address this problem, *C. lanceolata* are increasingly mixed with broadleaf *Schima superba* Gardn. & Champ. (Theaceae). The success of these mixed plantations relies on introducing each species in the appropriate sequence, which requires understanding how tree species respond to light variations. We therefore compared *S. superba* and *C. lanceolata* seedling light tolerance in shaded houses under five light gradients (5%, 15%, 40%, 60%, and 100% sunlight). Our findings showed that *S. superba* seedlings exhibited greater net height increment (ΔHt), net diameter growth (ΔDia), leaf area, root mass, stem mass, leaf mass, and total mass under low light conditions (15% sunlight). However, as sunlight increased, these growth variables became higher in *C. lanceolata* seedlings. With more sunlight, both species experienced a drop in height to diameter ratio (HDR), and specific leaf area (SLA), but an elevated root to shoot ratio. Additionally, under the same light levels, *S. superba* seedlings exhibited greater leaf area and root to shoot ratio than *C. lanceolata* seedlings. Our results suggested that *S. superba* might be more suitable for underplanting beneath a heavy canopy due to its shade-tolerant traits. In contrast, *C. lanceolata* was less shade-tolerant, having an optimum seedling growth under full sunlight. These findings suggest that underplanting *S. superba* seedlings in *C. lanceolata* monoculture plantation (i.e., underplanting regeneration approach) could be a better silvicultural alternative than simultaneously planting both seedlings.

Keywords: biomass allocation, leaf morphology, phenotypic plasticity, shade tolerance, silviculture, underplanting.

1. Introduction

Demand for commercial timber has increased global forest plantations from 168 × 10^6 ha in 1990 to 278 × 10^6 ha in 2015, a shift from 4.06% of total forest area to 6.95% (FAO, 2015; Keenan et al., 2015; Payn et al., 2015). In China alone, plantations cover ~ 69 × 10^6 ha and account for 25% of the global forested area, ranking first in the world (Yang et al., 2018). However, most of these plantations are monocultures, especially those located in southern China, focusing on a few select species, such as *Cunninghamia lanceolata*, *Eucalyptus* spp., and *Pinus massoniana* (CSFB, 2014). These plantations have some undesirable characteristics, including simple structure, low biodiversity, low ecosystem services, low soil fertility, and poor natural regeneration (Erskine et al., 2006; Richards et al., 2010; Wang et al., 2009; Zhang and Fu, 2009). Converting single-species plantations into mixed, broadleaf-conifer forests may be ideal for resolving these issues while gaining additional benefits such as yield increase, environmental restoration, and biodiversity conservation (Alem et al., 2015; Carnevale and Montagnini, 2002; Kelty, 2006; Piotto et al., 2004; Redondo-Brenes and Montagnini, 2006).

Chinese fir, *Cunninghamia lanceolata* (Lamb.) Hook (Taxodiaceae), an evergreen conifer, is the most important plantation tree by area both in China and the globe (Yang et al., 2018). Currently, *C. lanceolata* plantations take up 17 × 10^6 ha, which represent approximately 24% of the forest plantations in China and 6.1% of the global (FAO, 2015; Yang et al., 2018). These forests are nutrient-poor, with shallow fertile soils (Chen et al., 2000). Like other monocultures, the sustainability of *C. lanceolata* plantations is threatened by biodiversity reduction, production loss, soil degradation, and a lack of self-regeneration (Chen et al., 2014; Luo et al., 2014; Ma et al., 2007; Yang et al., 2004). In an attempt to address this problem, *Schima superba* Gardn. & Champ. (Theaceae) are increasingly mixed into the understory of *C. lanceolata* stands (Chen et al., 2013; Huang et al., 2004; Xiong, 2007). *Schima superba* is a dominant evergreen broadleaf tree with a wide distribution in southern China. Being known locally as 'Mu He', *S. superba* is also an ecologically and economically important tree (Li et al., 2011; Niu et al., 2012; Yang et al., 2017a). The tree of *S. superba* has thick leaves with high water content and can grow quickly in various soil types; features that are suitable for reforestation and plantation-restoration programs (Li et al., 2011). Previous studies showed that mixed *C. lanceolata* and *S. superba* forests generally have improved stand structure, soil quality, ecological functions, natural regeneration and economic return to landowners (Cai et al., 2012; Chen and Chen, 2002; Yang et al., 2010, Yang et al., 2017b).

