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REGULAR ARTICLE

Changes in nitrogen and phosphorus cycling suggest a transition to phosphorus limitation with the stand development of larch plantations

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Abstract
Aims The changes of nutrient limitation status for tree growth across a plantation chronosequence have great implications for plantation management. The underlying mechanisms for such a shift, however, have seldom been addressed. While plant nutrient use strategies would change in response to soil nutrient alteration, they may also create feedback on soil nutrient dynamics and thus plant nutrient limitation status.
Methods We examined soil and foliar nutrients of larch (*Larix kaempferi*), the dominant timber species in Northeast China, across a plantation chronosequence.
Results Total soil N increased but total soil P decreased across the chronosequence. Similarly, N concentrations in the green leaves were positively correlated, and P concentrations were negatively correlated with stand age. Foliar N:P ratios, N and P resorption efficiencies and PRE:NRE were positively correlated with stand age, indicating the shift from N-limitation to P-limitation across the chronosequence. P concentration in senesced leaves decreased and N:P ratios increased across the chronosequence, which has implications for decomposition and nutrient release.
Conclusions Nutrient resorption, soil pH, biomass P sequestration and imbalanced inputs of N and P would contribute to the occurrence of P-limitation with increased stand age. Furthermore, adaptive fertilization management strategies should consider the shift of nutrient limitation patterns across the chronosequence.

Keywords Stand development · Nutrient restranslocation · Ecological stoichiometry · Stoichiometric ratio · Plant-soil feedback

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Introduction

Nitrogen (N) and phosphorus (P) have been shown to strongly limit forest growth and productivity (Elser et al. 2007; Vitousek et al. 2010). Plantation forests in temperate zones are generally more frequently limited by soil N availability (Vitousek and Howarth 1991; Magnani et al. 2007; Iversen and Norby 2008), especially for young stands (Hayes et al. 2014; Mediavilla et al. 2014). Nevertheless, P tends to progressively become limiting in aging forests and with increased tree sizes (Vitousek and Howarth 1991; Hayes et al. 2014; Chen et al. 2016). Moreover, older stands of temperate plantations are stronger sinks for N than younger stands, and the imbalanced inputs of N and P may result in a shift from N- to P-limitation for plantation ecosystems (Deng et al. 2016; Sun et al. 2016). Such changes of nutrient limitation status across the plantation chronosequence would be influential for tree growth and have great implications for plantation management.

Nutrient resorption from senescing organs is one of the most important mechanisms by which plants conserve and optimize the use of nutrients (Aerts 1996; Brant and Chen 2015). This process can facilitate the reuse of internal nutrients directly in further growth, and make plants less dependent on soil nutrient supply (Aerts 1996; Kobe et al. 2005). Therefore, nutrient resorption is beneficial for the growth, reproduction and competitive ability of plants (May and Killingbeck 1992). It is commonly accepted that nutrient resorption can be negatively determined by the availability of soil nutrients (Aerts and Chapin 2000; Tully et al. 2013). However, multiple studies have suggested that it is not the case that plants growing on lower fertility soil consistently have higher rates of nutrient resorption (Aerts 1996), and fertilization studies do not show consistent responses of resorption to increasing soil nutrient status (Deng et al. 2016; Huang et al. 2016). In addition to soil, plant nutrient status also exerted positive (Yan et al. 2016), negative (Kobe et al. 2005) and even no effect (Aerts 1996) on leaf nutrient resorption. With the development of forest plantations, the associated nutrient supply and requirements are often changed (Gower et al. 1996; Yuan and Chen 2010; Sun et al. 2016). Such changes in soil and plant nutrient status would have substantial effects on plant nutrient conservation strategies (Kobe et al. 2005; Lü et al. 2012; Vergutz et al. 2012; See et al. 2015). Higher nutrient resorption decreases the litter quality and decomposition, which in turn decreases soil nutrient availability and reinforces plant nutrient limitation status (Aerts and Chapin 2000; Lü et al. 2012; Yan et al. 2016).

Variations of soil nutrients and plant ecophysiological traits have been demonstrated along ontogeny of trees (Mediavilla and Escudero 2004; England and Attiwill 2006; Yuan and Chen 2010). Such ontogenetic changes would be a source of variability in leaf nutrient resorption (Yuan and Chen 2010; Mediavilla et al. 2014; Sun et al. 2016). Knowledge of nutrient conservation strategy changes with plant age would help gain a better understanding of the plant adaptation to the changing environmental conditions. Among previous studies, the inconsistent results of the variations of nutrient resorption in response to stand development may be related to tree species and environmental conditions (Yuan and Chen 2010; Mediavilla et al. 2014; Zhou et al. 2016). Furthermore, it is still no clear how the resorption patterns in larch plantations, which would put insight into soil nutrient limitation, control and consequences.

