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A Comparative Analysis of the Hydraulic Strategies of Non-Native and Native Perennial Forbs in Arid and Semiarid Areas of China

Yanjun Dong [1,2], Zongshan Li [1,*], Maierdang Keyimu [3,4], Ying Chen [5], Guangyao Gao [1], Cong Wang [1] and Xiaochun Wang [5]

[1] State Key Laboratory of Urban and Regional Ecology, Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing 100085, China; dongyanjun19@mails.ucas.ac.cn (Y.D.); gygao@rcees.ac.cn (G.G.); congwang@rcees.ac.cn (C.W.)
[2] University of Chinese Academy of Sciences, Beijing 100049, China
[3] State Key Laboratory of Desert and Oasis Ecology, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi 830011, China; mhk@ms.xjb.ac.cn
[4] Xinjiang Key Laboratory of Desert Plant Roots Ecology and Vegetation Restoration, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi 830011, China
[5] Center for Ecological Research, Northeast Forestry University, Harbin 150040, China; cybbd1033@nefu.edu.cn (Y.C.); wangx@nefu.edu.cn (X.W.)
* Correspondence: zsli_st@rcees.ac.cn; Tel.: +86-1520-1157-915

Abstract: (1) Background: Water transport systems play an important role in maintaining plant growth and development. The plasticity responses of the xylem anatomical traits of different species to the environment are different. Studies have shown that there are annual growth rings in the secondary root xylem of perennial herbaceous species. Studies on xylem anatomical traits, however, have mainly focused on woody species, with little attention given to herbaceous species. (2) Methods: We set 14 sampling sites along a rainfall gradient in arid and semiarid regions, and collected the main roots of native (*Potentilla*) and non-native (*Medicago*) perennial forbs. The xylem anatomical traits of the plant roots were obtained by paraffin section, and the relationships between the xylem traits of forbs were analyzed by a Pearson correlation. (3) Results: In the fixed measurement area (850 µm × 850 µm), the vessel number (NV) of *Potentilla* species was higher than that of *Medicago* species, while the hydraulic diameter (Dh) and mean vessel area (MVA) of *Potentilla* species were lower than those of *Medicago* species. With the increase in precipitation along the rainfall gradient, the Dh (R^2 = 0.403, p = 0.03) and MVA (R^2 = 0.489, p = 0.01) of *Medicago* species increased significantly, and NV (R^2 = 0.252, p = 0.09) decreased, while the hydraulic traits of *Potentilla* species showed no significant trend with regard to the rainfall gradient. (4) Conclusions: The hydraulic efficiency of non-native *Medicago* forbs was higher than that of native *Potentilla* forbs, and the hydraulic safety of native *Potentilla* forbs was higher than that of non-native *Medicago* forbs. With the decrease in precipitation, the hydraulic strategies of non-native *Medicago* forbs changed from efficiency to safety, while native *Potentilla* forbs were not sensitive to variations in precipitation.

Keywords: hydraulic conductivity traits; water conveyance strategies; root vessel anatomy

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1. Introduction

Grasslands are one of the main biological communities on Earth, covering nearly 1/5 of the land surface [1]. In China, grassland is the vegetation type with the largest coverage area, and is distributed in arid and alpine areas with the most fragile ecological environment. The frequency and magnitude of drought events caused by global climate change are expected to be greater, affecting the structure and function of terrestrial ecosystems [2]. Climate change will affect water and carbon cycling, mineral cycling and the composition of the plant community, thus directly and indirectly affecting the primary productivity of grasslands [3,4]. Under the background of global climate change, the warm drought phenomenon in arid and semiarid areas of China has caused soil drought, and the natural water deficit has become an important factor limiting grassland productivity [5]. Grassland vegetation is sensitive to climate change [1], and research on the response of grassland to climate change has gradually attracted people's attention [6–8]. Studies have shown that the impact of climate change on grassland biomass varies with different grassland types [9] and is different throughout the growing season [10].

Although more than half of the Earth's land is covered by non-forest vegetation [11], vessel anatomical traits of plants are largely represented by anatomical and dendrochronological studies on trees and shrubs [12–23], with relatively few similar studies on herbaceous species [11,24–27]. Studies have shown that there are annual growth rings in the secondary root xylem of perennial herbaceous species [11,28], with wider vessels at the beginning of the growing season and narrower vessels at the end of the growing season [29]. The anatomy of herbaceous plants is of great significance to the development of herb chronology [30–32]. Recently, research on plasticity responses in vessel traits upon drought stress has gained importance because of frequent drought events, and there have been increasing studies focusing on the anatomical characteristics in the annual rings of plants [33,34]. The phenotypic plasticity of vessel traits enables plants to adjust their xylem structure to the water limitation experienced throughout their lifetimes [35]. The range of differences in vessel traits observed between two herbaceous species highlights the plasticity of hydraulic and vessel structures [36].

Plant xylem is prone to vessel embolism that blocks the process of water transport inside a conduit under drought stress [37], which could exert an adverse impact on the growth and development of the plant [38]. Severe water stress may cause the collapse of plant hydraulic systems, eventually causing plant death [39]. The increased level of embolism resistance, therefore, is one of the most important adaptations for plant survival under drought stress. The sensitivity of plants to embolism is determined by many anatomical traits, such as the thickness of intervessel pit membranes [40], vessel diameter [41] and mechanical characters [42], of which vessel diameter is directly related to embolism resistance [41]. It is generally believed that narrow xylem vessels have higher resistance to cavitation, but lower hydraulic conductivity than wide vessels [41], whereas wide vessels contribute to high hydraulic conductivity, but are vulnerable to hydraulic failure caused by gas embolism that forms under negative water potential [37,43]. Therefore, this may lead to trade-offs between efficiency and safety [43,44]; species with high hydraulic efficiency are prone to cavitation events, giving rise to low safety, while species with low water transport efficiency are safer and more resistant to embolism [45]. Differences in vessel plasticity responses and adaptation strategies between different species are necessary for exploring the plastic ability to adapt to climate change.

Medicago is a perennial deep-rooted forage introduced in arid and semiarid areas. *Potentilla* is a good ecological restoration species in this area that can adapt to different geological soils. The species of these two genera are sensitive to climate change and are often used in anatomical studies [28,46]. Previous studies have related the annual ring structures of plant roots [28], leaf anatomical structures [46,47] and the plasticity response of anatomical features to climate change [35,48]. It is not yet understood how the xylem anatomical features of the two genera respond to precipitation or what the differences are in xylem anatomical structure between non-native and native forbs.

In this study, we set eight sampling sites along a rainfall gradient in arid and semiarid regions of China and collected the main roots of *Medicago* and *Potentilla* forbs. We used the paraffin section method to obtain the vessel anatomical traits (vessel number, vessel fraction, vessel area, hydraulic conductivity and hydraulic diameter). Our aims were (1) to compare the differences in vessel anatomical traits between non-native and native forbs; (2) to examine the variation in vessel anatomical traits of non-native and native forbs along the precipitation gradient; (3) to explore the hydraulic strategies of non-native and native forbs growing in arid and semiarid regions.

