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Research paper

Variation of root resource acquisition and conservation strategies in a temperate forest is linked with plant growth forms

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Exploring why species of different plant growth forms can coexist in the same forest is critical for understanding the long-term community stability, but is poorly studied from root ecological strategies. The aim of this study was to explore the variation of root functional traits among different growth forms and their distribution patterns in root economics space to clarify how plant growth forms affect the root resource acquisition strategies of co-occurring species in a forest community. We sampled 115 co-occurring species with five growth forms (i.e., trees, shrubs, lianas, herbs and ferns) from a mega-plot (>50 ha) in temperate forest and measured seven root functional traits, including root morphological, anatomical and chemical traits, that are closely associated with root resource foraging and conservation strategies. We found that root specific length (SRL) and tissue density (RTD) showed wider variations than other traits among the five growth forms. Moreover, compared with clade and mycorrhizal type, variations of SRL and RTD were largely attributed to growth forms. Importantly, 115 co-occurring species were separately aggregated by growth forms along the trade-off dimension of SRL and RTD in root economics space, suggesting the diversity in root resource acquisition strategies at a local forest community is linked to plant growth forms. In particular, herbs were concentrated towards the side of high SRL and RN, by contrast, trees, shrubs and ferns were positioned at the side of high RTD and carbon/nitrogen, and lianas were located towards the middle. Diverse root resource acquisition strategies in plant growth forms allow them to occupy specific belowground ecological niches, thereby relieving the competition for the common resource. These findings advance our understanding of the mechanism for maintaining community species coexistence from a below-ground perspective.

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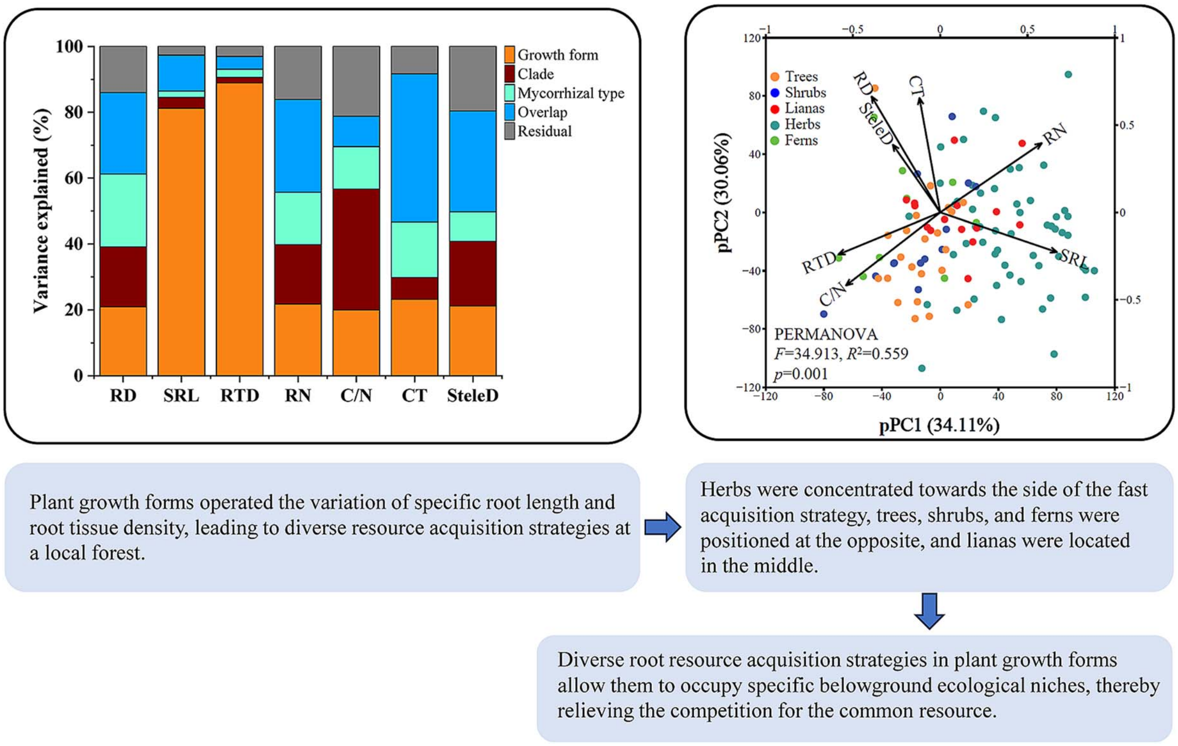
Graphical Abstract



Plant growth forms operated the variation of specific root length and root tissue density, leading to diverse resource acquisition strategies at a local forest.

Herbs were concentrated towards the side of the fast acquisition strategy, trees, shrubs, and ferns were positioned at the opposite, and lianas were located in the middle.

Diverse root resource acquisition strategies in plant growth forms allow them to occupy specific belowground ecological niches, thereby relieving the competition for the common resource.

Keywords: absorptive roots, plant life forms, root foraging strategy, root functional traits, root tissue density, specific root length.

