

Tree Physiology 35, 1106–1117
doi:10.1093/treephys/tpv076



Research paper

Nitrogen and phosphorus additions alter nutrient dynamics but not resorption efficiencies of Chinese fir leaves and twigs differing in age

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Received January 8, 2015; accepted July 18, 2015; published online September 9, 2015; handling Editor Heinz Rennenberg

It is unclear how or even if phosphorus (P) input alters the influence of nitrogen (N) deposition in a forest. In theory, nutrients in leaves and twigs differing in age may show different responses to elevated nutrient input. To test this possibility, we selected Chinese fir (*Cunninghamia lanceolata*) for a series of N and P addition experiments using treatments of +N1 – P (50 kg N ha⁻¹ year⁻¹), +N2 – P (100 kg N ha⁻¹ year⁻¹), –N + P (50 kg P ha⁻¹ year⁻¹), +N1 + P, +N2 + P and –N – P (without N and P addition). Soil samples were analyzed for mineral N and available P concentrations. Leaves and twigs in summer and their litters in winter were classified as and sorted into young and old components to measure N and P concentrations. Soil mineral N and available P increased with N and P additions, respectively. Nitrogen addition increased leaf and twig N concentrations in the second year, but not in the first year; P addition increased leaf and twig P concentrations in both years and enhanced young but not old leaf and twig N accumulations. Nitrogen and P resorption proficiencies in litters increased in response to N and P additions, but N and P resorption efficiencies were not significantly altered. Nitrogen resorption efficiency was generally higher in leaves than in twigs and in young vs old leaves and twigs. Phosphorus resorption efficiency showed a minimal variation from 26.6 to 47.0%. Therefore, P input intensified leaf and twig N enrichment with N addition, leaf and twig nutrients were both gradually resorbed with aging, and organ and age effects depended on the extent of nutrient limitation.

Keywords: evergreen tree species, nitrogen and phosphorus interaction, nitrogen deposition, nutrient resorption, red soil region.

Introduction

Human activities have substantially modified nitrogen (N) cycles as well as ecosystem phosphorus (P) availability (Perring et al. 2008, Marklein and Houlton 2012). Atmospheric N deposition leads to nutrient alteration and element imbalance in forest ecosystems (De Schrijver et al. 2011, Eastaugh et al. 2011). Although the mechanisms underlying these changes are complex, they hinge broadly on plant and soil responses to excess N, particularly on whether N leads to enhanced P conservation (Vitousek et al. 2010). Far less is understood about how the

availability of other elements such as P affect N cycling as the ecosystem receives increasing N inputs (Fornara et al. 2013), although forest growth limitation is profoundly influenced by the relative abundances of essential nutrients (Sardans et al. 2012). Even in temperate forests, where P availability less frequently limits biotic activity than N availability, P can significantly interact with N and thus influence N cycling rates and ecosystem productivity (Aber et al. 1998, Fenn et al. 1998). The synergistic interaction of P fertilization with atmosphere N deposition is predicted to be stronger in the subtropical and tropical regions

compared with temperate forests because these forests are generally poor in P and rich in N (Chen 2003, Chen et al. 2014). Unfortunately, the interactions between P input and N deposition in subtropical and tropical regions are infrequently reported (Cleveland and Townsend 2006), which limits our ability to forecast forest responses to globally increasing N deposition (Hietz et al. 2011).

Understanding plant nutrient internal cycling can increase our ability to predict the effects of nutrient addition on tree growth (Proe and Millard 1995). Even with high exogenous nutrient input, internal nutrient fluxes between forest trees and the soil and within individual trees are generally larger than the external nutrient fluxes associated with leaching and gaseous emissions (Nadelhoffer et al. 1999, Gundale et al. 2014). Resorption (i.e., the withdrawal of nutrients from senescing organs and the subsequent transportation to storage sites and growing organs) is a key process in internal, whole-plant nutrient cycling (Killingbeck 1996, Saur et al. 2000). It is also an important nutrient conservation strategy ensuring that nutrients are available for future growth and reducing the dependence on external nutrient availability, especially in poor nutrient ecosystems (Aerts 1996, Chen et al. 2012). In general, resorption is in balance with the acquisition of nutrients from the soil (Vergutz et al. 2012). High resorption plays an essential role in nutrient-poor environments, where the acquisition of nutrients from the soil is usually more energetically costly relative to resorption (Wang et al. 2014). Consequently, a broader understanding of tree nutrient use is required for developing models to predict the responses of forest ecosystems to changes in environmental conditions (Yuan and Chen 2009).

Another question is whether nutrient dynamics vary with the age of plant tissue. In species with a long leaf life span, such as many evergreen trees, nutrient concentrations as well as photosynthetic rates may tend to decrease as leaves age (Reich et al. 2009, Mediavilla et al. 2011) because light availability generally decreases vertically downward through the tree canopy (Wright et al. 2006). However, forest production models are generally parameterized only with respect to current-year foliage data (Escudero and Mediavilla 2003, Palmer et al. 2005), even though old leaves can comprise a large fraction of whole canopy foliage. In theory, nutrient retranslocation to younger leaves should increase the efficiency of nutrient resorbed because leaf aging usually reduces plant nutrient use efficiency (Escudero and Mediavilla 2003). Accordingly, the effects of leaf senescence and the removal of nutrients on total tree photosynthesis should depend on nutrient resorption throughout a leaf's life span, particularly as leaves become progressively shaded (Ackerly 1999).

In contrast to the intensive research on leaf nutrient responses to environment change, the effects of nutrient alteration on twig nutrient dynamics and resorption are rarely investigated (Mao et al. 2013), although the twigs of some plants have similar

nutrient resorption rates and generally larger biomass compared with leaves and play an important role in nutrient internal cycling (Freschet et al. 2010). Consequently, age effects on twig nutrients and nutrient resorption need to be considered, especially when twig and leaf age-spans are similar (Son et al. 2000).

