ORIGINAL ARTICLE

Response of the root anatomical structure of *Carex moorcroftii* to habitat drought in the Western Sichuan Plateau of China

Jia-Ying Yang[1] · Hong-Bin Wang[1] · Da-Cai Zhang[1]

Abstract

Main conclusion **The anatomical structures of *Carex moorcroftii* roots showing stronger plasticity during drought had a lower coefficient of variation in cell size in the same habitats, while those showing weaker plasticity had a higher coefficient of variation. The complementary relationship between these factors comprises the adaptation mechanism of the *C. moorcroftii* root to drought.**

Abstract To explore the effects of habitat drought on root anatomy of hygrophytic plants, this study focused on roots of *C. moorcroftii*. Five sample plots were set up along a soil moisture gradient in the Western Sichuan Plateau to collect experimental materials. Paraffin sectioning was used to obtain root anatomy, and one-way ANOVA, correlation analysis, linear regression analysis, and RDA ranking were applied to analyze the relationship between root anatomy and soil water content. The results showed that the root transverse section area, thickness of epidermal cells, exodermis and Casparian strips, and area of aerenchyma were significantly and positively correlated with soil moisture content ($P < 0.01$). The diameter of the vascular cylinder and the number and total area of vessels were significantly and negatively correlated with the soil moisture content ($P < 0.01$). The plasticity of the anatomical structures was strong for the diameter and area of the vascular cylinder and thickness of the Casparian strip and epidermis, while it was weak for vessel diameter and area. In addition, there was an asymmetrical relationship between the functional adaptation of root anatomical structure in different soil moisture and the variation degree of root anatomical structure in the same soil moisture. Therefore, the roots of *C. moorcroftii* can shorten the water transport distance from the epidermis to the vascular cylinder, increase the area of the vascular cylinder and the number of vessels, and establish a complementary relationship between the functional adaptation of root anatomical structure in different habitats and the variation degree of root anatomical structure in the same habitat to adapt to habitat drought. This study provides a scientific basis for understanding the response of plateau wetland plants to habitat changes and their ecological adaptation strategies. More scientific experimental methods should be adopted to further study the mutual coordination mechanisms of different anatomical structures during root adaptation to habitat drought for hygrophytic plants.

Keywords Anatomical structure · Coefficient of variation · Plasticity · Vascular cylinder · Vessel · Soil moisture gradient

Communicated by Dorothea Bartels.

✉ Da-Cai Zhang
dczhang24@163.com

1 Key Laboratory of National Forestry and Grassland Administration On Biodiversity Conservation in Southwest China, Southwest Forestry University, Bailongsi 300#, Kunming, Yunnan 650224, China

Introduction

Plant roots directly perceive soil moisture and are the first organ to respond to habitat stress, and the functions of their anatomical structures are enhanced or diminished accordingly (Machado et al. 2013; Chimungu et al. 2015; Donnelly et al. 2016). Plants with different ecological habits exhibit different responses in the face of the same stress (Pregitzer et al. 2002; Galindo et al. 2022). Xerophytes have gradually evolved their own drought-resistant anatomical structures during long-term adaptation to arid habitats (Boughalleb et al. 2014, 2015; Chen et al. 2017) and will change the size

of the structures in roots accordingly under drought stress (Brunner et al. 2015), thereby adjusting the strength of their functions in response to stress. Hygrophytes have long been adapted to habitats with high soil moisture content, and root anatomical structures have developed an adaptive relationship with their ecological habits (Singh et al. 2013; Yang et al. 2015; López et al. 2021). For example, in order to adapt to the habitat, the roots of hygrophytes generally have large aerenchyma, which facilitates the transfer of O_2 from the roots (Xiang et al. 2019). In order to screen the substances entering the roots, hygrophytes also have a strong ectoplasmic barrier structure, so that the root system will not be subjected to the persecution of hazardous substances, which ensures that the plant can be grown normally (Shoaib et al. 2022). Currently, more studies have focused on salinity tolerance and heavy metal uptake in the root anatomy of hygrophytes (Xie et al. 2021), and drought has become an important habitat factor that threatens the survival of hygrophytes. Thus, how will the root anatomy of hygrophytes change when experiencing drought stress?

Root anatomical structures differ in function and also in sensitivity when facing habitat change; that is, their plasticity varies (Karlova et al. 2021). Generally, plasticity is measured according to different plant habitats, and plants with high plasticity have strong adaptability (Yao et al. 2022; Zhang et al. 2022). Some studies have measured the habitat adaptability of plants by the coefficient of variation, and it is believed that if the coefficient of variation of plant morphology is large in different habitats, that is, if the plant morphology is diversified, the plant habitat adaptability is strong (Liu et al. 2018; Pang et al. 2019). It was shown that the plasticity of the anatomical structure and function of the root and the coefficient of variation of the morphology are particularly important for the plant to face the habitat changes, which is directly related to the physiological function of the root system, and thus affects the habitat adaptability of the plant (Zhu et al. 2015; Liu et al. 2016; Cris et al. 2019). In both cases, the adaptive capacity of structural functions and the coefficient of variation are measured as a single indicator, whereas in root anatomy, the horizontal transport structure (including the epidermis and exodermis) mainly absorb water and nutrients and transport them to the vascular cylinder, and the vertical transport structure (including the vascular cylinder and vessels) transport water and nutrients to the other organs of the plant (Eissenstat et al. 1999; Geng et al. 2018; Du et al. 2018; Kim et al. 2020). In the process of root adaptation to the environment, root anatomical structures may increase functional plasticity by increasing the functionality of horizontal and vertical transport structures, or may increase the degree of variability by increasing trait differences between horizontal and vertical transport structures to resisting habitat changes. Currently, the functional adaptation and coefficient of variation of plant anatomical

structures were measured in different habitats, and few studies have linked the functional adaptation of plant anatomical structures in different habitats to the variation degree of plant anatomical structures in the same habitat. Whether the relationship between these two indicators reveals new mechanisms of plant adaptation to different habitats is also unknown.

The wetlands on the Western Sichuan Plateau of China have a large area and are rich in hygrophytes, but under the dual interference of global climate change and human disturbance, the area of wetlands is rapidly decreasing (Xu et al. 2019; Zhang et al. 2021), and the living space for hygrophytes is diminishing. As a dominant species in the wetlands of the western Sichuan Plateau, *Carex moorcroftii* has the function of soil and water conservation and maintaining ecological balance; with the drought of the habitat, the importance value of *C. moorcroftii* in the plant community gradually declined (Xiao et al. 2014), and a lot of researches have been carried out on its geographic distribution, morphological characteristics and biomass in this process (Liu et al. 2018; Wang et al. 2021). During drought, the root anatomy of *C. moorcroftii* exhibit strong adaptations in functional traits, but the response mechanism is unclear.

To explore the effects of habitat drought on root anatomy of hygrophytic plants, our research focuses on the dominant species in the wetlands of the Western Sichuan Plateau. *C. moorcroftii* samples were collected along a gradient of habitat drought to analyze the relationship between root anatomical structure and ecological habits, variations in root anatomical structure characteristics along soil moisture gradients, the sensitivity of different anatomical structures to changes in soil moisture, and the ability of roots to adapt to habitat changes.

