EFFECT OF PROVENANCE AND CLIMATE ON XYLEM ANATOMY OF *HALOXYLON AMMODENDRON* (C. A. MEY) BUNGE IN THE GURBANTUNGGUT DESERT, CHINA

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Abstract. Although *Haloxylon ammodendron* is widely distributed in desert regions of both Asia and Africa, the anatomical structure of its xylem is rarely reported. In this study, the differences in xylem anatomical characteristics among five provenances in the southern Gurbantunggut Desert were compared and the effects of climatic factors on anatomical features were analyzed. The results showed that the xylem responded to low precipitation by increasing ray density and ray height to improve the storage of water and starch to combat drought stress. In an arid provenance (Jinghe), *H. ammodendron* had wide vessels to improve conductivity. Moreover, they increased the vessel wall thickness to decrease its sensitivity to embolism. Both average temperature in January and maximum wind velocity from April to June were significantly related to the wall thickness of the fiber ($P < 0.05$), indicating that a thicker fiber cell wall could provide higher mechanical resistance to steady stems and improve vessel conduction in low temperature and strong wind conditions. These results indicate that there is high plasticity in the xylem anatomical structures of *H. ammodendron* in response to different desert conditions and also explain the adaptation of the plant to a wide range of Asian and African deserts.
Keywords: *Saxoul; ray; vessel; fiber; precipitation; temperature; wind velocity; adaptation*

Introduction

Haloxylon ammodendron (C.A. Mey) Bunge belongs to the family Amaranthaceae, which is widely distributed in desert ecosystems across Asia and Africa (Pyankov et al., 1999; Tobe et al., 2000). In China, *H. ammodendron* is the dominant species of vegetation in the Gurbantunggut Desert (Huang et al., 2009). The plant is highly adaptable to drought, salinity, nutrient deficiency and intensive light (Fahn and Cutler, 1992; Huang et al., 2003), so in the Gobi region in southern Mongolia and the arid region of northwest China, *H. ammodendron* has become the main tree species for afforestation (Bedunah and Schmidt, 2000; Sheng et al., 2005; von Wehrden et al., 2009).

Trees with a wide geographical distribution must adapt to changes in ecological conditions through morphological and physiological variations. The growth characteristics of *H. ammodendron* vary across different regions of the Gurbantunggut Desert. The variations in appearance (e.g. tree height, basal diameter, crown area), seed quality (Lv et al., 2012, 2015) and seedling regeneration (Zhou and Song, 2015) may be

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caused by differences in climate and microhabitat. The xylem of plants provides mechanical support and the transportation and storage of water and nutrients (Esteban et al., 2010). Its microstructure reflects the adaptation of the plant to the natural environment (Carlquist, 2001). Many studies have confirmed that significant variations in the anatomical characteristics of xylems are caused by differences in ecological conditions among different provenances (Esteban et al., 2012; Zas et al., 2015). For a long period, *H. ammodendron* has lived in a desert environment with low precipitation so the xylem is already highly adapted to drought stress (Yang and Furukawa, 2003; Heklau et al., 2012; Li et al., 2015; Song and Zhou, 2015). However, existing studies have not considered the effects of climatic factors in different provenances on xylem anatomical variables.

Anatomical characteristics of the xylem change with environmental conditions, but the variation in xylem tissue among different species is inconsistent. For example, it is expected that wood density is higher and mechanical strength and cavitation resistance is stronger under drought stress (Christensen-Dalsgaard and Ennos, 2012; Plavcová and Hacke, 2012). Studies have also pointed out that with increasing drought stress, the cell wall area of fiber reduces, as a consequence of a decrease in wood density (Aref et al., 2013). Furthermore, contrasting results have been found in the correlations between drought stress and the diameter of vessels (Plavcová and Hacke, 2012; Aref et al., 2013; Menezes-Silva et al., 2015; Hajek et al., 2016) and rays (Margaris and Papadogianni, 1977; Martin et al., 2010). It is currently unclear how the anatomical structure of the xylem of *H. ammodendron* will respond to changes in desert environment.