To examine the dynamics of N and P, we selected Chinese fir (*Cunninghamia lanceolata*) as our model species because it is an evergreen conifer whose twigs and leaves generally grow and senesce at the same time and because it is one of the most important plantation tree species in China (Chen 2003). Consequently, Chinese fir provides a good experimental model system as well as an important economic species with which to study the responses of different age twigs and leaves to N and P additions. We used this species to evaluate whether (i) exogenous P addition increases tree N absorption under simulated N deposition situation and increases leaf and twig N concentrations, (ii) leaf and twig nutrient response patterns are similar to soil nutrient alterations, (iii) the nutrients in young and old leaves and twigs differ in their responses to N and P additions and (iv) nutrient resorption decreases with increasing nutrient availability irrespective of young and old leaves and twigs. The overarching goal of this study was to explore the responses to changes in N deposition and to test whether P addition can offset the effects of N deposition in a forest plantation community with poor soil conditions.

Materials and methods

Study region

The study site is located at the Qianyanzhou Ecological Research Station, Chinese Academy of Sciences, in Taihe County, Jiangxi Province of Southern China (26°42'N, 115°04'E). The site, which lies upon a red, nutrient-poor soil, has a subtropical moist monsoon climate, with a warm, dry summer and a cool, wet winter. The duration of the growing season is ~270 days. The average annual precipitation is 1600 mm with >50% of the total precipitation occurring from April to June. Maximum and minimum average monthly temperatures are 29.7 °C in July and 6.5 °C in January, while the average annual temperature is 17.9 °C. The clear-sky duration per year is 1306 h and the solar radiation is 4349 MJ m⁻². Most local soils are Typical Hapludult Ultisols (locally 'red soil'), which developed from Quaternary Red Clay and cover over 60% of 1.14 million km² of total land area in southeast China (Gong et al. 2013). The elevation is from 30 to 200 m above sea level.

Experimental design

At the end of 2011, we selected a 12-year-old Chinese fir plantation to simulate N deposition and exogenous P addition with six treatments including +N1 – P (50 kg N ha⁻¹ year⁻¹), +N2 – P (100 kg N ha⁻¹ year⁻¹), +N1 – P (50 kg N plus 50 kg P ha⁻¹ year⁻¹), +N2 – P (100 kg N plus 50 kg P ha⁻¹ year⁻¹), –N + P

(50 kg P ha⁻¹ year⁻¹) and -N - P (with and without, + and -, respectively). The plantation was established with 2 × 2 m spacing of fir trees after whole harvesting and slash burning. One-year-old seedlings were provided by the local Shixi forest farm and the seeds were collected from the second-generation Chinese fir seed plantation (~16 ha and 32 families) in Anfu county nearby our study area. The heritability of tree height and diameter at breast height (DBH) were ~0.76 and 0.78, respectively, with 8–10% variation coefficient (Zhu et al. 2013).

Five replications were established on five separate hilly slopes (5–15°); six treatments with 20 × 20 m plots, separated by at least 20 m, were randomly arranged within each replication (see Figure S1 available as Supplementary Data at *Tree Physiology* Online). All five blocks were arranged in north–south orientation, and six plots within a block were set up in similar slope aspect and position. Nitrogen and P were added four times each year [in March (30%), June (30%), September (20%) and December (20%)] in the form of NH₄NO₃ and NaH₂PO₄, respectively. The fertilizer was weighed, mixed with 8 kg of clean and dry fine sand and applied to each plot. The control plots received fine sand without N and P additions. To ensure better uniformity of N and P applications within a plot, we divided each plot into 16 (5 × 5 m) quadrates and equally distributed each application by hand. Dead fir twigs and leaves as well as all understory vegetation were moved from each plot in December 2011 so that new litter could accumulate and be evaluated for N and P contents in 2012 and 2013.

Sampling

Stand characteristics and soil general properties In November 2011, tree characteristics including density, DBH and height were measured in each of the 30 plots. Understory plant biomass was measured using eight random 1 × 1 m quadrates within each 20 × 20 m plot. In addition, soil (0–10 cm) was collected from 36 random points using 2.5-cm soil cores; subsamples were mixed to provide a single sample from each plot. All samples were immediately brought back from the field site, and their water contents were measured using a 105 °C drying method. The soil was cleared of roots and all organic debris and subsequently air-dried and stored for analyses of soil pH,

organic carbon (C), total N and total P. Soil pH was determined using pH meter with a soil : water ratio of 1 : 2.5. Air-dried soil samples were ground to pass through a 0.25-mm sieve. Organic C was determined using the Walkley–Black wet oxidation method (Allen 1989). Soil total N and total P concentrations were determined by the Kjeldahl method and by the molybdenum-antimony colorimetric method, respectively, after samples were digested with 1.84 M H₂SO₄ (Allen 1989). Soil bulk density was measured using a ringer sampler from the 0–5 and 5–10 cm layers.

To monitor tree growth dynamics, we randomly selected 20 trees in each plot that were then fitted with self-made devices that measured changes in tree diameter (see Figure S2 available as Supplementary Data at *Tree Physiology* Online). The girth growth rate at breast height was measured in June and December each year using a micrometer to obtain an average growth rate for a plot level.

Soil nutrient availability During the growing season (~30 days after fertilization in July) in 2012 and 2013, soil was collected at 36 random points with a core sampler in each plot. Soil samples were collected from a depth of 0–5 and 5–10 cm in each of the 36 random sampling points. For each soil layer, the samples were mixed completely to form a bulk sample from each plot to determine the mineral N concentration. A 25-g soil sample was mixed with 100 ml 2 M KCl, shaken for 0.5 h and left to stand overnight at 4 °C. The NH₄⁺-N and NO₃⁻-N in the supernatant were separately measured by spectrophotometry following filtration using the indophenol blue and the cadmium reduction methods (Allen 1989), respectively. A 5-g soil sample was mixed with 50 ml 0.5 M NaHCO₃, shaken for 0.5 h and the supernatant was used to determine the available P by means of the molybdenum-antimony colorimetric method (Allen 1989). Stand characteristics and soil properties are provided in Table 1.

