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REGULAR ARTICLE

Seasonal phosphorus and nitrogen cycling in four Japanese cool-temperate forest species

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Abstract

Purpose In plant-soil systems, phosphorus partitioning during the annual cycle related to nitrogen partitioning remains largely unknown. The present study aims at assessing the soil-plant P allocation patterns of four tree species along four phenological stages and its relationship with tissues and soil N concentrations.

Methods *Cryptomeria japonica, Larix kaempferi, Fagus crenata* and *Robinia pseudoacacia* trees were selected to sample coarse roots, sapwood, foliage, litter and soil during four phenological stages where total and Olsen extractable P and nitrogen content were measured respectively.

Results Intra- and inter plant tissue nitrogen correlated well with phosphorus during the four phenological stages, especially root nitrogen. *Fagus* and *Robinia* were phosphorus limited, *Larix* was nitrogen limited and *Cryptomeria* co-limited. All species reabsorbed phosphorus and nitrogen from foliage prior to leaf abscission and stored nitrogen in roots and sapwood. Phosphorus storage was solely found in sapwood of *Robinia*. Soil dissolved ammonium correlated positively with nitrogen reabsorption efficiency during the green leaf stage, while single soil nutrient variables did not correlate with phosphorus reabsorption efficiency.

Conclusions Plant tissues nitrogen partitioning correlated well with their respective phosphorus partitioning and the increase of soil NH_4^+ correlated positively with nitrogen reabsorption efficiency, regardless of tree species during the green leaf stage. The results of this study show the intricate

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relationship that exists between nitrogen and phosphorus in the soil-plant continuum as well as the tree species specific internal cycling of these nutrients.

Keywords *Cryptomeria japonica* · *Fagus crenata* · *Larix kaempferi* · *Robinia pseudoacacia* · N and P allocation · N:P ratio

Introduction

The availability of nitrogen (N) and phosphorus (P) is a driving force of plant community composition (Aerts and Chapin 2000; Kolb and Evans 2002; Güsewell and Gessner 2009) and their limitation or imbalance in forest ecosystems can reduce plant growth and photosynthetic activity (Güsewell and Gessner 2009; Zhang et al. 2014; Luo et al. 2015). Nitrogen is vital for the formation of proteins, nucleic acids and chlorophyll (Warren and Adams 2004; Ueda et al. 2011) and is affecting photosynthetic and other plant internal processes (Güsewell 2004), while P is a vital component of RNA, DNA, phospholipids and sugar phosphates and it is involved in cellular energy transfer (Marschner 1995; Rennenberg and Herschbach 2013; Li et al. 2017). In general, N and P cycles are linked in soils, where microorganisms, fungi and plants produce enzymes that mineralize organically bound nutrients (Olander and Vitousek 2000; Turner 2008). P demand and P mineralization form a slow strongly regulated single pathway cycle and when P demand exceeds P mineralization, the production of phosphatase enzymes is stimulated, resulting in higher P mineralization rates (Keller et al. 2012; Paul 2015; McQuillan et al. 2020) while high phosphate levels also repress phosphatase activity. Thus, if sufficient organic P is available in soils, plant P demand will be mostly met by P mineralization but never exceed it (Olander and Vitousek 2000). In contrast, N mineralization is predominantly driven by hydrolytic enzymes as well as by enzymes that mineralize C, which can contribute to release inorganic N during organic matter decomposition as C and N cycles are tightly linked (Olander and Vitousek 2000; Lang et al. 2017), resulting in a decoupling of N demand and N mineralization. Thus, N mineralization may exceed plant demand, ultimately leading to N saturation, as the comparably fast multi-pathway regulatory cycle between plant N demand and N mineralization may be weaker than that for P. On the other hand, N supply may stimulate phosphatase production because N is essential for enzyme synthesis and because N may boost plant and microbial productivity increasing P demand, whereas the converse is less evident in the literature (Olander and Vitousek 2000 and references therein).

Similarly, higher N content in foliage leads to an increased P demand as plants can increase their leaf area index, extend photosynthesis duration and improve nutrient uptake since all of these processes require P (Li et al. 2017). Kang et al. (2010) found indeed a significant positive correlation between leaf N and P content in woody plants.

Further, based on soil N and P content and availability, plants may develop highly efficient strategies for N and P uptake, utilization, storage, mobilization and resorption linking soils and plants. Through these links, plant species specific N and P cycling through ecosystems can be observed (Millard and Grelet 2010; Rennenberg and Herschbach 2013).

N and P fertilization experiments under N-limited or P-limited conditions typically conducted under laboratory conditions have investigated N and P cycling, often using saplings and focused on leaves (De Groot et al. 2003; Wright et al. 2005; Wright et al. 2011; Yavitt et al. 2011; Santiago et al. 2012; Mori et al. 2013). However, studies of other plant tissues with adult trees in forest ecosystems remain limited (Li et al. 2017). Furthermore, plant N cycling during the growing season has been extensively studied (Millard and Grelet 2010) but only limited data is available regarding plant P cycling (Rennenberg and Herschbach 2013; Li et al. 2017). Thus, information on P allocation of adult trees during the annual cycle in leaves, stem and root tissues, such as P storage, mobilization processes and the significance of soil P availability on plant allocation in relation to N allocation still remains scarce (Rennenberg and Herschbach 2013, Li et al. 2017). For instance, it is well known that N is predominantly stored in the woody tissues of deciduous trees with the amount being species specific (Millard and Grelet 2010) while tree P storage remains unknown. Increased sapwood P storage has been reported for *Pinus contorta* and *Pinus albicaulis* (Lahr and Sala 2014), while in *Pistacia vera* stored P was predominantly in canopy branches (Rosecrance et al. 1998). Furthermore, *Fagus sylvatica* L. seems to store P predominantly in root tissues (Zavišić and

Polle 2018) while Netzer et al. (2017) reported that P was stored in the bark and stem in the same species. In addition, high sapwood P content was observed in *F. sylvatica* L. during spring followed by a decrease throughout the year in P rich soils while low P sapwood values were reported in P poor soils (Yang et al. 2016). This is in contrast to Netzer et al. (2017) who reported no such changes of P content along a fertility gradient. Furthermore, no study has yet found a solid relationship between P resorption efficiency and soil nutrient status. Thus, even general patterns such as P allocation in plant tissues need to be further studied (Zavišić and Polle 2018) as well as the relationship between soil nutrient status and plant tissues P concentrations (Li et al. 2017).

Therefore, the present study aims to assess the plant P allocation patterns of four tree species during four phenological stages and the relationship between plant tissues N and P concentrations and soil nutrient status. The four studied tree species belong to different functional groups: evergreen conifer (*C. japonica*), deciduous conifer (*L. kaempferi*), deciduous broad-leaved (*Fagus crenata*), and deciduous leguminous (*R. pseudoacacia*).