Larch (*Larix* spp. mainly including *L. olgensis*, *L. principis-rupprechtii*, and *L. kaempferi*) is the dominant timber species in Northeast China (Zhu et al. 2008, 2010; Mason and Zhu 2014). The extensive area of larch plantation reaches 2.61 million hectares in Northeast China, and accounts for an estimated 85% of the total larch plantation area in China (Chinese Ministry of Forestry 2014). Most larch plantations were developed by replacing the secondary forests, which had been formed from primary forests after intensive human disturbances, and thus formed the mosaic plantation-secondary forest landscapes (Yang et al. 2013; Mason and Zhu 2014). However, compared with the adjacent secondary forests, soil carbon (C) and N were declined by 30% in the ca. 40-year-old larch plantations, because of the single species composition and mono-silviculture system (Yang et al. 2013). Chen et al. (2016) demonstrated a trend of decreased available P with the development of larch (*Larix olgensis*) plantations, especially for the older stages (e.g., 34- and 49-year-old stands). Therefore, the feedbacks between plant nutrient use strategy and soil nutrient availability across a plantation chronosequence would have great implications for larch plantation management.

In this study, we examined the changes of soil and foliar nutrients of larch (*L. kaempferi*) plantations across a chronosequence (10-, 21-, 34- and 55-year-old) in Northeast China. The objectives of this study were to (i) quantify the variations of N and P resorption across the larch plantation chronosequence and thus to assess the changes of nutrient use strategy in different aged larch plantations and (ii) explore the relationships between leaf nutrition and soil nutrient status and thus to assess the responses of leaf nutrients to the altered soil nutrient status in different aged larch plantations. We hypothesized that (i) nutrient resorption would increase along the larch plantation chronosequence, since nutrient demand may increase while soil nutrient availability decrease with stand development and (ii) nutrient resorption efficiency would negative and significant relationships with leaf and soil nutrient status, since nutrient resorption is an important nutrient conservation mechanism. Consequently, the results of this study have beneficial implications for nutrient conservation and management in larch plantations.

Material and methods

Study sites

This study was conducted at the Qingyuan Forest CERN (Chinese Ecosystem Research Network), Chinese Academy of Sciences, located in a mountainous region of Liaoning Province, China (41°51′N, 124°54′ E, elevation 500–1100 m above sea level). The climate of this region is a continental monsoon type with a humid, rainy summer and a cold, dry winter. The mean annual air temperature varies between 3.9 and 5.4°C, and the minimum and maximum temperatures are −37.6 and 36.5°C in January and July, respectively. Annual precipitation ranges from 700 to 850 mm, of which 80% falls from June to August. On average, the frost-free period lasts for 130 days, with the first frost in October and the last frost in April (Zhu et al. 2007).

Before the 1930s, this study site was covered by a primary mixed broadleaf-Korean pine (*Pinus koraiensis*) forest, and thereafter suffered from decades of excessive timber harvesting. In the early 1950s, the original forests were completely cleared by a large fire. Since that time, the study site has naturally regenerated as a secondary forest. *Fraxinus rhynchophylla*, *Juglans mandshurica*, *Phellodendron amurense*, *Quercus mongolica* and *Acer mono* were the dominant tree species of the natural secondary forests. Since the 1960s, patches of the natural secondary forests were cleared and replaced by larch plantations (*Larix* spp. mainly including *L. olgensis*, *L. principis-rupprechtii*, and *L. kaempferi*), resulting in a mosaic of larch plantation and secondary forest landscapes (Yang et al. 2013; Mason and Zhu 2014).

Experimental design

We selected four even-aged and pure larch (*Larix kaempferi*) plantation stands (10-, 21-, 34-, and 55-year-old, respectively) within the Qingyuan Forest CERN, CAS to represent a chronosequence. Three replicate 20 m × 20 m plots were established within each stand, and >10 m buffer zones between them (see details in Yan et al. 2017). Within each plot, five healthy individuals with different diameters at breast height (DBHs) were sampled to ensure that the sample trees were representative of that plot's DBH distribution, i.e., each individual represents a DBH class with a 2 cm interval from the minimum to maximum for the 21-, 34-, and 55-year-old stands, and a 1 cm interval from the minimum to maximum for the 10-year-old stand. To quantify the variability of leaf nutrient resorption within this chronosequence, we selected all the stands based on the following criteria. First, all the stands were topographically similar, i.e., all the sites were located in a well-drained middle slope position, with slopes ranging from 13 to 17°, and elevations ranging from 462 to 615 m above sea level (Table 1). The soils of all of the stands are typical brown forest soils and are classified as Udalfs based on the second edition of United States Department of Agriculture soil taxonomy, with 25.6% sand, 51.2% silt, and 23.2% clay on average (Yang et al. 2013), and soil depth was approximately 50 to 60 cm. Second, to reduce the influences from site conditions (Sun et al. 2016), the distance between any two stands was less than 2.3 km. Thus, all the stands shared similar climate and micro-environmental conditions. Third, all the larch plantation stands were in their first rotation, and were developed by replacing the secondary forests. The understory species (e.g., shrub and grass) of the 10- and 21-year-old stands were relatively species-poor, whereas those of the 34- and 55-year-old stands were species-rich.