Materials and methods

Study site

The study site was located in the ancient ice cap wetland in Yinduo Township, Xinlong County, Ganzi Prefecture, Sichuan Province, China, with geographic coordinates 31°24′25″ N, 99°49′48″ E and elevation of 4300–4450 m (Fig. 1a). It belongs to the subhumid climate zone of the Qinghai-Tibet Plateau. The terrain is plateau and mountainous, and the area between the two mountains is gentle and has a large area of swampy waters. *C. moorcroftii* is the monodominant species in swampy meadows in shallow-water areas. Alpine meadows are located on slopes, and the codominant species include *Kobresia humilis*, *K. macrantha*, and *C. moorcroftii*, and the accompanying species include *C. atrofusca* var. *minor*, *Poa alpina*, *P. arctica*, and *Stipa capillacea*. The study site formed a natural arid gradient
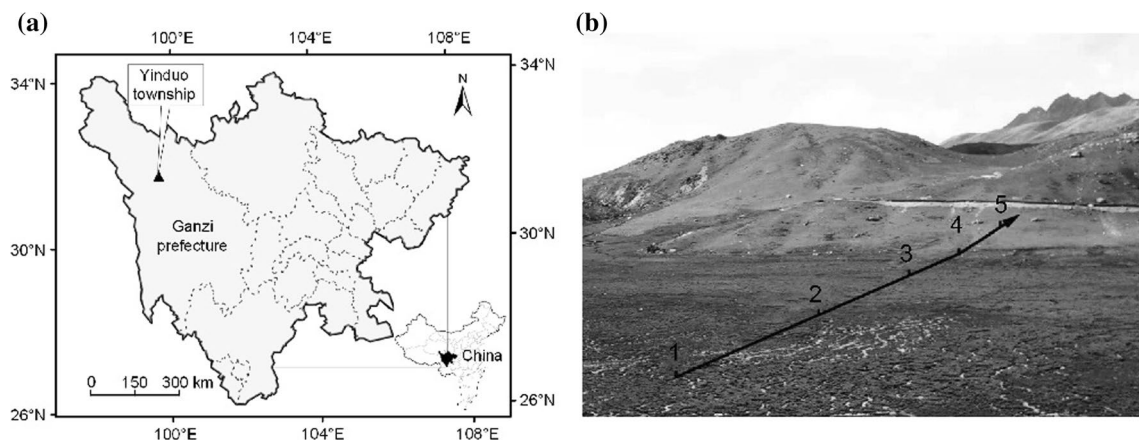
Fig. 1 Map of research setting (**a**) and sample plot setting (**b**)

from aquatic to humid habitats, which could objectively reveal the changes of anatomy with the drought of habitats for *C. moorcroftii*.

Material collection

Five 4 m × 4 m sample plots were set up from the low-lying flowing water area to the alpine meadow, among which two plots were located in the marsh meadow and three plots were located in the *Kobresia* meadow (Fig. 1b). *C. moorcroftii* were distributed in the five sample plots but with different spatial distribution patterns (Table 1). The image method (Guan et al. 2010) was used to measure the cover of *C. moorcroftii* in each sample plot, and a TSC-IW soil moisture meter was used to measure the volume moisture content of soil. The materials were collected in August 2018, and more than 30 plants of *C. moorcroftii* were randomly collected from each plot. One new white root was chosen from each plant, cleaned and placed in FAA fixative (HCHO:CH$_3$COOH:70% C$_2$H$_5$OH = 1:1:18, by vol.).

Paraffin method

The root was taken out of the fixative and an approximately 1-cm segment of the root was cut in half at 0.5 cm from the root tip. The samples were first washed with 70% ethanol and dehydrated with an increasing concentration series (70%, 85%, 90% and 100%) of tert-butanol-ethanol solutions for 2 h. Then, the samples were cleared with 100% tert-butanol 3 times for 2 h each time. Once transparent, the material was immediately dipped in pure paraffin wax and placed in a constant-temperature oven at 63 °C for 2 to 3 days. Then, the samples were embedded with a KD-BM II tissue embedding machine, sliced with a Leica RM 2145 microtome at a thickness of 8 to 10 μm, dried in a 40 °C oven, and dyed with safranin O–fast green (Cortaga and Sebidos 2019). Fifteen roots were taken from each plot, and each root has 2 slices. Thus, a total of 150 slices were taken from the 5 plots.

Data acquisition

The slices were viewed under a Leica DM 500 optical microscope, and images were obtained using LAS V4.4 software. More than 600 photos were obtained. ImageJ software was used to measure root transverse diameter (μm) and area (A$_1$, μm^2), epidermal cell thickness (μm), exodermis layer number (N$_1$) and thickness (μm), aerenchyma area (A$_2$, μm^2), Casparian strip thickness (μm), vascular cylinder diameter (μm) and area (A$_3$, μm^2), and vessel number (N$_2$), vessel area

Table 1 Information on the sample plots

Sample plot no	Terrain and habitat	Soil moisture content (%)	Spatial distribution pattern	C. moorcroftii cover (%)
1	Plain, swamp meadow	100	Uniformed	95
2	Plain, swamp meadow	80.07	Clustered	60
3	Gentle slope, alpine meadow	68.39	Random	25
4	Gentle slope, alpine meadow	51.04	Random	15
5	Steep slope, alpine meadow	28.78	Random	5

(A_4, μm^2) and vessel diameter (μm). Here, the thickness of the Casparian strip, exodermis and epidermal cells and the average area and average diameter of vessels were expressed as the mean of ten continuously distributed cells; the diameters of the vascular cylinder, root cross-section, and vessels were expressed as the mean of the horizontal and vertical diameters. According to the measurement data calculation, the vascular cylinder area ratio $= A_3/A_1$, aerenchyma area ratio $= A_2/A_1$, total vessel area $= A_4 \times N_2$, and total vessel area ratio $= (A_4 \times N_2)/A_3$.

Statistical analysis

Microsoft Excel software was used for data recording and sorting, and SPSS 26.0 software was used for data analysis. One-way ANOVA was used to analyze the difference in root anatomical structures among soil moisture levels ($P < 0.01$), and linear regression was used to analyze the variation in root anatomical structures along a soil moisture gradient. Canoco 5.0 software was used to analyze the ranking relationship between root anatomical structures and soil moisture content, and the ranking model was selected based on the gradient length in the detrended correspondence analysis results (Morris et al. 2015). In this study, when the maximum gradient length was greater than 3, the redundancy analysis linear ranking model was chosen. The first axis of the sorting diagram was taken as the horizontal axis ($-1,1$) and divided into three sections as the basis for the classification of plasticity strength. The first section is ($-0.25, 0.25$), and the plasticity is weak. The second section is ($-0.5, -0.25$) and ($0.25, 0.5$), and the plasticity is medium. The third section is ($-1, -0.5$) and ($0.5, 1$), and the plasticity is strong. The first axis of the sorting diagram was taken as the horizontal axis ($-1, 1$) as the basis for plasticity strength, and the length of the arrows projected to the first axis of each anatomical structure was divided by the sum of the projected

lengths of each index to measure the functional adaptation of the root anatomical structures in different soil moistures and was denoted plasticity 1. Coefficients of variation $= \left(\frac{SD}{M} \right) 100\%$. The difference between the maximum and minimum coefficients of variation of each anatomical structure under different soil moisture contents divided by the total difference was used to measure the variation degree of the root anatomical structures at the same soil moisture level and was denoted plasticity 2. Data were plotted with Origin 2018 software.