In this study, five sample plots were created on the Jinghe, Wusu, Shihezi, Caijiahu and Qitai, from West to East, of the southern Gurbantunggut Desert (*Fig. 1*). Among these sample plots, a significant difference was found in the growth of *H. ammodendron*, and the maximum was double the minimum in average annual precipitation (*Table 1*). The objectives of this paper were to: (1) compare the differences in xylem anatomical features among provenances; (2) analyze the effects of climatic factors on anatomical variables. We expected to clarify the adaptation of *H. ammodendron* xylem anatomy to ecological conditions, especially drought stress, in different areas.

Materials and Methods

Experimental set up and climatic conditions

Sample plots were located at Jinghe, Wusu, Shihezi, Caijiahu and Qitai in the southern Gurbantunggut Desert, China (*Fig. 1*); the plots have a temperate continental desert climate. Meteorological factors such as temperature, precipitation, wind velocity and sunshine are shown in *Table 1*. Five unbroken and representative sample trees in each plot were selected, totaling 25 trees. Branches (3–5) with a diameter of about 1 cm and length of about 15cm were sawn from each sample tree in order to measure the anatomical features of the xylem.

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Figure 1. *Sample plot in Gurbantunggut Desert of Xinjiang, China*

Table 1. *The climate conditions and growth characteristics of H. ammodendron in five provenances*

Variable	Jinghe	Wusu	Shihezi	Caijiahu	Qitai
Average height of tree (m)	1.23 ± 0.46 c	1.22 ± 0.42 c	1.70 ± 0.35 a	1.77 ± 0.41 a	1.44 ± 0.49 b
Average basal diameter of tree (cm)	3.99 ± 0.23 b	2.63 ± 0.15 c	5.69 ± 0.18 a	6.08 ± 0.23 a	4.00 ± 0.21 b
Average crown area of tree (m^2)	2.16 ± 0.19 b	1.50 ± 0.19 b	2.94 ± 0.17 a	3.22 ± 0.15 a	3.14 ± 0.28 a
Longitude (E)	82°53′35″	84°4′56″	86°14′44″	87°25′1″	88°53′20″
Latitude (N)	44°36′10″	44°22′57″	45°00′34″	44°39′10″	44°22′39″
Maximum velocity from April to June ($m.s^{-1}$)	5.39	5.11	5.61	6.25	6.52
Average annual temperature (°C)	8.42	8.71	8.09	6.69	5.54
Average temperature in July (°C)	33.31	32.86	32.73	34.03	30.46
Average temperature in January (°C)	-19.4	-18.45	-20.88	-24.26	-24.14
Average annual relative humidity (%)	61.84	59.41	63.55	61.61	61.87
Average sunlight (h)	2515.7	2547.8	2769.4	2834.8	2837.2
Average annual precipitation (mm)	111.2	180.4	225.3	153.8	205.9

Data are expressed as mean ± SE, different letters indicate a significant difference among different provenances at $P < 0.05$ level. Meteorological data are collected from China Meteorological Data Network (http://data.cma.cn/).

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Measurement of xylem anatomical characteristics

The bark of all sampled branches were stripped and then the xylem samples were embedded in paraffin without softening or dehydration. The cross sections, radial and tangential sections were prepared using a sliding microtome (MICROM HM430, Germany), with a thickness of 9 – 11, 4.5 – 5.5 and 4.5 – 5.5 μm, respectively. Sections were dehydrated and stained with safranin and hematoxylin and then the sections were placed on the microscopic slide using synthetic resin. The anatomical features were described according to the recommendations of the IAWA Committee (IAWA Committee, 2004).

To measure the length of the vessels and fibers, xylem samples were treated using Jeffery's method (10% chromic acid and 10% nitric acid were mixed according to V:V = 1:1; Wright and Endo, 1993). The isolated samples were placed on the microscopic slide (48 h after treatment), stained with safranin, and observed under a light microscope.

