

Article

Interrelationships and Environmental Influences of Photosynthetic Capacity and Hydraulic Conductivity in Desert Species *Populus pruinosa*

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Abstract: An improved understanding of the mechanisms underlying plant adaptation to habitat heterogeneity can be achieved by clarifying the climate-driving factors of the hydraulic and photosynthetic traits of different populations. With a focus on *Populus pruinosa* Schrenk, which is the predominant tree species in the desert riparian forests of the Tarim Basin, Xinjiang, this study investigated the hydraulic and photosynthetic trait relationships and their interactions with environmental factors in 11 *P. pruinosa* populations using a Pearson correlation analysis, plant trait networks, a redundancy analysis, and a least squares linear regression analysis. The results showed that the degree of variation in the hydraulic traits was higher than that in the photosynthetic traits. The net photosynthetic rate (P_n) showed a significantly positive correlation with leaf-specific conductivity (K_l) and the Huber value (Hv). The Hv exhibited a significantly positive correlation with the water-use efficiency and K_l , and the branch–leaf mass ratio significantly affected the hydraulic traits. The groundwater depth (GD) in natural *P. pruinosa* forest habitats ranged from 3.4 to 7.9 m. With an increase in the annual average temperature, the hydraulic conductivity of the xylem significantly increased; with an increase in GD, P_n and K_l significantly decreased. The temperature annual range, temperature seasonality (standard deviation), min temperature of the coldest month, and GD were significantly correlated with the diameter and average path length of the overall trait network parameters, and these environmental factors affected the coordination of the functional traits of *P. pruinosa*.

Keywords: functional traits; plant trait network; photosynthesis; hydraulic traits; intraspecific variation; groundwater depth; trait–climate relationships



Citation: Zhang, J.; Zhai, J.; Wang, J.; Si, J.; Li, J.; Ge, X.; Li, Z. Interrelationships and Environmental Influences of Photosynthetic Capacity and Hydraulic Conductivity in Desert Species *Populus pruinosa*. *Forests* **2024**, *15*, 1094. <https://doi.org/10.3390/f15071094>

Academic Editors: Stefan Arndt and José Javier Peguero-Pina

Received: 5 April 2024

Revised: 6 June 2024

Accepted: 21 June 2024

Published: 24 June 2024



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1. Introduction

Plant functional traits, which embody adaptations to environmental conditions, encompass morphological, physiological, and stoichiometric characteristics that directly influence the biological fitness, including growth, reproduction, and survival, of plants [1]. Functional traits are crucial in determining the distribution patterns of woody plants, which are essential for ecological understanding [2]. An improved carbon gain correlates with increased fitness, and thus, natural selection is likely to favor adaptations that maximize the carbon acquisition of populations [3]. Leaves are the central organ for gaining photosynthetic carbon; unsuitable environmental conditions for plant growth affect the photosynthetic carbon assimilation capacity of plants [4]. Plant hydraulic systems, which

are critical for terrestrial productivity, considerably influence the global carbon, water, and biogeochemical cycles. In addition, these systems determine the vulnerability of ecosystems to drought and climate change [5]. Plant xylem hydraulic traits are the primary determinants of drought response patterns, and they substantially affect the resilience and drought resistance of forest ecosystems. Typically, tree species in arid zones possess advanced hydraulic safety mechanisms, while those in humid areas present highly efficient water transport systems [6]. Plants in arid areas prevent xylem embolization through leaf shedding during drought but also maintain high sapwood-specific conductivity (K_s) levels during periods of sufficient water availability [7]. Hydraulic conductivity capacity critically influences the plant transpiration and photosynthesis and the growth, survival, and geographic distribution of a species. Woody plants possess a water transport system that efficiently transfers water from the soil to various organs, which guarantees a consistent water supply throughout the plant [8,9]. Given that most research has focused solely on individual organs, such as leaves or stems, our understanding of trait coordination and functional ecology at the whole-plant level has been limited [10]. Plants utilize optimal characteristic combinations to adapt to their changing surroundings [11]. Since the last century, ecologists have conducted relevant studies on plant functional traits [12–16]. However, studies barely investigated the connection between the hydraulic and photosynthetic traits of *P. pruinosa* in extremely arid regions.

Exploration of the relationship between the trait spatial distribution and environmental changes through the integration of environmental data can improve our comprehension of plant adaptation to their habitats. Wright et al. studied ecological drivers and broad-scale regional distribution patterns of key plant traits [17]. The intraspecific trait variation (ITV) contributes to the stabilization of plant communities, resistance to climate warming, and preservation of ecosystem functions [18]. Plant trait networks (PTNs) have been increasingly utilized to explore and analyze the complex relationships between multiple traits [19] because they facilitate the visualization of complex trait interconnections and the interdependence of traits across various growth forms [20]. In addition, the use of such networks enables the identification of central traits within them, which aids in the exploration of plant responses and adaptation strategies to environmental changes. The nodal parameters of a PTN are utilized to identify the topological roles of different nodes within it; traits with a high “degree” improve resource assimilation and utilization efficiency, and those with great “betweenness” serve as intermediaries in functional modules; a trait showing a high level of connectivity forms a strong association with other traits within the network [21]. From a comprehensive perspective, the multidimensional adaptation process of plants can be quantified using the overall parameters of the network. High edge densities in the network indicate a strong trait collaboration and improved ability of the plant to accumulate and transmit resources effectively. Traits characterized by a large diameter and average path length exhibit a high degree of overall independence. High modularity indicates the division of traits into distinct functional modules or “dimensions” for specialized functions. A large clustering coefficient suggests the grouping of specific traits into smaller clusters for environmental adaptation to distinguish the division of labor [20]. A degree of trait independence improves plants’ adaptability in function adjustment [22], contributes to a broad phenotypic diversity, and enables plants to adapt better to current environmental conditions [23,24]. PTNs exhibit pronounced modularity and low connectivity in extremely cold environments, whereas warm settings manifest the opposite pattern [25].

The Tarim Basin is located in an extremely arid area, where surface water and natural precipitation are scarce and cannot meet the normal growth needs of regional vegetation; therefore, groundwater is the most important water source for vegetation survival [26,27]. *P. pruinosa* is the dominant species in the desert riparian forests in extremely dry areas; it predominantly constructs the desert riparian ecosystem in the Tarim River Basin. *P. pruinosa* contributes to the prevention of desertification, conservation of biodiversity, and protection of the natural ecology of Xinjiang’s extreme arid desert regions. The species thrives predominantly in floodplains and riverbanks and benefits from adequate water levels

and low soil salinity [28]. However, in recent years, with global warming and the excessive exploitation of regional water resources, the continuous decrease in the groundwater level has directly affected the absorption of nutrients, supply of water, and various physiological and biochemical metabolic processes of plants, threatening the survival and development of desert vegetation and regional ecological security [29,30]. Groundwater plays a crucial role in shaping plant functional traits [31]. As most species in arid areas rely on groundwater or capillary water above the surface of groundwater for survival and growth, a reduction in groundwater can alter plant growth [32,33]. Furthermore, *P. pruinosa* is concentrated in the warm-temperate zone of the Tarim Basin and faces challenges in surviving the medium-temperate zone of the Junggar Basin across the Tianshan Mountains. Is this geographical distribution related to environmental factors? This study aimed to explore the relationship between the physiological traits and environmental factors of *P. pruinosa* in order to understand its ecological adaptation strategies and promote the restoration of desert vegetation.

