

N–P stoichiometry in soil and leaves of *Pinus massoniana* forest at different stand ages in the subtropical soil erosion area of China

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Received: 1 August 2015 / Accepted: 13 July 2016 / Published online: 21 July 2016
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Abstract Plant nitrogen (N)–phosphorus (P) stoichiometry is associated with important ecological processes. However, N–P stoichiometry in soil and plants and adaptive mechanisms of plants to infertile soils in the soil erosion areas remain unclear. We selected 15 plots with Masson pine forest of varying stand ages in typical subtropical soil erosion areas of Southern China. The total nitrogen (TN) and total phosphorus (TP) concentrations in green leaves of Masson pine forest (9.2 and 0.61 g/kg) were significantly lower than the national averages in China (18.6 and 1.21 g/kg). The N:P ratio (TN:TP) of green leaves (15.1:1) was higher than the national (14.4:1) and the global levels (11.8:1 or 11.0:1). Forest soil TN, TP concentrations (0.41 and 0.14 g/kg) were lower than the national averages. The high N:P ratio of green leaves and low soil TP, AP concentrations indicated that P was important in limiting Masson pine forest growth, especially for forests with stand age less than 10 years. Leaf TN, TP resorption efficiencies of Masson pine forests were 26.5 and 64.9 %, and TP in

senesced leaves of Masson pine with different stand ages was completely resorbed, suggesting that Masson pine was effective at adapting to nutrient-poor soils. Differences in leaf N–P stoichiometry among different stand ages indicated that nutrient demand varied with Masson pine forest growth stages. Changes in forest soil N–P stoichiometry suggested that Masson pine forest afforestation could greatly improve the soil quality in the eroded lands. However, the significant improvement would take at least a 30-year-long period.

Keywords N–P stoichiometry · Resorption efficiency · *Pinus massoniana* (Lamb.) · Subtropical soil erosion

Introduction

Ecological stoichiometry considers the relationship between organism, ecosystem structure, and function and multiple chemical elements in the environment (mainly carbon, nitrogen, and phosphorus) (Sterner and Elser 2002; Elser et al. 2010; Sardans et al. 2012). The elements carbon (C), nitrogen (N), and phosphorus (P) are the fundamental chemical elements of an organism. The stoichiometry of an organism is closely related to the important ecological processes such as ecosystem species composition and diversity, adaptation of organisms to environmental stress, and interspecific relationships (Venterink et al. 2003; Woods et al. 2003; Aerts et al. 2003; Güsewell et al. 2005).

Although plant has effective ability to maintain stoichiometric characteristics of its own (Elser et al. 2005; Feller et al. 2007), it can be affected by stoichiometry of the habitat (Güsewell et al. 2003; Hall et al. 2005). Availability and supply of nutrients in its habitat can significantly affect biosis (at the species level), biotic

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populations, biotic communities, and even ecosystems (Sardans et al. 2012). Large quantities of C were synthesized through photosynthesis, and N and P were consumed during plant growth, and the concentrations of these elements in habitats directly affect plant growth, thereby limiting ecosystem productivity (Vitousek and Howarth 1991; Elser et al. 2010).

Many studies showed that the concentrations of available N and P significantly influence plant growth (Aerts et al. 2003). High P leaching may lead to limitation of P for plant growth in areas with high rainfall and intense soil erosion, while N might restrict plant growth in those areas with low rainfall, weak soil erosion and thus relatively low P leaching (Aerts et al. 2003; Reich and Oleksyn 2004). In recent years, atmospheric N deposition results in an imbalance of the N:P ratio and an impact on the stoichiometry of ecosystems (Galloway et al. 2003; Feller et al. 2007; Elser et al. 2009). N can promote plant uptake efficiency and utilization of P in tropical and subtropical regions (Houlton et al. 2008). However, P becomes a main limiting factor for terrestrial ecosystems in these areas due to high P leaching (Reich and Oleksyn 2004). Therefore, many plants adapt to barren soil by resorption of nutrients from senesced leaves to relieve nutrient deficiency (Killingbeck 1996).

Soil and water loss is one of the global environmental problems that have long caused many concerns (Singha et al. 2006; Gu et al. 2013). Afforestation has been the most widespread policy for severely eroded areas in the world (Chirino et al. 2001; Deng et al. 2012). About 6–7 % of global forests are plantations, established to provide a variety of ecosystem services (Pawson et al. 2013; Sun et al. 2016). Afforestation offers great potential to improve soil quality of degraded or marginal lands by reducing soil disturbance and providing perennial ground cover (Zhou et al. 2002; Meira-Castro et al. 2012; Sauer et al. 2012). However, forest plantations are often limited by soil nutrient availability (Vitousek and Howarth 1991; Magnani et al. 2007) and also encounter increasing anthropogenic fertilizations (Galloway et al. 2008). The balance between nutrients supply and nutrient requirements for tree growth often changes following the developments of planted stands (Peri et al. 2006; Sun et al. 2016).

Evaluation of stand development and soil nutrient availability interact to affect plantations' internal nutrient cycling and demand is positive over the potential role of plantations in global climate warming. Masson pine [*Pinus massoniana* (Lamb.)] is one of the major pioneer species of afforestation in the erosion areas of Southern China (Cao et al. 2015). However, the relationship between Masson pine leaf N and P resorption capabilities, their stoichiometric characteristics and soil nutrients in these areas remains unclear. Therefore, this study aimed to: 1)

investigate ecological stoichiometry of N and P in leaves and soil of Masson pine forest with different stand ages and 2) analyze the resorption characteristics of N and P in the senesced leaves of Masson pine forest at different stand ages.