Based on the relationship between N and P cycles found in soils and plants, we hypothesized that i) plant tissues P allocation during four phenological stages is positively correlated to their respective N allocation; and ii) leaf N and P reabsorption efficiency and proficiency decreases with increasing availability of soil N.

Materials and methods

Study area

The research area is located in the Research Forest of Yamagata University along the coast of the Japanese Sea in north-eastern Japan. The climate is humid, with an annual mean temperature of 9.7 °C and a precipitation of 2558 mm (1987–2016) with approximately half of it corresponding to snow, covering the sampling sites from December to the end of April at an elevation ranging between 300 to 700 m above sea level.

The sampling sites are distributed within a radius of 3 km and were selected by accessibility, stand age and stand purity. The sampling points of each species were distributed within 3 ha to better represent their respective forest ecosystem following a deductive approach (Oksanen 2001). Nine Japanese cedar trees (*C. japonica* D. Don.) were sampled in a 50-year old plantation composed of exclusively *C. japonica* (CJ) with an understory vegetation of broad-leaf bamboo (*Sasa veitchii* (Carrière) Rehder) growing at an elevation of 300 to 400 m above sea level with an average diameter at breast height (DBH) of 42 cm and an average height of 24 m. Further, eight 40–50-year old Japanese larch trees (*L. kaempferi* Lamb.) with a DBH of 38 cm and a height of 24 m in a mixed forest dominated (~80–90%) by *L. kaempferi* (LK) at an elevation of 600–650 m above sea level were chosen. Next, nine 70–80 years old Japanese beech trees (*Fagus crenata* Blume) with a mean DBH of 30 cm and a mean height of 31 m growing in a pure stand at an elevation of 700–740 m above sea level were selected. Finally, five 7-year old Black locust trees (*R. pseudoacacia* L.) with a DBH of 12 cm and a height of 12 m growing in a pure stand were sampled at an elevation of about 400 m. Prior to the *R. pseudoacacia* (RP) trees, a CJ plantation was present, which was harvested and subsequently slash-and-burned. After the fire, RP quickly invaded the plot representing the only area where it currently distributes, which is only about 1 ha in size.

Plant and soil sample collection and treatments

Coarse roots (> 2 mm), sapwood and foliage samples were collected in 2017 from May 16 to 18 (shoot growth stage), August 1 to 3 (green leaf stage), October 19 (pre-abscission stage), and on November 29 (post-abscission stage) with fresh litter collected from litter traps (size: 1 m^2, placed on May 15 for CJ and on September 4 for the other species). The timing of sampling was carefully chosen to ensure that each tree species was in the same phenological stage: the shoot growth stage sampling was conducted once all species had freshly emerged leaves. Each of the studied tree species reaches its physiological maximum in August where the green leaf stage sampling was conducted. The timing of the pre-abscission sampling was chosen according to the timing of leaf discolouration, which started with RP, followed a few days later by the other species with LK being the last species to discolour over the course of 10 days. Coarse roots of single trees were dug out and cut from the trunk down

to a depth of 30 cm. Three samples surrounding each tree were taken and pooled. Tree cores were collected using a 10 mm diameter increment borer for LK and CJ while a 5 mm borer was chosen for the hard woods *Fagus crenata* (FC) and RP. Sapwood and heartwood were separated by colour. Further, leaves without damage were sampled with a telescopic pole saw from different canopy positions and foliage clusters to include possible variations in N and P content (Rosecrance et al. 1998; Özbucak et al. 2008). Needles of evergreen CJ were separated and analysed by year, as described in Seidel et al. (2019a). All plant samples were transported in plastic bags and directly oven dried in the laboratory. All plant material was dried to a constant weight at 60 °C for at least 48 h, following Rosecrance et al. (1998). Subsequently, they were ground and stored in a dark and cool place until further analysis.

Soils were sampled by fixed depth, after the identification of the horizons in the field following the FAO guidelines (FAO 2006). The organic layer was removed and only mineral soil samples were taken from three depths (0–5 cm, 5–15 cm and 15–30 cm) from August 1 to 3, 2017. Within 30 cm distance around each tree, samples were taken from three pits. In the same pits, the bulk density was assessed using the core method (Al-Shammary et al. 2018).

All samples were taken from the field in a cooler box, air dried for at least 48 h and then sieved (< 2 mm). Subsequently, samples from the three pits around each individual tree were pooled according to their depth, ground and stored in a fridge until further analysis. However, samples used for the determination of inorganic N were frozen after transport from the field and stored in the dark. Before analysis, they were thawed overnight in a refrigerator, sieved (< 2 mm) and pooled.

Soil analysis

Soil texture was measured in triplicate with a laser diffraction particle size analyzer (Coulter LS200 with an attached Fluid Module, Beckman Coulter GmbH, Germany), after treating the samples with H_2O_2 and $Na_4P_2O_7$. The pH was determined potentiometrically in a 1:2.5 soil: water suspension. The carbon (C) and N contents were analyzed by dry combustion using SUMIGRAPH NC-220F automatic high sensitive NC analyzer SCAS (Japan). The results were expressed on a dry-weight (105 °C) basis.

Total soluble N (TN_b) was extracted from the soil samples by shaking them with 50 ml of 1 M KCl. The supernatant was centrifuged, filtered (0.45 µm), stored in a refrigerator and analysed with a TOC/TN analyzer (vario TOC cube, Elementar, Germany) for TN_b determination. Ammonium content was determined using the alicylate-dichloroisocyanurate reaction in the presence of nitroprusside of Crooke and Simpson (1971), whereas nitrate content was determined by the Griess reaction following the method of Mulvaney (1996) modified by Miranda et al. (2001). Dissolved organic nitrogen in the extracts (DON) expressed in g kg^{-1} was calculated as follows:

$$DON = TN_b - \left(NH_4^+ + NO_3^-\right)$$

Olsen extractable P was extracted following Olsen et al. (1954) and determined colorimetrically using malachite-green (Kuo 1996).

The stocks of soil organic C and nutrients were calculated in each soil layer from the weighted means of the data and the soil bulk density. The 0–30 cm depth element stocks were computed by summing up the stocks of all layers.

Plant material analysis

For the determination of total N content, a Thermo Quest EA1110 Elemental Analyzer (Italy) connected to an IsoPrime (GV Instruments, UK) was used. Total phosphorus (TP) was determined by digesting the samples with potassium peroxydisulfate (Wetzel and Likens 2000). All samples were weighed and ignited at 550 °C for 2 h. Potassium peroxydisulfate was added and samples positioned in an autoclave (LSX-300 High pressure steam sterilizer, TOMY, Japan) for 1 h at 121 °C and then centrifuged (3000 rpm, 5 min). The concentration of TP was determined colorimetrically with a microplate reader (Multiscan GO, Thermo Scientific, USA).