Introduction

Plants have evolved diverse traits and strategies for capturing resources in different environments (Freschet et al. 2017, Iversen et al. 2017, McCormack et al. 2017), which can, in turn, affect community assembly and ecosystem functioning (McGill et al. 2006, Dorrepaal 2007, Weemstra et al. 2016, Laliberté 2017). The different trait combinations reflect the functional trade-off between resource acquisition (i.e., fast) and resource conservation (i.e., slow) in plant life-history strategies (Comas and Eissenstat 2009, Reich 2014, Weemstra et al. 2016). Species with acquisitive leaf traits, such as high nitrogen concentration and low leaf mass per area, may have great respiration rates and carbon dioxide (CO_2) fixation but short lifespans, contrasting the opposite performance of species with conservative traits (Reich et al. 1999, Wright et al. 2004). However, the variation of leaf traits at the global scale was much less than that at the local scale (Wright et al. 2004), because of local community constructed by different growth forms showing great leaf trait variation (Westoby and Wright 2006). For example, in a tropical forest, liana leaves with low tissue density and high nitrogen have cheaper construction costs than co-occurring trees, promoting their photosynthetic capacity and return on investment (Zhu and Cao 2010). Such differences in leaf traits were also found between trees and herbs in a temperate forest (Hikosaka et al. 1998), and between ferns and seed plants in a northern deciduous forest (Karst and Lechowicz 2007). These contrasting performances ultimately indicate that plant growth forms may play a key role in forming leaf economics spectrum at the local scale (e.g., Rossatto and Franco 2017, Funk et al. 2024, Matsuo et al. 2024), which may also occur in roots.

Within a community, some field studies have indeed found that the effect of growth forms on root morphology was significant such as specific root length (SRL) and root tissue density (RTD) (Roumet et al. 2008, Freschet et al. 2010, Laughlin et al. 2010), correspondingly changing root ecological strategies. For example, Liu et al. (2016) found that among three growth forms, herbaceous plants with fast growth rates had consistently lower RTD and shorter root lifespan than trees and shrubs in a desert community, and variation of both traits was narrower within growth form than across them. Likewise, Larson and Funk (2016) reported that herbaceous roots, compared with woody species, showed longer SRL in a Mediterranean community, which allows them to rapidly capture soil resources to support growth with less carbon investment. Furthermore, environmental pressures may also force each growth form to occupy specific resource niches for survival, such as coexisting grasses and trees at the same savanna site absorbing shallow water and deep water respectively (Rossatto et al. 2013), thereby avoiding strong competition for limited soil resources. As climate effect on root traits is weak, these findings provided important evidence that root strategies within a community may be also largely determined by plant growth forms. In forest communities, their structures are commonly composed by many growth forms, including not only trees, shrubs and herbs, but also ferns and lianas. These growth forms with different life-history strategies may play key roles in maintaining stand biodiversity and stability (Sharpe et al. 2010, Schnitzer 2018). It is natural to wonder whether such root eco-physiological strategies operated by growth forms are prevalent in forest ecosystems with more growth forms. More studies on this are therefore needed, as it could advance our understanding of the universal mechanism of long-term species coexistence at the forest community level.

Mounting studies have shown that applying the root trait dimension is a powerful approach to exploring root performances or strategies in changing environments (Kong et al. 2014, Kramer-Walter et al. 2016, Weemstra et al. 2016). This dimension reflects the trade-off between root construction cost, root lifespan and resource uptake efficiency, also called the root 'fast–slow' strategy (Reich 2014). As diverse root functions and soil resource heterogeneities, this framework has shifted from earlier one-dimension towards recent multi-dimensions (Weemstra et al. 2016), that is root economics space (RES) (Bergmann et al. 2020). In addition to a classical fast–slow gradient (i.e., RTD-RN axis), Bergmann et al. (2020) also added a novel 'collaboration' gradient (i.e., SRL-RD axis) representing the resource uptake strategies by roots and by mycorrhizal partner, respectively. The position of species along these axes are directly related to their ecological strategies in responding to environmental changes (Fort 2023). Roots of fast-growing species typically possess a lower RTD and higher RN to show higher metabolic activities, and a longer SRL or thinner RD to support their extensive resource foraging, all of which prompt them to separate from slow-growing species with opposite root traits in the RES (Bergmann et al. 2020). At the global scale, for instance, the separated pattern of herbaceous and woody plants was mainly along a collaboration gradient (Weigelt et al. 2021), reflecting the main difference in resource acquisition strategies between two major growth forms, which respectively depend on roots (e.g., herbaceous species) and mycorrhizal partners (e.g., woody species). Recently, many studies, however, have debated that the presence of patterns and trait relationships at a global scale may differ locally because the drivers of trait variation at global scale are not the same at local scale (Burton et al. 2020, Funk et al. 2024, Matsuo et al. 2024). Exploring how diverse plant growth forms in a local forest are organized along the major dimensions of root trait space, and which traits drive their distribution patterns, is, therefore, an important matter for understanding their role in community stability.

