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C:N:P stoichiometry and nutrient resorption in mixed-species and monoculture forest plantations on the Loess Plateau, China

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Abstract

Effects of mixed-species on leaf and soil stoichiometry of nitrogen (N), carbon (C), and phosphorous (P) and foliar nutrient resorption efficiency are unclear. We analyzed the effects of stand structure, understory plant species diversity, and soil properties associated with mixed plantations of *Robinia pseudoacacia* + *Amygdalus davidiana* (RPAD) and *R. pseudoacacia* + *Armeniaca sibirica* (RPAS) and monocultures of *R. pseudoacacia* (RP); *A. davidiana* (AD), and *A. sibirica* (AS) on tree leaf and soil C:N:P stoichiometry, resorption efficiency of N (NRE) and P (PRE) on the Loess Plateau. The soil total C content in RPAD and soil total N content in RPAS were greater than for monocultures RP, AD, and AS. The highest soil C:N and C:P ratios were recorded from RPAD and the lowest were recorded from RPAS; leaf P content was greater in RPAD than RP and AD, while leaf C:N and C:P ratios were lower. NRE and PRE was lower in the mixed plantations than in RP, and PRE was lower in RPAS than in RPAD. Stoichiometry of leaf and soil C:N:P in the mixed and monoculture plantations was affected by stand and canopy densities, average tree height (AH), soil available P, and electrical conductivity. NuRE was positively correlated with leaf N content and N:P ratios, and AH, and negatively correlated with leaf C:N ratios and soil total P content. The planting of RPAD mixed plantation to increase productivity and to improve biogeochemical cycling and contribute to the restoration of ecosystem function.

1 Introduction

Globally, the area of planted forests increased by 110.4 million ha between 1990 and 2015 (Payn et al., 2015), with impacts on water and mineral nutrient cycling between above- and below-ground ecosystems (Jiang et al., 2019; Zhong et al., 2020). Afforestation is a common practice to curb soil degradation and restore degraded ecosystems (Deng et al., 2017); however, plantations tend to comprise monocultures that reduce levels of biodiversity, soil fertility, and ecosystem stability (Lamb et al., 2005; Felton et al., 2010). Previous studies have showed greater forest productivity, ecosystem stability, and resilience to biotic stressors in mixed-species plantations than monoculture forests (Pretzsch and Schutze, 2016), indicating the potential value of mixed-species plantations to mitigate effects of global environmental change, such as increased drought conditions (Metz et al., 2016).

Forest stands of mixed tree species have been shown to capture limited resources, due to stratification of the canopy (Matzek and Vitousek, 2009; Dawud et al., 2016) and roots (Forrester et al., 2006), and functional complementarity (Coll et al., 2018). For example, in stands of mixed tree species, nitrogen (N) fixing species mainly utilize atmospheric N (N_2), resulting in less competition among non-N_2-fixers for soil N (Forrester et al., 2006), and the resulting greater availability of soil N accelerates nutrient cycling through increases in rates of litter decomposition (Voigtlaender et al., 2012), root exudates, and mycorrhizal network transport (Nygren and Leblanc, 2015), while increases in soil available N have been negatively associated with soil available P (Koutika et al., 2014), and the proportion of N_2-fixing *Albizia* planted with the non-N_2 fixing *Eucalyptus* is positively associated with soil content (upper 50 cm) of total N and C (Kaye et al., 2000). Thus, an improved understanding of nutrient balance dynamics in N_2-fixing species in monocrops and mixed species communities will lead to greater clarity of plant-soil nutrient cycling in forest plantation ecosystems.

Ecological stoichiometry is the study of the balance and interaction of chemical elements in ecological processes (Sterner and Elser, 2002), where carbon (C), nitrogen (N), and phosphorus (P) stoichiometric relationships between plants and soils indicate ecosystem function and biogeochemical processes (Peñuelas et al., 2019a; Peñuelas et al., 2019b). Thus, plant C:N:P ratios reflect plant-ecosystem nutrient balance relationships (Sardans et al., 2012; Peñuelas and Sardans, 2022), while soil C:N:P ratios reflect soil fertility-plant nutrient relationships (Bui and Henderson, 2013), where plant-soil C:N:P ratios are driven by plant physiology. Therefore, analysis of C:N:P stoichiometry allows for greater understanding of the relationships between above- and below-ground components of terrestrial ecosystems (Elser et al., 2010), due to the close links and feedbacks between plant and soil nutrients (Zhang et al., 2019).

The process of nutrient resorption in plants, when nutrients are transferred from senesced organs to living tissue (Freschet et al., 2010), is an important strategy for the optimization of use efficiency and conservation of nutrients (Aerts et al., 1996). Thus, nutrient resorption may directly affect the nutrient content of biomass and rates of litter decomposition, with impacts on plant productivity and nutrient cycling (Deng et al., 2019). However, understanding of effects of nutrient resorption efficiency (NuRE) on soil nutrient content is unclear, given the limited number of studies of effects of biotic and abiotic factors on variation in NuRE (Pang et al., 2021) and effects on drivers of nutrient cycling, along with contrasting reports of negative (Brant and Chen, 2015), positive (Yan et al., 2018), and lack of (Blanco et al., 2009) relationships, likely due to variations in environmental and biological factors (Drenovsky et al., 2019), such as microclimate, species composition, and soil properties (Zhang et al., 2019).

Historic anthropogenic damage to the natural vegetation communities of the loess Plateau of China (LPC) caused extensive drought and soil erosion across the region (6.4×10^5 km^2) and led to the introduction of the “Grain for Green” project in 1999 that increased forest plantation cover by 28% (Chen et al., 2015). However, the majority of these planted forests comprise monocultures that negatively impact the ecological environment of the LPC (Sang et al., 2013), such as through soil nutrient depletion (Chen et al., 2005). *Robinia pseudoacacia*, a non-native, fast-growing N-fixing tree species (Cierjacks et al., 2013; Tsunekawa et al., 2014), has been planted across > 7.0×10^4 ha on the LPC (Qiu et al., 2010); while its P-limited growth (Cao and Chen, 2017) intensifies with time (Zhang et al., 2019), its impacts on root networks and the mycorrhizal

system, when planted with non-N-fixing tree species, lead to greater nutrient absorption across soil depths (Zhang et al., 2016) and increases in litter decomposition and nutrient release (González et al., 2020). Thus, cultivation of *R. pseudoacacia* with native species, such as *Amygdalus davidiana* and *Armeniaca sibirica* that are widely planted on the LPC and provide ecological and economic benefits (Zhao, 2021; Xu et al., 2020), may improve the ecological function and stability of forest plantation ecosystems in this region. However, previous forest C:N:P stoichiometry and NuRE research has been restricted to monoculture plantations (*R. pseudoacacia* and *A. sibirica*) (Xu et al., 2020), limiting understanding of dynamics in mixed species plantations and the ability to improve sustainable forest management on the LPC.

Here, we address these knowledge gaps and provide new insights into nutrient cycling and ecosystem function of *R. pseudoacacia* plantations to improve LPC plantation management. Specifically, we analyzed C, N, and P content and stoichiometry of green and senesced leaf material and soil samples collected from *R. pseudoacacia* mixed and monoculture plantations to test the hypotheses that (1) content of C, N, and P in leaves and soils are greater in stands of mixed tree species than monocultures, with associated impacts on stoichiometry, and (2) NuRE varies between mixed and monoculture stands, due to differences in structure, understory plant species composition, and soil properties.