N and P reabsorption calculations

Reabsorption efficiency (*RE*) for N (NRE) and P (PRE) was calculated as:

$$Nutrient\ RE = \left(1 - \frac{Nu_{senesced}}{Nu_{green}}\right) \times 100$$

with $Nu_{senesced}$ representing the nutrient concentration in litter and Nu_{green} representing the nutrient concentration in foliage during the green leaf stage. N and P were expressed as mass per leaf dry mass (mg kg^{-1}).

Subsequently, N and P resorption proficiencies (NRP and PRP, respectively) were determined, since they represent more stable indicators of plant ability to recycle nutrients than NRE and PRE. Tree species that can reduce nutrient concentration to a lower level are more proficient for a specific nutrient from the biochemical point of view (Killingbeck 1996). The NRP and PRP are simply the nutrient concentration per leaf mass in senescing leaves (in % dry mass) (Killingbeck 1996) and were used to compare the four species.

The whole-tree foliage biomass was determined destructively in August 2018, by collecting, drying (40 °C, 72 h) and weighing all foliage from three individual trees of CJ, LK and RP that were of similar age and size as the ones sampled in August 2017 where needles of CJ, were additionally separated by needle age. For FC trees total leaf biomass was calculated with the following allometric equation (Tateishi et al. 2010) verified by litter trap measurements as these trees could not be safely felled in the steep slope.

$$\ln(ML) = p + q\ln(DBH)$$

where, (ML) is the foliage mass [g], p is a normalization coefficient and q is a scaling exponent ($p = 2.87$ and $q = 1.7$, respectively), and DBH is expressed in [cm].

For the deciduous species, total foliage mass represented the total litter weight while for evergreen CJ total litter weight was determined using and upscaling values gained from litter traps as described in Seidel et al. (2019a).

Statistical analysis

The differences in nutrient concentrations among sites, plant species and phenological stages were assessed through the analysis of variance with repeated measures (ANOVA), using a Tukey-Kramer test for post-hoc multiple comparison. Relationships between plant and soil characteristics were evaluated using Person's correlation coefficient. In all cases, a P level of 0.05 was selected as threshold for statistical significance. SPSS v.26 (IBM Corp. 2019) was used for data treatment.

Results

Soil characteristics

All soils were identified as brown forest soils (Haplic Cambisols) with a silty-loamy texture under FC, and sandy-loamy textures in all other plots. The soil parent material consisted mainly of granodiorite. The pH in the top 30 cm of the soil was the highest in RP plots and the lowest in FC plots ($P < 0.01$) (Table 1). Total C content of the top 30 cm was significantly lower in LK and significantly higher in CJ plots than in RP and FC ($P < 0.05$). Total and total dissolved N were the lowest in LK plots ($P < 0.05$). In the top 30 cm of soil, FC plots had the highest ammonium content ($P < 0.05$) while nitrate content was highest in RP plots ($P < 0.05$). DON content was the highest in CJ plots ($P < 0.05$) followed by LK, RP and FC plots. The C:N ratio was higher in FC and lower in CJ and RP ($P < 0.05$) plots. C, N and Olsen extractable P decreased from top to bottom ($P < 0.05$, Table S1) while Olsen extractable P content was similar in all plots.

N and P allocation in coarse root, sapwood and foliage

All species followed the same pattern of N depletion from coarse roots during the green leaf stage with respect to all other stages (Fig. 1). RP showed remarkably higher N concentrations in coarse roots ($P < 0.01$) than the other species. No significant changes in coarse roots P content throughout the season were visible although the seasonal P trends mirrored those of N (Fig. 1). The coarse roots of RP showed the highest P content, although not significantly different from that of CJ. LK and FC had the lowest P contents in coarse roots ($P < 0.01$) being 50% lower than that of CJ.

Sapwood N content of all species followed the same pattern; from the shoot growth stage, it decreased until the pre-abscission stage, and then increased in the post-abscission stage ($P < 0.05$). RP

Table 1 Average soil characteristics and stocks of nutrients in the first 30 cm of mineral soil (± SD) under *Cryptomeria japonica*, *Larix kaempferi*, *Fagus crenata* and *Robinia pseudoacacia* with ± denoting SD. Letters indicate significant differences between species. DON represents extracted dissolved organic nitrogen

Species	Texture	pH	total C kg/m^2	total N kg/m^2	C: N	Olsen extractable P g/m^2	total dissolved N g/m^2	NH_4^+-N g/m^2	NO_3^--N g/m^2	DON g/m^2
C. japonica	sandy loam	4.3 ± 0.4^{b}	18.3 ± 4.1^{a}	1.3 ± 0.3^{a}	13.7 ± 0.5^{b}	5.8 ± 3.5^{a}	58.8 ± 6.9^{a}	9.4 ± 5.9^{b}	2.9 ± 3.3^{ab}	45.0 ± 14.8^{a}
L. kaempferi	sandy loam	4.3 ± 0.4^{b}	11.5 ± 1.2^{b}	$0.7 \pm < 0.1^{c}$	16.6 ± 1.0^{ab}	3.4 ± 1.9^{a}	31.9 ± 1.0^{b}	2.0 ± 0.2^{b}	0.3 ± 0.4^{b}	30.7 ± 2.2^{ab}
Fagus crenata	silt loam	3.7 ± 0.2^{c}	16.1 ± 2.2^{ab}	$0.9 \pm < 0.1^{bc}$	17.6 ± 2.5^{a}	5.7 ± 2.2^{a}	55.9 ± 13.5^{a}	35.0 ± 22.1^{a}	0.7 ± 1.1^{b}	9.9 ± 5.4^{c}
Robinia pseudoacacia	sandy loam	5.4 ± 0.3^{a}	14.7 ± 2.1^{ab}	1.1 ± 0.1^{ab}	13.5 ± 0.5^{b}	5.1 ± 0.3^{a}	35.8 ± 2.0^{b}	1.7 ± 0.3^{b}	6.7 ± 0.1^{a}	26.0 ± 0.5^{b}

was the N-richest species also when considering the sapwood ($P < 0.01$), followed by FC and CJ, and LK (Fig. 2).

The annual trend in sapwood P was more variable among species (Fig. 2). There was no significant change throughout the seasons for CJ; LK and FC sapwood P content decreased ($P < 0.01$) through the year, while the sapwood of RP showed an increase of 40% in P content from the green leaf stage to the post-abscission stage ($P < 0.01$). On average, RP had the highest P content in the sapwood, followed by CJ and FC having 30% and 60% lower P content, respectively ($P < 0.01$), while LK had the lowest ($P < 0.01$).

