

The effect of hydraulic and leaf photosynthesis properties on the spread and distribution of *Dasiphora fruticosa* in Qinghai-Tibet Plateau alpine meadows

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Abstract

Background and Aims

Qinghai-Tibet Plateau is the largest alpine grassland area in the world. Alpine region is a typical and unique plateau ecosystem. Natural and human-induced factors have resulted in shrub encroachment in the Qinghai-Tibet Plateau alpine meadows. Yet, the role of functional traits of different plant organs in shrub encroachment remain insufficiently explored.

Methods

Here, we measured stem and leaf hydraulics, leaf photosynthesis characteristics, and other functional traits of *D. fruticosa* in different habitats.

Results

We found that hydraulic traits (K_L , K_S , π^0 , ϵ) and leaf photosynthetic capacity (A_a , A_m , g_s) were key factors in the shrub encroachment of *D. fruticosa*. In addition, variations in root average diameter (RAD) and specific root length (SRL) were mainly influenced by soil total nitrogen (STN) and soil total phosphorus (STP) between two habitats. On soil water and nutrient deficient sunny slopes, below-ground functional traits of *D. fruticosa* tend to favour a resource acquisition strategy to acquire more soil nutrients. On less stressful shady slopes, the above-ground organs of *D. fruticosa* exhibited higher hydraulic efficiency and photosynthetic capacity, and adopted a resource acquisition strategy. Thus it seems the below- and above-ground functional traits of *D. fruticosa* in different habitats are coordinated to comprise the whole plant ecological response.

Conclusion

Our study clearly shows hydraulic functional traits and leaf photosynthesis characteristics play key roles in shrub encroachment. This research also provides new insights for understanding the adaptation strategies of plant functional traits under different habitats.

Introduction

Shrub encroachment is mainly manifested by an increase in the abundance, coverage or biomass of plants (Deng et al. 2021). The factors driving shrub encroachment are complex, and include factors such as overgrazing, grassland fire, climate change and increases in atmospheric CO₂ concentrations (Eldridge et al. 2021), allowing shrub species better access to environmental resources leading to their colonization of grasslands. Nevertheless, there are no consistent conclusions on the impacts of shrub encroachment

on biodiversity or productivity of grassland ecosystems, with some studies suggesting that shrub encroachment significantly reduces grassland productivity and species richness (Brantley et al. 2009; Ratajczak et al. 2012). Other studies have noted that shrub spread is facilitated by increasing annual precipitation (Zhang et al. 2023). Despite intensive studies on how shrub encroachment affects ecosystems and community structure, the mechanism of shrub encroachment is still unknown when explored in terms of functional traits of the shrub itself.

Water transportation is vital for plant survival and growth. Hydraulic functional traits usually play a major role in water transport capability (Liang et al. 2019). The classic perspective of the hydraulic limitation hypothesis suggests that the resistance to tree water transport increases with trees height, and therefore limits the maximum height of trees in specific habitats (Liu et al. 2019). A growing number of researches have noted that trees hydraulics are correlated with leaf photosynthetic capacities, water-stress tolerance and nutrient use efficiencies (Joshi et al. 2022; Xu et al. 2021; Zhu et al. 2018). Generally, fast-growing species should have high leaf photosynthetic capacity and K_{leaf} (leaf hydraulic conductivity), which tends to result in increased competitiveness in acquiring resources, as contrasted with slow-growing species (Reich et al. 2014). In addition, the relationship between plants hydraulic safety and efficiency is an important hydraulic trade-off strategy (Liu et al. 2019). For plants, water transport efficiency is offset by increasing likelihood of hydraulic failure. Therefore, exploring hydraulic trade-off strategies may provide knowledge of plant growth strategies and distribution (Rosas et al. 2021), and important physiological-ecological mechanisms of plants.

The whole plant economics spectrum is represented by the sum of the functional traits and a study of the individual functional traits can provide insights into our mechanistic understanding of how plants garner environmental resources. Leaf economics spectrum as proposed by Wright et al. (2004) represents the trade-off strategy of the plant from the “low input-quick return” to the “high input-slow return” (Jardine et al. 2020). Thus, plants in a limited resource environment, will invest more resources in one functional trait, and at the same time will sacrifice the construction and maintenance of other traits in order to reduce the resources invested in other traits (Wright et al. 2005). Additionally, previous studies have demonstrated root trait correlation to the ecological strategy of individual species (Li et al. 2018; Ostonen et al. 2017). For example, fine roots are important for plant species productivity and ecosystem carbon sequestration (Chen et al. 2021; Gao et al. 2023) and can also represent a resource trade-off between acquisition and conservative strategy for plants (Li et al. 2022; Kong et al. 2019). However, an increasing number of studies exhibits a weak relationship between root traits at the species level (Ma et al. 2018; Silva et al. 2018). As described by Chen et al. (2021) RES (root economic spectrum) is a play off between fine roots inexpensively constructed and able to exploit nutritional “hotspots” and more expensively constructed longer roots able to exploit larger volumes of soil. At the present, LES has been extended into the wood economic spectrum (WES), with plant growth rates being closely related to trade-offs in a suite of wood traits and their resource availabilities (Fajardo et al. 2018). Nevertheless, the strength of coupling of functional traits between different organs may vary considerably (Carvajal et al. 2019; Vleminckx et al. 2021). For example, Liu et al. (2023), at a finer taxonomic level (*Artemisia*), using pair-wise correlations,

identified a 'fast-slow' resource management strategy. Other studies showed that different organs economic strategies of tropical trees, in Amazonian forests, are decoupled due to environmental impacts (Vleminckx et al. 2021). Hence, understanding the trade-offs or coordination relationship among the functional traits of plants is to better inform the adaptation strategies of plants in the context of specific habitats (He et al. 2020).

The area of Qinghai-Tibet Plateau alpine meadow account for more than 60% of the Qinghai-Tibet Plateau, and is representative of high alpine systems (Wang et al. 2022). Due to global climate warming, shrub encroachment has occurred in the Qinghai-Tibet Plateau alpine meadow (Zhou et al. 2021). *D. fruticosa* shrubs are now widely distributed in the Qinghai-Tibet Plateau alpine meadow and one of the important vegetation types. Its area is second only to the largest area of *Kobresia* meadow (Li et al. 2013). A recent study also noted that *D. fruticosa* shrubs have created microenvironments and heterogeneous microbial communities across different seasons and elevations in alpine meadows (Wang et al. 2023).

The functional traits allowing *D. fruticosa* shrubs to encroach on the high alpine meadows remain to be further investigated. Here, we measured the functional traits of different organs of *D. fruticosa* to explore which functional traits mainly dominant *D. fruticosa* shrub encroachment and whether it could use different adaptive strategies in different habitats. We test the following hypotheses: (1) Hydraulic functional traits and leaf photosynthetic capacity mainly dominate the widespread distribution of *D. fruticosa*; (2) Above and below-ground functional traits of *D. fruticosa* in different habitats use different adaptation strategies and trade-off relationships; (3) Variations in the whole-plant economic spectrum of *D. fruticosa* in different habitats.

Materials and methods

Study site and experimental design

The study region was near Hezuo city (E 102°88', N 34°94', at an average elevation of 2900 m), Gannan Tibetan Autonomous Prefecture, on the northeastern Qinghai-Tibetan Plateau, China. The climate is a typical plateau continental with long daylight hours and strong radiation. The average annual precipitation is 545mm, with most falling between August and September. The annual mean air temperature is 2°C, with a monthly minimum of -23°C in January and a monthly maximum of 28°C in July, there is no absolute frost-free period throughout the year. Meteorological data in the study regions were collected using grid data covering CRU TS4.04 (LAND) from 1901 to 2020, from the Royal Netherlands Meteorological Institute (<http://climexp.knmi.nl/>). The soil type is alpine meadow. The vegetation is typical alpine meadow, in which the plant community is dominated by *D. fruticosa* and herbaceous species, such as *Kobresia myosuroides*, *Elymus nutans*, *Kobresia humilis*, *Kobresia capillifolia*, *Stipa aliena*, *Potentilla anserina* etc.