Results

Anatomical characteristics of roots and variations in root transverse section area along a soil moisture gradient

The transverse section of the root is an irregular circle (Fig. 2a). The epidermal cells are an oblong monolayer with a stratum corneum. The exodermal cells are tightly packed, with 3 to 5 layers (Fig. 2b). Lysigenous aerenchyma accounts for 51–71% of the root transverse section area (Fig. 2a). The cells of the endodermis are arranged in a regular circle and thickened by "U" embolization to form the Casparian strip. The vascular cylinder is nearly round and consists of primary xylem, primary phloem, and parenchyma, with 7 to 10 rows of vessels (Fig. 2c). The pith is clearly visible, and the cell wall is thickened (Fig. 2c).

The area of the transverse section ranged from 37.4 to 92.5×10^4 μm^2, and is significantly and positively correlated with the soil moisture gradient ($P < 0.01$; Fig. 3).

Variations in the horizontal transport structure of roots along the soil moisture gradient.
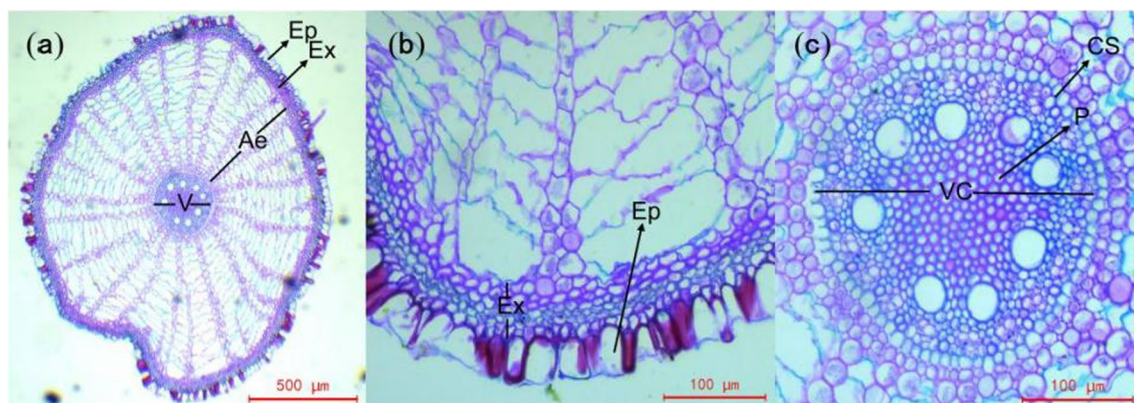

Fig. 2 Anatomical structure of the *C. moorcroftii* root. **a** Root transverse section. **b, c** Part of the root transverse section at higher magnification. Ep: Epidermis; Ex: Exodermis; Ae: Aerenchyma; CS: Casparian strip; VC: Vascular cylinder; P: Pith
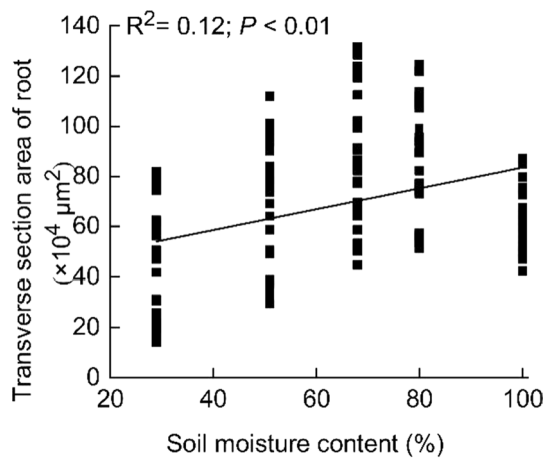
Fig. 3 Variations in root transverse section area correlated with soil moisture gradient. Mean values $\pm$ SE, $n = 150$

The epidermal cells of the root ranged in thickness from 7.93 to 22.63 μm (Fig. 4a), and those of the exodermis from 23.08 to 40.80 μm (Fig. 4b). The thickness of the Casparian strip ranged from 1.16 to 3.55 μm (Fig. 4c), the aerenchyma area ranged from 19.93 to 66.51×10^4 μm^2 (Fig. 4d), and the ratio of the aerenchyma area to the root transverse section area ranged from 0.51 to 0.71 (Fig. 4e); all of which were significantly and positively correlated with the soil moisture gradient ($P < 0.01$; Fig. 4).

Variations in the vertical transport structure of roots along the soil moisture gradient

The area of the vascular cylinder was 2.49 to 6.40×10^4 μm^2 (Fig. 5a), the ratio of vascular cylinder area to transverse section area was 0.03 to 0.13 (Fig. 5b), and the number of primary xylem vessels was 7 to 11 rows (Fig. 5c). The total area of vessels ranged from 2.31 to 3.63×10^3 μm^2 (Fig. 5d), and all were significantly and negatively correlated with the soil moisture gradient ($P < 0.01$; Fig. 5a–d). The ratio of total vessel area to vascular cylinder area ranged from 0.05 to 0.12, and was significantly and positively correlated with the soil moisture gradient ($P < 0.01$; Fig. 5e).

Plasticity analysis of root anatomical structures

The plasticity of the *C. moorcroftii* root anatomical structures can be divided into three types: strong plasticity, medium plasticity and weak plasticity. The structures with strong plasticity included the ratio of the vascular cylinder area to root transverse section area, thickness of the Casparian strip, thickness of epidermal cells, and diameter and area of the vascular cylinder. The medium plasticity structures were composed of the aerenchyma area and area ratio, root transverse section area, number of vessels, ratio of total

vessel area to root transverse section area, and number of exodermal layers. The weak plastic structures included the total vessel area, epidermal thickness, diameter of root transverse section, and diameter and area of vessels (Fig. 6a).

In the driest habitat, the coefficient of variation was the smallest for the vascular cylinder area ratio, which thus showed the strongest functional adaptation, and was the largest for the total vessel area, which thus showed the weakest functional adaptation (Table 2). In addition, the vascular cylinder area ratio, total vessel area, exodermis thickness and vessel diameter plasticity 1 and plasticity 2 were symmetrically distributed, while the plasticity 1 and plasticity 2 of the remaining anatomical structures were asymmetrically distributed (Fig. 6b).