As for foliage, N and P content decreased from spring to autumn, except for CJ (Fig. 3). Living needles of CJ showed an increase in N content throughout the year while P remained constant and litter was low in N and P contents. Furthermore, CJ needles showed no significant differences in P content among age groups (Fig. 4) in contrast to N content, which decreased from the youngest to the oldest needle by 25% as reported by Seidel et al. (2019b) (Fig. S1). RP leaves showed the highest N and P content ($P < 0.05$) among all species.

Prior to foliage abscission, all species reabsorbed N and P from foliage (Figs. 3 and 4) with the highest NRE observed for FC ($P < 0.05$), followed by CJ and LK, while RP showed the lowest value (Table 2). Additionally, N content of living remaining needles of CJ increased significantly during the post abscission stage ($P < 0.05$) (Fig. 3). Similar to NRE, FC showed the highest PRE ($P < 0.05$), followed by LK, RP and CJ being the least efficient. When all species are taken together, NRE was found to be related to soil NH_4^+ content ($P < 0.001$, Fig. 5).

Trees that can reduce N or P concentration in senescing foliage to a lower level are more proficient in reabsorbing N or P (Killingbeck 1996; Richardson et al. 2005). Therefore, the non-leguminous tree species were the most N and P proficient, while RP was the least proficient ($P < 0.01$) with values at least thrice as high for NRP and twice as high for PRP (Table 2).

During the shoot growth stage, all species foliage N:P ratios were lower than 14 (Table 3). During the green leaf stage, needles of LK remained below 14, needles of CJ shifted to a ratio of 15, while leaves of RP and FC values were above 16. During the pre-abscission stage, all non-leguminous tree species

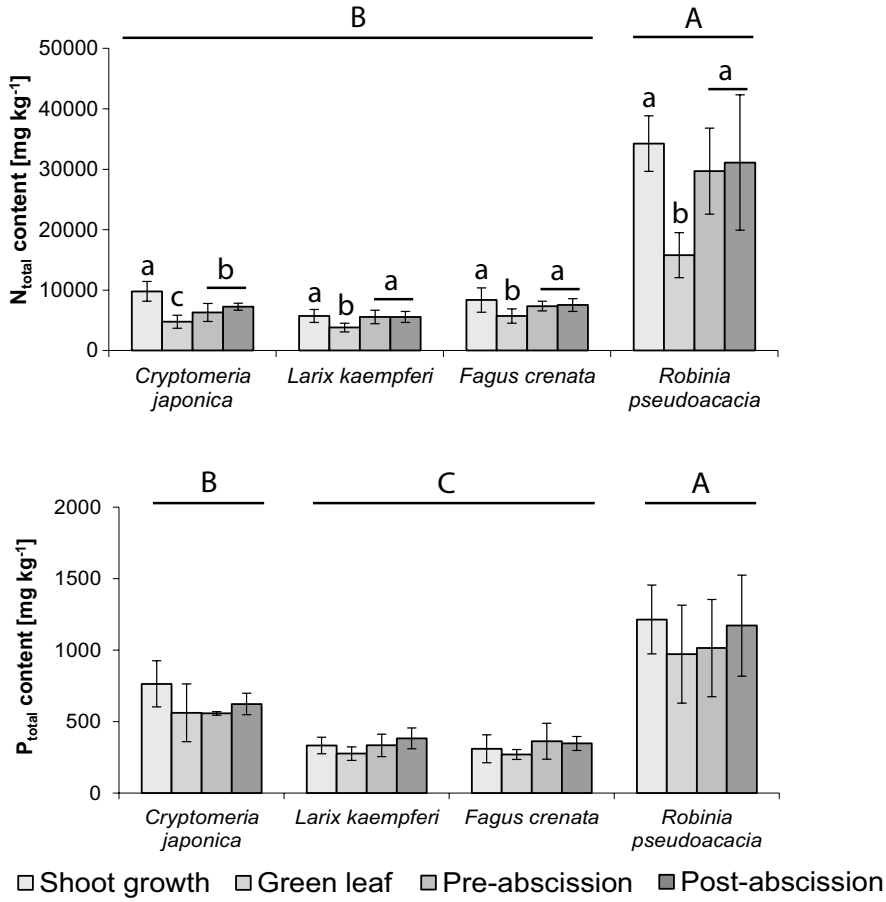

Fig. 1 Seasonal pattern of N (top) and P (bottom) content in coarse roots of *Cryptomeria japonica*, *Larix kaempferi*, *Fagus crenata* and *Robinia pseudoacacia*. The error bars denote SD (n = 9, 8, 9 and 5 per species respectively for N and n = 3 for P), capital letters indicate significant differences ($P < 0.05$) between species, lower case letters along the four phenological stages of the same species

foliage N:P ratios were close to 16 while RP remained above 16. During the post-abscission stage, remaining living needles of CJ did not change their ratio while litter N:P of all species followed their respective N and P resorption efficiencies.

Discussion

Plant internal N and P allocation

Comparing all plant tissues at any phenological stage, we could observe a common pattern: the highest N and P contents were found in foliage followed by coarse roots and sapwood (Figs. 1, 2 and 3). Only the evergreen CJ differed during the shoot growth stage where roots N and P contents were higher than foliage. The N cycle of all species followed a well-established pattern where the highest N content in plant tissues was found during the shoot growth stage when remobilization and transport of N from storage tissues and uptake from soil N (and atmospheric N in the case of RP) towards the canopy occurred (Millard and Grelet 2010; Marron et al. 2018). Subsequently, woody tissues (Figs. 1 and 2) showed reduced N content during the green leaf stage as N was bound in the leaf photosynthetic apparatus (Grassi et al. 2002; Millard et al. 2006; Ueda et al. 2011). All species displayed an increase in coarse root N content from the green leaf to the pre-abscission stage while sapwood N content increased during the post-abscission stage. This suggests that N was first stored in roots (Fig. 1) followed by sapwood (Fig. 2), and remaining living needles in the case of evergreen CJ (Fig. 3), which may be a general pattern of trees growing in the cold temperate zone (Seidel et al. 2019a, b). In agreement with Aerts and Chapin (2000), our data (Figs. 1, 2 and 3) suggested that roots N uptake controlled tree N status for all species which was further supported by the significant correlation of roots N content with

