

Sap flow characteristics and physiological adjustments of two dominant tree species in pure and mixed plantations in the semi-arid Loess Plateau of China Postprint

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Date: 2018-10-29T00:00:00+00:00

Abstract

It is essential to understand the water consumption characteristics and physiological adjustments of tree species under drought conditions, as well as the effects of pure and mixed plantations on these characteristics in semi-arid regions. In this study, the normalized sap flow (SF_n), leaf water potential, stomatal conductance (gs), and photosynthetic rate (Pr) were monitored for two dominant species, i.e., *Pinus tabuliformis* and *Hippophae rhamnoides*, in both pure and mixed plantations in a semi-arid region of Chinese Loess Plateau. A threshold-delay model showed that the lower rainfall thresholds (RL) for *P. tabuliformis* and *H. rhamnoides* in pure plantations were 9.6 and 11.0 mm, respectively, and the time lags (τ) after rainfall were 1.15 and 1.76 d for corresponding species, respectively. The results indicated that *P. tabuliformis* was more sensitive to rainfall pulse than *H. rhamnoides*. In addition, strong stomatal control allowed *P. tabuliformis* to experience low gs and Pr in response to drought, while maintaining a high midday leaf water potential (Ψ_m). However, *H. rhamnoides* maintained high gs and Pr at a low Ψ_m expense. Therefore, *P. tabuliformis* and *H. rhamnoides* can be considered as isohydric and anisohydric species, respectively. In mixed plantation, the values of RL for *P. tabuliformis* and *H. rhamnoides* were 6.5 and 8.9 mm, respectively; and the values of τ were 0.86 and 1.61 d for corresponding species, respectively, which implied that mixed afforestation enhanced the rainfall pulse sensitivity for both two species, especially for *P. tabuliformis*. In addition, mixed afforestation significantly reduced SF_n, gs, and Pr for *P. tabuliformis* ($P < 0.05$), while maintaining a high leaf water potential status. However, no significant effect of mixed afforestation of *H. rhamnoides* was observed at the expense of leaf water potential status in response to drought. Although inconsistent physiological responses were adopted by these species, the altered water consumption characteristics, especially for

P. tabuliformis indicated that the mixed afforestation requires further investigation.

Full Text

Sap Flow Characteristics and Physiological Adjustments of Two Dominant Tree Species in Pure and Mixed Plantations in the Semi-arid Loess Plateau of China

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Abstract: Understanding water consumption characteristics and physiological adjustments of tree species under drought conditions, as well as the effects of pure versus mixed plantations on these characteristics, is essential in semi-arid regions. This study monitored normalized sap flow (SF_n), leaf water potential, stomatal conductance (gs), and photosynthetic rate (Pr) for two dominant species—*Pinus tabuliformis* and *Hippophae rhamnoides*—in both pure and mixed plantations in the semi-arid Chinese Loess Plateau. A threshold-delay model revealed that the lower rainfall thresholds (RL) for *P. tabuliformis* and *H. rhamnoides* in pure plantations were 9.6 mm and 11.0 mm, respectively, with time lags (τ) of 1.15 d and 1.76 d after rainfall. These results indicated that *P. tabuliformis* was more sensitive to rainfall pulses than *H. rhamnoides*. Strong stomatal control allowed *P. tabuliformis* to maintain low gs and Pr in response to drought while preserving high midday leaf water potential (Ψ_m). In contrast, *H. rhamnoides* maintained high gs and Pr at the expense of low Ψ_m . Therefore, *P. tabuliformis* and *H. rhamnoides* can be considered isohydric and anisohydric species, respectively. In mixed plantations, RL values were 6.5 mm and 8.9 mm for *P. tabuliformis* and *H. rhamnoides*, respectively, with τ values of 0.86 d and 1.61 d. This implied that mixed afforestation enhanced rainfall pulse sensitivity for both species, particularly for *P. tabuliformis*. Additionally, mixed afforestation significantly reduced SF_n, gs, and Pr for *P. tabuliformis* ($P < 0.05$) while maintaining high leaf water potential status, whereas no significant effect was observed for *H. rhamnoides* except at the expense of leaf water potential status in response to drought. Despite these inconsistent physiological responses, the altered water consumption characteristics—especially for *P. tabuliformis*—indicate that mixed afforestation requires further investigation.

Keywords: normalized sap flow; physiological adjustments; mixed afforestation; *Pinus tabuliformis*; *Hippophae rhamnoides*

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1 Introduction

Vegetation restoration and reforestation of degraded land are effective forest management practices for soil erosion conservation and hydrological regime regulation [?, ?]. By increasing biodiversity and ecological niche variety, mixed plantations may exhibit greater resistance to external disturbances such as storms or disease attacks compared to pure plantations [?, ?]. However, vegetation deterioration and ecological degradation have been observed in some mixed plantations because water supplies could not meet the demands of co-existing species, particularly in arid and semi-arid regions [?, ?]. Water shortage profoundly influences water consumption, plant hydraulic system integrity, and carbon assimilation [?, ?]. Therefore, improved understanding of water consumption and drought tolerance strategies of species grown in pure and mixed plantations is needed to evaluate the most appropriate tree species, planting regimes, and forest management practices that will effectively respond to climate uncertainties in the future [?].