Shrub encroachment plays an important role in the Qinghai-Tibet Plateau. We selected two habitats of *D. fruticosa* for study, including shady slope and sunny slope (Table S1), three 5m×5m quadrants were

selected in each habitat. In each plot, *D. fruticosa* with similar base diameter were measured. Liao et al. (2018) suggested that more than 50% coverage is severe shrub encroachment, thus, for this study, we used the cover percentage of *D. fruticosa* to describe the state of shrub encroachment in different habitats (Table S1).

Soil sampling and measurements

We sampled soil at the same time as the vegetation surveys. A five-point sampling method was measured in each plot. Soil samples of each point were divided into two parts. One part packed into an aluminum box for transport to the laboratory where soil water content was measured after 24h drying in an oven at 105°C. The other part was brought back to the laboratory in plastic bags, then used to determine the soil nutrients. These soil samples were air-dried in the laboratory, passed through a 1 mm sieve and used for analysis of soil pH. Soil pH was measured from 1:1 (v/v) soil water solution. Soil was passed through an additional 0.25mm sieve before determining SOC, STP and STN. Soil organic carbon (SOC) was used by the potassium dichromate and sulfuric acid oxidation method. The sulfuric acid-perchloric acid digestion was used for both soil total nitrogen (STN) and soil total phosphorus (STP). Soil total nitrogen (STN) were followed by the indophenol blue spectrophotometry (Bremner & Mulvaney, 1982). Soil total phosphorus (STP) were followed by the molybdenum antimony anti-colorimetric method (Murphy and Riley 1962). Soil water content (SWC, %) was determined by the oven dried method.

Root functional traits

Root samples were gathered from different habitats, and returned to the lab for analysis. The study methodology broadly followed Liu et al. (2023). Fine roots (< 2mm) were carefully cleaned in water. Root systems were scanned. Fine root lengths were measured with a vernier scale. The total volume of fine roots was measured by the drainage method, weighed to acquire the dry mass after oven-dried at 60°C for 48h. Specific root length (SRL, m/g) was calculated as follows: fresh root length / root dry mass. Root tissue density (RTD, g/cm³) was calculated as follows: root dry mass/ fine roots volume. Specific root area (SRA, cm²/g) was calculated as follows: fine root surface area/ dry mass.

Leaf functional traits

At each habitat, we selected five health and robust plants with fully expanded leaves. Leaves were scanned using a CanoScan LIDE300 scanner and leaf fresh weight was weighed by electronic balance (accuracy of 0.0001g). Then the surfaces of the collected intact leaves were cleaned, leaf dry weight was measured after oven-dried at 60°C for 48h. Leaf area (LA) was quantified using ImageJ software analysis. Leaf mass per area (LMA) was expressed as leaf dry weight (LDW)/leaf area (LA) (Rosas et al. 2021). The nitrogen leaf content ($N_{\text{mass-leaf}}$) was measured by the indophenol blue spectrophotometry after H₂SO₄-H₂O₂ digestion (Bremner and Mulvaney 1982), total phosphorus leaf content ($P_{\text{mass-leaf}}$) was measured by H₂SO₄-H₂O₂ digestion and molybdenum-antimony anti-colorimetric method (Murphy and Riley 1962).

Maximum photosynthetic rate per unit leaf dry weight (A_m , $\text{nmol} \cdot \text{g}^{-1} \cdot \text{s}^{-1}$) was calculated as follows: maximum photosynthetic rate per unit leaf area (A_a , $\text{umol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) / leaf mass per area (LMA). Photosynthetic nitrogen use efficiency (PNUE, $\text{umol} \cdot \text{g}^{-1} \cdot \text{s}^{-1}$) was calculated as follows: $A_m / N_{\text{mass-leaf}}$. Photosynthetic phosphorus use efficiency (PPUE, $\text{umol} \cdot \text{g}^{-1} \cdot \text{s}^{-1}$) was calculated as follows: $A_m / P_{\text{mass-leaf}}$.

Stem and leaf hydraulic traits

In each habitat, sun-exposed branches from *D. fruticosa* shrubs were selected from the upper canopy in the morning. These were immediately put in water, then the ends of the branches were re-cut and were attached to a hydraulic conductivity measurement instrument to determine maximum hydraulic conductivity (K_{max}). The solution used was 20 mmol L^{-1} KCl solution, the pressure gradient was 5 KPa. The hydraulic conductivity (K_h , $\text{g m s}^{-1} \text{MPa}^{-1}$) was calculated as follows: $K_h = F / (dp/dx)$, where dp/dx (MPa m^{-1}) is the pressure gradient along the length of the segment and F (g s^{-1}) is the flow of water through the stem section per unit time. Stem sapwood specific conductivity (K_s , $\text{g m s}^{-1} \text{MPa}^{-1}$) was calculated as follows: the hydraulic conductivity (K_h , $\text{g m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) / the sapwood area (A_s , cm^2). Leaf specific hydraulic conductivity (K_L , $\text{g m s}^{-1} \text{MPa}^{-1}$) was calculated as follows: the hydraulic conductivity (K_h , $\text{g m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) / the distal leaf area (A_L , cm^2). Leaves were scanned and leaf area was quantified using ImageJ software. The Huber value (HV) was determined by the sapwood area (A_s , cm^2) / the distal leaf area (A_L , cm^2).

Stem vulnerability curve

Stem vulnerability curves (VCs) were determined by according to Sperry et al. (1988). Subsequently, branches with different water potential gradients were measured by bench drying methods, then were covered with black plastic bags to balance the water potential between stems and leaves. Measure the water potential of each branch with a pressure chamber (Model 1505D, PMS Instrument Company, Albany, USA). If the difference in water potential between two branch is < 0.2 MPa, the average of two branch was assumed to be the xylem water potential. After the actual hydraulic conductivity (K_i , $\text{g m s}^{-1} \text{MPa}^{-1}$) was determined, the branch segment was flushed with 20 mmol L^{-1} KCl solution under 0.15 MPa pressure for about 30 min, and the maximum hydraulic conductivity (K_{max}) was determined. PLC(%) were expressed by the formula: $\text{PLC}(\%) = (K_{\text{max}} - K_i) / K_{\text{max}} \times 100\%$, the vulnerability curves were plotted using PLC% as a function of the xylem water potential, and then fitted by an exponential sigmoid function: $\text{PLC}\% = 100 / \{1 + \exp^{a(\psi_i - b)}\}$, where ψ_i is xylem water potential, a is the maximum slope of the curve and b is the xylem water potential at 50% loss of hydraulic conductivity (P_{50}), which can reflect the resistance of branches to embolism.

Leaf pressure-volume curve

For two habitats, a branch was obtained from each of five individuals, and quickly wrapped in a black plastic bag. After rehydration to saturation ($\Psi_L > -0.3$ MPa), the branch was weighed to determine their saturated fresh weight (SW). After measuring the water potential (Ψ) with a pressure chamber, a leaf pressure-volume curve was evaluated using the bench drying procedure (Hao et al. 2010). The branch was allowed to dry on a bench for a certain time, and the corresponding fresh weight (FW) and Ψ_L were measured again; the measurements were repeated until Ψ did not decrease significantly (Aritsara et al. 2022). Then, the measurement of leaf area (LA) was conducted using a scanner and ImageJ software. Dry weight (DW) was measured in an oven at 70°C for 72 h. The relative leaf water content (RWC, %) and RWC were expressed by the following formula: $RWC = (FW - DW) / (SW - DW) \times 100\%$; $RWC_{tlp} = 100 - RWC$. Then using $100 - RWC_{tlp}$ and the corresponding $-1/\Psi$ to make the P-V curve, modulus of elasticity (ϵ) and leaf turgor loss point water potential (π^0) and were determined by the P-V curve (Bartlett et al. 2012).