In this study, we sampled 115 co-occurring species from five growth forms, including canopy trees, understory shrubs, herbs and ferns as well as lianas (woody climbers), in a mega-plot in temperate forests. These five groups cover almost all growth forms in temperate forests, and differ in root forms and functions, particularly in life-history strategies. Seven key functional traits were measured on first-order roots for each species (Table 1). In addition to root morphological and chemical traits, we also measured anatomical traits, as they can regulate root uptake and transport functions (Guo et al. 2008, Kong et al. 2017). This study aimed to investigate how root resource acquisition strategies were operated by plant growth forms in a coexisting forest community. To be specific, we attempted to test the following two hypotheses: (i) SRL and RTD are strongly affected by growth forms, as the key traits representing the fast–slow strategy variations across growth forms, given that many previous studies have demonstrated that both traits play a major role in affecting plant life-history strategies among growth forms within communities (Freschet et al. 2010, Larson and Funk 2016, Liu et al. 2016); and (ii) if the first hypothesis is accepted, we hypothesize that species with different growth forms vary mainly along the SRL-RTD gradient, both ends are occupied respectively by relatively fast-growing growth forms (e.g., herbs with longer SRL, Larson and Funk 2016) and relatively slow-growing growth forms (e.g., trees and shrubs with higher RTD, Liu et al. 2016).

Materials and methods

Study site and species selection

This study was conducted at the Maoershan Experimental Station (45°21–′45°25′N, 127°30′–127°34′E) located in Heilongjiang province, China. This region represents a continental temperate monsoon climate: the mean annual temperature is 2.8 °C and the mean annual precipitation is 730 mm (Wang et al. 2006), and the soils are Hap-Boric Luvisols with high organic matter (Gong et al. 1999). This site is predominantly occupied by secondary forests, which were naturally regenerated after the primary forests were harvested more than half a century ago. In more than 50 hectares of stand, where the forest type is composed by deciduous broadleaved tree species. For trees, shrubs and herbs, we sampled only the most abundant species in the canopy and understory, while for lianas and ferns, we collected almost all the species we found. A total of 115 species were selected in this study, which belong to 49 families and 92 genera and were classified into the following growth forms: trees (22), shrubs (13), lianas (15), herbs (56) and ferns (9) (Table S1 available as Supplementary data at *Tree Physiology* Online). The scientific names of all species were queried against the World Flora Online (WFO, http://www.worldfloraonline.org/).

Root sampling and trait measurements

All species were sampled in a common stand in July and August. For each tree, shrub and liana species, we sampled at least three mature individuals. For each individual, at least 10 intact root branches in the mineral soil layer (within 20 cm) were obtained based on the approach of Pregitzer et al. (2002). To identify the roots of each woody species, we used the method of tracing to the trunk base to collect root samples from the main lateral branches (Guo et al. 2008). For herbs and ferns, about five to 10 individuals of each species were randomly selected according to the size of root biomass (Dong et al. 2015), and obtained root samples from the mineral soil layer (within 20 cm). All root samples were divided into two sub-samples for later analysis of root morphology, chemistry and anatomy in the laboratory. One sub-sample for anatomical analysis was gently washed by using deionized water and placed into the FAA (formalin-aceto-alcohol) solution immediately (each 100 mL consists of 90 mL of 50% ethanol, 5 mL of 100% glacial acetic acid, as well as 5 mL of 37% methanol) (Wang et al. 2023). Another sub-sample for the analysis of morphological and chemical traits was placed into Ziploc bags. All samples were put into a cooler and transported to the laboratory in a few hours and were stored in a standard freezer for analysis at a later date.

For morphological analysis, the root samples of each species were carefully dissected by forceps based on the root branching order (Pregitzer et al. 2002), that is, the distal nonwoody roots (i.e., root tips) were considered as first-order roots. Subsequently, 150–300 first-order roots of each root sub-sample were randomly chosen and scanned by using a color scanner (Epson Expression 10,000XL, dpi = 800, Seiko Epson Cor.). Then, we used software for analyzing the root system (WinRhizo 2004b, Regent Instruments Inc.) to obtain the

Table 1. List and descriptive statistics of seven functional traits of first-order roots for all species in a temperate forest.

Traits	Unit	Abbreviation	Mean	Maximum	Minimum	CV[1]	Blomberg's *K*	Pagel's λ
Root diameter	mm	RD	0.263	0.522	0.093	0.305	**0.144**	0.763
Specific root length	m g^{-1}	SRL	322.776	1113.157	31.062	0.914	**0.195**	**0.964**
Root tissue density	g cm^{-3}	RTD	0.120	0.561	0.005	1.028	**0.148**	**0.897**
Root nitrogen concentration	mg g^{-1}	RN	25.308	53.653	11.926	0.283	**0.200**	**0.705**
Ratio of root carbon to nitrogen	—	C/N	19.205	49.722	8.350	0.351	**0.223**	**0.658**
Cortex thickness	μm	CT	82.572	186.450	14.770	0.421	**0439**	**0.601**
Stele diameter	μm	SteleD	67.420	219.125	23.060	0.436	0.054	0.000

[1] CV, the coefficient of variation. Bold values indicate traits that showed stronger phylogenetic signal than expected at random ($P < 0.05$).

mean values of root diameter (RD, mm) and length, as well as the volume of each sample. These samples were oven-dried at 65 °C and then weighted (nearest 0.0001 g). After calculating the SRL (m g^{-1}) and tissue density (RTD, g cm^{-3}), all dried root samples were ground to a fine powder for analyzing tissue nitrogen (RN, mg g^{-1}) and carbon (RC, mg g^{-1}) concentrations by using an elemental analyzer (Vario Macro, Elementar Co.), and the carbon to nitrogen ratio (C/N) was finally calculated.

