

Effects of light intensity on non-structural carbohydrate contents and C:N:P stoichiometry in *Cunninghamia lanceolata* and *Schima superba*

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Abstract

Background: An understanding of the light requirement of tree species has paramount importance in management of mixed species forests. Here, we examined changes in leaf morphological traits, non-structural carbohydrate contents and C:N:P stoichiometry in *Cunninghamia lanceolata* and *Schima superba* seedlings that were grown under five light intensity levels (5%, 15%, 40%, 60%, and 100% sunlight) in a shade house.

Results: Mean leaf area was significantly larger under 40% light intensity for *C. lanceolata* while maximum mean leaf area was observed under 15% light intensity for *S. superba* seedlings, whereas leaf mass per area decreased consistently with decreasing light intensity in *S. superba*; Non-structural carbohydrate content was higher for *S. superba* than *C. lanceolata* when seedlings were exposed to 100%, 15% and 5% light intensity; Leaf C:N ratio decreased while N:P ratio increased with decreasing light intensity; leaf C:P ratio was highest in 40% light intensity for *C. lanceolata* and in 60% light intensity for *S. superba*.

Conclusion: *S. superba* is better adapted to low light intensity than *C. lanceolata* through enlarged leaf area and increased carbohydrate reserves that allow the plant to better maintain C balance. From mixed species planting viewpoint, it would be advisable to plant *S. superba* later once the canopy of *C. lanceolata* is well developed but allowing enough sunlight (up to 15%-60%).

Introduction

The temporal and spatial distribution of light varies greatly during forest development and succession [1, 2]. This fluctuation hampers or accelerates plant growth intermittently, especially beneath the forest canopy [3, 4]. Under canopies, light intensity is greatly attenuated before reaching leaf surfaces of seedlings and saplings in the forest understory [5, 6]. Plants have therefore evolved strategies to avoid canopy shade and compete for light, ensuring a regular photosynthesis rate and maintaining nutrient balance [7]. Seedling establishment and juvenile growth are particularly light-sensitive stages of plant life cycles. The morphological and physiological attributes that form during these periods are critical for subsequent recruitment and survival of tree populations. Therefore, light is recognized as an indispensable factor influencing natural forest regeneration [8, 9, 10].

Light is probably the most heterogeneous environmental factor that affects plant growth. Therefore, plant survival, growth, and regeneration is strongly dependent on whether it can flexibly respond to these changing conditions [11]. Both high and low light conditions could limit plant performance [12]. Plants can respond to light fluctuations through metabolic, developmental, morphological, and physiological adjustments throughout their entire life cycle, but especially during the early stages [13, 14]. Previous studies have examined general growth, biomass allocation, and morphological plasticity of plants under different environments [4, 13, 15]. Leaf traits are particularly sensitive to environmental change and are the typical target of selection [16, 17]. Thus, they effectively reflect the adaptive mechanisms of plants to

environmental changes [18]. Light influences multiple leaf related characteristics, including area, branch number, and water content [19, 20, 21]. Plants often invest large amounts of photosynthate to construct supporting structures and enlarging leaf area during light competition with neighbors [22, 23, 24].

In addition to light, plants also require carbon, nitrogen, and phosphorus during their life cycle, similar to other organisms [25]. The content and ratios of these three essential elements reflect a plant's nutrient absorption and use strategy [26]. Indeed, some evidence shows that plant stress responses are associated with C:N:P ratios [27, 28, 29]. An important measure linking nutrient and light uptake is non-structural carbohydrate (NSC), including soluble sugars and starch contents in leaf tissue. This reflects the relationship between C uptake (photosynthesis) and consumption (respiration), as well as the energy stores (carbohydrates) available for stress responses [30]. Overall, leaf area, NSC content, and C:N:P stoichiometry are the main morphological and functional responses of leaves to differing light availability [30].