Wood density and Minimum water potential

Segments 3-5cm selected for hydraulic conductivity measurement were used to measure the sapwood density (WD, g cm⁻³) according to Hacke et al. (2000). Bark and pith material were separated from segments and Archimedes' drainage method was used to measure the volume of the fresh sapwood (V, cm³). The sapwood sample was dried out in an oven at 75°C for 72 h to determine the dry mass (W, g), and then used for determination of WD. WD was calculated by the following formula: $WD = \text{dry mass (W)} / \text{fresh sapwood (V)}$.

On a sunny day, five branches were selected between 12:00 noon-13:00 pm and quickly wrapped in a black plastic bag, and immediately taken to the laboratory. Minimum water potential (Ψ_{min}) was determined in a pressure chamber (Model 1505D, PMS Instrument Company, Albany, USA).

Gas exchange parameters measurements

The photosynthetic parameters were selected to be measured in close position to the branches used to determine the hydraulic traits. Three individuals were selected from each habitat, and the same photosynthetically active radiation PAR (1500 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) were settled in different habitats, and three leaves from every individual were measured from 9:00–11:30h. The net photosynthetic rate (P_n), intercellular CO₂ concentration (C_i), transpiration rate (T_r) and stomatal conductance (g_s) were measured with a portable photosynthesis system (GFS-3000, Heinz Walz GmbH, Effeltrich, Germany) during continuous sunny days. WUE was expressed by the following formula: $\text{net photosynthetic rate (} P_n \text{)} / \text{transpiration rate (} T_r \text{)}$.

Data analysis

All traits were tested for normality and all original data were log₁₀-transformed. One-way ANOVA and the least significant difference (LSD) method were used to determine community structure traits and soil nutrient difference. Differences in branch hydraulic structure and photosynthetic capacity relationships

between shady and sunny slopes of *D. fruticosa* were compared with independent-samples t-test. Pearson correlations and linear regression analysis were performed for pairwise combinations of traits. Additionally, to assess the relationships between fine root functional traits and soil variables, we conducted stepwise multiple regressions analysis. To assess relationships between shrub encroachment and functional traits, PCA was performed using all functional traits and vegetation cover. All statistical analyses were performed using SPSS 26.0 software, and figures were drawn with Origin 2022.

Results

Differences in population characteristics and soil physicochemical properties of *D. fruticosa* in different habitats

Our result indicated that plant density, height and cover changed significantly ($p < 0.05$) between the two habitats (shady slope and sunny slope). Density, height and cover of *D. fruticosa* on the shady slope increased by 2.46, 0.19, 7.85 times compared with the sunny slope (Table S1). One-way ANOVA analysis also showed that SOC, STP, STN, pH were significantly different ($p < 0.05$) between the shady and sunny slopes. In addition, SWC, SOC, STP and pH of the shady slope was greater by 18.73%, 23.31%, 32.88%, 1.38% and 13.76% compared with the sunny slope (Table S2).

Differences in functional traits of *D. fruticosa* between two habitats

Differences in the fine root functional traits

Results clearly indicated significant differences between the SRL and RAD on the shady and sunny slopes ($p < 0.05$) (Fig. 1b 1c). Compared to the shady slope, the SRL and SRA on the sunny slope were larger by 117.5% and 7.5%, respectively (Fig. 1a 1c). Compared to the sunny slope, the RAD, RTD on the shady slope were significantly larger ($p < 0.05$) by 60% and 56.7%, respectively (Fig. 1b 1d).

Differences in the leaf functional traits

Our results demonstrated that LMA, N_{mass} , P_{mass} changed significantly ($p < 0.05$) between the shady and sunny slopes (Fig. 2a, 2b, 2c). Additionally, N_{mass} , P_{mass} , PPUE, PNUE on the shady slope were increased by 54.44%, 89.38%, 14.34% and 17.14% over the sunny slope ($p < 0.05$) (Fig. 2b, 2c, 2d, 2e). LMA on the shady slope was decreased by 42.31% compared with sunny slope ($p < 0.05$) (Fig. 2a).

Differences in branch and leaf traits of *D. fruticosa* between two habitats

Differences in the branch vulnerability curve between shady and sunny slopes

From the stem vulnerability curves for the shady and sunny slopes, it can be seen that the P_{50} value is -0.97MPa on shady slope (Fig. 3a), and -1.43MPa on the sunny slope (Fig. 3b). This results indicate a

higher embolism resistant capacity for plants growing on the sunny slope compared to those on the shady slope.

Differences in hydraulic and photosynthetic traits

Leaf and stem traits vary significantly between the sunny and shady slopes. K_L , K_S , HV, π^0 , Ψ_L , A_a , A_m , T_r , P_n , g_s on the sunny slope was significantly lower than for the shady slope ($p < 0.05$) (Table 1). However, ϵ and WD on the shady slope was significantly lower than for the sunny slope ($p < 0.05$). WUE on the shady slope was also lower than for the sunny slope ($p > 0.05$) (Table 1).

Table 1
Differences in hydraulic and photosynthetic traits between shady and sunny slope (mean $\pm$ SE)

Traits	units	Shady slope	Sunny slope	t	p
KS	g m ⁻¹ s ⁻¹ MPa ⁻¹	26.60 $\pm$ 9.70	11.64 $\pm$ 3.52	-5.240	0.000
K_L	g m ⁻¹ s ⁻¹ MPa ⁻¹	1.10 $\pm$ 0.31	0.03 $\pm$ 0.02	-12.441	0.000
HV	cm ² cm ⁻²	4.59 $\pm$ 1.85	2.62 $\pm$ 1.92	-2.967	0.012
WD	g cm ⁻³	0.63 $\pm$ 0.09	0.71 $\pm$ 0.07	2.767	0.011
π^0	MPa	-0.59 $\pm$ 0.14	-1.03 $\pm$ 0.17	-7.406	0.000
ϵ	MPa	15.71 $\pm$ 2.47	22.46 $\pm$ 2.40	7.192	0.000
Ψ_L	MPa	-1.79 $\pm$ 0.48	-2.10 $\pm$ 0.31	-1.996	0.057
A_a	umol.m ⁻² . s ⁻¹	21.64 $\pm$ 1.10	15.74 $\pm$ 1.28	-12.867	0.000
A_m	nmol. g ⁻¹ . s ⁻¹	222.49 $\pm$ 75.01	118.76 $\pm$ 28.58	-4.675	0.000
T_r	mmol.m ⁻² . s ⁻¹	4.69 $\pm$ 0.29	2.93 $\pm$ 0.46	7.199	0.000
P_n	umol.m ⁻² . s ⁻¹	13.25 $\pm$ 0.67	8.76 $\pm$ 1.30	6.850	0.000
g_s	mol.m ⁻² . s ⁻¹	0.49 $\pm$ 0.03	0.28 $\pm$ 0.07	5.925	0.000
WUE	umol. mmol ⁻¹	2.82 $\pm$ 0.26	3.13 $\pm$ 1.01	1.111	0.277
$C_i:C_a$	/	0.88 $\pm$ 0.01	0.86 $\pm$ 0.03	1.270	0.240

Note: K_S , sapwood-specific hydraulic conductivity; K_L , leaf-specific hydraulic conductivity; WD, sapwood density; HV, Huber value; WUE, photosynthetic water use efficiency; g_s , stomata conductance; $C_i:C_a$, intercellular CO₂ concentration: intracellular CO₂ concentration; ϵ , bulk modulus of elasticity; π^0 , turgor loss point water potential; Ψ_L , minimum leaf water potential; A_m , maximum leaf mass-based photosynthesis rate; A_a , maximum leaf area-based photosynthesis rate; P_n , net photosynthetic rate; T_r , leaf transpiration rate

Influence of fine-roots functional traits and shrub encroachment on soil properties

Our results indicated that the presence of *D. fruticosa* shrubs was associated with significant differences in soil properties and nutrients (Fig. S1). SWC, SOC, STN, STP and pH were all positively related to cover.