The shift in preference from monoculture plantations to mixed broadleaf-conifer forests has highlighted the need for research on how tree species develop under different light environments resulting from management interventions (Alem et al., 2015; Carnevale and Montagnini, 2002; Kelty, 2006). The response of different species to variable light conditions is complex (Valladares et al., 2002), involving both plant-environment interactions, and plant-plant interactions. Although *C. lanceolata* is considered to be light-demanding throughout its life cycle (Xue et al., 2017), we know little of how light gradients influence seedling growth, morphology, and biomass allocation. In contrast, *S. superba* is considered more shade-tolerant during the seedling stage (Wang and Guo, 2007; Zhu et al., 2017). In most cases, these categorizations were drawn from traditional, silvics-based shade-tolerance classes, rather than from empirical research that evaluate species-specific responses to varying shade levels. Thus, management of mixed broadleaf-conifer forests would be aided through understanding how light influences seedling survival and growth during early post-planting stages. 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. To the best of our knowledge, little is known regarding the effects of variable light intensity on growth and biomass allocation in broadleaf-conifer combinations. Therefore, such research will enhance forest management practices that emphasize multifunctional and biodiversity-oriented objectives.

The aim of this study was to examine the effects of shading on the early growth, morphology, and biomass allocation of *C. lanceolata* and *S. superba*. Artificial shading is a practical alternative to fieldwork for investigating interspecific differences in light tolerance (Madsen, 1994), because it removes potential confounding factors in a variable forest environment. Seedlings of both species were exposed to different shade levels that mimic underplanting conditions, while access to other resources (e.g., water and nutrients) was kept constant. This manipulation allowed us to separate the effects of these prominent confounding factors and focus only on plant response to light gradient. Our specific objectives were to: (i) identify how growth, morphology, and biomass allocation change across light gradients; and (ii) determine the light requirements for the optimal growth of *C. lanceolata* and *S. superba*.

2. Materials and methods

2.1. Experimental design and shade treatments

The study was constructed in a flat, open area at the Fujian Agriculture and Forestry University. Five light gradients (100%, 60%, 30%, 15%, and 5% full sunlight) were created using shade houses covered with black nylon shade cloth at increasingly higher mesh gauges. Specifically, mesh gauges of 2, 3, 6, and 8 were used to intercept 40%, 60%, 85%, and 95% irradiance, resulting in conditions of 60%, 40%, 15% and 5% sunlight, respectively (relative irradiance was estimated with a light meter on a clear day in summer, Table 1). The 100% sunlight control did not use a shade cloth (Kennedy et al., 2007; Saldaña-Acosta et al., 2009). Shade houses were 2.0 m high, 6.0 m×2.5 m in length and width, and were placed parallel to the sun's daily track to minimize spatiotemporal variation in solar radiation. Distance between the shade houses was maintained at 5.0 m to minimize interaction effects. A 10 cm opening between the soil surface and the shade cloth was left for ventilation. Shade houses were not water-proofed; more rainfall was blocked as mesh gauges increased. To guarantee sufficient soil moisture for seedlings establishment, all seedlings were watered 2-3 times weekly.

In July 2016, *C. lanceolata* and *S. superba* seedlings were purchased from a container nursery in Zhangping Wuyi Forest Farm, Fujian, China. Seeds were sown during February 2016 in one of the nursery's greenhouses, following standard practice. Purchased seedlings were transplanted to pots containing potting compost and were grown for one month in glasshouse at the experimental site. In August 2016, 6-mouth old seedlings were placed in shade houses, and randomly divided into five groups per species with five seedlings. Each group was subjected to a different light gradient: 100% (control), 60%, 40%, 15%, and 5% full sunlight. Initial seedling height and diameter did not differ significantly between the individuals of each species (based on measurements from five randomly selected individuals per species; see section 2.2). Seedling pots were treated as replicates and were randomly positioned to ensure they obtained similar light irradiation with no mutual shading. Seedlings grown under the same shade house were completely independent. Pots were rotated weekly to ensure homogeneous conditions.

2.2. Growth and biomass measurements

Prior to light treatment, seedlings of both species were measured to determine initial heights and stem diameters. Height from the soil surface to the highest point of the live crown was obtained with a measuring tape. Stem diameter was measured to the nearest 0.01 mm using Vernier calipers. The position and direction of the stem diameter measurements were marked on the stem using a permanent marker; subsequent measurements were made at this position to maintain consistency.