Discussion

Relationship between root anatomical structures and ecological habit

The anatomical structures of the roots of *C. moorcroftii* were similar to those of most monocotyledonous plants in wetlands (Soukup et al. 2005; Yang et al. 2019a), but there are differences in the ratio of the structures. First, the ratio of aerenchyma area to the transverse section area of the root is 0.51–0.71 (Fig. 2a), which is extremely high. Aerenchyma is an oxygen channel for plants to survive in aqueous habitats (Efremov et al. 2016), and a larger area ratio indicates a higher water content in the plant habitat (Leandro et al. 2022). This ratio is still high in the driest habitats, indicating that the ecological habits of *C. moorcroftii* are not easily changeable. Second, the ectoplasmic barrier structure is prominent (Fig. 2b, c), including the exodermis, endodermis and Casparian strip, which is consistent with the anatomical structure of the root of *Eichhornia crassipes* (Madhubala et al. 2021). The nutrition and water of roots in wet habitats need to be controlled by barrier structures (Andersen et al. 2021; Beisson et al. 2012) to prevent harmful substances from entering the root vascular cylinder and prevent the loss of nutrients from the roots, which are the fundamental structures of plant hygrophytes (Barberon et al. 2016). These structures, formed in the process of long-term habitat evolution, have given rise to the ecological habits of *C. moorcroftii* and have ensured its dominance in wetlands.

Adaptation of root anatomical structures to soil moisture gradient

The response strategies of the horizontal and vertical transport structures of the *C. moorcroftii* root to drought are different. During drought, the transverse section area of roots decreases with decreasing soil moisture (Fig. 3), and the

Fig. 4 Variations in the horizontal transport structure in relation to the soil moisture gradient. Mean values ± SE, $n = 150$
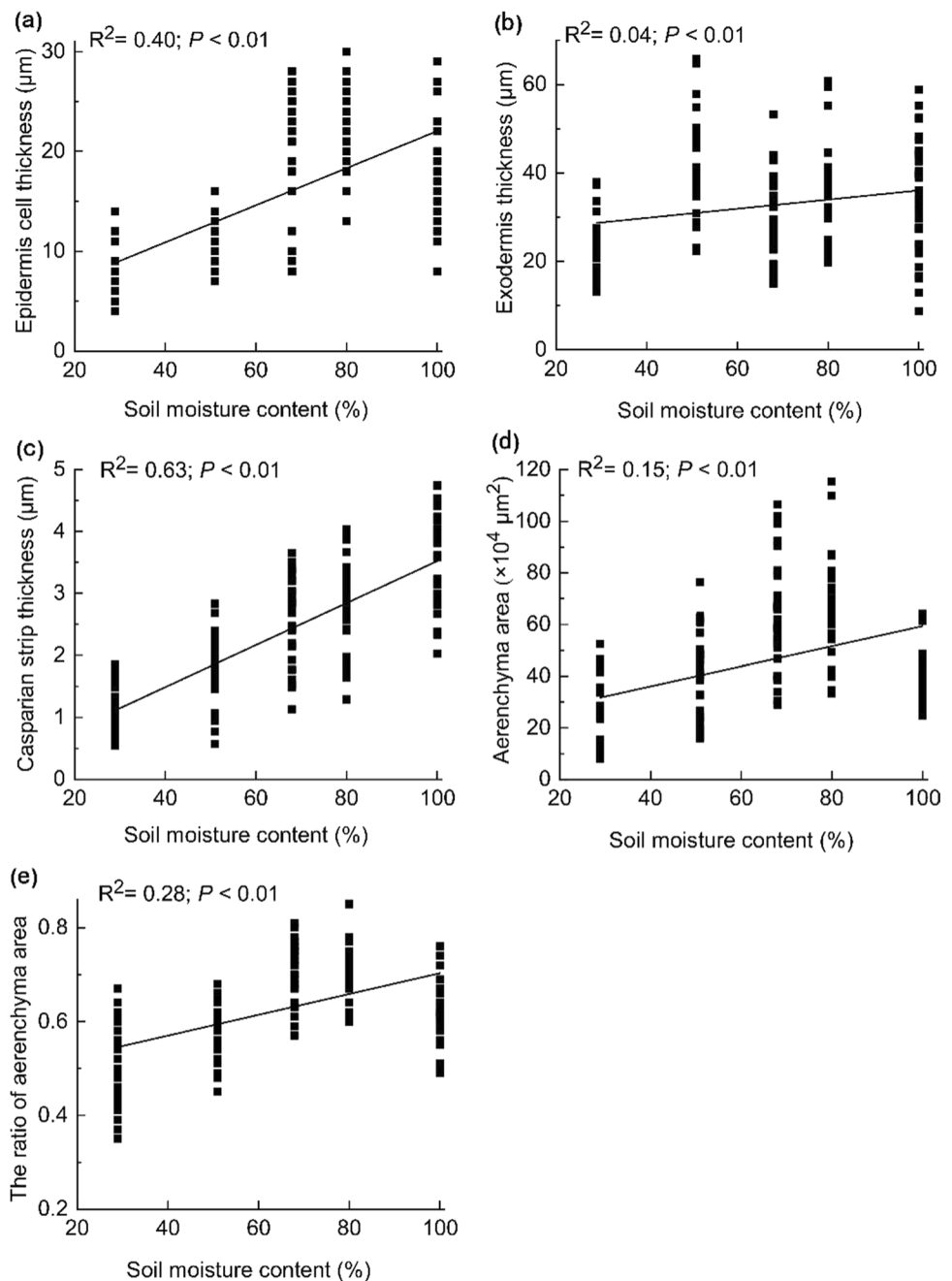
horizontal and vertical transport structures exhibit opposite changing trends. The thickness of the epidermis and exodermis, the area of the aerenchyma, the ratio of the aerenchyma area to the root transverse section area, and the thickness of the Casparian strip were all significantly and positively correlated with soil moisture content (Fig. 4). The epidermis absorbs water, but epidermal cells also consume water through respiration in water-deficient habitats (Xiao et al. 2020; Halder et al. 2022; Kou et al. 2022). Therefore, reducing the thickness of the epidermis is a water retention strategy in *C. moorcroftii*. When water enters the root vascular cylinder, it is first transported horizontally, and the thickness of the exodermis is related to the horizontal water transport efficiency, so reducing the thickness of the exodermis is a manifestation of reduction in the horizontal water transport distance in *C. moorcroftii*. Aerenchyma is a channel for oxygen in wet and hypoxic habitats (Bartlett et al. 2022), so it has less significance in arid habitats, resulting in a decrease in its area and in the ratio of its area to the root transverse section area. The change in the thickness of the Casparian strip is contrary to the research results of increased Casparian strip thickness when *Populus przewalskii* responds to