The PCA showed that *D. fruticosa* in different habitats are mainly affected by SRL and RAD (Fig. 4, Table S3). In addition, the stepwise multiple regression analyses showed that STN and STP were determined as the most affected factors on RAD and SRL (Table 2).

The abbreviations for fine root traits as shown in Fig. 1

Table 2

Summarized results of the stepwise multiple regression analyses with root functional traits (SRL, SRA, RAD, RTD) as dependent variables and soil nutrients (SOC, STP, STN, SWC, pH) as independent variables. Coefficients (β) and *P-values* for each independent variable as well as coefficient of determination (R^2) and *P-values* and *F-values* in each model are shown. STP and STN were predictors and SWC, SOC and pH were excluded variables in model. See Table S2 for abbreviations of soil properties.

Independent variable	SRL		RAD		SRA		RTD	
	β	<i>P-values</i>	β	<i>P-values</i>	β	<i>P-values</i>	β	<i>P-values</i>
STN	-0.098	0.776	0.666	< 0.001	0.562	0.163	-0.91	0.019
SWC	-0.024	0.3	0.124	0.458	-0.357	0.136	0.109	0.614
STP	-0.451	0.018	0.235	0.41	-0.979	0.085	0.907	0.084
SOC	-0.127	0.58	-0.045	0.81	-0.464	0.177	0.641	0.049
pH	0.435	0.248	-0.23	0.92	0.929	0.096	-0.467	0.354
<i>F-values</i>	6.931		19.977		1.05		1.941	
R^2	0.172		0.422		0.01		0.153	
<i>P-values</i>	0.018		< 0.001		0.415		0.13	

Relationships between functional traits

Our result showed that K_L and K_s were positively related to A_a , A_m , P_{mass} , N_{mass} , g_s , and RAD ($p < 0.05$) (Fig. 5e-l) and negatively correlated with SRL, WD, RWC_{tip} , ϵ , π^0 (Table S4). Whereas WD was positively correlated with ϵ , π^0 ($p < 0.05$) (Table S4). SRL was negatively correlated with RAD, P_{mass} and RTD ($p < 0.01$) (Fig. 5b-5d). Additionally, SRL was negatively related to A_a and g_s ($p < 0.05$), and RAD was positively related to P_{mass} , A_a , A_m and g_s ($p < 0.05$) (Table S4). LMA was negatively related to K_L , K_s , A_m , PPUE, PNUE (Fig. 5n-5p) and positively correlated with RWC_{tip} , ϵ , π^0 ($p < 0.05$) (Fig. 5m) (Table S4).

Principal component analysis between functional traits and shrub encroachment of different habitats

The Principal Component Analysis (PCA) indicated that PC1 and PC2 explained 58.50% of the total variance. Among the first PC accounted for 43.5% of the total variation, the two PC accounted for 15.0% of the total variation (Table 3). The PC axis 1 was loaded by Cover, K_L , K_S , HV, A_a , A_m , P_n , g_s , P_{mass} , N_{mass} , PPUE, PNUE, RAD, RTD. the PC axis 2 was loaded by π^0 , ε , RWC_{tlp} , Ψ_L , SRA, SRL, LMA, WD and WUE (Fig. 6). *D. fruticosa* on the shady slope was clustered to the right of the PCA plot, whereas *D. fruticosa* on the sunny slope was clustered to the left of the PCA plot. These results indicated that *D. fruticosa* shrubs on shady slopes showed positively correlation with K_L , K_S , A_a , A_m , g_s , P_{mass} , whereas *D. fruticosa* shrubs on sunny slopes showed positively correlation with π^0 , ε , RWC_{tlp} (Fig. 6). Additionally, tested traits of *D. fruticosa* on sunny and shady slopes were distributed along the diagonal line between the PC axis 1 and 2, meaning that the functional traits of different organs together determine the different adaptive strategies by which *D. fruticosa* are enabled to be distributed in different habitats (Fig. 6).

Table 3
The Eigenvalue of each axis of PCA ordination of different habitats and correlation coefficients of functional traits with each axis

Principal component	PC1	PC2	PC3
Eigenvalue	10.00	3.45	2.35
Percentage of total variance (%)	43.50	15.01	10.22
Cumulative percentage (%)	43.50	58.50	68.72
Factor loading			
K_L	0.30	0.07	-0.02
K_S	0.22	0.13	-0.11
WD	-0.16	-0.05	0.15
HV	0.20	-0.01	0.08
RWC_{tlp}	-0.23	0.20	-0.08
π^0	-0.29	0.09	0.15
ε	-0.26	-0.02	0.28
Ψ_L	-0.15	0.20	-0.26
SRL	-0.18	-0.30	-0.10
SRA	-0.06	-0.36	-0.15
RAD	0.19	0.13	0.17
RTD	0.02	0.27	-0.07
N_{mass}	0.22	-0.14	-0.39
P_{mass}	0.25	0.22	-0.22
LMA	-0.17	0.35	0.11
A_a	0.30	0.02	0.13
A_m	0.26	-0.26	-0.04
PNUE	0.11	-0.20	0.39
PPUE	0.04	-0.49	0.17
g_s	0.26	0.11	0.21

Principal component	PC1	PC2	PC3
WUE	-0.04	-0.08	-0.21
$C_i:C_a$	0.15	0.12	0.47

Discussion

The dominant role of hydraulic and leaf photosynthetic traits enabling shrub encroachment of *D. fruticosa*

Our PCA results indicated that K_L , A_a , g_s , bulk modulus of elasticity(ϵ) and leaf turgor loss point(π^0) were significantly correlated with vegetation coverage (Fig. 6), which verifies our first hypothesis. A recent study at global scale has identified a significant correlation between maximum tree height and different hydraulic traits (Liu et al. 2019) and a study by Li et al. (2021) also revealed that fast-growing plants species exhibited high xylem hydraulic conductivity. Trees usually have a high K_L when growing on sites which provide sufficient water for photosynthesis and ensures a faster rate of gas exchange to strength their competitive advantage (Brodribb et al. 2007), whereas in species growing under water stress, the stomata open little or remain closed even in the morning when sunlight is abundant. Hence, plant water supply and ability to deliver water to the leaf canopy determines the photosynthetic capacity. Thus *D. fruticosa* growing on a shady slope with fast water conductivity rate and photosynthetic capability has a higher degree of shrub encroachment compared to the sunny slope. However, the hydraulic conductivity and carbon assimilation came at the cost of increased risk of hydraulic failure under the influence of global climate change. We found that *D. fruticosa* on sunny slopes had a lower P_{50} value than those growing on shady slopes. Hence, when *D. fruticosa* on shady slopes experienced water stress, it was more likely to develop embolism due to its weaker xylem resistance, resulting in hydraulic failure and death. However, this may be alleviated by the presence of other drought tolerance indicators such as bulk modulus of elasticity(ϵ) and leaf turgor loss point (π^0) (Santiago et al. 2018).