In August 2017 (the experiment lasted for one year), all seedlings were harvested and separated into roots, stems, and leaves. Roots were washed carefully using distilled water. Leaf area was determined with a portable leaf meter (Yaxin-1241, Shanghai, China) from 10 randomly selected leaves per seedling. All plant tissues were placed in paper bags and oven-dried at 105°C for 30 min, then at 80°C for at least 24 h to a constant dry weight. Dry weights of stems, leaves, and roots were measured separately. The following major growth-related indices were calculated: net height increment (ΔHt, plant height at the end of experiment minus initial height, cm); net diameter growth (ΔDia, plant stem diameter at the end of experiment minus initial diameter, cm); height to diameter ratio (HDR, ratio of height to stem diameter at 3 cm above ground at the end of experiment); leaf area (per leaf, cm^2); specific leaf area (SLA, leaf area per unit leaf dry mass, cm^2 g^{-1}); leaf mass ratio (leaf dry mass/total seedling dry mass, g g^{-1}); stem mass ratio (stem dry mass/total seedling dry mass, g g^{-1}); root mass ratio (root dry mass/total seedling dry mass, g g^{-1}); root to shoot ratio (root dry mass/aboveground dry mass, g g^{-1}); leaf to root ratio (leaf dry mass/root dry mass; g g^{-1}); and Ht/Stem-mass (The length gained per unit mass invested, calculated as main stem length divided by stem dry weight, cm g^{-1}) (Sevillano et al., 2016).

2.3. Data analysis

All statistical analyses were performed using SPSS version 24.0 for Windows (SPSS Inc., Chicago, IL, USA). Fixed effects were light, species, and their interaction. Normal distribution of errors and homogeneity of variance were assessed and data with residuals that did not conform to these assumptions were transformed using Box–Cox transformations. The data are presented as means ± standard error (SE) for different treatments. Tukey's tests were used for multiple comparisons of means within significant explanatory variables under the ANOVA. Significance level was set at $p = 0.05$.

3. Results

3.1 Seedling survival and growth responses to light

Seedling net height increment (ΔHt) and net diameter increment (ΔDia) varied significantly across species and light gradients (Table 2). For both species, ΔHt increased as shade increased, peaking under 15% sunlight and then declining under 5% sunlight (Fig. 1A). However, ΔDia differed across species, increasing with increasing shade for *S. superba* (except under 5% sunlight), and decreasing with increasing shade for *C. lanceolata* (Fig. 1B). For both species, HDR increased significantly with increasing shade (Fig. 1C). Significant interspecific differences in HDR were found under 100% and 60% sunlight.

3.2 Foliage morphology responses to light

The largest leaf area of *S. superba* and *C. lanceolata* occurred under 15% and 40% sunlight, respectively (Fig. 2A). Leaf area was significantly larger in *S. superba* (26.99±1.48 cm^2, averaged over treatments) than in *C. lanceolata* (0.90±0.03 cm^2) across all light gradients (Fig. 2A). Both species experienced increases in SLA with increasing shade, with values in full sunlight being 54.96% (*S. superba*) and 53.68% (*C. lanceolata*) smaller than values under 5% sunlight (Fig. 2B). *Schima superba* consistently had greater SLA than *C. lanceolata* (138.34±5.28 cm^2 g^{-1}versus 114.97±4.36 cm^2 g^{-1}, averaged over treatments) across all light gradients (Fig. 2B).

3.3 Biomass and biomass allocation responses to light

Root biomass, stem biomass, leaf biomass, and total biomass differed significantly across all light gradients in both species (Table 2). Biomass variables were higher under 15% sunlight than under any other light treatment for *S. superba* seedlings, but decreased with increasing shade for *C. lanceolata* (Fig. 3). Significant interspecific differences in biomass (except for root biomass) were found under 100% and 60% sunlight (Fig. 3). For both species, root mass ratio and root to shoot ratio decreased as shade increased (Fig. 4A, D). Root mass ratio and root to shoot ratio were significantly larger in *S. superba* (0.44±0.02 g, 0.85±0.06 g, respectively, averaged over treatments) than in *C. lanceolata* (0.35±0.02 g, 0.57 ± 0.05 g) across all light gradient (Fig. 4A, D). In contrast, stem mass ratio, leaf mass ratio, and leaf to root ratio increased as shade decreased (Fig. 4). Finally, Ht/Stem-mass tended to increase with increasing shade in *C. lanceolata*, but except under 5% sunlight, the index decreased in *S. superba*. Under100%, 60% and 40% sunlight, Ht/Stem-mass was significantly larger in *S. superba* than in *C. lanceolata* (Fig. 4F).

