

Contribution of Soil and Litter Nutrient Characteristics to Plant Nutrients in a Natural Secondary Mixed Forest in the Qinling Mountains, China

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Research Article

Keywords: soil and litter nutrient characteristics, plant nutrient characteristics, plant organs, plant functional groups, C:N:P stoichiometry

Posted Date: April 26th, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-372614/v1>

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Version of Record: A version of this preprint was published at Environmental Science and Pollution Research on July 31st, 2021. See the published version at <https://doi.org/10.1007/s11356-021-15632-5>.

Abstract

Soil and litter play important roles in ecosystem nutrient storage and cycling, which both affect plant growth and ecosystem productivity. However, the potential contributions of soil and litter nutrient characteristics to the nutrient characteristics of different plant functional groups (PFGs) remain unclear. In this study, we investigated the carbon (C), nitrogen (N) and phosphorus (P) concentrations of different organs of three PFGs (trees, shrubs and herbs), litter and soil in nine natural secondary mixed forests in the Qinling Mountains. The results showed that leaves had the highest N and P concentrations and N:P ratios at the organ level, whereas the C:N and C:P values were lowest in leaves. At the PFG level, the N and P concentrations of the same organs in herbaceous plants were significantly higher than those in woody species, while the N:P ratio was significantly lower in herb leaves than in tree and shrub leaves. Tree organs had significantly higher C concentrations and C:N and C:P ratios than shrub and herb organs. The leaf N:P ratios of all PFGs were less than 14, suggested that plant growth was limited by N in the study region. The nutrient contents and stoichiometric ratios in plant organs had different degrees of linkages with those in litter and soil. Soil nutrient characteristics were the main factors affecting the nutrient characteristics of the different PFGs, and litter nutrient characteristics also had important contributions to the nutrient characteristics of PFGs, showing the following order: herbs > trees > shrubs. Our results indicate that the functional difference in plant organs resulted in diverse nutrient concentrations; and varied nutrient connections exist among different ecosystem components. Furthermore, nutrient characteristics of litter and soil can together affect the nutrient characteristics of PFGs.

Introduction

Plants are composed of approximately 30 nutrient elements (Marschner 2013; Zhao et al. 2016), of which carbon (C), nitrogen (N) and phosphorus (P) are key elements for organism construction and play vital roles in plant function and biogeochemical cycles (Güsewell 2004; Sterner and Elser 2002). Of these, C is a main element in the dry matter of organisms and acts as a relatively stable skeleton of plants (Zhang et al. 2018c). N is involved in the synthesis of all plant enzymes and can influence plant metabolism, growth and reproduction (Reich and Oleksyn 2004). P is crucial in plant energy storage and genetic material because of its presence in ATP, DNA and RNA (Elser et al. 2000; Reich et al. 2009). Furthermore, a widely accepted view is that N and P are limiting elements for primary producers (Reich and Oleksyn 2004; Vitousek and Howarth 1991), and that the concentrations and ratio of C, N and P might affect ecosystem functions and succession to some extent (Allen and Gillooly 2009; Song et al. 2014). Therefore, comprehensive knowledge about plant C, N and P composition and variation is important for the understanding of plant physiological regulation mechanisms.

Ecological stoichiometry concerns the balance and interactions among multiple chemical elements in ecological processes (Kennish 2016) and provides an integrative and effective approach for exploring nutrient concentrations and the ratio of C, N and P in natural plant communities. Although many ecological researchers are devoted to this field of research and have made great achievements, there remain knowledge gaps in our understanding of plant ecological stoichiometry. First, although most

previous studies have analyzed the stoichiometric characteristics of plant organs at regional and global scales, they have mainly focused on certain organs, such as leaves and roots (Chen et al. 2013; Elser et al. 2007; Han et al. 2005; Yang et al. 2018). Therefore, the understanding of the stoichiometric characteristics of multiple plant organs remains limited, even though different plant organs perform various functions and cooperate with each other to support plant adaptation to environmental stress (Zhang et al. 2018b). Second, prior studies have focused on the nutrient element content of plant tissues among dominant species at the community level, which greatly advanced research regarding stoichiometry (Hou et al. 2018; Sun et al. 2019). However, plant communities are composite system of different functional groups (Zhang et al. 2018a), which includes the adaptation of species to environment and mutual competition between them. Therefore, the stoichiometric characteristics of organs, including those of different functional species, should be investigated at the community level to better reflect the reality of community structure and functional attributes. In view of the above deficiencies, quantifying nutrient element stoichiometric variation in multiple plant organs, including those of different functional species, is urgently needed to understand the functional diversity of vegetation, community succession and biogeochemical processes.

It is well known that soil is the main nutrient source for plants, determining the species composition, productivity, and stability of communities (Ordoñez et al. 2009; Richard et al. 2013). Therefore, numerous studies have reported patterns related to nutrient exchange between plants and soil at different scales and revealed the relationships and feedback between plants and soil and the factors influencing the plant-soil system (Fan et al. 2015; Hendriks et al. 2015; Stein et al. 2017). However, in addition to considering the soil factor, we cannot neglect the contribution of litter nutrients to plants in an ecosystem (Swift et al. 1979). Litter plays important roles in ecosystem nutrient storage and cycling (Sayer et al. 2012; Stefano et al. 2008) and also affects the plant nutrient allocation mechanism and ecosystem productivity (Guo and Sims 1999; Yang et al. 2018). For instance, early studies reported that plants obtain more than 90% of their N and P from the nutrients that plants had returned to the soil in previous years (leaf litter and rhizodeposition) (Chapin et al. 2011). These studies indicated that soil and litter nutrient characteristics together influence the nutrient characteristics of plant communities. Therefore, clarifying the intrinsic connections between plant nutrients and the nutrient characteristics of soil and litter could improve our understanding of plant nutrient limitations and ecosystem dynamics, especially according to stoichiometric theory (Elser et al. 2010).

The Qinling Mountains are covered by typical mountain forest in the transitional region between the subtropical and warm temperate zones that run across central China. During the 1960s and 1970s, forests in the Qinling Mountains suffered from extensive logging, which promoted the regeneration of diverse natural secondary forests. Aiming toward advancing forest resource protection and cultivation, the Chinese government launched a series of projects to improve the ecological environment, such as the “Natural Forest Protection Program” (NFP) (Wei et al. 2014). Through decades of effort, these projects have restored the structure and function of the plant communities and enhanced the carbon storage of the ecological systems (Cao and Chen 2015). Previous studies have evaluated the variation in the species composition, soil physical and chemical properties, carbon budget, and plant and soil C:N:P stoichiometry

among these natural secondary mixed forests (Chai and Wang 2016; Hou et al. 2018; Hou et al. 2016; Zheng et al. 2017). However, stoichiometric variation in multiple plant organs among PFGs and the contributions of soil and litter nutrient characteristics to the nutrients in different plant functional groups (PFGs) have rarely been evaluated.

In this study, we evaluated the variation in C, N, and P contents and stoichiometry in overstory trees, understory plants, litter, and soil collected from nine natural secondary mixed forests in the Qinling Mountains. We hypothesized that (i) the nutrient contents and stoichiometry of plant organs differs among PFGs due to the functional differences among organs, (ii) and the nutrient contents and stoichiometry in plant organs is correlated with litter and soil nutrient characteristics because of the control of biological processes and their cycling in the same ecosystem. In addition, we predicted that (iii) the nutrient characteristics of both soil and litter affect plant nutrient characteristics. Therefore, our objectives were to (1) examine the differences in C:N:P stoichiometric characteristics in multiple plant organs among PFGs, (2) analyze the relationships between the C:N:P stoichiometry of plant organ and that in soils and litter, and (3) explore the potential contributions of soil and litter nutrient characteristics to the nutrient characteristics of different PFGs.