Thus, we investigated the effects of light intensity on leaf morphology, non-structural carbohydrate content and C:N:P stoichiometry in *Cunninghamia lanceolata* (Lamb.) Hook and *Schima superba* Gardn. & Champ – the two most important forest species in subtropical China, which are intended for establishment of mixed species forest. It has been shown that *S. superba* seedlings under low light exhibited greater net height increment, net diameter growth and total biomass than *C. lanceolata* [31]. However, we still know little about the effect of varying light intensities on leaf morphological and functional responses in these two species. We hypothesized that (1) *S. superba* will have larger leaf area but smaller leaf mass per unit area under low light intensity than *C. lanceolata*, and (2) *S. superba* produces more NSC under low light intensity than *C. lanceolata*; and (3) C:N:P stoichiometry varies among light intensity levels with marked inter-species variation. To test these hypotheses, we conducted an experiment by altering light intensity along a gradient to determine the differential effects on leaf morphological traits, NSC content and C:N:P stoichiometry in *C. lanceolata* and *S. superba*. We also examined variation in soluble sugar and starch contents as well as leaf C, N, and P contents. Finally, we looked for potential relationships between leaf NSCs, C:N:P stoichiometry, and their combined effects on plant survival mechanisms. The study will provide valuable insights about optimum light conditions for the establishment and growth of both species under mixed planting scheme.

Results

Leaf morphological responses to light

Leaf traits differed significantly ($p < 0.05$) across light treatment and species (Tables 2 and 3). *Schima superba* leaf length, width, and area were the greatest under 15% light. For Chinese fir, leaf length, width, and area were the greatest under 15%, 40%, and 40% light, respectively. Leaf mass per unit area was positively correlated with light for both species. *Schima superba* seedlings had smaller leaf mass per unit area but greater leaf length, width, and area than Chinese fir seedlings across all light treatments.

Responses of carbohydrate content to light intensity gradient

Soluble sugar content, NSC content and soluble sugar/starch ratio varied significantly between species, among light intensity levels and their interaction, whereas the main effects of light and species significantly influenced starch content (Table 2). Soluble sugar content was higher for *C. lanceolata* seedlings exposed to 40%, 60% and 100% light intensity than 5% and 15% light intensity, whereas it was higher for *S. superba* seedlings exposed to 60% and 100% light intensity than 5%, 15% and 40% light intensity (Fig. 1A). However, the soluble sugar content was higher for *S. superba* than *C. lanceolata* seedlings exposed to 5% and 15% light intensity. Starch content was higher for *S. superba* than *C. lanceolata* across all light intensity levels, and in both species the highest starch content was observed in seedlings exposed to 60% light intensity (Fig. 1B). The NSC content was higher for *S. superba* than *C. lanceolata* when seedlings were exposed to 100%, 15% and 5% light intensity, and in both species NSC content was the highest in seedlings exposed to 60% light intensity (Fig. 1C). The soluble sugar to starch ratio was larger for *C. lanceolata* than *S. superba* across all levels of light intensity (Fig. 1D). While there was no significant difference in soluble sugar to starch ratio across all levels of light intensity for *S. superba*, it was the highest in *C. lanceolata* seedlings exposed to full sunlight, followed by those exposed to 40% and 60% light intensity and the least being in 5% and 15% light intensity. Averaged across all light treatments, *S. superba* had significantly higher soluble sugar, starch, and NSC content ($18.87 \pm 0.76 \text{ mg} \cdot \text{g}^{-1}$, $7.89 \pm 0.33 \text{ mg} \cdot \text{g}^{-1}$, $26.76 \pm 1.02 \text{ mg} \cdot \text{g}^{-1}$, respectively) than *C. lanceolata* ($17.76 \pm 1.35 \text{ mg} \cdot \text{g}^{-1}$, $4.35 \pm 0.24 \text{ mg} \cdot \text{g}^{-1}$, $22.10 \pm 1.52 \text{ mg} \cdot \text{g}^{-1}$, respectively), while as soluble sugar to starch ratio was significantly greater in *C. lanceolata* ($4.09 \pm 0.26 \text{ mg} \cdot \text{g}^{-1}$) than in *S. superba* ($2.41 \pm 0.07 \text{ mg} \cdot \text{g}^{-1}$).