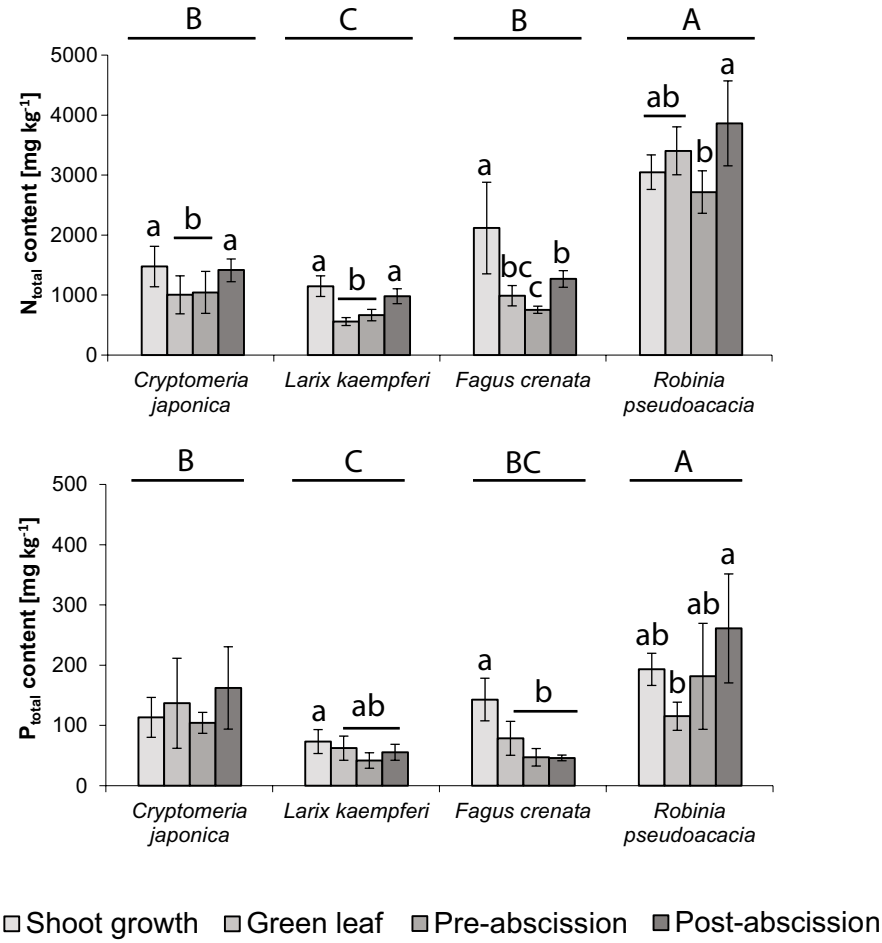

Fig. 2 Seasonal pattern of N (top) and P (bottom) content in sapwood of *Cryptomeria japonica*, *Larix kaempferi*, *Fagus crenata* and *Robinia pseudoacacia*. The error bars denote SD (n = 9, 8, 9 and 5 per species respectively for N and n = 3 for P), capital letters indicate significant differences ($P < 0.05$) between species, lower case letters along the four phenological stages of the same species

the sapwood N content (r = 0.71, $P < 0.01$) and with foliage N content (r = 0.41, $P < 0.05$) during all phenological stages.

Li et al. (2017) found that needle N content strongly controlled needle P content in *Larix principis-rupprechtii* (Mayr.) plantations of different ages. This was in agreement with our findings (Fig. 3) in addition to a good correlation between N and P content in LK (r = 0.71, $P = <0.001$). Similar correlation coefficients were also found for the other species (i.e. from 0.53 to 0.79, P always <0.01). In detail, foliage N and foliage P content of all species positively correlated during the shoot growth (r = 0.84, $P < 0.01$) and the pre-abscission stage (r = 0.86, $P < 0.001$), and during the green leaf stage for CJ and LK (r = 0.55, $P < 0.01$). The lack of significant correlation ($P > 0.05$) during the green leaf stage for FC and RP was possibly caused by insufficient P supply from the soil as indicated by the leaf N:P ratio (Koerselman and Meuleman 1996) as opposed to N limited LK and N and P co-limited CJ trees (Table 3). The foliage N:P ratio is used to determine N or P limitation (Koerselman and Meuleman 1996), where ratios lower than 14 indicate growth under N limited conditions, while values over 16 indicate growth under P limited conditions. If the values are between 14 and 16, plants are co-limited in both N and P.

Generally, woody plant tissues P concentrations tended to follow their respective N content with intrinsically lower P values and their variability between individual trees (Netzer et al. 2017) (Figs. 1 and 2). The positive correlations we found for root N and root P content (r = 0.66, $P < 0.05$) during all phenological stages as well as for sapwood N and P content (r = 0.48, $P < 0.05$) seems to point to a link of N and P cycles in sapwood and roots as it has been observed for leaves (Li et al. 2017).

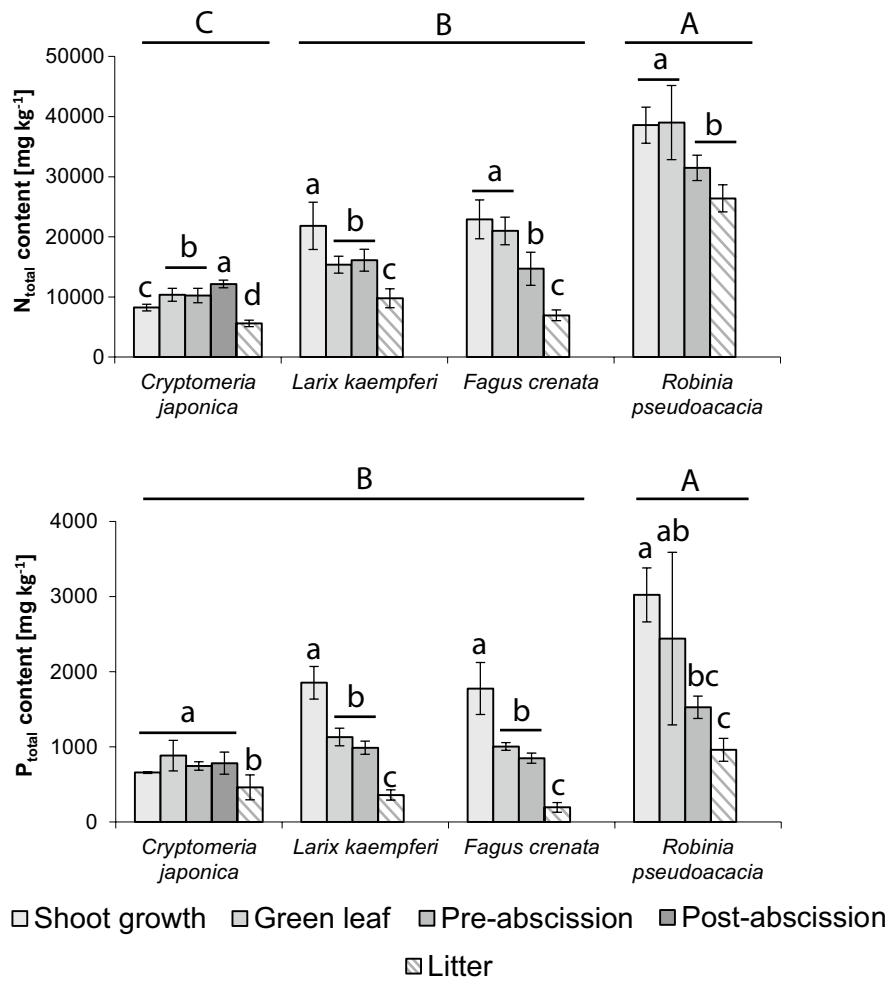

Fig. 3 Seasonal pattern of N (top) and P (bottom) content in leaves of *Cryptomeria japonica*, *Larix kaempferi*, *Fagus crenata* and *Robinia pseudoacacia*. The error bars denote SD (n = 9, 8, 9 and 5 per species respectively for N and n = 3 for P), capital letters indicate significant differences ($P < 0.05$) between species, lower case letters along the four phenological stages of the same species