We found that wood density is correlated with leaf turgor loss point (π^0), bulk modulus of elasticity(ϵ) and minimum penitential(Ψ_L) and (Table S4), which is agreed with previously published studies, such as Markesteijn (2011) who found that wood density correlated with leaf economic traits and xylem embolism resistance in tropical dry forest species. *D. fruticosa* on sunny slopes have high wood density, low water conductivity rates and photosynthetic capability. This is because dense wood is correlated with reduced hydraulic efficiency (Eller et al. 2018). Also, the minimum leaf water potential (Ψ_L) and leaf turgor loss point(π^0) could be used to predict the plant response to drought. *D. fruticosa* on sunny slopes had a lower π^0 and minimum leaf water potential and thus greater xylem resistance to embolism and ability to resist leaf dehydration. Consequently, plants could maintain stomatal conductance, allowing photosynthesis under lower water availability (Zhu et al. 2018). As a result, *D. fruticosa* are able to grow on water deficient sunny slopes.

Different resource use strategies between *D. fruticosa* on sunny and shady slopes

Our results showed that *D. fruticosa* growing on resource-rich shady slopes, exhibited acquisitive strategies in above-ground functional traits and conservative strategies in below-ground functional traits. Whereas growth on sunny slopes is mainly limited by soil moisture and nutrients, where below-ground functional traits tend to acquisitive strategies and above-ground functional traits tend to conservative strategies (Bricca et al. 2023). These findings also support our second hypothesis.

We found that SRL and RAD are the major fine roots factors accounting for the distribution of *D. fruticosa* in different habitats (Fig. 4). SRL and RAD could respond to the plant's requirement for the availability of soil nutrients. A stepwise regression indicated that STN and STP are major influence factors for SRL and RAD (Table 2). This is compatible with the findings of Liu et al. (2023) who found that plants growing in phosphorus-limited soils tend to have finer and deeper roots. High SRL could increase soil nutrients acquisition and faster growth, which related to plants producing deeper and thinner roots enabling acquisition of water and nutrients under drought conditions. It represents an effective strategy in nutrient-poor environments (Bricca et al. 2023). Moreover, in our study, *D. fruticosa* growing on shady slopes had higher RAD. Thicker roots have been reported to be linked to resource conservative strategies, this is because thicker roots have higher root dry mass and lignin content, and display greater root life span (Li et al. 2019). While *D. fruticosa* growing on sunny slopes was limited by soil nutrients, its nutrient acquisition capacity or competitiveness was improved by increasing specific root length (SRL). In addition, we found that RAD and RTD were not correlated ($p > 0.05$). This result is consistent with work from Kong et al. (2019), which suggested that root functional trait relationships among species are mostly nonlinear. The main reason for this is the anisotropic relationship with the root anatomy. Fine-root traits may be responsive to soil nutrients alone or a combination of other factors (Li et al. 2019). Roots can adjust their morphology to respond to heterogeneous distribution of soil nutrients (Hodge et al. 2010). Thus the root systems of *D. fruticosa* adapt their use strategies to different habitats with different resources.

Our results also showed clear differences in the aspects of carbon gain and water use strategies between *D. fruticosa* on shady and sunny slopes. Higher hydraulic conductivity and photosynthetic capacity enable *D. fruticosa* on shady slopes to have faster growth. However, *D. fruticosa* on sunny slopes have more conservative water use strategies and greater xylem-cavitation resistance, which results in better drought tolerance. *D. fruticosa* on shady and sunny slopes operate a trade-off relationship between water transfer efficiency and safety. In accordance with Hagen-Poiseuille's law, the trade-off relationship is likely to be closely related to vessel diameter (Hacke et al. 2000). This also means that plants with lower water transport efficiency and have higher safe hydraulic structure, decreasing the risk of xylem embolism (Jin et al. 2016).

LMA is generally considered to be related to leaf carbon-fixation capacity and plant-growth strategies (Rosas et al. 2021). Pearson correlation results indicated that LMA was significantly negative correlated to K_L , A_m (Table S4), meaning that leaf structure was indicative of carbon allocation to its water transport. Higher LMA indicates thicker leaves, which tend to have a longer diffusional pathways in the mesophyll, which increases water movement resistance outside leaf xylem and decreases hydraulic conductivity (Xu

et al. 2021). LMA was also significantly positively related to π^0 , which also confirms that increased leaf turgor maintenance related to leaf carbon investment (Zhu et al. 2018). Our results showed that *D. fruticosa* on sunny slopes have higher LMA and more negative π^0 than those growing on shady slopes. The devotion of resources to leaf structure building, thus reduces the resources available for photosynthetic and respiratory functions, resulting in lower photosynthetic and respiratory rates. This is indicative of trait coordination in agreement with a 'fast-slow' leaf spectrum (Wright et al. 2004). The results of our study are in accord with those of Maréchaux et al. (2020).

As we have observed, our findings also confirm the third hypothesis. Our results demonstrated the existence of a trade-off relationship between above-ground and below-ground functional traits of *D. fruticosa* between the two habitats. We found that RAD are significantly positive related to K_s , K_L , g_s , A_a , P_{mass} (Table S4). Weemstra et al. (2021) determined that RAD was the best predictor of tree growth. In contrast, SRL are significantly negative related to K_L , g_s , A_a (Table S4). On the one hand, thicker roots will have greater mycorrhizal colonization than thinner roots, through which trees can increase access to soil nutrients and faster growth. On the other hand, thicker roots also related to low roots foraging efficiency, which is caused by low SRL but higher SRL with high roots foraging efficiency by roots themselves (Kong et al. 2019). In our study, RAD was negative related to SRL between the two habitats because of higher competition for light for above-ground functional traits of *D. fruticosa* on shady slopes. These plants will allocate relatively more carbon to above-ground organs, resulting in better water transport efficiency and greater photosynthetic capacity than those growing on sunny slopes (Bricca et al. 2023). In contrast, on the stressful sunny slope, below-ground organ of *D. fruticosa* competes for soil water and nutrients, using fine-roots strategies (High SRL), and above-ground conservative strategies (Low K_L , g_s , A_a). In addition, SRL was positive related to LMA, but they have no significance. This result is compatible with the findings of Liu et al. (2023), and with SRL associating with mycorrhizal fungi. Roots outsource nutrient uptake to root mutualistic symbionts, resulting in root trait variation (Bergmann et al. 2020). Root trait variation weakens coordination among organs. Thus, different organs have different strength of coordination and adaptation strategies to adapt to specific habitats. The reasons for this coordination also may be the continuous anatomical structures of stems, roots and leaves are very different (Liu et al. 2023). Therefore, the different organs have traits that are clearly correlated, and together they form the whole-plant economic spectrum of *D. fruticosa* on different habitats.

Conclusion

Our study demonstrates that shrub encroachment is closely related to hydraulic traits and leaf photosynthetic capacity. In addition, SRL and RAD are major root factors driving the distribution of *D. fruticosa* in different habitats. High SRL represents a high root foraging efficiency. On sunny slopes, limited by low soil nutrient and water, *D. fruticosa* has a high acquisition root system. But higher LMA on sunny slopes means more resources dedicated to leaf building, and thus decreased leaf photosynthesis and respiration. The above-ground functional traits of *D. fruticosa* on sunny slope display conservative strategies. Although shady slopes have higher soil nutrients and water, thicker roots are considered as

“conservative”. *D. fruticosa* can invest more carbon in above-ground organs to compete for light. Above-ground and below-ground functional traits of *D. fruticosa* on shady slope exhibits resource acquisition and conservative strategies. Therefore, above-ground and below-ground organs of *D. fruticosa* in different habitats coordinated to form the whole-plant economic spectrum.