Materials And Methods

Study site description

The field experiment was conducted at the Huoditang Experimental Forest Farm of Northwest A&F University in Ningshaan County (33°18'-33°28'N, 108°21'-108°39'E), Shaanxi Province, China. The landform of the farm is characterized by an abrupt and broken landscape with altitudes ranging from 800 to 2500 m and a mean slope of approximately 35°. The soil in this area is composed of Cambisols, Umbrisols and Podzols (FAO), and the mean soil depth is 50 cm. The climate in this region is classified as warm temperate. The average annual precipitation in this region is 1000 mm, most of which falls from July to September. The average frost-free period is approximately 170 days, and the average annual temperature is 10.5°C (Pang et al. 2020).

Experimental design and sampling

This study was conducted from July to August 2017 at the Huoditang Experimental Forest Farm. Nine replicate plots (20 × 20 m) were randomly established in a 111.3 ha compartment dominated by natural secondary mixed forest (Fig. 1). All plots had a similar stand age and elevation topography and experienced no fertigation (or tending measures). For each variable, the average value of the nine replicated plots was taken as the observation for the whole site. Detailed information regarding the plots is presented in Table 1.

Table 1

Characteristics of the sample plots (mean \pm standard error; n = 9). DBH: diameter at breast height

| Habitat factors description | | Tree species | Shrub species | Herb species |
|-------------------------------|------------------|----------------------------------------|--------------------------------|---------------------------------|
| Altitude (m) | 1800–2000 | <i>Quercus aliena var. auteserrata</i> | <i>Schisandra sphenanthera</i> | <i>Matteuccia intermedia</i> |
| Slope aspect | Northwest | <i>Pinus tabuliformis</i> | <i>Viburnum betulifolium</i> | <i>Tripterospermum chinense</i> |
| Slope position | Central | <i>Pinus armandii</i> | <i>Rubus mesogaeus</i> | <i>Athyrium sinense</i> |
| Slope gradient (°) | 16–20 | <i>Betula albosinensis</i> | <i>Smilax china</i> | <i>Carex duriuscula</i> |
| Fertigation | NO | <i>Larix principis-rupprechtii</i> | <i>Lonicera fragrantissima</i> | <i>Lysimachia christinae</i> |
| Age (similar age) | Same | <i>Picea asperata</i> | | <i>Viola verecunda</i> |
| DBH (cm) | 16.5 \pm 0.61 | <i>Populus davidiana</i> | | |
| Height (m) | 13.23 \pm 0.99 | other broad leaf species | | |
| Density (n ha ⁻¹) | 1151 | | | |

Within each plot, all trees (diameter at breast height (DBH) \geq 5 cm) were classified and numbered, and DBH and height (H) were measured. Samples were taken from different organs for each tree species. Fully expanded and sun-exposed leaves and branches (diameter < 1 cm, collected randomly) were collected from the east, west, south and north directions in the upper, middle and lower parts of the canopies. Stem (sampled using an increment borer) and bark samples were obtained from the DBH location. Roots (diameter < 1 cm) were randomly excavated from the shallow soil (0–20 cm), and root samples were collected by removing the surrounding soil along a main root of a specific plant species until roots appeared. All the organ samples from the trees were transported to the lab and oven dried at 70°C to a constant weight. Based on the DBH and tree height, the biomass of the components (leaves, branches, stems, bark and roots) of each tree species in the community was calculated using published species-specific allometric equations developed for trees within or near the study area (Table S1). To better reflect the relative contributions of multiple tree species at the community level, the different organ samples of the species were mixed according to the ratios calculated from the allometric equations.

Five shrub subplots (2 \times 2 m) and five herb subplots (1 \times 1 m) were established along the diagonals of each plot. Shrub and herb samples were collected using the total harvest method. The whole shrubs were separated into leaf, branch and root components, and the herbs were separated into leaves and roots. Because there are no corresponding allometric equations for shrubs and herbs in the study area, the

same components of shrubs, herbs and litter were mixed uniformly into one sample. For ground litter sampling, all organic material within five 1 × 1 m subplots was collected from each plot. The subsamples were transported to the lab and oven dried at 70°C to a constant weight.

For soil sampling, nine replicate sampling points were established along an “S” shape in each plot (Fig. 1). Soil samples (0–20 cm) were obtained from each point using a soil auger (400 mm inner diameter) after removing the litter layer and biological crusts. These nine replicated soil samples were fully homogenized to form one composite soil sample per plot such that nine soil samples were ultimately collected from the nine plots. After removing the plant roots, large stones and debris by hand, the soil samples were sieved (< 2 mm) and air dried at room temperature for physicochemical analysis.

Chemical analyses

The C, N, and P contents in the tree, shrub and herb tissue and litter were analyzed after the samples were ground into a powder with a plant-sample mill (1093 Sample Mill, Hoganas, Sweden). All chemical analysis referred to the method described by Bao (2000) (Bao 2000). The organic carbon (OC) content of the plant and soil samples was measured using the $K_2Cr_2O_7$ oxidation method. The total nitrogen (TN) and total phosphorus (TP) concentrations of the plant and soil samples were determined with an automatic discontinuous elemental analyzer (Clever chem200+, Germany) after digestion with H_2SO_4 and H_2O_2 .

Data analysis

The differences in C, N, P contents and stoichiometric ratios among the different plant organs and PFGs were tested using one-way ANOVA with least significant difference (LSD) multiple comparisons ($p < 0.05$). Regression analysis and Pearson correlation analysis were used to evaluate the relationships between the C, N, P contents and stoichiometric ratios in plant organs and those in soil and litter. Variation partitioning analysis (VPA) was used to determine the potential contributions of soil and litter nutrient characteristics to nutrient patterns in the different PFGs. The VPA was implemented by using the ‘*Vegan*’ package (Oksanen et al. 2013). All statistical analyses were performed using R version 4.0.3 (R Development Core Team, 2017).

Results

C:N:P stoichiometric characteristics in the organs of different PFGs, litter and soil

The stoichiometry varied greatly in different plant organs among the different PFGs (Fig. 2). Among the organs, leaves had the highest N and P concentrations, while the C concentration exhibited inconsistent tendency for different PFGs (Fig. 2a, b, c). The N and P concentrations were also relatively higher in the tree and shrub branches and roots and herb roots (Fig. 2b, c). At the PFG level, the C concentration in tree organs was significantly higher than that in shrub and herb organs (Fig. 2a). The N and P concentrations in the same organs in herbaceous plants were significantly higher than those in woody species (shrubs and trees) (Fig. 2b, c).

The highest values of the C:N and C:P ratios were observed in stem of trees, branches of shrubs and roots of herbs, whereas the lowest values were observed in the leaves of all PFGs (Fig. 2d, e). The tree organs had significantly higher C:N and C:P ratios than the shrub and herb organs (Fig. 2d, e). In terms of the N:P ratio, leaves were observed to have the highest N:P ratio among the different organs of all PFGs (Fig. 2f). The N:P ratio was significantly lower in herb leaves than in tree and shrub leaves, while the opposite result was observed in roots (Fig. 2f).

The average C, N, and P concentrations were 25.43, 2.36, and 0.77 g kg⁻¹ for soil and 438.61, 16.03, and 1.54 g kg⁻¹ for litter, respectively (Table 2). The C, N, and P concentrations and stoichiometric ratio were higher in the litter than in the soil (Table 2).