2 Materials And Methods

2.1 Study site

The plantation study sites were located on the central LPC, at Heping, Shaanxi Province (36°35'49"–109°35'56"N, 109°13'18"–109°13'32"E, 1195–1212 m a.s.l), where the average annual temperature is 8.8 ℃ and average annual rainfall is 510 mm; precipitation during the rainy season (June–September) accounts for 72.9% of the annual total. The soils are classified as Calcic Cambisols according to the FAO classification system (FAO, 1974). Areas afforested since 1999 are dominated by the tree species *R. pseudoacacia, Pinus tabuliformis*, *Platycladus orientalis*, *A. davidiana*, and *A. sibirica*, the shrub species *Hippophae rhamnoides* and *Caragana korshinskii*, and herbs including *Medicago sativa*, *Herba artimisiae*, *Stipa bungeana*, and *Bothriochloa ischaemum*.

2.2 Experimental design

In April 2021, we selected mixed plantations of *R. pseudoacacia* with *A. davidiana* (RPAD) and *R. pseudoacacia* with *A. sibirica* (RPAS), along with monoculture plantations of *R. pseudoacacia* (RP), *A. davidiana* (AD), and *A. sibirica* (AS) that were distributed across a similar soil type (loess), topographical orientation (southwest), and stand age (16–25 years) for measurement of stand and canopy densities (SD and CD, respectively), tree diameter at breast height (DBH), and average height (AH) (Table 1). Within each plantation type, we established three 20 × 20-m plots that were surrounded by a 5-m buffer to avoid edge effects; the distance between plots was < 3 km. (Fig. 1).

Table 1
Analysis of variation in mean stand structure, understory plant species, and soil properties among plantation types. Data are means ± SD.

Plantation	Dominant tree species composition (%)	Stand structure				Understory plant species		Soil properties					
		SD (trees ha^{-1})	DBH (cm)	AH (m)	CD (%)	*H*	*EH*	BD (g·cm^{-3})	SWC (%)	SAN (mg·kg^{-1})	SAP (mg·kg^{-1})	pH	EC (μg·g^{-1})
RPAD	R. *pseudoacacia* (75), *A. davidiana* (25)	1633 ± 31 a	8.80 ± 0.48 ab	7.67 ± 0.35 b	0.82 ± 0.05 a	1.51 ± 0.01 b	0.75 ± 0.05 a	1.26 ± 0.07 ab	9.80 ± 0.50 a	13.67 ± 0.63 a	1.67 ± 0.14 a	8.64 ± 0.22 b	97.52 ± 1.97 a
RPAS	*R. pseudoacacia* (75), *A. sibirica* (25)	1225 ± 89 b	9.28 ± 0.89 ab	7.48 ± 0.87 b	0.69 ± 0.05 b	1.76 ± 0.07 a	0.70 ± 0.03 a	1.25 ± 0.13 a	9.29 ± 0.15 a	13.63 ± 0.35 a	1.50 ± 0.13 ab	8.66 ± 0.05 b	91.13 ± 1.63 b
RP	*R. pseudoacacia* (100)	1125 ± 89 b	11.33 ± 1.80 a	9.41 ± 0.74 a	0.49 ± 0.02 c	1.19 ± 0.00 d	0.66 ± 0.07 a	1.23 ± 0.09 ab	8.43 ± 0.31 a	12.72 ± 0.24 a	1.74 ± 0.18 a	8.80 ± 0.01 a	93.91 ± 1.06 ab
AD	*A. davidiana* (100)	733 ± 47 c	5.65 ± 0.91 b	3.58 ± 0.17 c	0.36 ± 0.02 d	1.31 ± 0.00 c	0.63 ± 0.06 a	1.21 ± 0.05 b	9.59 ± 0.20 a	11.33 ± 0.41 a	1.18 ± 0.12 b	8.85 ± 0.09 a	83.52 ± 1.03 ab
AS	*A. sibirica* (100)	733 ± 94 c	10.09 ± 1.08a	3.46 ± 0.06 c	0.32 ± 0.03 d	1.06 ± 0.06 e	0.73 ± 0.01 a	1.28 ± 0.14 a	8.63 ± 0.37 a	11.06 ± 0.54 a	1.31 ± 0.10 ab	8.87 ± 0.04 a	88.22 ± 1.51 ab
F	/	50.96	7.20	48.73	75.40	84.53	2.14	3.09	0.92	0.45	3.60	9.21	2.40
p	/	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	0.15	0.02	0.46	0.77	< 0.01	< 0.01	0.06

RPAD: *R. pseudoacacia* and *A. davidiana*; RPAS: *R. pseudoacacia* and *A. sibirica*; RP: *R. pseudoacacia*; AD: *A. davidiana*; AS: *A. sibirica*; SD: stand density; DBH: diameter at breast height; AH: average tree height; CD: canopy density; *H*: understory plant species diversity (Shannon-Wiener); *EH*: understory plant species evenness (Shannon-Wiener); BD: bulk density; SWC: soil water content; SAN: soil available nitrogen; SAP: soil available phosphorus; and, EC: electrical conductivity. Different lowercase letters indicate plantation type differences at $p < 0.05$.

2.3 Understory plant diversity and soil properties

We measured soil bulk density (BD), water content (SWC), available N (SAN), available P (SAP), pH, and electrical conductivity (EC) and, using the equations for the Shannon-Wiener indexes reported by Stirling and Wilsey (2001), we calculated the diversity (*H*) and evenness (*EH*) of understory plant species for each plot (Table 1):

$$H = -\sum_{i=1}^{s}(Pi \ln Pi) \quad (1)$$

$$EH = -\sum_{i=1}^{s}\frac{(Pi \ln Pi)}{\ln s} \quad (2)$$

where *s* is the total number of species and *Pi* is the proportion of the community comprising species *i*, calculated as *i/s*.

2.4 Leaf sample collection and analysis

Maximum biomass of the growing season (early April to late October) is reached between late July and mid-August, while leaf fall is largely complete by mid-December. Therefore, we randomly selected five trees per plot, with similar DBH and height, from which we sampled healthy and intact green leaves from the mid-canopy in early August 2021, using high branch shears, and falling senesced leaves in mid-December 2021 collected in nylon nets (1 × 1 m, 0.1-mm gauge) that were suspended beneath the trees. The composition of leaf samples from the mixed

plantations represented the proportion of tree species (Table 1) and the samples were oven-dried at 105°C for 15 min, followed by 70°C to a constant mass.

In mid-August 2021, we collected samples of soil from five loci per plot, arranged in an “S” shape, at five depths (0–10, 10–20, 20–30, 30–50, and 50–100 cm) using a 4-cm auger; samples were combined to form a single composite sample per depth. Roots, stones, and debris were manually removed from the samples, before the soils were passed through a 2-mm mesh screen. Then, the samples were divided into two parts, where one was air-dried, ground, and passed through a 0.15-mm sieve prior to chemical analysis, and the other was dried in the shade and passed through a 1-mm pore sieve prior to analysis of soil pH and EC. Single samples of soil across an entire 1-m depth profile were collected from each plot using a ring knife (100 cm^3) for analysis of soil BD and SWC.

Leaf C content (TC) was measured using titration, following digestion in a K_2CrO_7-H_2SO_4 solution, heated using an oil bath, while leaf N content (TN) was determined using the Kjeldahl method (Kjeltec 2300 Analyser Unit, Foss Tecator, Hoganas, Sweden), following digestion in H_2SO_4-H_2H_2 solution; leaf P content (TP) was determined using the molybdenum yellow method (U-2800 spectrophotometer, Shanghai, China).

We determined soil organic C (SOC) concentrations using the potassium dichromate-external heating method (Nelson and Sommers, 1982) and soil total N (TN) concentrations using the Kjeldahl method (Bremner and Mulvaney, 1982), while SAN was assayed using the alkaline-hydrolysis diffusion method (Bao. 2000); soil total P (TP) and SAP were determined using the molybdenum blue method (Murphy and Riley, 1962). Soil BD and SWC were measured using the cutting ring method (Bao, 2000), soil pH was measured using an automatic acid-base titrator (water-soil ratio 2.5:1), and EC was determined using a conductivity meter (DDSJ-308F, INESA Scientific InstrumentCo., Ltd, Shanghai, China).