Materials and methods

Study area

The research was conducted in Hetian Town, Changting County, Fujian Province of China (25°33'–25°48'N, 116°18'–116°31'E). This site belongs to a subtropical monsoon climate with an average annual temperature of 19 °C, an average frost-free period of 260 days, an annual precipitation of 1621 mm with over 50 % falling in April–June and an annual evaporation of 1444 mm (Gu et al. 2011, 2013). Soils with a high sand content (about 45 % of >1 mm gravel) are developed from coarse-grained granite and classified as humic Planosols (FAO-WRB). As a typical soil erosion area in the mid-subtropics of Southern China, it has an area of serious water loss and soil erosion of 158.4 km² accounting for 46.7 % of the total land area. Masson pine forests were reconstructed since the primary evergreen broadleaf forests were destroyed in the early 1980s, which had contributed to the development of Masson pine plantations with different stand ages.

The Masson pine forests selected for this study had stand ages of ≤10 years (PF0), 10–20 years (PF1), 20–30 years (PF2), and >30 years (PF3) with different vegetation properties (Table 1). The PF0 forests were dominated by Masson pine in the tree layer, with scattered distributed shrubs, a minimal quantity of herbs, and large areas of bare soil surfaces. The PF1 forests were Masson pine in the tree layer, with some shrubs and herbs which were tolerant to drought and barren. The PF2 forests had mostly Masson pine and occasionally other tree species in the tree layer, and a high amount of shrubs and herbs with the covers more than 80 %. The PF3 forests were dominated by Masson pine accompanying with diversified tree species and had more than 90 % coverage of understory vegetation dominated by Masson pine saplings, a high amount of shrubs and herbs.

Leaf and soil sampling

In August of 2011 and 2012, Masson pine forests were selected from sites with similar conditions such as altitude, slope, and aspect. Fifteen plots (each with dimensions of 20 m × 20 m, 4 plots for PF0, PF1, PF2, respectively, and 3 plots for PF3) were selected that was more than 30 m away from the forest edge, in which Masson pine grew

Table 1 Vegetation properties of the experimental plots in the study area

Stand ages	Density of trees (plants/hm ²)	Dominant tree species	Dominant shrub species	Dominant herb species
PF0	650–750	<i>Pinus massoniana</i> (Lamb.)	<i>Syzygium buxifolium</i> Hook et Arn, <i>Baekkea frutescens</i> Linn	<i>Dicranopteris dichotoma</i> (Thunb.) Bernh., <i>Eulalia speciosa</i> (Debeaux) Kuntze, <i>Eriachne pallescens</i> R. Br
PF1	900–1100	<i>Pinus massoniana</i> (Lamb.)	<i>Lespedeza bicolor</i> Turcz., <i>Syzygium buxifolium</i> Hook & Arn, <i>Adinandra millettii</i> (Hook & Arn) Benth & Hook f. ex Hance	<i>Dicranopteris dichotoma</i> (Thunb.) Bernh., <i>Eulalia speciosa</i> (Debeaux) Kuntze
PF2	1200–1400	<i>Pinus massoniana</i> (Lamb.), <i>Schima superba</i> Gardner & Champ	<i>Lespedeza bicolor</i> Turcz. and <i>Syzygium buxifolium</i> Hook & Arn	<i>Dicranopteris dichotoma</i> (Thunb.) Bernh., <i>Digitaria longiflora</i> (Retz.) Pers
PF3	1300–1400	<i>Pinus massoniana</i> (Lamb.), <i>Sophora japonica</i> L., <i>Sapium sebiferum</i> (L.) Roxb., <i>Liquidambar formosana</i> Hance, <i>Cunninghamia lanceolata</i> (Lamb.) Hook, <i>Schima superba</i> Gardner & Champ	Masson pine saplings, <i>Camellia oleifera</i> Abel, <i>Gardenia jasminoides</i> J. Ellis, <i>Syzygium buxifolium</i> Hook & Arn, <i>Lespedeza bicolor</i> Turcz., <i>Adinandra millettii</i> (Hook & Arn) Benth & Hook f. ex Hance	<i>Dicranopteris dichotoma</i> (Thunb.) Bernh., <i>Melastoma dodecandrum</i> Lour., <i>Woodwardia japonica</i> (L.f.) Sm., <i>Digitaria longiflora</i> (Retz.) Pers

PF0 ≤10 years, PF1 10–20 years, PF2 20–30 years, PF3 >30 years

well. For estimation of forest stand age, the cores of selected Masson pine trees were taken using growth cones based on the diameter class (5 cm as a diameter class, 3 replicates for each class), and the tree with a diameter at breast height < 5 cm was removed from its trunk at ground level. The basal area of all selected trees was also measured. The stand age of the Masson pine forest was determined by a weighted average method, and the forest was classified by 10 years as an age class (Meng 1996).

In each plot, three well-growing Masson pine trees were taken, and 12 branches of each sample tree were harvested from four opposite compass sides of the crown with three branches from each side. Mature needles without pests were collected from the 12 branches and evenly mixed to make up a composite sample. Additionally, senesced leaves that had just fallen off from the sampled trees to ground were collected. Five soil samples (0–30 cm depth) were randomly taken from each plot using a soil auger (30 mm in diameter) and mixed uniformly as a composite sample.