Rainfall is essential for preventing plant mortality caused by drought [?]. Analyzing the effects of rainfall pulses on plant water consumption is fundamental to understanding species sensitivity to rainfall pulses and how these responses affect species adaptation to their habitats [?]. The threshold-delay model has been widely used to describe rainfall pulse effects on plant water consumption [?]. This model incorporates a threshold level of rainfall that stimulates plant water use and evaluates the time lags of tree and shrub responses [?, ?].

Plants undergo different physiological adjustments in the trade-off among water consumption, leaf water potential, and carbon gain to adapt to frequent drought stress [?, ?]. These adjustments include reliance on deep root systems [?], delayed stomatal closure [?], maintenance of high photosynthetic rates [?], and adjustments in leaf water potential [?]. The classification of isohydric and anisohydric species has been widely used to identify the balance between stomatal control, leaf water potential status, and carbon gain under drought conditions [?, ?]. Isohydric species experience smaller variations in leaf water potential through stomatal control regardless of carbon gain, whereas anisohydric species maintain stable carbon gain and stomatal conductance (gs) at the expense of leaf water potential [?]. However, Franks et al. [?] found that some anisohydric species, such as *Eucalyptus gomphocephala*, exhibit strong stomatal regulation under limited soil water conditions and show isohydrodynamic characteristics. Zapater et al. [?] attributed these altered physiological characteristics to a trade-off strategy between water consumption and carbon allocation, also relating it to root architecture systems. Research into water consumption and root systems, along with further investigation of physiological variables such as leaf water potential, stomatal control, and carbon gain, is needed to fully understand plant

strategies for drought tolerance.

To combat severe soil erosion and habitat degradation in the Chinese Loess Plateau, the government launched the “Grain-for-Green” project in the last decade, and plantations now occupy more than 59% of the region’s total forest area [?]. Due to their high drought tolerance and economic value, *Pinus tabulaeformis* and *Hippophae rhamnoides* are the main plantation species used for ecological restoration in this region [?]. Mixed afforestation with these two species has been widely employed during the initial plantation stage, as mixed plantations generally show higher plant survival rates and soil conservation capacity compared to pure plantations [?]. However, evapotranspiration far exceeds annual precipitation in the Loess Plateau, and this imbalance may become acute for plant growth [?, ?]. Seasonal variations in water consumption under drought conditions for *P. tabulaeformis* or *H. rhamnoides* in pure plantations have been investigated in this region [?, ?, ?], but physiological adjustments to drought and the effects of mixed afforestation on water consumption and physiological adjustments of these species have not been examined.

The year 2015 was the driest year recorded in the Loess Plateau, with only 58.9% of the average precipitation since 1988. For species selection and plantation management practices in this region, we examined variations in water consumption and physiological variables—including stem sap flow (SF), leaf water potential, g_s , and photosynthetic rate (Pr)—for 14-year-old planted *P. tabulaeformis* and *H. rhamnoides* in pure and mixed plantations in 2015. The objectives were to (1) investigate the rainfall pulse sensitivities and physiological adjustments of the two species under drought conditions in pure plantations, and (2) identify whether water consumption characteristics and physiological adjustments for specific species were altered in mixed plantations.

2.1 Study Area and Description of Plantations

The study was conducted at the Ansai Station of the Chinese Academy of Sciences (36.51°N, 109.19°E; 1231 m a.s.l.) in the central part of the Chinese Loess Plateau. The climate is temperate semi-arid, with mean annual precipitation of 492.7 (± 129.4) mm and annual mean air temperature of 10.4°C (± 0.5)°C, according to meteorological records during the period 1988–2015 in Ansai County. The loess in this region is characterized as silt loam with a depth of 50–190 m, depending on topography, with low organic carbon and nutrient contents [?].

Three adjacent plantations planted in 2002 were selected: a pure *P. tabulaeformis* plantation, a pure *H. rhamnoides* plantation, and a *P. tabulaeformis*-*H. rhamnoides* mixed plantation. A study plot of 20 m \times 20 m was established for each plantation type. The plantation densities in the pure *P. tabulaeformis* plantation and 10,000 stems/hm² in the pure *H. rhamnoides* plantation. The stem densities in the corresponding mixed plantations were 1111 and 3333 stems/hm², respectively.

According to a plot survey conducted in July 2015, the stem densities of *P. tabuliformis* and *H. rhamnoides* in pure plantations were 1175 and 1900 stems/hm², respectively. For *P. tabuliformis*, the average height was 3.39 (± 0.47)m, average trunk diameter at breast height (1.3m) was 59.5 (± 2.3)mm, and average canopy radius was 1.41 (± 0.1)m. For *H. rhamnoides*, the average height was 3.3 (± 0.58)m, average trunk diameter at ground height (0.3m) was 51.1 (± 1.1)mm, and average canopy radius was 1.81 (± 0.54)m in the pure *P. tabuliformis* plantation and 1.81 (± 0.54)m in the pure *H. rhamnoides* plantation, according to monthly monitored values using an LAI-2000 plant canopy analyzer (LI-Cor, Lincoln, Nebraska, USA). The dominant herbaceous species were *Glycyrrhiza uralensis* and *Bothriochloa ischaemum* in the pure *P. tabuliformis* and *H. rhamnoides* plantations, respectively.