2.5 Data analysis

We calculated NuRE (%), following Vergutz et al. (2012):

$$NuRE = \left(1 - \frac{N_s}{N_g} \times MLCF\right) \times 100\% \qquad (3)$$

where *Ns* and *Ng* are nutrient concentrations (g kg^{-1}) in senesced and green leaves, respectively, and *MLCF* is the correction factor for mass loss in angiosperms (= 0.784).

Ratios of C:N, C:P, and N:P for green and senesced leaves and soil samples were calculated from TC (SOC), TN, and TP concentrations. Data were checked for normality and homogeneity of variance, and log-transformed where appropriate. We used one-way analysis of variance (ANOVA), followed by Tukey's multiple comparison test, to test for plantation type differences in NuRE and leaf C:N:P stoichiometry, while associations between NuRE, leaf and soil nutrient content and stoichiometry, soil properties, stand structure, and understory plant diversity were tested using Pearson’s correlation coefficient; tests were conducted using SPSS 23.0 (SPSS Inc., Chicago, USA). Relationships between C:N:P stoichiometry and plant-soil variables were tested using redundancy analysis (RDA) in Canoco 5.0 (ter Braak and Smilauer, 2012).

3 Results

3.1 Stand structure, understory plant diversity, and soil properties

The mixed plantations RPAD and RPAS were characterized by greater SD, CD, AH, and *H*, and lower soil pH than monoculture plantations, while in RPAD, *H* was lower and SD and CD were greater than in RPAS (Table 1).

3.2 Soil C:N:P stoichiometry

Highest levels of soil C, N, and P content were recorded in the upper soil profile (0–10 cm), and decreased with soil depth (Fig. 2). There were main effects of plantation type on soil C, N, and P content and stoichiometry (Fig. 3), where RPAD was characterized by highest levels of soil C content and highest C:N and C:P ratios; RPAS and RP were characterized by lowest C:N ratios and RP was characterized by lowest levels of soil C and P and highest ratios of N:P (Fig. 3). The monoculture plantations AD and AS were characterized by highest levels of soil P content, moderate C:N ratios, and lowest N:P ratios (Fig. 3).

3.3 Leaf C:N:P stoichiometry and NuRE

Levels of green and senesced leaf C, N, and P content and stoichiometry varied with plantation type (Fig. 4). Green leaf C content was greatest in AD and lowest in RPAD and RPAS, while green leaf N content differed among all plantation types, where it was greatest in RP and lowest in AS; green leaf P content was greatest in RPAD and RP, and lowest in AS, whereas C:N and C:P ratios were lowest in RPAD and RP. Green leaf ratios of C:N and C:P were higher in the AD and AS monocultures than the RP monoculture and the two mixed plantations, while N:P ratios were the highest in RP and lowest in AS.

Senesced leaf content of N and P, and N:P ratios were greater in RPAD than in RP and AD, while C:N and C:P ratios were lower; senesced leaf C:N ratios were higher in RPAS than in RPAD, while N and P content and N:P ratios were lower. Senesced leaf N and P content and N:P ratios were greatest in RP, and C content and C:N and C:P ratios were lowest; senesced leaf N and P content and N:P ratios were lowest in AS.

There were variations in NuRE for N (NRE) and P (PRE) among the plantation types, where they were greatest in RP; lowest levels of NuRE were recorded in AS (NRE) and RPAS, AD, and AS (PRE) (Fig. 5a–c). Ratios of NRE:PREs were highest in AD and lowest in AS (Fig. 5c). There were positive associations between NRE and PRE in the mixed and monoculture plantations, where increases in NRE led to greater increases in PRE in the mixed plantations (Fig. 5d).

3.4 Relationships between soil with leaf C:N:P stoichiometry and NuRE

For NRE, there were positive associations with green leaf N and P content, green leaf N:P ratios, senesced leaf N and P content, senesced leaf N:P ratios, and soil N:P ratios, and negative associations with green and senesced leaf C:N and C:P ratios, and soil P content (Fig. 6). For PRE, there were positive associations with green leaf N and P content and N:P ratios, senesced leaf N content and N:P ratios, and soil C:P and N:P ratios, and negative associations with green leaf C:N and C:P ratios, senesced leaf C content and C:N ratios, and soil P content (Fig. 6).

3.5 Drivers of variation in soil C:N:P stoichiometry among plantation types

Plantation stand characteristics and soil properties explained 86.24% of the variation in soil elemental composition and stoichiometry (Fig. 7). Soil C:N:P stoichiometry was affected by EC ($F = 28.8$), AH ($F = 28.0$), SD ($F = 15.7$), and SAN ($F = 12.8$). EC was positively related to soil C:P and C:N ratios, and negatively related to soil P content; AH was positively associated with soil C:P and N:P ratios, and negatively related to soil P content, while SD was positively related to soil C content and C:N and C:P ratios. Soil available N was positively related to soil C:P and N:P ratios, and negatively related to soil P content.

3.6 Leaf C:N:P stoichiometry and NuRE associations with plantation characteristics

Green and senesced leaf C:N:P stoichiometry and NuRE were correlated with stand structure and understory plant communities (Fig. 8). Stand and canopy densities were positively associated with leaf N and P concentrations and N:P ratios, and negatively associated with leaf C content and C:N and C:P ratios; DBH was negatively correlated to senesced leaf C content and AH was positively associated with NRE and PRE, green leaf N and P content and N:P ratios, and senesced leaf N content and N:P ratios, and negatively correlated to leaf C:N and C:P ratios. Understory plant species diversity was positively associated with senesced leaf P content and negatively associated with green leaf C:N ratios and senesced leaf C:P ratios.

Leaf C:N:P stoichiometry and NuRE were correlated with soil properties (Fig. 8). Soil BD was positively associated with green leaf C:N ratios and negatively associated with NRE. Soil available N was positively associated with green leaf N and P content and N:P ratios, and senesced leaf N content and N:P ratios, and negatively correlated to leaf C content and C:N and C:P ratios, while SAP was positively correlated to PRE and senesced leaf N:P ratios, and negatively associated with senesced leaf C content. There were positive associations between EC and PRE, green leaf N and P content and N:P ratios, and senesced leaf N content and N:P ratios, and negative associations with leaf C content and C:N and C:P ratios.

4 Discussion

4.1 Soil C:N:P stoichiometry in mixed and monoculture plantations

In partial support of hypothesis 1, we found soil C content of the mixed stand, RPAD, was greater than the monoculture stands of RP and AD along the vertical soil profile (Fig. 2a, b; Fig. 3a, b), indicating a lower storage of C in monocultures of species than when they are planted in mixes. Although tree species diversity is positively associated with soil C stocks, species of tree is a stronger driver of the soil properties we studied here (Dawud et al., 2016). Our finding that soil TN content was greater in RPAS than in monocultures (Fig. 2a, b; Fig. 3a, b) supports findings of increased soil N retention in mixed species plantings that may lead to reductions in N losses (Lang et al., 2014), possibly due to the presence of the N_2-fixing tree species that increased soil N content and reduced species competition for SAN (Forrester et al., 2006).

In soils, P is largely derived from weathered parent geology, litter decomposition, and root exudates; given plant growth continuously utilizes SAP, and the soil parent material and growth environment were similar across the study sites, the lower recorded soil P content of RP than AD and AS is likely to reflect the balance between lower levels of plant litter and litter decomposition rates and greater root absorptive capacity of *R. pseudoacacia* (Yuan and Chen, 2015; Cao and Chen, 2017; Wei et al., 2018). Similarly, it is likely that the greater soil content of P in RPAD than RP was related to high decomposition rates of senesced leaves and low absorption capacity of the root system (Fig. 4c).