Light-induced changes in leaf C:N:P stoichiometry

Contents of C, N and P as well as C:N:P stoichiometry varied significantly between species, among light intensity levels and their interaction (Table 2). Generally, leaf C content was higher for *S. superba* than *C. lanceolata*, and it was higher in 100% light level for *C. lanceolata* and in 15% and 100% light levels for *S. superba* (Fig. 2A). Leaf N content in both species showed an increasing tendency with decreased light intensity, and it appeared to be higher for *C. lanceolata* than *S. superba* (Fig. 2B). In both species, the highest leaf N content was observed in 5% light intensity compared to other light intensity levels. Leaf P content in *C. lanceolata* showed 70% drop from 100% ($3.13 \pm 0.02 \text{ mg} \cdot \text{g}^{-1}$) to 40% light ($0.93 \pm 0.01 \text{ mg} \cdot \text{g}^{-1}$), before increasing slightly afterwards as light level decreased (Fig. 2C). Full exposure to sun light and 5% light intensity increased leaf P content in *S. superba* compared to other light intensity levels. As a whole, leaf P content was significantly higher for *C. lanceolata* than *S. superba*. For both species, leaf C:N ratio decreased as light intensity decreased (Fig. 2D); peaking at 60% (58.01 ± 0.30 for *C. lanceolata* and 75.24 ± 3.42 for *S. superba*). Similarly, leaf N:P ratio in both species increased from 100% to 5% light intensity (Fig. 2E); ranging from 3.38–12.17 for *C. lanceolata* to 14.37–22.59 for *S. superba*. Averaged across all light intensity levels, leaf N:P ratio for *S. superba* (18.93 ± 0.96) was significantly higher than for *C. lanceolata* (8.43 ± 0.69). Leaf C:P ratio was highest in 40% light intensity for *C. lanceolata*, while it was

highest in 60% light intensity for *S. superba* (Fig. 2F). Averaged overall light intensity levels, leaf C:P ratio was 2.62 times greater for *S. superba* (939.65 ± 46.12) than for *C. lanceolata* (358.71 ± 27.38).

Correlations between carbohydrate content and C:N:P stoichiometry

Soluble sugar content was negatively correlated with N content and N:P ratio in both species while a positive correlation was observed between soluble sugar content and C:N ratio in *C. lanceolata* and between soluble sugar content and C content and C:N ratio in *S. superba* (Table 2). Starch content was negatively correlated with N content in *C. lanceolata* and with N and P contents in *S. superba* while positive correlations were observed with C:N ratio in *C. lanceolata* and C content, C:N and C:P ratio in *S. superba*. NST content was negatively correlated with N content and N:P ratio in both species whereas a positive correlation was observed between NSC and C:N ratio in *C. lanceolata* and with C content and C:N ratio in *S. superba*. The soluble sugar to starch ratio was positively correlated with C and P contents while it had a negative correlation with N content and N:P ratio in *C. lanceolata*. There was no significant correlation between soluble sugar to starch ratio and C:N:P stoichiometry in *S. superba*.

Discussion

The considerable variation in leaf morphology and structure reflects the organ's phenotypic plasticity [32]. Therefore, leaf characteristics are often used as an indicator of plant acclimation potential and adaptation mechanism [33]. Because excessive irradiance has a detrimental impact on photosynthetic tissues, plants must produce smaller and thicker leaves with higher leaf mass per area under high light conditions. This morphology allows heat dissipation, avoiding damage from overheating and high transpiration rates [2, 34]. Conversely, shaded conditions result in increasing area and decreasing thickness of leaves [22, 31], with low leaf mass per unit area [12]. Increasing leaf area allows plants to acquire more light for photosynthesis [5, 35] and is thus an adaptation to low-light environments [34]. In this study, we observed larger leaf area under 5% and 15% light intensity levels for *S. superba* and under 40% light intensity for *C. lanceolata*. Our findings are in line with previous research on *Elaeagnus angustifolia* leaves, which became smaller and thicker under high light [34].