Fig. 5 Variations in the vertical transport structure in relation to the soil moisture gradient. Mean values ± SE, $n = 150$
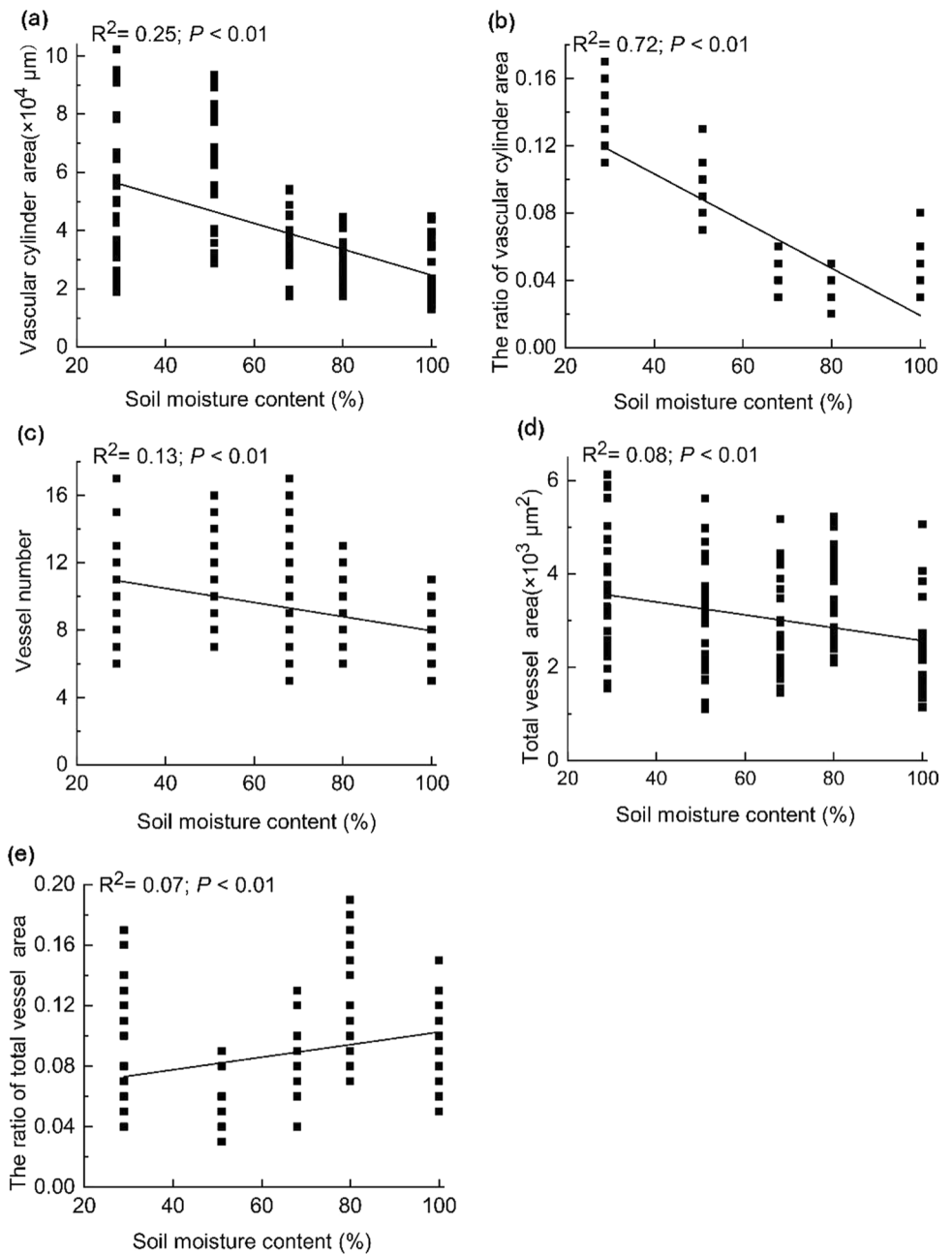
arid habitats (Yu et al. 2020), because *C. moorcroftii* is a hygrophytic plant, and the Casparian strip is more adapted to wet habitats. As one of the structures of the extracellular barrier, the Casparian strip mainly has the function of preventing harmful substances from entering the root vascular cylinder in wet habitats. However, in arid habitats, Casparian strips have less significance, which means that reducing their thickness is beneficial for water transport. Compared with the ability of xerophytes to absorb and retain water in response to drought by increasing the thickness of the epidermis and Casparian strip (Zhao et al. 2011; Grzesiak et al. 2019), *C. moorcroftii* has its own special drought adaptation

mechanism, that is, to reduce the thickness of the epidermis and Casparian strip and the area of each horizontal transport structure to increase the efficiency of water horizontal transport.

The area of the vascular cylinder, ratio of vascular cylinder area to root transverse section area, number of vessels, and total area of vessels were significantly and negatively correlated with soil moisture (Fig. 5). The vascular cylinder transports water and nutrients vertically in plants (Gu et al. 2014) and is closely related to plant mechanical support (Liu et al. 2005). The number and area of vessels are directly related to the efficiency of water transport (Köcher et al.
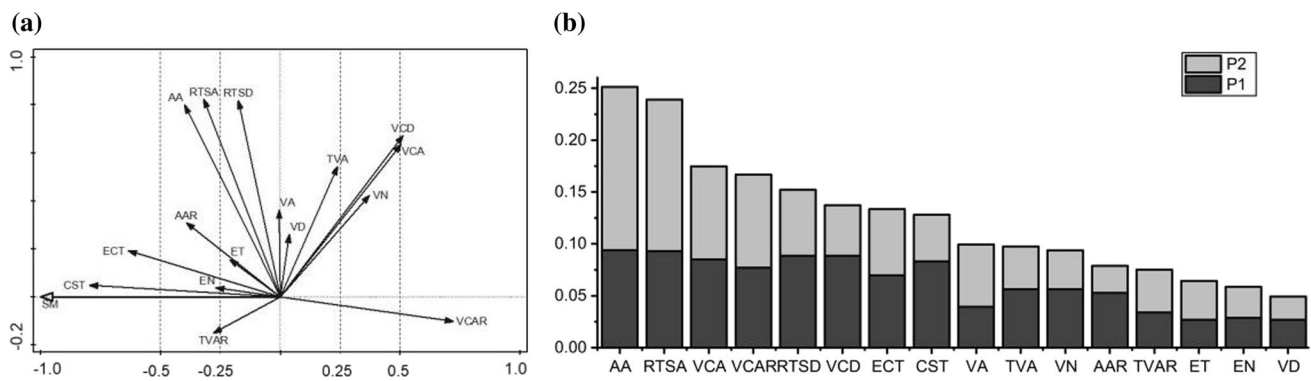
(a)   **(b)**

Fig. 6 Redundancy analysis ordination diagram of root anatomical structures and soil moisture gradient (**a**) and plasticity 1 and plasticity 2 of each anatomical structure (**b**). *SM* soil moisture, *P1* plasticity 1, *P2* plasticity 2, *VCAR* vascular cylinder area ratio, *CST* Casparian strip thickness, *ECT* epidermis cell thickness, *VCD* vascular cylinder diameter, *VCA* vascular cylinder area, *AA* aerenchyma area, *AAR* aerenchyma area ratio, *RTSA* root transverse section area, *VN* vessel number, *TVAR* total vessel area ratio, *EN* exodermis layer number, *TVA* total vessel area, *ET* exodermis thickness, *RTSD* root transverse section diameter, *VD* vessel diameter, *VA* vessel area. Values (-0.25, 0.25), the plasticity is weak; -0.5, -0.25) and (0.25, 0.5), the plasticity is medium; (-1, -0.5) and (0.5, 1), the plasticity is strong

Table 2 Coefficient of variation of root anatomical structures in different soil moistures (CV%)

SM	VCAR	CST	ECT	VCD	VCA	AA	AAR	RTSA	VN	TVAR	EN	TVA	ET	RTSD	VD	VA
100	0.34	0.21	0.27	0.18	0.38	0.27	0.12	0.20	0.20	0.38	0.26	0.38	0.38	0.32	0.17	0.28
80	0.20	0.27	0.17	0.15	0.29	0.30	0.09	0.24	0.21	0.28	0.18	0.28	0.33	0.15	0.14	0.29
68	0.18	0.27	0.38	0.15	0.29	0.34	0.09	0.31	0.30	0.36	0.20	0.36	0.30	0.15	0.22	0.42
51	0.17	0.30	0.21	0.17	0.33	0.40	0.10	0.34	0.25	0.39	0.18	0.39	0.28	0.19	0.19	0.28
29	0.10	0.33	0.34	0.28	0.53	0.69	0.16	0.59	0.28	0.35	0.22	0.35	0.31	0.30	0.15	0.26

2012; Wang et al. 2022). The efficiency of water transport in arid habitats is particularly important; therefore, by increasing the total area of vessels, *C. moorcroftii* increases the ratio of the area of the vascular cylinder to that of the root transverse section area and thus increases the water transport efficiency. The ratio of vessel area to vascular cylinder area decreases with decreasing soil moisture, indicating that other structures of the vascular cylinder also increase in size to increase the ratio of the vascular cylinder to the root, enhancing the efficiency of vertical water and nutrient transport as well as their own mechanical support.