Ratios of soil C:N indicate soil quality and affect the cycling of organic C and N, where lower ratios, as a result of low levels of soil organic matter enrichment from leaf litter, as found at our study sites (Liu, 1985; Wei et al., 2018), reflect low N use efficiency in plant-soil systems (Cleveland et

al., 2007). We found C:N ratios were lower in RP than RPAD (Fig. 3), indicating lower N use efficiency, likely related to lower litter inputs in the monoculture than the mixed stand. Soil C:N ratios are inversely proportional to organic matter decomposition rates (Vitousek et al., 2010), where mineralization rates are more rapid in soils with low C:N ratios (< 25) (Bui and Henderson, 2013). We found that average soil C:N ratios (5.6) (Fig. 3d) were less than the national (25) and global (20.6 in temperate regions) averages (Tian et al., 2010), indicating a greater N mineralization capacity in the study area. Compared with the monoculture plantations, largest soil C:N ratios were recorded from RPAD and lowest ratios were recorded from RPAS (Fig. 3d), supporting our finding of greater soil N mineralization in RPAS than in RPAD (Fig. 3b). There were no differences in soil C:N ratios between RPAS and RP (Fig. 3d), possibly because the mixed planting of *A. davidiana* and *R. pseudoacacia* promoted acidic root exudates, resulting in relatively stable soil N mineralization (Forrester et al., 2006; Pang et al., 2021).

Soil C:P ratios are related to P mineralization capacity, where lower C:P ratios indicate higher levels of available P (Bui and Henderson, 2013). Across the plantation types, average soil C:P ratio (7.2, Fig. 3e) was lower than the national (60) and global (52.6) means (Tian et al., 2010), indicating greater soil P availability in the study area. We found the greatest and lowest soil C:P ratios were recorded from RPAD and AS, respectively (Fig. 3e), indicating that SAP is greater when *R. pseudoacacia* is planted with *A. sibirica* and lower when *R. pseudoacacia* is planted with *A. davidiana*. Soil C:P ratios were higher for RPAD than RPAS (Fig. 3e), likely due to the higher levels of EC and extreme pH that increase immobilization of P (Table 1), leading to greater proportions of total soil P content and lower SAP (Sardans et al., 2012).

Our RDA showed that soil C:N:P stoichiometry in mixed and monoculture plantations is associated with variations in stand structure and soil properties, particularly AH, SD, EC and SAN (Fig. 7). Average tree height was positively related to soil C:P ratios and negatively related to soil total P content, indicating that demand for soil P is greater in stands with taller than average trees (Blank and Morgan, 2014). Stand density was positively related to soil C:N and C:P ratios, reflecting the negative associations between SD with SAN and SAP (Sterner and Elser, 2002), due to greater demand for SAN and SAP in dense tree stands to support physiological and biochemical reactions that subsequently lead to decreases in soil TN and TP content (Dawud et al., 2016). There was a positive association between EC and soil C:P ratio and a negative association between EC and soil TP content, indicating a negative association between EC and mineralization of soil TP (Zhang 2008). Moreover, precipitation of P in soils as a salt, leading to increases in EC, due to an increase in cations in solution, may be indicated by the positive correlation between soil total P content and soil pH (Fig. 7). Our finding that SAN was positively related to soil TN and negatively related to soil TP indicates that soil TN promoted activity of N_2-fixing microbes that require SAN (Zhao et al., 2013), such as in mycorrhiza for RNA production, and the intensification of N competition between N_2-fixing trees and neighboring species (Nygren and Leblanc 2015). However, we found a lack of correlation between soil C:N:P stoichiometry and ecological factors, especially for understory characteristics (Fig. 8), possibly because of weak association between topsoil nutrient content and understory plants (Pang et al., 2021).

4.2 Green and senesced leaf C:N:P stoichiometry in mixed and monoculture plantations

Support for hypothesis 1 was compromised, because we found no differences in green leaf C content among mixed and monoculture plantation types (Fig. 4a), possibly because plants maintain C concentrations to support their cytoskeleton (Zhang et al., 2019). While we found that green leaf N content was similar across the mixed and monoculture plantations, levels were lower in RPAS than RPAD (Fig. 4b), and although there was no association with soil TN content, there was a negative association with soil TP content (Fig. 9a) and P mineralization rates were greater in RPAS than RPAD (Fig. 3e); it is likely that this mixed plantation variation in green leaf N concentration derived from differences in species responses to soil conditions (Peñuelas and Sardans, 2009). Green leaf P content was greatest in monoculture plantations and RPAD and lowest in RPAS (Fig. 4c), while CD was greatest in RPAD, followed by RPAS and monoculture plantations (Table 1), indicating that higher levels of CD in stratified canopies may indirectly restrict plant growth through limited P required for chlorophyll and RNA production (Forrester et al., 2006; Schuler et al., 2017).

Green leaf ratios of C:N and C:P indicate NUE (Turner, 2020); low levels of NUE have been recorded in plants where soil nutrient availability is high, with the converse in nutrient-poor soils (Vitousek, 2010). In this study, green leaf C:N and C:P ratios were lowest in RPAD and RP (Fig. 4d, e), likely reflecting the greater green leaf content of N and P in N_2-fixing species than non-legumes (Reich and Oleksyn, 2004;Vitousek, 2010; Turner, 2020), indicating low levels of N and P use efficiency and abundant levels of SAN and SAP (Table 1). Leaf N:P ratios of < 14, 14–16, and > 16 indicate N limitation, N and P co-limitation, and P limitation, respectively (Koerselman and Meuleman, 1996) and, in this study, we found the average green leaf N:P ratio (18.2; Fig. 4f) confirmed P limitation on the LPC (Cao and Chen, 2017). Our finding that growth of the mixed plantations and RP was limited by P, while growth in AS was limited by N and P indicates that *A. sibirica* benefits from fixed N_2 provided by *R. pseudoacacia* (Voigtlaender et al., 2012). Green leaf C:N:P stoichiometry was related to SD, AH, CD, *H*, SAN, and EC (Fig. 8), likely reflecting the impacts of multiple factors on soil nutrients (Voigtlaender et al., 2012; Nygren and Leblanc, 2015).

Senesced leaf C, N, and P content differed between mixed and monoculture plantations (Fig. 4a, b, c), supporting hypothesis 1 and indicating that plant and soil traits influence the release of nutrients from senesced leaves to the topsoil. However, we found that senesced leaf N content was positively correlated to SAN and EC (Fig. 8), reflecting the positive plant-soil feedback of N during leaf decomposition (García-Palacios et al.,

2016), and the associations of senesced leaf N and P content with SD and CD indicate canopy-restricted leaf growth, due to long-distance transport of nutrients (Schuler et al., 2017).

Microbial activities tend to be greater when litter C:N and C:P ratios are lower, leading to increased litter decomposition and nutrient release (Zhang et al., 2018). Here, average senesced leaf C:N and C:P ratios (27.3 and 443.7) (Fig. 4d, e) were lower than the global averages for temperate forests (55.9 and 1052, respectively) (McGroddy et al., 2004), indicating more rapid decomposition of senesced leaves and nutrient release in this study region (Deng et al., 2019). We found that senesced leaf C:N ratios were lower in RPAD than RP and AD, whereas senesced leaf C:N ratios in RPAS were intermediate to those in RP and AS; these results indicate a rapid release of N from senesced leaves in RPAD, as demonstrated for other mixed plantations (Forrester et al., 2006; Brant and Chen, 2015; Zhang et al., 2016). We found evidence for effects of senesced leaf decomposition on soil P mineralization processes (Güsewell, 2005), because senesced leaf C:N and C:P ratios were negatively related to SAN and EC (Fig. 8).