Furthermore, here we observed decreasing leaf mass per area and increasing leaf area with decreasing light intensity, again in both species. In agreement with our results, *Alocasia macrorrhiza* displays the same adaptations (larger and thinner leaves) to optimize photosynthetic efficiency under low light [36]. Low light intensity also resulted in greater leaf mass per area for *Citharexylum*, *Dendropanax*, *Fraxinus*, *Quercus*, and *Magnolia* [4]. Interestingly, our study revealed between-species differences in the response of mean leaf area to decreasing light intensity. Specifically, mean leaf area was greatest at 40% light intensity in *C. lanceolata*, but at 15% light intensity in *S. superba*. The latter species also had significantly larger mean leaf area than *C. lanceolata*. These traits enhanced the ability of *S. superba* to tolerate low light intensity (shade) compared with *C. lanceolata*. Our finding is in line with the carbon gain hypothesis, which proposes that leaf area is higher in shade-tolerant seedlings than in intolerant seedlings [37], and implies that *S. superba* is better adapted to low light. As a whole, the findings support our first hypothesis

that *S. superba* will have larger leaf area but smaller leaf mass per unit area under low light intensity than *C. lanceolata*.

Previous studies have shown that *C. lanceolata* seedlings adapt to shaded conditions through adjusting morphological characteristics [38]. However, seedlings had difficulty maintaining a C balance under extremely shaded (5% sunlight) conditions, causing poor growth and survival. The issue of negative C and relatedly NSC balance under low light is a common problem plants face. For instance, a study made on *Pinus koraiensis* and *Quercus mongolica* demonstrated that low light induced carbohydrate deficiency and therefore high seedling mortality, with none surviving at 1% light intensity [39]. Similarly, under extremely shaded conditions, *Quercus aliena* seedlings had difficulty maintaining C balance and thus experienced mortality [40]. To overcome the lack of an energy source under low light intensity, plants store NSC to enhance growth and survival [12, 39, 41, 42]. Here, we found that 60% light intensity results in significantly higher soluble sugar, starch, and NSC content for both species. Once under low light intensity, all three variables decreased, presumably as a result of seedlings using their energy stores for growth. In addition, when averaged across all light treatments, the carbohydrate contents were significantly larger in *S. superba* than in *C. lanceolata*. Moreover, *C. lanceolata* had a larger soluble sugar/starch ratio across all light treatments, despite considerable variability as light intensity decreased. This result demonstrates that *S. superba* seedlings had an advantage under shaded conditions and, moreover, could flexibly adjust to a vast range of light conditions. In terms of mechanism, exposure to high light intensity would result in greater C gain than demand, leading to NSC storage [12, 43]. Once light becomes a limiting resource, plants will mobilize NSC to support growth and survival [44]. The results support our second hypothesis that *S. superba* produces more NSC under low light intensity than *C. lanceolata*.

Both genetic and environmental factors influence plant nutrient uptake, as demonstrated by interspecific differences, along with intraspecific differences under various habitats [45]. In our study, *S. superba* and *C. lanceolata* used C, N, and P differently under varying light intensities, suggesting species-specific strategies in balancing nutritional metabolism and adapting to environmental stress. Light level, species, and their interaction significantly altered C, N, P content and stoichiometry. Notably, leaf C content decreased with decreasing light intensity. Both species had higher C content under full sunlight, likely due to strong photosynthetic efficiency resulting in heightened synthesis of organic matter and C accumulation. Importantly C content was significantly larger in *S. superba* than in *C. lanceolata*. Given previous research linked higher C content with greater photosynthetic efficiency and resilience to adverse environments [46], our findings imply that *S. superba* is better adapted to low light than *C. lanceolata*. Also in agreement with our results, some studies have suggested that shade-tolerant plants have higher NSC accumulation and C pool than non-tolerant plants [41, 42]. In further support of light-dependent changes in strategy, we observed higher P and N contents in both two species under 100% and 5% light intensity, respectively. P and N are essential macro-elements for plant growth and development, which participate in a number of metabolic processes, such as photosynthetic phosphorylation, ATP production, the production and export of triose-P and ribulose-1, 5-bisphosphate regeneration as well as synthesis of amino acids [47]. This outcome is the vigorous growth under strong photosynthetic ability in full sunlight,

leading to greater requirements for proteins and nucleic acids. On the contrary, seedlings of both species may use more N resources to synthesize light-trapping proteins under low light intensity. This is further evidenced in our study where NST content was negatively correlated with N content and N:P ratio in both species whereas a positive correlation was observed between NSC and C:N ratio in *C. lanceolata* and with C content and C:N ratio in *S. superba*. Our findings are corroborated by previous research showing that plants growing under low light intensity will have increased leaf N content and allocate more N to photosynthetic pigments. This strategy increases light use efficiency and maintain normal photosynthetic function [48]. The findings give credence to our third hypothesis where C:N:P stoichiometry varies with light intensity with marked inter-species variability.