Table 2
Soil and litter nutrient properties (mean ± standard error; n = 9)

| | C (g · kg ⁻¹) | N (g · kg ⁻¹) | P (g · kg ⁻¹) | C:N | C:P | N:P |
|---------------|---------------------------|---------------------------|---------------------------|--------------|----------------|--------------|
| Soil | 25.43 ± 2.18 | 2.36 ± 0.21 | 0.77 ± 0.06 | 10.84 ± 0.18 | 34.09 ± 3.14 | 3.15 ± 0.29 |
| Litter | 438.61 ± 12.65 | 16.03 ± 0.70 | 1.54 ± 0.06 | 27.91 ± 1.68 | 288.87 ± 15.38 | 10.40 ± 0.19 |

Connections between plant organ, soil and litter C:N:P stoichiometry

The C:N:P stoichiometry of the various organs among the different PFGs responded differently to soil and litter nutrient stoichiometry (Fig. 3–6 and Table 3, Table 4). The C concentration in tree organs was negatively correlated with the soil organic carbon (SOC) concentration (significantly for tree leaves and stem, p < 0.05) and positively correlated with the organic carbon in litter (significantly for tree branches and roots, p < 0.05), while no clear relationship was found for shrub and herb C (Fig. 3–6).

Table 3

Pearson's correlation coefficients between tree organs and soil and litter stoichiometric ratios. The bold fonts indicated significant correlations. * $p < 0.05$, ** $p < 0.01$

| Organs | Stoichiometry | Soil | | | Litter | | |
|--------|---------------|---------------|----------------|----------------|----------------|----------------|--------|
| | | C:N | C:P | N:P | C:N | C:P | N:P |
| Leaf | C:N | 0.461 | -0.373 | -0.446 | 0.836** | 0.773* | -0.469 |
| | C:P | 0.416 | -0.186 | -0.247 | 0.778* | 0.793* | -0.222 |
| | N:P | 0.062 | 0.196 | 0.197 | 0.246 | 0.387 | 0.340 |
| Branch | C:N | 0.327 | -0.070 | -0.126 | 0.605 | 0.633 | -0.088 |
| | C:P | 0.686* | -0.251 | -0.359 | 0.857** | 0.801** | -0.471 |
| | N:P | 0.707* | -0.215 | -0.324 | 0.778* | 0.712* | -0.492 |
| Stem | C:N | 0.533 | 0.259 | 0.173 | 0.874** | 0.898** | -0.276 |
| | C:P | 0.324 | -0.610 | -0.654 | 0.704* | 0.627 | -0.448 |
| | N:P | -0.362 | -0.778* | -0.710* | -0.211 | -0.291 | -0.093 |
| Bark | C:N | 0.577 | -0.241 | -0.327 | 0.864** | 0.807** | -0.473 |
| | C:P | 0.644 | -0.457 | -0.561 | 0.762* | 0.668* | -0.532 |
| | N:P | 0.422 | -0.623 | -0.695* | 0.347 | 0.257 | -0.345 |
| Root | C:N | 0.533 | -0.422 | -0.502 | 0.869** | 0.776* | -0.585 |
| | C:P | 0.720* | 0.059 | -0.064 | 0.687* | 0.673* | -0.281 |
| | N:P | 0.168 | 0.594 | 0.551 | -0.405 | -0.286 | 0.507 |

Table 4

Pearson's correlation coefficients between shrub and herb organs and soil and litter stoichiometric ratios. The bold fonts indicated significant correlations. * $p < 0.05$, ** $p < 0.01$

| Species | Organ | Stoichiometry | Soil | | | Litter | | |
|---------|--------|---------------|--------|---------------|----------------|--------|---------------|---------------|
| | | | C:N | C:P | N:P | C:N | C:P | N:P |
| Shrub | Leaf | C:N | -0.242 | 0.646 | 0.681* | -0.142 | -0.071 | 0.168 |
| | | C:P | -0.376 | 0.749* | 0.811** | -0.214 | -0.046 | 0.518 |
| | | N:P | -0.415 | 0.587 | 0.660 | -0.312 | -0.097 | 0.766* |
| | Branch | C:N | 0.306 | -0.317 | -0.363 | 0.493 | 0.560 | 0.112 |
| | | C:P | -0.401 | 0.493 | 0.554 | -0.380 | -0.275 | 0.415 |
| | | N:P | -0.427 | 0.437 | 0.501 | -0.561 | -0.564 | 0.114 |
| | Root | C:N | 0.316 | 0.606 | 0.541 | 0.385 | 0.418 | -0.099 |
| | | C:P | 0.406 | 0.301 | 0.217 | 0.434 | 0.420 | -0.225 |
| | | N:P | 0.370 | -0.345 | -0.421 | 0.296 | 0.220 | -0.285 |
| Herb | Leaf | C:N | -0.053 | 0.479 | 0.486 | -0.085 | 0.013 | 0.268 |
| | | C:P | -0.179 | 0.722* | 0.754* | 0.153 | 0.320 | 0.382 |
| | | N:P | -0.197 | 0.663 | 0.698* | 0.263 | 0.420 | 0.327 |
| | Root | C:N | -0.425 | -0.191 | -0.102 | 0.141 | 0.145 | -0.058 |
| | | C:P | 0.331 | 0.395 | 0.339 | 0.538 | 0.709* | 0.310 |
| | | N:P | 0.499 | 0.467 | 0.373 | 0.394 | 0.535 | 0.281 |

The N concentration of tree organs was significantly correlated positively with that in litter and soil (excluding branches), while P concentration of tree leaves and branches was significantly correlated positively with that in litter and soil (Fig. 3–4, $p < 0.05$). The N and P concentrations of shrub organs had no clear relationship with those in litter and soil (Fig. 5, $p > 0.05$). The P concentration of herb organs was significantly correlated positively with that in soil and litter (excluding the correlation between P in herb leaves and litter P) (Fig. 6).

The C:N and C:P ratios in tree organs were generally significantly positively correlated with those in litter, while N:P ratio in tree stems and barks was significantly negatively correlated with the soil N:P ratio (Table 3, $p < 0.05$). The C:P and N:P ratios of shrub leaves linearly increased with the soil C:P and litter N:P ratios, respectively (Table 4, $p < 0.05$). The C:P and N:P ratios of herb leaves were significantly positively correlated with the soil C:P and N:P ratios, respectively, and the root C:P ratio was also significantly positively correlated with the litter C:P ratio (Table 4, $p < 0.05$).

Contributions of soil and litter nutrient characteristics to the nutrient characteristics of different PFGs

Using variation partitioning analysis (VPA), we found that the percentages of the variation associated with the soil and litter nutrient concentrations were 56.4% and 49.7% for tree nutrients, 41.4% and 7.7% for shrub nutrients and 23.9% and 25.4% for herb nutrients, respectively (Fig. 7a, b, c). The soil and litter nutrient concentrations explained 56.1% and 37.2% of the variation in stoichiometric ratios for trees, 30.7% and 4.5% for shrubs and 41.5% and 15.1% for herbs, respectively (Fig. 7d, e, f).

