



Effects of nitrogen and phosphorus supply on growth and physiological traits of two *Larix* species



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ABSTRACT

To investigate how nitrogen (N) and phosphorus (P) fertilization affect plant growth, biomass accumulation and allocation, leaf N and P concentration, and also eco-physiological responses of *Larix* species with contrasting growth characteristics, slow growing (*L. olgensis*) and fast growing (*L. kaempferi*) saplings grown in larch plantation soil were exposed to different N and P regimes. The results showed that N and combined N and P (NP) fertilization promoted growth with a higher biomass accumulation, height growth rate (GR_H), net photosynthesis rate (P_n), and photosynthetic P-use efficiency (PPUE) in both species, while P fertilization alone had a positive effect on the growth of *L. olgensis* but a negative effect on that of *L. kaempferi*. Moreover, N and NP fertilization increased the photosynthetic N-use efficiency (PNUE) of *L. olgensis*, while all fertilization treatments decreased that of *L. kaempferi*. Furthermore, P fertilization increased the N concentration of *L. olgensis* leaves but had no influence on that of *L. kaempferi* leaves, while it decreased the NSC concentration of *L. olgensis* leaves but stimulated the accumulation of starch, fructose and NSC in *L. kaempferi* leaves. In addition, *L. kaempferi* with higher GR_H showed a greater biomass accumulation, growth, P_n , PNUE, and PPUE when compared to *L. olgensis*, except for biomass and PPUE under P fertilization and PNUE under N fertilization. These results indicated that the N and P balance rather than the absolute amount of them enhances the growth of *L. kaempferi* effectively, and P fertilization affects the morphological and physiological traits of the two larch species differently. We propose that the distinct effects of P fertilization on the two larch species were related to different regulation effects of P fertilization on the N concentration, and on the accumulation and transportation of photosynthetic products.

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1. Introduction

Nitrogen (N) and phosphorus (P) are essential macronutrients for plant growth and development, and they are also nutrients that

most frequently limit primary productivity in all ecosystems in the biosphere (Aerts and Chapin, 2000; Hall et al., 2005; Elser et al., 2007). Previous studies have showed that N and P deficiencies cause negative effects on plants (Boyce et al., 2006; Turnbull et al., 2007; Kant et al., 2011; Warren, 2011; Zhang et al., 2014), and photosynthesis always decreases under N and P deficiencies (Zhang et al., 2014; Luo et al., 2015). N is a vital constituent in proteins, nucleic acids, chlorophylls and many secondary metabolites of plants (Luo et al., 2013a), and therefore it plays an essential role in the enzymatic activities of photosynthetic processes (Güsewell, 2004). A strong linear relationship between leaf N concentration and photosynthetic capacity has been well established (Field and Mooney, 1986; Evans, 1989; Wright et al., 2004;

Abbreviations: AM, aboveground dry mass; B/A ratio, belowground dry mass/aboveground dry mass; BD, basal diameter; LM, leaf dry mass; N, nitrogen; NSC, non-structural carbohydrate; P, phosphorus; P_n , net photosynthesis rate; PNUE, photosynthetic N-use efficiency; PPUE, photosynthetic P-use efficiency; GR_D , basal diameter growth rate; GR_H , height growth rate; RM, root dry mass; SM, stem dry mass; TM, total dry mass.

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Takashima et al., 2004; Zhang et al., 2014). P is involved in cellular energy transfer (Marschner, 1995), and it is a component of numerous plant metabolites (Gan et al., 2015). However, limited information is available regarding the regulation of eco-physiological processes of many trees, for instance larches, exposed to P fertilization. Many studies have showed that N and P fertilization could shift some ecosystems from N to P limitation or to N and P co-limitation (Braun et al., 2010; Elser et al., 2010; Sardans et al., 2012). Menge and Field (2007) found that N fertilization led to P limitation in six out of eleven previously N-limited ecosystems, mainly because N input could accelerate P cycling rates across a wide variety of terrestrial ecosystems (Marklein and Houlton, 2012). Nevertheless, most investigations on P fertilization have been conducted in N-rich (Wright et al., 2011; Yavitt et al., 2011; Santiago et al., 2012; Mori et al., 2013) or P-limited conditions (De Groot et al., 2003; Wright et al., 2005), while only few studies have investigated how P fertilization influences productivity in N-limited ecosystems (Blevins et al., 2006; Carlson et al., 2014; Gotore et al., 2014).

Numerous investigations have suggested that species with contrasting growth rates exhibit different eco-physiological traits and responses to N and P treatments (Miller and Hawkins, 2007; Gan et al., 2015). The fast-growing ones possess greater N and P use efficiencies and higher enzymatic activities related to N assimilation and P mobilization (Gan et al., 2015). The fast-growing broadleaved tree *Populus alba* × *P. glandulosa* is more sensitive to increasing N availability (Li et al., 2012), while the slowly growing *P. popularis* is more sensitive to decreasing N availability (Luo et al., 2013b). Also, fast growing *P. deltoides* females are more sensitive to inorganic nitrogen forms than the slow growing male trees (Li et al., 2015). Among conifers, the fast growing spruce families show more plasticity in biomass allocation than do the slowly growing ones under different nitrogen supplies (Miller and Hawkins, 2007), and the fast growing species *Pinus radiata* allocates more to the aboveground biomass under N and P fertilization (Carson et al., 2004; Bown et al., 2009). Yet, limited information is available about the responses of larches with contrasting growth strategies under N and P fertilization.