Leaf and soil sampling

Green leaves were collected in mid-August 2015, when the leaves were at peak biomass, and senesced leaves were collected in October, during the period of maximum abscission (Yan et al. 2016). A sufficient quantity of needles from the lower to upper canopy for each individual were sampled (leaves with obvious diseases and/or insect pests were excluded) for the subsequent chemical analysis. Senesced leaves were also directly collected from trees rather than from litter to avoid underestimation of nutrient concentrations in the senesced leaves due to decomposition and leaching (Vergutz et al. 2012; Li et al. 2013). We considered leaves ready to fall off if they were completely yellow, dry without any signs of deterioration, and would fall from the branch with just a gentle shake or touch (Killingbeck and Whitford 2001; Wright and Westoby 2003; Yan et al. 2016).

Table 1 Summary of the four age stand properties of larch plantations in Northeast China

	Stand age (years)			
	10	21	34	55
Elevation (m)	507 ± 2.9	615 ± 3.8	517 ± 4.1	462 ± 3.8
Slope (°)	13 ± 0.9	15 ± 1.2	16 ± 1.0	17 ± 0.6
Soil type	Typical brown forest soil	Typical brown forest soil	Typical brown forest soil	Typical brown forest soil
Leaf biomass (kg tree^{-1})	1.5 ± 0.2	3.7 ± 0.7	3.0 ± 0.8	5.4 ± 0.6
AGB (kg tree^{-1})	8.5 ± 0.2	99.2 ± 4.2	149.4 ± 11.7	322.0 ± 31.4
DBH (cm)	6.3 ± 0.1	15.3 ± 0.2	17.3 ± 0.5	25.6 ± 0.4
Tree height (m)	7.2 ± 0.3	18.2 ± 0.1	20.8 ± 0.5	23.8 ± 0.8
Density (trees ha^{-1})	4725 ± 340	1967 ± 225	1292 ± 58	500 ± 29

Note: DBH and AGB are the abbreviations of diameter at breast height and above-ground biomass, respectively. Values are mean ± SE ($n = 3$)

As the surface soil (0–10 cm) is the most closely related to plant nutrients and strongly susceptible to litter decomposition (Yang and Zhu 2015), four soil samples were randomly taken at 0–10 cm (after removing the litter layer) within 1 m of the base of each selected tree with a metal tube (5 cm Ø) and pooled to obtain one composite soil sample per tree (Li et al. 2013). Soil samples were air-dried, cleaned of small stones and any visible plant and root residues, then ground and passed through a 0.25-mm sieve for total C, N and P analysis.

Chemical analysis

All plant samples were taken to the laboratory immediately, oven dried at 65°C for at least 48 h to constant mass and then ground to pass through a 60-mesh sieve (0.25 mm). Leaf and soil total C and N were determined by Elementar vario MICRO cube (Germany). Leaf and soil total P were measured by a molybdenum blue colorimetric method after digestion in sulfuric acid-hydrogen peroxide and nitric acid-perchloric acid-hydrofluoric acid, respectively. Soil pH was determined using a 1:2.5 soil/water ratio slurry.

Definitions and calculations

Nutrient resorption efficiency (NuRE) was used to quantify the nutrient resorption. NuRE was defined as the relative amount of nutrients resorbed during senescence (Aerts 1996).

However, leaf mass would be reduced due to the carbon resorption during senescence (Aerts 1996; Mediavilla et al. 2014). Thus, nutrient resorption efficiency based on leaf mass would be underestimated (van Heerwaarden et al. 2003; Mediavilla et al. 2014). To corrected the unbiased resorption value, Vergutz et al. (2012) introduced the mass loss correction factor (MLCF) based on 86 studies and ~1000 data points in six plant types across climates globally. Therefore, nutrient resorption efficiency was calculated as follows: NuRE (%) = $[(N_g - N_s \times \mathrm{MLCF}) / N_g] \times 100$, where the MLCF value was 0.745 for conifers, and N_g and N_s represent nutrient concentrations in green and senesced leaves, respectively (Vergutz et al. 2012).