Conclusions

The results demonstrate that both *C. lanceolata* and *S. superba* seedlings acclimatize morphologically and physiologically to different light availability. Nevertheless, *S. superba* is better adapted to low light than *C. lanceolata* through enlarged leaf area and larger carbohydrate reserves that allow the plant to better maintain C balance. The findings have great implication for establishment and maintenance of mixed species stand. As *S. superba* is better adapted to low light intensity (shade tolerant), it would be advisable to plant *S. superba* later once the canopy of *C. lanceolata* is well developed but allowing enough sunlight (up to 15%-60%). Conversely, in dense stands of *C. lanceolata*, thinning to allow sufficient light to reach the understory would be recommended to expedite the natural regeneration and subsequent growth of *S. superba* as we observed better growth of *S. superba* under low light intensity [31].

Materials And Methods

Experimental design and treatments

We conducted an experiment in a flat, open area at the Fujian Agriculture and Forestry University. Five light intensity levels (100%, 60%, 40%, 15%, and 5% of full sunlight) were created using shade houses covered with black nylon shade cloth of differing mesh size [31]. The relative irradiance was estimated with a light meter on a clear day in summer and summarized in Table 1. More importantly, shade houses were placed parallel to the sun's daily track to minimize spatiotemporal variation in solar radiation. In July 2016, *C. lanceolata* and *S. superba* seedlings were purchased from a container nursery in Zhangping Wuyi Forest Farm, Fujian, China. Purchased seedlings were transplanted to pots containing potting compost and were grown for 1 month in a glasshouse. During August 2016, well-developed seedlings of uniform height were selected and randomly divided into five groups. Each group comprised four seedlings per species and was assigned to light intensity treatment. Although we used only one shade structure for each light level, the four seedlings under each light intensity levels were grown individually in pots. And individual seedling pots were treated as replicates and randomly positioned to ensure each obtained similar light irradiation with no mutual shading. Pots were widely spaced from each other to minimize any interplant competition and rotated weekly to remove positional effects. Weeds were periodically cleared from the experimental plot and seedlings were watered as needed.

Leaf morphology measurements

All plants were maintained under their assigned light intensity levels for 1 y. To estimate mean leaf area, 10 healthy and fully expanded green leaves were randomly collected from seedlings of comparable height in the same plot. Samples were placed in ice and immediately taken to the laboratory for further analysis. Individual leaf area (cm^2) was determined with a portable leaf area meter (Yaxin-1241, Shanghai, China). Leaves were then individually placed in paper bags and oven-dried for 30 min at 105°C , followed by at least 24 h at 80°C . Upon reaching a constant dry mass, the dry mass of each leaf was determined. Leaf mass per unit area (LMA, $\text{mg}\cdot\text{cm}^{-2}$) was computed as the oven-dry mass per leaf divided by the corresponding area.

Determination of carbohydrate content

Leaves were randomly collected from seedlings of both species across all light treatments, cleaned with distilled water, and ground to powder. Samples (0.2 g) were mixed with 5 mL of distilled water in a test tube. After 30 min in a boiling water bath, the supernatant was collected. This process was repeated twice to ensure complete sugar extraction. The two extracts were collected in a centrifuge tube and distilled water was then added to achieve a 25 mL constant volume. Thereafter, sediments from the soluble sugar extraction were dried before the addition of perchloric acid to extract starch. Soluble sugar and starch content were determined using the anthrone colorimetric method. Absorbance at 630 nm was measured to calculate soluble sugar and starch content according to the glucose standard curve. Non-Structural Carbohydrate content was calculated as the sum of soluble sugar and starch content. The analysis was replicated four times per treatment.