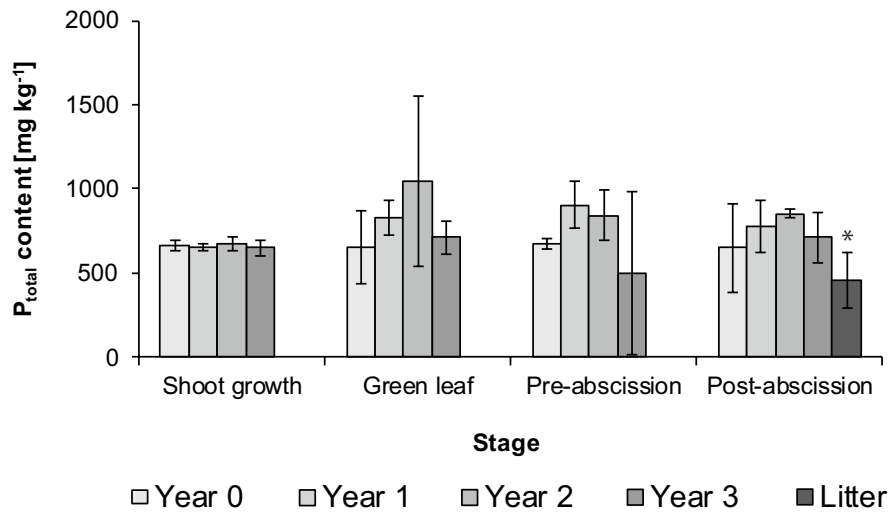

Fig. 4 Seasonal pattern of P content in leaves of *Cryptomeria japonica* separated by leaf age (n = 3 per leaf age class). Asterisks indicate significant differences ($P < 0.05$)

Table 2 N and P reabsorption efficiency [%] (NRE and PRE, respectively), N and P proficiency [% dry mass] (NRP and PRP, respectively), leaf/litter biomass [kg] of *Cryptomeria japonica*, *Larix kaempferi*, *Fagus crenata* and *Robinia pseudoacacia* with ± denoting SD. N related values are based on n = 9, 8, 9 and 5 trees per species respectively, P values are based on n = 3 trees per species. Letters indicate significant differences between species

Species	NRE		NRP	PRE	PRP	Leaf / Litter biomass	
	[%]		[% dry mass]	[%]	[% dry mass]	[kg]	
C. japonica	0-year old leaf	49 ± 9^{b}	0.6 ± 0.1^{c}	53 ± 10^{bc}	0.05 ± 0.01^{b}	living leaf	101.4 ± 20.7
	3-year old leaf	34 ± 3^{cd}				litter	6.9 ± 0.9^{b}
L. kaempferi	36 ± 13^{cd}		0.9 ± 0.1^{b}	68 ± 7^{abc}	0.04 ± 0.01^{b}	4.0 ± 0.8^{c}	
Fagus crenata	67 ± 4^{a}		0.7 ± 0.1^{bc}	80 ± 7^{a}	0.02 ± 0.01^{b}	8.7 ± 0.2^{a}	
R. pseudoacacia	32 ± 12^{d}		2.6 ± 0.2^{a}	55 ± 20^{b}	0.09 ± 0.02^{a}	4.8 ± 0.9^{c}	

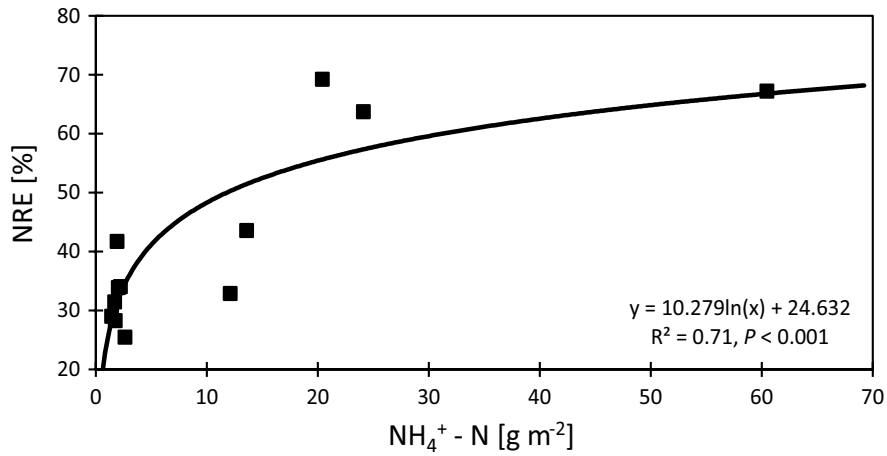

Fig. 5 Logarithmic relationship between soil ammonium (NH_4^+-N) and nitrogen reabsorption efficiency (NRE) in stands of *Cryptomeria japonica, Larix kaempferi, Fagus crenata* and *Robinia pseudoacacia* (n = 12) during the green leaf stage

Table 3 Leaf N: P ratio of *Cryptomeria japonica*, *Larix kaempferi*, *Fagus crenata* and *Robinia pseudoacacia* (n = 3 per species) with ± indicating SD. Capital letters indicate significant differences between species, lower case letters between phenological stages

Phenological stage	*Cryptomeria Japonica*	*L. kaempferi*	*Fagus crenata*	*Robinia pseudoacacia*
shoot growth	13.9 ± 0.2^{A}	9.7 ± 1.4^{Bc}	13.4 ± 0.9^{ABb}	12.9 ± 2.7^{ABb}
green leaf	15.0 ± 2.8^{AB}	12.8 ± 1.0^{Bc}	21.6 ± 3.2^{Ab}	19.3 ± 5.9^{ABab}
pre-abscission	16.2 ± 2.5	16.46 ± 2.4^{b}	16.0 ± 2.5^{b}	21.1 ± 3.6^{ab}
post-abscission	$\frac{\text{living leaf/litter}}{16.0 \pm 0.8B / 15.1 \pm 1.7B}$	26.3 ± 2.3^{ABa}	35.9 ± 9.8^{Aa}	28.1 ± 2.9^{ABa}