2. Materials and Methods

2.1. Study Area and Field Sampling

In this study, samples were collected annually in arid and semiarid regions of China in July and August from 2017 to 2020. To avoid the influence of plant size on vessel size, healthy, mature and similar-sized *Medicago* and *Potentilla* forbs were carefully sampled. The average annual precipitation ranged from 230 mm to 500 mm, the average annual temperature ranged from −2.08 °C to 8.2 °C and the altitude ranged from 275 m to 1526 m in the entire sampling area (Table 1). Climate data from 1981 to 2019 were obtained from the China Meteorological Information Center (http://data.cma.cn/, accessed on 3 June 2021). A total of 120 healthy *Medicago* and *Potentilla* forbs (5 per species) were sampled (Table 1). Main roots of forbs were collected from approximately 3–10 cm beneath the ground surface and placed into FAA fixation solution (70% ethanol: 35–40% formaldehyde: acetic acid = 90:5:5) for preservation. They belong to the taproot system with obvious distinctions between main roots and lateral roots (Figure 1).

2.2. Experimental Procedure

The collected samples were made into sections according to the paraffin section method [49]. With a Leica RM2245 rotary microtome (Leica, Heidelberg, Germany), the 8–12 µm thick sections were obtained. Safranine and Fast Green were used for double dyeing. Finally, the samples were observed and photographed with the same magnification (×40) under an Olympus DP73 light microscope (Olympus, Tokyo, Japan) after sealing on the slides with neutral balsam.

Table 1. Site characteristics of non-native and native herbaceous species in arid and semiarid areas of China.

Site Code	Location (Latitude N, Longitude E)	Precipitation (mm)	Temperature (°C)	Elevation (m)	Species	Number of Samples
S1	37.10°, 108.22°	445	7.80	1372	MF, MS	10
S2	36.65°, 108.32°	500	8.20	1526	MF, MS, ML, MR, MM, PT	30
S3	44.27°, 116.53°	282	1.39	1140	MR, PT	10
S4	43.55°, 116.67°	321	1.51	1260	MS	5
S5	50.20°, 119.39°	357	−2.08	525	MR	5
S6	43.91°, 115.50°	227	1.80	1131	MR	5
S7	45.14°, 121.53°	404	5.76	275	MR	5
S8	36.98°, 107.85°	430	6.80	1405	PT, PC	10
S9	44.37°, 116.11°	253	2.58	938	PT	5
S11	43.55°, 116.67°	320	1.52	1271	PT, PA, PC	15
S12	47.94°, 117.32°	230	0.60	595	PT	5
S13	45.04°, 118.92°	358	1.03	1015	PT	5
S14	48.52°, 119.74°	360	−1.31	749	PT, PA	10

MF—*Medicago falcata*; ML—*M. lupulina*; MM—*M. minima*; MR—*M. ruthenica*; MS—*M. sativa*; PA—*Potentilla acaulis*; PC—*P. chinensis*; PT—*P. tanacetifolia*.

Figure 1. The picture of the research material (*Potentilla tanacetifolia*). The yellow box indicates the intercepted part.

2.3. Data Processing and Statistical Analysis

The ImageJ program (http://rsb.info.nih.gov/ij/index.html, accessed on 11 May 2021) was used to analyze the images. To reduce the effects of different ages on the results, an analyzed area (850 μm × 850 μm) was selected from the xylem periphery (close to the periderm), and the percentage of parenchyma rays in the fixed area should be equal to the percentage of parenchyma rays in each cross-section (Figure 2). Vessel number (NV), mean vessel area (MVA, μm^2), major and minor axis of the cross-section of each vessel and vessel fraction (VF, %) were measured. The vessel fraction was determined as the ratio of the total vessel area to the measured area. Annual rings were analyzed by recognizing earlywood and latewood in root xylem [50]. Plant age was determined by counting the number of annual rings in the digital images [35] (Figure 3). Since the cross-sections of vessels are mostly elliptical, the diameter of the vessel lumen was calculated as follows:

$$D = [3(ab)^3/(2a^2 + 2b^2)]^{1/4}, \quad (1)$$

where a and b are the major and minor axis dimensions, respectively [51]. According to the Hagen–Poiseuille law [37], the potential hydraulic conductivity (Kh, kg m MPa^{-1} s^{-1}) was calculated as follows:

$$Kh = \left(\frac{\pi\rho}{128\eta}\right)\sum_{i=1}^{n}(D_i)^4, \quad (2)$$

where ρ is the density of water (998.2 kg m^{-3}) and η is the viscosity of water at 20 °C (1.002 × 10^{-9} MPa s). The hydraulic diameter (Dh, μm) [52] was calculated as follows:

$$Dh = \sum_{i=1}^{n}(D_i)^5 / \sum_{i=1}^{n}(D_i)^4. \quad (3)$$

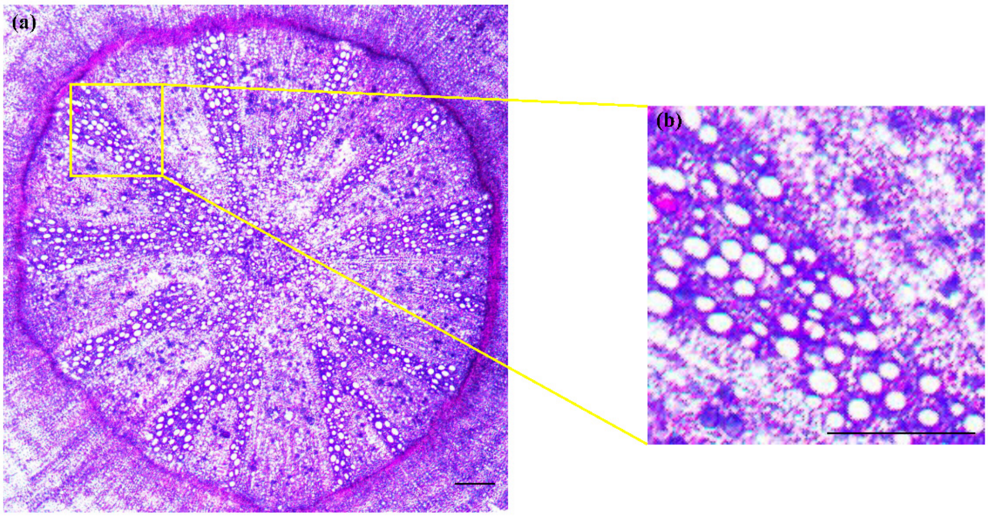

Figure 2. Root cross-section of *Potentilla chinensis*. (**a**,**b**) Cross-section from the same individual. The percentage of parenchyma rays in root cross-section (**a**) is 50.96%; the percentage of parenchyma rays in the analyzed area (**b**) is 51.09%. Scale bars = 200 µm.

