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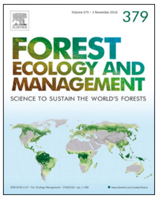

Responses of Chinese fir and *Schima superba* seedlings to light gradients: Implications for the restoration of mixed broadleaf-conifer forests from Chinese fir monocultures

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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.

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

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(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, 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.

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 (μmol m^{-2} 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

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