Leaf and twig nutrients During the growing season in 2012 and 2013, three representative trees were selected on the basis of the average DBH and height determined for each plot. Leaves and twigs from one first-order branch were collected from each tree. Leaves and twigs were divided into young (the first order of

Table 1. The ratios of N resorption proficiency to P resorption proficiency for various age leaves and twigs experiencing N and P additions in Chinese fir plantations growing in a hilly red soil region. Mean ± 1 standard error. Two-factor ANOVA of N addition, P addition and their interaction was adopted. Different letters indicate the significant differences among the six treatments ($P < 0.05$, randomized complete block design ANOVA followed by multiple comparison tests).

| N addition | P addition | Young needle leaf litter | Old needle leaf litter | Young twig litter | Old twig litter |
|------------|------------|--------------------------|------------------------|-------------------|-----------------|
| -N | -P | 25.86 ± 3.19a | 24.21 ± 2.21b | 19.52 ± 1.27ab | 18.03 ± 1.51b |
| +N1 | | 26.59 ± 2.07a | 28.02 ± 2.00a | 23.97 ± 0.86a | 22.72 ± 1.77a |
| +N2 | | 24.90 ± 2.84a | 21.96 ± 1.43c | 20.89 ± 2.30ab | 22.37 ± 2.60a |
| -N | +P | 20.96 ± 1.28b | 18.26 ± 1.66d | 16.19 ± 2.22b | 14.68 ± 1.52c |
| +N1 | | 20.47 ± 1.52b | 22.70 ± 2.55c | 19.48 ± 1.95ab | 17.83 ± 1.47b |
| +N2 | | 20.64 ± 1.45b | 21.47 ± 1.71c | 17.72 ± 1.43b | 16.51 ± 1.21bc |

branching) and old (the second or third orders of branching) (see Figure S3a available as Supplementary Data at *Tree Physiology* Online). The same components (leaves vs twigs) were mixed together to obtain a composite sample for each plot. The samples were washed with deionized water to remove dust, oven-dried, and ground and screened with a 0.25-mm sieve. Total N and total P were determined using the micro-Kjeldahl method and molybdenum-antimony colorimetric method, respectively.

Nutrient resorption Litterfall was collected from November 2013 to April 2014 using perforated plastic boxes under the canopies of three representative trees within each plot to measure leaf and twig nutrient resorption during 2013. Since Chinese fir litter generally falls in the form of whole branches, we used the previously described protocols to assemble composite samples of young vs old leaf needle litters and young vs old twig litters (see Figure S3b available as Supplementary Data at *Tree Physiology* Online). Each component in each plot was analyzed to determine total N and total P concentrations using the micro-Kjeldahl method and molybdenum-antimony colorimetric method, respectively (Allen 1989). The biomass of each component was also determined (and expressed as a percentage of the whole).

Nutrient resorption proficiency and nutrient resorption efficiency were used as indices of nutrient conservation (Wright and Westoby 2003, Mao et al. 2013). The former is defined as the concentration of the nutrient remaining in the litter produced in any one year (Killingbeck 1996). In this study, N and P resorption proficiencies (NRP and PRP) for young and old leaves and for young and old twigs were calculated as the N and P concentrations in the litterfall collected between November and April.

Nutrient resorption efficiency was calculated using the formula of Aerts (1996), i.e., nutrient resorption efficiency = [(nutrient in living leaf or twig tissue – nutrient in the litter component corresponding to the same organs)/(nutrient in living leaf or twig tissue)] × 100%.

This formula was applied to data collected from live leaves and twigs from the representative trees sampled in July and to data collected for nutrients in leaf and twig litter from under the canopies of the representative trees in November–April. Nitrogen and P resorption efficiencies (NRE and PRE) were determined separately for young and old leaves and for young and old twigs removed from the branches of representative trees and for the litter collected from under the canopies of representative trees. In this study, the leaf and twig mass loss during senescence was not taken into consideration, which may lead to underestimate nutrient resorption (van Heerwaarden et al. 2003, Vergutz et al. 2012).

Data analyses

The data were tested for homogeneity of variances (Brown and Forsythe's variation of Levene's test) before statistical analysis.

The variables were analyzed by analysis of variance (ANOVA) in randomized complete block design. Least significant difference methods were used to compare the differences among the three N addition levels. SPSS software (SPSS 2007) was used to perform all analyses. The standard 0.05 level was used throughout as a cutoff for statistical significance.

Results

The responses of tree growth and soil nutrient availability to N deposition and P input

The general characteristics of the stands including density, DBH, average height and understory vegetation biomass were not significantly different among the experimental plots (see Table S1 available as Supplementary Data at *Tree Physiology* Online). Girth growth rate at breast height increased with N deposition and P input in 2013 but not in 2012 (presumably reflecting a lag in treatment effects); no interactions of N deposition and P input were found. Meanwhile, tree growth rates across all treatments were much higher in the first than the second half of both years (Figure 1).

Soil general properties such as bulk density, organic C, total N, total P and their ratios showed minimal variations among the different treatments (see Table S1 available as Supplementary Data at *Tree Physiology* Online). Soil $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$, mineral N and available P were influenced by a main factor (i.e., N addition, P addition, soil depth and sampling year) with the exception of single P input on $\text{NO}_3^-\text{-N}$ (see Table S2 available as Supplementary Data at *Tree Physiology* Online). Soil $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$ and mineral N increased with increasing levels of N addition in both 2012 and 2013 at 0–5 cm depth and at 5–10 cm depth. Increases in $\text{NH}_4^+\text{-N}$ and mineral N diminished significantly with N addition due to P input at a soil depth of 0–5 cm but not at a depth of 5–10 cm in 2012 and for both soil depths in 2013. Soil $\text{NO}_3^-\text{-N}$ was not altered by P input at either depth in both years (Figure 2a–c). In contrast, soil available P was more than four times higher in plantations treated with P input than without P input at a soil depth of 0–5 cm and increased by 80% at a soil depth of 5–10 cm (Figure 2d).

Leaf and twig nutrient concentrations and stoichiometry

Young and old leaf N concentrations were unaffected by N addition in 2012 (see Figure S4a available as Supplementary Data at *Tree Physiology* Online), but young leaf N concentration significantly increased with N addition in 2013 (Figure 3a). The N concentration of young but not old leaves increased with P addition in 2013 (Figure 3a). Young and old leaf P concentrations were higher in plantations treated with P input than without P input from 2012 to 2013 but did not change with N addition (Figure 3c). Old leaf N/P ratios generally decreased with P input, but young leaf N/P ratios did not change with N and P additions (Figure 3e).