Statistical analysis

The normality of data was checked by Kolmogorov-Smirnov's test, and the homogeneity of variances was examined by Levene's test. We used one-way analysis of variance (ANOVA) to test the differences of soil nutrients and stoichiometric ratios among the different aged larch plantations; if the difference was significant, then post hoc multiple comparisons were conducted using the LSD test. Relationships between the stand age and leaf nutrient concentration, stoichiometric ratio, nutrient resorption efficiency and PRE:NRE were estimated by using linear regressions. Stand age was log-transformed to comply with normality assumptions. Pearson bivariate correlations were used to determine the relationships between nutrient resorption efficiency, senesced leaf nutrient status and soil nutrient concentrations and stoichiometric ratios. All the statistical analyses were performed with SPSS 13.0 (SPSS Inc., Chicago, IL, USA) for windows.

Results

Soil total N and P concentrations and N:P ratio

Soil total N was significantly increased and soil total P was significantly decreased with stand age ($P < 0.05$). Soil N:P ratio was significantly increased across the plantation chronosequence ($P < 0.05$, Table 2).

Leaf N and P concentrations, N:P ratio, NRE and PRE

Green leaf N concentrations were significantly increased ($P = 0.027$), ranging from 2.12 to 2.86%, but no significant differences were found for senesced leaf N concentrations with stand age (Fig. 1a). In contrast, green leaf P concentrations were significantly decreased ($P < 0.001$), ranging from 0.25 to 0.14%, and senesced leaf P concentrations were also significantly decreased ($P < 0.001$), ranging from 0.18 to 0.03% with stand age (Fig. 1b). Both green and senesced leaves N:P ratios were significantly increased (all $P < 0.001$) with stand age, ranging from 8.91 to 18.79 and from 6.82 to 26.28, respectively (Fig. 1c and d).

NRE and PRE were significantly increased ($P = 0.008$ and $P < 0.001$, respectively) with stand age (Fig. 2a). Specifically, NRE ranged from 57.98 to 76.54%, and PRE ranged from 44.60 to 83.71% in the 10- and 55-year-old stands, respectively. PRE:NRE were increased ($P < 0.001$) along the stand age chronosequence (Fig. 2b).

Correlations of nutrient resorption efficiency, nutrient concentration, and stoichiometry in senesced leaf and soil

Soil total N was positively correlated with NRE, PRE and N:P in senesced leaves ($P = 0.001$, $P = 0.002$ and $P = 0.020$, respectively), but negatively correlated with N and P concentrations in senesced leaves ($P = 0.006$ and $P = 0.018$, respectively) (Table 3). Soil total P was only negatively correlated with N:P in senesced leaves ($P = 0.021$), whereas soil N:P was negatively ($P = 0.030$) and positively ($P = 0.007$) correlated with P concentration and N:P in senesced leaves, respectively (Table 3). NRE and PRE were positively and negatively correlated with green-leaf N and P concentrations, respectively ($P = 0.037$ and $P = 0.003$, respectively) (Table 3).

Discussion

Nutrient use strategies across the plantation chronosequence

An increase in soil total N but a decrease in soil total P were observed across the stand age chronosequence (Table 2). Our findings are in agreement with the results of Kuznetsova et al. (2011), who found that soil N concentration increased and soil P concentration and soil pH decreased with increasing stand age for black alder (*Alnus glutinosa* (L.) Gaertn.), silver birch (*Betula pendula* Roth.), and scots pine (*Pinus sylvestris* L.) plantations. Similar findings were also observed in trembling aspen (*Populus tremuloides*) for soil total N (Yuan and Chen 2010), and larch (*Larix olgensis*) for soil total P with stand development (Chen et al. 2016; Deng et al.

Table 2 Nutrient concentrations, stoichiometric ratios and pH of the top soil (0–10 cm depth) along the chronosequence

	Stand age			
	10	21	34	55
Soil pH	5.97 ± 0.09a	5.80 ± 0.06ab	5.73 ± 0.03b	5.48 ± 0.04c
Soil total C (%)	2.49 ± 0.09c	2.81 ± 0.06b	2.90 ± 0.04b	3.56 ± 0.05a
Soil total N (%)	0.23 ± 0.01c	0.27 ± 0.01b	0.26 ± 0.01b	0.30 ± 0.02a
Soil total P (g kg^{-1})	0.70 ± 0.03a	0.79 ± 0.04a	0.49 ± 0.06b	0.57 ± 0.02b
Soil N:P	3.34 ± 0.08b	3.85 ± 0.56ab	5.58 ± 0.88a	5.49 ± 0.43a

Different letters within the same line indicate significant differences among stand ages ($P < 0.05$). Values are mean ± SE ($n = 3$)