Laboratory procedure

Soil samples were air-dried after removal of seeds, roots, gravel, and other debris. The leaf samples were dried at 75 °C in an oven to a constant weight. Then, leaf and soil samples were ground and passed through a 100-mesh sieve. The leaf and soil samples were digested using the Kjeldahl procedure for total nitrogen (TN) and total phosphorus (TP)

concentration determinations. Available soil nitrogen (AN, ammonium, and nitrate) was determined using a KCl extracting technique (Stubbs and Pyke 2005). A soil sub-sample (about 20 g) was extracted with 50 mL of NH₄F (0.03 M)–HCl (0.025 M) and shaken for 30 min. The available soil phosphorus (AP) was measured by the molybdenum blue method with ascorbic acid as a reductant (Murphy and Riley 1962). A soil subsample (about 20 g) was extracted with 50 mL of NaHCO₃ (0.5 M) and shaken for 30 min. TN and TP of leaf and soil samples, AN and AP of soil samples were determined on a continuous flow analyzer (SEAL AutoAnalyzer 3, SEAL Analytical Ltd, Norderstedt, German). Soil bulk density, total porosity, and capillary porosity were measured following the methods proposed by Liu (1996).

Data analysis

All data analyses were performed using PASW Statistics 18.0 (SPSS Inc.), and figures were generated by Sigma-plot 10.0 (Systat Software Inc). Significances of differences in the leaf TN and TP, and measured soil physical and chemical properties among forest stand ages were analyzed by least square difference (LSD) tests. Leaf N and P resorption efficiencies (RE) were calculated by the formula proposed by Du et al. (2011): RE_x = (A₁ – A₂)/A₁ × 100 %, where RE_x represents the resorption efficiency of a certain nutrient, A₁ and A₂ represent the nutrient concentration of green matured and senesced leaves (g/kg).

Results

N, P concentrations of leaves and soil quality at different stand ages of Masson pine forest

As the Masson pine forest stands developed, leaf TN concentration first declined and then increased, and leaf TP concentration first increased and then decreased (Fig. 1). The leaves of PF0, PF1, PF2, and PF3 had 8.9–10.6, 7.2–8.8, 8.5–8.8, 11.4–12.6 g/kg for TN, and 0.4–0.46, 0.62–0.85, 0.6–0.63, 0.66–0.76 g/kg for TP, respectively. The leaf TN concentrations of PF0 and PF3 were significantly higher than that of PF1 and PF2 ($P < 0.05$), while the PF1 had the lowest leaf TN concentration. The leaf TP concentration was lowest in PF0 and highest in PF1.

The planted Masson pine forests improved the soil quality significantly in the study area (Table 2). The soil TN, TP concentrations of PF3 were higher than those of other stand ages ($P < 0.05$). The soil AN and AP concentrations of PF2 and PF3 were higher than those of PF0 and PF1 ($P < 0.01$). The soil bulk density decreased gradually following increased Masson pine forest stands. The soil total porosity increased slowly, while the capillary porosity did not show significant improvement.

N:P ratio patterns of leaves and soils at different stand ages of Masson pine forest

With increasing forest stand age, leaf N:P ratio (TN:TP) showed a first downward then upward trend, while soil N:P ratio (TN:TP) showed a gradual upward trend (Fig. 2). Leaf N:P ratios of PF0, PF1, PF2, and PF3 were 22.0–25.1, 9.1–13.0, 13.9–14.2, and 16.6–18.8, respectively. Soil N:P ratio of PF0, PF1, PF2, and PF3 is 1.3–2.7, 1.9–3.1,

2.1–2.9, and 3.9–4.8, respectively. The PF0 showed the highest leaf N:P ratio than those of other stand ages, while the lowest ratio was in the PF1. The soil N:P ratio of the PF3 was significantly higher than those of other stand ages ($P < 0.001$). However, the soil N:P ratio between PF0, PF1, and PF2 did not show significant fluctuation.

Nutrient resorption of senesced leaves at different stand ages of Masson pine forest

Senesced leaves revealed a first downward then upward trend in TN, TP concentrations with increasing forest stand age (Fig. 3a), while both the RE_N and RE_P showed first upward then downward trends (Fig. 3b). TN concentrations in senesced leaves of PF0, PF1, PF2, and PF3 were 6.8–9.0, 4.3–5.3, 4.8–6.0, and 8.2–9.3 g/kg, while the RE_N were 11.4–3.9, 28.8–46.7, 31.3–42.8, and 25.9–29.5 %, respectively. TP concentrations in senesced leaves of PF0, PF1, PF2, and PF3 were 0.14–0.23, 0.14–0.22, 0.14–0.18, and 0.23–0.28 g/kg, while the RE_P were 44.6–68.9, 71.6–81.0, 71.7–76.5, and 62.4–65.1 %, respectively.

Both the PF0 and PF3 showed significant higher TN, TP concentrations in senesced leaves than those of PF1 and PF2 ($P < 0.05$). The highest TN, TP concentrations were found in senesced leaves of PF3. The senesced leaves of PF0 revealed the lowest RE_N and RE_P , but the RE_N and RE_P between other stand ages showed non-significant differences.