Litter decomposition tends to be N-limited for plants grown at N:P ratios < 22 (Güsewell and Freeman, 2005) and P-limited at leaf N:P ratios > 25 (Güsewell and Verhoeven, 2006). In this study, the average senesced leaf N:P ratio (21.2) (Fig. 4d) was lower than the threshold (22 or 25) and higher than for temperate (17.6) and boreal (15.0) forests (Yuan and Chen, 2009), indicating greater nutrient release from senesced leaves in the study area. We found senesced leaf decomposition was N- and P- limited in RPAD and AS, but not in RPAS, indicating higher rates of senesced leaf decomposition and nutrient cycling in RPAS (Richards et al., 2010), likely due to effects of *A. sibirica* on nutrient limitation in the mixed plantation. Our finding that senesced leaf N:P ratios were positively related to SAN, SAP, and EC (Fig. 8) provides evidence for the importance of soil available nutrients in plant growth.

4.3 NuRE in mixed and monoculture plantations

NuRE is a key plant strategy for the conservation of nutrients, influencing nutrient cycling and improving plant adaptation to nutrient-poor conditions (Drenovsky et al., 2019). In this study, average NRE (45.0%) and PRE (52.8%) (Fig. 5a, b) were higher than for evergreen forests in eastern China (34.0 and 37.1%, respectively) and lower than the global averages (62.1 and 64.9%, respectively) (Huang et al., 2007; Vergutz et al., 2012), indicating moderate levels of NuRE in these plantations on the LRC with scarce nutrient availability (Cao and Chen, 2017).

We found that NuRE of AS and AD were lower than for RP (Fig. 5a, b), possibly due to the greater SD, AH, and CD of RP that led to a larger nutrient pool (Fig. 7) and greater resorption of nutrients from senesced leaves (Peng et al., 2019). NRE of the mixed plantation was lower than for RP, supporting hypothesis 2; however, the lack of associations between NRE and soil total N concentrations or SAN (Fig. 6, Fig. 8), as reported elsewhere (Yuan and Chen, 2015), indicates tree species effects on NuRE. In contrast, NRE was correlated with soil total P concentrations, and C:N and N:P ratios (Fig. 8), indicating that soil N and P mineralization is linked to NRE (Drenovsky et al., 2019; Zhang et al., 2019). Similarly, differences in NRE between the mixed plantations (RPAD > RPAS; Fig. 5a) indicate NRE is affected by species composition (Qiu et al., 2020).

In support of hypothesis 2, we found that PRE was lower for the mixed plantations than the RP monoculture (Fig. 5b), reflecting previous findings for *Populus tremuloides* in late successional mixed stands during late succession (Chen and Chen, 2022). Thus, we suggest this mixed plantation may have entered a late successional stage of development, given this result and the large-scale slow growth, dry canopy, and plant mortality in the RP plantation (Li et al., 2010; Wei et al., 2018).

We found no evidence for consistent relationships between NuRE and leaf and soil nutrients, as stated in hypothesis 2. For example, PRE was positively correlated with leaf N concentrations, as reported for *Larix kaempferi* plantations in northeast China (Yan et al., 2018) and *L. principis-rupprechtii* plantations in northern China (Qiu et al., 2020), but not correlated with soil total N content (Fig. 8), possibly as a result of release of nutrients from senesced leaves to the topsoil (Pei et al., 2017). In contrast, we found that PRE was negatively related to soil total P content (Fig. 6), consistent with previous studies (Qiu et al., 2020; Pang et al., 2021). Unexpectedly, PRE was positively related to SAP, perhaps reflecting the association between soil N and P (See et al., 2015) and indicating that the balance between soil available and total P may affect PRE (Zhang et al., 2019). In this study, green leaf P content was positively correlated with PRE (Fig. 8), in contrast to findings of previous studies (Xu et al., 2020; Qiu et al., 2020); thus, this relationship may be affected by other factors, such as biological and methodological influences (Kobe et al., 2005).

Consistent allocation of nutrients to various biochemical pools (enzymes, structural proteins) of differing solubility and potential for export, including under variable levels of availability, may lead to constant levels of resorption efficiency (Chapin and Ked-rowski, 1983); the resource optimization theory states that plant growth under N or P-limited conditions leads to greater reabsorption of foliar N and P (Güsewell, 2005). When NRE:PRE ratios are > 1, N-limitation is greater than P-limitation and the converse when ratios are < 1 (Reed et al., 2012); we found that green leaf N:P ratios and average NRE:PRE ratios were < 1 (Figs. 4 and 5c, respectively), indicating greater P than N-limitation on the LPC, where RPAD was P-limited and RPAS was N-limited. Consistent with hypothesis 2, the relationship between PRE and NRE was stronger in the mixed plantations (r = 0.91) than in the monoculture plantations (r = 0.76) (Fig. 5d), indicating a potential decrease in P-limitation in the mixed stands, likely due to the regulation of NuRE by the relative limitations of N and P (Güsewell, 2005). Therefore, we conclude that the study area is mostly P-

limited and this condition was exacerbated in the presence of *R. pseudoacacia*, due to its capacity to fix N. Overall, our results show a greater nutrient balance in the RPAD plantation, based on greater NuRE and higher levels of soil C content.

5 Conclusions

The study area of the LPC is P limited, while N is also scarce. The mixed plantations, particularly RPAD, improved P retention capacity. Variations in green leaf N content are likely to have derived from species responses to soil conditions. The mixed plantations, particularly RPAD, retained higher levels of C and P in soils than the RP monoculture plantation.

Declarations

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Supplementary materials

Non

Availability of data and material

Data and materials can be obtained by contacting the corresponding authors.

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Author contributions

Y.M. Chen and S.B. Lu conceived and designed the study; S.B. conducted the experiment; S.B., Y.M., J.S., and J.P analyzed the results, wrote and edited the manuscript.

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Figures

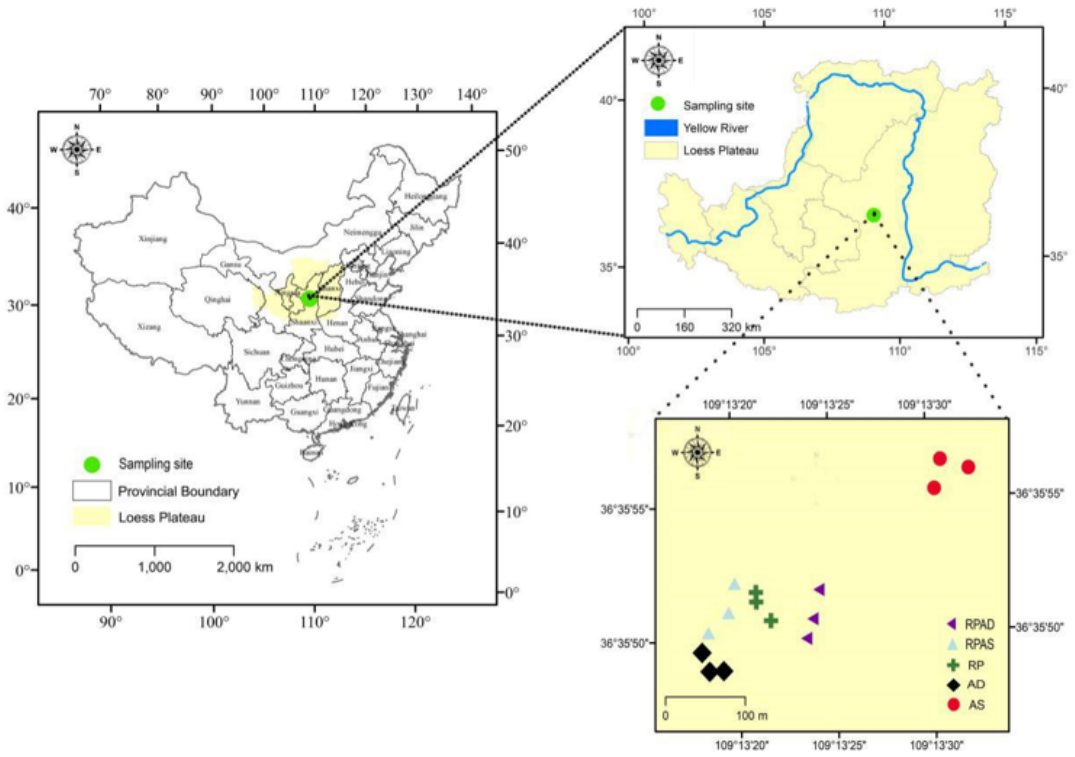


Figure 1

Location of the mixed and monoculture plantation study plots on the Loess Plateau, China. RPAD: *R. pseudoacacia* and *A. davidiana* mixed plantation; RPAS: *R. pseudoacacia* and *A. sibirica* mixed plantation; RP: *R. pseudoacacia* monoculture; AD: *A. davidiana* monoculture; and, AS: *A. sibirica* monoculture.