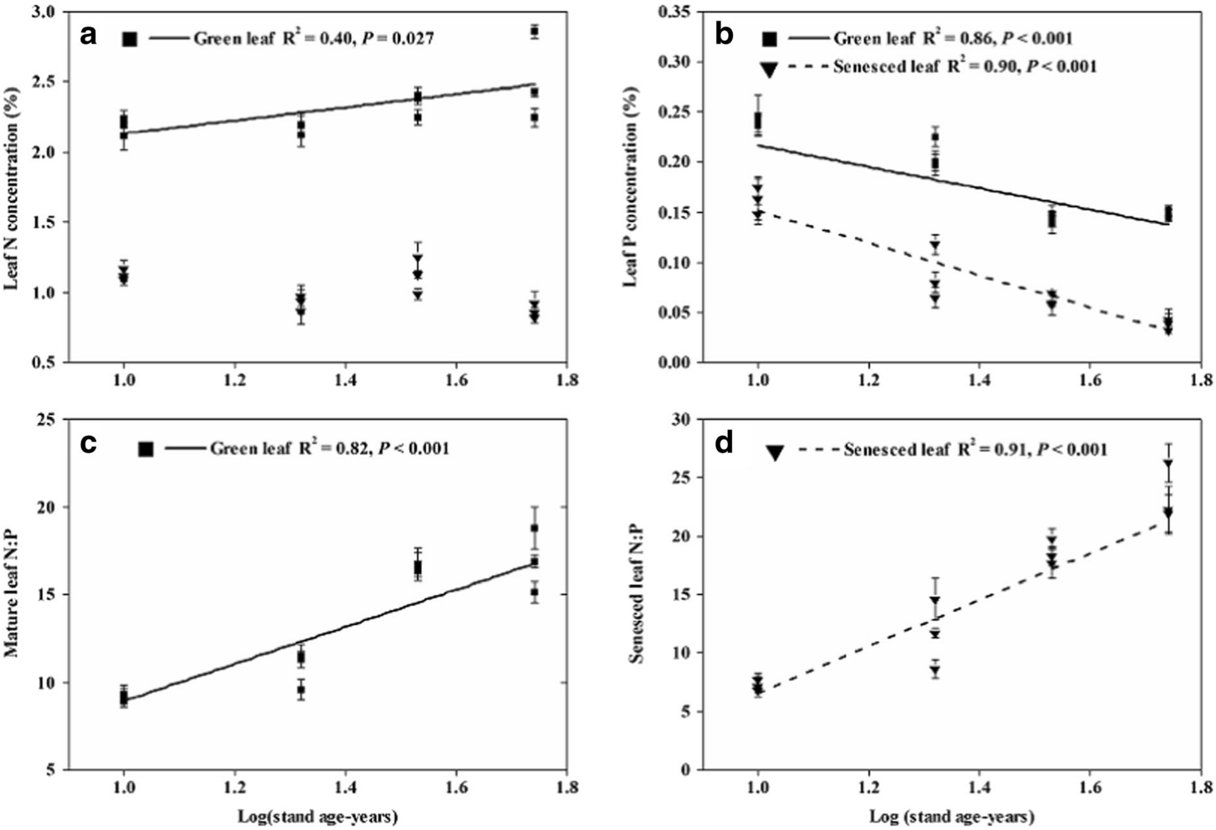

Fig. 1 Changes in N (**a**), P (**b**) concentrations and N:P ratios in green (**c**) and senesced leaves (**d**) along the stand age chronosequence of larch plantations in Northeast China. Data are shown as the mean ± SE. Only significant regressions are displayed

2016). In our study, the increase of N and decrease of P concentrations in green leaves (Fig. 1) could be directly driven by the specific changes of soil nutrients availability (Aerts 1996; Lambers et al. 2008; Li et al. 2013).