Ability of root anatomical structures to adapt to habitat

The anatomical structures of the roots of *C. moorcroftii* have strong adaptability to different habitats. Except for the weak plasticity of the diameter and area of the vessels, thickness of the epidermis, and diameter of the root transverse section, all other structures have strong plasticity, including the vascular cylinder diameter, area and area ratio (Fig. 6a). Plasticity reflects the sensitivity of root anatomical structures to soil moisture (Hou et al. 2017; Potocka et al. 2018; Shelden et al. 2023). When soil moisture is lacking, the

vascular cylinder in the *C. moorcroftii* root quickly responds to drought and increases its area in arid habitats. As the main water transport structure in the vascular cylinder, the number of vessels gradually increases with decreasing soil moisture, and the plasticity of the number of vessels is stronger than that of vessel diameter, which indicates that the number of vessels is the first parameter to increase in response to arid habitats. This is similar to the strategy of *Bombax ceiba* to improve water delivery efficiency, in which the diameter of the vessels is reduced and the number of vessels is increased in dry and hot valleys (Zhao et al. 2016). In the absence of soil moisture, longer vessels and narrower lumens will not cause lumen embolism (Ding et al. 2016; Wang et al. 2019; Li et al. 2022), which is more conducive to vertical water transport over long distances.

Moreover, the vascular cylinder area ratio, the total vessel area, exodermis thickness and vessel diameter plasticity 1 and plasticity 2 are symmetrically distributed, while the plasticity 1 and plasticity 2 of the Casparian strip thickness, epidermis cell thickness, aerenchyma area, root transverse section area, vessel number, exodermis number and exodermis thickness are asymmetrically distributed and plasticity 1 and plasticity 2 form a complementary relationship (Fig. 6b). When the functional adaptation of plant

anatomical structures is strong in different habitats, the variation coefficient of plant anatomical structures is low in the same habitats, indicating that the plant anatomical structures were more sensitive to habitat changes (Schneider et al. 2022). Similarly, Casparian strip thickness, exodermis number, epidermis cell thickness and vessel number in the root anatomical structure of *C. moorcroftii* showed strong structural functional plasticity with low coefficients of variation in the soil moisture gradient, indicating that these structures have a major role in enhancing structural function in response to habitat drought. When the functional adaptation of plant anatomical structures is weak in different habitats, the variation coefficient of plant anatomical structure is high in the same habitats, indicating that the plant shows structural diversity in changing habitats (Yang et al. 2019b; Zhao et al. 2016). *C. moorcroftii* show strong variability in the exodermis thickness, aerenchyma area, and root transverse section area, while structural functional plasticity is low, indicating that these structures have a major role in enhancing structural diversity in response to habitat drought. At the population level, nutrients and water of *C. moorcroftii* can be transported among clones through the asexual network formed by the clonal building constructs, enabling resource sharing across the asexual lineage as a means of improving the population's adaptive capacity to the habitat (Liu et al. 2009). In our study, at the individual plant level, the simultaneous changes in the functional adaptation of root anatomical structures in different habitats and the variation degree of root anatomical structures in the same habitats, and this complementary relationship between structural function and structural diversity make the habitat adaptability of *C. moorcroftii* stronger.

Conclusion

The aerenchyma, which accounts for more than half of the area of the root transverse section and is the extracellular barrier structure controlling the entry of harmful substances into the root vascular cylinder of *C. moorcroftii*, is formed by long-term adaptation to wetland habitats and has achieved its own ecological habits. During drought, *C. moorcroftii* adopts the strategy of shortening the horizontal water transport distance while increasing the number of vessels to accelerate vertical water transport to enhance its ability to resist drought. At the same time, the functional adaptation of root anatomical structures in different habitats and the variation degree of root anatomical structures in the same habitats are complementary, and the two factors coordinate with each other to form a unique adaptation mechanism, which makes *C. moorcroftii* more adaptive to changes in its habitat. The results of this study further supplement the research on the response of plants to habitat drought in plateau wetlands,

and provide a scientific basis for the response of plateau wetlands to habitat drought. Based on the current context of habitat drought, it is necessary to increase the depth and breadth of research on more plateau wetland plants in the future, and to observe the changes of wetland plants from all nutrient organs of plants, in order to have a more comprehensive understanding of wetland plants response to habitat changes.

Author contribution DCZ conceived and designed research. HBW collected samples and conducted experiments. JYY analyzed data and wrote the manuscript. All authors read and approved the manuscript.

Data availability The data sets generated and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

References

Andersen TG, Molina D, Kilian J, Franke RB, Ragni L, Geldner N (2021) Tissue-autonomous phenylpropanoid production is essential for establishment of root barriers. Curr Biol 31(5):965–977. https://doi.org/10.1016/j.cub.2020.11.070

Barberon M, Vermeer JE, Bellis DD, Wang P, Naseer S, Andersen TG, Humbel BM, Nawrath C, Takano J, Salt DE, Geldner N (2016) Adaptation of root function by nutrient-induced plasticity of endodermal differentiation. Cell 164(3):447–459. https://doi.org/10.1016/j.cell.2015.12.021

Bartlett MK, Sinclair G, Fontanesi G, Knipfer T, Walker MA, McElrone AJ (2022) Root pressure-volume curve traits capture rootstock drought tolerance. Ann Bot-London 129(4):389–402. https://doi.org/10.1093/aob/mcab132

Beisson F, Li-Beisson Y, Pollard M (2012) Solving the puzzles of cutin and suberin polymer biosynthesis. Curr Opin Plant Biol 15(3):329–337. https://doi.org/10.1016/j.pbi.2012.03.003

Boughalleb F, Abdellaoui R, Ben-Brahim N, Neffati M (2014) Anatomical adaptations of Astragalus gombiformis Pomel under drought

stress. Cent Eur J Biol 9(12):1215–1225. https://doi.org/10.2478/s11535-014-0353-7

Boughalleb F, Abdellaoui R, Hadded Z, Neffati M (2015) Anatomical adaptations of the desert species *Stipa lagascae* against drought stress. Biologia 70:1042–1052. https://doi.org/10.1515/biolog-2015-0125