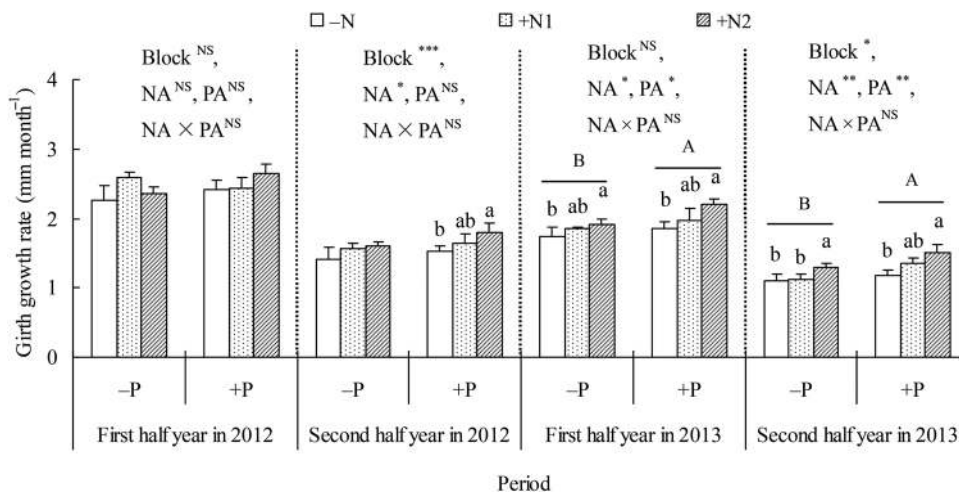


Figure 1. Girth growth rate at breast height varied with N and P additions in Chinese fir plantations of a hilly red soil region. The bars represent standard error. NA, nitrogen addition; PA, phosphorus addition. Different small and capital letters indicate the significant differences among three levels of N additions and between two P addition treatments, respectively ($P < 0.05$, randomized complete block design ANOVA followed by multiple comparison tests). NS, not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

The young twig N concentration increased with P input in 2013 (Figure 3b), but not in 2012 (see Figure S4b available as Supplementary Data at *Tree Physiology* Online). Young and old twig P concentrations were higher in plantations treated with P input than without P input from 2012 to 2013, but did not change with N addition (Figure 3d). Young and old twig N/P ratios decreased with P input, but were not altered by N addition in either of the 2 years (Figure 3f; Figure S4f available as Supplementary Data at *Tree Physiology* Online).

Nutrient resorption of different age leaves and twigs

Nitrogen resorption proficiency of young leaf litter generally decreased with N addition and P input, while NRP of old leaf litter was unaltered by N addition and P input except in the case of old leaf litter treated by P addition (Figure 4a and b). The PRP of all young and old leaf and twig litters decreased with P input but showed minimal variations with N addition (Figure 4c and d). Nitrogen resorption proficiency was lower for young and old leaf litters than for young or old twig litters. Phosphorus resorption proficiency did not significantly differ between young leaf and young twig litters, but it was lower for old leaf litter than for old twig litter (Figure 4). Nitrogen resorption proficiency to PRP ratios were influenced by N addition only for old leaf and twig litters, and were generally lower in plantations treated with +N1 - P rather than +N2 - P, or treatments lacking N addition. In contrast, all NRP/PRP ratios were higher in plantations treated with P input than without P input. No significant interaction of N addition and P input was observed on any of the NRP/PRP ratios (Table 1).

Nitrogen resorption efficiency and PRE of the four litter components were not significantly different among the plantations treated with N and P additions (Table 2). Nitrogen resorption efficiency was much higher for young (21.2–29.6%) than old

twig litters (1.2–14.6%) and ranged between 29.8 and 39.4% and between 21.4 and 33.4% for young and old leaf litters, respectively. Phosphorus resorption efficiency ranged between 26.6 and 46.8% and was not significantly different among the four litter components (Table 2). Phosphorus resorption efficiency was generally higher than NRE for each of the litter components, and NRE/PRE ratio was higher for leaves than for twigs (Table 2). Finally, total NRE and PRE and NRE/PRE ratios within whole branches were not significantly different among the six different treatments; the NRE/PRE of all treatments was < 1 , whereas NRE and PRE were not significantly different in plantations treated with higher N addition (+N2 - P and +N2 + P) (Table 2).

Discussion

The interaction of P input and various levels of N addition has been seldom reported, especially in subtropical forests. Our results show that the plant internal N cycle is altered by P input and increases with increasing N addition levels and that P limitation can be enhanced with increasing N addition dosage. Each of these observations is discussed in the following sections.

N and P accumulations with exogenous N and P inputs

Our data show that N and P concentrations in the soil and storage in plant tissues generally increase with exogenous N and P application, which is consistent with the hypothesis that motivated this study as well as with the observations reported in previous studies. For example, Xu and Timmer (1999) found that N uptake in Chinese fir seedlings increased from 18 to 65% in a pot experiment with four different levels of N application (i.e., from 0 to 90 mg tree⁻¹). Proe and Millard (1995) investigated the response of Sitka spruce (*Picea sitchensis*) seedlings