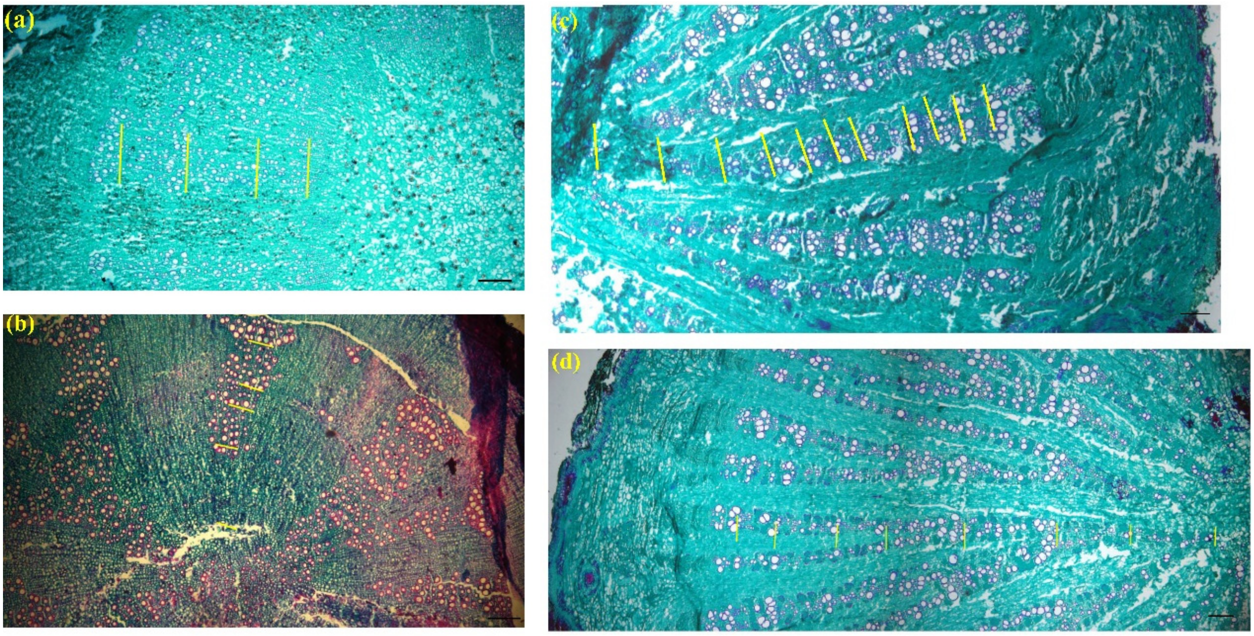

Figure 3. Root cross-sections of perennial forbs. (**a**) *Potentilla chinensis*; (**b**) *Potentilla tanacetifolia*; (**c**) *Medicago falcata*; (**d**) *Medicago sativa*. Yellow markers indicate annual ring boundaries. Scale bars = 200 µm.

The formula for calculating plasticity index is as follows:

$$PI = 1 - x/X, \quad (4)$$

where x is the minimum mean value and X is the maximum mean value [53].

To increase the normality of the distributions, the original data were $\log_{10}$-transformed [54]. Pearson correlations were used to analyze the relationship between precipitation and vessel anatomical and hydraulic traits, as well as the relationship between vessel area and vessel number.

3. Results

3.1. Vessel Anatomical Traits of Non-Native and Native Forbs

By comparing the root vessel structure of *Medicago* and *Potentilla* forbs (Figure 4), we found that there were few differences in their age, vessel fraction (VF) and the potential hydraulic conductivity (Kh). The average ages of the *Medicago* and *Potentilla* forbs were (5 ± 2.29) years and (7 ± 2.61) years, respectively; the average vessel fractions were (7.50 ± 3.04)% and (8.61 ± 3.57)% and the average potential hydraulic conductivities were (165.11 ± 102.05) kg m MPa^{-1} s^{-1} and (106.51 ± 81.82) kg m MPa^{-1} s^{-1}, respectively. In the fixed measurement area, the average vessel number (NV) of *Potentilla* (147 ± 35.06) was higher than that of *Medicago* (86 ± 31.97), while the mean vessel area (MVA) and hydraulic diameter (Dh) of *Potentilla* were lower than those of *Medicago*.

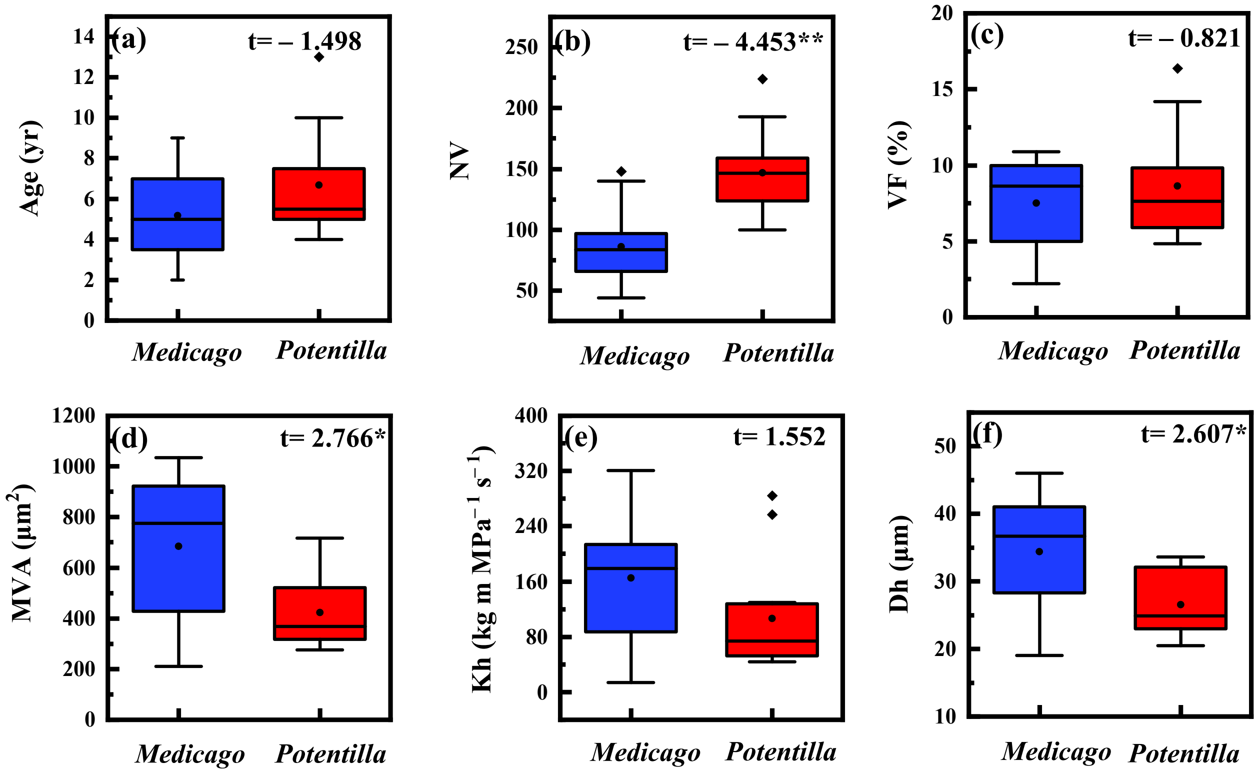

Figure 4. Boxplot of the major hydraulic traits in secondary root xylem of non-native and native forbs in arid and semiarid areas. (**a**) age; (**b**) vessel number (NV); (**c**) vessel fraction (VF); (**d**) mean vessel area (MVA); (**e**) the potential hydraulic conductivity (Kh); (**f**) hydraulic diameter (Dh). The blue and red boxes indicate *Medicago* and *Potentilla* herbaceous species, respectively. The *t*-test results between *Medicago* and *Potentilla* forbs are highlighted. * $p < 0.05$; ** $p < 0.01$.

The ranked order of the plasticity index (PI) of root vessel anatomical traits of *Medicago* was as follows: Kh > MVA > VF > NV > Dh. The ranked order of the PI of root vessel anatomical traits of *Potentilla* was as follows: Kh > VF > MVA > NV > Dh (Table 2). The plasticity index of all vessel anatomical traits of *Medicago* species was higher than that of *Potentilla* species.