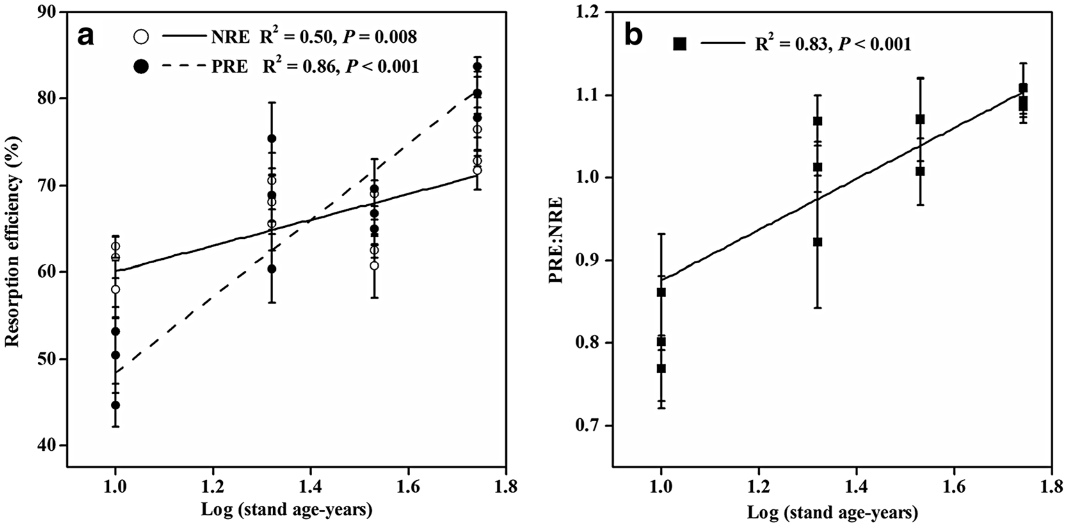

Fig. 2 Changes in N and P resorption efficiency (**a**) and PRE:NRE (**b**) along the chronosequence of larch plantations in Northeast China. Data are shown as the mean ± SE

Table 3 Pearson correlations between nutrient resorption efficiency, nutrient concentration, and stoichiometry in senesced leaf and soil

	Soil total N	Soil total P	Soil N:P	Green N concentration	Green P concentration
NRE	0.815 (**0.001**)	−0.122 (0.705)	0.346 (0.271)	0.604 (**0.037**)	−0.507 (0.093)
PRE	0.787 (**0.002**)	−0.316 (0.316)	0.517 (0.085)	0.606 (**0.037**)	−0.778 (**0.003**)
Senesced N concentration	−0.744 (**0.006**)	−0.119 (0.712)	−0.167 (0.604)	−0.272 (0.392)	0.256 (0.422)
Senesced P concentration	−0.666 (**0.018**)	0.483 (0.112)	−0.624 (**0.030**)	−0.578 (**0.045**)	0.913 (< **0.001**)
Senesced N:P ratio	0.659 (**0.020**)	−0.656 (**0.021**)	0.727 (**0.007**)	0.756 (**0.004**)	−0.926 (< **0.001**)

NRE and PRE represent N and P resorption efficiency, respectively. Values given are Pearson correlations and *P* values for the coefficient were shown in the parentheses. Bold data indicated significant correlation at the 0.05 level (two-tailed)

Moreover, both the soil and leaf element-specific responses to stand age suggested that older stands may have higher ability to absorb N but lower ability to absorb P from soil than younger stands (Wang et al. 2014).

In accordance with our first hypothesis, both NRE and PRE increased (the increments were from 58 to 77% and from 45 to 84%, respectively) with stand age (Fig. 2), indicating that larch plantations became more efficient in using the N and P across the plantation chronosequence. This was consistent with some previous studies, which reported that the fractions of N and P retranslocated in older stands were significantly higher than those in younger stands (Hayes et al. 2014; Mediavilla et al. 2014; Sun et al. 2016), but was dissimilar with the results of other studies (Yuan and Chen 2010; Li et al. 2013; Zhou et al. 2016). Three possible mechanisms for such NRE and PRE patterns in response to the stand development. First, the nutrient requirements for leaf biomass production increased with stand age, because a substantial proportion of the resorbed nutrients was used for leaf production for deciduous plants (Nambiar and Fife 1991; Sun et al. 2016). Younger larch individuals had relatively smaller and lighter needles whereas the older larch individuals had relatively bigger and heavier ones (our personal observation). The age-related changes of nutrient resorption were correlated with the annual leaf biomass production of larch plantations, which indicated that the nutrient requirement for growth, especially of leaves, was indeed a crucial determinant for nutrient resorption (Brant and Chen 2015; Sun et al. 2016). In addition, root uptake and leaf nutrient resorption are the two main sources for nutrient supply to support the growth of plants (Cleveland et al. 2013; Brant and Chen 2015). Although soil N increased with stand development, root N uptake from soil may be insufficient for the demand of larch individuals. Consequently, an increase in leaf NRE was observed to facilitate growth. Second, the increased nutrient resorption efficiency may be driven by the nutrients competition between larch individuals and the understory species. Because the understory species (e.g., shrub and grass) of the 10- and 21-year-old stands were relatively species-poor, whereas those of the 34- and 55-year-old stands were species-rich. Third, the increased NRE may be regulated by the increased PRE. Nutrient resorption is an important nutrient conservation mechanism for plants to reduce their dependence on soil nutrient supply, especially for those in infertile environment (Aerts 1996; Kobe et al. 2005; Yuan and Chen 2015). More N or P would be resorbed when plants are growing in N- or P-limited conditions (Han et al. 2013). Therefore, larch individuals would hydrolyze more immobile P to enhance PRE during leaf senescence, which resulted from a decrease of soil P concentration with increasing stand age. Due to the close relationship between N and P (Koerselman and Meuleman 1996; Treseder and Vitousek 2001; Vitousek et al. 2010; Deng et al. 2016), the process of P hydrolysis requires a greater cost of N (Hidaka and Kitayama 2011; Hofmann et al. 2016), and thus result in an increase of leaf NRE. This is also a possible explanation as to why NRE increased with increasing soil N but PRE increased with decreasing soil P. The diverse responses of NRE and PRE to respective soil N and P concentrations were further confirmed by the positively and negatively correlations between NRE and PRE with N and P concentrations in green leaves (Table 3). Taken together, since the process of resorption depends on environmental conditions and plant ecophysiologic traits (Mediavilla et al. 2014; Sun et al. 2016), perhaps NRE are more regulated by plant-soil system as a whole than by soil total N concentration per se in larch plantations.