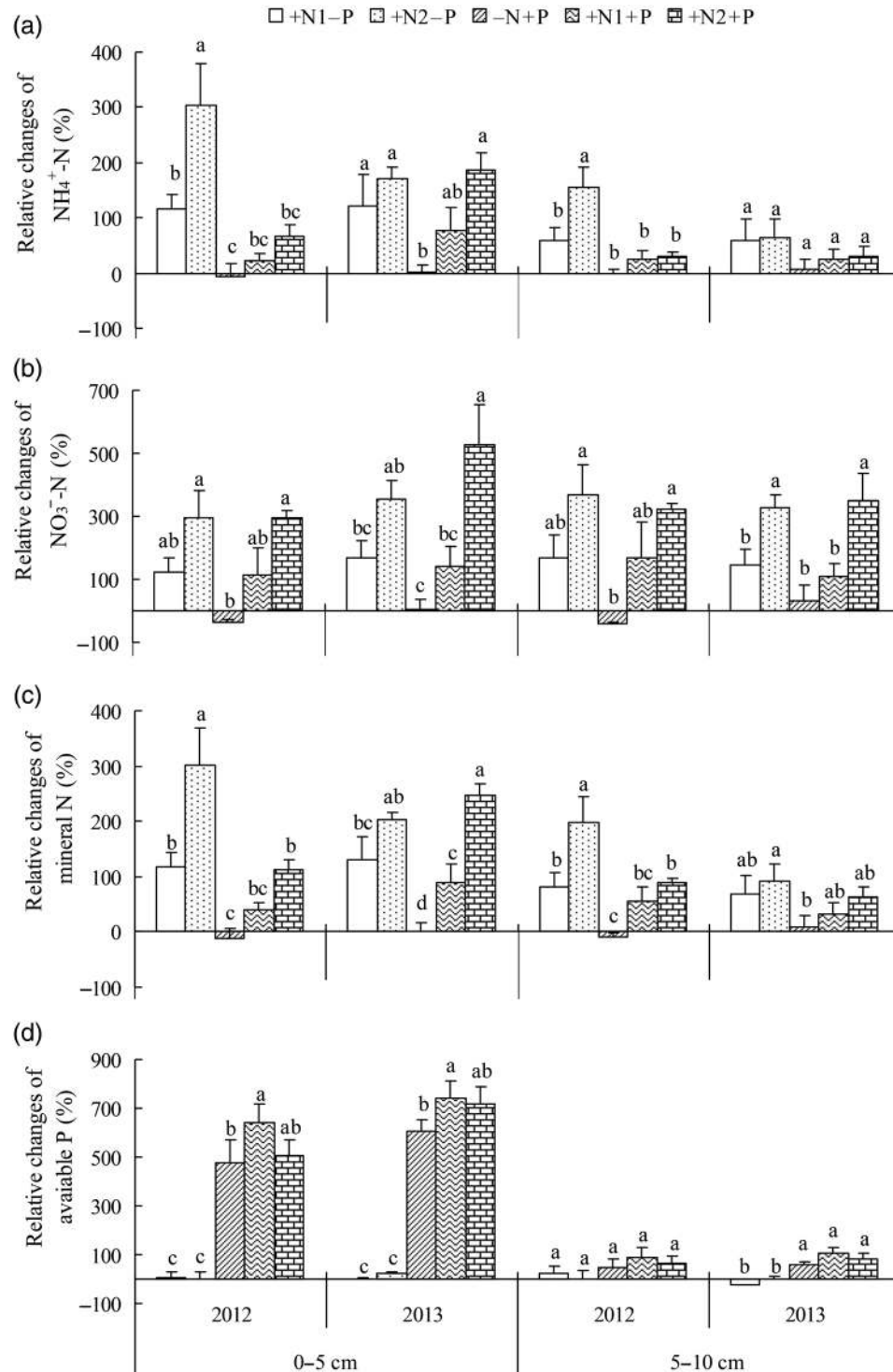


Figure 2. Relative change of soil $\text{NH}_4^+\text{-N}$ (a), $\text{NO}_3^-\text{-N}$ (b), mineral N (c) and available P (d) concentrations to control treatment varied with different treatments, soil depths and sampling year in Chinese fir plantations of a hilly red soil region. The bars represent standard error. Different letters indicate the significant differences among the six treatments ($P < 0.05$, randomized complete block design ANOVA followed by multiple comparison tests).

to P fertilization and found that P tissue content and seedling growth increased eight and three times, respectively. In subtropical China, leaf N and P concentrations of slash pine (*Pinus elliottii*) were, respectively, 24% (Chen et al. 2010) and 20% (Hu et al. 2011) higher in urban as opposed to rural sites due to urban N

deposition and P input (Chen et al. 2014). Therefore, it seems to be generally true that nutrients in plant tissues increase in response to increasing soil nutrient concentrations.

At a more highly resolved level of nutrient partitioning within the individual plant, our data highlight the differences in where