3.2. Correlations of the Major Hydraulic Traits of Non-Native and Native Forbs

There were negative correlations between NV and MVA, and Dh in *Medicago* species, but these correlations were not significant, while there were no correlations between NV and MVA, and Dh in *Potentilla* (Figure 5a,c). In contrast to *Medicago*, there was a positive correlation between NV and Kh in *Potentilla*, but it was not significant (Figure 5b). The correlations between VF and hydraulic traits (MVA, Kh and Dh) reached the extremely significant level in both *Medicago* and *Potentilla* species (Figure 5d–f).

Table 2. Plasticity index (PI) of anatomical traits of non-native and native forbs.

Traits	Genera	
	Medicago	*Potentilla*
NV	0.430	0.295
VF (%)	0.558	0.466
MVA (μm^2)	0.568	0.430
Kh (kg m MPa^{-1} s^{-1})	0.684	0.697
Dh (μm)	0.364	0.285
PI mean	0.521	0.435

NV—vessel number; VF—vessel fraction; MVA—mean vessel area; Kh—the potential hydraulic conductivity; Dh—hydraulic diameter.

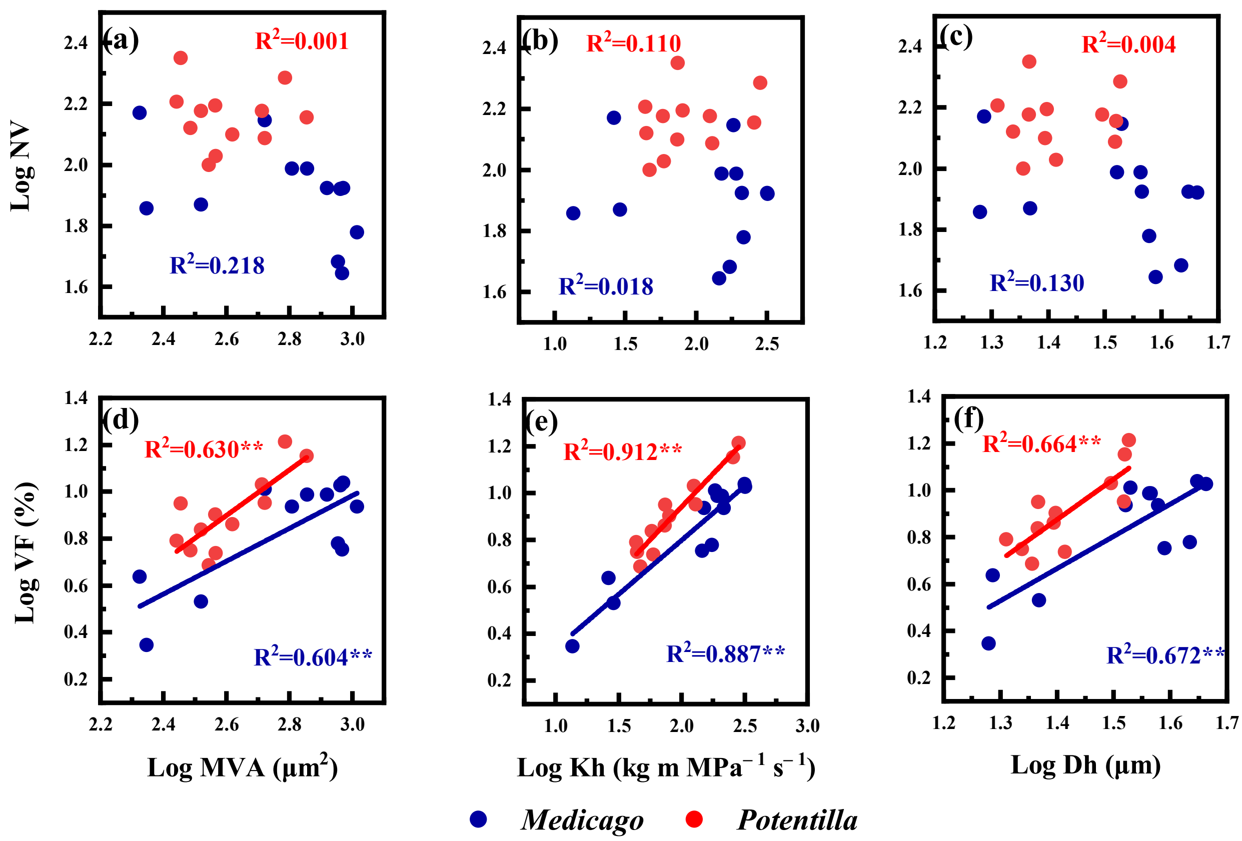

Figure 5. Correlation relationships between NV, VF and major hydraulic traits in secondary root xylem of non-native and native forbs in arid and semiarid areas. (**a**–**c**) Relationships between vessel number and hydraulic traits; (**d**–**f**) Relationships between vessel fraction and hydraulic traits. NV—vessel number; VF—vessel fraction; MVA—mean vessel area; Kh—the potential hydraulic conductivity; Dh—hydraulic diameter. The blue and red dots indicate *Medicago* and *Potentilla* herbaceous species, respectively. ** $p < 0.01$.

3.3. Variation in Vessel Anatomical Traits of Non-Native and Native Forbs along a Precipitation Gradient

With the increase in precipitation, there were no significant changes in NV and VF for the *Medicago* species (Figure 6b,c), but there were significant uptrends in age (Figure 6a). There were significant positive correlations between precipitation and MVA (r = 0.699, $p < 0.05$), and Dh (r = 0.635, $p < 0.05$) in *Medicago* species (Figure 6d,f). Precipitation was positively correlated with Kh in *Medicago*, but not significantly (Figure 6e). On the rainfall gradient, the age and all xylem anatomical traits of *Potentilla* species had a stable fluctuation without notable changing trends (Figure 6).

