Differential response of plant water consumption to rainwater uptake for dominant tree species in the semiarid Loess Plateau

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Abstract Whether uptake of rainwater can increase plant water consumption in response to rainfall

15 pulses requires investigation to evaluate the plant adaptability, especially in water limited regions where rainwater is the only replenishable soil water source. In this study, the water sources from rainwater and three soil layers, predawn (Ψ_{pd}), midday (Ψ_m) and gradient ($\Psi_{pd}-\Psi_m$) of leaf water potential, and water consumption in response to rainfall pulses were analyzed for two dominant tree species, *Hippophae rhamnoides* and *Populus davidiana*, in pure and mixed plantations during the growing period (June–

20 September). In pure plantations, the relative response of daily normalized sap flow (SF_R) was significantly affected by rainwater uptake proportion (RUP) and $\Psi_{pd}-\Psi_m$ for *H. rhamnoides*, and was only significantly influenced by $\Psi_{pd}-\Psi_m$ for *P. davidiana* ($P < 0.05$). Meanwhile, the large $\Psi_{pd}-\Psi_m$ was consistent with high SF_R for *H. rhamnoides*, and the small $\Psi_{pd}-\Psi_m$ was consistent with the low SF_R for *P. davidiana*, in response to rainfall pulses. Therefore, *H. rhamnoides* and *P. davidiana* exhibited

25 sensitive and insensitive responses to rainfall pulses, respectively. Furthermore, mixed afforestation significantly enhanced RUP, SF_R, and reduced the water source proportion from the deep soil layer

(100–200 cm) for both species (P < 0.05). The SF_R was significantly influenced by RUP and $\Psi_{pd}-\Psi_m$ for both species in the mixed plantation. Lower Ψ_m and higher Ψ_{pd} were adopted by *H. rhamnoides* and *P. davidiana* in mixed plantation, respectively, to enlarge $\Psi_{pd}-\Psi_m$, enhance rainwater uptake, and decrease water source competition from the deep soil layer. These results indicate that mixed afforestation enhanced the influence of rainwater uptake to water consumption after rainfall pulse, regardless of sensitivity to rainfall pulses. This study provides insights into suitable plantation species selection and management considering the link between rainwater uptake and consumption in water limited regions.

Keywords: Leaf water potential; Loess Plateau; Plant water consumption; Rainwater uptake; Water stable isotope

1 Introduction

Rainwater uptake by plant and water consumption in response to rainfall pulses drive the survival of plant species and ecosystem ecohydrological processes, especially in arid and semiarid regions where rainwater is the only replenishable soil water source (Berkelhammer et al., 2020; Gebauer and Ehleringer, 2000; West et al., 2012). Generally, rainwater uptake is refers to the uptake of rainwater by plant roots, and plant water consumption is refers to the absorbed water transported to leaves through stems for transpiration, and can be quantified through water stable isotope and thermal dissipation methods, respectively (Meier et al., 2018; Tfwala et al., 2019; Zhang et al., 2019). The variability and intermittency of rainfall, which plays an important role in plant water uptake and consumption (Swaffer et al., 2014; Wang et al., 2020), have been predicted to increase in water limited regions (Klein et al., 2014; Mendham et al., 2011). Clarifying the influence of rainwater uptake to plant water consumption after rainfall pulses is essential to understand the process of plant species adaptation in water limited regions (Meier et al., 2018; Tfwala et al., 2019).

Rainwater uptake by plant is expected to increase water consumption after a rainfall pulse (Cheng et al., 2006; Liu et al., 2019; Xu et al., 2012). However, the uptake of rainwater may also be mainly used to reduce the water uptake from deep soil layers or decrease the risk of cavitation in stems for some

plant species (Plaut et al., 2013; Tfwala et al., 2019). The controversial rainfall pulse response between

55   water uptake and consumption may be mainly attributed to an inconsistent influence of plant leaf

physiological characteristics (West et al., 2007), root morphology adjustment (Wang et al., 2020), or

environmental conditions (Tfwala et al., 2019) on these two water processes. Generally, water

consumption is observed to increase after rainfall pulses for plants with shallow (Liu et al., 2019) or

dimorphic root systems (Swaffer et al., 2014); meanwhile, no increase or a decrease in water

60   consumption is observed for plants with deep rooting systems (West et al., 2012). However, regardless

of the root distribution, the plant leaf water potential gradient (the difference between predawn (Ψ_{pd})

and midday (Ψ_{m}) leaf water potential) has been observed to regulate water consumption after rainfall

pulses (De Guzman et al., 2016; Liu et al., 2019). Thus, taking into consideration plant leaf

physiological or root morphological parameters could help in understanding the mechanisms underlying

65   the influence of rainwater uptake on plant water consumption in response to rainfall pulses.