Photos of sections were taken with a digital camera (Nikon 4500) mounted on a light microscope with 40 × optical magnification (or 10 × optical magnification for the measurement of density of rays [dR]). The WinCELL image analysis system (Regent Instruments Inc., Québec, Canada) was used to measure the anatomical variables: height of ray (hR), width of ray (wR), ray cell length (RCl), ray cell width (RCw), wall thickness of ray cell (wtRC), pit diameter of vessel (PdV), diameter of vessel (dV), length of vessel (lV), wall thickness of vessel (wtV), wall thickness of fiber (wtF) and length of fiber (lF). The dR was calculated by counting the number of rays in an area of 1 mm^2. For each variable, 50 random measurements were taken and the mean value per tree was calculated.

Statistical analysis

All data were analyzed using SPSS 19.0 software. The regression analyses were carried out using Pearson two-tailed tests between the mean value by provenance of the xylem variables and the meteorological factors (from 1991 to 2008), and between each of the xylem variables. The differences in anatomical variables between different provenances were analyzed using a Tukey test for multiple comparisons. The significance of explained variation was analyzed using a generalized linear model (GLM, type III sum of squares; McCullagh and Nelder, 1989), which was set up as follows:

$$Y = \mu + R + T(R) + \varepsilon \qquad \text{(Eq.1)}$$

In this model, *Y* was the response variable, μ was the general mean, *R* was the effect of the provenance, *T*(*R*) was the effect of the trees (within provenance) and ε was the error term.

A principal component analysis (PCA) was used to analyze the xylem anatomical variables. The scores of principal components were used to draw the scatter plot, which was used to analyze the combinations of anatomical variables between different plots.

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Results

Variation in H. ammodendron xylem anatomy

The GLM showed that provenance significantly affected ($P < 0.05$) the anatomical features of the xylem, apart from in RCl, RCw, PdV and lF ($P > 0.05$). The tree factor (within provenance) was significant only in RCl, RCw, PdV and lF ($P < 0.05$, *Table 2*). For most of the anatomical features (8 out of a total of 12), the provenance significantly explained the total variation. The variation explained was particularly high for the effect of provenance on dR, which was up to 186.07.

Table 2. *The Sources of variation and its significance in anatomical characteristics of H. ammodendron xylem*

Anatomical characteristic	Variable	Source: Provenance	Source: Tree (Within-provenance)
Rays	Density of rays (n/mm^2)	186.07***	1.12 ns
	Height of rays (μm)	83.93***	0.08 ns
	Width of rays (μm)	19.53**	0.82 ns
	Ray cell length (μm)	2.73 ns	9.99***
	Ray cell width (μm)	1.01 ns	27.24***
	Wall thickness of ray cell (μm)	17.96**	0.22 ns
Vessels	Diameter of vessels (μm)	26.85***	0.43 ns
	Wall thickness of vessels (μm)	5.33*	0.59 ns
	Pit diameter of vessels (μm)	3.30 ns	10.17***
	Length of vessels (μm)	85.46***	0.38 ns
Fibers	Wall thickness of fibers (μm)	9.10*	1.99 ns
	Length of fibers (μm)	2.33 ns	11.23***

Asterisks indicate significant sources at $P < 0.05$ (*), $P < 0.01$ (**) and $P < 0.001$ (***); *ns* not significant.

H. ammodendron xylem anatomy in the five provenances

There were significant differences ($P < 0.05$) between the xylem anatomical characteristics of *H. ammodendron* in different provenances. Some anatomical parameters significantly changed with the different climate of each provenance. For instance, the average annual precipitation was highest in Shihezi and lowest in Jinghe (*Table 1*) and significant differences in dR, hR, wR, RCl, wtRC and dV were found between Jinghe and Shihezi ($P<0.05$; *Table 3*). The average annual precipitation in Wusu, Caijiahu and Qitai was between Shihezi and Jinghe, and the dR, hR, wtRC and dV of Wusu, Caijiahu and Qitai were similar (*Tables 1 and 3*). The highest values of dR, hR, wR, RCw, dV, lV, wtV and lF were found in Jinghe, the highest value of PdV was found in Wusu, the highest values of RCl and wtRC were found in Shihezi and the highest value of wtF was found in Caijiahu.