4. Discussion

Our study showed that *S. superba* and *C. lanceolata* experienced greater net height increment (ΔHt) at lower light levels, except for a decline under 5% sunlight (Fig. 1). The greatest ΔHt in both species occurred under 15% sunlight. Furthermore, given that their height decreased under 5% sunlight, both species are likely to experience inhibited growth under a closed overstory. *Schima superba* exhibited greater height increments than *C. lanceolata* under 15% and 5% sunlight (Fig. 1A). This finding confirmed the traditional perception of shade-tolerant species exhibiting higher height-increment rates than shade-intolerant species under lower light conditions (Chen et al., 1997), likely because this mechanism facilitates escape from darker regions in natural ecosystems (e.g., Sevillano et al., 2016).

Studies on multiple tree species have observed significant reductions of net diameter increment (ΔDia) with reduced light availability (Chen et al., 1997; Wang et al., 2006; Cheng et al., 2013; Sevillano et al., 2016), although the opposite response has also been reported (Barnett, 1989). In our study, ΔDia in two species showed opposing trends under increasing shade, with *C. lanceolata* decreasing and *S. superba* generally increasing (Fig. 1B). *Schima superba* exhibited greater ΔDia than *C. lanceolata* under 40%, 15%, and 5% sunlight (Fig. 1B). These results are consistent with previous studies demonstrating that the shade-tolerant species have a higher diameter increase than the shade-intolerant species under low light conditions (Chen et al., 1996; Sevillano et al., 2016).

In some tree species, shade influences the slenderness index (HDR) (Chen 1997; Sevillano et al., 2016). Corresponding to these previous findings, our study did not observe interspecific differences in HDR, which consistently increased with decreasing light availability (Fig. 1C) (Chen and Klinka, 1997; Sevillano et al., 2016). Overall, under our low-light conditions, ΔHt per plant was greater than the corresponding increase in stem biomass. Similar findings have been reported for beech (*Fagus sylvatica* L.), oak (*Quercus robur* L.) seedlings (Sevillano et al., 2016), and Douglas fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) (Chen, 1997). Our findings partially confirmed the hypothesis that trees tend to grow taller more rapidly under low light conditions as a light-capture mechanism (Valladares and Niinemets, 2008). Taken together, the data suggest that shaded seedlings prioritize biomass allocation towards increasing height at the expense of increasing in diameter (Sevillano et al., 2016; Sumida et al., 1999; Wang et al., 2006), which is necessary to support the crown mechanically and physiologically. This trade-off is also confirmed by the greater increase Ht/Stem-mass under heavy shade (Fig. 4F; Bloor and Grubb et al., 2004; Sevillano et al., 2016).

Plants can efficiently acclimate to different light environments through altering leaf traits. In general, to enhance light capture under low light conditions, plants allocate more biomass to produce thin leaves with high SLA (Poorter, 1999), a trait that describes light-capture efficiency relative to biomass invested in leaf tissue (Marshall and Monserud, 2003). Under high light conditions, plants reduce transpiration losses and increase carbon gain by forming small, thick leaves with low SLA (Poorter, 1999). Here, we observed a significant SLA increase as light levels decreased (Fig. 2B), consistent with previous studies showing an association between greater SLA and higher light-capture efficiency under low light environments (Chen, 1997; Sevillano et al., 2016; Wang et al., 2006). Increasing SLA is a frequent phenotypic response of trees to shade. For example, beech and other shade-tolerant species have higher SLA under low light than less shade-tolerant species like oak (Groninger et al., 1996; Sevillano et al., 2016) (but see Chen et al., 1996). Similarly, we observed greater SLA (less dense, larger leaves) in *S. superba* seedlings than in *C. lanceolata* seedlings (smaller, heavier leaves) (Fig. 2A, B; Fig. 3C), indicating that *S. superba* could be more shade tolerant than *C. lanceolata*. Overall, in shade-tolerant species appear to employ low SLA as a successful strategy for survival and growth in poor-light environments.

Our findings on other plant properties beside traits also support the differential light requirements of *S. superba* and *C. lanceolata*. Although shading generally reduced root biomass more than aboveground biomass, total root, stem, and leaf biomasses of *S. superba* seedlings increased with increasing shade, indicating considerable shade-tolerance. In contrast, total root, stem, and leaf biomass of *C. lanceolata* seedlings declined significantly with increasing shade, similar to other shade-intolerant trees such as Douglas fir (Williams et al., 1999) and silver fir (*Abies alba* Mill) (Robakowski et al., 2003, 2004). The higher root to shoot ratios of *S. superba* allow it to compete more effectively for soil nutrients than *C. lanceolata* and other trees with lower root to shoot ratios (Allaby, 1998). The trade-off in this allocation strategy is important for survival during light and other resource limitation, as well as recovery from herbivore damage.