Abbreviations

Fine functional traits	SRA	Specific root area
	RAD	Root average diameter
	SRL	Specific root length
	RTD	Root tissue density
Leaf functional traits	LMA	Leaf mass area
	N _{mass}	The nitrogen leaf content
	P _{mass}	The phosphorus leaf content
	PPUE	Photosynthetic phosphorus use efficiency
	PNUE	Photosynthetic nitrogen use efficiency
Hydraulic and wood traits	K _S	sapwood-specific hydraulic conductivity
	K _L	leaf-specific hydraulic conductivity
	WD	sapwood density
	HV	Huber value
	ε	bulk modulus of elasticity
	π ⁰	turgor loss point water potential
	Ψ _L	minimum leaf water potential
Leaf photosynthetic traits	WUE	photosynthetic water use efficiency
	g _s	stomata conductance
	Ci:Ca	Intercellular CO ₂ concentration: intracellular CO ₂ concentration
	A _m	maximum leaf mass-based photosynthesis rate
	A _a	maximum leaf area-based photosynthesis rate
	P _n	net photosynthetic rate
	T _r	Leaf transpiration rate
Soil physicochemical properties	STN	Soil total nitrogen
	STP	Soil total phosphorus
	SOC	Soil organic carbon
	SWC	Soil water content

Declarations

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Author Contributions

B.L.F. designed the study, revised the first draft and led the writing on subsequent revisions. N.N.D. collected and analyzed the data and wrote the first draft. Data from the field study was also collected by P. F. G., T.T.T., D. X.A., Y. K.W. and K. S. provided input regarding the study design. All authors approved the final version of the manuscript.

Data Availability

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

Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

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Figures

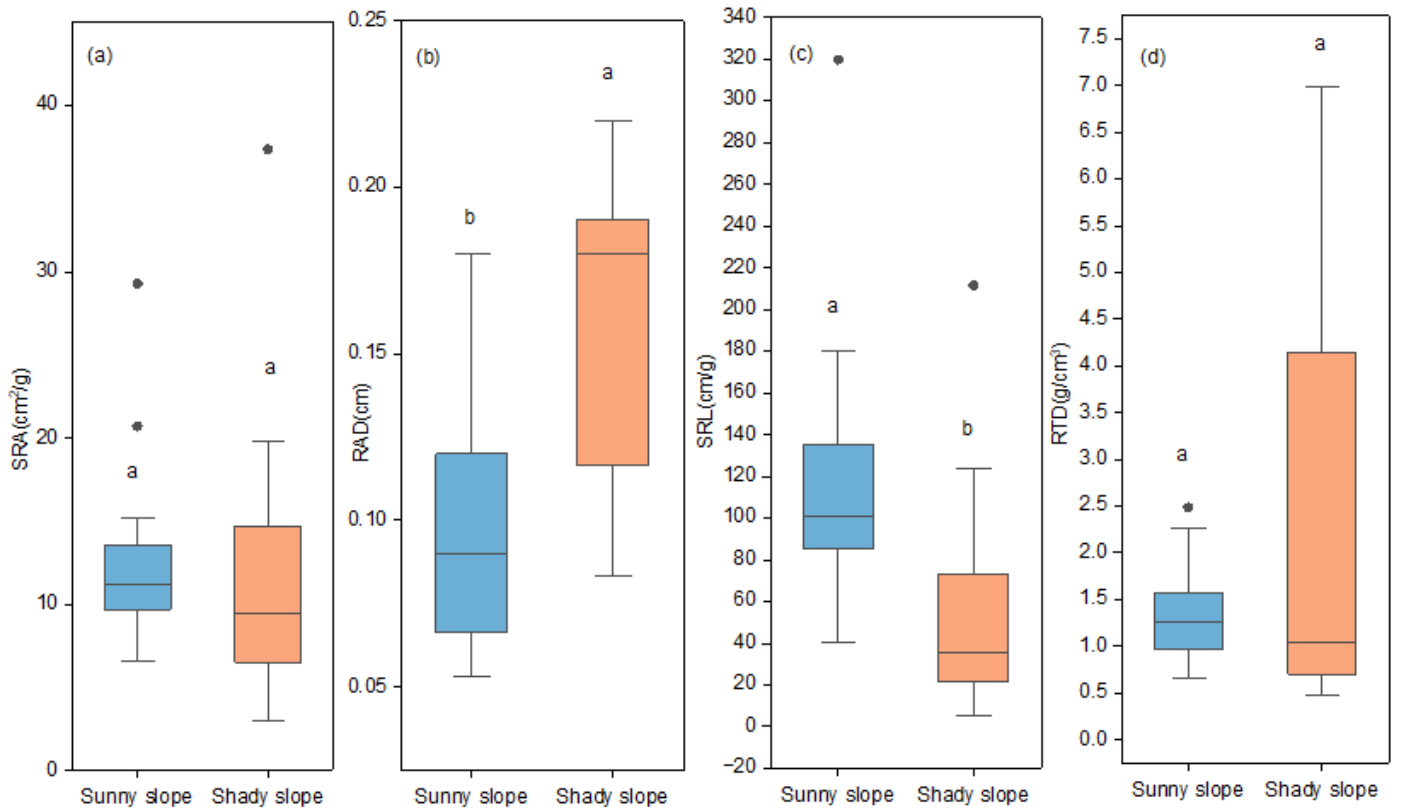


Figure 1

Comparisons of root functional traits of *D. fruticosa* between sunny and shady slopes (a) specific root area (SRA), (b) Root average diameter (RAD), (c) specific root length (SRL), (d) Root tissue density (RTD)

Note: The top and bottom lines of the boxes represent the 25th and 75th percentiles, respectively, the horizontal line in each box represents the median. The horizontal lines extending from the box represent the lowest and highest values within a range of 1.5× interquartile, the vertical line represents the 1.5×interquartile. The dots represent outliers. Dates are from 4-5 replicates. Different lowercase letters indicate significant difference ($p<0.05$) or very significant difference ($p<0.001$)