2. Materials and Methods

2.1. Study Area

Eleven representative natural *P. pruinosa* forest sampling sites in Xinjiang, China, were selected for this study, and their latitudes and longitudes were in the ranges of 36.9291°–43.8444° N and 76.1722°–85.4831° E, respectively (Figure 1). The groundwater depth (GD) ranged from 3.4 to 7.9 m. The mean annual temperature (MAT) varied from 9.73 °C to 12.67 °C, and the mean annual precipitation (MAP) ranged from 28 to 217 mm. The altitude spanned from 543 m to 1400 m. The aridity index (AI) refers to the ratio of the MAP to the potential evapotranspiration [34]. All the sampling sites had AI values between 0.0184 and 0.1432 (Table 1). More climatic information of the sampling sites can be found in Supplementary Table S1. The common species in the study area included *Tamarix chinensis* Lour. (Tamaricaceae), *Phragmites australis* (Cav.) Trin. ex Steud. (Poaceae), *Lycium ruthenicum* Murr. (Solanaceae), *Halimodendron halodendron* (Pall.) Voss (Fabaceae), and *Sophora alopecuroides* L. (Fabaceae).

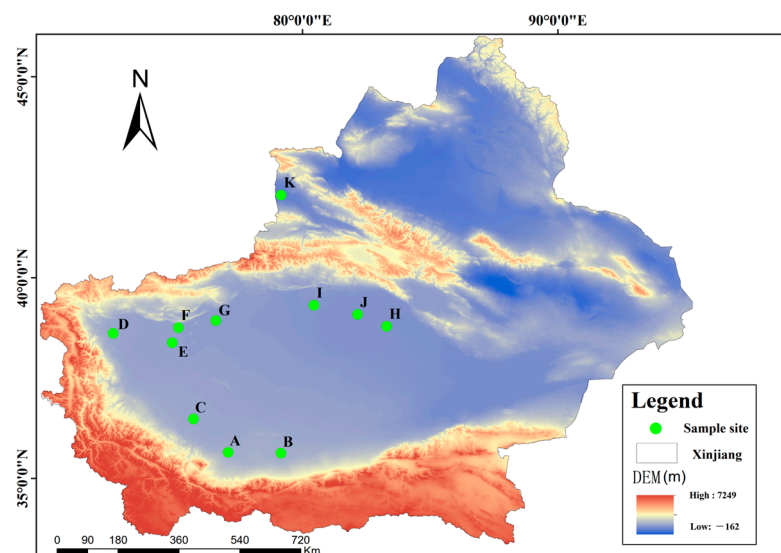


Figure 1. *P. pruinosa* sampling sites. Different capital letters represent different sites in the figure, and the specific corresponding information is shown in Table 1.

Table 1. Sampling sites' climatic characteristics (ascending order of latitude). MAT: mean annual temperature, MAP: mean annual precipitation, AI: aridity index, and GD: groundwater depth.

Zone	Site	GD (m)	Altitude (m)	Longitude (°)	Latitude (°)	MAT (°C)	MAP (mm)	AI
Cele, Hotan	A	3.9	1400	81.02	36.93	12.63	33	0.0222
Minfeng, Hotan	B	3.7	1292	82.79	37.22	11.65	28	0.0184
Moyu, Hotan	C	6.8	1279	79.63	37.58	12.67	32	0.0203
Shule, Kashgar	D	7.9	1270	76.17	39.17	11.94	76	0.0493
Maigaiti, Kashgar	E	6	1145	78.25	39.36	12.45	39	0.0248
Bachu, Kashgar	F	5.9	1127	78.31	39.79	12.55	51	0.0316
Keping, Aksu	G	4.9	1059	79.52	40.22	11.90	49	0.0299
Yuli, Bayingolin	H	7.7	894	85.48	41.08	11.75	48	0.0300
Shaya, Aksu	I	3.4	952	82.78	41.22	11.66	118	0.0702
Luntai, Bayingolin	J	6.1	920	84.38	41.23	11.24	80	0.0433
Qapqal, Ili	K	6	543	80.68	43.84	9.73	217	0.1432

2.2. Experimental Design and Sampling

A total of 20 mature *P. pruinosa* trees with similar diameters at breast height, tree heights, and growth patterns were selected at each site (the populations of *P. pruinosa* in China are concentrated in the Tarim Basin; therefore, the sampling sites were selected based on the concentrated forest region in Xinjiang, which had at least 20 trees with a concentrated distribution of *P. pruinosa*). Painted markings were placed on the bark facing the Sun and we recorded the longitude and latitude. All functional traits at each site were measured on the same 20 trees. Measurements of photosynthetic parameters were conducted site by site in July and August 2021 at all sampling sites. In August 2022, the GD of the sampling sites was detected using ground-penetrating radar (GPR, TS-WGR1201 (A), Tensense Geotech, Wuhan, China). Before measuring the groundwater level of all the sampling points, we selected a typical sampling site (Shaya, Aksu) and used GPR to detect the GD. Subsequently, the Luoyang shovel was used to measure the GD, and after verification, the appropriate radar system parameters for detecting the groundwater depth in natural *P. pruinosa* forests were determined. And field measurements of hydrological parameters were conducted in July and August of 2022. Table 2 lists all the studied traits.

Table 2. Traits measured in this study, with abbreviations, definitions, and units.

Abbreviation	Definition	Units
T_r	Transpiration rate	$\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$
P_n	Net photosynthetic rate	$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$
G_s	Stomatal conductance	$\mu\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$
C_i	Intercellular carbon dioxide concentration	$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$
WUE	Water-use efficiency	$\mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{ H}_2\text{O}$
LDMC	Leaf dry matter content	g g^{-1}
LMA	Leaf mass per area	g m^{-2}
TLMR	Branch–leaf mass ratio	g g^{-1}
K_s	Sapwood-specific conductivity	$\text{kg} \cdot \text{m}^{-1} \text{ s}^{-1} \text{ Mpa}^{-1}$
$K_{s\text{max}}$	Maximum sapwood-specific conductivity	$\text{kg} \cdot \text{m}^{-1} \text{ s}^{-1} \text{ Mpa}^{-1}$
K_w	Wood-specific conductivity	$\text{kg} \cdot \text{m}^{-1} \text{ s}^{-1} \text{ Mpa}^{-1}$
$K_{w\text{max}}$	Maximum wood-specific conductivity	$\text{kg} \cdot \text{m}^{-1} \text{ s}^{-1} \text{ Mpa}^{-1}$
PLC	Percent loss of hydraulic conductivity	%
K_l	Leaf-specific conductivity	$\text{kg} \cdot \text{m}^{-1} \text{ s}^{-1} \text{ Mpa}^{-1}$
Hv	Huber value	$\text{cm}^2 \text{ cm}^{-2}$
$\delta^{13}\text{C}$	Carbon isotope signature	‰

2.3. Measurement of Photosynthetic Traits

An LI-6800 Portable Photosynthesis System (LI-COR Biosciences, Lincoln, NE, USA) was used to measure the photosynthetic gas exchange parameters. Measurements began at 9:00 a.m. on clear, windless days. At a tree height of about 5–6 m, we used an averruncator to cut a branch with leaves. Twenty trees were measured at each sampling site, and three healthy leaf measurements were repeated for each tree. Each leaf was measured thrice, and the mean was considered one biological repeat. A red and blue light source was used to provide a standard light intensity of $1200 \mu\text{mol}/(\text{m}^2 \cdot \text{s})$ in a 25°C measurement chamber, which contained $400 \mu\text{mol}/\text{mol CO}_2$ and a $500 \mu\text{mol}/\text{s}$ flow rate. A small branch with broad and oval-shaped leaves was cut from each tree using an averruncator at a height of 5–6 m, and the branches were promptly placed in a bucket filled with water from the base. We determined the net photosynthetic rate (P_n), transpiration rate (T_r), stomatal conductance (G_s), and intercellular CO_2 concentration (C_i), and calculated the WUE as follows:

$$\text{WUE} = P_n / T_r \quad (1)$$

where P_n refers to the net photosynthetic rate, and T_r indicates the transpiration rate.