We also found that Ht/Stem-mass increased in *C. lanceolata* seedlings and decreased in *S. superba* seedlings under increasing shade, leading to longer but weaker seedlings in the former species under low light conditions. Etiolation-related increases in seedling height was then reflected in the greater allocation of biomass belowground (Fig. 4D). These results support the functional equilibrium theory that suggests plants increase allocation to shoots or leaves when aboveground biomass decreases, and increase allocation to roots when belowground biomass decreases (Poorter and Nagel, 2000). In general, the observed morphological shifts in both species imply a dynamic response to light conditions that balances trade-offs between aboveground growth (for light interception) and root growth (for nutrient and water acquisition).

5. Conclusions

Our results showed that light differentially affected seedling growth, morphology, and biomass allocation in *S. superba* and *C. lanceolata*. However, light availability did not influence seedling survival rates of either species. Considering that *S. superba* seedlings achieved their best growth under light conditions as low as 15% sunlight, this species could be shade-tolerant and suitable for underplanting beneath a heavy canopy. The strategy of underplanting has been successfully applied to enrich existing stands, convert even-aged monocultures to more complex systems, and rehabilitate non-productive stands (Kenk and Guehne, 2001; Pretzsch and Rais, 2016). In contrast, we consider *C. lanceolata to* be shade-intolerant due to its superior growth and biomass accumulation at full sunlight. We therefore suggest using the underplanting regeneration approach-specifically inserting *S. superba* below the canopy of existing *C. lanceolata* forests to improve biodiversity in *C. lanceolata* monoculture plantations.

Because our experiment was conducted under controlled conditions, we cannot fully extrapolate our results to the field. In a natural environment, abiotic and biotic factors such as water, nutrients, temperature, and plant litter, intra- and interspecific competition are more variable. Moreover, the effect of light on growth, morphology and biomass allocation may age dependent. Therefore, long-term field studies are necessary to fully understand the complex environmental interactions that influence growth thresholds of plants experiencing light gradients in forest plantation ecosystems. Nonetheless, our findings suggest that light play an important role in determining seedling performance of in *C. lanceolata* and *S. superba*.

Conflict of interest

The authors declare that there are no conflicts of interest.

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Table 1 Light gradients in experiment shade houses. Different letters indicate significant differences in light conditions across shade houses.

Shade house /light gradient (%)	Illuminance (Lux)	PPFD ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	Red/far red ratio
100%	61860.11±1170.73a	1101.88±22.81a	1.07±0.01a
60%	37214.13±885.93b	669.76±32.12b	1.07±0.01a
40%	24805.29±424.82c	453.88±16.17c	1.06±0.01a
15%	9357.80±374.01d	166.91±6.62d	1.06±0.01a
5%	2889.60±89.48e	51.60±1.59e	1.06±0.02a

Table 2 Summary of ANOVA for the main effects of species (df = 1), light (df = 4), and their interaction (df = 4) on growth, foliage characteristics, and biomass.

Traits	Species		Light		Species × Light	
	F	P	F	P	F	P
Height increment (cm)	32.01	<0.001	40.12	<0.001	7.55	<0.001
Diameter increment (cm)	2.87	0.098	15.45	<0.001	28.69	<0.001
Height to diameter ratio	1.24	0.273	44.37	<0.001	7.52	<0.001
Leaf area (cm^2)	86.89	<0.001	87.58	<0.001	2486.04	<0.001
Specific leaf area ($cm^2 \cdot g^{-1}$)	251.27	<0.001	487.93	<0.001	17.73	<0.001
Root biomass (g)	86.65	<0.001	36.42	<0.001	37.04	<0.001
Stem biomass (g)	61.16	<0.001	17.22	<0.001	27.05	<0.001
Leaf biomass (g)	156.73	<0.001	10.21	<0.001	24.10	<0.001
Total biomass (g)	123.66	<0.001	20.37	<0.001	34.20	<0.001
Root weight ratio	158.11	<0.001	165.70	<0.001	2.49	0.058
Stem weight ratio	12.88	0.001	65.10	<0.001	1.93	0.123
Leaf weight ratio	213.71	<0.001	48.70	<0.001	0.48	0.753
Root to shoot ratio	135.10	<0.001	114.63	<0.001	6.54	<0.001
Leaf weight root ratio	52.57	<0.001	36.93	<0.001	5.92	0.001
Ht/Stem-mass ($cm^{-1} \cdot g$)[1]	46.10	<0.001	18.63	<0.001	20.03	<0.001

[1] Length gained per unit mass invested

Figure captions

Fig. 1 Net height increment (A), net diameter growth (B), and height to diameter ratio (C) of *Schima superba* and *Cunninghamia lanceolata* seedlings under different light gradients. Bars show means ± SE. Different lowercase letters indicate significant between-treatment variations; different capital letters indicate significant between-species variations.