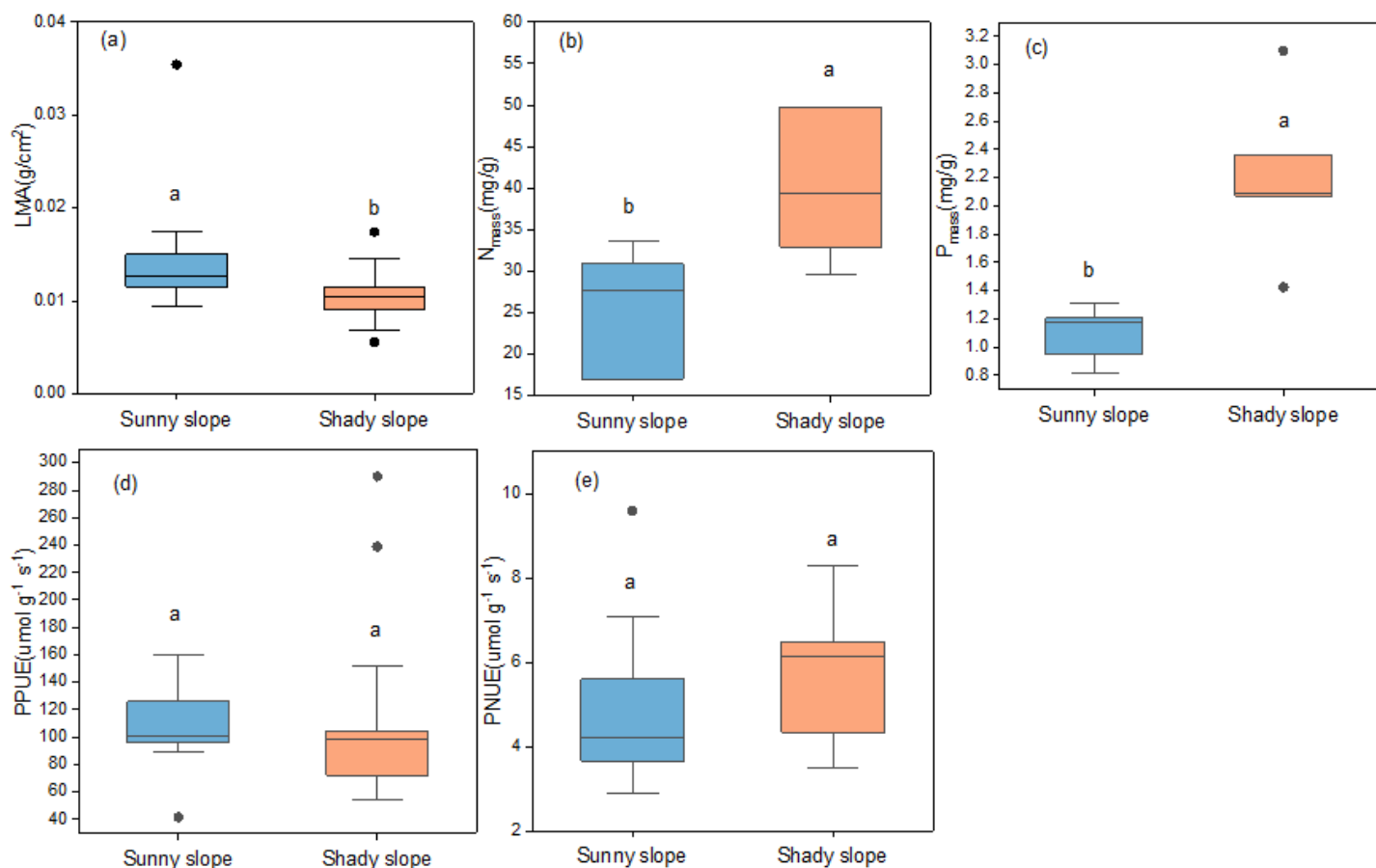


Figure 2

Comparisons of leaf functional traits of *D. fruticosa* between sunny and shady slopes. (a) leaf mass area (LMA), (b) The nitrogen leaf content (N_{mass}), (c) The phosphorus leaf content (P_{mass}), (d) Photosynthetic phosphorus use efficiency (PPUE), (e) Photosynthetic nitrogen use efficiency (PNUE)

Note: The top and bottom lines of the boxes represent the 25th and 75th percentiles, respectively, the horizontal line in each box represents the median. The horizontal lines extending from the box represent the lowest and highest values within a range of 1.5× interquartile, the vertical line represents the 1.5×interquartile. The dots represent outliers. Dates are from 4-5 replicates. Different lowercase letters indicate significant difference ($p < 0.05$) or very significant difference ($p < 0.001$)

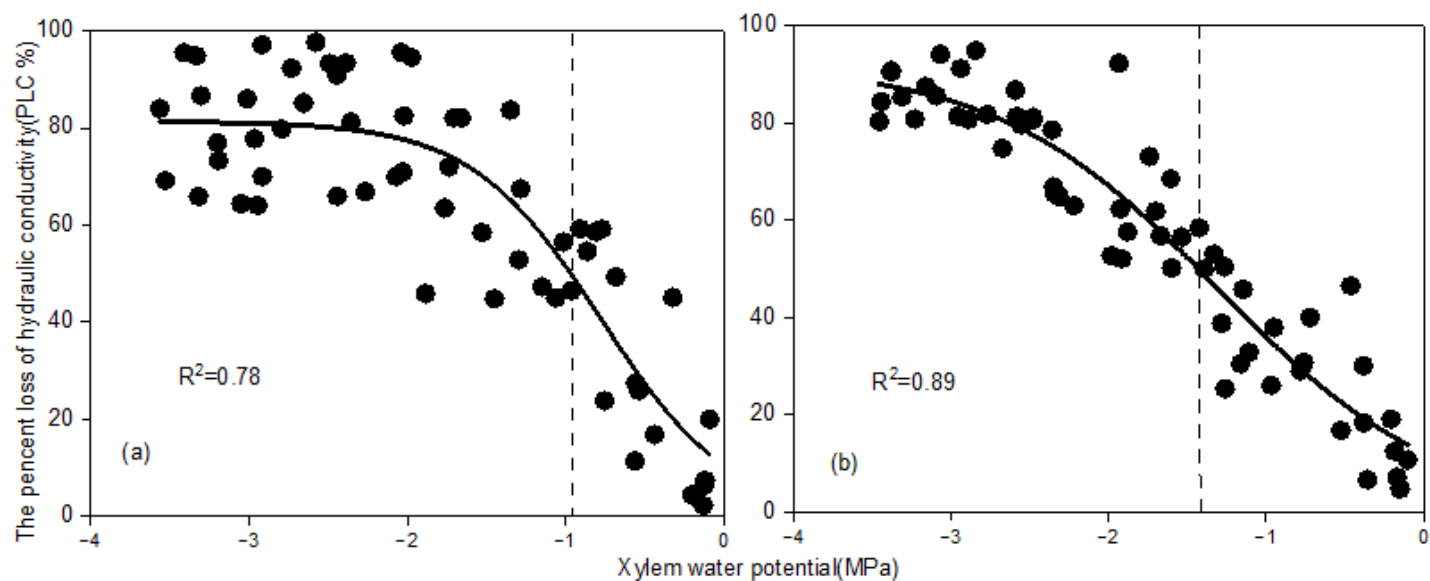


Figure 3

Stem vulnerability curves (VCs) for the shady (a) and sunny slopes (b). Vertical dashed lines show xylem water potential (Ψ_{leaf}) at 50 % loss of hydraulic conductivity

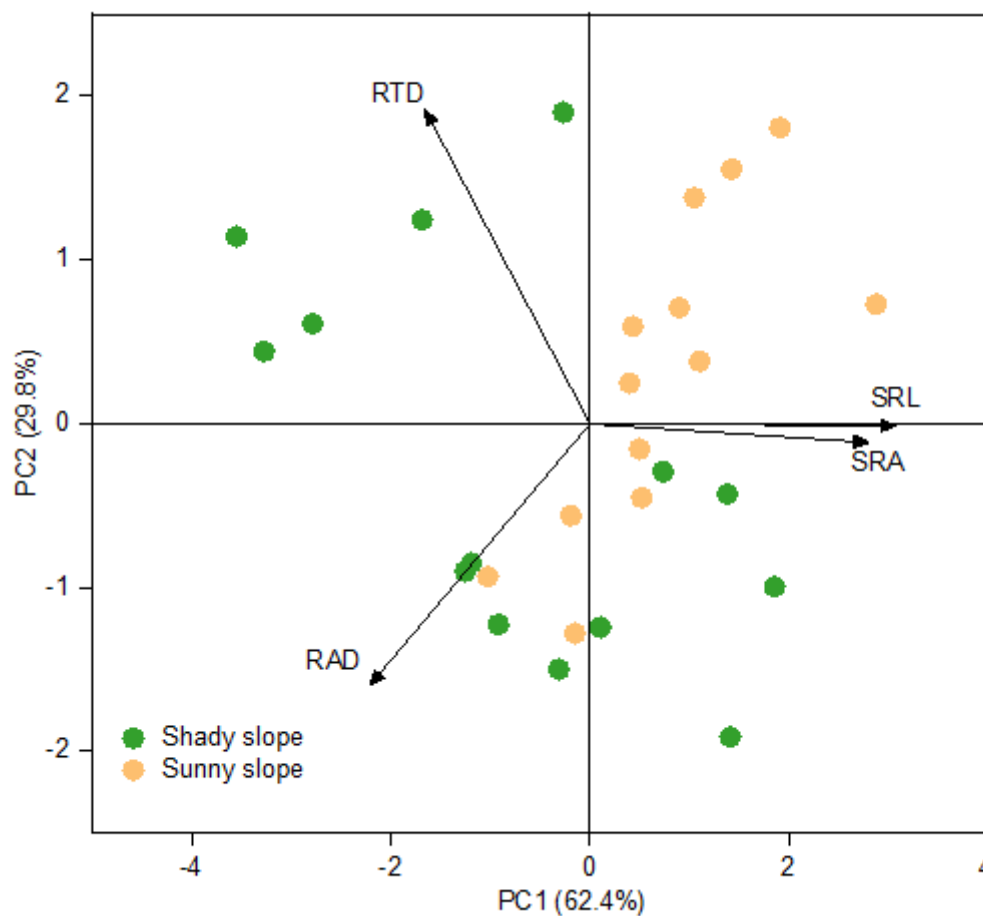


Figure 4

Principal components analysis (PCA) among fine-root functional traits.