Leaf C, N, P determination

After the light intensity experiments, all leaves of the same species under the same treatment were pooled, grounded into uniformly fine powder, and sieved with a 1 mm mesh before chemical analysis. Total C and N content ($\text{mg}\cdot\text{g}^{-1}$, dry mass basis) were measured via dry combustion using an elemental analyzer (VARIO MAX CN; Elementary, Germany). Total P concentration ($\text{mg}\cdot\text{L}^{-1}$) was determined with ICP-OES (Optima 8000, PerkinElmer) after $\text{H}_2\text{SO}_4\text{-HClO}_4$ solution digestion and dilution. After converting to $\text{mg}\cdot\text{g}^{-1}$, the C:N, C:P and N:P ratios were calculated. All chemical analyses were replicated four times per light treatment and species.

Statistical analysis

Two-way ANOVA was performed to test the effects of light, species, and their interaction on leaf morphology, carbohydrate content, and C:N:P stoichiometry, with light intensity and species as independent variables. Between species differences under each light intensity level were determined with independent t tests. Correlation analysis was performed to examine the relationship between non-structural carbohydrate content and C:N:P stoichiometry. Data are presented as means \pm SE for different light treatments and species. Statistical significance was set at $P < 0.05$. All statistical analyses were performed in SPSS version 20.0 for Windows (SPSS Inc., Chicago, IL, USA).

Declarations

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Authors' contributions

BL conceived the study. BL and QQL designed the experiments. QQL, ZJH, YFC, and ZMW performed the experiments. QQL and BL analysed the data. QQL, BL and MT wrote the manuscript. All authors read and approved the final manuscript.

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Competing interests

The authors declare that they have no competing interests

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Tables

Table 1. Light intensity in different shade treatments (mean ±SE). Different letters indicate significant differences in light conditions across shade treatments.

Light intensity (% of full sunlight)	Illuminance/(Lux)	Photosynthetic Photon Flux Density/($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	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. Results of ANOVA, showing main effects of light (df=4), species (df=1), and their interaction (df=4) on leaf morphology, NSC content, and C:N:P stoichiometry.

Traits	Light		Species		Light × Species	
	F	P	F	P	F	P
Leaf mass per unit area (mg·cm ²)	482.023	<0.001	240.537	<0.001	10.859	<0.001
Soluble sugar content(mg·g ⁻¹)	82.097	<0.001	5.322	0.028	8.588	<0.001
Starch content(mg·g ⁻¹)	22.203	<0.001	253.800	<0.001	2.023	0.116
NSC content(mg·g ⁻¹)	105.117	<0.001	80.982	<0.001	6.779	0.001
Soluble sugar/Starch	14.793	<0.001	134.778	<0.001	9.815	<0.001
Leaf C content (mg·g ⁻¹)	75.973	<0.001	144.258	<0.001	19.281	<0.001
Leaf N content (mg·g ⁻¹)	383.990	<0.001	91.432	<0.001	11.155	<0.001
Leaf P content (mg·g ⁻¹)	498.269	<0.001	2929.903	<0.001	351.043	<0.001
Leaf C:N ratio	136.738	<0.001	46.735	<0.001	6.208	0.001
Leaf N:P ratio	82.692	<0.001	865.569	<0.001	15.100	<0.001
Leaf C:P ratio	132.876	<0.001	2360.670	<0.001	50.798	<0.001

Table 3. Leaf color and leaf traits of *Schima superba* and Chinese fir in response to different light intensities.