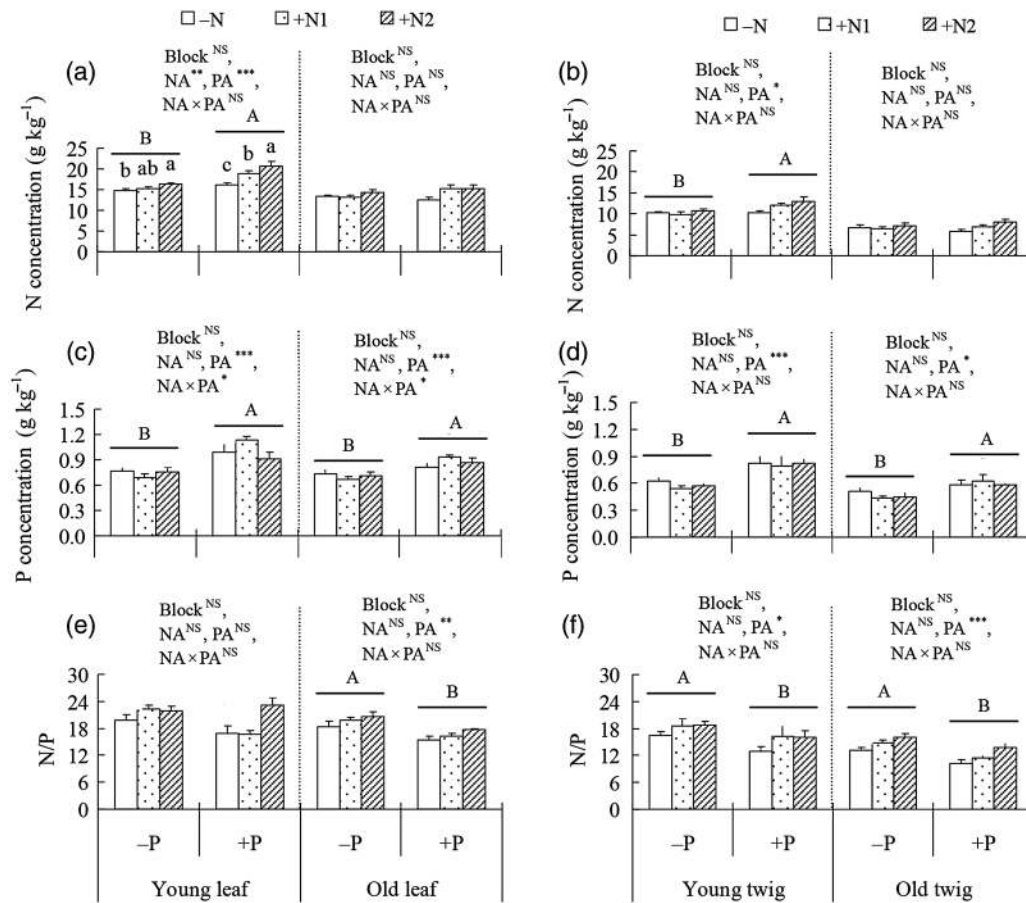


Figure 3. Nitrogen and P concentration and N/P in the leaves (a, c and e, respectively) and twigs (b, d and f, respectively) varied with N and P additions in 2013 in Chinese fir plantations of a hilly red soil region. The bars represent standard error. NA, nitrogen addition; PA, phosphorus addition. Different small and capital letters indicate the significant differences among three levels of N additions and between two P addition treatments, respectively ($P < 0.05$, randomized complete block design ANOVA followed by multiple comparison tests). NS, not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

(and in what form) N and P are stored. In general, plants tend to store N as structural amino acids and proteins (Chapin et al. 1990), whereas plants generally store P in vacuoles and cytoplasm, although inorganic P moves through xylem and phloem (Bloom et al. 1985, Sinclair and Vadez 2002). Our data also show that the leaves and twigs of plants respond more rapidly and to a greater degree to increasing levels of P compared with increasing levels of N. This is also consistent with other studies. For example, using a long-term fertilization protocol in a Hawaiian tropical forest, Ostertag (2010) found that foliar P levels increased much more rapidly than N. This pattern has been detected in many other ecosystems, including pine forests (Sword Sayer et al. 2004), mangroves (Feller et al. 2003) and wetlands (Güsewell 2005). Consequently, it is reasonable to conclude that it is a general phenomenon, although exceptions are known. For example, in semi-arid grassland with a N-limited ecosystem, factorial N x P addition experiments revealed that leaf N accumulated at a greater rate than P accumulation, both over the short term (1 year) (Chen et al. 2010) and over the long term (5 years) (Li et al. 2012).

The effects of N addition and those when coupled with P input

Taken in isolation, the effects of N addition on plant–soil nutrient dynamics and ecosystem productivity are known to vary with site characteristics, N input dosage, duration and plant species (Gundersen et al. 1998, Lü et al. 2013, Mayor et al. 2014). These effects can be positive (Perring et al. 2008, Pregitzer et al. 2008), negative (De Schrijver et al. 2011, Wei et al. 2013) or insignificant (van Heerwaarden et al. 2003, Gundale et al. 2014). In our study, N addition alone increased soil mineral N and tree growth rate over the short term (Xu and Timmer 1999, Lü et al. 2013), but in general had no effect on leaf or twig N concentrations (most likely because of the ‘dilution of N’ with increasing plant biomass; see Holub and Tuma 2010, Mao et al. 2013).

However, a novel and potentially important observation in our study is that P input significantly increased young leaf N concentrations in tandem with N deposition. Previous studies have shown that essential elements do not cycle independently at the ecosystem level, and that N and P are closely linked in soil

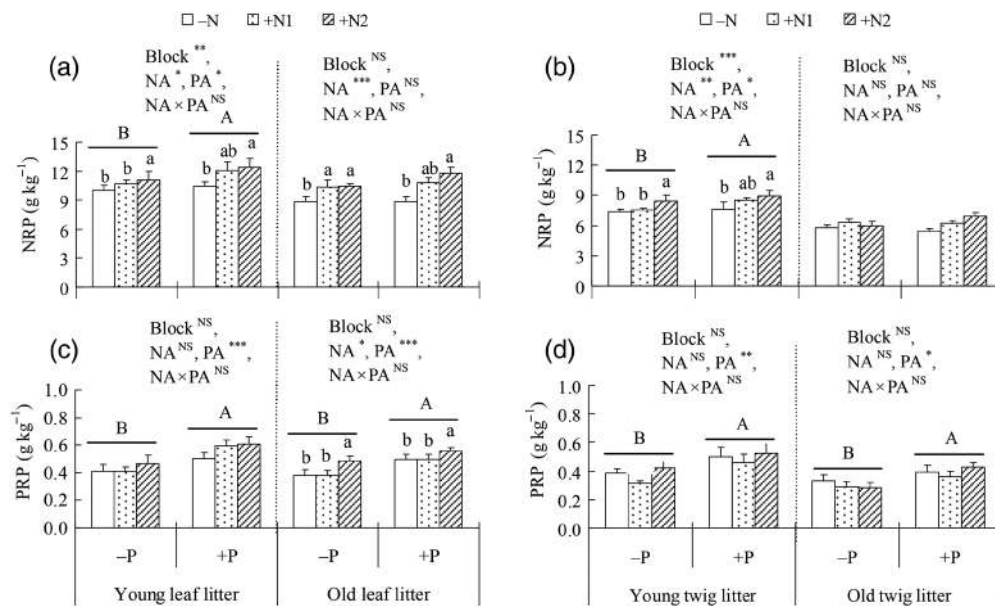


Figure 4. Nitrogen and P resorption proficiencies (NRP and PRP) for various age leaves (a and c) and twigs (b and d) varied with N and P additions in Chinese fir plantations of a hilly red soil region. The bars represent standard error. NA, nitrogen addition; PA, phosphorus addition. Different small and capital letters indicate the significant differences among three levels of N additions and between two P addition treatments, respectively ($P < 0.05$, randomized complete block design ANOVA followed by multiple comparison tests). NS, not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Table 2. Nitrogen and P resorption efficiencies (NRE and PRE, %) for various age leaves and twigs varied with N and P additions in Chinese fir plantations of a hilly red soil region. Mean ± 1 standard error. Different lower and capital letters indicate the significant differences among the four litter components and among the six treatments ($P < 0.05$, randomized complete block design ANOVA followed by multiple comparison tests).