For determining root anatomical traits, roots in FAA solution were also carefully dissected by forceps according to branching orders (Pregitzer et al. 2002). For each species, we randomly chose 30–50 first-order roots and adopted the paraffin section technique to make 8-μm-thick root cross-section slides for measuring root anatomical traits (Guo et al. 2008, Gu et al. 2014, Wang et al. 2023). We used a compound microscope (BX-51, Olympus Corporation) to photograph all root cross-section slides, and used Motic Images Advanced 3.2 software (Motic Corporation) to measure cortical thickness (CT, μm) and the stele diameter (SteleD, μm) for each species. In addition, we used a compound microscope (BX-51, Olympus Corporation) to determine the mycorrhizal types for first-order root of each species, the mycelia of arbuscular mycorrhizal (AM) penetrate inside the cortical cells to form various haustoria, and the mycelia of ectomycorrhiza (EM) form a dense sheath on the root tips' surface and have Hartig net around epidermal cells (Brundrett 2004).

Data analysis

In each species, we calculated the mean and standard error by using the data of trait measurements. And then we calculated the values of the mean, maximum and minimum as well as coefficient of variation (CV), respectively, among and within growth forms. The differences for each trait among growth forms were tested by using MANOVA in SPSS software (V.27.0.1.0, SPSS Inc.).

To assess the influence of plant evolutionary history on root trait variation of all species, we performed the 'phylo.maker' function (R package V.Phlomaker; Jin and Qian 2019) for constructing a phylogenetic tree. Then, we conducted the 'phyloSignal' function (R package Phylosignal; Keck et al. 2016) to calculate the phylogenetic signal of all root traits and used the 'abouheif.moran' function (R package Adephylo; Jombart et al. 2010) to perform Abouheif's test (Abouheif 1999).

We used original data and phylogenetically independent contrasts (PICs) data by performing SPSS software (V.27.0.1.0, SPSS Inc.) and the 'pic' function (R package Ape; Paradis et al. 2004) respectively, for conducting the Pearson's correlation analyses among and within growth forms. We used the 'phyl.pca' function (R package Phytools; Revell 2012) to perform phylogenetically informed principal component analysis (pPCA) for seven functional traits and four core traits (i.e., RD, SRL, RTD and RN) among and within each growth form for investigating the multivariate correlations and the root economics space (Bergmann et al. 2020). We also performed the 'adonis' function (R package Vegan; Dixon 2003) to conduct a permutational analysis of variance (PERMANOVA) based on Bray-Curtis distance measurements under different growth forms to ensure whether species with different growth forms could be differently distributed in the root economics space. We also used SPSS software (V.27.0.1.0, SPSS Inc.) to perform a discriminant function analysis (DFA) to investigate which trait affects the differences of distributions among growth forms in the root economics space (Ramayah et al. 2010).

Finally, to further explore the specific effect of growth form, clade and mycorrhizal type on the variation of each root trait, we constructed a linear mixed model to perform variance partitioning analysis across all plants. Each root trait was defined as a dependent factor; for the model, 'clade' was a fixed factor, and per 'growth form' and 'mycorrhizal type' nested in 'clade' were random factors (Weemstra et al. 2021). The variance could not be attributed to independent effects of individual factors but might be explained by the full model being labeled as 'overlap' (Valverde-Barrantes et al. 2017, An et al. 2022). These statistical tests were carried out in the R package lme4 (Bates et al. 2015). All phylogenetic-related analyses were performed in R software 4.0.3 (R Core Team 2020).

Results

Variation of root traits

The seven root functional traits varied largely across 115 co-occurring species (Table 1) and among the growth forms (Figure 1). RTD and SRL showed high variation, 112-fold (CV = 1.028) and 36-fold (CV = 0.914), whereas RD, RN and C/N showed low variation, less than 6-fold. The CT and SteleD had moderate variation, 9 to 12-fold (Table 1). To be specific, herbs exhibited the thinnest RD and the longest SRL, while shrubs showed the opposite trend (Figure 1a and b, Table S2 available as Supplementary data at *Tree Physiology* Online). Moreover, herbs also showed the lowest RTD, while trees showed the highest (Figure 1c, Table S2 available as Supplementary data at *Tree Physiology* Online). Additionally, herbs had the highest RN and the lowest C/N, respectively, whereas ferns possessed the lowest RN and the highest C/N (Figure 1d and e, Table S2 available as Supplementary data at *Tree Physiology* Online). There was no significant difference in CT (except ferns) and SteleD among the five growth forms (Figure 1f and g).