Discussion

Fluctuation of TN, TP concentrations in green leaves of Masson pine forest

Leaf TN and TP concentrations reflect nutrient demands of plants in different stages of growth and nutrient conditions in its habitat. Geometric means for green leaf TN and TP concentrations of the Masson pine in our study area were 9.2 and 0.61 g/kg, which were significantly lower than the national averages in China (18.6 and 1.21 g/kg) (Han et al. 2005), and the global averages of the genus *Pinus* (11.5 and 1.21 g/kg or 11.3 and 1.22 g/kg) (Reich and Oleksyn 2004; Wright et al. 2004). Moreover, the results were also lower than the averages of the Masson pine in the subtropical regions of China (11.1 and 0.81 g/kg) (Han et al. 2005). The changes in TN, TP concentrations of the Masson pine leaves were closely associated with plant growth. In the early stages, plant growth is slow with small biomass, but has a potent ability to undergo cell division, and thus requires a large amount of protein (Gorokhova and Kyle 2002), resulting in relatively high TN concentration in plant leaves. The Masson pine forest at 13–20 years in the

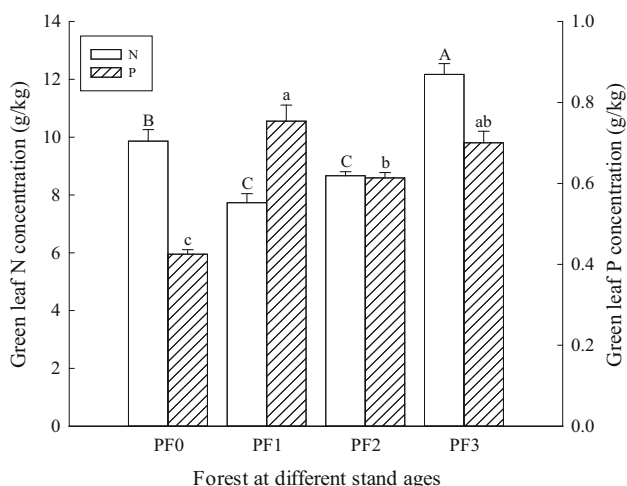


Fig. 1 TN, TP concentrations of green leaves in different stand ages of Masson pine forest

Table 2 Physical and chemical properties of soil in the experimental plots

Stand ages	Bulk density (g/cm ³)	Total porosity (%)	Capillary porosity (%)	Total nitrogen (g/kg)	Available nitrogen (mg/kg)	Total phosphorus (g/kg)	Available phosphorus (mg/kg)
PF0	1.51 ± 0.05a	43.47 ± 1.90b	33.98 ± 1.77b	0.21 ± 0.04b	11.36 ± 0.85c	0.10 ± 0.01c	0.07 ± 0.02c
PF1	1.35 ± 0.02b	49.13 ± 0.73a	38.49 ± 1.12a	0.33 ± 0.03b	13.96 ± 0.99c	0.14 ± 0.01b	0.17 ± 0.016b
PF2	1.34 ± 0.01b	49.79 ± 0.09a	36.51 ± 0.49ab	0.37 ± 0.03b	65.11 ± 1.62b	0.15 ± 0.01ba	0.28 ± 0.02a
PF3	1.29 ± 0.06b	50.97 ± 1.71a	36.29 ± 2.31ab	0.84 ± 0.16a	101.11 ± 20.29a	0.19 ± 0.03a	0.38 ± 0.05a

Different lowercase letters in the same column indicate significant differences ($P < 0.05$) with a least significant difference test
 PF0 ≤10 years, PF1 10–20 years, PF2 20–30 years, PF3 >30 years

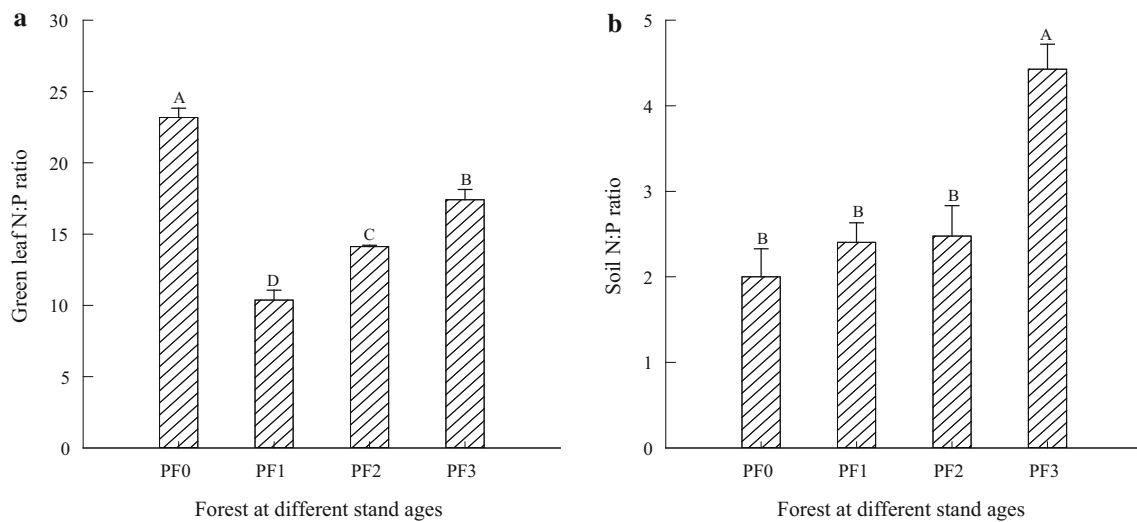


Fig. 2 N:P ratio of green leaves (a) and soil (b) in different stand ages of Masson pine forest. The ratios of leaf and soil refers to TN:TP. Error bars are SEM. Different capital letters indicate significant differences ($P < 0.05$) with a least significant difference test