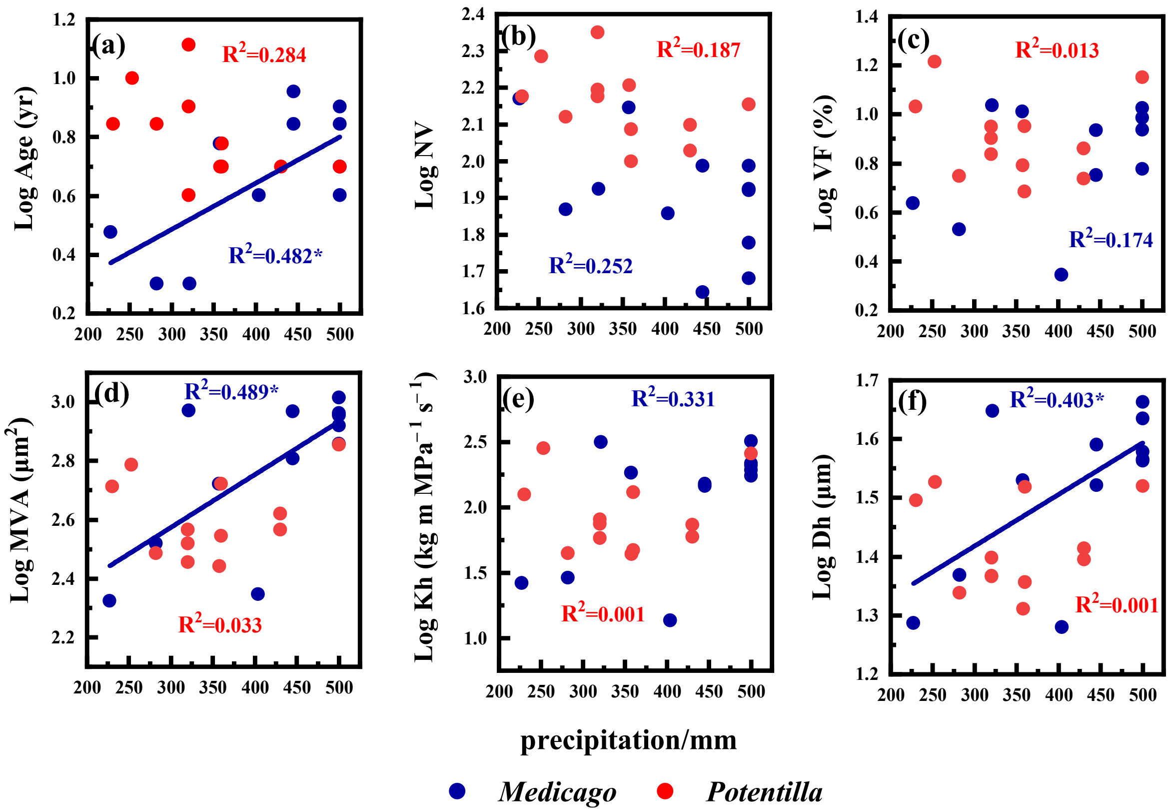

Figure 6. The changing trends of age and the major hydraulic traits in secondary root xylem of non-native and native forbs along a precipitation gradient in arid and semiarid areas. (**a**) age; (**b**) vessel number (NV); (**c**) vessel fraction (VF); (**d**) mean vessel area (MVA); (**e**) the potential hydraulic conductivity (Kh); (**f**) hydraulic diameter (Dh). The blue and red dots indicate *Medicago* and *Potentilla* herbaceous species, respectively. * $p < 0.05$.

4. Discussion

4.1. Differences in Xylem Features and Plasticity between Native and Non-Native Forbs

The xylem anatomical features of perennial forbs varied from species to species, which was consistent with the observations of xylem anatomical structures in other regions [55,56]. In this study, there were notable differences in the vessel anatomical traits between native *Potentilla* forbs and non-native *Medicago* forbs. The vessel size (MVA and Dh) of *Medicago* was larger than that of *Potentilla* (Figure 4d,f). Studies have shown that most leguminous plants have relatively wide vessels compared with other forbs, which allows leguminous plants to have a higher growth rate and larger root systems [57]. The NV of *Potentilla* is significantly higher than that of *Medicago* (Figure 4b), and there is no difference in Kh and VF between the two genera (Figure 4e), which may suggest that *Potentilla* forbs compensate for the small vessels with more vessels to ensure the required water transport.

Under stress conditions, the xylem pressure becomes more negative, which increases the risk of xylem embolism [43]. Embolisms could then spread from gas-filled conduits to adjacent water-filled conduits through interconduit pit membranes, a process known as air-seeding [58]. The larger a conduit's diameter is, the larger the pitted area will be, which will reduce the resistance of end walls and improve hydraulic efficiency, but give rise to vulnerability to cavitation [59]. A high vessel density contributes to hydraulic safety by leaving a larger proportion of vessels functional when cavitation occurs [60,61]. Moreover, intervessel pit characters also seem to play a role in ensuring hydraulic safety [40]. The larger vessel size in *Medicago* means that non-native *Medicago* forbs have higher hydraulic efficiency, while the smaller vessel size and more vessels in *Potentilla* mean that native *Potentilla* forbs may have higher hydraulic safety. Additionally, some studies have reported that compared with native grassland, *Medicago* grassland can strongly deplete deep soil water, even to the degree of desiccation in deeper soil layers, which eventually results in serious degradation of alfalfa grassland [62,63]. Therefore, more suitable native species should be selected in ecological restoration programs [57].

The evolution of plants in heterogeneous environments may lead to adaptation to a wide range of environments, and phenotypic plasticity plays an important role in this adaptation [64]. The plasticity index can reflect the ability of plants to overcome heterogeneous environments, and species with high plasticity often have extensive tolerance to different environmental conditions [64]. The xylem anatomical traits of plants with strong resilience often have good plasticity. The plasticity indexes of xylem anatomical traits in *Medicago* were higher than those of *Potentilla* (Table 2), which may suggest that *Medicago* forbs have a wider range of adaptation to the environment. The greater plasticity of key traits can promote an organism's establishment in a short time [65], which corresponds with greater plasticity of xylem traits in non-native *Medicago* forbs.

4.2. Differences in the Relationship between Vessel Traits of Non-Native and Native Forbs

There was a negative correlation between NV and MVA in *Medicago* (Figure 5a), which was consistent with the hypothesis of a trade-off between hydraulic efficiency and safety [43]. The size and number of vessels are related to the efficiency and safety of water transport. To ensure the efficiency and safety of water transport, there is usually a trade-off between the size and number of vessels [43]. Small vessels and many vessels are not prone to embolism under drought stress and have high hydraulic safety; large vessels and few vessels have high water transport efficiency, but they are more prone to embolism [66,67]. However, there was no similar trade-off relationship in *Potentilla* species (Figure 5a), and a positive correlation between NV and Kh (Figure 5b), which may indicate that *Potentilla* species can improve hydraulic efficiency while maintaining a high level of hydraulic safety. The significant positive correlations between VF and MVA, and Kh of *Potentilla* were higher than those of *Medicago* (Figure 5d,e), which may be related to the fact that there was almost no trade-off relationship between the vessel number and size in *Potentilla*.

The trade-off between efficiency and safety is not only related to xylem structures, but also affected by the plant growth environment. If plants grow in soil with high moisture, there is no need to reduce hydraulic efficiency to ensure safety. On the contrary, if the root system is seriously subjected to water stress, it is necessary to improve the hydraulic safety to ensure normal water transport [68]. However, some studies have also shown that the trade-off between efficiency and safety is independent of the moisture status of the plant growth environment [69]. Therefore, the trade-off between xylem efficiency and safety may be affected by many factors and is likely to be species-specific.

4.3. Response Differences of Vessel Traits of Non-Native and Native Forbs to Precipitation

Precipitation is one of the important factors influencing plant growth, particularly in arid and semiarid areas [70]. For *Medicago* forbs, precipitation was positively correlated with hydraulic traits (MVA, Kh and Dh) (Figure 6d–f), indicating that *Medicago* species may improve hydraulic efficiency in areas with more precipitation and ensure hydraulic safety to survive in areas with less precipitation. Species' embolism resistance would vary with the degree of drought the species experienced; species in water-limited environments are more cavitation-resistant than plants in good water conditions [71]. García-Cervigón et al. [72] studied the variation in xylem traits of *Embothrium coccineum* along the precipitation gradient, and results showed that the hydraulic diameter decreased significantly, the vessel density increased significantly, but the vessel fraction did not change significantly from wet sites to dry sites. Boughalleb et al. [73] designed a water control experiment to study the effects of water deficit on *Astragalus gombiformis* Pomel., and the results showed that the vessel diameter of root xylem decreased and the vessel density increased under water deficit, which was consistent with the results of our study. *Quercus canariensis* in the Mediterranean region responded to water stress by reducing the vessel area and increasing the vessel density [12], which was consistent with the results of this paper. There was no correlation between the xylem anatomical features of *Potentilla* and precipitation, which may suggest that precipitation has little effect on the hydraulic strategies of *Potentilla*. Some studies have reported that introduced species were more sensitive to climatic factors than native species [57,74], which was consistent with our results. Other climatic factors such as temperature may also affect xylem features [25,75]. More studies are needed to reveal the response mechanism of xylem traits of *Potentilla* to other abiotic and maybe biotic factors.