The abbreviations for fine root traits as shown in Fig. 1

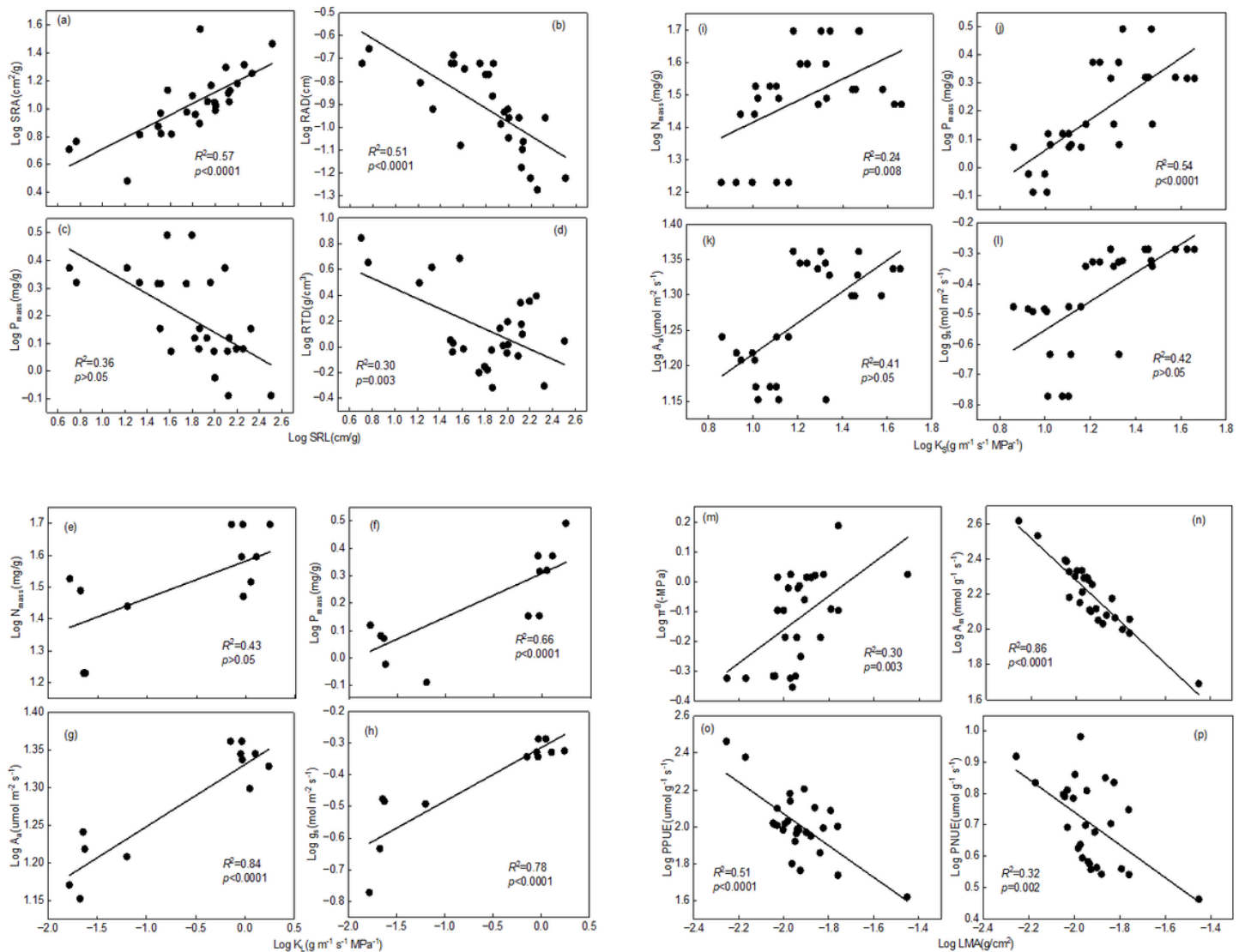


Figure 5

Linear regression relationship between root traits and stem and leaf hydraulic traits. (a-d) Correlations between SRL and SRA, RAD, RTD, P_{mass} ; (e-h) Correlations between K_L and N_{mass} , P_{mass} , A_a , g_s ; (i-l) Correlations between K_s and N_{mass} , P_{mass} , A_a , g_s ; (m-p) Correlations between LMA and π^0 , A_m , PPUE, PNUE. Line indicates best fit and R-values indicate correlation coefficients

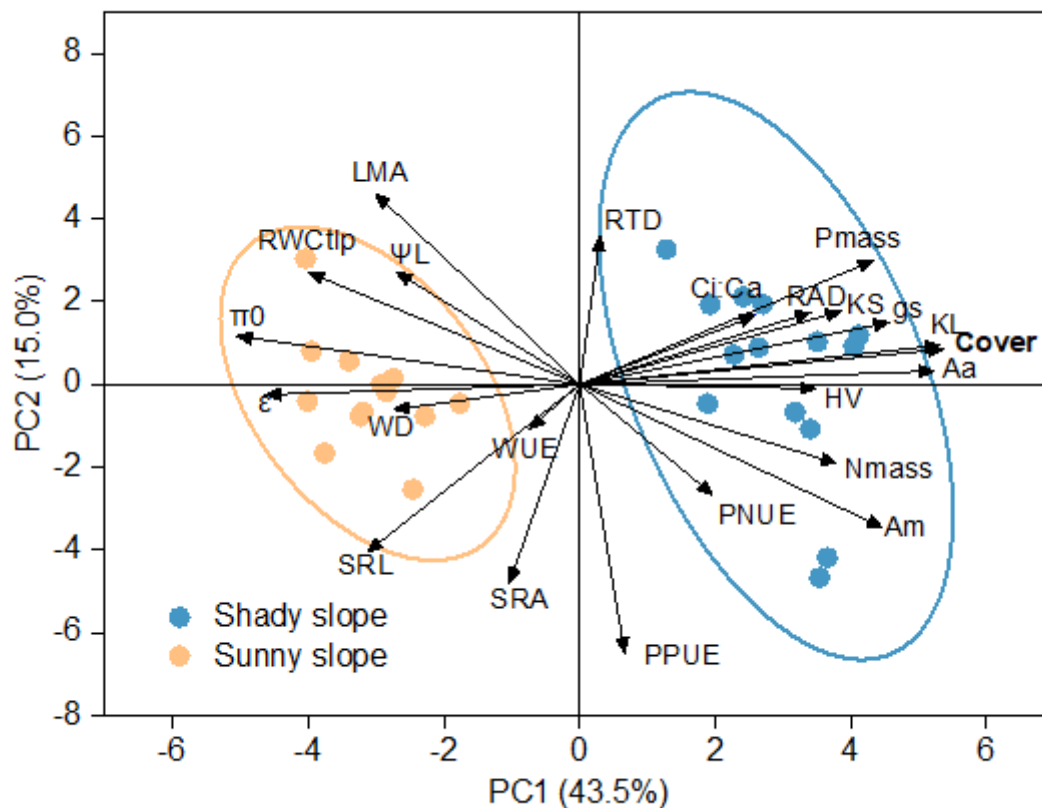


Figure 6

PCA ordination of shady slope and sunny slope on vegetation cover and all functional properties. The arrows show factor loadings of each variable on each axis, the dots denote the scores of PC1 (x axis) and PC2 (y axis), and the percentages of variance explained by the first two PCs are shown in the axis labels. Circles show the different habitats

Supplementary Files

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