Discussion

C, N, and P contents and stoichiometric ratio characteristics in the organs of different PFGs

Significant differences in C, N, P contents and stoichiometries were detected in multiple organs among the different PFGs (Fig. 2). Our results proved that the plants of the different PFGs allocated most of their N and P to leaves, followed by roots and branches (Fig. 2b, c). This is in general agreement with the results of previous studies conducted in forests, shrubs and grasslands systems (Hong et al. 2014; Yan et al. 2016; Zhang et al. 2018b). Leaves with relatively high metabolic activity are responsible for many physiological functions and require higher quantities of N and P for biochemical reactions than organs with lower metabolic activity (Wright et al. 2004). In addition, roots are responsible for nutrient and water absorption, while branches are responsible for bud initiation and nutrient exchange (Zhang et al. 2018a). Therefore, relatively higher N and P concentrations in roots and branches represent high rates of nutrient recycling and could allow the higher levels of transport loading (Zhang et al. 2018b). The significantly higher N and P concentrations in the leaves than in the other organs resulted in lowest leaf C:N and C:P ratios (Fig. 2d, e). Previous studies also showed that C:N and C:P ratio values were lower in leaves than in other organs (Cao and Chen 2017; Jiang et al. 2017). In comparison, the N:P ratio in leaves was much higher than that in other organs (Fig. 2f). This is because leaves with high metabolic rates (“metabolic” organs) can maintain a relatively constant N:P ratio to meet the diverse physiological needs of metabolic processes, while other organs (“structural” organs), with P concentrations rising faster than N concentrations, show a decrease in the N:P ratio (Kerkhoff et al. 2006; Zhang et al. 2018a). These results indicate that the functional differences among plant organs resulted in diverse nutrient concentrations; and that more metabolically active organs had higher N and P nutrient contents.

At the PFG level, tree organs had significantly higher C concentrations and C:N and C:P ratios than shrub and herb organs (Fig. 2a, d, e). A possible explanation for this result is that to support their large skeletal structures, trees synthesize more photosynthate and accumulate more organic matter than understory plants (Cleveland et al. 2011). Herbaceous plants had significantly higher N and P concentrations than the woody species (Fig. 2b, c). This result may be explained by the fact that herbs require high nutrient investment to support their rapid growth and reproduction during the relatively short growing season (Zheng and Shangguan 2007). Furthermore, plant nutrients exhibit a size scaling pattern in which N and P concentrations are diluted with increasing plant size; therefore, small plants (herbs) have high N and P concentrations (Elser et al. 2010). In the present study, herb leaves were observed to have lower N:P ratios

than tree and shrub leaves (Fig. 2f). This is consistent with the growth rate hypothesis, which indicates that rapidly growing organisms have a low N:P ratio (Elser et al. 2000). However, the N:P ratio in herb roots was higher than that in the woody plant roots (Fig. 2f), which is inconsistent with previous research (He et al. 2008). This inconsistency might be caused by the roots not being classified into more fine classes, as fine roots (diameter < 2 mm) were not evaluated separately, because fine roots have higher N and P nutrient concentrations than coarse roots (Shen et al. 2017). Previous studies have proposed that a leaf N:P ratio < 14 indicates N limitation, while a N:P > 16 indicates P limitation (Koerselman and Meuleman 1996). In this study, the leaf N:P ratios of all PFGs were less than 14 (Fig. 2f), which suggests the occurrence of N limitation in the study area.

Contributions of soil and litter nutrient characteristics to the nutrient characteristics of different PFGs

In our study, the C concentration in the tree organs was negatively correlated with the SOC content (Fig. 3). First, SOC is mainly derived from the metabolism of amino acid, which results in a positive relationship between SOC and plant organ N and P (Sinsabaugh et al. 2010; Zhang et al. 2019). Simultaneously, previous study reported that the fixation of C during the process of plant metabolism requires the participation of a large number of proteases (which consumes a high amount of N) and that the assembly of proteases requires the replication of a large number of nucleic acids (which consumes a great deal of P), which results in negative relationships of C with N and P in plant organs (Elser et al. 2000). Thus, plant C has a negative correlation with SOC. The C concentration in the tree organs was positively correlated with the organic carbon in the litter (Fig. 4), because litter C is derived from that in plant organs (Zhang et al. 2017). In contrast, we found no clear relationship between the C concentration in shrub and herb organs and soil and litter organic carbon (Fig. 5–6). A possible explanation for this result may be that trees produce a higher amount of litter biomass annually and can recycle more C than shrubs and herbs by microorganisms (Liu et al. 2018), which may obscure the relationship between the C concentration in shrub and herb organs and soil and litter organic carbon.

In present studies, the N and P contents in the tree organs and P contents in herb organs were generally positively correlated with those in the soil and litters, and the stoichiometric ratios in the different organs of the trees and herbs were also correlated to some extent with those of the soil and litter (Fig. 3, 4, 6 and Tables 3, 4). These finding aligns with previous studies showed that organisms and their environments are closely connected by the exchange of chemical elements (Ladanai et al. 2010; Odum et al. 1972). Litter is the main form of nutrient restitution, and plants primarily absorb nutrients from the soil (Hatton et al. 2015; Townsend et al. 2007); consequently, the dynamic cycling of nutrients among plants, litter and soil supports their close relationship. Moreover, the inconsistent nutrient connections between plant organs and soil and litter indicated the different PFGs had different nutrient utilization strategies in the ecosystem (Zhang et al. 2019). However, our results revealed the decoupling of the relationship between nutrient elements in shrub organs and that in soil and litter (Fig. 5). One possible explanation for this might be that shrubs can obtain nutrients from different sources, e.g., atmospheric nutrient deposition and biological fixation (especially for N) (Gundale et al. 2010; Phoenix et al. 2010), which might lead to the observed decoupling phenomenon. Additionally, earlier studies had proved that the decoupling of

nutrient cycling relationships among different components of the ecosystem can be observed when plants respond passively to external environmental conditions (Ladanai et al. 2010). In our study region, shrubs are often passively disturbed by herbivores; therefore, the state in which nutrient elements are retained in shrub organs may have changed, resulting in the decoupling of the cycling of nutrients among the shrub organs, soil and litter. In general, these results confirm our hypothesis that C, N, P contents and stoichiometries in plant organs is correlated with litter and soil nutrient characteristics.

The aim of this study was to examine the potential contributions of soil and litter nutrient characteristics to the nutrient characteristics of different PFGs. Our VPA results show that soil nutrient characteristics were the main controlling factors of the nutrient characteristics of the different PFGs (Fig. 7). As mentioned in the Introduction, soil is the main nutrient source for plants; therefore, soil nutrients play a dominant role in the nutrient characteristics of plants (Han et al. 2011). In addition, the litter nutrient characteristics also had important contributions to the nutrient characteristics of the three PFGs, showing the following order: herbs > trees > shrubs (Fig. 7). Because nutrient release from litter is a continuous process, nutrients infiltrate the soil from the top to the bottom (Zeller et al. 2001). Furthermore, plant roots show some degree of below ground niche partitioning, and the root systems of different PFGs have different depth distributions (Carrera et al. 2000; Cremer et al. 2016). These two factors lead to a hierarchy order of plants absorbing nutrients released from the litter, which in turn leads to litter nutrients having different influences on the nutrient characteristics of different PFGs. Previous studies have also reported that herbaceous roots are mainly distributed in shallower soil than woody plant roots; hence, herbs can preferentially absorb nutrients returned from the litter (Ren et al. 2017; Zhang et al. 2019). Thus, litter nutrient characteristics contribute more to the nutrient characteristics of herbaceous plants than woody species. Overall, these VPA results imply that both soil and litter nutrients play the important roles in plant nutrient cycling.

Conclusion

Our results demonstrate that soil nutrient characteristics were the main factors affecting the nutrient characteristics of the different PFGs, and litter nutrient characteristics also had important contributions to the nutrient characteristics of the PFGs; these contributions were especially important for herbs. In addition, significant differences in C:N:P stoichiometry were observed in multiple organs in the different PFGs, indicating that the functional differences among plant organs resulted in diverse nutrient concentrations. Plants allocated the most N and P to leaves, followed by roots and branches, suggesting that more metabolically active organs have higher N and P nutrient contents. The leaf N:P ratios of all PFGs were less than 14, indicating that all the PFGs are limited by N in the study area. Furthermore, the relationship between plant organ C:N:P stoichiometry and that in soils and litter and the different contributions of soil and litter nutrients to plant nutrient characteristics together imply that different PFGs had different nutrient utilization strategies in the ecosystem. Collectively, our findings provide valuable data for elucidating the mechanisms of nutrient cycling in plant-litter-soil systems and basis for establishing new forest ecosystem models.

