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Variation in survival and growth strategies for seedlings of broadleaved tree species in response to thinning of larch plantations: Implication for converting pure larch plantations into larch-broadleaved mixed forests

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ABSTRACT

In Northeast China, larch (*Larix* spp.) plantations exchanged from broadleaved secondary forests to meet the demand of timber consumption are facing some serious problems, including soil fertility decline, acidification of surface runoff and low levels of biodiversity. How to promote the regeneration of broadleaved tree species in larch plantations and convert the pure larch plantations into mixed larch-broadleaved forests would be a top priority to solve some of these issues. The success of this conversion mainly depends on the seedling performances of the selected broadleaved tree species. Seedlings of four dominant broadleaved tree species (intermediate shade tolerant species: *Fraxinus mandshurica* and *Acer mono*, shade intolerant species: *Juglans mandshurica* and *Quercus mongolica*) from the secondary forests were planted in the thinned pure larch stands (0%, 25%, 50% and 100% thinning) to explore the adaptive strategies (biomass accumulation, leaf structural, nutrient and physiological traits) of two shade-tolerant types of broadleaved tree species responding to the thinning in larch plantations. We found that compared with the intermediate shade tolerant group, the shade intolerant species had higher leaf construction cost (CC), carbon:phosphorus (C:P) ratio, nitrogen:phosphorus (N:P) ratio, and nonstructural carbohydrate concentration (NSC) in stems and roots at all thinning treatments, and had higher leaf ash and specific leaf area (SLA) only in the larch plantations with a canopy openness more than $25 \pm 1\%$ (i.e., the 50% and 100% thinning intensity). Across all the thinning treatments, higher survival rates were found for the shade intolerant species relative to the intermediate shade tolerant species, but relative height growth (RHG) did not differ significantly between the groups. When the canopy openness of larch plantations was less than 21% (i.e., 0% and 25% thinning intensity), the intermediate shade tolerant group could utilize essential growth resources more efficiently by investing less energy per unit of RHG, and had a greater photosynthetic capacity at minimal costs relative to the shade intolerant species. However, regression analyses indicated that across all the thinning treatments (and hence all the light irradiance in this study), at a given NSC, there was a higher RHG for the shade intolerant group; also at a common SLA, there were a lower CC and lower area-based N for the shade intolerant group. Ordination using 15 eco-physiological and chemical traits of plants indicated that the major axis of shade intolerant-intermediate shade tolerant dichotomy was primarily driven by leaf NSC, CC and C:P ratio, and was significantly linked with RHG. These results demonstrated that it is a potentially feasible practice for building uneven-aged larch-broadleaved mixed forests by thinning and planting seedlings of native broadleaved tree species in pure larch plantations. Furthermore, the regeneration of the intermediate shade tolerant group and the shade intolerant species could be promoted in larch

Abbreviations: N_{mass}, mass-based nitrogen concentration; N_{area}, area-based nitrogen concentration; C, carbon concentration; P, phosphorus concentration; NSC, nonstructural carbohydrate concentration; Ash, mineral ash; HC, heat of combustion; SLA, specific leaf area; CC_{mass}, mass-based construction cost; CC_{area}, area-based construction cost; $\delta^{13}C$, isotopic carbon; RHG, relative height growth; RGR, relative growth rate; WUE, water use efficiency; C:P, carbon:phosphorus ratio; N:P, nitrogen: phosphorus ratio; C:N, carbon:nitrogen ratio.

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plantations with the canopy openness less than 21% and more than 25%, respectively. This study may provide an insight into uneven-aged and mixed silviculture for larch plantation forests.

1. Introduction

To meet the increasing demand for timber, large areas of plantation forests have been transformed from the natively broadleaved secondary forests in China, which are the major forest resources (accounting for more than 50% of the total area of national forests) (Zhu et al., 2007). Particularly in Northeast China, pure larch plantations (*Larix* spp.: native *L. olgensis* Henry and *L. gmelinii* Rupr., and exotic *L. keampferi* (Lamb.) Carr.) have been established since the 1960s and occupied one-third of the plantation area of China (Mason and Zhu, 2014). Compared with the secondary forests with complex species composition and stand structure, however, there are some serious problems in larch plantations, including soil fertility decline caused by soil acidification and nutrient leaching (Yang et al., 2010, 2013), decreased biodiversity resulted from simple stand structure and mono-species compositions (Yan et al., 2013), and unsustainable forest development (including poorer ecosystem services and lower productivity) due to poor natural regeneration and soil fertility decline (Zhu et al., 2010). To resolve some of these issues, converting the mono-species coniferous forests (e.g., pure larch plantations) into mixed-species forests (e.g., mixed larch-broadleaved forests) may be a top priority (Hooper et al., 2005; Yan et al., 2013; Yang et al., 2013).