Light intensity	<i>Schima superba</i>				<i>Cunninghamia lanceolata</i>			
	LL (cm)	LW(cm)	LS (cm ²)	LMA (mg·cm ⁻²)	LL (cm)	LW(cm)	LS (cm ²)	LMA (mg·cm ⁻²)
5%*	17.20±0.67a	3.21±0.12b	32.46±1.51a	5.11±0.08e	5.16±0.22bc	0.25±0.02ab	0.83±0.02c	5.92±0.10c
15%*	8.18±0.50c	3.95±0.16a	43.02±1.82b	6.43±0.16d	6.17±0.14a	0.29±0.02ab	0.92±0.04b	9.10±0.25b
40%*	12.65±0.59b	3.09±0.17bc	22.62±0.72c	7.69±0.12c	5.34±0.26b	0.30±0.03a	1.23±0.03a	9.15±0.14b
60%*	13.49±0.57b	2.72±0.16c	21.94±0.71c	8.32±0.12b	4.67±0.15cd	0.26±0.04ab	0.80±0.03cd	9.41±0.10b
100%*	18.29±0.78a	2.21±0.18d	14.91±0.48d	11.33±0.19a	4.44±0.17d	0.21±0.03b	0.74±0.02d	12.75±0.17a

Data are represented as means ± SE. Different lowercase letters indicate significant difference (ANOVA, Tukey's test, $p < 0.05$) among treatments within each species. An asterisk after light intensity indicates significant differences between the two species; LL= Leaf length, LW=leaf width, LS=leaf size, LMA=leaf mass per unit area.

Table 4. Correlations between leaf carbohydrate contents and C:N:P stoichiometry of *C. lanceolata* and *S. superba* seedlings under different light gradients.

Species		Soluble sugar	Starch	NSC	Soluble sugar/Starch
<i>C. lanceolata</i>	C	0.443	-0.136	0.371	0.768**
	N	-0.879**	-0.788**	-0.903**	-0.477*
	P	0.248	-0.319	0.168	0.663*
	C:N	0.898**	0.841**	0.929**	0.443
	N:P	-0.731**	-0.282	-0.692**	-0.762**
	C:P	-0.023	0.407	0.045	-0.434
<i>S. superba</i>	C	0.555*	0.539*	0.587**	0.024
	N	-0.820**	-0.774**	-0.860**	-0.082
	P	-0.242	-0.497*	-0.339	0.330
	C:N	0.781**	0.735**	0.819**	0.080
	N:P	-0.725**	-0.436	-0.681**	-0.402
	C:P	0.341	0.583**	0.441	-0.306