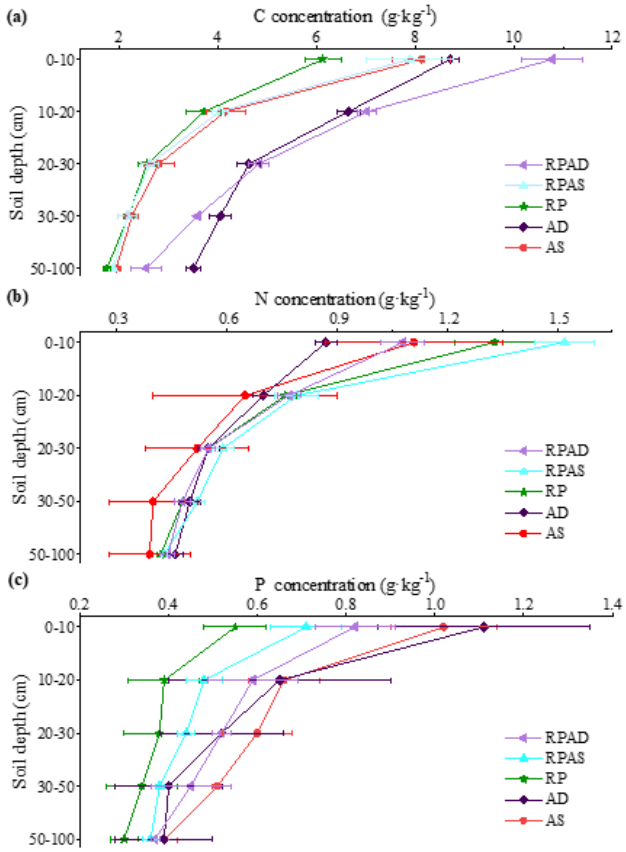


Figure 2

Plantation type variation in C, N, and P content along a vertical depth gradient. RPAD: *R. pseudoacacia* and *A. davidiana* mixed plantation; RPAS: *R. pseudoacacia* and *A. sibirica* mixed plantation; RP: *R. pseudoacacia* monoculture; AD: *A. davidiana* monoculture; and, AS: *A. sibirica* monoculture. Data are means ±SD.

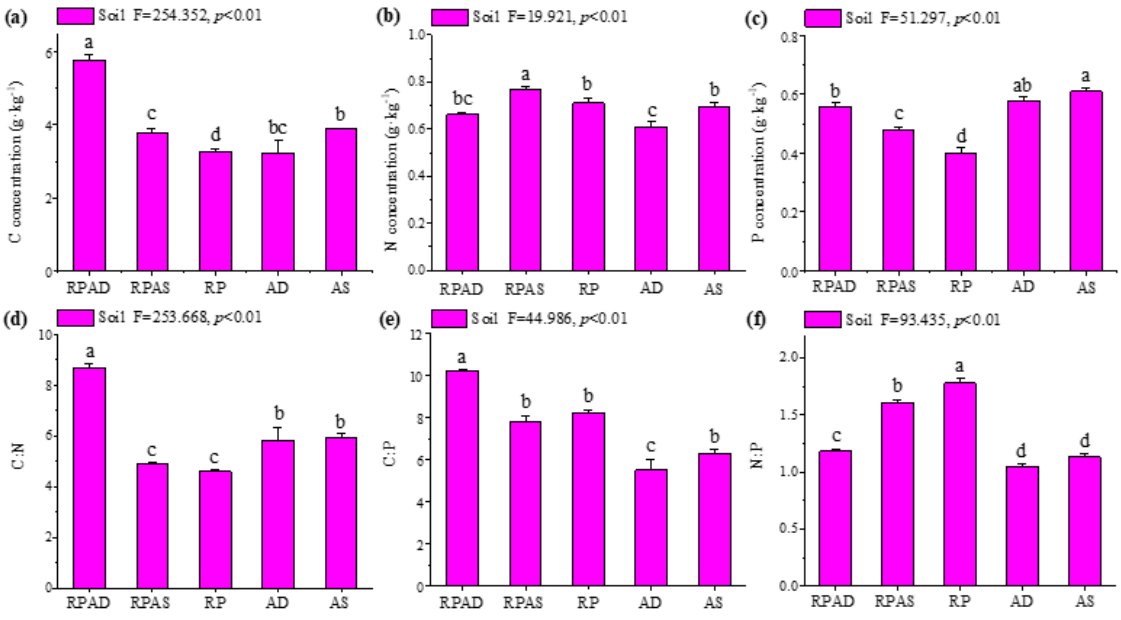


Figure 3

Analysis of plantation type variation in soil C, N, and P content (a, b, c) and stoichiometric ratios (d, e, f) (0–100 cm). RPAD: *R. pseudoacacia* and *A. davidiana* mixed plantation; RPAS: *R. pseudoacacia* and *A. sibirica* mixed plantation; RP: *R. pseudoacacia* monoculture; AD: *A. davidiana* monoculture; and, AS: *A. sibirica* monoculture. Data are means ±SD; different lowercase letters indicate plantation type differences at $p<0.01$.