5. Conclusions

Our study revealed the hydraulic strategies to cope with precipitation of native and non-native forbs in arid and semiarid areas of China by comparing their xylem anatomical traits. Our results showed that there were notable differences in xylem anatomical traits between native *Potentilla* and non-native *Medicago* forbs in arid and semiarid areas of China. The water transport system of native *Potentilla* forbs, built of higher vessel number, and smaller vessel size, contrasts with that of non-native *Medicago* forbs and is expected to be safer. Because vessel traits are only part of the plant system, other anatomical and functional traits have to be studied to verify these results. There was a trade-off between safety and efficiency in the xylem of *Medicago* forbs, while there was no similar trade-off relationship in *Potentilla* species. The plasticity of vessel traits in non-native forbs was greater, which gave *Medicago* forbs higher hydraulic efficiency in areas with more precipitation and higher hydraulic safety in areas with less precipitation, whereas native *Potentilla* forbs were not sensitive to variation in precipitation. Further research is needed to explore the effects of other abiotic and maybe biotic factors on the hydraulic strategies and growth of perennial herbs in arid and semiarid areas of China.

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References

1. Zavaleta, E.S.; Shaw, M.R.; Chiariello, N.R.; Thomas, B.D.; Cleland, E.E.; Field, C.B.; Mooney, H.A. Grassland responses to three years of elevated temperature, CO_2, precipitation, and N deposition. *Ecol. Monogr.* **2003**, *73*, 585–604. [CrossRef]
2. Easterling, D.R. Climate extremes: Observations, modelling, and impacts. *Science* **2000**, *289*, 2068–2074. [CrossRef] [PubMed]
3. Brookshire, E.N.J.; Weaver, T. Long-term decline in grassland productivity driven by increasing dryness. *Nat. Commun.* **2015**, *6*, 7148. [CrossRef]
4. Liu, H.Y.; Mi, Z.R.; Lin, L.; Wang, Y.H.; Zhang, Z.H.; Zhang, F.W.; Wang, H.; Liu, L.L.; Zhu, B.; Cao, G.M.; et al. Shifting plant species composition in response to climate change stabilizes grassland primary production. *Proc. Natl. Acad. Sci. USA* **2018**, *115*, 4051–4056. [CrossRef]
5. Knapp, A.K.; Briggs, J.M.; Koelliker, J.K. Frequency and extent of water limitation to primary production in a mesic temperate grassland. *Ecosystems* **2001**, *4*, 19–28. [CrossRef]
6. Gao, Q.Z.; Zhu, W.Q.; Schwartz, M.W.; Ganjurjav, H.; Wan, Y.F.; Qin, X.B.; Ma, X.; Williamson, M.A.; Li, Y. Climatic change controls productivity variation in global grasslands. *Sci. Rep.* **2016**, *6*, 26958. [CrossRef] [PubMed]
7. Grime, J.P.; Brown, V.K.; Thompson, K.; Masters, G.J.; Hillier, S.H.; Clarke, I.P.; Askew, A.P.; Corker, D.; Kielty, J.P. The response of two contrasting limestone grasslands to simulated climate change. *Science* **2000**, *289*, 762–765. [CrossRef]
8. White, S.R.; Carlyle, C.N.; Fraser, L.H.; Cahill, J.F. Climate change experiments in temperate grasslands: Synthesis and future directions. *Biol. Lett.* **2012**, *8*, 484–487. [CrossRef]