Additionally, we found positive correlations between plant tissues. Root N correlated positively with sapwood P content in the shoot growth ($r = 0.54$, $P < 0.05$) and post-abscission stage ($r = 0.51$, $P < 0.05$), while root P content positively correlated with N and P content of the sapwood ($r = 0.61$, $P < 0.05$ and $r = 0.47$, $P < 0.05$, respectively) except during the pre-abscission stage. This suggests that during the post-abscission stage N storage in roots may affect P content of sapwood and foliage during the following shoot growth stage, stressing the importance of N storage during the post-abscission stage for N and P allocation for the next year (Han et al. 2013). Besides, root N positively correlated with foliage P content during the shoot growth ($r = 0.53$, $P < 0.05$) and pre-abscission

stage ($r = 0.73$, $P < 0.05$). Sapwood N content was positively correlated with foliage N ($r = 0.49$, $P < 0.05$) and foliage P content ($r = 0.46$, $P < 0.05$) during all phenological stages. In the pre-abscission stage during N and P reabsorption and storage, plant N content, P content and foliage N:P ratio correlated strongly with root N content ($r = 0.88$, $P < 0.001$, $r = 0.82$, $P < 0.05$ and $r = 0.78$, $P < 0.05$, respectively). If plant tissue growth would significantly attenuate these correlations, there should be a clear seasonal pattern of correlation strength. However, we found no such pattern within and across plant tissues and time. Additionally, perennial roots and sapwood tissue do not grow as rapidly as leaves do and thus, growth seems to only play a minor role in these tissues compared with leaves. The results showed that N and P cycles were linked on whole-tree level in all phenological stages, which has, to our knowledge, not yet been shown for adult trees in a forest ecosystem.

Remarkably, although growth of LK was generally N limited as indicated by the leaf N:P ratio (Table 3), CJ was N and P co-limited and FC and RP were P limited, all species reabsorbed P from foliage more efficiently than N (Table 2) suggesting that P conservation had a higher priority than N. Furthermore, although we found a link between N and P changes in plant tissues, NRE and PRE as well as NRP and PRP were not correlated with plant N or P content suggesting that other factors had a stronger effect on N and P reabsorption efficiency and proficiency, such as plant specific traits or differences in soil nutrient status (Yan et al. 2018). Further, the fate of the resorbed P remains unclear, as P storage tissues seemed to differ from N storage tissues suggesting that, other significant P storage tissues are in play such as seeds, bark and twigs as found in Alaskan tree species, pistachio trees, pitch pine and Japanese larch (*Larix leptolepis)* (Chapin III and Kedrowski 1983, Rosecrance et al. 1998, Son et al. 2000).

Overall, our data suggested that N and P cycling was tightly coupled regardless of the tree species. This was in partial agreement with our first hypothesis showing that plant tissues N allocation was positively correlated with their respective P allocation and foliage P content followed foliage N content. However, we did not find storage of P in the same tissues where N was stored except for RP, where P storage was observed in sapwood.

Soil and plant N and P interaction

The availability of nutrients in forest soils is typically controlled by the amounts and turnover of organic matter (Jobbágy and Jackson 2001). Both factors seemed to play a role in CJ and LK, where the highest and the lowest amounts of TOC are coupled with the stocks of total dissolved N during the green leaf stage (Table 1). These trends were however not visible for the other two species. The species-specific behaviour of nutrients is further confirmed by the distribution of N forms during the green leaf stage. The RP plots were dominated by NO_3^-, while NH_4^+ was predominant in CJ, LK and FC, forming up to 90% of the inorganic forms in the FC plots (Table 1). The striking abundance of NH_4^+ in FC is likely to be related to the lower soil pH of these sites that inhibit nitrification (De Boer and Kowalchuk 2001). In a poorly buffered soil system like in these plots, the high quantity of litter, the large root biomass and high root activity may have an acidifying effect, which did not affect only the rhizosphere but was also visible in the bulk soil (Braun et al. 2001; Jacob et al. 2010). On the opposite side, a faster organic matter turnover and a more complete nitrification are expected in the RP plots. In all plots during the green leaf stage, the extractable dissolved organic N forms formed the greatest part of the total dissolved N pool, despite the differences in the amounts shown in Table 1, related to a high organic matter availability, which may cause a decoupling between N mineralization and plant demand. The relative low proportion of DON combined with the high amounts of NH_4^+ found in the FC plots highlighted that organic matter decomposition was relatively high and led to mineralization of organic N into NH_4^+, a process less affected by pH than nitrification (De Boer and Kowalchuk 2001). In fact, the inverse correlation ($r = -0.62$, $P < 0.05$) between NH_4^+ and DON showed that at least the first stage of N mineralization normally occurred in all stands during the green leaf stage.

The efficiency of plants to reabsorb nutrients depends on the available nutrient contents in the soils (Millard and Grelet 2010). NH_4^+ seemed to exert the strongest control and acted differently depending on whether the plot was NH_4^+ − rich or poor, as shown by the logarithmic relationship ($r = 0.71$, $P < 0.001$); at low ammonium contents, even small increases in the soil enhanced NRE, but when the concentration

in the top 30 cm of soil is above 25 g m^{-2}, as in the FC stands, the increase in NRE is less correlated due to the large abundance of the nutrient in soil and to the high degree of N mineralization (Fig. 5). Similarly, Wang et al. (2014) found that NRE increased with increasing soil NH_4^+ while it decreased with increasing soil NO_3^- content in leaves of leguminous *Medicago sativa*. The latter was also observed in RP ($P<0.05$) but was insignificant in CJ, LK and FC plots suggesting that this pattern may be typical for leguminous species. Additionally, we found that DON correlated negatively with NRE in CJ ($r=-0.95$, $P<0.001$) and RP ($r=-0.96$, $P<0.001$) plots suggesting that soil DON may be a direct source of N for these species compared to LK and FC.

Soil Olsen extractable P was always rather high (Table 1) likely due to the relevant contribution of P-bearing minerals, since these soils are at relatively low stages of pedogenesis (Wang et al. 2016). Olsen extractable P was instead unrelated to the amounts of organic matter ($P>0.05$), confirming the fact that P is mineralized independently of C through catalysis by phosphatases (McGill and Cole 1981). In addition, the high amount of Olsen extractable P did not drive reabsorption trends during the phenological stages, causing a lack of correlation between soil Olsen extractable P and reabsorption efficiency as well as with plant tissues P content conversely to the much closer link between soil total dissolved N and plant tissues N content. However, we found the lowest values in PRE and PRP in LK and FC (Table 2), in relation to the lowest Olsen extractable P and pH (Table 1), respectively, confirming that combined factors in soil nutritional status may drive the response of trees to recycle nutrients (Yan et al. 2018). Thus, foliage NRE/NRP and PRE/PRP did not decrease with increasing availability of soil N but NRE varied with the form of total dissolved Nin the soil while PRE/PRP was not directly affected by a single soil nutrient but by a combination of soil variables. Therefore, despite soil nutrient forms were determined only once in a year, the contents obtained at the green-leaf stage, seem to be adequate to relate efficiency and proficiency to soil conditions. This is likely because the seasonal trend of nutrient forms is similar within the same climatic region (Chen et al. 2013).