In the mixed plantation, the stem densities of *P. tabuliformis* and *H. rhamnoides* were 850 and 1775 stems/hm², respectively. For *P. tabuliformis*, the average height was 3.68 (± 0.39)m, average trunk diameter was 62.7 (± 1.8)mm, and average canopy radius was 1.26 (± 0.29)m. For *H. rhamnoides*, the average height was 3.13 (± 0.47)m, average trunk diameter was 53.6 (± 1.9)mm, and average canopy radius was 1.81 (± 0.54)m in the mixed plantation. The dominant herbaceous species were *B. ischaemum* and *Artemisia gmelinii* in the mixed plantation.

2.2 Environmental Variables

Meteorological variables have been measured less than 400 m from the selected plantation plots since 1999. Half-hourly net radiation (Rn) (Model CNR-1, Kipp & Zonen Inc., Delft, The Netherlands), air relative humidity and temperature (HMP45C, Campbell Scientific Inc., Logan, UT, USA), rainfall amount (Model 52203, RM Young Inc., Traverse City, MI, USA), and soil heat flux (Model HFP01, Campbell Scientific Inc., USA) were measured and stored using a CR1000 datalogger (Campbell Scientific Inc., USA). Soil water content (SWC) was continuously monitored at depths of 10, 20, 50, 100, and 150 cm in the three plantation plots using EM50 (Decagon Inc., Pullman, WA, USA).

Daily potential evapotranspiration (ETP, mm) was calculated as follows [?]:

$$ETP = \frac{s}{s + \gamma} \cdot \frac{R_n - G}{\lambda}$$

where Rn and G are net radiation (W/m²) and soil heat flux (W/m²), respectively; s is the slope of a function relating saturation vapor pressure to temperature (kPa/K); and γ is the psychrometric constant (kPa/K).

2.3 Sap Flow Measurements

Using Granier-type thermal dissipation probes (TDP) following Granier (1987), SF was monitored in a total of 25 individuals of these species during the growing season from 5 June (DOY 156) to 26 September (DOY 269), 2015 (Table 1).

To preserve the monitored trees, we established the relationship between trunk diameter and sapwood width based on 20 unmonitored individual core samples for each species. Core samples were obtained using an increment borer, and the color difference between sapwood and heartwood was distinct.

In the pure plantation, 7 individuals of *P. tabuliformis* were selected with trunk diameters of 42–65 mm and canopy radii of 1.01–1.56 m. Six individuals were selected for *H. rhamnoides* with trunk diameters of 36–63 mm and canopy radii of 0.84–1.17 m. In the mixed plantation, it was important to select *H. rhamnoides* individuals adjacent to selected *P. tabuliformis* individuals, as one objective was to identify the mixed plantation effect on water consumption and physiological adjustments for these two species. First, we selected 6 individuals of *P. tabuliformis* with trunk diameters of 43–70 mm and canopy radii of 1.18–1.48 m. Each *H. rhamnoides* was selected within 2 m of a *P. tabuliformis* trunk, creating 6 pairs (Fig. S1). The 6 selected *H. rhamnoides* individuals had trunk diameters of 38–67 mm and canopy radii of 0.89–1.24 m. The 2-m radius was used to ensure potential interactions between *P. tabuliformis* and *H. rhamnoides* individuals. In our earlier work, we showed that the majority of lateral roots for *P. tabuliformis* and *H. rhamnoides* extended twice the distance of the corresponding canopy radius. The minimum canopy radius for selected *P. tabuliformis* individuals was 1.18 m; therefore, we calculated that the minimum radius of the majority of lateral roots was approximately 2.36 m.

A pair of TDPs with diameters of 10 mm and 2 mm was used for both *P. tabuliformis* and *H. rhamnoides*, respectively. The probes were uniformly and horizontally installed on the north side of the trunks at breast and ground heights for selected *P. tabuliformis* and *H. rhamnoides* individuals. The probes were packaged in aluminum foil to prevent thermal influences from ambient environmental variation. SF data were measured at 30-s intervals and stored as half-hour averages using a CR1000 data logger (Campbell Scientific Inc., USA) with an AM16/32A multiplexer (Campbell Scientific Inc., USA).

The standard sap flux density (F_d , $\text{g}/(\text{m}^2 \cdot \text{s})$) can be calculated according to the equation suggested by Granier (1987):

$$F_d = 119 \cdot \left(\frac{\Delta T_M - \Delta T}{\Delta T} \right)^{1.231}$$

where ΔT_M is the maximum temperature ($^{\circ}\text{C}$) and ΔT is the temperature difference between unheated and heated probes ($^{\circ}\text{C}$).

The probe length was longer than the sapwood thickness of some sampled trees. To avoid underestimation of F_d , we used corrected values (ΔT_C) rather than measured values (ΔT) in these trees [?]:

$$\Delta T_C = \frac{\Delta T - (1 - a) \cdot \Delta T'_M}{a}$$

where ΔT_C and $\Delta T'_M$ are the actual temperature differences between heated and unheated probes in the conductive sapwood and in the inactive xylem ($^{\circ}\text{C}$), respectively; a is the length ratio of sapwood to probe; and $\Delta T'_M$ is equal to ΔT_M in Equation 2.