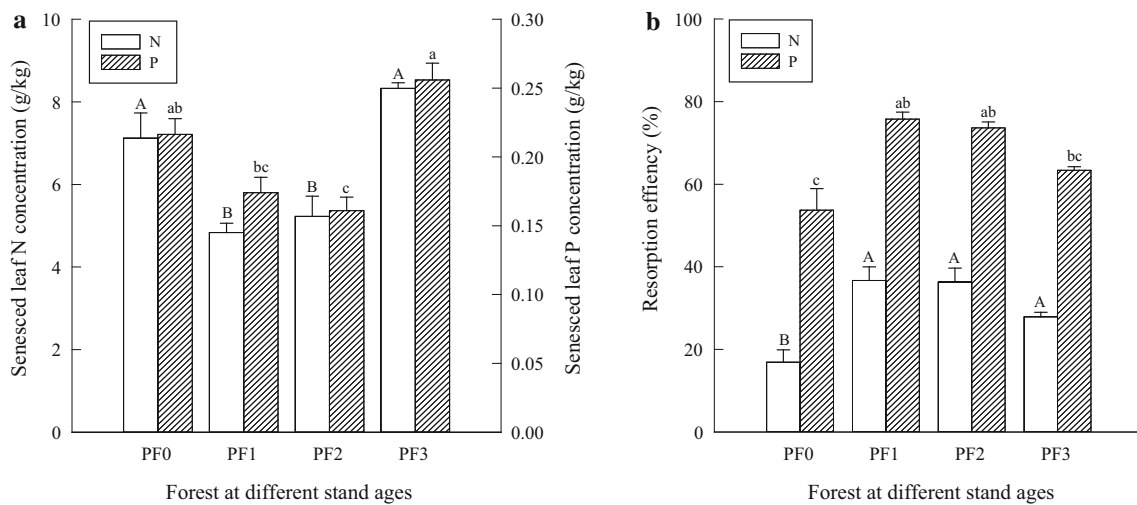


Fig. 3 TN, TP concentrations (a) and resorption efficiency (b) in senesced leaves of Masson pine forest at different stand ages. Error bars are SEM. Different capital or lowercase letters indicate significant differences ($P < 0.05$) with a least significant difference test

mid-subtropics of China is in fast-growing stages and can accumulate biomass rapidly (Zhou 2001). Its high growth rate can lead to increased TP concentration, which is consistent with the previously proposed growth rate hypothesis (Sterner and Elser 2002; Elser et al. 2003). Also, changes in the growth rate can alter the leaf TN concentration of the fast-growing Masson pine (Sun and Chen 2001). In the mature stages, the growth rate and the TP concentration of the Masson pine decreased, but TN concentration in the pine had increased. However, as the soil TP, AP concentrations increased, the leaf TP concentration remained higher than that found in the early stages of growth.

The improvement in soil quality with the developments of Masson pine forest stands

TN, TP, and AP concentrations in the surface soil averaged 0.41 g/kg, 0.14 g/kg, and 0.20 mg/kg, respectively, which were lower than the averages (0.71–1.73 g/kg, 0.8–1.7 g/kg, and 3.7–6.7 mg/kg, respectively) of red soil in China (Gong et al. 2014). The trends of soil nitrogen and phosphorus in our study area were associated with local community growth conditions and the sources of soil nitrogen and phosphorus in different stand ages of the Masson pine forest.

In the early growth stages, low soil nutrients were associated with low understory vegetation coverage and plant litter quantity which induced large exposed soil surface area and high soil nutrient leaching. As the forest stand age increased, the understory vegetation of the Masson pine forest gradually developed, the litter increased, and broadleaf species such as *S. japonica*, *S. sebiferum*, *L. formosana*, *S. superba* developed. Therefore, soil nitrogen concentrations gradually enhanced as the forest stand age increased with the development of understory plant by reducing soil erosion and increasing inputs of organic materials. However, soil phosphorus released from the weathering of rocks is very slow and gentle (Aerts and Chapin 2000; Reich and Oleksyn 2004), and the biological process has weak regulation on the process. Furthermore, high concentrations of Fe and Al in red soil will reduce the availability of P through the synthesis of Fe–P and Al–P (Solomon et al. 2002; Yang et al. 2005). These factors led to low concentration and non-significant fluctuation of phosphorus in the study area.

The development of Masson pine forest facilitated the functional restoration of soils by increasing surface vegetation coverage and plant litter. However, the improvement in soil quality was slow following the development of the Masson pine forest stands. The bulk density of soil decreased 11.26 %, and total porosity, TN, and AN increased 14.53, 76.19, and 50.00 % in PF2 compared to

PF0. Most of the soil physical and chemical properties showed significant improvement at the stage of PF3 which indicated the practice of afforestation in erosion area to restore the soil quality would take a very long process.