Larch (*Larix*) forests are the dominant forest type through northeastern Asia to central Siberia (Liang et al., 2004). As one of the most common species and as an important timber resource, it is also one of the most widely used plantation tree species in China, especially in cold and medium temperate zones of China (Chen et al., 1997). *L. olgensis* and *L. kaempferi* are the major plantation tree species in this region (Liu et al., 2005). According to previous reports, these two larches possess different growth strategies. *L. kaempferi* exhibits higher growth rates and carbon storage but a lower wood density than does *L. olgensis* (Yin et al., 2008; Guo et al., 2016). A previous study reported that larch plantation soil possesses lower concentrations of available nitrogen and phosphorus than secondary forest soil, and that constrains plant growth (Yang et al., 2012). Soil degradation has been found, for instance, in Chinese *L. olgensis* and *L. kaempferi* plantations (Liu et al., 1998). Understanding how these plants react to N and P fertilization could enhance our ability to predict and improve plantation productivity. In this study, *L. olgensis* and *L. kaempferi* saplings planted in larch plantation soil were employed to investigate the influence of N and P fertilization on the growth and eco-physiological traits of larch species. Specifically, growth, biomass accumulation and allocation, leaf N and P concentrations, and physiological responses (including photosynthetic capacity, N and P use efficiency (PNUE and PPUE), and non-structural carbohydrates) were determined to address the following questions: (a) How does enhanced N and P supply affect the growth and the eco-physiology of two contrasting larches? (b) Do these two larch species respond differently to N and P fertilization?

2. Materials and methods

2.1. Plant material and experimental design

Healthy one-year old saplings of *L. olgensis* and *L. kaempferi* were collected from the state-owned forest farm located in Qingyuan Manchu Autonomous County Dasuhe, Liaoning Province, China. In May 2012, *L. olgensis* and *L. kaempferi* saplings were planted separately in 50-L plastic pots (one sapling per pot) with 40 kg larch forest soil under ambient conditions at the Qingyuan Experimental Station, Institute of Applied Ecology, Chinese Academy of Sciences (CAS), located in a montane region in the eastern part of the Liaoning Province, Northeast China (41°51'N, 124°54'E, 500–1100 m above sea level). The climate characteristics have been described in Zhu et al. (2007). In May 2013, after one year of acclimation to natural conditions, when the saplings were two years old and had been sprouting and growing for about two weeks, 80 *L. olgensis* and 80 *L. kaempferi* saplings with a similar crown size and root collar diameter were chosen for the experiment. The treatments started on the 20th of May 2013, and the plants were harvested on the 10th of September 2013.

The experiment had a completely randomized design with eight factorial combinations of three factors (2 species (*L. olgensis* and *L. kaempferi*), 2 N conditions (control and fertilization) and 2 P conditions (control and fertilization)). Thus, the two species were subjected to 4 regimes: control (C, with neither N nor P fertilization); N fertilization (N, with 13.8 g N per tree); P fertilization (P, with 7.2 g P per tree); and combined N and P fertilization (NP, with 13.8 g N and 7.2 g P per tree, simultaneously). N and P fertilizers were supplied on three occasions during the whole experiment, 4.6 g N and 2.4 g P at each time, respectively. When supplied, the fertilizer was first dissolved in spring water and then applied into a 5-cm deep groove around each tree trunk. After fertilization, the grooves were filled up with soil. Grooves were dug carefully to avoid damaging the root. Each treatment included twenty saplings and was replicated four times (with five saplings in each replicate). All saplings were watered every two days to avoid the drought effect.

2.2. Growth measurements

The height (H) and basal diameter (BD) of each sapling were monitored monthly during the experiment. The height growth rate (GR_H , cm day⁻¹) and the diameter growth rate (GR_D , mm day⁻¹) were calculated as follows: $GR_H = (H_{t2} - H_{t1}) / (t_2 - t_1)$, $GR_D = (BD_{t2} - BD_{t1}) / (t_2 - t_1)$, where the denominator is the time elapsed between the initial and final measurements. At the end of the experiment, after the final H and BD measurements, one sapling among the five saplings of each replicate was harvested randomly (thus, four saplings per treatment) and divided into leaves, stems and roots. Then, the samples were dried (70 °C, 48 h) to a constant weight and weighed, i.e. the dry mass of leaves (LM), stems (SM) and roots (RM). The total dry mass (TM), aboveground dry mass (AM) and the ratio of belowground to aboveground mass (B/A ratio) were calculated.

2.3. Net photosynthesis rates and the analysis of chemical elements

One sapling was selected randomly among the five saplings of each replicate (thus, four saplings per treatment) and used for measurements. The upper and mature needle leaves from each sapling were used for the net photosynthesis rate (P_n) measurements using a portable photosynthesis measuring system, LI-COR 6400 (Li-Cor Inc., Lincoln, NE, USA), under the following conditions: leaf temperature of 25 °C, leaf air vapour pressure deficit of 1.5 ± 0.5 kPa, photosynthetic photon flux density (PPFD)

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