9. Ma, W.H.; Fang, J.Y.; Yang, Y.H.; Mohammat, A. Biomass carbon stocks and their changes in northern China's grasslands during 1982–2006. *Sci. China Life Sci.* **2010**, *53*, 841–850. [CrossRef]
10. Ma, W.H.; Liu, Z.L.; Wang, Z.H.; Wang, W.; Liang, C.Z.; Tang, Y.H.; He, J.S.; Fang, J.Y. Climate change alters interannual variation of grassland aboveground productivity: Evidence from a 22-year measurement series in the Inner Mongolian grassland. *J. Plant Res.* **2010**, *123*, 509–517. [CrossRef]
11. Büntgen, U.; Psomas, A.; Schweingruber, F.H. Introducing wood anatomical and dendrochronological aspects of herbaceous plants: Applications of the Xylem Database to vegetation science. *J. Veg. Sci.* **2014**, *25*, 967–977. [CrossRef]
12. Gea-Izquierdo, G.; Fonti, P.; Cherubini, P.; Martín-Benito, D.; Chaar, H.; Caellas, I. Xylem hydraulic adjustment and growth response of *Quercus canariensis* Willd. to climatic variability. *Tree Physiol.* **2012**, *32*, 401–413. [CrossRef]
13. Martínez-Sancho, E.; Dorado-Lián, I.; Heinrich, I.; Helle, G.; Menzel, A. Xylem adjustment of sessile oak at its southern distribution limits. *Tree Physiol.* **2017**, *37*, 903–914. [CrossRef] [PubMed]
14. Pérez-de-Lis, G.; Rozas, V.; Vázquez-Ruiz, R.A.; García-González, I. Do ring-porous oaks prioritize earlywood vessel efficiency over safety? Environmental effects on vessel diameter and tyloses formation. *Agric. For. Meteorol.* **2018**, *248*, 205–214. [CrossRef]
15. Hallinger, M.; Manthey, M.; Wilmking, M. Establishing a missing link: Warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia. *New Phytol.* **2010**, *186*, 890–899. [CrossRef]
16. Schweingruber, F.H.; Hellmann, L.; Tegel, W.; Braun, S.; Nievergelt, D.; Büntgen, U. Evaluating the wood anatomical and dendroecological potential of Arctic dwarf shrubs communities. *IAWA J.* **2013**, *34*, 485–497. [CrossRef]
17. Buras, A.; Lehejček, J.; Michalová, Z.; Morrissey, R.C.; Svoboda, M.; Wilmking, M. Shrubs shed light on 20th century Greenland Ice Sheet melting. *Boreas* **2017**, *46*, 667–677. [CrossRef]
18. Unterholzner, L.; Carrer, M.; Bär, A.; Beikircher, B.; Dämon, B.; Losso, A.; Prendin, A.L.; Mayr, S. Juniperus communis populations exhibit low variability in hydraulic safety and efficiency. *Tree Physiol.* **2020**, *40*, 1668–1679. [CrossRef]
19. Rodríguez-Ramírez, E.C.; Vázquez-García, J.A.; García-González, I.; Alcántara-Ayala, O.; Luna-Vega, I. Drought effects on the plasticity in vessel traits of two endemic *Magnolia* species in the tropical montane cloud forests of eastern Mexico. *J. Plant Ecol.* **2020**, *13*, 331–340. [CrossRef]
20. Rodríguez-Ramírez, E.C.; Valdez-Nieto, J.A.; Vázquez-García, J.A.; Dieringer, G.; Luna-Vega, I. Plastic responses of *Magnolia schiedeana* Schltdl., a relict-endangered Mexican Cloud Forest tree, to climatic events: Evidences from leaf venation and wood vessel anatomy. *Forests* **2020**, *11*, 737. [CrossRef]
21. Zhang, H.X.; Yuan, F.H.; Wu, J.B.; Jin, C.J.; Pivovaroff, A.L.; Tian, J.Y.; Li, W.B.; Guan, D.X.; Wang, A.Z.; McDowell, N.G. Responses of functional traits to seven-year nitrogen addition in two tree species: Coordination of hydraulics, gas exchange and carbon reserves. *Tree Physiol.* **2021**, *41*, 190–205. [CrossRef] [PubMed]
22. Ganthaler, A.; Mayr, S. Subalpine dwarf shrubs differ in vulnerability to xylem cavitation: An innovative staining approach enables new insights. *Physiol. Plantarum* **2021**, *172*, 2011–2021. [CrossRef] [PubMed]
23. García-Cervigón, A.I.; García-López, M.A.; Pistón, N.; Pugnaire, F.I.; Olano, J.M. Co-ordination between xylem anatomy, plant architecture and leaf functional traits in response to abiotic and biotic drivers in a nurse cushion plant. *Ann. Bot.* **2021**, *127*, 919–929. [CrossRef]
24. Schweingruber, F.H.; Dietz, H. Annual rings in the xylem of dwarf shrubs and perennial dicotyledonous herbs. *Dendrochronologia* **2001**, *19*, 115–126.
25. Olano, J.M.; Almería, I.; Eugenio, M.; von Arx, G.; Tjoelker, M. Under pressure: How a Mediterranean high-mountain forb coordinates growth and hydraulic xylem anatomy in response to temperature and water constraints. *Funct. Ecol.* **2013**, *27*, 1295–1303. [CrossRef]
26. Dee, J.R.; Palmer, M.W. Application of herb-chronology: Annual fertilization and climate reveal annual ring signatures within the roots of U.S. tallgrass prairie plants. *Botany* **2016**, *94*, 277–288. [CrossRef]
27. Hummel, I.; Vile, D.; Violle, C.; Devaux, J.; Ricci, B.; Blanchard, A.; Garnier, E.; Roumet, C. Relating root structure and anatomy to whole-plant functioning in 14 herbaceous Mediterranean species. *New Phytol.* **2007**, *173*, 313–321. [CrossRef]
28. Dietz, H.; Fattorini, M. Comparative analysis of growth rings in perennial forbs grown in an alpine restoration experiment. *Ann. Bot.* **2002**, *90*, 663–668. [CrossRef]
29. Dietz, H.; von Arx, G.; Dietz, S. Growth increment patterns in the roots of two alpine forbs growing in the center and at the periphery of a snowbank. *Arct. Antarct. Alp. Res.* **2004**, *36*, 591–597. [CrossRef]
30. Schweingruber, F.H.; Büntgen, U. What is 'wood'—An anatomical re-definition. *Dendrochronologia* **2013**, *31*, 187–191. [CrossRef]
31. Dietz, H.; von Arx, G. Climatic fluctuation causes large-scale synchronous variation in radial root increments of perennial forbs. *Ecology* **2005**, *86*, 327–333. [CrossRef]
32. Dee, J.R.; Stambaugh, M.C. A new approach towards climate monitoring in Rocky Mountain alpine plant communities: A case study using herb-chronology and *Penstemon whippleanus*. *Arct. Antarct. Alp. Res.* **2019**, *51*, 84–95. [CrossRef]
33. Fonti, P.; von Arx, G.; García-González, I.; Eilmann, B.; Sass-Klaassen, U.; Gärtner, H.; Eckstein, D. Studying global change through investigation of the plastic responses of xylem anatomy in tree rings research. *New Phytol.* **2010**, *185*, 42–53. [CrossRef] [PubMed]
34. Venegas-González, A.; Chagas, M.P.; Anholetto Júnior, C.R.; Alvares, C.A.; Roig, F.A.; Tomazello Filho, M. Sensitivity of tree ring growth to local and large-scale climate variability in a region of southeastern Brazil. *Theor. Appl. Climatol.* **2016**, *123*, 233–245. [CrossRef]