Larch plantations would alter nutrient conservation and use strategy with stand age. To maximize N- and P-use efficiencies in the older stands, more conservative P-use strategies were observed, via increased PRE and decreased leaf P concentration. In contrast, a more conservative N-use strategy was obtained via increased NRE but not decreased leaf N concentration. Similar results were also found by Hayes et al. (2014) in plants of contrasting nutrient-acquisition strategies along a 2-million-year dune chronosequence. It is generally considered that nutrient resorption efficiency was negatively related with specific leaf nutrient concentrations (Kobe et al. 2005; Yuan and Chen 2010), because green leaf nutrient concentrations, in some instances, could reflect soil fertility (Aerts 1996; Lambers et al. 2008). In this study, partly agreed with our second hypothesis, NRE was positively correlated with green leaf N concentrations while PRE was negatively correlated with green leaf P concentrations (Table 3), indicating that green leaf nutrient concentration was good indicator for nutrient resorption efficiency, but the direction would vary with specific nutrient elements. Besides, soil total N was positively and significantly correlated with NRE, PRE and N:P ratio and negatively correlated with N and P concentrations in senesced leaves, but in contrast, only negative and significant relationship was observed between soil total P and senesced N:P ratio (Table 3), which suggested that soil total N was more closely linked with leaf nutrient status (e.g., nutrient resorption and leaf nutrient concentration) than soil total P. Our results supported the multiple-element explanations for nutrient resorption patterns proposed by See et al. (2015), which detected that soil N positively affects leaf P resorption in a northern hardwood forest. The tightly controlled plant-soil interactions would be of great importance for nutrient cycling and tree growth.

Implications for nutrient conservation and management

The significant correlations between N:P ratios of both green and senesced leaves with stand age (Fig. 1) impling that the growth of larch plantations tends to be more P-limited. Green leaf N:P ratios were 9.17, 10.78, 16.57 and 16.93 for the 10-, 21-, 34- and 55-year-old stands, respectively. Following the criteria proposed by Koerselman and Meuleman (1996), our results suggest that nutrient limitation status of larch plantations would shift from relative N-limitation to relative P-limitation across the chronosequence. In other words, the 10- and 21-year-old stands were relatively more N-limited, whereas the 34- and 55-year-old stands were relatively more P-limited (Fig. 1). Some previous studies have demonstrated that younger trees were more susceptible to N limitation (Laliberté et al. 2012; Mediavilla et al. 2014; Brant and Chen 2015), while evidence from Chen et al. (2016) showed P-deficiency in older *Larix olgensis* plantations (e.g., 34- and 49-year-old) in Northeast China. Similar findings have also been demonstrated by Hayes et al. (2014), which showed that long-term ecosystem development tended to cause a shift from N- to P-limitation in southwest Australia.

Additionally, our findings demonstrate a positive correlation between PRE:NRE and stand age (Fig. 2), indicating that relatively more P was resorbed with increased plantation age. This supported the relative resorption hypothesis that plants would resorb proportionally more N or P when under N- or P-limited conditions (Reed et al. 2012; Han et al. 2013). The relative changes of PRE and NRE gave further evidence for the N-limitation in young stands and P-limitation in old stands. The emerges of P limitation with stand development may be driven by the following reasons. First, P concentration in senesced leaves decreased and N:P ratios in senesced leaves increased across the chronosequence (Fig. 1). Compared with the younger stands, less P would remain in the leaf litter and return to the soils for the older stands, thus reduce the release of P from litter decomposition, and thereby reducing soil P availability (See et al. 2015). The positive plant-soil feedback may lead to more severe P-limitation for the older stands. Therefore, larch plantations would alter nutrient cycling through a plant-mediated pathway with stand age. Second, the decreased soil P may be caused by the decreased soil pH, which controls the solubility of P (Lambers et al. 2008; Kuznetsova et al. 2011; Barrow 2016). P nutrition may be improved via the decrease of soil pH, and more available P was absorbed and assimilated by trees (i.e., P sequestration in biomass) across the plantation chronosequence (Šourková et al. 2005; Kuznetsova et al. 2011). A substantial amount of the P sequestered in biomass was frequently removed from the sites by harvesting or thinning (Yan et al. 2017), and thus caused a decrease of soil total P with stand development (Deng et al. 2016). Third, input of P to the ecosystems mainly comes from rock weathering with an extremely slow rate (Wang et al. 2007; Achat et al. 2016). Therefore, P output may exceed P input for the ecosystem; thus, P recovers very slowly by natural processes (Gómez-García et al. 2016), consequently, results in a decrease of soil P concentration across the plantation chronosequence. Fourth, the continual increase in anthropogenic nitrogen (N) deposition relative to that of phosphorus (P) creates a strong imbalance in the inputs of N and P to the ecosystems, which in turn, may cause a shift in the temperate forest ecosystems from N- to P-limitation (Vitousek et al. 2010; Peñuelas et al. 2013; Deng et al. 2016). However, more N- and P- addition experiments are needed to assess whether the N- and P-limitation have truly been occurred with stand development of larch plantations. Furthermore, we have only measured soil P in the top layer (0–10 cm), and soil P in the deeper layers were remains unknown.