Brunner I, Herzog C, Dawes MA, Adrend M, Sperisen C (2015) How tree roots respond to drought. Front Plant Sci 6:547. https://doi.org/10.3389/fpls.2015.00547

Chen X, Xu Y, Liu H, Li Q, Kang X (2017) Root/stem anatomical characteristics of four *Malus* plants in Western Sichuan Plateau and their drought adaptation strategy. Acta Bot Boreali-Occidentalia Sinica 37(07):1296–1302. https://doi.org/10.7606/j.issn.1000-4025.2017.07.1296

Chimungu JG, Loades KW, Lynch JP (2015) Root anatomical phenes predict root penetration ability and biomechanical properties in maize (*Zea mays*). J Exp Bot 66(11):3151–3162. https://doi.org/10.1093/jxb/erv121

Cortaga CQ, Sebidos RF (2019) Drought-induced modifications on the outer part of the root (OPR) and root endodermis of selected rice genotypes. J Crop Sci Biotechnol 22(2):131–138. https://doi.org/10.1007/s12892-019-0018-0

Ding J, Zhang X, Chu G, Liu N (2016) Vessel characteristics and their plasticity in three desert plants. J Arid Land Resources Environ 30(09):171–177

Donnelly L, Jagodziński AM, Grant OM, O'Reilly C (2016) Above- and below-ground biomass partitioning and fine root morphology in juvenile Sitka spruce clones in monoclonal and polyclonal mixtures. Forest Ecol Manag 373:17–25. https://doi.org/10.1016/j.foreco.2016.04.029

Du X, Wei X (2018) Definition of fine roots on the basis of the root anatomy, diameter, and branch orders of one-year old *Fraxinus mandshurica* seedlings. J for Res 29(05):1321–1327. https://doi.org/10.1007/s11676-017-0561-x

Efremov AN (2016) Anatomy and morphology of vegetative organs and inflorescence of *Stratiotes aloides* L. (Hydrocharitaceae). Inland Water Biol 9(1):27–38. https://doi.org/10.1134/S1995082916010041

Eissenstat DM, Achor DS (1999) Anatomical characteristics of roots of citrus rootstocks that vary in specific root length. New Phytol 141(2):309–321. https://doi.org/10.1046/j.1469-8137.1999.00342.x

Galindo-Castañeda T, Lynch JP, Six J, Hartmann M (2022) Improving soil resource uptake by plants through capitalizing on synergies between root architecture and anatomy and root-associated microorganisms. Front Plant Sci. https://doi.org/10.3389/fpls.2022.827369

Geng D, Chen P, Shen X, Zhang Y, Li X, Jiang L, Xie Y, Niu C, Zhang J, Huang X, Ma F, Guan QM (2018) MdMYB88 and MdMYB124 enhance drought tolerance by modulating root vessels and cell walls in apple. Plant Physiol 178(3):1296–1309. https://doi.org/10.1104/pp.18.00502

Grzesiak MT, Hordyńska N, Maksymowicz A, Grzesiak S, Szechyńska-Hebda M (2019) Variation among spring wheat (*Triticum aestivum* L.) genotypes in response to the drought stress II- root system structure. Plants-Basel 8(12):584. https://doi.org/10.3390/plants8120584

Gu J, Xu Y, Dong X, Wang H, Wang Z (2014) Root diameter variations explained by anatomy and phylogeny of 50 tropical and temperate tree species. Tree Physiol 34(4):415–425. https://doi.org/10.1093/treephys/tpu019

Guan F, Liang Z, Wang Z (2010) Comparison of digital image method and graticulation method for vegetation coverage measurement in salinized grassland. J Northeast Agric Univ 41(01):130–133

Halder T, Choudhary M, Liu H, Chen Y, Yan G, Siddique KHM (2022) Wheat proteomics for abiotic stress tolerance and root system architecture: current status and future prospects. Proteomes 10(2):17. https://doi.org/10.3390/proteomes10020017

Hou X, Tigabu M, Zhang Y, Ma X, Cai L, Wu P, Liu A, Wang C, Qiu H (2017) Root plasticity, whole plant biomass, and nutrient accumulation of *Neyraudia reynaudiana* in response to heterogeneous phosphorus supply. J Soils Sediments 17:172–180. https://doi.org/10.1007/s11368-016-1517-z

Karlova R, Boer D, Hayes S, Testerink C (2021) Root plasticity under abiotic stress. Plant Physiol 187(3):1057–1070. https://doi.org/10.1093/plphys/kiab392

Kim Y, Chung YS, Lee E, Tripathi P, Heo S, Kim KH (2020) Root response to drought stress in rice (*Oryza sativa* L.). Int J Mol Sci 21(4):1513–1534. https://doi.org/10.3390/ijms21041513

Köcher P, Horna V, Beckmeyer I, Leuschner C (2012) Hydraulic properties and embolism in small-diameter roots of five temperate broad-leaved tree species with contrasting drought tolerance. Ann Forest Sci 69(6):693–703. https://doi.org/10.1007/s13595-012-0189-0

Kou X, Han W, Kang J (2022) Responses of root system architecture to water stress at multiple levels: A meta-analysis of trials under controlled conditions. Front Plant Sci 9(13):1085409. https://doi.org/10.3389/fpls.2022.1085409

Leandro TD, Manvailer V, de Oliveira Arruda RDC, Scremin-Dias E (2022) Pantanal flood pulse reveals constitutive and plastic features of two wild rice species (Poaceae, Oryzoideae): implications for taxonomy, systematics, and phylogenetics. Braz J Bot 45:1261–1278. https://doi.org/10.1007/s40415-022-00835-y

Li T, Ren J, He W, Wang Y, Wen X, Wang X, Ye M, Chen G, Zhao K, Hou G, Li X, Fan C (2022) Anatomical structure interpretation of the effect of soil environment on fine root function. Front Plant Sci. https://doi.org/10.3389/fpls.2022.993127

Liu F, Liu Q, Liang X, Huang H, Zhang S (2005) Morphological, anatomical, and physiological assessment of Ramie [*Boehmeria Nivea* (L.) Gaud.] tolerance to soil drought. Genet Resour Crop Ev 52(5):497–506

Liu WS, Wei W, Dong M (2009) Clonal and genetic diversity of *Carex moorcroftii* on the Qinghai-Tibet plateau. Biochem Syst Ecol 37(04):370–377. https://doi.org/10.1016/j.bse.2009.07.003

Liu G, Liu G, Lan Q, Li H, Cao R, Wang J, Liu L (2016) Comparative study on morphological characteristics and ecological adaptability of vessel elements of *Salix gordejevii* and *S.microstachya var bordensis*. Acta Bot Boreali-Occidentalia Sinica 36(02):316–322. https://doi.org/10.7606/j.issn.1000-4025.2016.02.0316

Liu WS, You JL, Zeng WB, Qi DH (2018) Predicting of the geographical distribution of *Carex moorcroftii* under global climate change based on MaxEnt model. Chinese J Grassland 40(05):43–49

López-Herrera A, Avalos-Borja M, García-Nava JR, Trejo-Téllez LI, Alarcón A, Patrón-Soberano A, Conde-Martinez V, Zavaleta-Mancera HA (2021) Interaction of silver nanoparticles with the aquatic fern *Azolla filiculoides*: root structure, particle distribution, and silver accumulation. J Nanopart Res 23(1):1–15. https://doi.org/10.1007/s11051-020-05120-1