2.4. Determination of Hydraulic Traits

Experiments were conducted following the methodology described by Fang et al. [35]. Twenty trees were selected at each sample site. At around 6 am, one straight branch with fewer forks (1 m in length and 6–8 mm in diameter) on the sunny side of each sample tree was cut using an averruncator at a height of about 5–6 m. The branch was submerged in a plastic bucket filled with water and then covered with a black plastic bag. This procedure was conducted to prevent air from entering the exposed xylem. The branches were immediately transported to the nearest experimental station (the distance varied in the range of tens of kilometers). At the experimental station, we started the experiment using our self-made hydraulic-conductivity-measuring device. The branches were fully submerged in water, and a 20 cm stem segment from the middle of each branch was cut underwater and retained for measurement. The remaining branch ends, with each extending by 15 cm, were also submerged in water to determine the sapwood area (SA). A total of 20 mmol/L potassium chloride solutions prepared with pure water (Wahaha pure water) was used to measure the hydraulic conductivity. One end of the branch was connected to the potassium chloride solution and passed through a $0.2 \mu\text{m}$ filter under a 0.005 MPa pressure gradient. The other end was attached to a graduated pipette. A syringe was used for bubble elimination. The solution flowed through the xylem vessels into the pipette. The scale and time on the pipette were recorded, and the flow rate of the solution through the branch's xylem (volume of liquid flowing per unit time, J_v) was determined. Each branch was measured twice, and the average value was obtained. The initial hydraulic conductivity (K_h) of the branches was also determined [36]. A 1 mm slice at both ends was cut along the part in water (to prevent the wound flow from clogging the ends of the branch), and one end of the branch was connected to a deaerated KCl solution; a pressure of 15 PSI was applied to the KCl solution to ensure that it flowed out through the xylem of the branch; rinsing was performed for 15–20 min [37]. Then, the branches were removed, and the hydraulic conductivity measurement was repeated using the same method to determine K_h . The maximum hydraulic conductivity ($K_{h\text{max}}$) of *P. pruinosa* was also quantified. The branch was removed, and the hydraulic conductivity was measured via the same method as the measurement of K_h . $K_{h\text{max}}$ refers to the maximum hydraulic conductivity of the xylem conduit of the branch. After the hydraulic conductivity tests, 5 cm portions of the branch were cut and immersed in water from both ends of the remaining segments. A 1 cm length bark was peeled off from each segment underwater. One end of the branch was connected to a 0.01% magenta solution in deaerated pure water (Wahaha pure water) and subjected to a 50 cm height pressure gradient to enable continuous flow through one end of the 5 cm branch segment. After 24 h, the branch was removed, and a 2 mm slice was cut

from its central part. This slice was scanned into an image, and the stained SA and total cross-sectional area of the xylem (CA) were measured using ImageJ software (Version 1.53o) Fiji version (<https://imagej.net/software/fiji/>, accessed on 3 October 2023) to calculate the SA for each branch.

The total leaf area was determined using ImageJ software. A photograph of all the leaves from the branch segment where hydraulic conductivity was measured was laid flat against black cardboard with an attached scale. Hydraulic parameters, including K_l , Hv (a comprehensive trait that connects the plant branches and leaves and represents their carbon-to-water coupling relationship [38]), sapwood-specific conductivity (K_s), wood-specific conductivity (K_w), and percent loss of hydraulic conductivity (PLC) were calculated using the following equations:

$$K_h = J_v / (\Delta P / \Delta L) \quad (2)$$

where J_v refers to the velocity of water flow through a section of the branch, ΔP indicates the pressure provided by a 50 cm high water column (50 cm = 0.005 MPa), and ΔL denotes the branch length (m).

$$K_s = K_h / SA \quad (3)$$

where K_h means the initial hydraulic conductivity of the branch, and SA corresponds to the xylem sapwood area.

$$K_w = K_h / CA \quad (4)$$

where CA is the entire cross-sectional xylem area.

$$K_l = K_h / TAL \quad (5)$$

where TAL refers to the area of all leaves per branch.

$$Hv = SA / TAL \quad (6)$$

where SA refers to the xylem sapwood area, TAL corresponds to the area of all leaves per branch [39].

$$PLC = 100 \times (K_{hmax} - K_h) / K_{hmax} \quad (7)$$

K_h was replaced with K_{hmax} to obtain the maximum sapwood-specific conductivity (K_{smax}) and maximum wood-specific conductivity (K_{wmax}).

After the hydraulic conductivity measurement was taken, the photographed leaves and stem segments were weighed to determine them for fresh weight, air-dried for several days, and then oven-dried at 80 °C for 48 h until a constant weight was achieved. Using an electronic balance accurate to one ten-thousandth, their dry weights were measured for calculations of the leaf mass per area (LMA), leaf dry matter content (LDMC), and branch–leaf mass ratio (TLMR). The leaf carbon isotope signature ($\delta^{13}C$) was determined using isotope ratio mass spectrometry, specifically by the Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences.

2.5. Establishment of PTNs

The construction of PTNs aimed at elucidating the interrelations between traits across various *P. pruinosa* populations. In these networks, traits and their correlation strengths were represented as nodes and edges, respectively. The overall network parameters comprised the edge density, average path length, clustering coefficient, and modularity, which can be used to quantify the tightness and complexity of the PTNs [20]. The PTN node parameters—degree, closeness, and betweenness—were utilized to identify adaptations for various traits [40]. He et al. comprehensively explained the network topological parameters [19]. First, the absolute value of the Pearson correlation ($|r|$, $r > 0.2$) was used to calculate the strengths of relationships between traits, and a matrix of trait–trait relationships (r) was calculated [10]. A threshold of $|r| > 0.2$ was used to avoid spurious correlations between traits, indicating significant trait correlations at $p < 0.05$. Next, trait–trait correlations below

this threshold were assigned a value of 0 and those above it a value of 1. An adjacency matrix $A = [a_{ij}]$, with $a_{ij} \in [0, 1]$, was yielded. In addition, the absolute value of the correlation coefficient was used to weigh the edges between any pair of plant traits. Then, the “igraph” package in R [25] (version 4.3.2; <https://www.r-project.org>, accessed on 10 November 2023) was used to visualize the networks and calculate the node parameters and overall network parameters. The average value for 20 trees was obtained for every trait in each site, with each site having an established PTN, and finally, a total network was constructed.

2.6. Data Analysis

A GPS was used to determine the latitude, longitude, and altitude of the sampling sites. A total of 19 climatic factors of the *P. pruinosa* sampling sites were collected from the WorldClim database (<http://www.worldclim.org>, accessed on 3 September 2023), and the AI (the ratio of yearly precipitation to potential evapotranspiration) data were according to CGIAR-CSI (<https://www.cgiar-csi.org>, accessed on 3 September 2023) from 1970 to 2000 [41] based on the field determination of the GD. In total, 21 environmental factors were collected. We identified eight factors as fixed variables to eliminate collinearity between the environmental factors. Among these identified factors, four (MAT, MAP, AI, and GD) were directly retained. The remaining four (isothermality, average temperature of the wettest quarter, precipitation in the wettest month, and seasonal variation of precipitation) were selected through dimensionality reduction using principal component analysis.

The quartile coefficient of dispersion (QCD) was employed as a more robust measure of variance for each trait compared with the coefficient of variation (CV) [42]. The calculated QCD of each trait was used to evaluate its variability. Pearson correlation analysis was performed to analyze the relationship between pairs of traits. Complex relationships between multiple traits were explored through the construction of PTNs. Redundancy analysis (RDA) was conducted to investigate the primary environmental factors that influenced the alterations in the functional traits of *P. pruinosa*. The relationship between environmental factors and overall network parameters was analyzed via least squares linear regression analysis. Data preprocessing was carried out using Microsoft Excel 2019, and statistical analysis was performed with SPSS 27.0. The RDA was completed using Canoco 5.0. The charting was completed using Origin Pro 2021, and the network construction was accomplished via the “igraph” package from R version 4.3.2.