As F_d values are correlated with whole-tree water consumption [?], this value was used as an index to evaluate variations in transpiration. In addition, species-specific calibration has been suggested [?], and the underestimated value with the thermal dissipation method should be considered when Granier-type probe data are used for whole-tree water consumption calculation [?]. Therefore, normalized F_d (SFn) rather than whole-tree water consumption was used for diurnal and daily variation analyses as suggested by Du et al. (2011). The SFn was calculated by dividing all F_d values for each replicate tree by the maximum during the observation period. Each replicate tree had a maximum SFn of 1, and the average normalized SFn was calculated among replicates within species.

Table 1 Biometric variables of monitored species, including tree height, trunk diameter at breast or ground height, sapwood width, and canopy radius for *P. tabuliformis* and *H. rhamnoides* in both pure and mixed plantations .

2.4 Investigation of Root Systems

In July 2015, 3 individual trees of *P. tabuliformis* and *H. rhamnoides* with approximately average trunk diameter and canopy radius (standard individuals) were selected around each of 3 corresponding research plantations for whole-plant root excavation. In the pure plantation, the average canopy radius for standard individuals of *P. tabuliformis* and *H. rhamnoides* was $1.38 (\pm 0.15)\text{m}$ and $0.92 (\pm 0.09)\text{m}$, respectively. In the mixed plantation, the average canopy radius for standard individuals of *P. tabuliformis* and *H. rhamnoides* was $1.19 (\pm 0.08)\text{m}$ and $0.9 (\pm 0.11)\text{m}$, respectively. Therefore, the corresponding radius of the majority of lateral roots was approximately 2.76 m and 1.84 m for *P. tabuliformis* and *H. rhamnoides* in pure plantations, respectively, and approximately 2.38 m and 1.80 m for *P. tabuliformis* and *H. rhamnoides* in mixed plantations, respectively. The 3-m radius and 2-m depth for root excavations captured the majority of lateral and vertical roots for each selected standard individual. A spade was used to dig up the roots at 10-cm depth intervals, starting from the plant trunk to the edge of the plant canopy. Fine roots (diameter < 2 mm) were manually selected, and their surface area was calculated for each 10 cm of the depth profile using WinRHIZO (Regent Instruments Inc., Quebec, Canada).

2.5 Leaf Water Potential, Stomatal Conductance, and Photosynthetic Rate Measurements

We examined leaf water potential, g_s , and Pr in 16 of the 25 SF-monitored individuals (4 individuals per species in each plantation) at midday (11:00-14:00 LST) three times per month from June to September 2015 (Table 1). Three well-expanded leaves were selected from each monitored individual. A LI-6400 analyzer (Li-Cor Inc., USA) was used to measure g_s and Pr under approximately natural conditions [?]. In addition, predawn leaf water potential (Ψ_{pd} , 05:00-06:00) and midday leaf water potential (Ψ_m , 11:00-14:00) were measured on nearby leaves on the same individual used for g_s and Pr measurements with a PMS-1515D analyzer (PMS Instrument, Corvallis, OR, USA).

2.6 Threshold-Delay Model

The threshold-delay model suggests that upper and lower precipitation thresholds stimulate plant water consumption [?]. This model incorporates the duration of rainfall pulses and the speed of plant response [?]:

$$y_t = y_{t-1} + (\delta_t - \delta_{t-1}) \cdot \frac{R_{t-\tau} - R_L}{R_U - R_L} \cdot (y_{max} - y_{t-1}) - k \cdot (y_{t-1} - y_{min})$$

where y_t is the SFn in this study; y_{t-1} is the antecedent SFn; y_{max} is the maximum response SFn; δ_t , δ_{t-1} , and δ_{max} are the potential, actual, and maximum potential response parameters, respectively; R_U and R_L are the upper and lower rainfall thresholds (mm), respectively; $R_{t-\tau}$ is the effective rainfall amount (mm); τ is the time lag when significant increases in SFn were observed after $R_{t-\tau}$ (d); k is the reduction rate (d^{-1}); and t is the response time (d).

After testing for normal distribution and homogeneity of variance, we identified the rainfall threshold through one-way analysis of variance (ANOVA) and Tukey's HSD test. The threshold-delay model was then calculated by multiple linear regression [?].

2.7 Statistical Analysis

Relative response in daily SFn was calculated as $(X_{max} - X_{before}) / X_{before} \times 100\%$, where X_{before} and X_{max} represent the SFn from the first day before rainfall and the maximum SFn after rainfall, respectively. Significant relative changes in SFn for *P. tabuliformis* in pure and mixed plantations and *H. rhamnoides* in pure and mixed plantations in response to rainfall were identified through ANOVA and Tukey's HSD test after testing for normal

distribution and homogeneity of variance. Rainfall classes of 0–5, 5–10, and >15 mm were used for significance testing; the 10–15 mm class was not used because only 11 mm of rainfall (DOY 222–226) was observed during the study period.