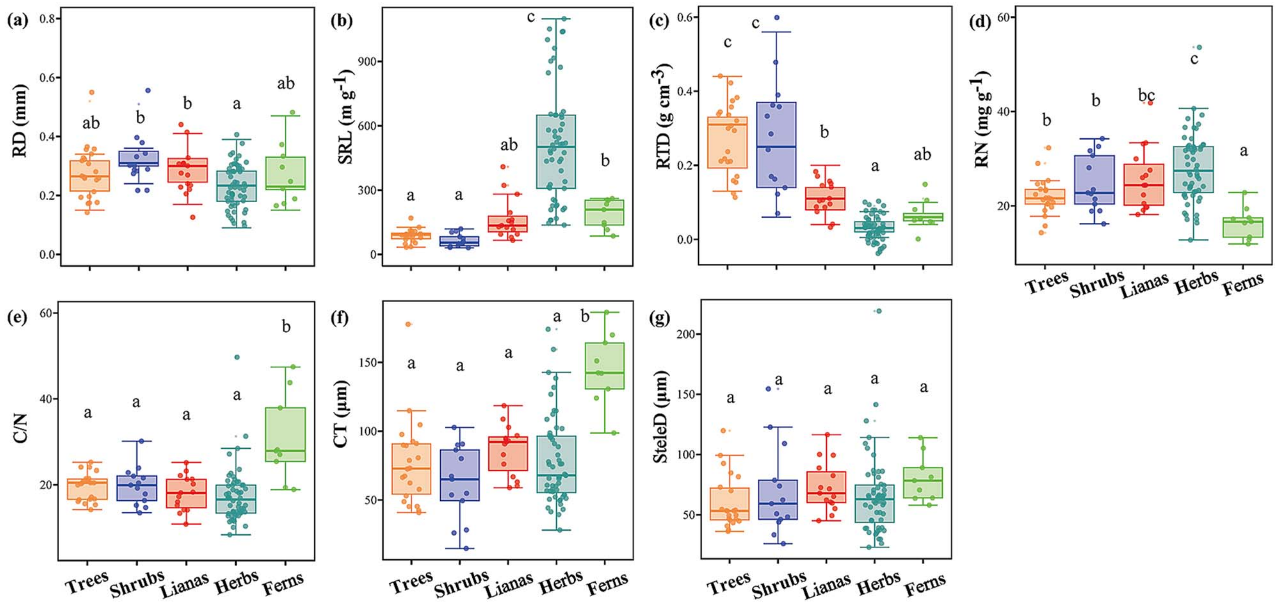


Figure 1. Distribution of seven functional traits of first-order roots for five growth forms in a temperate forest. Boxplots include the median (horizontal line within boxes), the first and third quartiles (bottom and top parts of the box, respectively), and the two whiskers (10th and 90th percentiles). Different letters indicate significant differences between the five plant growth forms ($P < 0.05$). Trait abbreviations are provided in Table 1.

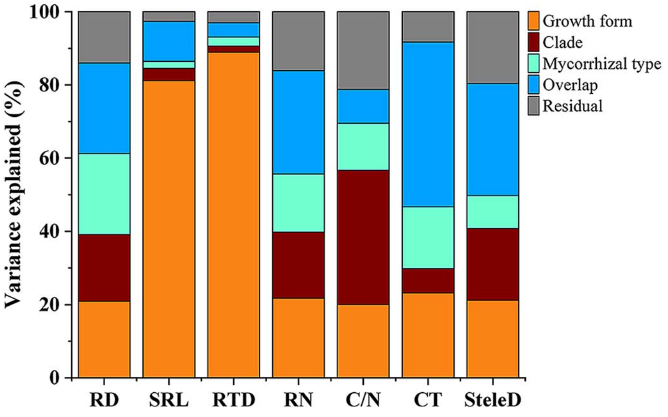


Figure 2. Variance partitioning of growth form, clade and mycorrhizal type of seven functional traits of first-order roots for all species in a temperate forest. Trait abbreviations are provided in Table 1.

Factors contributing to root trait variations

Variance partitioning analysis showed that growth form, clade and mycorrhizal type all together explained about 47–93% of the total variance among root traits (Figure 2). However, growth form greatly influenced the variation of SRL and RTD, explaining 81% and 88% of the variation in these two traits, but less than 25% of the variation in other traits (Figure 2). Despite, nearly all traits showed phylogenetic signals (except for SteleD, Table 1), the contributions of the clade, an indicator of plant phylogenetic structure, to variation accounted for 6–36% in RD, RN, C/N, CT and SteleD, and 3% and 2% in SRL and RTD (Figure 2). The contribution of mycorrhizal type accounted for 8–22% in RD, RN, C/N, CT and SteleD, respectively, and less than 3% in SRL and RTD (Figure 2).

Trait correlations

Across 115 co-occurring species, RD represented a negative correlation with SRL and positive correlations with CT and SteleD (Table 2). The SRL was negatively correlated with RTD, C/N, CT and SteleD, but positively covaried with RN (Table 2). There was also a negative correlation between RTD and RN, and a positive correlation between RTD and C/N (Table 2). Similar trends also occurred in PICs analysis (Table 2) and each growth form (Table S3 available as Supplementary data at *Tree Physiology* Online), but the degree of correlations showed somewhat different.

Trait dimensions and distribution patterns of the five growth forms

By using the approach of pPCA, we found that the seven root functional traits of 115 co-occurring species exhibited multidimensional (Figure 3), even in each growth form (Figure S1 available as Supplementary data at *Tree Physiology* Online). The first PC axis captured 34.11% of the total variation and had strong loadings on SRL, RTD and C/N, where SRL and RN showed trade-offs with RTD and C/N (Figure 3a, Table 3). The second axis, which accounted for 30.06% of the total variation, had strong loadings on RD and CT,

Table 2. Pearson's correlation coefficients for pairwise comparisons of seven functional traits of first-order roots for all species in a temperate forest.