35. Von Arx, G.; Archer, S.R.; Hughes, M.K. Long-term functional plasticity in plant hydraulic architecture in response to supplemental moisture. *Ann. Bot.* **2012**, *109*, 1091–1100. [CrossRef]
36. Castagneri, D.; Carrer, M.; Regev, L.; Boaretto, E. Precipitation variability differently affects radial growth, xylem traits and ring porosity of three Mediterranean oak species at xeric and mesic sites. *Sci. Total Environ.* **2020**, *699*, 134285. [CrossRef]
37. Tyree, M.T.; Ewers, F.W. The hydraulic architecture of trees and other woody plants. *New Phytol.* **1991**, *119*, 345–360. [CrossRef]
38. Choat, B.; Jansen, S.; Brodribb, T.J.; Cochard, H.; Delzon, S.; Bhaskar, R.; Bucci, S.J.; Feild, T.S.; Gleason, S.M.; Hacke, U.G.; et al. Global convergence in thevulnerability of forests to drought. *Nature* **2012**, *491*, 752–755. [CrossRef]
39. McDowell, N.G. Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. *Plant Physiol.* **2011**, *155*, 1051–1059. [CrossRef]
40. Schmitz, N.; Jansen, S.; Verheyden, A.; Kairo, J.G.; Beeckman, H.; Koedam, N. Comparative anatomy of intervessel pits in two mangrove species growing along a natural salinity gradient in Gazi Bay, Kenya. *Ann. Bot.* **2007**, *100*, 271–281. [CrossRef]
41. Cochard, H.; Tyree, M.T. Xylem dysfunction in *Quercus*: Vessel sizes, tyloses, cavitation and seasonal changes in embolism. *Tree Physiol.* **1990**, *6*, 393–407. [CrossRef] [PubMed]
42. Hacke, U.G.; Sperry, J.S.; Pockman, W.T.; Davis, S.D.; McCulloh, K.A. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* **2001**, *126*, 457–461. [CrossRef] [PubMed]
43. Sperry, J.S.; Meinzer, F.C.; Mcculloh, K.A. Safety and efficiency conflicts in hydraulic architecture: Scaling from tissues to trees. *Plant Cell Environ.* **2008**, *31*, 632–645. [CrossRef] [PubMed]
44. Hacke, U.G.; Jacobsen, A.L.; Pratt, R.B. Xylem function of arid-land shrubs from California, USA: An ecological and evolutionary analysis. *Plant Cell Environ.* **2009**, *32*, 1324–1333. [CrossRef]
45. Hacke, U.G.; Sperry, J.S.; Wheeler, J.K.; Castro, L. Scaling of angiosperm xylem structure with safety and eficiency. *Tree Physiol.* **2006**, *26*, 89–701. [CrossRef]
46. Kołodziejek, J.; Glińska, S.; Michlewska, S. Seasonal leaf dimorphism in *Potentilla argentea* L. var. *tenuiloba (Jord.) Sw. (Rosaceae). Acta Bot. Croat.* **2015**, *74*, 53–70. [CrossRef]
47. Munir, M.; Khan, M.A.; Ahmad, M.; Abbasi, A.M.; Zafar, M.; Khan, K.Y.; Tariq, K.; Tabassum, S.; Ahmed, S.N.; Habiba, U.; et al. Taxonomic potential of foliar epidermal anatomy among the wild culinary vegetables of Pakistan. *J. Med. Plants Res.* **2011**, *5*, 2857–2862.
48. Liu, W.S.; Zheng, L.; Qi, D.H. Variation in leaf traits at different altitudes reflects the adaptive strategy of plants to environmental changes. *Ecol. Evol.* **2020**, *10*, 8166–8175. [CrossRef]
49. Purnobasuki, H.; Nurhidayati, T.; Hariyanto, S.; Jadid, N. Data of root anatomical responses to periodic waterlogging stress of tobacco (*Nicotiana tabacum*) varieties. *Data Brief* **2018**, *20*, 2012–2016. [CrossRef]
50. von Arx, G.; Dietz, H. Growth rings in the roots of temperate forbs are robust annual markers. *Plant Biol.* **2006**, *8*, 224–233. [CrossRef]
51. Lewis, A.M.; Boose, E.R. Estimating volume flow rates through xylem conduits. *Am. J. Bot.* **1995**, *82*, 1112–1116. [CrossRef]
52. Sperry, J.S.; Nichols, K.L. Xylem embolism in ring-porous, diffuse-porous, and coniferous trees of Northern Utah and Interior Alaska. *Ecology* **1994**, *75*, 1736–1752. [CrossRef]
53. Ashton, P.M.S.; Olander, L.P.; Berlyn, G.P.; Thadani, R.; Cameron, I.R. Changes in leaf structure in relation to crown position and tree size of Betula papyrifera within fire-origin stands of interior cedar-hemlock. *Can. J. Bot.* **1998**, *76*, 1180–1187.
54. Kerkhoff, A.J.; Enquist, B.J. Multiplicative by nature: Why logarithmic transformation is necessary in allometry. *J. Theor. Biol.* **2009**, *257*, 519–521. [CrossRef]
55. Liu, Y.B.; Zhang, Q.B. Growth rings of roots in perennial forbs in Duolun Grassland, Inner Mongolia, China. *J. Integr. Plant Biol.* **2007**, *49*, 144–149. [CrossRef]
56. Dietz, H.; Schweingruber, F.H. Annual rings in native and introduced forbs of lower Michigan, USA. *Can. J. Bot.* **2002**, *80*, 642–649. [CrossRef]
57. Shi, S.L.; Li, Z.S.; Wang, H.; von Arx, G.; Lü, Y.H.; Wu, X.; Wang, X.C.; Liu, G.H.; Fu, B.J. Roots of forbs sense climate fluctuations in the semi-arid Loess Plateau: Herb-chronology based analysis. *Sci. Rep.* **2016**, *6*, 28435. [CrossRef]
58. Brodribb, T.J.; Bowman, D.; Nichols, S.; Delzon, S.; Burlett, R. Xylem function and growth rate interact to determine recovery rates after exposure to extreme water deficit. *New Phytol.* **2010**, *188*, 533–542. [CrossRef]
59. Sperry, J.S.; Hacke, U.W.; Wheeler, J.K. Comparative analysis of end wall resistivity in xylem conduits. *Plant Cell Environ.* **2005**, *28*, 456–465. [CrossRef]
60. Schmitz, N.; Verheyden, A.; Beeckman, H.; Kairo, J.G.; Koedam, N. Influence of a salinity gradient on the vessel characters of the mangrove species *Rhizophora mucronata*. *Ann. Bot.* **2006**, *98*, 1321–1330. [CrossRef]
61. Verheyden, A.; De Ridder, F.; Schmitz, N.; Beeckman, H.; Koedam, N. High-resolution time series of vessel density in Kenyan mangrove trees reveal a link with climate. *New Phytol.* **2005**, *167*, 425–435. [CrossRef] [PubMed]
62. Yang, L.; Wei, W.; Chen, L.D.; Mo, B.R. Response of deep soil moisture to land use and afforestation in the semi-arid Loess Plateau, China. *J. Hydrol.* **2012**, *475*, 111–122. [CrossRef]
63. Liu, B.X.; Shao, M.A. Modeling soil-water dynamics and soil-water carrying capacity for vegetation on the Loess Plateau, China. *Agric. Water Manag.* **2015**, *159*, 176–184. [CrossRef]
64. Abrams, M.D.; Kubiske, M.E.; Mostoller, S.A. Relating wet and dry year ecophysiology to leaf structure in contrasting temperate tree species. *Ecology* **1994**, *75*, 123–133. [CrossRef]

65. Nicotra, A.B.; Davidson, A. Adaptive phenotypic plasticity and plant water use. *Funct. Plant Biol.* **2010**, *37*, 117–127. [CrossRef]
66. Zimmermann, M.H. Hydraulic architecture of some diffuse-porous trees. *Can. J. Bot.* **1978**, *56*, 2286–2295. [CrossRef]
67. Yáñez-Espinosa, L.; Terrazas, T.; López-Mata, L. Effects of flooding on wood and bark anatomy of four species in a mangrove forest community. *Trees* **2001**, *15*, 91–97. [CrossRef]
68. Cochard, H. Vulnerability of several conifers to air embolism. *Tree Physiol.* **1992**, *11*, 73–83. [CrossRef]
69. Kavanagh, K.L.; Bond, B.J.; Aitken, S.N.; Gartner, B.L.; Knowe, S. Shoot and root vulnerability to xylem cavitation in four populations of Douglas-fir seedlings. *Tree Physiol.* **1999**, *19*, 31–37. [CrossRef]
70. Wilcox, K.R.; von Fischer, J.C.; Muscha, J.M.; Petersen, M.K.; Knapp, A.K. Contrasting above- and belowground sensitivity of three Great Plains grasslands to altered rainfall regimes. *Glob. Chang. Biol.* **2015**, *21*, 335–344. [CrossRef]
71. Pockman, W.T.; Sperry, J.S. Vulnerability to xylem cavitation and the distribution of Sonoran Desert vegetation. *Am. J. Bot.* **2000**, *89*, 1287–1299. [CrossRef]
72. García-Cervigón, A.I.; Olano, J.M.; von Arx, G.; Fajardo, A. Xylem adjusts to maintain efficiency across a steep precipitation gradient in two coexisting generalist species. *Ann. Bot.* **2018**, *122*, 461–472. [CrossRef] [PubMed]
73. Boughalleb, F.; Abdellaoui, R.; Ben-Brahim, N.; Neffati, M. Anatomical adaptations of *Astragalus gombiformis* Pomel. under drought stress. *Cent. Eur. J. Biol.* **2014**, *9*, 1215–1225. [CrossRef]
74. Williams, A.L.; Wills, K.E.; Janes, J.K.; Schoor, J.; Newton, P.; Hovenden, M.J. Warming and free-air CO_2 enrichment alter demographics in four co-occurring grassland species. *New Phytol.* **2007**, *176*, 365–374. [CrossRef] [PubMed]
75. Zhu, L.J.; Liu, S.J.; Arzac, A.; Cooper, D.J.; Jin, Y.; Yuan, D.Y.; Zhu, Y.; Zhang, X.; Li, Z.S.; Zhang, Y.D.; et al. Different response of earlywood vessel features of *Fraxinus mandshurica* to rapid warming in warm-dry and cold-wet areas. *Agric. For. Meteorol.* **2021**, *307*, 108523. [CrossRef]