N–P stichometry and nutrient limitation in leaves and soil

In most terrestrial ecosystems, N–P availability can limit plant growth and affect plant traits, community composition, and biodiversity (Aerts et al. 2003; Güsewell et al. 2005). Thus, the plant N:P ratio is one of the most simple and effective indicators for assessing limiting elements in plant growth (Koerselman and Meuleman 1996; Güsewell 2004). In our study area, leaf N:P ratio had a geometric mean of 15.1:1, which was higher than the national average of China (14.4:1) (Han et al. 2005) and the global average (11.8:1 or 11.0:1) (Reich and Oleksyn 2004; Wright et al. 2004). However, it was lower than the leaf N:P ratio (16.3:1) of the Masson pine in the subtropics of China (Han et al. 2005), and higher than the global average (10.0:1 or 9.6:1) of the genus *Pinus* species (Reich and Oleksyn 2004; Wright et al. 2004).

The leaf N:P ratio averaged 23.2:1 in the PF0, 10.3:1 in the PF1 and PF2, and 15.7:1 in the PF3. According to the breakpoints proposed by Koerselman and Meuleman (1996) and Güsewell (2004), Masson pine growth in PF0 was markedly limited by P because large area of bare soil surface induced high phosphorus loss in the soil at the early stages of plant growth. Nitrogen became the limit elements of Masson pine at fast-growing stages due to the high growth rate-induced phosphorus increases and nutrient dilution (Sun and Chen 2001; Gorokhova and Kyle 2002). Although the growth rate of the Masson pine in PF3 decreased, its large biomass and different sources of nitrogen and phosphorus could cause phosphorus to become a limiting factor for the Masson pine growth. The growth of the Masson pine was mostly limited by the availability of phosphorus in our study areas, which was concordant with the law of P deficiency in the low-latitude region (Hedin 2004; Han et al. 2005; Zhang et al. 2005).

The mean soil N:P ratio under the Masson pine forest was 2.5:1, which was lower than that reported by the previous study in the same area and in the southern subtropics of China (Huang 2009; Liu et al. 2010; Hou et al. 2012). The soil N:P ratio under the Masson pine forest of PF0, PF1, PF2, and PF3 averaged 1.9:1, 2.4:1, 2.5:1, and 4.4:1, respectively. The soil N:P ratio under the Masson pine forest had increased with increasing forest stand age, and at least two reasons might account for this. One reason was that vegetation restoration increased vegetation coverage and reduced surface runoff, thereby increasing the concentration soil nitrogen and decreasing phosphorus

release from the soil parent material (Yan et al. 2008). The other reason was due to differences in nutrient turnover rate caused by different sources of soil nitrogen and phosphorus (Yan et al. 2008; Liu et al. 2010).

Adaptation strategy of leaf TN, TP resorption to nutrient limitation

Leaf nutrient resorption is an important strategy that enables plants to maintain appropriate nutrition levels, which can affect its interspecific competition, nutrient uptake and productivity (Killingbeck 1996; Liu et al. 2010). The changes in TN, TP concentration and RE in senesced leaves are closely related to the growth of the Masson pine forest. Studies indicate that stands with higher growth potential require more nutrients to support biomass production, and therefore should have a higher RE (Nambiar and Fife 1991; Sun et al. 2016).

In early and mature growth stages, the RE was low due to the low nutrient consumption induced by lower growth potential of the Masson pine forest. The nutrient demands of the Masson pine forests were high in the fast-growing stage. Therefore, the RE was high due to high senesced leaf nutrient transfer to Masson pine. Content of 0.7 % TN and 0.04 % TP in senesced leaves represents ultimate nutrient resorption (Killingbeck 1996). According to the proposed breakpoints, the senesced leaf TN of the Masson pine forest could be considered as incomplete resorption in PF0 and PF3, but TP of senesced leaf could be regarded as ultimate resorption in all the study sites. The RE_P was higher than that of TN, which reflected the deficiency of phosphorus in soils of low-latitude regions, or differences in the relative amounts of nitrogen and phosphorus that were leached from the leaves. Some studies believe that the high RE of evergreen leaves reflect the adaptation of plants to oligotrophic habitats, and can help plants to gain a competitive advantage in barren soils (Aerts and Chapin 2000; Du et al. 2011). However, others argue that high RE of nitrogen or phosphorus is not an important adaptive mechanism of plants to oligotrophic habitats (Yan et al. 2008), but instead represents an inherent characteristic of the phylogenetic position. The differences in leaf RE of different plants depend on genetic differences of individual plant species rather than important adaptive mechanisms of plants to barren habitats (Killingbeck 1996).

Conclusions

With increasing forest stand age, leaf TN, TP concentrations of the Masson pine in the study area showed opposite trends in that TN concentrations first decreased and then

increased, while TP concentrations increased then decreased. These trends might be caused by differences in nutrient demands of plants at different growth stages. Leaf TN, TP concentrations of the Masson pine forest were significantly lower than the national averages in China, while the N:P ratio was higher than the national and global averages. This result suggested that the growth of the Masson pine forest was mainly limited by the availability of phosphorus in the study area. Concordant with the stand age, the study showed that soil TN, AN, TP and AP concentrations and soil N:P ratio under the forest canopy increased. The soil phosphorus in the study area was significantly lower than the national average in China and was one of the key limiting factors of plant growth. Masson pine forest revealed high nutrient RE to adapt to such barren soils. Complete TP resorption of senesced leaves at different growth stages also indicated phosphorus deficiency in this area.

Acknowledgments The National Natural Science Foundation of China (41071281) and 135 Development Plan of YIC-CAS, and Shuangchuang Talent Plan of Jiangsu Province supported this work. We are grateful to all of the staff of Fujian Changting Monitoring Station of Soil and Water Conservation for providing the experimental sites, and in helping the field sample collections.