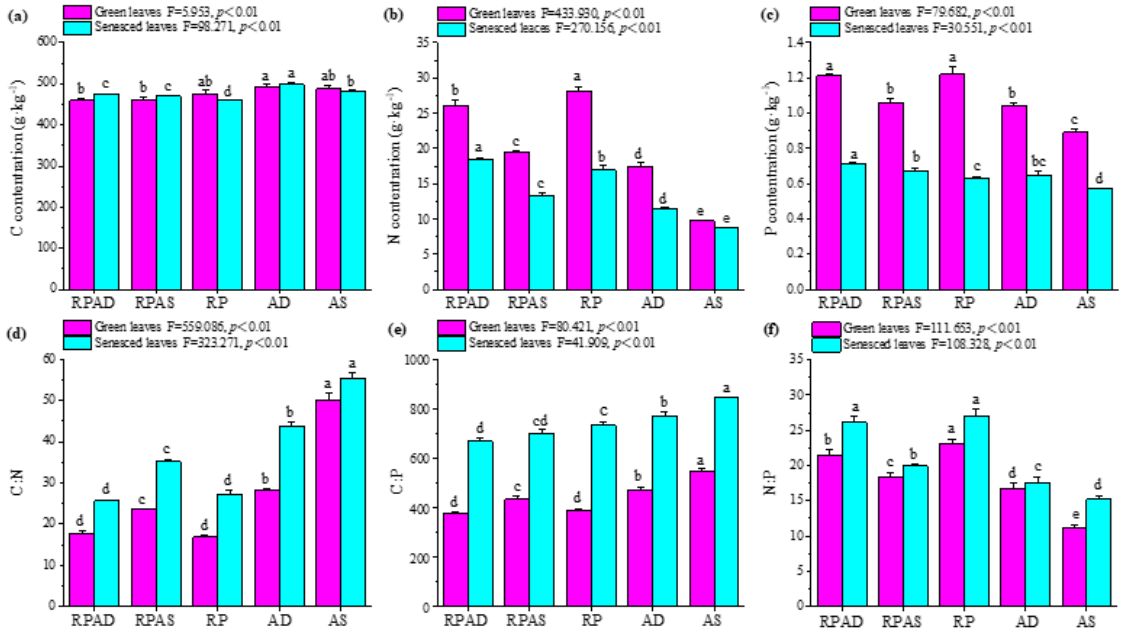


Figure 4

Analysis of plantation type variation in green and senesced leaf C, N, and P content and stoichiometric ratios. RPAD: *R. pseudoacacia* and *A. davidiana* mixed plantation; RPAS: *R. pseudoacacia* and *A. sibirica* mixed plantation; RP: *R. pseudoacacia* monoculture; AD: *A. davidiana* monoculture; and, AS: *A. sibirica* monoculture. Data are means ±SD; different lowercase letters indicate plantation type differences at $p<0.01$.

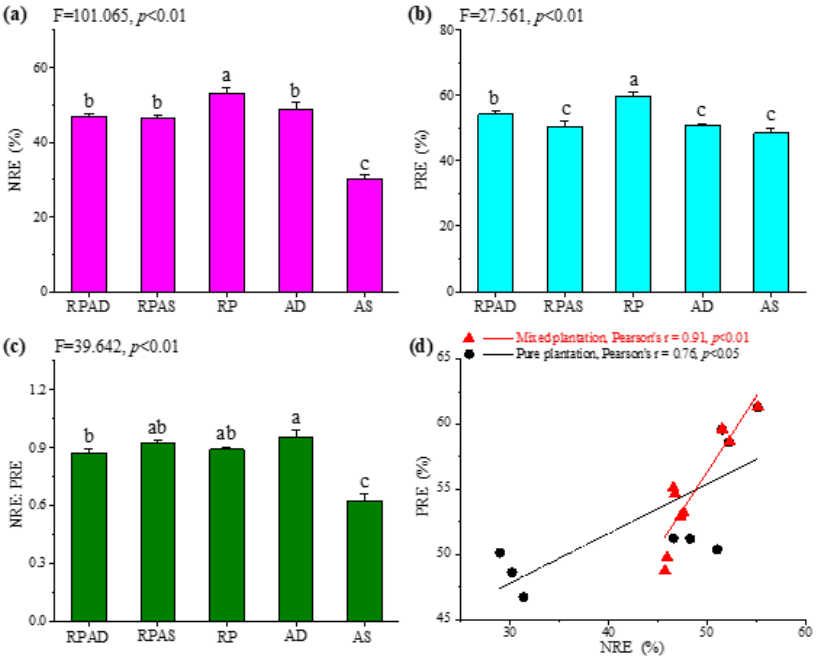


Figure 5

Analysis of plantation type variation in mean (±SD) foliar nutrient resorption efficiency (NuRE) (a–c) and association between proportions (%) of P resorption efficiency (PRE) and N resorption efficiency (NRE) in *R. pseudoacacia* mixed and monoculture plantations (d). RPAD: *R.*

pseudoacacia and *A. davidiana* mixed plantation; RPAS: *R. pseudoacacia* and *A. sibirica* mixed plantation; RP: *R. pseudoacacia* monoculture; AD: *A. davidiana* monoculture; and, AS: *A. sibirica* monoculture. Different lowercase letters (a–c) indicate plantation type differences at $p<0.05$.

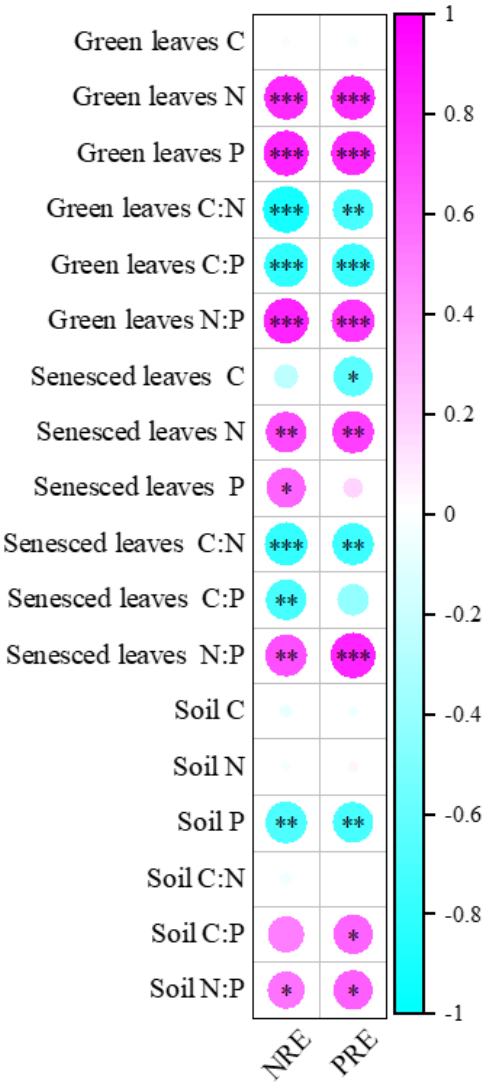


Figure 6

Pearson's correlation analysis of associations between resorption efficiencies of N and P (NRE and PRE, respectively) and C, N, and P content and stoichiometry of green and senesced leaves and soils. Positive and negative associations are shown in purple and cyan, respectively; *$p<0.05$, **$p<0.01$, ***$p<0.001$.

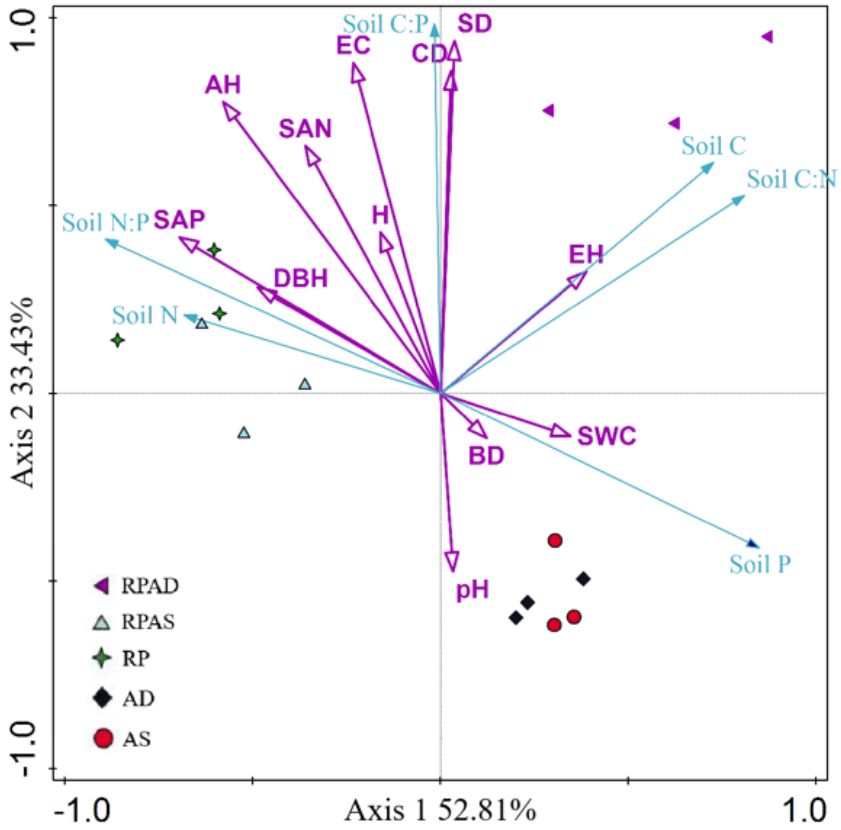


Figure 7

Redundancy analysis of soil C, N, and P content and stoichiometry (black arrows), and stand structure, understory plant species, and soil properties (red arrows) in contrasting mixed species and monoculture forest stands. SD: stand density; DBH: diameter at breast height; AH: average tree height; CD: canopy density; *H*: understory species diversity (Shannon-Wiener); *EH*: understory species evenness (Shannon-Wiener); BD: soil bulk density; SWC: soil water content; SAN: soil available nitrogen; SAP: soil available phosphorus; EC: electrical conductivity; RPAD: *R. pseudoacacia* and *A. davidiana* mixed plantation; RPAS: *R. pseudoacacia* and *A. sibirica* mixed plantation; RP: *R. pseudoacacia* monoculture; AD: *A. davidiana* monoculture; and, AS: *A. sibirica* monoculture.