3. Results

3.1. Variability and Interrelationships of Functional Traits

The PLC and K_w exhibited the greatest variability, and the $\delta^{13}C$ and intercellular carbon dioxide concentration (C_i) showed the least (Figure 2). The hydraulic parameters showed more variation than the photosynthetic traits, with K_s displaying 65% more variation than K_l . According to Supplementary Table S2, site B had the highest Hv and K_l , site E had the highest K_s and K_w , and site K had the lowest K_l , K_s , and K_w .

The following findings were observed: a synergistic relationship between Hv and K_l ; a highly significant positive correlations between $\delta^{13}C$, K_l , and the xylem hydraulic traits (K_s , K_{smax} , K_w , and K_{wmax}) ($p < 0.01$); highly significant negative correlations between the TLMR, the LMA, Hv, and the xylem hydraulic traits ($p < 0.01$); synergistic links ($p < 0.01$) between P_n , K_l , and Hv; and a trade-off relationship between the WUE and LMA (Figure 3).

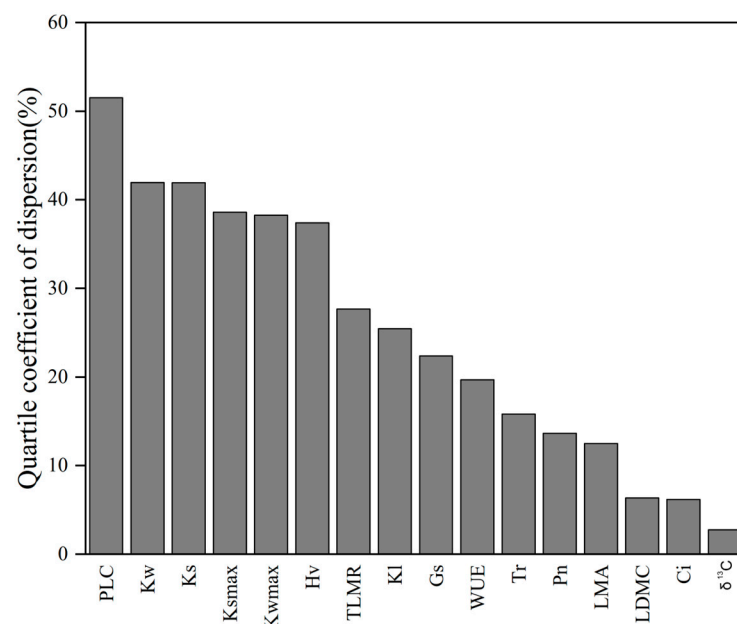


Figure 2. QCDs of functional traits across all measurements in the study ($n = 220$). Traits are ordered from highest to lowest (left to right). PLC: percent loss of hydraulic conductivity, K_w : wood-specific conductivity, K_s : sapwood-specific conductivity, K_{smax} : maximum sapwood-specific conductivity, K_{wmax} : maximum wood-specific conductivity, Hv: Huber value, TLMR: branch–leaf mass ratio, K_l : leaf-specific conductivity, G_s : stomatal conductance, WUE: water-use efficiency, T_r : transpiration rate, P_n : net photosynthetic rate, LMA: leaf mass per area, LDMC: leaf dry matter content, C_i : intercellular carbon dioxide concentration, and $\delta^{13}C$: carbon isotope signature.

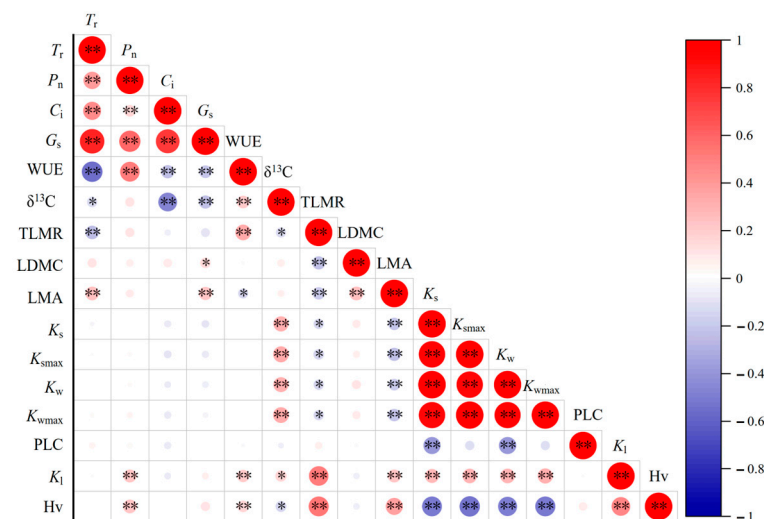


Figure 3. Pearson's correlation analysis of functional traits ($p < 0.05$: *; $p < 0.01$: **; $n = 220$). The scale on the right represents the strength of the correlation. PLC: percent loss of hydraulic conductivity, K_w : wood-specific conductivity, K_s : sapwood-specific conductivity, K_{smax} : maximum sapwood-specific conductivity, K_{wmax} : maximum wood-specific conductivity, Hv: Huber value, TLMR: branch–leaf mass ratio, K_l : leaf-specific conductivity, G_s : stomatal conductance, WUE: water-use efficiency, T_r : transpiration rate, P_n : net photosynthetic rate, LMA: leaf mass per area, LDMC: leaf dry matter content, C_i : intercellular carbon dioxide concentration, and $\delta^{13}C$: carbon isotope signature.

3.2. Central traits and Comprehensive Profile of PTNs

The different populations showed variations in the coordination between multiple plant traits (Figure 4). A module refers to a cluster of closely connected plant traits. The

main modules in the network were marked with different colors, with two modules found at site K. Meanwhile, the remaining samples all consisted of three or four modules. The modules of the overall network were closely interconnected, and the module tightness of each population varied between different populations.