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Table 3. *Anatomical characteristics of H. ammodendron xylem in differenc provenances*

Anatomical characteristic	Variable	Jinghe	Wusu	Shihezi	Caijiahu	Qitai
Rays	Density of rays (n/mm^2)	7.71 ± 1.80 a	2.41 ± 0.74 c	1.46 ± 0.77 d	3.57 ± 1.10 b	3.43 ± 1.11 b
	Height of rays (μm)	223.74 ± 88.11 a	202.70 ± 73.38 ab	170.62 ± 78.80 c	197.48 ± 57.93 abc	194.50 ± 68.25 bc
	Width of rays (μm)	29.40 ± 12.01 a	22.34 ± 8.49 bc	20.80 ± 11.52 bc	20.17 ± 6.01 c	23.97 ± 6.42 b
	Ray cell length (μm)	19.98 ± 3.68 b	24.08 ± 5.45 a	24.98 ± 5.99 a	23.74 ± 5.70 a	18.67 ± 5.10 b
	Ray cell width (μm)	11.86 ± 2.26 a	10.04 ± 2.06 b	10.57 ± 1.73 b	9.25 ± 2.05 c	9.91 ± 1.30 bc
	Wall thickness of ray cell (μm)	2.85 ± 0.42 b	3.02 ± 0.66 ab	3.08 ± 0.44 a	2.89 ± 0.49 ab	2.97 ± 0.47 ab
Vessels	Diameter of vessels (μm)	60.88 ± 11.64 a	57.47 ± 13.18 ab	49.06 ± 14.74 c	58.60 ± 15.84 ab	55.50 ± 11.92 b
	Wall thickness of vessels (μm)	5.53 ± 1.18 a	5.37 ± 1.18 ab	5.15 ± 0.79 b	5.32 ± 1.28 ab	5.28 ± 0.98 ab
	Pit diameter of vessels (μm)	3.28 ± 0.72 b	3.50 ± 0.71 a	3.06 ± 0.64 c	2.89 ± 0.48 c	3.45 ± 0.77 ab
	Length of vessels (μm)	78.03 ± 14.56 a	60.57 ± 10.05 c	71.25 ± 11.92 b	64.70 ± 10.57 c	71.41 ± 10.66 b
Fibers	Wall thickness of fibers (μm)	2.79 ± 0.41 b	2.64 ± 0.40 c	2.72 ± 0.38bc	2.97 ± 0.43 a	2.94 ± 0.41 a
	Length of fibers (μm)	263.48 ± 3.89 a	234.51 ± 4.02 bc	276.24 ± 4.31 a	247.85 ± 3.71 b	228.41 ± 3.70 c

Data are expressed as mean ± SD, different letters indicate a significant difference among different provenances at $P < 0.05$ level.

Principal component analysis of anatomical features

The PCA results showed the classification of climatic characteristics in the five provenances (*Fig. 2A*), and certain anatomical features of *H. ammodendron* were well distinguished by provenance, according to climatic characteristics (*Fig. 2B*). The dR, hR, wR, dV and wtV were in accordance with positive scores of PC1 and characterized the climatic features of Jinghe. The RCl and wtRC were in agreement with the negative scores of PC1 and characterized the climatic features of Shihezi. The PdV was in accordance with positive scores of PC3 and characterized the climatic features of Wusu. The wtF was in agreement with the negative scores of PC3 and characterized the climatic features of Caijiahu.