Uptaking contrasting water sources between coexisting species usually shows water source separation

and can minimize water source competition (Munoz-Villers et al., 2020; Silvertown et al., 2015);

however, overlapping water sources among plant species may lead to competition in arid and semiarid

regions (Tang et al., 2019; Yang et al., 2020). Rainfall pulses have been observed to relieve or eliminate

70   water competition and thus maintain or increase plant water consumption in some water limited regions

(Du et al., 2011; Tfwala et al., 2019). Meanwhile, plant species with strong rainwater uptake ability

generally exhibit more competitiveness than coexisting weak rainwater uptake ability species (Stahl et

al., 2013; West et al., 2012). However, Liu et al. (2019) attribute opposite rainwater uptake ability to the

stable coexistence of species in mixed plantations in semiarid regions, where the rainfall events are

75   variable and less rainwater is uptake by one of the coexisting plant species. In addition, coexisting

species may also cope with or minimize water resource competition through plant leaf water potential or

root distribution adjustment (Chen et al., 2015; Silvertown et al., 2015). It is still unclear whether these

adjustments could influence the rainwater uptake and water consumption for coexisting species in water

limited regions.

80   The "Grain for Green project" has increased vegetation coverage by 25% in the Loess Plateau

through afforestation activities since the 1990s, to deal with vegetation degradation and water and soil loss (Tang et al., 2019; Wu et al., 2021). *Hippophae rhamnoides* and *Populus davidiana* are typical dominant tree species, with high survival rate and drought tolerance, and occupy nearly 30% of the plantation area in this region (Liu et al., 2017; Tang et al., 2019). In addition to *H. rhamnoides* and *P.*

85 *davidiana* pure plantations, mixed plantations of these two species were also widely promoted due to the higher soil and water conservation capacity than pure plantations in the original afforestation stage (Tang et al., 2019; Wang et al., 2020). Rainwater has obvious seasonal variability and is the only replenished soil water source in this region because of the soil is approximately 100 m deep (Li et al., 2016; Zhang et al., 2017). The imbalance between rainwater input and plant water demand may weaken

90 the sustainability of plantations with further plant growth (Jia et al., 2020; Wu et al., 2021). Previous investigations in the region quantified the water sources from different soil depths (Wang et al., 2020; Wu et al., 2021) and characterized the water consumption (Zhang et al., 2017) during drought stress periods for plantation species in pure plantations. To understand the adaptation of plantation species in this study, the water consumption, water sources from rainwater and different soil layers, and plant leaf

95 water potential for *H. rhamnoides* and *P. davidiana* in pure and mixed plantations were analyzed. The specific objectives were as follow: (1) to investigate the influence of rainwater uptake and leaf water potential on water consumption after rainfall events, and (2) to assess the mixed afforestation effect on these influences.

100 **2 Materials and methods**

2.1 Study site

The study was conducted in the Ansai Ecological Station in the semiarid Loess Plateau (36.55 °N, 109.16 °E), Northern China. The study area has a semiarid continental climate. The annual average (mean ± SD) rainfall amount and air temperature are 493.1 ± 127.9 mm and 10.7 ± 0.5 °C (1985–2017),

105 respectively. The soil is characterized as a silt loam soil according to United States soil taxonomy (Tang et al., 2019).

Three plantations were chosen for the study: pure *H. rhamnoides* plantation, pure *P. davidiana*

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plantation, and *H. rhamnoides–P. davidiana* mixed plantation. All plantations were planted in 2004, and

three adjacent plots were selected (16 m × 10 m) for each plantation type. In pure plantations, the

110 original planted spacing for each individual plant was 2.0 m × 2.0 m. In the mixed plantation, *P. davidiana* was originally planted between the 4.0 m gaps in rows of *H. rhamnoides*, each individual

plant was also spaced 2.0 m × 2.0 m. Based on a survey performed in July 2018, in pure plantations, the

average tree trunk diameter (at 1.2 m height above the ground) and height were 50.5 ± 3.6 mm and 4.11