	RD	SRL	RTD	RN	C/N	CT	SteleD
RD	1	**−0.542**	**−0.233**	0.110	−0.113	**0.661**	**0.439**
SRL	**−0.541**	1	**−0.269**	0.142	**−0.226**	**−0.259**	−0.172
RTD	0.114	**−0.614**	1	**−0.231**	**0.483**	**−0.424**	−0.021
RN	0.091	**0.340**	**−0.358**	1	**−0.647**	0.184	−0.095
C/N	−0.116	**−0.244**	**0.227**	**−0.780**	1	−0.159	0.071
CT	**0.513**	**−0.201**	**−0.277**	−0.031	0.082	1	0.007
SteleD	**0.449**	**−0.219**	−0.077	−0.094	0.046	**0.255**	1

Upper-right diagonal is PICs data and lower-left diagonal is original data. Bold values represent significant correlations ($P < 0.05$). Trait abbreviations are provided in Table 1.

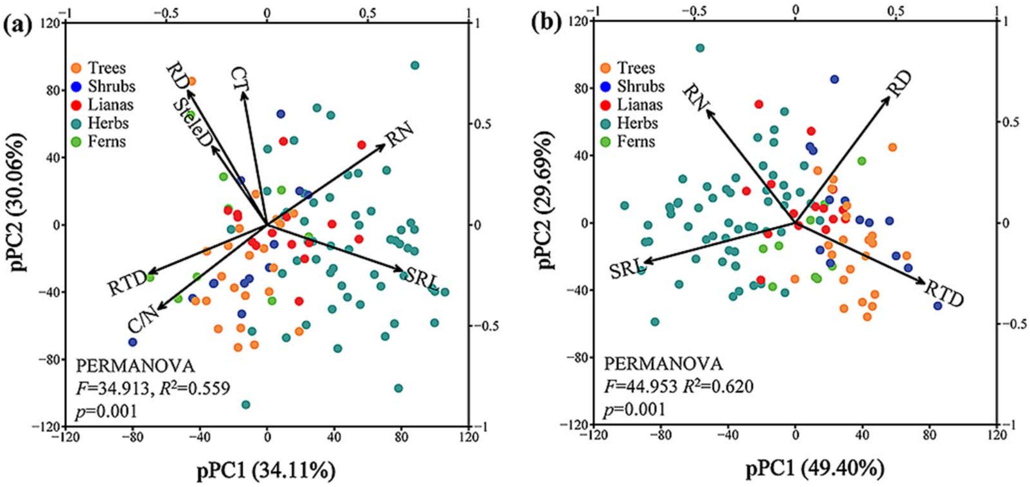


Figure 3. Phylogenetically informed principal component analyses (pPCA) of seven functional traits (a) and four core traits (b) of first-order roots for five growth forms in a temperate forest. Loading scores are shown in Table 3. Points indicate the position of species along the first two axes. F, R^2 and P-values represent permutational multivariate analysis of variance test (PERMANOVA) based on Bray-Curtis distance measurements under different plant growth forms. Trait abbreviations are provided in Table 1.

and both traits exhibited a positive correlation (Figure 3a, Table 3). The results of PERMANOVA showed that the species among the five growth forms distributed differently in the RES ($P = 0.001$) (Figure 3a). Herbs were concentrated towards the side of high SRL and RN, by contrast, trees, shrubs and ferns were positioned at the side of high RTD and C/N, and lianas were located towards the middle (Figure 3a). These aggregation patterns were driven by SRL and RTD according to the test of the discriminant function analysis (DFA) (Table S6, Figure S2a available as Supplementary data at *Tree Physiology* Online). Similar results were also found in pPCA for four core traits (Figure 3b, Table 3, and Table S7, Figure S2b available as Supplementary data at *Tree Physiology* Online).

Table 3. Loading scores of seven functional traits (Figure 3a) and four core traits (Figure 3b) of first-order roots in the pPCA for all species in a temperate forest.

	pPC1	pPC2
Variation explained	34.11%	30.06%
RD	−0.471	0.796
SRL	0.802	−0.273
RTD	−0.700	−0.288
RN	0.698	0.476
C/N	−0.647	−0.501
CT	−0.143	0.786
SteleD	−0.326	0.465
Variation explained	49.40%	29.69%
RD	0.557	0.746
SRL	−0.895	−0.236
RTD	0.768	−0.360
RN	−0.524	0.668

Trait abbreviations are provided in Table 1.

Discussion

Plant growth forms reflect the key functional response of plants concerning their habitats and may provide important insights into the ecological strategies acting on the community assembly and ecological processing (Adler et al. 2013, Taylor et al. 2023). Based on investigating seven root traits of the five growth forms (i.e., trees, shrubs, lianas, herbs and ferns), two important findings were obtained in our study. First, compared with other factors, variation of SRL and RTD was largely influenced by growth forms, across 115 co-occurring species in a temperate forest community. Second, we further found that the five growth forms aggregated separately in the root trait space, such aggregation pattern was mainly along the trade-off axis which is formed by SRL and RTD. These findings, consistent with our two hypotheses, suggest that diversity in belowground resource acquisition strategies in a local forest community is linked overall to plant growth forms.