Fig. 2 Leaf area (A) and specific leaf area (B) of *S. superba* and *C. lanceolata* seedlings under different light gradients. Bars show means ± SE. Different lowercase letters indicate significant between-treatment variations; different capital letters indicate significant between-species variations.

Fig. 3 Root biomass (A), stem biomass (B), leaf biomass (C), and total biomass (D) of *S. superba* and *C. lanceolata* seedlings under different light gradients. Bars show means ± SE. Different lowercase letters indicate significant between-treatment variations; different capital letters indicate significant between-species variations.

Fig. 4 Root mass ratio (A), stem mass ratio (B), leaf mass ratio (C), root to shoot ratio (D), leaf to root ratio (E), and Ht/Stem-mass (length gained per unit mass invested) ratio (F) in *S. superba* and *C. lanceolata* seedlings under different light gradients. Bars show means ± SE. Different lowercase letters indicate significant between-treatment variations; different capital letters indicate significant between-species variations.

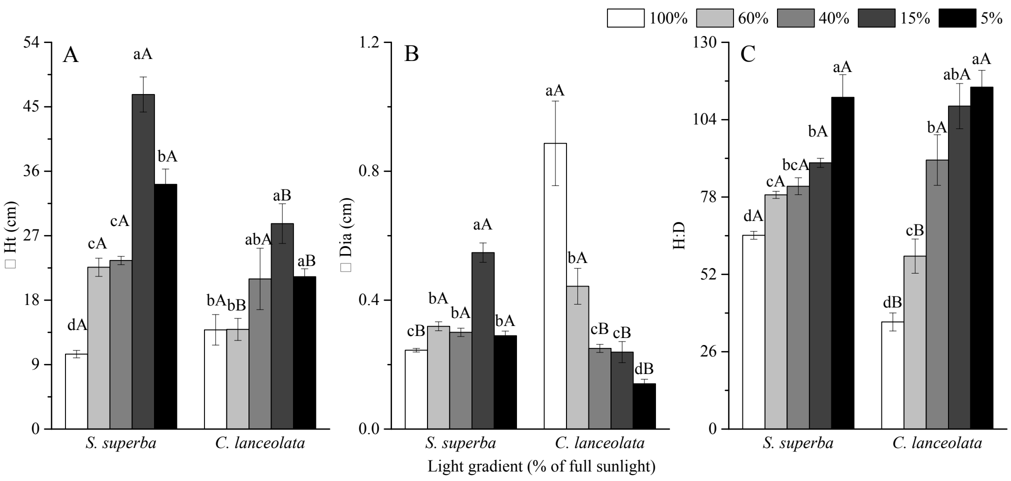
100%
60%
40%
15%
5%
A
Ht (cm)
0
9
18
27
36
45
54
dA
cA
cA
aA
bA
bA
bB
abA
aB
aB
S. superba
C. lanceolata
B
Dia (cm)
0.0
0.4
0.8
1.2
cB
bA
bA
aA
bA
aA
bA
cB
cB
dB
S. superba
C. lanceolata
Light gradient (% of full sunlight)
C
H:D
0
26
52
78
104
130
dA
cA
bcA
bA
aA
dB
cB
bA
abA
aA
S. superba
C. lanceolata

Fig. 1

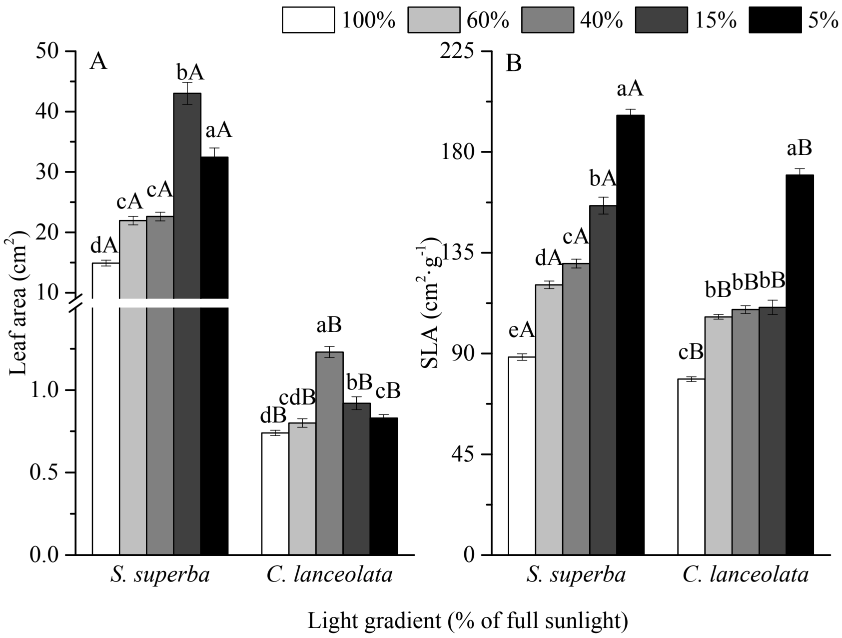
100%
60%
40%
15%
5%
A
B
Leaf area (cm^2)
50
40
30
20
10
1.0
0.5
0.0
dA
cA
cA
bA
aA
dB
cdB
aB
bB
cB
SLA (cm^2·g^{-1})
225
180
135
90
45
0
eA
dA
cA
bA
aA
cB
bB
bB
bB
aB
S. superba
C. lanceolata
S. superba
C. lanceolata
Light gradient (% of full sunlight)