| N addition | -N | +N1 | +N2 | -N | +N1 | +N2 |
|---------------------------|-------------------|------------------|-------------------|--------------------|-------------------|-------------------|
| P input | -P | | | +P | | |
| NRE (%) | | | | | | |
| Young leaf litter | 32.6 \pm 4.0Aa | 29.8 \pm 1.9Aa | 32.4 \pm 5.7Aa | 35.0 \pm 1.8Aa | 35.2 \pm 6.2Aa | 39.4 \pm 5.1Aa |
| Old leaf litter | 33.4 \pm 3.5Aa | 21.4 \pm 5.4Aa | 26.8 \pm 3.7Aa | 26.6 \pm 9.2Aa | 28.0 \pm 5.3Aa | 21.6 \pm 5.4Abc |
| Young twig litter | 27.4 \pm 1.9Aa | 23.0 \pm 6.5Aa | 21.2 \pm 5.4Aab | 25.2 \pm 5.1Aa | 28.4 \pm 4.2Aa | 29.6 \pm 5.3Aab |
| Old twig litter | 8.6 \pm 11.2Ab | 1.2 \pm 6.6Ab | 14.6 \pm 8.0Ab | 2.8 \pm 9.4Ab | 7.2 \pm 7.9Ab | 11.0 \pm 6.6Ac |
| PRE (%) | | | | | | |
| Young leaf litter | 45.6 \pm 7.4Aa | 40.2 \pm 4.7Aa | 39.0 \pm 5.8Aa | 45.4 \pm 8.9Aa | 46.8 \pm 5.2Aa | 32.4 \pm 6.5Aa |
| Old leaf litter | 46.0 \pm 8.8Aa | 43.2 \pm 6.8Aa | 30.4 \pm 5.9Aa | 37.4 \pm 7.1Aab | 47.0 \pm 5.6Aa | 34.4 \pm 5.8Aa |
| Young twig litter | 37.8 \pm 5.2Aab | 41.0 \pm 5.1Aa | 26.8 \pm 8.2Aa | 34.6 \pm 11.5Aab | 35.6 \pm 14.2Aa | 35.2 \pm 8.9Aa |
| Old twig litter | 29.8 \pm 14.1Ab | 33.6 \pm 7.8Aa | 36.8 \pm 5.6Aa | 29.6 \pm 11.5Ab | 36.0 \pm 12.6Aa | 26.6 \pm 4.8Aa |
| Within a branchlet | | | | | | |
| NRE (%) | 38.1 \pm 3.2Ab | 34.8 \pm 2.9Ab | 35.9 \pm 4.1Aa | 37.9 \pm 2.4Ab | 31.8 \pm 6.0Ab | 34.6 \pm 3.5Aa |
| PRE (%) | 55.0 \pm 3.4Aa | 57.2 \pm 7.1Aa | 46.1 \pm 8.5Aa | 58.8 \pm 7.5Aa | 60.9 \pm 5.5Aa | 41.5 \pm 4.9Aa |
| NRE/PRE | 0.71 \pm 0.09A | 0.63 \pm 0.07A | 0.86 \pm 0.16A | 0.70 \pm 0.12A | 0.51 \pm 0.07A | 0.90 \pm 0.18A |

nutrient dynamics as well as within internal plant nutrient cycles (Marklein and Houlton 2012, Sardans et al. 2012). Our data show that soil mineral N decreases with P input, and that P input simulated N absorption from the soil (Vitousek et al. 2010). Nitrogen storage in understory vegetation increased between 20 and 30% in sites with P input compared with those without P input (data not shown). In contrast, N addition did not alter leaf and twig P dynamics regardless of whether P was provided or not provided. It is relevant to note that Perring et al. (2008) developed a plant–soil nutrient model to examine the

coupling of N and P with respect to plant biomass and found that N addition is predicted to have no effect on P dynamics when N is sufficient for optimal growth, i.e., plant growth and P demand are unresponsive to elevated supraoptimal N levels.

Nitrogen deposition can induce a more conservative usage of P in forest ecosystems in ways that maintain stoichiometric homeostasis (Sardans et al. 2012) and promote plant growth (Perring et al. 2008, Vitousek et al. 2010). We found that the rate of girth growth at breast height increased between 6 and 12% in sites experiencing P input compared with those without

P input. The fastest rate of growth was found in the plantation treated by combined N and P additions. Cleveland and Townsend (2006) conducted a field-fertilization experiment in a P-poor tropical rain forest in Costa Rica, and found P fertilization stimulated soil respiration mostly as a result of increasing fine root biomass, but especially in the plots receiving N input. Therefore, it is not surprising that our data show the NRE/PRE <1.0 in leaves and twigs (i.e., a higher P use efficiency) regardless of P or N additions. The inferences that can be drawn from this observation are limited, however, because ecosystem short-term responses to soil nutrient alteration generally differ from long-term responses and because soil properties will likely change as a result of multi-year N and P inputs, e.g., soil acidification following long-term N deposition, with an attending decrease in P availability (Marklein and Houlton 2012). Clearly, the accumulative effect of exogenous P input in subtropical forest N cycles and long-term N addition and P input interaction need to be examined in detail (Reich et al. 2009, Sardans et al. 2012).

Organ and age effects on nutrient internal cycle

Changes in the nutrient levels of young and old leaves and twigs were generally similar in response to N and P additions. Accordingly, irrespective of organ position or age, the nutrient levels of leaves and twigs appear to be physiologically coordinated in response to exogenous nutrient levels (Wright et al. 2006). Although the absolute N and P concentrations in these organs varied depending on soil nutrient supply, the N/P ratios in leaves vs twigs and young organs vs old organs were relatively stable, which is consistent with the supposition that these ratios reflect stoichiometric constraints and perhaps maintain electrical neutrality in vacuoles; see Broadley et al. (2004) as posited by the plant physiological relative balance theory (Glynn et al. 2007).