± 0.81 m for *H. rhamnoides*, respectively, and the corresponding values were 52 ± 4.6 mm and 4.05 ±

115 0.63 m for *P. davidiana*. Meanwhile, in mixed plantations, the average trunk diameter and tree height

were 51.3 ± 2.9 mm and 4.49 ± 0.7 m for *H. rhamnoides*, respectively, and the corresponding values

were 56.3 ± 3.8 mm and 4.23 ± 0.79 m for *P. davidiana*. *Bothriochloa ischaemum* and *Glycyrrhiza*

uralensis were the dominant herbaceous species in *H. rhamnoides* and *P. davidiana* pure plantations,

respectively; meanwhile, *B. ischaemum* was dominant in the mixed plantation.

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2.2 Environmental parameter measurements and reference evapotranspiration calculation

Net radiation (R_n, CNR4, Kipp &Zone Inc., Netherlands), atmospheric pressure (CS105, Vaisala Inc.,

Finland), air temperature (T_a) and relative humidity (HMP45D, Vaisala Inc.), and wind velocity (Ws,

A100R, Vector Inc., UK) were measured using a weather station nearly 500 m from the research plots.

125 Soil heat flux (G) and rainfall amount were measured at 5 cm below ground using two HFT-3 plates

(Campbell Scientific Inc., USA) and a TE525 rain gauge (Campbell Scientific Inc.), respectively. At

each plot, soil water content (SW) was measured at 5, 30, 50, 100, 150, and 200 cm below ground

(SW_{5cm}, SW_{30cm}, SW_{50cm}, SW_{100cm}, SW_{150cm}, and SW_{200cm}) by CS615 TDR probes (Campbell Scientific

Inc.). All these parameters were measured and stored at 30 min interval by a CR3000 datalogger

130 (Campbell Scientific Inc.).

Reference evapotranspiration (ET_0) was used to indicate atmospheric evaporative demand (Allen et

al., 1998): $ET_0 = (0.408 \times s \times (R_n - G) + \gamma \times \dfrac{900}{T_a + 273} \times W_s \times VPD)/(s + \gamma \times (1 + 0.34 \times W_s))$ (1)

where γ and s are the psychrometric constant (kPa K^{-1}) and the slope between saturation vapor pressure

and air temperature (kPa K^{-1}), respectively. The units of R_n and G are W m^{-2}, and of W_s is m s^{-1}.

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2.3 Sap flow observation

Three standard individuals, with approximately mean height and trunk diameter, for specific species were chosen in each of the nine plots (Table S1). In each plot in the mixed plantation, three individuals of *H. rhamnoides* were chosen firstly, then a neighboring *P. davidiana* individual was selected at

140   approximately 2 m distance from each chosen *H. rhamnoides* individual. The sap flow was monitored by a pair of Granier-type thermal dissipation probes 10 mm in length and 2 mm in diameter in 36 selected individuals. During the plant growing season and ranging from 1 June (DOY 152) to 30 September (DOY 273) in 2018, the 30 s original and 30 min average sap flow values were monitored using a CR3000 data logger (Campbell Scientific Inc.). Waterproof silicone and aluminum foil were

145   used to avoid the impact of the external environment on and physical damage to TDPs (Du et al., 2011). The standard sap flow density (F_d, ml m^{-2} s^{-1}) was calculated as follows (Granier, 1987):

$$F_d = 119((\Delta t_{max} - \Delta t) / \Delta t)^{1.231} \tag{2}$$

where Δt and Δt_{max} are the temperature difference of heated and unheated probes at 30 min intervals and the maximum Δt in each day, respectively.

150   Steppe et al. (2010) suggested that F_d should have a species specific calibration to validate Eq. (2). Meanwhile, the possibility of underestimating the F_d value with the Granier-type thermal dissipation method (Du et al., 2011) should be considered when the whole tree water consumption is calculated. However, with the lack of species specific calibration for Eq. (2) in the present study, the daily normalized F_d for each replicate individual was calculated as the index of plant water consumption,

155   through dividing F_d by the maximum value from DOY 152 to DOY 273. Thus, each monitored individual had a maximum daily normalized F_d of 1. In each plantation type, the average daily normalized F_d for plant species was calculated in each plot to determine the water consumption characteristics rather than the absolute water consumption amount (Du et al., 2011).