References

- Aerts R, Chapin FI (2000) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Adv Ecol Res* 30:1–67
- Aerts R, Caluwe HD, Beltman B (2003) Is the relation between nutrient supply and biodiversity co-limited by the type of nutrient limitation? *Oikos* 101:489–498
- Cao LX, Liang Y, Wang Y, Lu HZ (2015) Runoff and soil loss from *Pinus massoniana* forest in southern China after simulated rainfall. *Catena* 129:1–8
- Chirino E, Sánchez JR, Bonet A, Bellot J (2001) Effect of afforestation and vegetation dynamics on soil erosion in semi-arid environment (SE Spain). In: Villacampa Y, Brebbia CA, Uso JL (eds) *Ecosystems and sustainable development III*. WIT Press, Southampton, pp 239–248
- Deng L, Shangguan ZP, Li R (2012) Effects of the grain-for-green program on soil erosion in China. *Int J Sediment Res* 27:120–127
- Du YX, Pan GX, Li LQ, Hu ZL, Wang XZ (2011) Leaf N:P ratio and nutrient reuse between dominant species and stands-predicting phosphorus deficiencies in Karst ecosystems, Southwestern China. *Environ Earth Sci* 64:299–309
- Elser JJ, Acharya K, Kyle M (2003) Growth rate-stoichiometry couplings in diverse biota. *Ecol Lett* 6:936–943
- Elser JJ, Schampel JH, Garcia-Pichel F, Wade BD, Souza V, Eguiarte L, Escalante A, Farmer JD (2005) Effects of phosphorus enrichment and grazing snails on modern stromatolitic microbial communities. *Freshw Biol* 50:1808–1825
- Elser JJ, Andersen T, Baron JS, Bergstrom AK, Jansson M, Kyle M, Nydick KR, Steger L, Hessen DO (2009) Shifts in lake N:P stoichiometry and nutrient limitation driven by atmospheric nitrogen deposition. *Science* 326:835–837