In the absence of optimal soil nutrient levels, plants appear to adaptively conserve nutrient levels in response to nutrient deficiencies (Aerts and Chapin 2000). This supposition is supported by the observation that nutrient resorption indexes are in balance with soil nutrient acquisition and depend on the relative energy consumption of these two processes (Wright and Westoby 2003, Vergutz et al. 2012). For example, in our study, NRP and PRP for both old and new leaf and twig litters generally decreased with increasing N deposition and P input. Average leaf NRP decreased from 9.5 mg g⁻¹ (which is lower than the global mean value of 10.0 mg g⁻¹) (Yuan and Chen 2009) to ~10.5–11.5 mg g⁻¹ (which is significantly higher than global mean value) with elevated N addition, especially in tandem with P input. In contrast, average leaf PRP was higher than the global mean value (0.70 mg g⁻¹) (Yuan and Chen 2009) even in sites experiencing P input, i.e., Chinese fir has a 'complete PRP' and an 'incomplete NRP' (sensu Killingbeck 1996) such that tree growth is P-limited rather than N-limited (Chen 2003).

It is interesting to note that decreasing NRP and PRP can, under some circumstances, add larger amounts of N and P to the

soil provided that litter quantity is maintained (Mirmanto et al. 1999). Moreover, litters with higher nutrient concentrations tend to decompose faster and thereby accelerate nutrient cycles (van Huysen et al. 2013). Another interesting observation is that the ratios of NRP/PRP in old leaf and twig litters are altered by N and P additions, but those in young leaf and twig litters decreased with P input. Finally, the NRP of young leaf litter and the PRP of old leaf litter decreased with P input and N addition, indicating that N and P are likely tightly coupled during the transition from young to old organs (Yang et al. 2014).

In contrast, NRE within entire branches for all treatments ranged from 32 to 38%, which is much lower than the global value (i.e., 50% based on uncorrected data, Aerts 1996; 62% when corrected for mass loss, Vergutz et al. 2012), while PRE was close to the global value (i.e., 52% based on uncorrected data, Aerts 1996; 65% when corrected for mass loss, Vergutz et al. 2012). Thus, Chinese fir might either expend less energy to obtain N than P from the soil or more easily resorb P from aging leaves and twigs than absorb P from the soil (which is often the case in subtropical and tropical forests; see Yuan and Chen 2009, Chen et al. 2012, Vergutz et al. 2012).

Our data indicate that NRE and PRE do not significantly vary among the various litters in response to N deposition and P input. This is consistent with many studies showing that resorption efficiency is generally unaffected by increasing nutrient availability (Aerts 1996, Aerts and Chapin 2000, Yuan and Chen 2009, Chen et al. 2010). The efficiency of resorption reflects plant physiology and metabolic processes, whereas proficiency is directly linked with decomposition processes and hence overall nutrient cycling (Chen et al. 2012). Further, our results agree with the observations of Norris and Reich (2009) and Chen et al. (2010) that resorption proficiency is more sensitive to nutrient alteration than resorption efficiency (Killingbeck 1996).

An additional insight into these interactions is provided by a comparison of nutrient dynamics and resorption between leaves vs twigs and young vs old leaves or twigs. Our data confirm that N and P concentrations and the N/P ratios in leaves are higher than those in twigs. This is not surprising since leaves are the primary photosynthetic organs of trees and because they contain a larger fraction of living biomass compared with twigs (Chen et al. 2012). Mao et al. (2013) also found that leaves and other organs (such as stems) respond differentially to N addition. Further, NRP, PRP and PRP/NRP were lower for leaf than twig litters, which sheds light on why foliar litter is more easily decomposed compared with twig litter (and is the dominant litter in nutrient-poor soil; see van Huysen et al. 2013). Taken together, these trends indicate that leaves are the principal organs affecting adaptive nutrient use patterns in response to environment change (Phoenix et al. 2003).

In addition, N and P concentrations and N/P, NRP/PRP ratios were higher for young compared with old leaves and twigs.

Interestingly, NRE was generally higher for young compared with old litters, whereas PRE was not significantly different. These observations suggest that Chinese fir preferentially absorbs N directly from the soil rather than transfer N from old to young leaves and twigs, whereas the acquisition of P from the soil is more energetically costly relative to resorption from old litters even under exogenous P input. Additional observations indicate that excess N in the ecosystem of our study sites might decrease forest P internal cycle rates and would likely accelerate P limitation (Vitousek et al. 2010). As mentioned above, soil acidification due to long-term N deposition leads to decreased P availability, thus P limitation would be enhanced with N deposition (Marklein and Houlton 2012). Therefore, P fertilization could be a good management practice to improve leaf N concentration and biomass production, especially under an elevated N deposition situation in subtropical forest (Mirmanto et al. 1999, Ostertag 2010). In addition, other optional management practices, such as applying an appropriate amount of lime or plant ash, to raise soil pH might also contribute to increasing soil P availability in this ecosystem (Haynes 1982).

Overall, our data indicate that the internal cycling of essential nutrients within Chinese fir trees is spatiotemporally complex since it involves the transfer of N and P from new to old leaves and stems that responds to the magnitudes of exogenous applications of N and P to the soil. This complexity is amplified further because of a feedback loop between the nutrient concentrations of old and young leaf and twig litter (which depends on the previous year's soil nutrient concentrations) whose decomposition affects soil nutrient concentrations (which affects the nutrient concentrations of new leaves and twigs in the following year). The dynamics in N and P cycling both within trees and between trees and the soil in which they grow are undoubtedly dependent on ambient soil conditions, but it is also likely species dependent (e.g., the functional nutrient cycling traits of leaves and twigs). Additional studies are required to evaluate this complexity sufficiently to provide a predictive model in which all the variables of interest can be modified to emulate the behavior of different species in response to different soil types.

Supplementary data

Supplementary data for this article are available at [Tree Physiology Online](http://www.treephysiology.com).

Acknowledgments

The authors thank Wen Ren, Ming-Quan Yu and Xue Feng for their field work and soil analyses.

Conflict of interest

None declared.

Funding

This study was supported by grants from National Basic Research Program of China (973 Program, 2012CB416903), National Natural Science Foundation of China (31160107 and 31360179) and Jiangxi Provincial Department of Science and Technology (20122BCB23005).

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