Relationships between xylem anatomical characteristics and climatic factors

The regression analyses between the xylem anatomical variables showed the following significant relationships ($P < 0.05$; *Table 4*): dR was positively related to wR (r = 0.89), dR was positively related to wtV (r = 0.88), hR was positively related to dV (r = 0.95), hR was positively related to wtV (r = 0.99) and dV was positively related to wtV (r = 0.92).

The regression analysis between the climatic characteristics and anatomical variables showed the following significant relationships ($P < 0.05$; *Table 5*): average annual precipitation was negatively correlated with dR (r = -0.89, Eq. 1), hR (r = -0.91, Eq. 2), wtV (r = -0.93, Eq. 5) and dV (r = -0.90, Eq. 4), and positively correlated with wtRC (r = 0.91, Eq. 3). Maximum wind velocity from April to June was positively related to wtF (r = 0.92, Eq. 6), and average temperature in January was negatively related to wtF (r = -0.93, Eq. 7).

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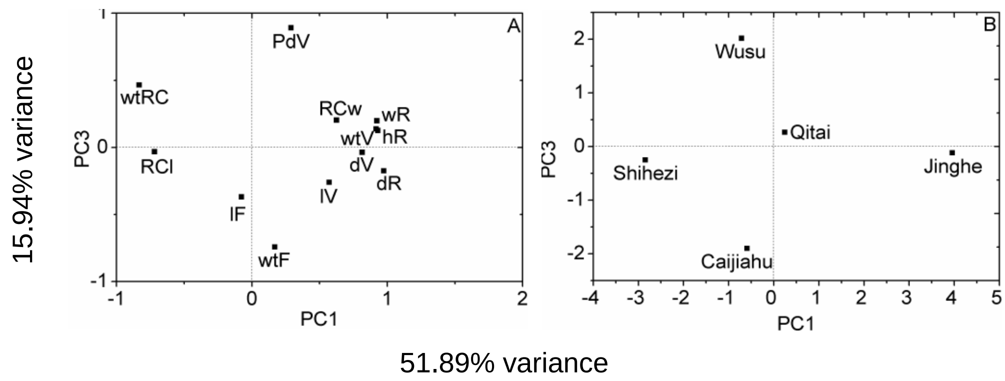

Figure 2. *Principal component analysis (PCA) of the anatomical characteristics of H. ammodendron from Gurbantunggut Desert, China*

Table 4. *Correlation matrix between anatomical variables of H. ammodendron xylem*

	Height of rays	Width of rays	Diameter of vessels	Wall thickness of vessels
Density of rays	0.88	0.89	0.77	0.88
Height of rays		0.78	0.95	0.99
Width of rays			0.56	0.79
Diameter of vessels				0.92

Significant correlations shown in underlined ($P<0.05$). Anatomical variables not included in the table were not significantly related other variables.

Table 5. *Correlation matrix between meteorological factors and anatomical variables of H. ammodendron xylem*

Variables	Linear equation	r	*P*	No.
Average annual precipitation (x) and density of rays (y)	y = -0.047x + 12.03	-0.89	0.04	(1)
Average annual precipitation (x) and height of rays (y)	y = -0.384x + 265.2	-0.91	0.03	(2)
Average annual precipitation (x) and wall thickness of ray cell (y)	y = 0.001x + 2.619	0.91	0.04	(3)
Average annual precipitation (x) and diameter of vessels (y)	y = -0.09x + 72.08	-0.9	0.04	(4)
Average annual precipitation (x) and wall thickness of vessels (y)	y = -0.002x + 5.832	-0.93	0.02	(5)
Maximum velocity from April to June (x) and wall thickness of fibers (y)	y = 0.220x + 1.537	0.92	0.03	(6)
Average temperature in January (x) and wall thickness of fibers (y)	y = -0.048x + 1.763	-0.93	0.02	(7)

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Discussion

This paper studied the branch xylem anatomy of *H. ammodendron* from five provenances in the Gurbantunggut Desert. For most anatomical characteristics, more variation was explained by provenance than by tree (within-provenance variation), which showed that the anatomical characteristics of *H. ammodendron* xylems were notably affected by provenance (*Table 3*).