Significant differences in SFn, leaf water potential, gs, and Pr between species in pure and mixed plantations were identified by independent samples t-test after testing for normality and homogeneity of variances. We also evaluated the effects of mixed afforestation on SFn, leaf water potential, gs, and Pr through independent samples t-test based on significant difference analyses of these variables for specific species in pure and mixed plantations.

Additionally, the relationship between Ψ_{pd} and corresponding maximum SFn has been used to assess the effect of stomatal control on hydraulic characteristics [?]. The significant difference in the slope of SFn and Ψ_{pd} linear regression can be tested through a General Linear Model (GLM) [?]. SPSS 18.0 was used for all statistical and regression analyses (SPSS Inc., Chicago, IL, USA), and the significance level was set at $P < 0.05$.

3.1 Variation of Environmental Variables

There was 120.8 mm of rainfall during the observation period (DOY 156–269), which was the lowest value since 1988 and accounted for 33.8% of the mean annual precipitation amount between 1988 and 2014 for the corresponding period. Although rainfall gradually increased during the later observation period (Fig. 1a [Figure 1: see original paper]), the daily average rainfall (1.1 ± 2.4 mm/d) represented only 8.4% of the corresponding ETP. This lack of sufficient rainfall and high water demand may have resulted in drought stress for these studied plantations, according to the monthly variation of Budyko's aridity index (Table 2).

The SWC at 10 cm depth showed the largest fluctuation with rainfall (Fig. 1; Table 3), while SWCs at 100 cm and 150 cm depths gradually decreased during the observation period for all three plantations, suggesting that rainfall had less effect on SWC in deep soil. The highest daily averaged SWCs were observed at 50 cm depth for the pure *P. tabuliformis* plantation, 100 cm depth for the pure *H. rhamnoides* plantation, and 150 cm depth for the mixed plantation. The lowest daily averaged SWCs also experienced the smallest coefficient of variation (CV) for each plantation, occurring at 150 cm depth for the pure *P. tabuliformis* plantation, 20 cm depth for the pure *H. rhamnoides* plantation, and 50 cm depth for the mixed plantation (Table 3).

Fig. 1 Daily variation of environmental variables from DOY 156 to 269 (5 June–26 September). (a) Rainfall amount (P) and potential evapotranspiration (ETp); soil water content (SWC) at depths of 10, 20, 50, 100, and 150 cm (SWC10, SWC20, SWC50, SWC100, and SWC150) in (b) pure *P. tabuliformis* plantation,

(c) pure *H. rhamnoides* plantation, and (d) mixed plantation. Vertical arrows in Figure 1a indicate leaf water potential, gs (stomatal conductance), and Pr (photosynthetic rate) observation dates [Figure 1: see original paper].

3.2 Daily and Diurnal Variations in SFn and Responses to Rainfall

Daily SFn for *P. tabuliformis* and *H. rhamnoides* in pure plantations generally exhibited a decreasing trend during the observation period, whereas daily SFn for both species in mixed plantations exhibited a “U-shaped” pattern, with higher values occurring in June and September (Fig. 2 [Figure 2: see original paper]). The variation of daily SFn for *P. tabuliformis* in pure plantation was significantly different ($t = 4.95$, $P < 0.01$, $df = 226$) from that for the same species in mixed plantation. However, there was no significant difference ($t = 1.95$, $P = 0.053$, $df = 226$) in daily variation of SFn for *H. rhamnoides* between pure and mixed plantations.

Generally, the relative response of SFn for both species significantly increased ($P < 0.05$, $df = 2$) across three rainfall classes in both pure and mixed plantations (Fig. 3 [Figure 3: see original paper]), when the 10–15 mm class was excluded. However, no significant difference was observed either between rainfall classes of 5–10 mm and >15 mm for *P. tabuliformis* in pure plantation ($P = 0.09$, $df = 7$), or between rainfall classes of 0–5 mm and 5–10 mm for *H. rhamnoides* in pure plantation ($P = 0.14$, $df = 7$). Moreover, the CVs of SFn for *P. tabuliformis* and *H. rhamnoides* in pure plantation were 39.1% and 37.59%, respectively, and were 43.64% and 36.58% for the corresponding species in mixed plantation, respectively (Table 4).

Figures 4 show the diurnal variation of SFn. Values of SFn for *P. tabuliformis* and *H. rhamnoides* in pure plantations increased from a minimum at midnight to a maximum at noon, exhibiting a unimodal curve (Figs. 4a and c). In pure plantation, the half-hourly average SFn values for *P. tabuliformis* and *H. rhamnoides* after rainfall increased from $0.27 (\pm 0.26)$ to $0.32 (\pm 0.30)$ and from $0.24 (\pm 0.23)$ to $0.35 (\pm 0.33)$, respectively. The SFn for *P. tabuliformis* in mixed plantation followed a similar diurnal variation as that in pure plantation. However, *H. rhamnoides* in mixed plantation showed a bimodal curve before rainfall and a unimodal curve after rainfall (Fig. 4d [Figure 4: see original paper]). Furthermore, the half-hourly average SFn values for *P. tabuliformis* and *H. rhamnoides* in mixed plantation after rainfall increased from $0.23 (\pm 0.24)$ to $0.3 (\pm 0.31)$ respectively.