Declarations

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Availability of data and materials

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Competing interests

The authors declare that they have no competing interests.

Funding

This study was financially supported by the National Natural Science Foundation of China (No. 31470644); and Humanities and social science research special project of Xi'an University of Technology (No. 2020RY004); and Social Science Fund Project of Shaanxi Province (No. 2020N004).

Authors' contributions

YP designed the experiment; YP, JT, LL and LH carried out the field work; YP analyzed the data and wrote the manuscript; and D W revising the draft manuscript.

Acknowledgments

We sincerely thank Xinping Zhang for his help in making the figures.

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Figures

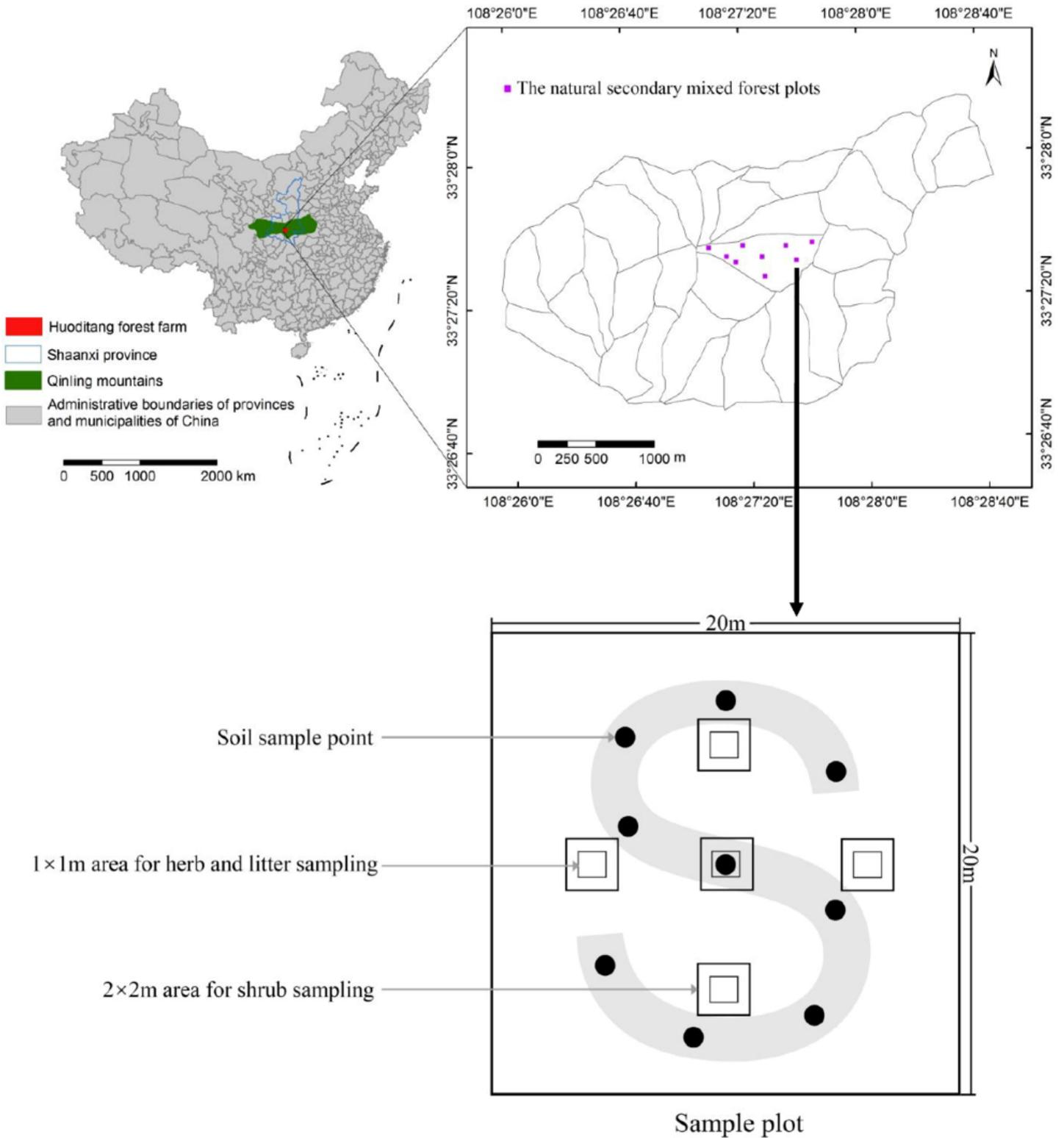


Figure 1

Geographic location of the Huoditang Experimental Forest Farm and the sampling process Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