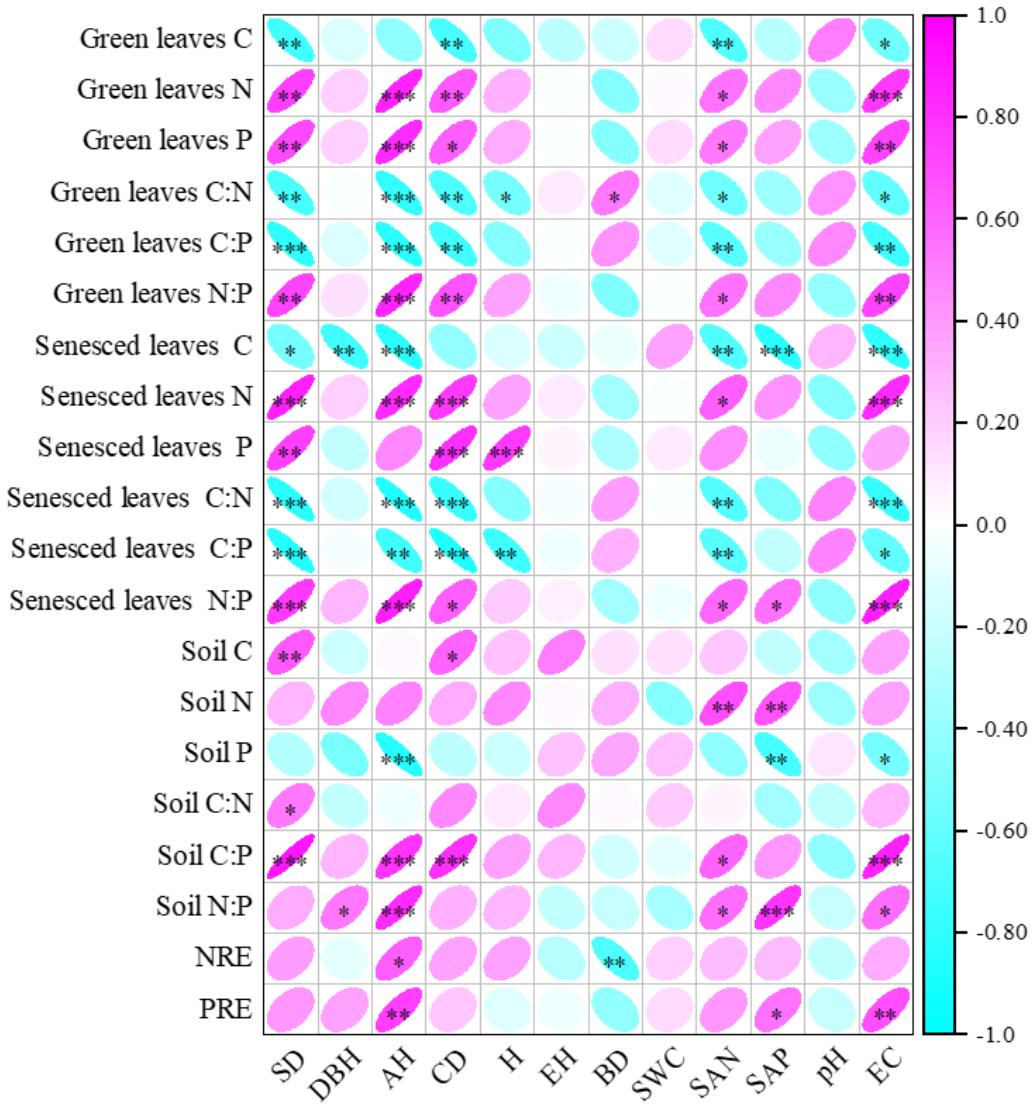


Figure 8

Pearson's correlation analysis of associations between C, N, and P content and stoichiometry of green and senesced leaves and resorption efficiencies of N and P (NRE and PRE, respectively) with stand structure, understory plant species, and soil properties. SD: stand density; DBH: diameter at breast height; AH: average tree height; CD: canopy density; *H*: species diversity (Shannon-Wiener); *EH*: species evenness (Shannon-Wiener); BD: soil bulk density; SWC: soil water content; SAN: soil-available nitrogen; SAP: soil-available phosphorus; and, EC: electrical conductivity. Positive and negative associations are shown in purple and cyan, respectively; *p<0.05, **p<0.01, ***p<0.001.

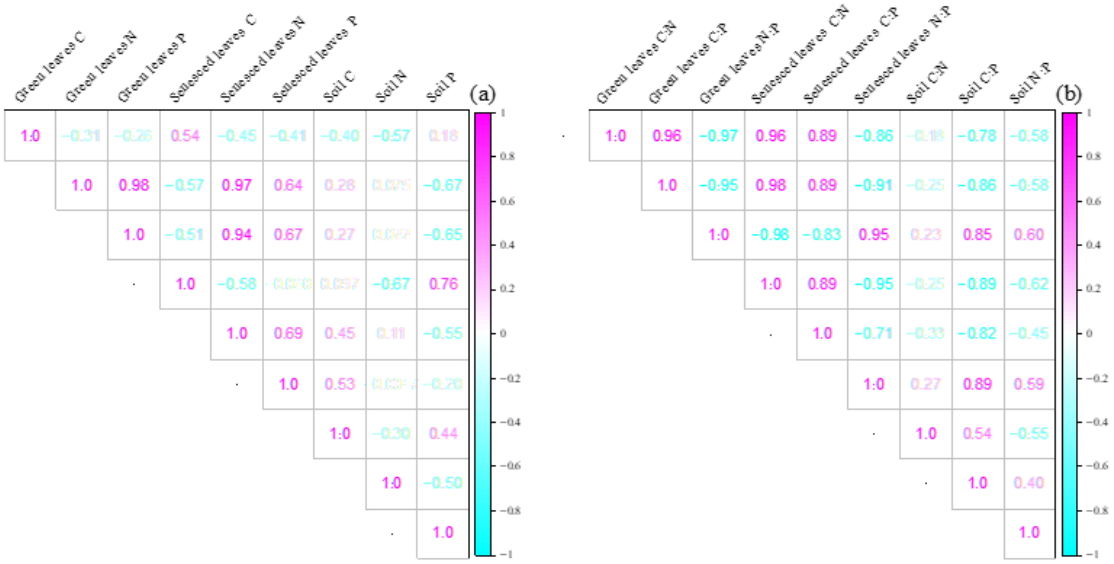


Figure 9

Pearson correlation analysis between green and senesced leaves, and soil C:N:P stoichiometric. Positive and negative associations are shown in purple and cyan, respectively; *p<0.05, **p<0.01, ***p<0.001.