160   **2.4 Rainwater, plant stem and soil water collection, and water source determination**

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From April to October 2018, at the end of each rainfall event, 19 rainwater samples were collected immediately using a rain gauge cylinder placed in the middle of the plantation plots, and stored at 4 ℃. To avoid the influence of sample collection on sap flow observation, one standard individual for the specific species nearby each sap flow monitored individual was selected for plant stem and soil water

165   collection. In the mixed plantation, the distance was approximately 2 m between the selected *H. rhamnoides* and *P. davidiana* standard individuals in each plot for sample collection. For plant stem and soil water collection, five rainfall events were selected: 3.4 mm (DOY 194), 7.9 mm (DOY 266), 15.4 mm (DOY 249), 24 mm (DOY 204), and 35.2 mm (DOY 156). These rainfall events were selected with an interpulse period longer than 7 days to eliminate the potential influence of the previous rainfall event.

170   At each of successive three days after every selected rainfall event, one suberized stem after removing the bark was collected at midday (11:30–13:30) for each standard individual. Meanwhile, approximately 0.5 m around the stem of each standard individual in the pure plantations and at the middle between two species in the mixed plantation, one soil core at seven depths (0–10, 10–20, 20–30, 30–50, 50–100, 100–150, and 150–200 cm) was collected through soil drilling. The suberized stem and

175   one part of the collected soil samples were placed into glass bottles. These bottles were sealed with parafilm and stored at –15 ℃.

A vacuum line (LI-2100, LICA Inc., China) was used to extract water from soil samples and plant stems. The water isotopic values of rainwater, soil samples, and plant stems were determined using a DLT-100 water isotope analyzer (LGR Inc., USA), with accuracy of ± 0.1 (δ^{18}O) and ± 0.3 ‰ (δD).

180   The potential influence of organic matter on water isotopic values produced during water extraction from stems was eliminated using the method of Yang et al. (2015). The isotopic values (‰) were calculated as follows:

$$\delta^{18}\text{O(D)} = (R_{sample} - R_{standard}) / R_{standard} \times 1000‰$$
(3)

where $R_{standard}$ and R_{sample} indicate the ^{18}O/^{16}O (D/H) molar ratios of water sample relative to the Vienna

185   Standard Mean Ocean Water, respectively. The average water δ^{18}O and δD of plant stems for specific species and corresponding soil samples was calculated in each plot for further analysis.

In the present study, the rainwater uptake proportion (RUP, %) for plant is calculated as the

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proportion of rainwater in plant stem as follows (Cheng et al., 2006):

$$\delta^{18}O\,(D)_P = PAP \times \delta^{18}O\,(D)_{rain} + (1-PAP) \times \delta^{18}O\,(D)_{swb} \tag{4}$$

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$$RUP = (\delta^{18}O(D)_p - \delta^{18}O(D)_{swb})/(\delta^{18}O(D)_{swa} - \delta^{18}O(D)_{swb}) \times 100\% \tag{5}$$

where $\delta^{18}O(D)_{rain}$ and $\delta^{18}O(D)_p$ are the isotopic values for rainwater and plant stem after rainfall, respectively; $\delta^{18}O(D)_{swb}$ and $\delta^{18}O(D)_{swa}$ are the isotopic values of soil water immediately before and after rainfall, respectively. Equation (5) is derived through the linear mixing model for water isotopic value in plant stem after rainfall in Eq. (4).

195 Equations (4) and (5) are based on the assumption that little or no soil water is lost through evaporation. Thus, in this study, only the values of plant stem and soil water collected on the first day immediately after rainfall were used, and only the RUP on the first day after each rainfall event was calculated.

In this study, the $\delta^{18}O(D)_{swb}$ cannot be directly accurately determined through soil water sample

200 collection, due to unpredictable natural rainfall events. A linear mixed model can be used to calculate the $\delta^{18}O(D)_{swb}$, based on the isotopic values for rainwater and soil water after rainfall, and soil depth interval weighted SW before (sw_b, $m^3\ m^{-3}$) and after (sw_a, $m^3\ m^{-3}$) rainfall:

$$\delta^{18}O(D)_{swb} = SW_b/SW_a \times \delta^{18}O(D)_{swa} + (1-SW_b/SW_a) \times \delta^{18}O(D)_{rain} \tag{6}$$

In addition, on the first day after rainfall, the relative water uptake proportions from different soil

205 depths were calculated using the MixSIR program (Moore and Semmens, 2008). The model input parameters were the average $\delta^{18}O$ and δD values in plant stem water, soil water at seven depths in each plot, and rainfall water. The SD for $\delta^{18}O$ and δD at each soil depth was used to accommodate the uncertainties of these values, and no fractionation was considered during water source uptake by plant roots. In addition, the calculated water uptake proportions from seven soil depths were combined into

210 three soil layers (shallow, middle, and deep) to facilitate water source comparisons, for soil depths of 0–30, 30–100, and 100–200 cm, respectively.