Fig. 2

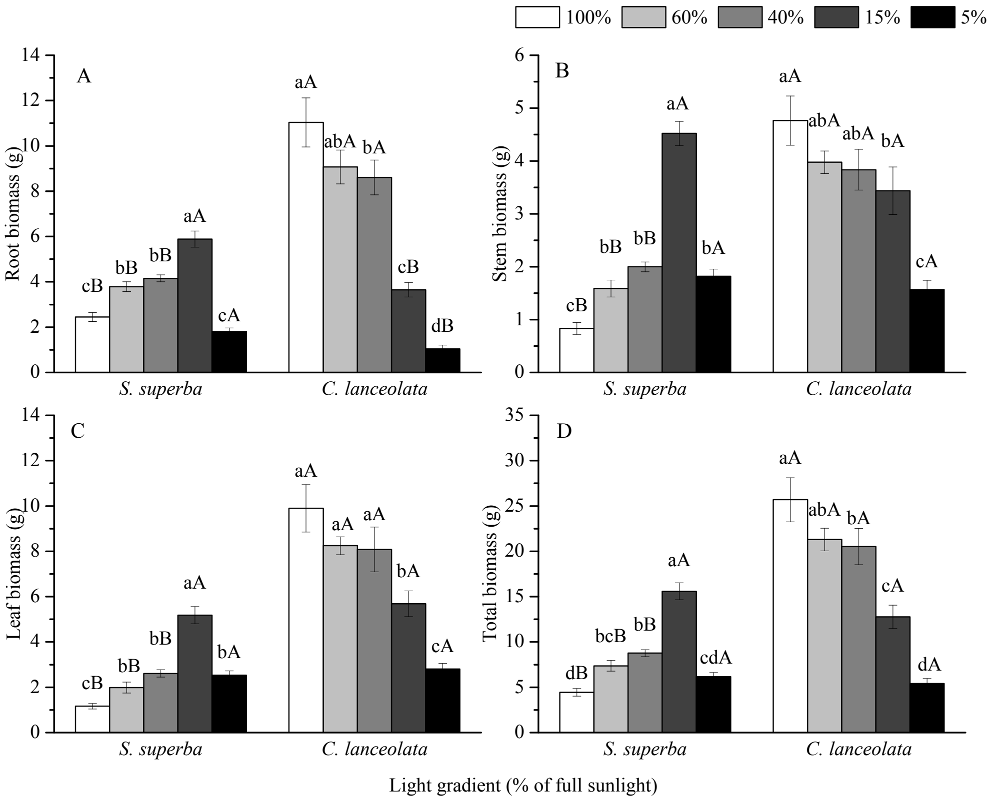
100%
60%
40%
15%
5%
A
Root biomass (g)
0
2
4
6
8
10
12
14
cB
bB
bB
aA
cA
aA
abA
bA
cB
dB
S. superba
C. lanceolata
B
Stem biomass (g)
0
1
2
3
4
5
6
cB
bB
bB
aA
bA
aA
abA
abA
bA
cA
S. superba
C. lanceolata
C
Leaf biomass (g)
0
2
4
6
8
10
12
14
cB
bB
bB
aA
bA
aA
aA
aA
bA
cA
S. superba
C. lanceolata
D
Total biomass (g)
0
5
10
15
20
25
30
35
dB
bcB
bB
aA
cdA
aA
abA
bA
cA
dA
S. superba
C. lanceolata
Light gradient (% of full sunlight)