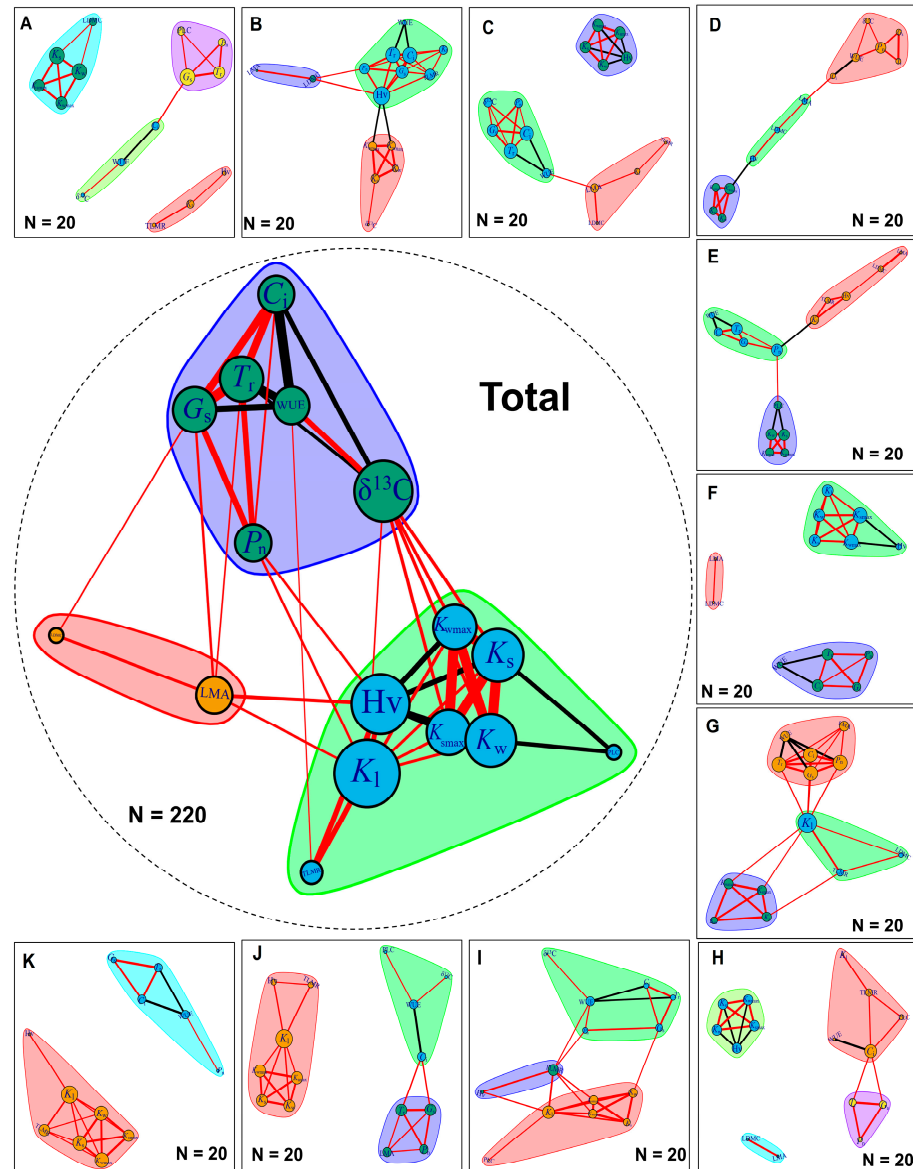


Figure 4. PTNs of 11 populations. The subfigures (A–K) represent the PTNs of different populations. Traits sharing the same background color belong to the same module. The size of the circle around a trait denotes its importance in the network. Lines represent associations between and within modules, with the line thickness reflecting the correlation strength. Red and black lines indicate positive and negative correlations, respectively. Traits without a correlation with others were omitted from the network. Based on the distance between two nodes, the independence and cooperation between traits were evaluated. PLC: percent loss of hydraulic conductivity, K_w : wood-specific conductivity, K_s : sapwood-specific conductivity, K_{smax} : maximum sapwood-specific conductivity, K_{wmax} : maximum wood-specific conductivity, H_v : Huber value, TLMR: branch–leaf mass ratio, K_1 : leaf-specific conductivity, G_s : stomatal conductance, WUE: water-use efficiency, T_r : transpiration rate, P_n : net photosynthetic rate, LMA: leaf mass per area, LDMC: leaf dry matter content, C_i : intercellular carbon dioxide concentration, and $\delta^{13}C$: carbon isotope signature.

The central traits of the *P. pruinosa* trait networks, which varied between populations, were identified through node parameters: K_w was central at sites A and E (Figure 5A,E), H_v at site B (Figure 5B), C_i at sites C and H (Figure 5C,H), K_{wmax} at sites D and F (Figure 5D,F), and K_i at sites G, I, J, and K (Figure 5G,I–K). This study focused on degree changes given the consistent order of the degree, betweenness, and closeness of all traits within any network. Supplementary Figures S1 and S2 illustrate the alterations in “betweenness” and “closeness”.

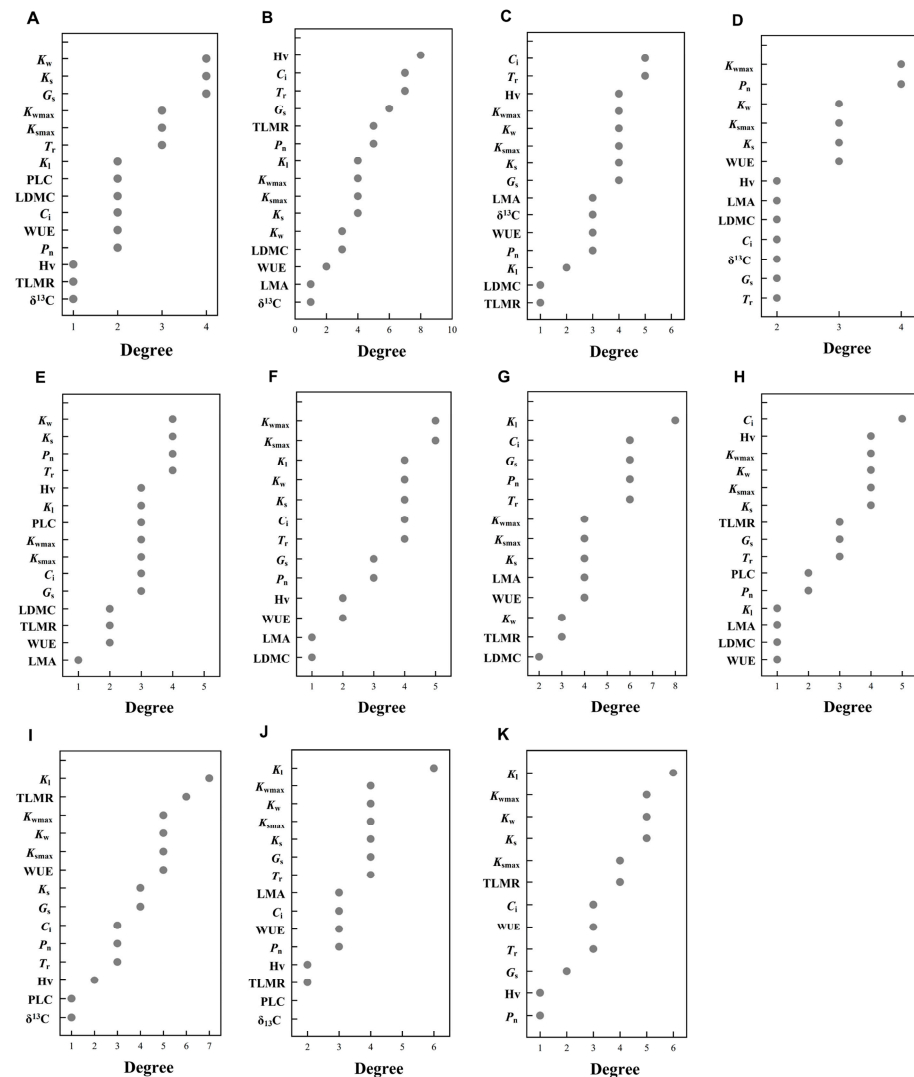


Figure 5. Variations in the network node parameter “degree” for functional traits (the sample size for each sampling point was 20). The subfigures (A–K) represent the variations of “degree” of different populations. Among the 11 populations, traits with the highest degree were considered “central traits” in the network. PLC: percent loss of hydraulic conductivity, K_w : wood-specific conductivity, K_s : sapwood-specific conductivity, K_{smax} : maximum sapwood-specific conductivity, K_{wmax} : maximum wood-specific conductivity, H_v : Huber value, TLMR: branch–leaf mass ratio, K_i : leaf-specific conductivity, G_s : stomatal conductance, WUE: water-use efficiency, T_r : transpiration rate, P_n : net photosynthetic rate, LMA: leaf mass per area, LDMC: leaf dry matter content, C_i : intercellular carbon dioxide concentration, and $\delta^{13}C$: carbon isotope signature.

Analysis of the overall PTN parameters across eleven populations revealed significant variations in the edge density, clustering coefficient, modularity, and average path length (Table 3). The networks attained an average edge density of 0.26, with site G displaying the highest (0.38) and site A displaying the lowest (0.17) values. Site F exhibited the highest

clustering coefficient (0.83) and site I exhibited the lowest (0.52). The network achieved an average clustering coefficient of 0.68. In addition, the network analysis indicated the highest modularity at site A (0.62) and the lowest at sites B and I (0.34). The average path length was 1.43, with the longest path observed at site D (2.62) and the shortest at site K (0.93).