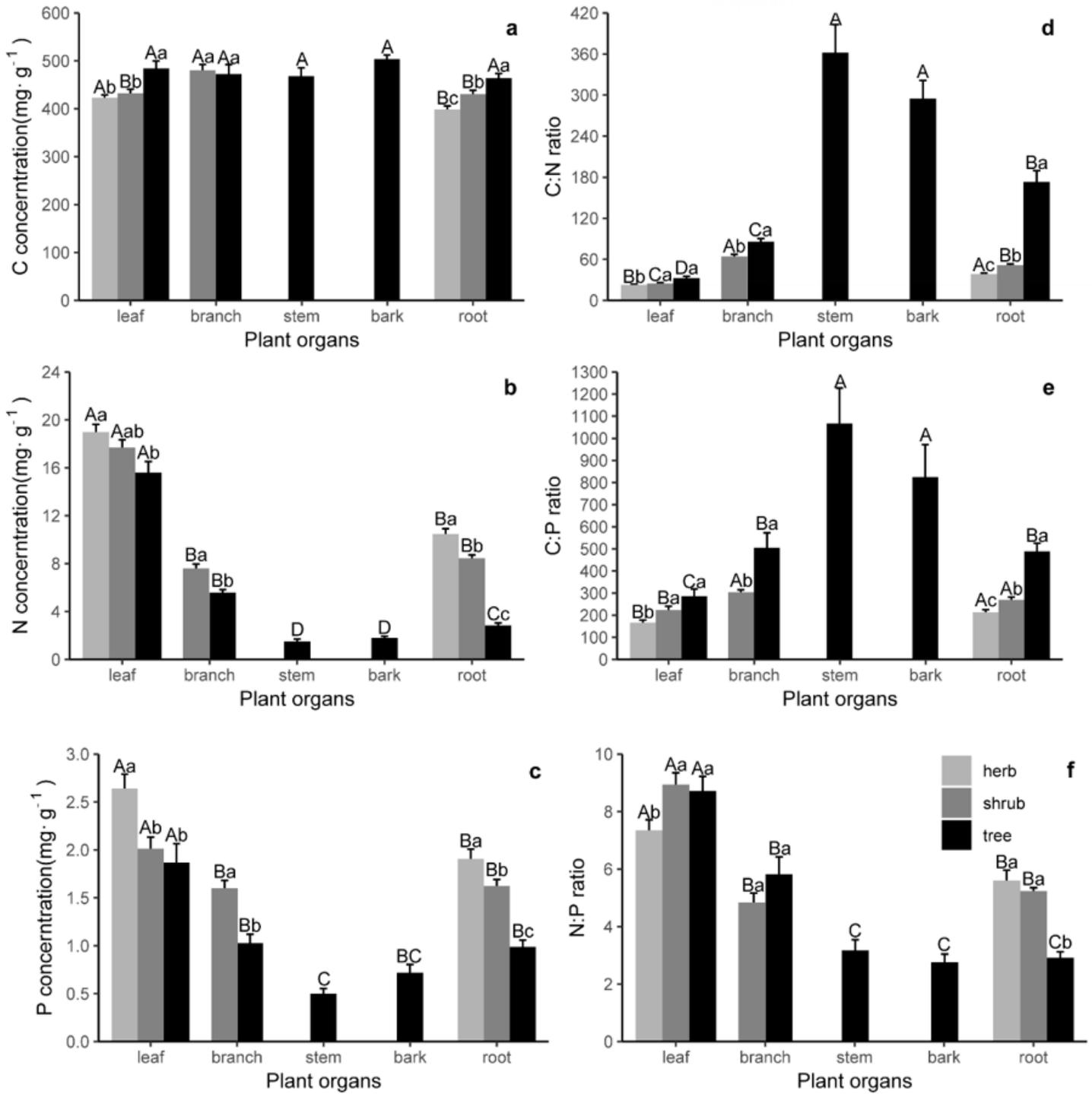


Figure 2

Stoichiometric characteristics of tree, shrub and herb tissue C, N, and P in natural secondary mixed forests (means \pm SE; n = 9). Different lowercase letters above the bars indicate significant differences among PFGs for the same organ ($p < 0.05$), while different uppercase letters indicate significant differences among organs for the same PFG ($p < 0.05$)

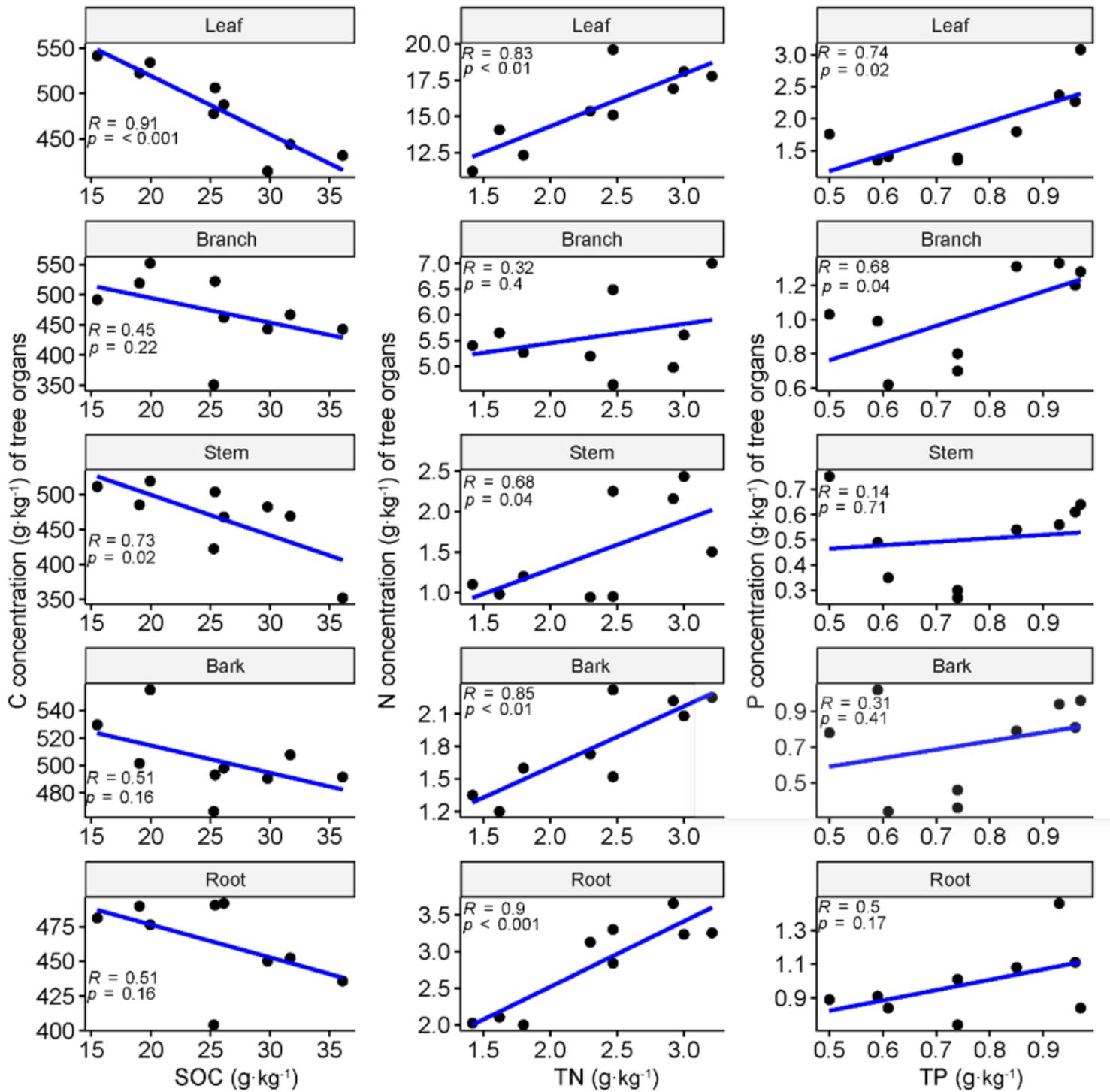


Figure 3

Correlations between tree organs and soil in C, N, and P contents in natural secondary mixed forest ecosystems. SOC: soil organic carbon; TN: soil total nitrogen; TP: soil total phosphorus