Fig. 3

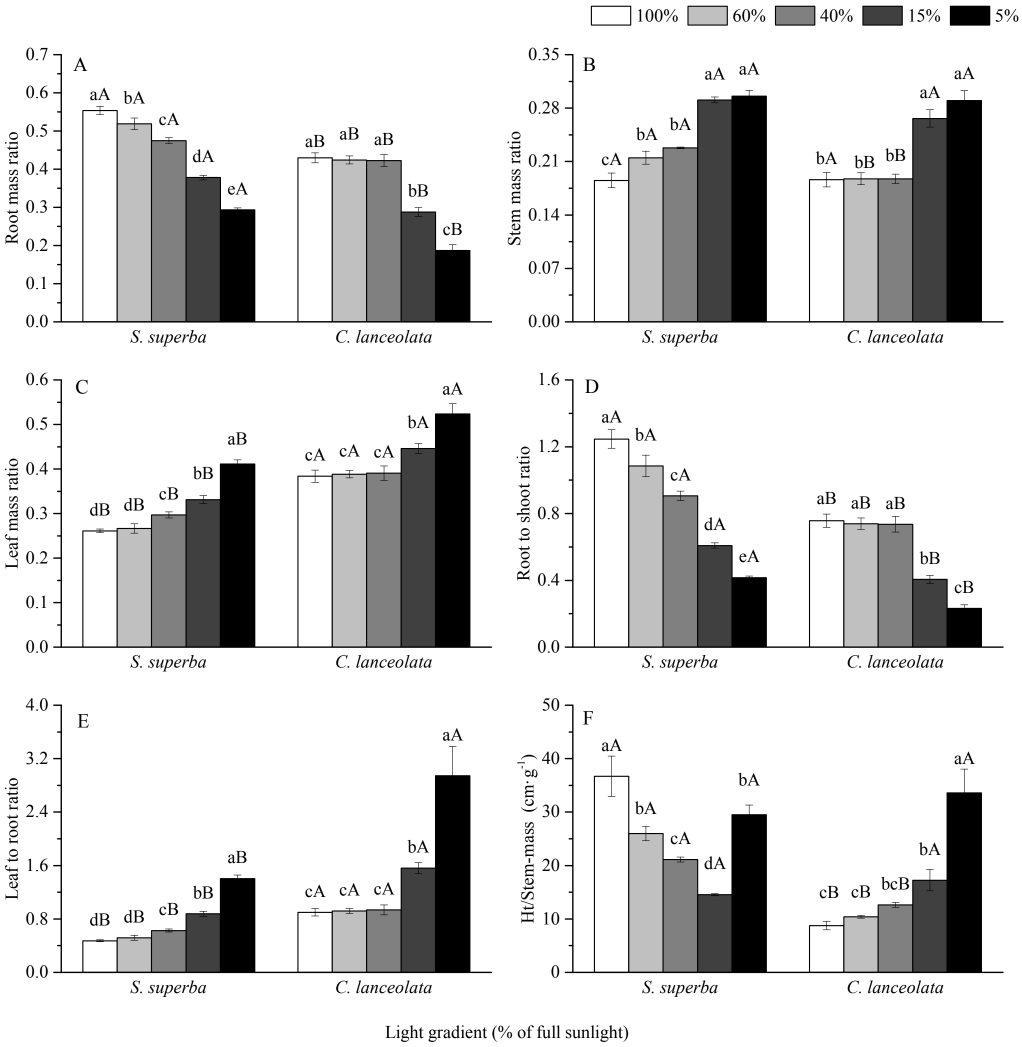
100%
60%
40%
15%
5%
A
Root mass ratio
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
aA
bA
cA
dA
eA
aB
aB
aB
bB
cB
S. superba
C. lanceolata
B
Stem mass ratio
0.00
0.07
0.14
0.21
0.28
0.35
cA
bA
bA
aA
aA
bA
bB
bB
aA
aA
S. superba
C. lanceolata
C
Leaf mass ratio
0.0
0.1
0.2
0.3
0.4
0.5
0.6
dB
dB
cB
bB
aB
cA
cA
cA
bA
aA
S. superba
C. lanceolata
D
Root to shoot ratio
0.0
0.4
0.8
1.2
1.6
aA
bA
cA
dA
eA
aB
aB
aB
bB
cB
S. superba
C. lanceolata
E
Leaf to root ratio
0.0
0.8
1.6
2.4
3.2
4.0
dB
dB
cB
bB
aB
cA
cA
cA
bA
aA
S. superba
C. lanceolata
F
Ht/Stem-mass (cm·g⁻¹)
0
10
20
30
40
50
aA
bA
cA
dA
bA
cB
cB
bcB
bA
aA
S. superba
C. lanceolata
Light gradient (% of full sunlight)

Fig. 4