Table 3. Variation in the network-level parameters among the eleven sampling sites. *D*: diameter; *AL*: average path length; *AC*: average clustering coefficient.

Site	<i>D</i>	<i>AL</i>	<i>AC</i>	Modularity
A	5.92	2.32	0.48	0.68
B	5.47	2.07	0.58	0.51
C	3.18	1.50	0.49	0.57
D	4.51	2.11	0.42	0.54
E	4.12	1.64	0.63	0.67
F	2.86	1.27	0.66	0.59
G	3.19	1.40	0.69	0.27
H	2.25	1.07	0.62	0.69
I	3.15	1.46	0.54	0.43
J	2.35	1.20	0.55	0.70
K	4.94	2.20	0.66	0.58

3.3. Environmental Drivers That Affected Functional Traits and Their Linkages with Traits

The two-dimensional ordination diagram obtained from the redundancy analysis (RDA), which related the photosynthetic and hydraulic parameters of *P. pruinosa* to environmental factors (Figure 6), shows the top three important factors: BIO1 (annual mean temperature), AI (aridity index), and GD (groundwater depth). The cumulative explanatory rate of environmental factors for the photosynthetic and hydraulic parameters of *P. pruinosa* reached 83.3%, with the first and second ordination axes explaining 33.27% and 24.80% of the total, respectively. BIO1 was a significant influencing factor ($p < 0.05$) and accounted for 20% of the explanatory rate for photosynthetic and hydraulic traits, followed by the AI (14%) and GD (12.4%) (Table 4).

The RDA identified the top three environmental factors that influenced the functional traits of *P. pruinosa*: annual average temperature (BIO1), aridity index (AI), and groundwater depth (GD) (Figure 7). The Pearson correlation results for the three environmental factors and functional traits indicate that K_s , K_{smax} , K_w , and K_{wmax} significantly increased ($p < 0.05$) with the rise in annual average temperature. The aridity index showed a slightly negative correlation with K_l , K_{smax} , and K_{wmax} , and a slightly positive correlation with G_s ($p > 0.05$). As the GD increased, K_l and P_n significantly decreased ($p < 0.05$), and $\delta^{13}C$ showed a slight downward trend ($p = 0.13$).

Table 4. The explanatory rates of environmental factors on photosynthetic and hydraulic traits. BIO1: annual average temperature, BIO3: isothermality, BIO8: average temperature of the wettest quarter, BIO12: annual precipitation, BIO13: precipitation in the wettest month, BIO15: seasonal variation of precipitation, AI: aridity index, GD: groundwater depth.

	Environmental Factors	Explanatory Rate (%)	F Value	p Value
Functional traits	BIO1	20	2.2	0.03
	AI	14	1.7	0.10
	GD	12.4	1.6	0.13
	BIO12	9.6	1.3	0.31
	BIO13	8.6	1.2	0.37
	BIO3	7.2	0.9	0.52
	BIO15	6.5	0.8	0.57
	BIO8	5.1	0.6	0.65

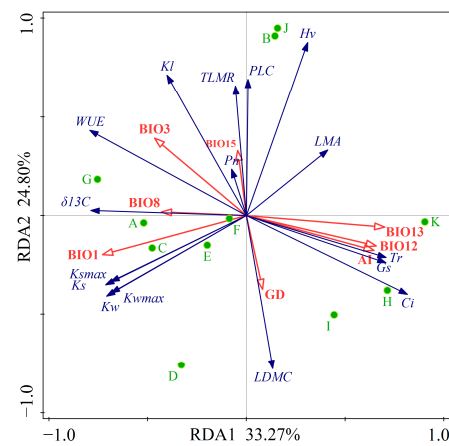


Figure 6. RDA of functional traits and seven important environmental factors ($n = 11$). Green dots represent different sites, blue arrows denote functional traits, and red arrows indicate climate factors. PLC: percent loss of hydraulic conductivity, K_w : wood-specific conductivity, K_s : sapwood-specific conductivity, K_{smax} : maximum sapwood-specific conductivity, K_{wmax} : maximum wood-specific conductivity, H_v : Huber value, TLMR: branch–leaf mass ratio, K_l : leaf-specific conductivity, G_s : stomatal conductance, WUE: water-use efficiency, T_r : transpiration rate, P_n : net photosynthetic rate, LMA: leaf mass per area, LDMC: leaf dry matter content, C_i : intercellular carbon dioxide concentration, and $\delta^{13}C$: carbon isotope signature. BIO1: annual average temperature, BIO3: isothermality, BIO8: average temperature of the wettest quarter, BIO12: annual precipitation, BIO13: precipitation in the wettest month, BIO15: seasonal variation of precipitation, AI: aridity index, GD: groundwater depth.

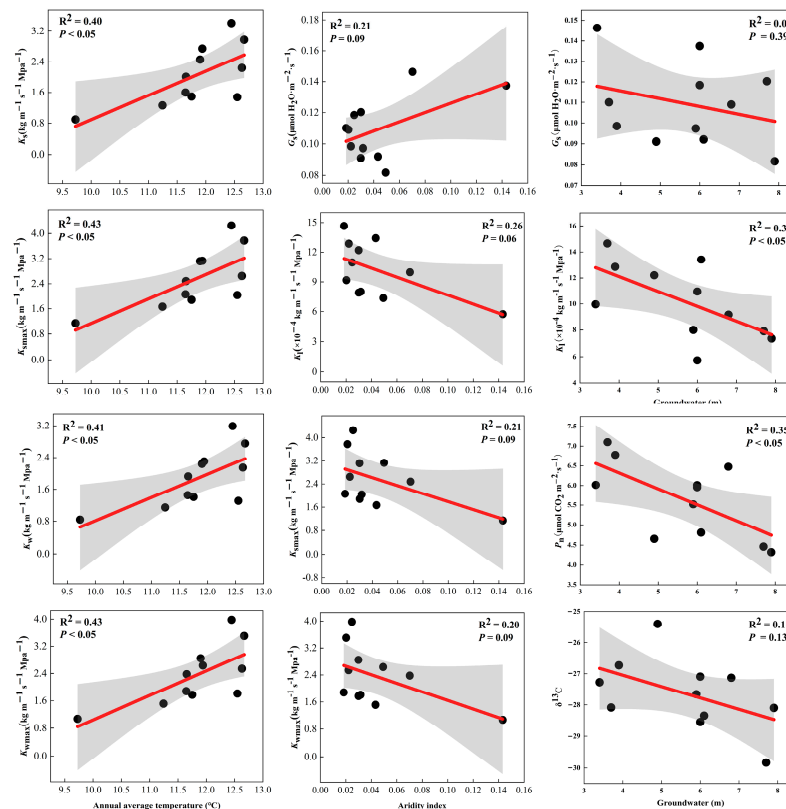


Figure 7. Relationship between the functional traits and important environmental factors ($n = 11$). The shaded area represents the 95% confidence interval, and the red line indicates the linear regression fitting line. K_w : wood-specific conductivity, K_s : sapwood-specific conductivity, K_{smax} : maximum sapwood-specific conductivity, K_{wmax} : maximum wood-specific conductivity, K_l : leaf-specific conductivity, G_s : stomatal conductance, P_n : net photosynthetic rate, and $\delta^{13}C$: carbon isotope signature.

The network's overall parameters were significantly correlated with some temperature-related climate factors and groundwater depth (Figure 8). Specifically, a significant negative correlation was identified between the network's diameter and average path length and the seasonal temperature variation coefficient and annual temperature range ($p < 0.05$). In addition, the lowest temperature of the coldest month and groundwater depth showed a significantly positive correlation with the average path length ($p < 0.05$).