Fig. 2 Variation of daily normalized sap flow (SFn). (a) *P. tabuliformis* and (b) *H. rhamnoides* in both pure and mixed plantations during DOY 156–269 (5 June to 26 September). Error bars indicate the standard deviation [Figure 2: see original paper].

Fig. 3 Relative response of SFn to rainfall class. Error bars indicate the

standard deviation. Lowercase letters indicate a significant difference in daily SFn responses among rainfall classes for the specific species in pure or mixed plantation. The ANOVA test parameters for relative response of SFn among three rainfall classes (0–5, 5–10, and >15 mm) are also presented. The rainfall class of 10–15 mm was not used for the significance test [Figure 3: see original paper].

The lower rainfall thresholds for *P. tabuliformis* and *H. rhamnoides* in pure plantation were 9.6 mm and 11.0 mm, respectively, and the values for corresponding species in mixed plantation were 6.5 mm and 8.8 mm, respectively, based on the threshold-delay model (Table 5). The upper rainfall thresholds for *P. tabuliformis* and *H. rhamnoides* in pure plantation were 16.7 mm and 20.9 mm, respectively, and the values for corresponding species in mixed plantation were 19.6 mm and 22.1 mm, respectively. The lag times after an effective rainfall event were 1.15 d and 1.76 d for *P. tabuliformis* and *H. rhamnoides* in pure plantation, and 0.86 d and 1.61 d for corresponding species in mixed plantation, respectively.

3.3 Variation of Leaf Water Potential and Relationship Between Ψ_{pd} and Maximum SFn

In both pure and mixed plantations, Ψ_{pd} and Ψ_m for *P. tabuliformis* and *H. rhamnoides* generally exhibited a “U-shaped” pattern, with higher values occurring in June and September (Fig. 5 [Figure 5: see original paper]). Increased Ψ_m was also observed for *H. rhamnoides* in pure and mixed plantations during DOY 171–174. Both in pure ($t = 0.55$, $P = 0.59$, $df = 22$) and mixed ($t = 1.88$, $P = 0.74$, $df = 22$) plantations, Ψ_{pd} did not significantly differ between *P. tabuliformis* and *H. rhamnoides*. However, in both pure ($t = 2.2$, $P < 0.05$, $df = 22$) and mixed ($t = 5.41$, $P < 0.001$, $df = 22$) plantations, Ψ_m in the former species was significantly higher than in the latter.

Mixed afforestation did not significantly affect Ψ_{pd} ($t = 0.40$, $P = 0.7$, $df = 22$) or Ψ_m ($t = 0.74$, $P = 0.47$, $df = 22$) for *P. tabuliformis*; however, it significantly decreased Ψ_{pd} ($t = 2.26$, $P < 0.05$, $df = 22$) and Ψ_m ($t = 2.85$, $P < 0.01$, $df = 22$) for *H. rhamnoides*. Furthermore, mixed afforestation enhanced the CVs of Ψ_{pd} for both *P. tabuliformis* and *H. rhamnoides*, but had less effect on the CVs of Ψ_m for these species (Table 4).

In pure and mixed plantations, there were no significant relationships between Ψ_{pd} and maximum SFn for *H. rhamnoides*; however, maximum SFn gradually dropped with decreasing Ψ_{pd} for *P. tabuliformis* in these plantations (Table 6). Additionally, mixed afforestation significantly offset the sensitivity of maximum SFn to Ψ_{pd} for *P. tabuliformis* ($F = 5.78$, $P < 0.05$, $df = 1$), suggesting that this species in mixed plantation experienced stronger stomatal control on water consumption than in pure plantation.

Fig. 5 Variation of predawn (Ψ_{pd}) and midday leaf water potential (Ψ_m). (a) *P. tabuliformis* in pure plantation, (b) *P. tabuliformis* in mixed plantation, (c) *H. rhamnoides* in pure plantation, and (d) *H. rhamnoides* in mixed plantation during DOY 156-269 (5 June-26 September). Error bars indicate the standard deviation [Figure 5: see original paper].

Table 6 Maximum SFn as a function of predawn leaf water potential (Ψ_{pd}) for *P. tabuliformis* and *H. rhamnoides* in pure and mixed plantations .

3.4 Variation of gs and Pr

In pure and mixed plantations, gs and Pr for *P. tabuliformis* and *H. rhamnoides* exhibited similar variation to leaf water potential, with higher values occurring in June and September (Fig. 6 [Figure 6: see original paper]). Increased gs was observed for *H. rhamnoides* in pure and mixed plantations during DOY 171-174. Increased Pr was also observed for *P. tabuliformis* in pure and mixed plantations and for *H. rhamnoides* in pure plantation during DOY 171-174. In pure plantation, both gs and Pr for *H. rhamnoides* were significantly higher ($t = 2.15$, $P < 0.05$, $df = 22$ and $t = 2.17$, $P < 0.05$, $df = 22$, respectively) than the corresponding values for *P. tabuliformis*. In mixed plantation, both gs and Pr for *H. rhamnoides* were also significantly higher ($t = 3.47$, $P < 0.05$, $df = 22$ and $t = 3.7$, $P < 0.01$, $df = 22$, respectively) than the corresponding values for *P. tabuliformis* (Fig. 6).