The variation in dR, hR and wR among different provenances was significant; the variation in dR was higher than other anatomical characteristics (*Table 2*). Generally, ray tissues are related to the storage and transport of water and nutrients. The higher ray frequency means that the xylem can accumulate more water and starch, and the starch can provide metabolites to reduce the impact of water stress (Esteban et al., 2012). For example, *Acacia tortilis* subsp. *raddiana* (Savi) Brenan increased its ray density to cope with the shortage of water under drought stress (Aref et al., 2013).

In this study, the average annual precipitation in Jinghe was the lowest of the studied provenances, but the values of dR, hR and wR were the highest (*Table 3*). This may be because drought stress favored the production of ethylene in the plants (Chen et al., 2002) and ethylene promoted anticlinal division in fusiform initials, increasing the density and/or size of rays (Pramod et al., 2013). The dR and hR were negatively related to average annual precipitation ($P < 0.05$; *Table 5*, Eq. 1 and Eq. 2), which shows that the xylem rays of *H. ammodendron* favor efficiency over safety, meaning that rays were tall and wide to reduce water shortages under water stress (Leal et al., 2006).

The increase in ray size often leads to a decrease in the mechanical strength of the xylem (Carlquist et al., 1984; Rahman et al., 2005). However, we did not find an increase in wtRC in *H. ammodendron* in response to drought stress. Of the five provenances, the maximum wtRC was found in Shihezi, which has the highest average annual precipitation, rather than in Jinghe, which has the lowest average annual precipitation (*Table 3*). The regression analysis showed that wtRC was positively related to the average annual precipitation ($P < 0.05$; *Table 5*, Eq. 3). Therefore, it was difficult to explain the variations in wtRC according to changes in precipitation. The ray cell may have thick or thin walls (Carlquist, 2001; Rajput et al., 2013), but only a few species have thick-walled rays. For example, rays in *Symbolanthus macranthus* G. Don are thick-walled, with a thickness of 2.5 μm (Carlquist and Grant, 2005). Although the wall thickness of rays in *H. ammodendron* did not increase with decreasing precipitation, the walls of rays in all five provenances were generally thickened, with a mean thickness of 2.96 μm. This implies that the rays of *H. ammodendron* have thick walls to increase the safety of storage and radial transport of water. The decrease in mechanical strength caused by the increase in ray size and density could be improved by other aspects of growth. For example, the tree height, basal diameter and crown area in Jinghe was lower than in Shihezi ($P < 0.05$; *Table 1*), which could decrease the trees' requirement for mechanical strength (Alves and Angyalossy-Alfonso, 2002).

The precipitation in Jinghe was low, but the values of dV and lV in *H.*

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ammodendron were higher in Jinghe than in other provenances, which indicated that the efficiency of water transport was the priority in xylem anatomy (*Table 3*; Zanne et al., 2010). Plants growing in drought stress often have narrow vessels to increase cavitation resistance and hydraulic safety (Cai and Tyree, 2010). However, in our experiment the dV was negatively related to the average annual precipitation ($P < 0.05$; *Table 5*, Eq. 4). Vessels with large diameters were susceptible to embolization due to drought stress (Al-Khalifah et al., 2006). In *H. ammodendron*, there was an increase in the diameter of vessels to improve transport under sparse precipitation, which likely compensates for the reduction in transport induced by cavitation (Galle et al., 2010). Our results are in accordance with the studies on xylem hydraulic properties in *Fagus sylvatica* L. and *Salix psammophila* C. Wang et Ch. Y. Yang (Hajek et al., 2016; Li et al., 2016). However, this did not mean that transport safety was not considered in the structure of the vessels. The wtV may be related to drought adaptation because the vessel wall is thicker when arid-adapted plants experience greater negative xylem pressures (Kohonen and Helland, 2009), which could decrease the sensitivity to embolism (Hacke et al., 2001).