As trees in the RP plot were young compared to the other species, their impact on the soil-plant interactions may be lower than for the other, much older species. As RP was invading this area after the slash and burn of a CJ plantation, we saw that already after 7 years this species increased available forms of N, which is typical for this species (Lopez et al. 2014) while the higher pH of RP plots could be linked to natural soil variability.

Additionally, when considering the effect of litter biomass on soil processes (Kara et al. 2008), our data showed that LK produced the least amount of litter followed by RP and CJ while FC produced the most (Table 2). Based on the N and P content in the litter, the effect on soil N and P cycling is expected to be strongest in FC plots followed by RP, CJ and finally LK. As the RP trees in our experiment were not adult, their impact on N and P cycling may increase with time as leaf biomass will increase due to asymmetrical growth of young versus adult trees (Blujdea et al. 2012) and this will contribute to soil fertilization (Lopez et al. 2014).

Plant specific N and P allocation patterns

The four investigated tree species belong to four different functional groups and some species-specific behaviours were visible.

We observed generally the highest foliage P concentrations in the early growing season (Fig. 3), as plants require P-rich ribosomal RNA to initiate growth and energy in the form of ATP (Kim et al. 2006; Li et al. 2017) with CJ being the exception. This may be related to the time of sampling, since the evergreen CJ starts its initial growing phase earlier with a peak in needle P content that may have already occurred, unlike deciduous tree species that needed to start their leaf growth from a bare leafless crown. It is unlikely that soil P contents have affected this behaviour, being the P contents comparable with that of FC (Table 1). Furthermore, compared with deciduous trees, evergreen trees tend to have lower needle N and P concentrations, as their photosynthetic rates per mass are generally lower (Ishida et al. 2006).

Besides, CJ could not only reabsorb P from shedding needles, but also possibly store it in the large amount of remaining living needles, as it was the case for N (Fig. 3). However, we found a non-significant decrease in P content in remaining winter needles contrasting the results of Chapin III and Kedrowski (1983) who found that evergreen spruce (*Picea mariana*) stored P mainly in remaining living

needles. Further, P content did not differ among the four needle age classes (Fig. 4), unlike the significant decrease in N content observed with age, where the youngest needles contained 25% more N than the oldest ($P < 0.05$) (Fig. S1, taken from Seidel et al. 2019b). Thus, by separating needles by age, 0-year old needles N:P ratios were higher than in 2 and 3-year old needles ($P < 0.05$, data not shown) during all phenological stages. This indicated that the older needles were rather N limited, while the 0-year-old needles followed the pattern of the weighted mean N:P ratio. This suggested that younger needles may be more photosynthetically active (Güsewell 2004). Further, the slope of the relationship between N and P content in needles of CJ proposed that it had a higher photosynthetic P-use efficiency than the other species, as it is typical for fast growing tree species (Son et al. 2000; Gan et al. 2015). Additionally, CJ allocated more P to its woody tissues than the deciduous non-leguminous trees of this study (Figs. 1 and 2), as it was also found for evergreen *Quercus oleoides* (Waring et al. 2015). Together with its low litter production and evergreen trait, CJ incorporated more N (Seidel et al. 2019a) and P in its plant tissues than all other species (data not shown) while balancing between N and P limitation, thus displaying a rather nutrient conservative strategy.

In contrast, LK showed low N and P contents in woody plant tissues throughout all phenological stages among the species of this study (Figs. 1 and 2) while growing in the nutrient poorest soil (Table 1). Its needle N and P content was much higher than that of CJ (Fig. 3), in agreement with other studies for evergreen tree species (Prokushkin et al. 2018; Enta et al. 2019). Although CJ was rather N limited based on the N:P ratio, it still recycled P more efficiently than N (Tables 2 and 3). Our results presented LK as a rather low nutrient demanding tree that is able to grow well in low soil available nutrient conditions.

FC was highly efficient in recycling N and P from leaves in comparison to evergreen coniferous trees (Ishida et al. 2006; Kang et al. 2010) (Table 2). FC sapwood P content peaked during the shoot growth stage as it has been also reported for FC grown along a P fertility gradient (Yang et al. 2016), which is in agreement with our findings (Fig. 2) but in disagreement with Netzer et al. (2017) who reported no changes or a decrease of P in sapwood in sites differing strongly in P availability during the same phenological stage. Netzer et al. (2017) further suggested that FC sapwood acts as P storage, which was supported by Zavišić et al. (2018) with the addition of P storage in roots, which we both did not find. Our study showed that FC is N and P demanding (Figs. 1, 2 and 3) and simultaneously highly efficient in recycling N and P.

As expected, the leguminous tree species RP was independent on soil N availability, but its N_2 fixing capacity and consequent growth was strongly P limited (Table 3). P was stored in sapwood (Fig. 2), which may be related to tree age; other older tree species store P in branches (Rosecrance et al. 1998; Son et al. 2000; Marron et al. 2018), and since RP trees were young and had not a fully developed crown yet, sapwood could act as a temporary storage in addition to branches until the trees mature and P storage in sapwood may become redundant. RP followed an exploitative nutrient strategy, enabling it to acquire the highest amounts of N and P, supporting rapid growth.

Conclusions

To our knowledge, the present study is the first attempt to clarify the internal P allocation patterns of four typical tree species in Japan, as related to their N allocation patterns in root, sapwood and foliage along four phenological stages. Our results showed that plant tissues N allocation was positively correlated to their respective P allocation regardless of the tree species, revealing that especially roots N content correlated well with trees internal N and P allocation throughout all phenological stages. N was stored in roots and sapwood, while P was not, with sapwood P storage of RP as the exception. Further, foliage NRE and PRE as well as NRP and PRP were not affected by absolute availability of soil N, but instead by the form of the total dissolved N, with NRE increasing where NH_4^+ was more present. Further, tree species PRE and PRP were not affected only by soil N status but rather by a combination of soil nutrient variables. The results of this study showed the strong interaction of internal N and P cycling in four tree species along the whole annual cycle in relation to soil N and P status with a much closer link between soil and plant N interactions than their respective P interactions.

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Declarations

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