Across all species, SRL and RTD exhibited particularly wider variation than other traits (Table 1), such wide variation suggests that these co-occurring species in a local forest can support their diverse resource acquisition strategies by varying root functioning in soil resource exploration, root tissue turnover and metabolic activity (McCormack et al. 2017, Freschet et al. 2021). Additionally, variance partitioning analysis clearly showed that over 80% of the variation in SRL and RTD was caused by growth forms, rather than by phylogenetic clade or the mycorrhizal type (Figure 2). The reason for smaller effects in the latter two is not clear, perhaps the two major clades (i.e., Asterids and Rosids, which account for 75% of the total species) in our study forest contain all growth forms (except ferns, Table S1 available as Supplementary data at *Tree Physiology* Online), and about 95% of species are AM species (Table S1 available as Supplementary data at *Tree Physiology* Online), consequently, their effects on both trait variations might be weakened or obscured by growth forms. Although the minor contribution of the clade, most root traits displayed significant phylogenetic signals according to Blomberg's *K* and Pagel's λ tests (Table 1), suggesting that their variations were also constrained by plant phylogeny (Comas and Eissenstat 2009, Kong et al. 2014). However, this phylogenetic constraint was weakly in each growth form (Table S8 available as Supplementary data at *Tree Physiology* Online). At the global scale, macroclimate and plant phylogeny are two important factors driving root trait variations that have been proposed in many previous studies (Freschet et al. 2017, Valverde-Barrantes et al. 2017, Ma et al. 2018). In the same stand with similar climates, however, our findings demonstrated that growth form may also contribute more to variations in some specific root traits, particularly in SRL and RTD. On the other hand, nearly all root traits (except for SteleD) showed significant differences among growth forms (Table S2 available as Supplementary data at *Tree Physiology* Online), but the ranking of trait size in SRL and RTD can regularly distinguish the species with different growth forms (Figure S3b and c available as Supplementary data at *Tree Physiology* Online), such arrangement patterns further highlight the significance of growth form on the variation of the two root functional traits in local forests.

In the current study, we found that the root trait framework was multidimensional in all species of five growth forms (Figure 3), in line with previous research at regional and global scales (Kong et al. 2014, Kramer-Walter et al. 2016, Ma et al. 2018). Linking the framework of the RES (Bergmann et al. 2020), all root traits were loaded on two leading dimensions (Figure 3). One was called the 'collaboration' gradient composed by SRL, RD and CT, as well as SteleD, representing two alternative strategies of root resource foraging by roots themselves or relying on mycorrhizal partners. Another dimension was called the traditional fast–slow 'conservation' gradient formed by RTD, C/N and RN, reflecting a trade-off between carbon investment and resource return (Bergmann et al. 2020). Such leading dimensions also occurred in most growth forms in this study (Figure S1 available as Supplementary data at *Tree Physiology* Online), but had somewhat difference in shrubs as RD had a weak relationship with CT and SteleD (Figure S1c available as Supplementary data at *Tree Physiology* Online). In shrub roots, the CVs of both anatomical traits, indicative of the capacity of root resource uptake and transportation, were the highest and showed more than double that of RD (Table S2 available as Supplementary data at *Tree Physiology* Online), which in turn may confer their roots to have more flexible strategies to balance resource uptake and transport (Kong et al. 2017), and beneficial for their long-term ecological adaption and diversity maintenance under seasonal canopy openness (Wang et al. 2009). The result in shrub roots also suggests that the understory environments may alter the strategy framework of the root traits in some growth forms. Importantly, we found that these five growth forms separated regularly along the SRL-RTD trade-off axis in the RES (Figure 3). From herbs to lianas to shrubs, trees and ferns, such separation patterns reflect that they occupied different belowground ecological niches showing diverse resource foraging strategies within the same stand of temperate forests.

Canopy trees, as dominant species in forest ecosystems, govern the eco-physiological performances of the most understory species in their habitats (Barbier et al. 2008, Caplan et al. 2017), particularly their wide canopy and high above- and below-ground biomass could confer them to have a competitive advantage over other growth forms in capturing light and soil resources (Riegel et al. 1992, Bakker et al. 2006). Compared with other growth forms, however, trees had conservative root trait syndromes in temperate forests, with relatively lower SRL and higher RTD (Figure 1b and c), which put them to occupy the side of corresponding to slow life-history strategies in the RES (Figure 3). Trees cost much carbon to construct highly dense roots, which may reduce SRL and lead to overall low resource exploration and acquisition capacity and enhance root lifespan (Comas and Eissenstat 2004, Reich 2014, Freschet et al. 2017), but all of these could be more beneficial for the long-term stability of forest structure and function. For shrubs, Putz et al. (2024) recently found that shrubs and trees did not differ in nutrient-absorbing capacities or efficiencies in a temperate forest, consistent with our finding that both growth forms loaded on the side of high RTD in the RES (Figure 3). Moreover, there were no significant differences in all root traits between shrubs and trees (Figure 1), indicating similar root ecological strategies between two growth forms in a temperate forest although distinction in phenotype and growth rate aboveground.