In this study, on the first day after rainfall, the water uptake proportions from rainwater and soil

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layers were calculated separately. The sum of RUP and relative water uptake proportions from three soil layers were larger than 100%. Thus, no significant difference was determined between RUP and water sources from different soil layers in the following analysis.

2.5 Leaf water potential measurement

On the same day as plant stem and soil sample collections, the Ψ_{pd} and Ψ_m were measured by a PMS1515D analyzer (PMS Instrument, Corvallis Inc., OR, USA) at 4:30–5:30 (predawn) and 11:20–12:40 (midday), respectively. One leaf was selected for each sap flow monitored individual, and the average value for each species in each plot was used for further analysis. The diurnal variation in leaf water potential (Ψ_{pd}–Ψ_m) was used to illustrate the leaf water potential gradient.

2.6 Plant fine root investigation

In August 2018, six soil cores were dug around each selected standard individual for plant stem and soil water collection, through a soil drill with diameter 20 cm to investigate plant fine roots. The collected soil depths were 0–10, 10–20, 20–30, 30–50, 50–70, 70–100, 100–130, 130–160, 160–200 cm, with approximately 0.5 m around the stem of each species standard individual. WinRHIZO (Regent Instruments Inc., Quebec, Canada) was used to determine the fine root (diameter < 2 mm) surface area at each soil depth. The sum of fine root surface area for six soil cores was used to determine the fine root distribution for each selected standard individual.

2.7 Statistical analysis

In the present study, the first day after rainfall was the maximum normalized F_d within 3 days for *H. rhamnoides* and *P. davidiana* in both plantation types, except after 24 and 35.2 mm for *P. davidiana* in pure plantation. The maximum normalized F_d for *P. davidiana* in pure plantation was observed on the second day after these two rainfall events. However, for *P. davidiana* in pure plantation, there was no significant difference (P > 0.05) in diurnal sap flow between the first and second day after each of these two rainfall events based on independent-sample *t*-test (Fig S1). Therefore, the normalized F_d on the

240 first day after each selected rainfall amount was used in Eq. (7) to calculate the relative response of

daily normalized F_d (SF_R, %) to rainfall pulses:

$$SF_R = ((X_{after} - X_{before}) / X_{before}) \times 100\%$$ (7)

where X_{after} and X_{before} are the normalized F_d on the first day after and on the day before the rainfall

event, respectively.

245 Meanwhile, none of Ψ_{pd}, Ψ_m nor $\Psi_{pd} - \Psi_m$ showed significant differences between the first and second

day after each rainfall events ($P > 0.05$) for these two species in both plantation types (Table S2). The

Ψ_{pd}, Ψ_m, and $\Psi_{pd} - \Psi_m$ on the first day after each rainfall event were used in the following analysis to

illustrate the influence of leaf water potential on SF_R in response to rainfall pulses.

A repeated ANOVA (ANOVAR) was used to analyze the differences in water consumption, water

250 sources, and plant physiological parameters between these species in pure and mixed plantations,

respectively. This analysis was conducted with SF_R, RUP, relative water uptake proportions from three

soil depths, and $\Psi_{pd} - \Psi_m$ as response variables, and "species" and "rainfall" as between-subject and

within-subject factors. The same analysis was used to detect mixed afforestation effect on response

variables for each plant species, with "plantation type" and "rainfall" as the between-subject factor.

255 Furthermore, significant differences in fine root proportion for each soil layer (shallow, middle, and

deep) for each species between pure and mixed plantations were detected through independent-sample

t-test. All of these analyses were calculated with SPSS 18 (IBM Inc., New York, US), after data normal

distribution and homogeneity of variance analysis were tested.