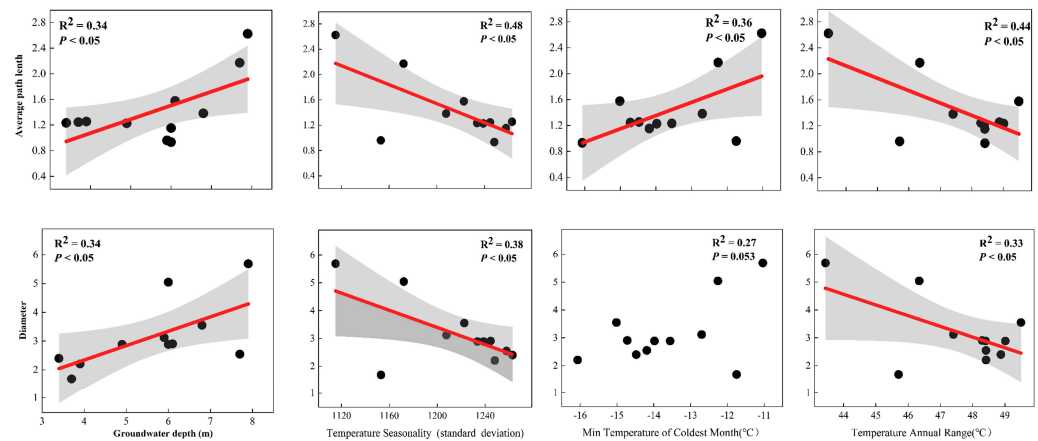


Figure 8. Relationships between overall network parameters and environmental factors ($n = 11$). The figures only display significant regression lines ($p < 0.05$). The shaded area represents the 95% confidence interval, and the red line indicates the linear regression fitting line.

4. Discussion

4.1. Variability and Interrelationships of Functional Traits

Through the evaluation of these traits in diverse environments, we delineated alterations in traits on a geographical scale and inferred plant adaptations to global climate change [43]. The ITV offers valuable insights into ecological processes and dynamics. However, current research often disregards this variation and mostly focuses on average traits at the species level. Studies on the ITV have substantially deepened our comprehension of the mechanisms underlying plant responses to stressors and their adaptation to environmental changes at the biological and geographical levels [44]. Siefert et al. examined the extent of the ITV at the community level via a global meta-analysis [45]. Hydraulic traits, such as H_v and K_s , exhibit extensive variability. Trait variability spans from individual organs (leaves, stems, and roots) to more integrated traits found across multiple organs [42]. This study revealed the greater variability of *P. pruinosa* hydraulic traits compared with its photosynthetic traits, which may have been due to the increased sensitivity of *P. pruinosa* hydraulic conductivity to changes in the drought gradient.

Trait coordination is indicated by a positive correlation, and trade-offs are denoted by a negative correlation [46]; these correlations reflect the strategies employed by plants throughout their life cycle. Desert plants adapt to drought stress through a balanced interaction with various functional traits [28]. This complexity poses challenges to organisms with optimally competitive phenotypes [10,47]. Xylem structural traits or leaf functional characteristics alone are insufficient to infer plant survival strategies. The failure to integrate these types of traits can lead to plant mortality [48]. Significant correlations have been observed between economic and leaf hydraulic traits [11,49]. Variations in hydraulic traits influence the plant growth and survival and the economic attributes of leaves. Simonin et al. observed a significant negative correlation between the LMA and K_1 . The efficiency and capacity of water transfer in xylem tissue, exemplified by the hydraulic conductivity of plant branches, also influence plant growth, survival, and distribution patterns [50]. K_1 governs the WUE of an entire plant [51]. H_v serves as a crucial component of the plant hydraulic architecture [6], representing carbon distribution in stems and leaves and the

balance between water supply and loss. A high H_v indicates the need for increased branch tissue allocation for water supply per unit leaf area. Plants with a low H_v typically exhibit a low $\delta^{13}C$ and LMA. In the presence of a high P_n , leaves fix more carbon, which necessitates an increase in G_s , and consequently, elevates water loss [52]. This study revealed the low coupling between photosynthetic and hydraulic traits. The dissociation of stem hydraulic traits and leaf photosynthesis may be attributed to their representation of distinct physiological metabolic processes, with each process affected by varying factors. A trade-off was observed between the hydraulic traits, TLMR, and LMA and between the xylem hydraulic conductivity, K_l , and H_v . This finding was due to the decreased water-use and transmission efficiencies in plants that resulted from the increase in leaf construction costs and the required branch tissue input for water supply per unit leaf area. As a result, the xylem hydraulic conductivity was consequently reduced. The growth relationship between the branch of *P. pruinosa* and its leaf functional traits exhibited a dynamic adjustment in response to environmental fluctuations.

4.2. Trait Network Analysis in Plant Adaptability Research

PTNs provide a comprehensive and visual perspective; they quantify inter-trait relationships, identify central traits via an integrated and pragmatic approach, and offer valuable insights into plant adaptation strategies under varying environmental and resource conditions [53]. To increase their survival rate and capacity to recover from stress, plants integrate multiple phenotypes, thereby increasing their competitiveness and ability to adapt to a changing external environment [25,54,55]. As highlighted by Kleyer et al., stem traits refer to the primary characteristics of perennial herbaceous plants [10]. In this study, *P. pruinosa* might have prioritized the connection of hydraulic characteristics to improve the WUE given the plant's small vessel diameter and low water transport efficiency [56]. This finding suggests that *P. pruinosa*'s hydraulic characteristics are easily preferred as central traits. Thus, at high latitudes, for *P. pruinosa* populations, K_l was selected as the central trait, whereas in lower-latitude populations, the xylem hydraulic conductivity (K_w and K_s) played a key role in plant adaptation. This result may have been due to the relatively moist environments of higher-latitude populations, which allowed for the increased investment in leaf structure [4]. Meanwhile, the leaf and stem hydraulic traits were coordinated [15,57], and differences were observed in the selection of central traits between populations. These differences imply the complexity of hydraulics and subtle variations that reflect various aspects of plant physiology [24]. Through the alteration of K_l , and thus, transpiration, population differences resulted in changes in trait composition, network topology, and characteristics of the PTN.

In this study, site K attained the highest AI (indicating the wettest climate) and the highest degree of synergy between population traits in its PTN. Photosynthetic and hydraulic traits formed two independent modules, indicating strong interactions within each module but loose ones between them. This result aligns with the researchers' conclusions regarding the decoupling of economic and hydraulic traits in humid areas and their coupling in drier regions [23]. This phenomenon might be attributed to the increased sensitivity and fragility of ecosystems in arid regions, with trait relationships being strongly controlled by a few traits and a low water availability [58]. Plants stably combine economic and hydraulic traits to adapt to drought. In more humid areas, this decoupling aids plants in forming various trait combinations in resource-rich environments, improving their adaptation to the environment [23].