Our study indicated that precipitation in Jinghe was low, but the wtV in this region of 5.53 ± 0.67 μm was the highest of all the provenances (*Table 3*). The wtV was negatively related to the average annual precipitation ($P < 0.05$; *Table 5*, Eq. 5) and was positively related to the dV ($P < 0.05$; *Table 4*). These correlations indicate that in the more arid Jinghe, the *H. ammodendron* had wide vessels to improve conductivity and increased wtV to guarantee transport safety. Similar results were reported for *Acacia ehrenbergiana* Hayne (Aref et al., 2013). The positive correlation between wtV and dV indicated no trade-off between efficiency and safety, which is in agreement with many studies (Maherali et al., 2006; Plavcová and Hacke, 2012; Hajek et al., 2016). The trade-off between efficiency and safety is based on pit-level traits (Sperry et al., 2006; Christman et al., 2012), so if the plasticity of dV and wtV in *H. ammodendron* is high enough, we might not find the trade-off between efficiency and safety during the development of the xylem.

Fibers provide mechanical strength to steady stems and vessel conduction against implosion due to negative pressure (Sperry, 2003; Jacobsen et al., 2005). In the Gurbantunggut Desert, the maximum wind velocity of the year occurred from April to June. This maximum was positively related to the wtF, indicating that the wtF is adapted to variation in wind velocity in the Gurbantunggut Desert. In other words, a thicker fiber cell wall could provide higher mechanical resistance and protect the transport safety of vessels in strong wind conditions (Alves and Angyalossy-Alfonso, 2002).

The stress of freeze-thaw can result in embolism and cavitation in plants (Sevanto et al., 2012). Many studies have reported that smaller vessels are less sensitive to this embolism and cavitation (Davis et al., 1999; Feild et al., 2002). The average temperature in January in Caijiahu was the lowest of all the study sites, but the dV of *H. ammodendron* was not the smallest in this provenance (*Table 3*), showing that the xylem of the plant did not decrease the dV in response to the stress of freeze-thaw. The area of fiber cell wall is positively related to cavitation resistance (Jacobsen et al.,

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2005), indicating that a thicker wtF would mean higher cavitation resistance. The average temperature in January was negatively related to the wtF ($P < 0.05$; *Table 5*, Eq. 7), implying that wtF increased in order to enhance resistance to cavitation under cold stress (Jacobsen et al., 2005).

The results of PCA indicated that the PC1 of Jinghe, with a maximum positive score, characterized the lowest precipitation and was in accordance with the highest values of dR, hR, wR, dV and wtV. This indicates that the high water storage and transport by the xylem was a response to the sparse precipitation, as also illustrated by the negative correlations between average annual precipitation and dR, hR, dV and wtV (*Table 5*). The PC3 of Wusu, with a maximum positive score, characterized the lowest value of maximum wind velocity from April to June, which was in accordance with the lowest values of wtF, indicating low mechanical properties. The wtF in Caijiahu was the highest among the five provenances, indicating that the higher the value of maximum wind speed, the thicker the wtF in xylems, as also evidenced by the positive correlation between wtF and maximum wind velocity from April to June (*Table 5*, Eq. 6).

The present study showed how anatomical features of xylems in *H. ammodendron* responded to climatic factors. The xylem responded to more arid conditions by increasing the dR and hR to improve water and starch storage. The xylem increased in both dV and wtV to account for both efficiency and safety in the xylem, which did not support the suggestion of a trade-off between efficiency and safety (Plavcová and Hacke, 2012; Hajek et al., 2016). The plants responded to the low temperature in January and strong winds from April to June by increasing wtF. These results indicate that there is high plasticity of xylem characteristics in *H. ammodendron* in response to different desert environmental conditions, explaining the adaptation of this plant to a wide geographical range across Asian and African deserts.

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