Moreover, mixed afforestation significantly decreased both gs ($t = 2.96$, $P < 0.01$, $df = 22$) and Pr ($t = 3.04$, $P < 0.01$, $df = 22$) for *P. tabuliformis*, but had no significant effect on gs ($t = 1.72$, $P = 0.10$, $df = 22$) and Pr ($t = 1.51$, $P = 0.15$, $df = 22$) for *H. rhamnoides*. In addition, mixed afforestation enhanced the CVs of gs and Pr for *P. tabuliformis*, but had less effect on the corresponding values for *H. rhamnoides* (Table 4).

Fig. 6 Variations of stomatal conductance (gs) and photosynthetic rate (Pr). *P. tabuliformis* in (a) pure and (c) mixed plantations, *H. rhamnoides* in (b) pure and (d) mixed plantations during DOY 156-269 (5 June-26 September). Error bars indicate the standard deviation [Figure 6: see original paper].

4.1 Sap Flow Characteristics and Its Response to Rainfall in Pure Plantations

Similar to other studies in semi-arid regions [?, ?], the differential SFn response to rainfall pulses for *P. tabuliformis* and *H. rhamnoides* indicated that sap flow response to rainfall pulses under drought was species-dependent. Previous studies indicated that coniferous species usually exhibited strong self-regulation to maintain water consumption under drought conditions and were more sensitive

to rainfall than broad-leaved species [?, ?, ?]. Moreover, the SFn response to rainfall pulses also depends on both rainfall characteristics [?] and other environmental conditions, such as drought extent [?]. Large rainfall events may relieve drought conditions, while small rainfall amounts may only wet the plant surface [?]. Previous studies in shrubs [?] and trees [?] reported that 5.0 mm was the threshold rainfall amount to effectively influence water consumption in the Loess Plateau. However, 9.6 mm and 11.0 mm were required as the lowest rainfall amounts to significantly increase SFn for *P. tabuliformis* and *H. rhamnoides* in pure plantations, respectively, which may be attributed to severe drought stress because rainfall in 2015 was the lowest since 1988 (Fig. 2). Zhao and Liu (2010) and Jian et al. (2016) also suggested that 13.0 mm was the upper rainfall threshold affecting plant water consumption in the Chinese Loess Plateau. However, 16.7 mm and 20.9 mm were required as the upper rainfall amounts for *P. tabuliformis* and *H. rhamnoides*, respectively, which may also be attributed to severe drought stress.

Moreover, diverse root vertical distribution explained the different species responses to rainfall events [?, ?]. For example, shallow-rooted *Hibbertia hypericoides* responded rapidly to rainfall pulses, whereas deep-rooted *Banksia ilicifolia* did not respond to rainfall even when it reached 10.0 mm [?]. In the studied pure plantations, more fine roots distributed in the upper soil layer of *P. tabuliformis* could partially explain its shorter time response ($\tau = 1.15$ d) to rainfall compared with *H. rhamnoides* ($\tau = 1.76$ d; Fig. 7 [Figure 7: see original paper]). The higher R_U, smaller R_L, and shorter τ for *P. tabuliformis* indicated that this species experienced high water demand and was more sensitive to rainfall pulses than *H. rhamnoides*. These results are consistent with studies in the hilly region of the Chinese Loess Plateau by Wen et al. (2017), which suggested that *P. tabuliformis* was more sensitive to rainfall than *H. rhamnoides* by comparing the relative response of diurnal variation in transpiration before and after rainfall. Furthermore, the anatomical structure of xylem needs further analysis to better understand the water demand and rainfall pulse responses of each species [?].

Fig. 7 Vertical distribution of surface area of fine root (diameter < 2 mm) for *P. tabuliformis* and *H. rhamnoides* in (a) pure and (b) mixed plantations. Error bars indicate the standard deviation [Figure 7: see original paper].

4.2 Trade-off Between Stomatal Control, Leaf Water Potential, and Photosynthesis in Pure Plantations

Previous studies suggested that contrasting hydraulic traits among species under identical weather conditions probably resulted from both water uptake capacity [?] and their optimized trade-off between carbon gain and water loss through photosynthesis [?]. Ψ_{pd} can substitute for soil water potential in contact with the roots [?]. Although there was no significant difference in Ψ_{pd}

between these two species, significantly ($P < 0.05$) higher Ψ_m was observed for *P. tabuliformis* than for *H. rhamnoides*. These results indicated that the former species maintained stable water status to avoid embolism damage and protect the water-conducting system.