- Elser JJ, Fagan WF, Kerkhoff AJ, Swenson NG (2010) Biological stoichiometry of plant production: metabolism, scaling and ecological response to global change. *New Phytol* 186:593–608
- Feller I, Lovelock CE, Mckee KL (2007) Nutrient addition differentially affects ecological processes of *Avicennia germinans* in nitrogen versus phosphorus limited mangrove ecosystems. *Ecosystems* 10:347–359
- Galloway JN, Aber JD, Erisman JW, Seitzinger SP, Howarth RW, Cowling EB, Cosby BJ (2003) The nitrogen cascade. *Bioscience* 53:341–356
- Galloway JN, Townsend AR, Erisman JW, Bekunda M, Cai Z, Freney JR, Martinelli LA, Seitzinger SP, Sutton MA (2008) Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. *Science* 320:889–892
- Gong ZT, Huang RJ, Zhang GL (2014) *Pedogeography of China*. Science Press, Beijing (in Chinese)
- Gorokhova E, Kyle M (2002) Analysis of nucleic acids in daphnia: development of methods and ontogenetic variations in RNA–DNA content. *J Plankton Res* 24:511–522
- Gu ZJ, Shi XZ, Li L, Yu DS, Liu LS, Zhang WT (2011) Using multiple radiometric correction images to estimate Leaf Area Index (LAI). *Int J Remote Sens* 32:9441–9454
- Gu ZJ, Wu XX, Zhou F, Luo H, Shi XZ, Yu DS (2013) Estimating the Effect of *Pinus massoniana* Lamb plots on soil and water conservation during rainfall events using vegetation fractional coverage. *Catena* 109:225–233
- Güsewell S (2004) N:P ratios in terrestrial plants: variation and functional significance. *New Phytol* 164:243–266
- Güsewell S, Koerselman W, Verhoeven JTA (2003) Biomass N:P ratios as indicators of nutrient limitation for plant populations in wetlands. *Ecol Appl* 13:372–384
- Güsewell S, Bailey KM, Roem WG, Bedford BL (2005) Nutrient limitation and botanical diversity in wetlands: can fertilisation raise species richness? *Oikos* 109:71–80
- Hall SR, Smith VH, Lytle DA, Leibold MA (2005) Constraints on primary producer N:P stoichiometry along N:P supply ratio gradients. *Ecology* 86:1894–1904
- Han WX, Fang JY, Guo D, Zhang Y (2005) Leaf nitrogen and phosphorus stoichiometry across 753 terrestrial plant species in China. *New Phytol* 168:377–385
- Hedin LO (2004) Global organization of terrestrial plant nutrient interactions. *PNAS* 101:10849–10850
- Hou EQ, Chen CR, McGroddy ME, Wen DZ (2012) Nutrient limitation on ecosystem productivity and processes of mature and old-growth subtropical forests in China. *PLoS ONE* 7:e52071
- Houlton BZ, Wang YP, Vitousek PM, Field CB (2008) A unifying framework for dinitrogen fixation in the terrestrial biosphere. *Nature* 454:327–330
- Huang SY (2009) Effects of different ecological restoration measures on soil fertility in red soil eroded degradation land. *Res Soil Water Conserv* 16(38–42):47 (in Chinese)
- Killingbeck KT (1996) Nutrient in senesced leaves: keys to the research for potential resorption and resorption proficiency. *Ecology* 77:1716–1727
- Koerselman W, Meuleman AFM (1996) The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. *J Appl Ecol* 33:1441–1450
- Liu GS (1996) Soil physical and chemical analysis and description of soil profiles. Standards Press of China, Beijing
- Liu XS, Zhou GY, Zhang DQ, Liu SZ, Chu GW, Yan JH (2010) N and P stoichiometry of plant and soil in lower subtropical forest successional series in southern China. *Chin J Plant Ecol* 34:64–71 (in Chinese)
- Magnani F, Mencuccini M, Borghetti M, Berbigier P, Berninger F, Delzon S, Grelle A, Hari P, Jarvis PG, Kolari P, Kowalski AS, Lankreijer H, Law BE, Lindroth A, Loustau D, Manca G, Moncrieff JB, Rayment M, Tedeschi V, Valentini R, Grace J (2007) The human footprint in the carbon cycle of temperate and boreal forests. *Nature* 447:849–851
- Meira-Castro A, Shakesby RA, Espinha Marques J, Doerr SH, Meixedo JP, Teixeira J, Chamine HI (2012) Effects of afforestation with four unmixed plant species on the soil–water interactions in a semiarid Mediterranean region (Sicily, Italy). *J Soils Sediments* 12:1222–1230
- Meng XY (1996) *Forest measurements*. China forestry publishing house, Beijing (in Chinese)
- Murphy J, Riley JP (1962) A modified single solution method for the determination of phosphate in natural waters. *Anal Chim Acta* 27:31–36
- Nambiar EKS, Fife DN (1991) Nutrient retranslocation in temperate conifers. *Tree Physiol* 9:185–207
- Pawson SM, Brin A, Brockerhoff EG, Lamb D, Payn TW, Paquette A, Parrotta JA (2013) Plantation forests, climate change and biodiversity. *Biodivers Conserv* 22:1203–1227
- Peri PL, Gargaglione V, Pastur GM (2006) Dynamics of above- and below-ground biomass and nutrient accumulation in an age sequence of *Nothofagus antarctica* forest of Southern Patagonia. *For Ecol Manag* 233:85–99
- Reich PB, Oleksyn J (2004) Global patterns of plant leaf N and P in relation to temperature and latitude. *PNAS* 101:11001–11006
- Sardans J, Rivas-Ubach A, Peñuelas J (2012) The C:N:P stoichiometry of organisms and ecosystems in a changing world: a review and perspectives. *Perspect Plant Ecol* 14:33–47
- Sauer TJ, James DE, Cambardella CA, Hernandez-Ramirez G (2012) Soil properties following reforestation or afforestation of marginal cropland. *Plant Soil* 360:375–390
- Singha R, Tiwarib KN, Malb BC (2006) Hydrological studies for small watershed in India using the ANSWERS model. *J Hydro* 318:184–199
- Solomon D, Lehmann J, Mano T, Fritzsche F, Zech W (2002) Phosphorus forms and dynamics as influenced by land use changes in the sub-humid Ethiopian highland. *Geoderma* 105:21–48
- Sterner RW, Elser JJ (2002) *Ecological stoichiometry: the biology of elements from molecules to the biosphere*. Princeton University Press, Princeton
- Stubbs MM, Pyke DA (2005) Available nitrogen: a time-based study of manipulated resource islands. *Plant Soil* 270:123–133
- Sun SC, Chen LZ (2001) Leaf nutrient dynamics and resorption efficiency of *Quercus liaotungensis* in the Dongling Mountain region. *Acta Phytoecol Sinica* 25:76–82 (in Chinese)
- Sun ZZ, Liu LL, Peng SS, Peñuelas J, Zeng H, Piao SL (2016) Age-related modulation of the nitrogen resorption efficiency response to growth requirements and soil nitrogen availability in a temperate pine plantation. *Ecosystems*. doi:10.1007/s10021-016-9962-5
- Venterink HO, Wassen MJ, Verkoost AWM, Ruiter PCD (2003) Species richness-productivity patterns differ between N-, P-, and K-limited wetlands. *Ecology* 84:2191–2199
- Vitousek PM, Howarth RW (1991) Nitrogen limitation on land and in the sea: How can it occur? *Biogeochemistry* 13:87–115
- Woods HA, Makino W, Cotner JB, Hobbie SE, Harrison JF, Acharya K, Elser JJ (2003) Temperature and the chemical composition of poikilothermic organisms. *Funct Ecol* 17:237–245
- Wright JJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas ML, Niinemets U, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ, Villar R (2004) The worldwide leaf economics spectrum. *Nature* 428:821–827

- Yan ER, Wang XH, Zhou W (2008) N:P stoichiometry in secondary succession in evergreen broad-leaved forest, Tiantong, east China. *J Plant Ecol* 32:13–22 (in Chinese)
- Yang JC, Huang JH, Pan QM, Tang JW, Han XG (2005) Soil phosphorus dynamics as influenced by land use changes in humid tropical, Southwest China. *Pedosphere* 15:24–32
- Zhang C, Tian HQ, Liu JY, Wang SQ, Liu ML, Pan SF, Shi XZ (2005) Pools and distributions of soil phosphorus in China. *Glob Biogeochem Cycle* 19:GB1020. doi:[10.1029/2004GB002296](https://doi.org/10.1029/2004GB002296)
- Zhou ZX (2001) Masson pine in China. China forestry publishing house, Beijing
- Zhou GY, Morris JD, Yan JH, Yu ZY, Peng SL (2002) Hydrological impacts of reforestation with eucalyptus and indigenous species: a case study in southern China. *For Ecol Manag* 167:209–222