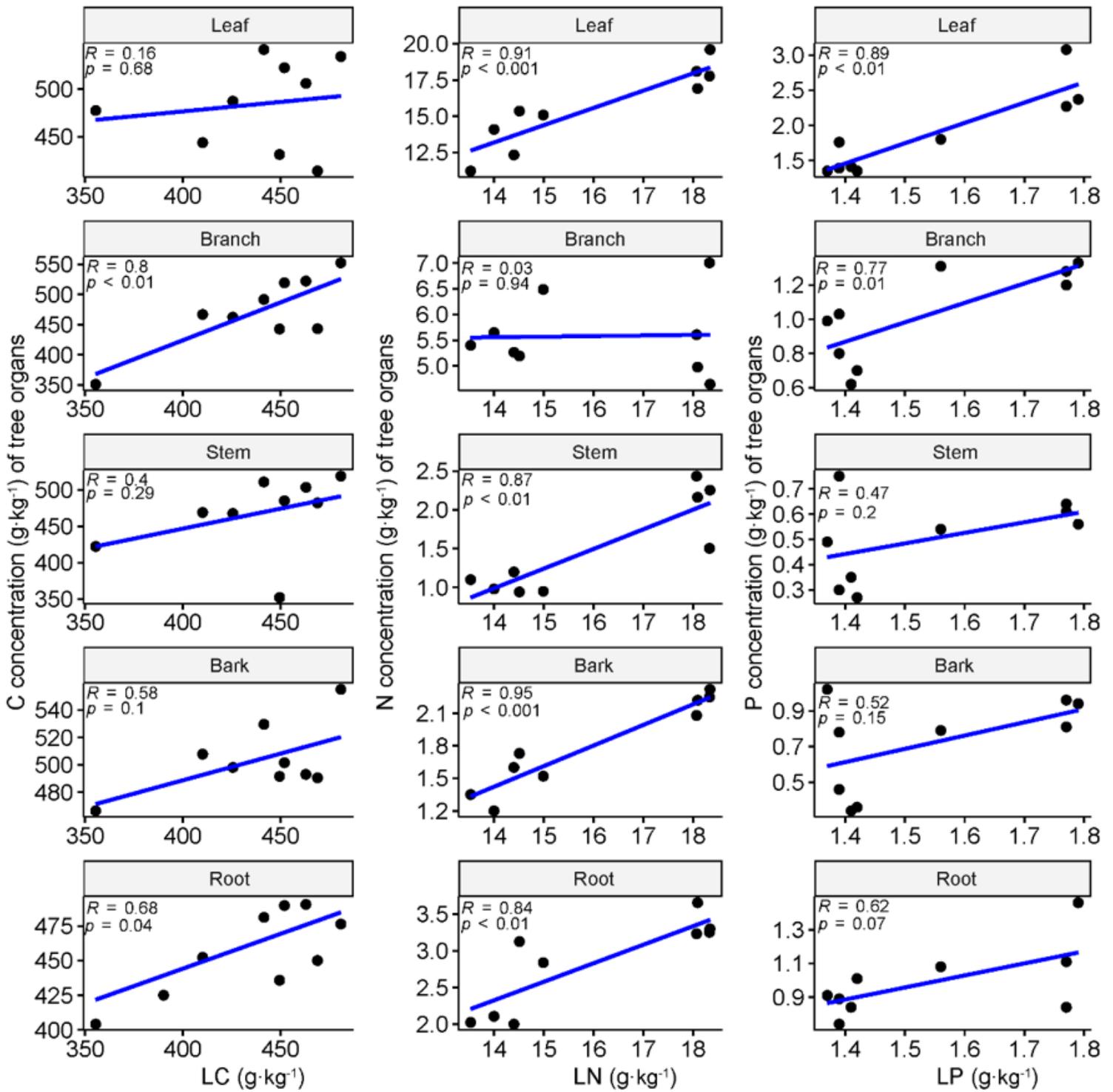


Figure 4

Correlations between tree organs and litter in C, N, and P contents in natural secondary mixed forest ecosystems. LC: litter carbon; LN: litter nitrogen; LP: litter phosphorus

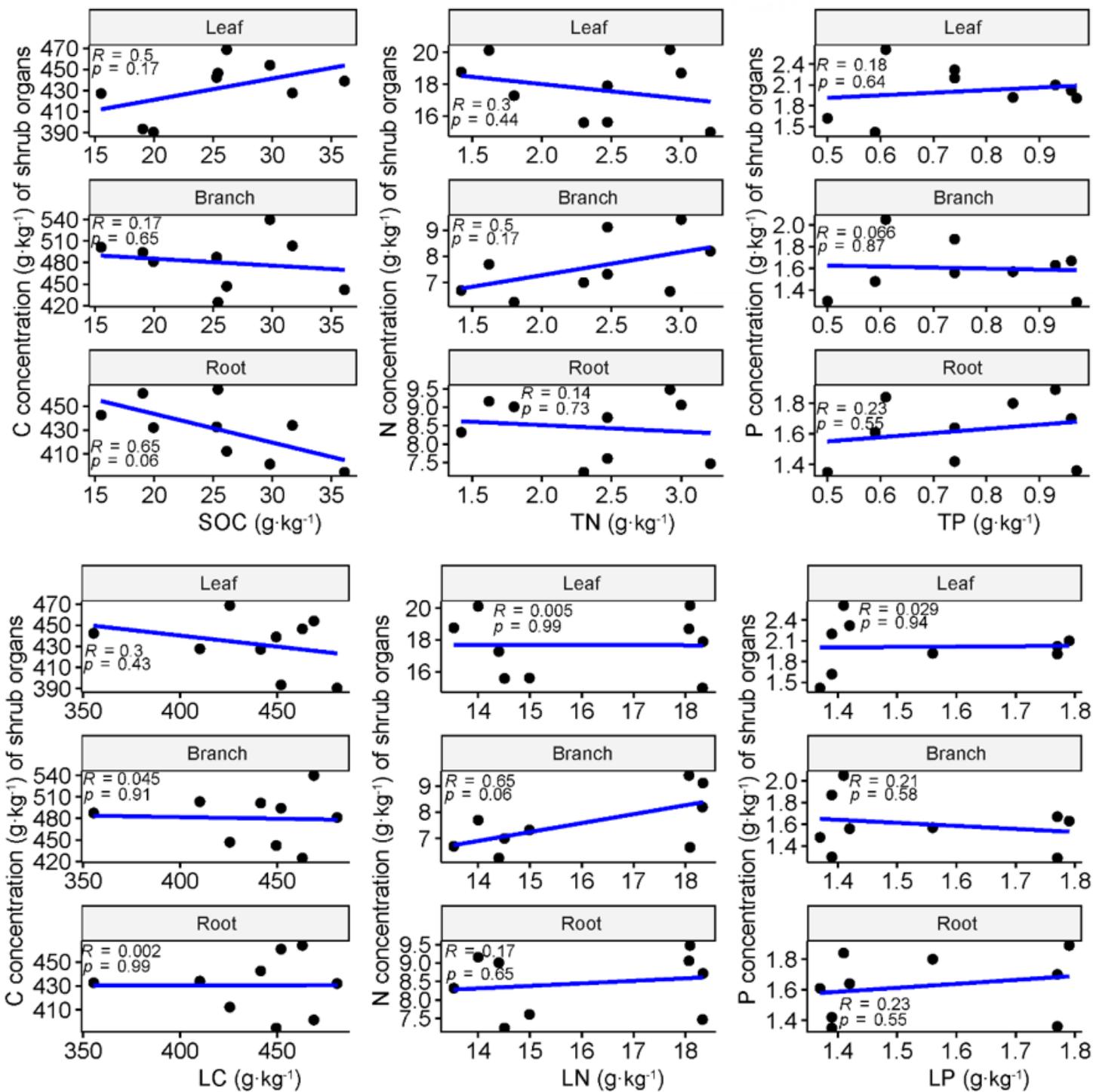


Figure 5

Correlations between shrub organs and soil and litter in C, N, and P contents in natural secondary mixed forest ecosystems. SOC: soil organic carbon; TN: soil total nitrogen; TP: soil total phosphorus; LC: litter carbon; LN: litter nitrogen; LP: litter phosphorus