4.3. Interplay between Functional Traits and Environmental Factors

Environmental changes trigger a synergistic response between functional traits [59–63]. Previous research at local-to-regional scales has attributed most variations in plant hydraulic traits to fluctuations in environmental climatic conditions [64]. Global warming results in not only elevated average temperatures but also in an increased probability of extreme heat events. Temperature variations directly affect the physiological and ecological characteristics of plants,

including metabolic rates and surface evapotranspiration. In this study, the annual average temperature was determined as the primary environmental climatic factor explaining the alterations in photosynthetic and hydraulic properties. Correspondingly, other research has depicted a relationship between temperature and functional traits. The mean annual temperature is a key factor that influences the variability of the intraspecific leaf traits of *Cunninghamia lanceolata* [65]. This study revealed a significant positive correlation between the maximum and wood specific conductivities with the annual average temperature. As a result of competition for light and rapid growth, warmer climates may necessitate high photosynthetic rates and water transport capacities [66]. Conversely, in colder areas, the risk of an embolism from freeze–thaw cycles increases due to elevated xylem hydraulic conductivity [67]. Extremely low temperatures are primary climatic factors that impair plant hydraulic systems, potentially reducing the productivity or causing plant mortality [68]. In this study, the coordination of traits showed a significant correlation with the lowest minimum temperature of the coldest month, implying that low-temperature stress influences the ITV and may lead to adaptive differentiation between populations. Conversely, strong trait coordination within a population reduces the likelihood of forming functional modules that support the population's healthy and stable development, particularly in environments with small seasonal and interannual temperature variability. Although structural traits exhibit less sensitivity and can adapt to environmental changes, physiological traits, such as photosynthetic characteristics and hydraulic conductivity, show increased susceptibility to environmental fluctuations given their important role in ensuring plant survival. Under the influence of natural selection, plants can improve their photosynthesis by adapting their long-term hydraulic systems and short-term physiological responses to environmental changes [69]. The predominant distribution of *P. pruinosa* in the Tarim Basin south of the Tianshan Mountains and its sparse allocation to the north may be associated with the species' preference for warmer climates. We speculated that the latitudinal distribution limit of *P. pruinosa* depends on a low-temperature climatic boundary.

In arid desert areas, water is one of the important factors that restrict plant growth and distribution. Precipitation is insignificant for plant growth, and, typically, no water is stored in surface soils because the annual potential evaporation is about 156 times higher than precipitation in the Tarim Basin [70]. Groundwater is a relatively stable and persistent water source that can not only be directly utilized by plants but can also provide water to the root-zone soil through capillary ascent [71]. Therefore, groundwater is considered the foundation for maintaining the functionality of desert ecosystems. An increase in groundwater depth can trigger adaptive adjustments in plant functional traits. For example, under the condition of increasing groundwater depth, the leaf carbon isotope content reflecting plant water-use efficiency and the net photosynthetic rate reflecting plant photosynthesis both decrease [72,73]. The net photosynthetic rate of *Haloxylon ammodendron* decreases [71]. In this study, the net photosynthetic rate and leaf specific conductance of *P. pruinosa* significantly decreased with an increased GD, indicating that when the groundwater depth was shallow, *P. pruinosa* adopted a resource acquisition strategy, which exhibited high photosynthetic and hydraulic capacities. As the depth of the groundwater increased, the photosynthetic capacity and xylem hydraulic function of *P. pruinosa* began to decline, which may have been due to the increased resistance of hydraulic transportation. The xylem hydraulic function of *P. pruinosa* began to decline because of increased hydraulic transportation resistance. *P. pruinosa* gradually adopted a resource conservation strategy. Meanwhile, in this study, $\delta^{13}\text{C}$ decreased with increasing GD. The low water-use efficiency may further decrease the groundwater level, which can induce a cycle [74]. The relationship between the overall parameters of the trait network and environmental factors indicated that under significant temperature fluctuations, extreme low temperatures, and increased groundwater depth, the coordination of the traits of *P. pruinosa* was poor, leading to a significant decrease in production efficiency and resource utilization, which had an adverse impact on its growth and geographical distribution.

5. Conclusions

Based on the results of this study, it could be concluded that the hydraulic conductivity of *P. pruinosa* was more sensitive to environmental responses than the photosynthetic traits. The photosynthetic and hydraulic traits presented low coupling. *P. pruinosa* adjusted its hydraulic conductivity to adapt to the environmental changes through alterations in the growth relationship between the branch and leaf functional traits. The traits related to xylem hydraulic conductivity (K_l , K_w , and H_v) were more likely to be selected as central traits, suggesting that these traits may play a central role in the regulation of the plant's ability to perform a specific function. With an increase in the annual average temperature, the hydraulic conductivity of the xylem significantly increased; with an increase in the GD, the photosynthetic capacity, hydraulic conductivity, and water-use efficiency of *P. pruinosa* decreased to varying degrees. The temperature annual range, temperature seasonality (standard deviation), min temperature of the coldest month, and GD substantially affected the coordination of the traits of *P. pruinosa*. Large temperature fluctuations, extreme low temperatures, and an increase in groundwater depth will have an adverse impact on the production efficiency and resource utilization of *P. pruinosa*. If extreme weather events occur in the future, the natural forest condition of *P. pruinosa* should be monitored, and ecological restoration methods (such as ecological water conveyance) can be used to protect this species.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f15071094/s1>, Figure S1: Variation in the network node parameter “closeness” for functional traits Among 11 populations (The sample size for each sampling point is 20). The traits abbreviation were mean percent loss of hydraulic conductivity (PLC), Wood-specific conductivity (K_w), Sapwood-specific conductivity (K_s), Maximum sapwood-specific conductivity (K_{smax}), Maximum wood-specific conductivity (K_{wmax}), Huber value (H_v), Branch leaf mass ratio (TLMR), Leaf-specific conductivity (K_l), Stomatal conductance (G_s), Water use efficiency (WUE), Transpiration rate (T_r), Net photosynthetic rate (P_n), Leaf mass per area (LMA), Leaf dry matter content (LDMC), Intercellular carbon dioxide concentration (C_i), Carbon isotope signature ($\delta^{13}C$); Figure S2: Variation in the network node parameter “betweenness” for functional traits Among 11 populations (The sample size for each sampling point is 20). The traits abbreviation were mean percent loss of hydraulic conductivity (PLC), Wood-specific conductivity (K_w), Sapwood-specific conductivity (K_s), Maximum sapwood-specific conductivity (K_{smax}), Maximum wood-specific conductivity (K_{wmax}), Huber value (H_v), Branch leaf mass ratio (TLMR), Leaf-specific conductivity (K_l), Stomatal conductance (G_s), Water use efficiency (WUE), Transpiration rate (T_r), Net photosynthetic rate (P_n), Leaf mass per area (LMA), Leaf dry matter content (LDMC), Intercellular carbon dioxide concentration (C_i), Carbon isotope signature ($\delta^{13}C$); Table S1: Sampling sites climatic characteristics; Table S2: Functional traits (mean $\pm$ SD) of *P. pruinosa* across 11 populations (The sample size for each sampling point is 20). The traits abbreviation were mean percent loss of hydraulic conductivity (PLC), Wood-specific conductivity (K_w), Sapwood-specific conductivity (K_s), Maximum sapwood-specific conductivity (K_{smax}), Maximum wood-specific conductivity (K_{wmax}), Huber value (H_v), Branch leaf mass ratio (TLMR), Leaf-specific conductivity (K_l), Stomatal conductance (G_s), Water use efficiency (WUE), Transpiration rate (T_r), Net photosynthetic rate (P_n), Leaf mass per area (LMA), Leaf dry matter content (LDMC), Intercellular carbon dioxide concentration (C_i), Carbon isotope signature ($\delta^{13}C$).

Author Contributions: Z.L. conceived the study. J.Z. (Jinlong Zhang), J.Z. (Juntuan Zhai), J.W., and X.G. performed the field measurements and laboratory analyses. J.Z. (Jinlong Zhang) analyzed the results and wrote the manuscript. Z.L., J.S., J.L., and J.Z. (Juntuan Zhai) modified the manuscript. All authors have read and agreed to the published version of the manuscript.

Funding: This work received funding from the grant provided by the National Natural Science Foundation of China (project no. 32371838), the Second Batch of “Tianshan Talents” Support Program—Science and Technology Innovation Team (2023TSYCTD0019), and the Tarim University graduate research and innovation project (TDGRI202205).

Data Availability Statement: Dataset available on request from the authors.

Acknowledgments: We are grateful to Houji Liu, Xiaoli Han, Mingyu Jia, Yin Wang, and Binglei Liu for their efforts in the sample collection, and to Jing Li and Hongyan Jin for their work in measuring samples.

Conflicts of Interest: The authors declare no conflicts of interest.

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