In the studied pure plantations, the observed decrease in maximum SFn with decreasing Ψ_{pd} for *P. tabuliformis* was consistent with the hypothesis of Meinzer et al. (1999), who stated that high hydraulic constraints and water demand can lead to strong stomatal limitations on photosynthesis and transpiration. In contrast, no significant relationship between maximum SFn and Ψ_{pd} was observed for *H. rhamnoides*, indicating weak stomatal limitation on transpiration and photosynthesis for this species. Xu et al. (2011) suggested that high concentrations of osmotically active substances in *H. rhamnoides* allowed wide osmotic adjustment and maintenance of stable leaf cell turgor pressure, thus enabling stomatal opening and photosynthesis maintenance. Moreover, similar to *P. deulsis* [?] and *Virola michelii* [?], *P. tabuliformis* can be considered an isohydric species that adequately maintains Ψ_m through strong stomatal limitation, with low g_s and P_r during drought. In contrast, *H. rhamnoides* can be considered an anisohydric species that maintains g_s and P_r at the expense of low Ψ_m . Similar physiological adjustments were observed in *Juniperus osteosperma* [?] and *E. grandis* [?].

4.3 Mixed Afforestation Effects on *P. tabuliformis* and *H. rhamnoides*

Facilitative interactions related to water resources can lead to stable co-existence, whereas competition for water resources may induce species exclusion [?]. Co-existing species in natural forests usually exhibit different physiological or morphological adjustments to minimize competition for water during prolonged drought periods [?, ?]. This facilitative interaction has also been observed among species in plantations even in seasonal drought or semi-arid water-limited regions [?, ?]. For example, Zhang et al. (2017) suggested that the dense canopy cover of *P. tabuliformis* can reduce soil water evaporation in surface layers, which may benefit co-existing species such as *Platycladus orientalis* in the dryland Loess Plateau of China. However, in the semi-arid Loess Plateau of China in the present study, although contrasting physiological adjustments of *P. tabuliformis* and *H. rhamnoides* were observed in mixed plantations (Figs. 5 and 6), mixed afforestation significantly altered SFn characteristics and rainfall pulse sensitivity in *P. tabuliformis*. Mixed afforestation reduced R_L and τ for *P. tabuliformis* by 32.3% and 25.2%, respectively. However, the effect of mixed plantation only reduced the corresponding values of R_L and τ by 19.1% and 8.5% for *H. rhamnoides* (Table 5). In addition, mixed plantation increased R_U by 26.3% and 13.2% for *P. tabuliformis* and *H. rhamnoides*, respectively. Previous studies also indicated that, compared with isohydric species, anisohydric species such as

Acer saccharum and *E. gomphocephala* may be more suitable for drought-prone habitats [?, ?]. However, under prolonged drought and reduced precipitation input, anisohydric species may experience xylem embolism or even mortality [?], while isohydric species may suffer from carbon starvation [?]. The threshold value of leaf water potential causing 100% stem cavitation for *P. tabuliformis* and the carbon gain required to avoid carbon starvation for *H. rhamnoides* need further investigation to assess the drought adaptive capacity of these two species.

Competition among co-occurring species may be apparent through root morphology characteristics such as fine root system architecture [?, ?]. Although accurate water sources were not analyzed using stable isotopes in the present study, overlap in root distribution of co-occurring species may result in water competition [?]. In response to prolonged drought in desert regions, *H. rhamnoides* also exhibited root morphology plasticity [?]. In the studied mixed plantation, *H. rhamnoides* developed more shallow roots and a root distribution similar to *P. tabuliformis*, especially in the upper 40 cm of soil (Fig. 7). West et al. (2007) suggested that shallow roots may maximize water extraction before it is lost to evaporation and maximize nutrient uptake, as nutrient concentrations are highest near the soil surface. Indeed, the total nitrogen (0.53%) and phosphorus (0.04%) contents at 0–40 cm soil depth were 2.20 and 1.97 times greater than those at 40–100 cm soil depth. Thus, *H. rhamnoides* and *P. tabuliformis* in mixed plantation may have competed for limited water and nutrient reserves. Therefore, competition for both water and nutrients should be further investigated to adequately evaluate mixed afforestation of these species.

5 Conclusions

This study demonstrated that *H. rhamnoides* and *P. tabuliformis* adopted contrasting strategies to cope with drought in 2015. Compared with *H. rhamnoides*, *P. tabuliformis* was more sensitive to rainfall pulses in pure plantation. *P. tabuliformis* displayed isohydric behavior through strong stomatal limitation, while *H. rhamnoides* displayed anisohydric behavior. Mixed afforestation enhanced rainfall pulse sensitivity and water demand for *P. tabuliformis*. However, mixed afforestation did not significantly affect the rainfall pulse sensitivity of *H. rhamnoides* except at the expense of decreased leaf water potential status. Therefore, the mixed afforestation of these two species should be further considered for “Grain-for-Green” projects in this region.

Acknowledgments

This research was supported by the National Key R&D Program of China (2017YFA0604801), the National Natural Science Foundation of China

(41501576), the China Special Fund for Meteorological Research in the Public Interest (Major Projects) (GYHY201506001-3), and the Fundamental Research Funds for the Central Universities (2452016105).

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Supplementary Figure

Fig. S1 Schematic of the local neighborhood for 6 pairs of selected *P. tabuliformis* and *H. rhamnoides* individuals in mixed plantation. A distance of 2 m was measured from the center of the trunk to the edge of the canopy for each *P. tabuliformis* individual, and the numbers (1-6) around each *P. tabuliformis* individual correspond to the same tree individual numbers in Table 1 for the mixed plantation.

Note: Figure translations are in progress. See original paper for figures.

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