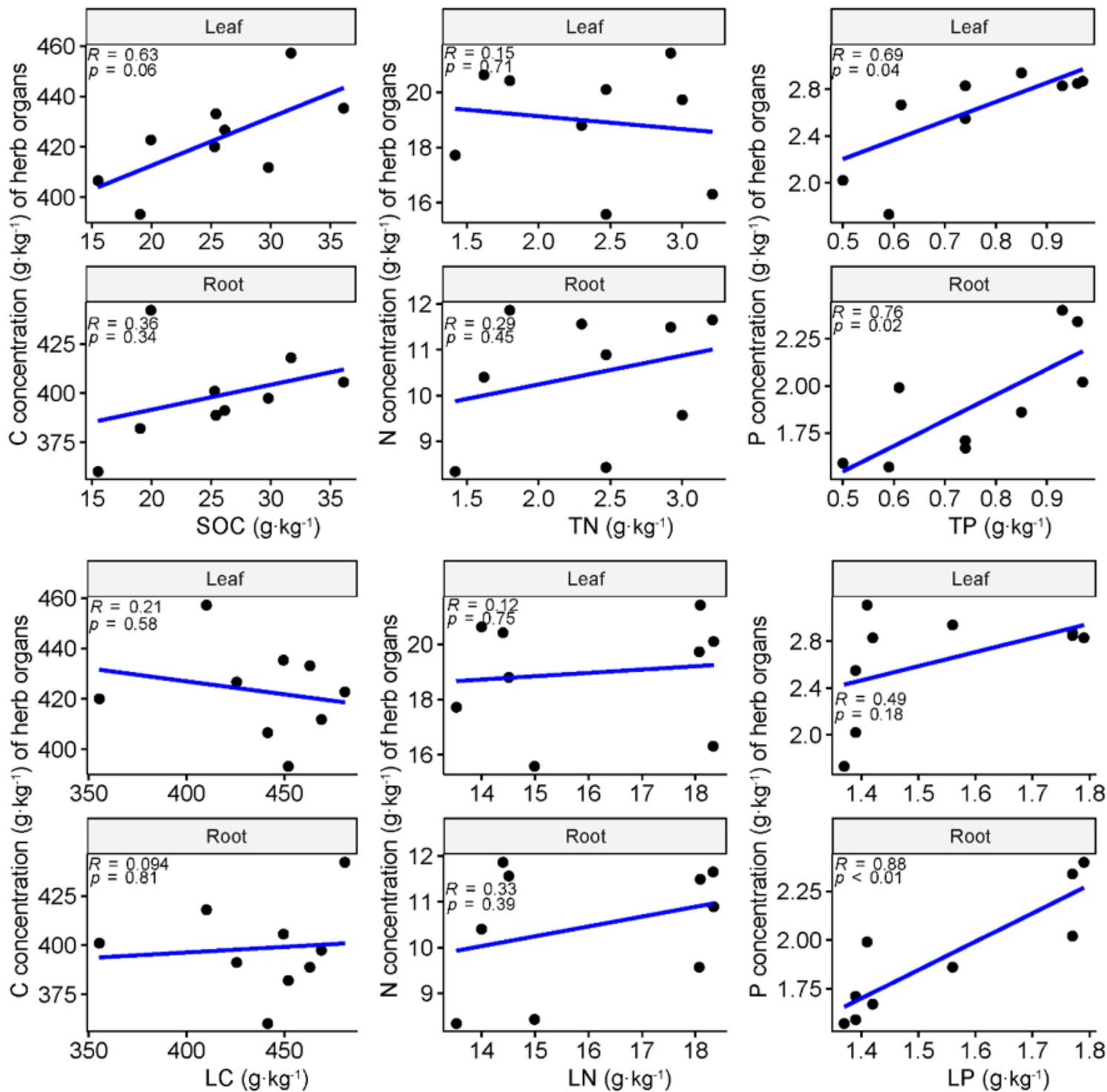


Figure 6

Correlations between herb organs and soil and litter in C, N, and P contents in natural secondary mixed forest ecosystems. SOC: soil organic carbon; TN: soil total nitrogen; TP: soil total phosphorus; LC: litter carbon; LN: litter nitrogen; LP: litter phosphorus

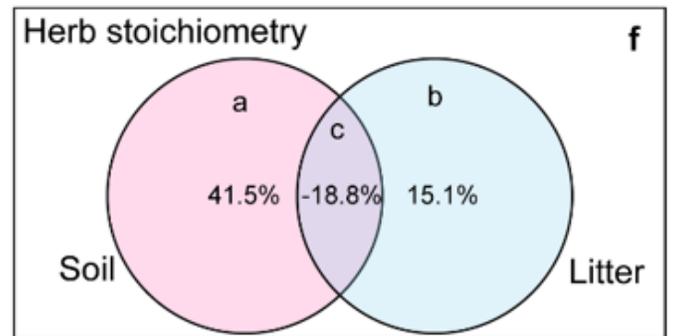
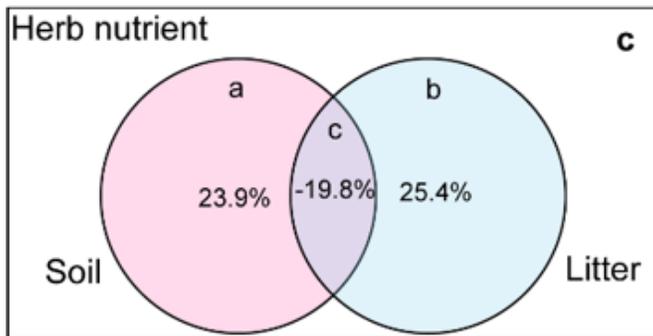
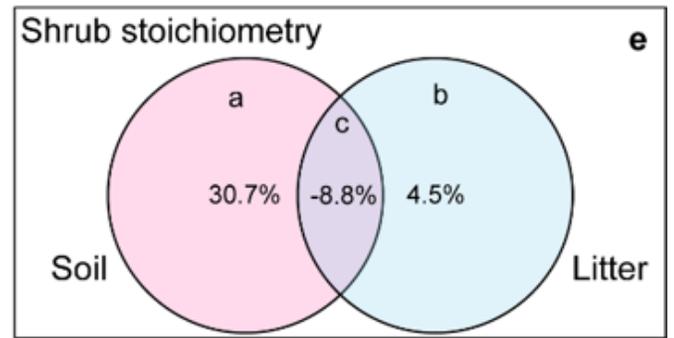
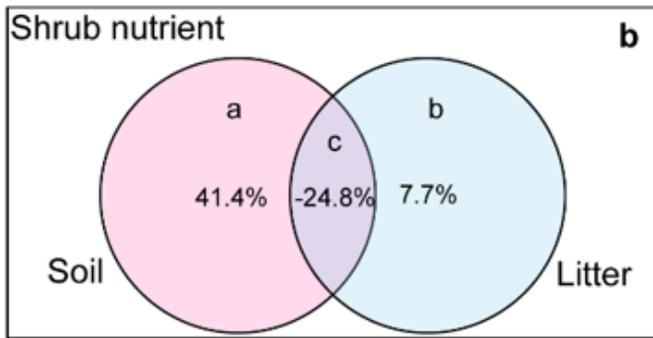
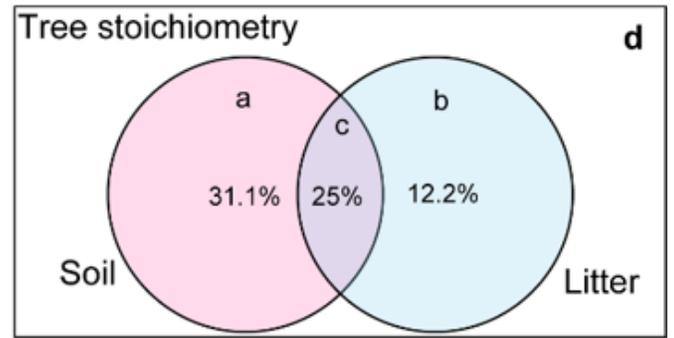
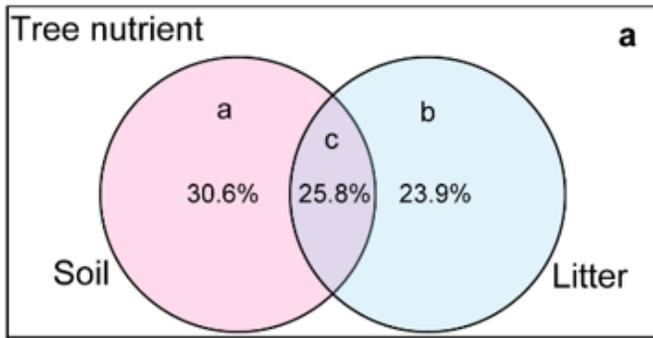


Figure 7

Variation partitioning of soil and litter nutrient characteristics (C, N and P) to account for variation in the nutrient concentrations and stoichiometric ratios of C, N and P in different PFGs. a and b are the individual effects; c is the explanatory part of the collinearity of a and b (a, b and c are all corrected values). For ecological interpretation, the negative correction values of a, b and c can be ignored or treated as 0 values

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