Lianas are a unique growth form in the forest community (Schnitzer 2018) and occupy the middle of the SRL-RTD trade-off axis compared with other growth forms in this study (Figure 3). Several possible reasons may help to explain our findings. Firstly, this aggregation pattern may reflect the differences in root demography among growth forms. For example, Chen and Brassard (2013) reported that the lifespan of liana roots is shorter than that of trees, but longer than that of herbs, which was in line with the ecological performance of lianas in the root trait space (Figure 3). Secondly, such aggregation pattern of lianas may be related to their life-history strategies. On one hand, lianas are considered as a fast-growing species among woody plants (Toledo-Aceves 2015, Schnitzer 2018), and they should have fast functional traits to perform their competitive abilities (Comas and Eissenstat 2004, Reich 2014). Some field studies, for instance, have observed that lianas possess more acquisitive root strategies for limited soil resource uptake compared with trees (Collins et al. 2016, Wang et al. 2023), such as higher RN and SRL, and lower RTD (Figure 1). On the other hand, unlike self-supporting woody species that invest much carbon to construct a relatively large root system to support aboveground biomass and upward growth, most lianas have slender stems and rely more on host trees to climb to the top of the forest canopy (Schnitzer 2018). This habit, thus, may confer that the major function of liana roots is resource uptake (Collins et al.

2016, Wang et al. 2023). These merits might allow liana roots to quickly forage soil resources to support fast growth with less carbon investment.

In our study, herbs exhibited the highest SRL and lowest RTD (Figure 1a and c), consequently, occupying the fast side of the RES among all growth forms (Figure 3). This result observed in temperate local forests is in line with the findings of some recent studies at global and regional scales (Weigelt et al. 2021, An et al. 2022). As fast-growing species, many field studies have reported that herbaceous roots have strong competitive traits over other growth forms such as co-occurring trees or shrubs in the same community (Rossatto et al. 2013, Larson and Funk 2016, Liu et al. 2016), due to they have evolved thin RD, long SRL and low dense roots (Freschet et al. 2017, Valverde-Barrantes et al. 2017, Ma et al. 2018, An et al. 2022). With these root trait syndromes, herbaceous roots exhibit higher precision or sensitivity of response to soil resource (e.g., nutrients and water) patches (Einsmann et al. 1999), and absorb soil nutrients more rapidly and efficiently than woody plants with the same investment in belowground carbon (Larson and Funk 2016). Even in the understory of temperate forests with shorter growing seasons, herbs are also strong competitors for capturing resources in below-ground.

Interestingly, ferns and herbs are both understory and typically shade-tolerant species growing within the same forest, yet the two groups differed notably in their root strategies. Ferns showed lower SRL and RN, and higher RTD representing a relatively conservative strategy for resource acquisition compared with herbs (Figure 1). The exact mechanism is unclear, but might be related to the unique evolutionary history toward conservative functional traits adapted to shade and wet environments (Page 2002, Jin et al. 2020). Compared with seed plants or other vascular plants, some studies have demonstrated that understory ferns also exhibit exceptionally slow growth (Page 2002, Sharpe et al. 2010), potentially related to their low photosynthetic rate caused by the low nitrogen and phosphorus content in leaves (Brodribb et al. 2005, 2007, Han et al. 2005, Richardson and Walker 2010). Consistent with these observations, fern roots possessed the lowest RN and the highest C/N among the five growth forms (Figure 1), like trees and shrubs it is reasonable to occupy the high resource conservative side in the RES (Figure 3). This strategy may be a better way for ferns to maintain their long-term survival in the understory.

Conclusion

Our study links 115 co-occurring species from a temperate forest to their growth forms to explore root trait variation and aggregation patterns in the RES. The growth form potentially plays a critical role in forming diverse root ecological strategies in a local temperate forest community. The variation of SRL and RTD was primarily attributed to plant growth forms. All species were separately aggregated by growth forms along the trade-off dimension of SRL and RTD in the RES. This separation pattern overall reflected the trade-off between root foraging strategies (i.e., high SRL to confer roots with rapid resource exploration) and life-history strategies (i.e., high RTD to confer roots to have long lifespan for resource conservation) of different growth forms within forest communities. Such trait strategy frameworks may enable co-occurring species to occupy specific belowground ecological niches, which could be more beneficial for relieving resource competition and maintaining species coexistence at the community levels. These findings advance our understanding of the potential mechanisms of community assembly and stability from a below-ground perspective. Considering global climate change, further researches are needed to determine whether these findings are consistent in other ecological biomes, such as tropical and subtropical forests with more rich plant growth forms.

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Supplementary data

Supplementary data for this article are available at *Tree Physiology* Online.

Authors' contributions

T.S. and S.Y.W. conceived the ideas; S.Y.W. performed field sampling, laboratory works and data analyses; S.Y.W., L.H.C., P.B.R., M.L.M., R.P.P., J.C.G. and T.S. interpreted the data and wrote the manuscript. The authors declare no conflict of interest.

Conflict of interest

None declared.

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Data availability

The data underlying this article will be shared on reasonable request to the corresponding author.

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