Machado A, Pereira H, Teixeira RT (2013) Anatomy and development of the endodermis and phellem of *Quercus suber* L. roots. Microsc Microanal 19(03):525–534. https://doi.org/10.1017/S1431927613000287

Morris C (2015) Multivariate analysis of ecological data using CANOCO 5, 2nd edn. Afr J Range for Sci 32(4):289–292. https://doi.org/10.2989/10220119.2015.1015053

Pang Z, Lu W, Jiang L, Jin K, Qi Z (2019) Leaf traits of different growing plants in karst area of Shilin. China. Guihaia 39(08):1126–1138

Potocka I, Szymanowska-Pulka J (2018) Morphological responses of plant roots to mechanical stress. Ann Bot-London 122(05):711–723. https://doi.org/10.1093/aob/mcy010

Pregitzer KS, Deforest JL, Burton AJ, Allen MF, Ruess RW, Hendrick RL (2002) Fine root architecture of nine north american trees. Ecol Monogr 72(02):293–309. https://doi.org/10.1890/0012-9615(2002)072[0293:FRAONN]2.0.CO;2

Schneider HM (2022) Characterization, costs, cues and future perspectives of phenotypic plasticity. Ann Bot-London 130(02):131–148. https://doi.org/10.1093/aob/mcac087

Shelden MC, Munns R (2023) Crop root system plasticity for improved yields in saline soils. Front Plant Sci 14:1120583. https://doi.org/10.3389/fpls.2023.1120583

Shoaib M, Banerjee BP, Hayden M, Kant S (2022) Roots' drought adaptive traits in crop improvement. Plants-Basel 11(17):2256. https://doi.org/10.3390/plants11172256

Singh A, Shamim M, Singh KN (2013) Genotypic variation in root anatomy, starch accumulation, and protein induction in upland rice (*Oryza sativa*) varieties under water stress. Agr Res 2(01):24–30. https://doi.org/10.1007/s40003-012-0043-5

Soukup A, Seago JL, Votrubová O (2005) Developmental anatomy of the root cortex of the basal monocotyledon, *Acorus calamus* (Acorales, Acoraceae). Ann Bot-London 96(3):379–385. https://doi.org/10.1093/aob/mci190

Wang H, Wang Z, Dong X (2019) Anatomical structures of fine roots of 91 vascular plant species from four groups in a temperate forest in Northeast China. PLoS ONE 14(5):0215126. https://doi.org/10.1371/journal.pone.0215126

Wang HB, Zhang YK, Zhang DC (2021) Morphological and biomass allocation of *Carex moorcroftii* along soil moisture gradient. Acta Agrestia Sinica 29(03):522–530

Wang L, Dai Y, Zhang J, Meng P, Wan X (2022) Xylem structure and hydraulic characteristics of deep roots, shallow roots and branches of walnut under seasonal drought. BMC Plant Biol 22:440. https://doi.org/10.1186/s12870-022-03815-2

Xiang J, Ming J, Yin H, Zhu Y, Li Y, Long L, Ye Z, Wang H, Wang X, Zhang F, Yang Y, Yang C (2019) Anatomy and histochemistry of the roots and shoots in the aquatic selenium hyperaccumulator *Cardamine hupingshanensis* (Brassicaceae). Open Life Sci 14:318–326

Xiao Y, Chen M, Zhou J, Guo Z (2014) Plant community features of *Carex moorcroftii* steppe at different degradation degrees in the interior of Qinghai-Tibetan Plateau. Chinese J Appl Environ Biol 20(04):639–645. https://doi.org/10.3724/SP.J.1145.2014.01052

Xiao S, Liu L, Zhang Y, Sun H, Zhang K, Bai Z, Dong H, Liu Y, Li C (2020) Tandem mass tag-based (TMT) quantitative proteomics analysis reveals the response of fine roots to drought stress in cotton (*Gossypium hirsutum* L.). BMC Plant Biol 20(01):328. https://doi.org/10.1186/s12870-020-02531-z

Xie HH, Ye ZH (2021) Research advances in the relationship between root morphological structure, radial oxygen loss and salt/heavy metal uptake, accumulation and tolerance of wetland plants. Chinese J Ecol 40(03):864–875

Xu T, Weng B, Yan D, Wang K, Li X, Bi W, Li M, Cheng X, Liu Y (2019) Wetlands of international importance: status, threats, and future protection. Int J Env Res Pub He 16(10):1818. https://doi.org/10.3390/ijerph16101818

Yang C, Li S, Deng S, Yao L, Yuan L, Zhang X (2015) Study of the anatomy and apoplastic barrier characteristics of *Imperata cylindrica*. Acta Pratacul Sin 24(03):213–218

Yang C, Zhang X, Wang T, Hu S, Zhou C, Zhang J, Wang Q (2019a) Phenotypic plasticity in the structure of fine adventitious *Metasequoia glyptostroboides* roots allows adaptation to aquatic and terrestrial environments. Plants-Basel 8(11):501. https://doi.org/10.3390/plants8110501

Yang JT, Schneider HM, Brown KM, Lynch JP (2019b) Genotypic variation and nitrogen stress effects on root anatomy in maize are node specific. J Exp Bot 70(19):5311–5325. https://doi.org/10.1093/jxb/erz293

Yao L, Wang D, Wang D, Li S, Chen Y, Guo Y (2022) Phenotypic plasticity and local adaptation of leaf cuticular waxes favor perennial alpine herbs under climate change. Plants 11(1):120. https://doi.org/10.3390/plants11010120

Yu Y, Liu C, Fan S, He X (2020) Effects of drought stress and ABA on the development of endodermis in poplar root. J Chinese Electron Microscopy Soc 39(03):300–306. https://doi.org/10.3969/j.issn.1000-6281.2020.03.012

Zhang Y, Yan J, Cheng X, He X (2021) Wetland changes and their relation to climate change in the Pumqu basin, Tibetan plateau. Int J Env Res Pub He 18(05):2682. https://doi.org/10.3390/ijerph18052682

Zhang L, Chen A, Li Y, Li D, Cheng S, Cheng L, Liu Y (2022) Differences in phenotypic plasticity between invasive and native plants responding to three environmental factors. Life 12(12):1970. https://doi.org/10.3390/life12121970

Zhao X, Dong K, Zhang Y, Zhu H, Yang W, Yang M (2011) Drought resistance and root anatomy of *Lespedeza davurica* (Laxm.) Schindl. Acta Agrariae Sinica 19(01):13–19. https://doi.org/10.3969/j.issn.1007-0435.2011.01.003

Zhao G, Ping P, Ma H (2016) Comparison of moisture transmission anatomical structure of three kinds of Bombacaceae plants in the dry-hot valleys. J Arid Land Resources Environ 30(01):162–168

Zhu G, Deng R, Ma Y, Wei X (2015) Changes in the vessel morphology of *Ziziphus jujuba* var. *spinosa* plants in response to natural drought-gradient ecotopes. Acta Ecol Sinica 35(24):8268–8275. https://doi.org/10.5846/stxb201404280852