**Significant at $P < 0.01$, * significant at $P < 0.05$.

Figures

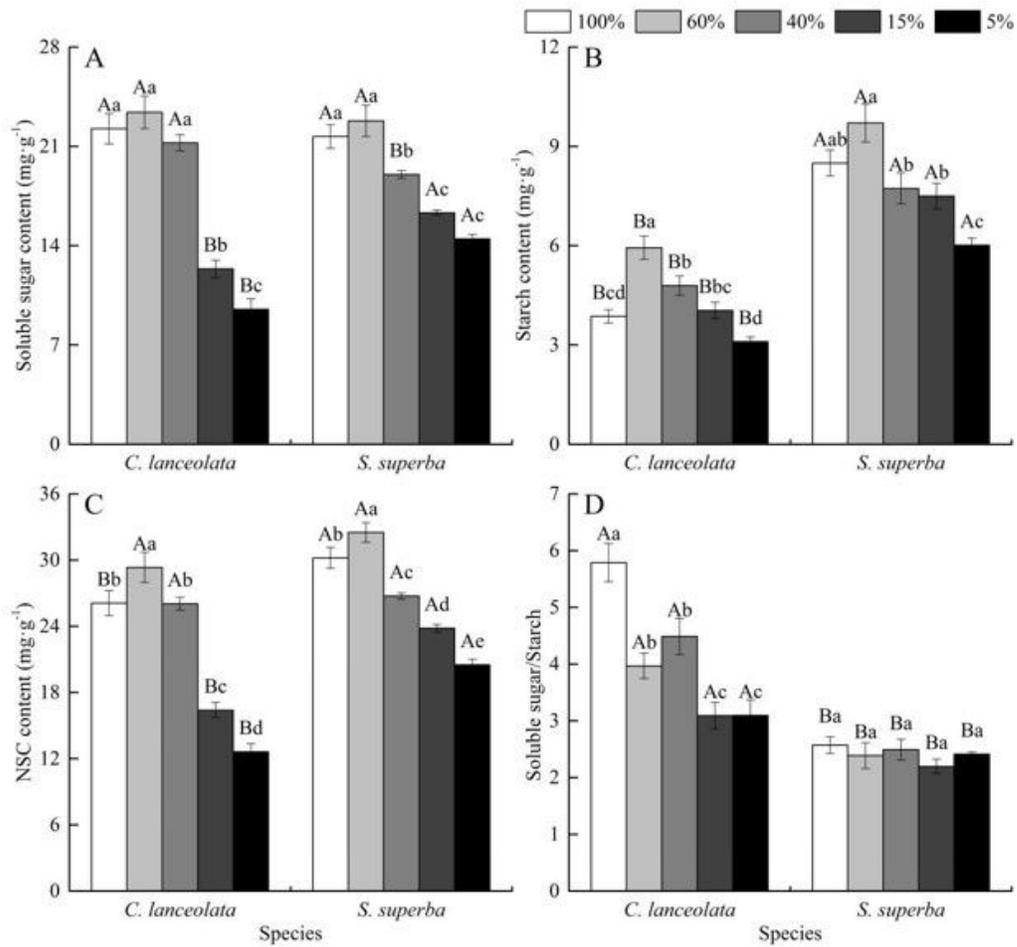


Figure 1

Soluble sugar content (A), starch content (B), NSC content (C), and NSC allocation (D) in leaves of *C. lanceolata* and *S. superba* seedlings under different light gradients. Bars with different capital letters represent significant differences among species of the same light intensity at 0.05 level. Bars with different lower letters represent significant differences among light intensity levels of the same species at 0.05 level.

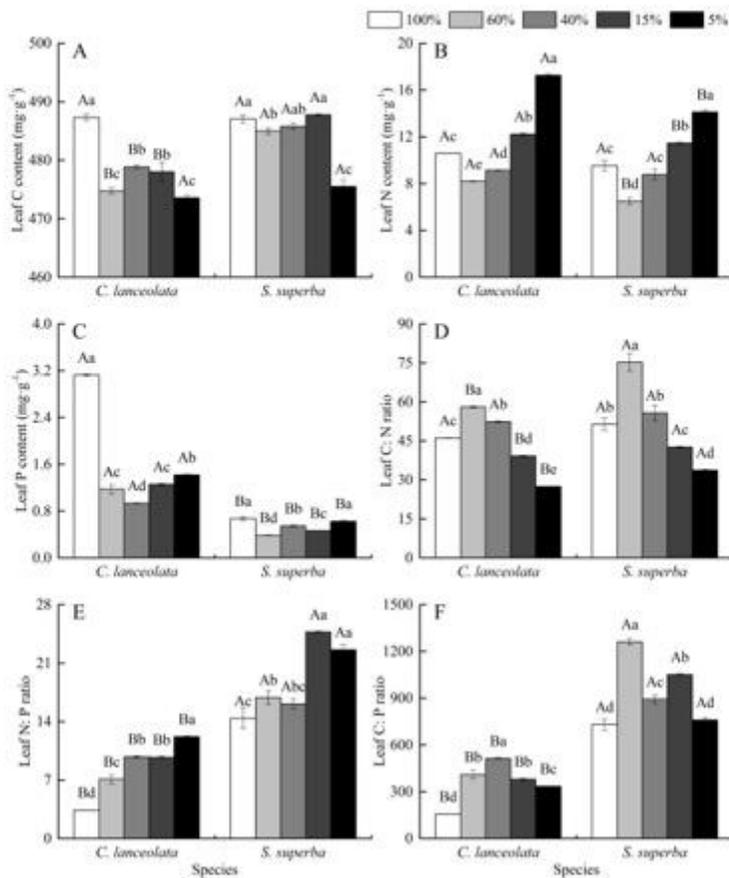


Figure 2

C content (A), N content (B), P content (C), C:N ratio (D), N:P ratio (E), C:P ratio (F) in leaves of *C. lanceolata* and *S. superba* seedlings under different light gradients. Bars with different capital letters represent significant differences among species of the same light intensity at 0.05 level. Bars with different lower letters represent significant differences among light intensity levels of the same species at 0.05 level.