All in all, our results show that plant internal nutrient cycling during leaf senescence, soil pH, P sequestration in biomass and imbalanced inputs of N and P would contribute to the occurrence of P-limitation with increased stand age. Adaptive fertilization management strategies e.g., P fertilization, may be of particularly importance for older stands. Wang et al. (2007) showed that the introduction of N-fixing species could improve the soil N and P availabilities at N-limited sites. Because the N-fixing species would supply highly decomposable leaf-litter (via higher N concentration, Aerts 1997) to the soil, higher N input would stimulate soil phosphatase activity, and greatly enhance soil P availability and P cycling rates (Wang et al. 2007; Deng et al. 2016). Therefore, N-fixing species may produce more available P than they need and thus improve both soil N and P availabilities (Forrester et al. 2006; Wang et al. 2007; Houlton et al. 2008). These results suggested that it may be a potentially feasible practice to improve and balance the soil nutrients by planting N-fixing species in the reforestation (or afforestation) of larch plantations (Wang et al. 2011).

Larch is the dominant timber species in Northeast China, it would be common for thinning and clear-cutting during the management of larch plantations. Such silvicultural measures would remove large quantities of nutrients from the site, particularly for the harvesting associated with logging residues (e.g., bark, branches and leaves) (Yan et al. 2017). Furthermore, the nutrients resorbed during leaf senescence were mainly transported and stored in branch and stem-bark of deciduous plants (Cooke and Weih 2005; Estiarte and Peñuelas 2015). Combined nutrient resorption efficiency and leaf biomass, each tree harvesting in mid-October (i.e., when leaves were completely abscised) would increase the nutrient export with 55 g N and 4 g P, in comparison with tree harvesting in mid-August (i.e., when leaves were at peak biomass). Therefore, if logging residues (e.g., bark, branches and leaves) could be remained on the sites, i.e., only stem wood harvesting, we strongly recommended that tree harvesting should be carried out after August but before mid-October (i.e., before resorption occurred) to reduce nutrient loss, and maintain soil nutrient availability, consequently, induce the minimal effect on the growth of the remaining trees. It should note that further studies need to be done to confirm whether the above findings were representative of other plantations as well, because each stand in our study is just one relatively small forest stand and thus getting more information from additional sites would be valuable.

Conclusions

The nutrient resorption efficiency for both N and P and PRE:NRE were positively correlated with stand age of larch plantations, which indicated that the larch plantations become more conservative and efficient in using N and P and that relatively more P is resorbed with increased stand age. Decreased P concentration in senesced leaves and increased N:P ratios across the chronosequence would reduce litter quality and thus litter decomposition, which in turn creates a positive feedback on soil nutrient availability and may potentially lead to more severe P-limitation with stand age. Highly conservative P-use strategies were observed in the older stands that maximize P-use efficiency by maintaining higher PRE and lower leaf P concentration, while highly conservative N-use strategies were only obtained through higher NRE, but not through lower leaf N concentration. Based on leaf nutrient concentrations, green leaf N:P ratios and nutrient resorption, our results suggested that larch plantations may shift from N-limitation in the 10- and 21-year-old stands to P-limitation in the 34- and 55-year-old stands. In summary, our results demonstrate that the changes in nutrient resorption, soil pH, biomass P sequestration and imbalanced inputs of N and P would contribute to the occurrence of P-limitation with increased stand age in larch plantations, and P fertilization would be of great importance for the older stands. Additionally, if logging residues (e.g., bark, branches and leaves) could be retained on the sites, we recommended that tree harvesting should be implemented after August but before mid-October to reduce nutrient loss and potentially maintain soil nutrient availability.

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