Aiming to facilitate this conversion, the widely used and primary approach is to plant seedlings of broadleaved tree species directly in coniferous plantations. For example, seedlings of birch are planted in a mixture with Sitka spruce plantations in Britain (Quine and Malcolm, 2007), and seedlings of Manchurian ash, Manchurian walnut, Amur cork tree, Mongolian oak, maple, and birch are widely established in a mixture with larch plantations in China (Wang et al., 2000; Mason and Zhu, 2014). All of these measures are trying to form an even-aged and mixed larch-broadleaved forest. For the existed pure larch plantation forests, little is known about the feasibility of building uneven-aged larch-broadleaved mixed forests by planting seedlings of native broadleaved tree species. The success of the transformation from a pure coniferous forest to a mixed broadleaf-conifer forest mainly depends on the seedling performances of regeneration for proper species selected in mixture. This is mainly because the seedling survival and establishment phase are the key bottlenecks in the life-history dynamics of trees, and strongly rely on both abiotic factors (e.g., the light environment) and inherent biotic factors (e.g., shade tolerance of tree species) (Poorter and Kitajima, 2007). It has been known that in low-light conditions, the shade-tolerant juveniles have a higher survival rate but the shade-intolerant ones have a high mortality; in the canopy openings, the shade-intolerant juveniles grow better relative to the shade-tolerant ones (Gravel et al., 2010). Thus, how to select proper broadleaved tree species according to these abiotic and biotic factors determines the conversion of forest types.

The trade-off between growth and survival could possibly arise from the contribution of plant adaptive traits to fitness (Reich et al., 2003; Wright et al., 2004), resource capture efficiency per unit investment (Wright et al., 2004), and a balance between carbon allocation to growth and allocation to storage/defense (Poorter and Kitajima, 2007). Plant fitness contains three traits, of which relative growth rate (RGR) and total biomass can influence niche occupation, and specific leaf area (SLA) can regulate carbon assimilation per unit energy investment (Reich et al., 2003; Wright et al., 2004). Therefore, plasticity of these traits is expected to enhance fitness in multiple environments. For example, shade-tolerant species have different sets of fitness traits at various light environments (Walters and Reich, 1999). Low leaf construction cost (CC) is characterized as low resource requirements for photosynthesis and is deemed to have the ability of increasing the competitive ability of a plant species (Poorter et al., 2006). This is because in the tissues of plant species with lower CC, more of the fixed carbon (C) is left for growth and reproduction. It has been reported that CC is closely associated with growth rate and shade tolerance (D'Andrea et al., 2013). If the carbon demand for growth is lower than the carbon gain, nonstructural carbohydrate (NSC) will be deposited in plants and activated later to support survival, growth or other functions (Valladares and Niinemets, 2008). Thus NSC storage, an important type of carbon investment, is favorable for seedling survival and growth in stressful habitats (e.g., shaded condition) (Myers and Kitajima, 2007).

Thinning is a useful stand management practice in plantation forests to change stand structure (mainly shown as canopy openness) (Zhu et al., 2008), subsequently to modify environmental factors (e.g., light availability and soil temperature) in the stands (Schnitzler and Closset, 2003; Lochhead and Comeau, 2012). It has been reported that regeneration (especially bottleneck phases of seedling survival and establishment) of broadleaved tree species in conifer plantation stands is closely linked to the changing environment conditions due to thinning (Seiwa et al., 2012). Examining how plant functional traits may change in relation to environmental gradients (especially light conditions) and to strategies of resource capture and survival is an important research focus (Villar-Salvador et al., 2012). Based on this examination, proper trees with different shade tolerance attributes can be selected in a mixture of plantation forest with different thinning intensities (and hence various canopy openness (light irradiance)).

Four dominant broadleaved tree species in secondary forests of Northeast China, including intermediate shade tolerant species (*Fraxinus mandshurica* Rupr. and *Acer mono* Maxim.) and shade intolerant species (*Juglans mandshurica* Maxim. and *Quercus mongolica* Fisch. ex Ledeb.) (Wu et al., 2013), can be successfully established in larch plantations to form an even-aged mixed forest (Shi et al., 1991; Wang et al., 2000) and soil fertility in these four mixed larch-broadleaf forests can also be greatly improved relative to pure larch plantations (Yang and Zhu, 2015). However, little is known about the feasibility of building uneven-aged larch-broadleaved mixed forests by planting seedlings of native broadleaved tree species in the existed pure larch plantation forests. In view of the shade tolerance of these four woody species, furthermore, thinning may contribute to their seedling regeneration performance in larch plantations. Thus, data on seedling regeneration performance (including fitness, leaf chemistry (covering the stable carbon isotope (a measure of long-term water use efficiency (WUE)) and CC), and NSC) of the same group of intermediate shade tolerant and shade intolerant species responding to changes in light due to thinning are presented in this study. We expect to: (1) determine the suitable thinning intensity (and hence appropriate light environment (canopy openness)) promoting the seedling survival and growth rates of two shade-tolerant types of broadleaved species in larch plantations to establish uneven-aged mixed larch-broadleaved forests; (2) explain the adaptive strategies of resource needs