260 **3 Results**

3.1 Variation in environmental parameters and plant fine root vertical distribution

The rainfall amount during the study period (265.7 mm, DOY 152–273) was 11.8% lower than the

average value during 2008–2017. Rainfall varied seasonally with 36 consecutive days had no rainfall

event (DOY 157–192) and 5 days had successive rainfall events (DOY 237–241) (Fig 1). The ET_0

265 (554.7 mm) was approximately twice the rainfall amount during the study period, with the higher and

lower values during the low and high rainfall event periods, respectively (Fig 1). The SW increased and

subsequently decreased by different degrees following rainfall events, with shallow soil layer (0–30 cm) exhibited higher variation than the corresponding value below 30 cm in the three plantations (Fig 1). The coefficients of variation (CVs) in the shallow soil layer were 19.22%, 18.56%, and 16.61% in *H.*

270 *rhamnoides* and *P. davidiana* pure plantations and the mixed plantation, respectively. The SW for shallow and middle (30–100 cm) soil layers exhibited lower values than some deep soil layers (100–200 cm) during the less rainfall event period (such as DOY 157–192) in the three plantations. In addition, compared with shallow and middle soil layers, the deep soil layer SW exhibited a time lag response to rainfall events.

275 The *H. rhamnoides* and *P. davidiana* in pure plantations exhibited different fine root vertical distributions, with more than 40% of fine roots observed in shallow and deep soil layers, respectively (Fig S2). In the mixed plantation, approximately 40% of *H. rhamnoides* fine roots were in the shallow soil layer. Meanwhile, no significant differences in fine root proportion were observed for *H. rhamnoides* for each soil layer in pure and mixed plantations (P > 0.05). The proportion of *P. davidiana*

280 fine roots in the shallow soil layer, was significantly increased from 21.94% in pure plantation to 31.28% in the mixed plantation ($df = 4$, $t = 7.15$, P < 0.01).
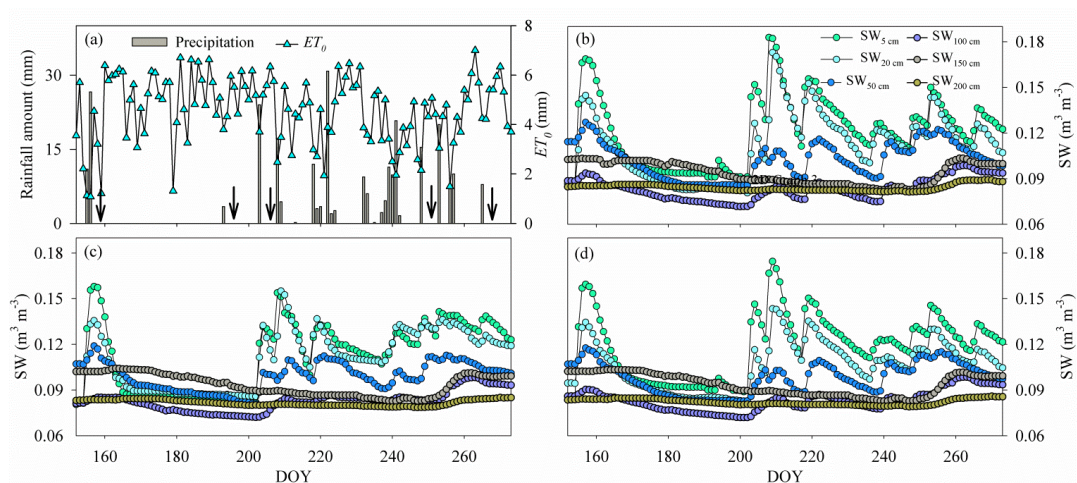

Figure 1. Variation of (a) rainfall amount, reference evapotranspiration (ET_0), and averaged soil water content (SW) in (b) *H. rhamnoides* pure plantation, (c) *P. davidiana* pure plantation, and (d) mixed

285 plantation from DOY 152 to 273 (1 June to 30 September). Standard deviation bars for SW at each soil layers are not shown to allow clear display of variation of SW for each plot. Arrows in (a) indicate dates

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of sample collection: DOY 157–159 (6–8 June), DOY 194–196 (12 –14 July), DOY 204–206 (23–25

July), DOY 249–251 (6–8 September), and DOY 265–267 (22–24 September).

290 **3.2 Variations in sap flow**

Daily normalized F_d for *H. rhamnoides* and *P. davidiana* fluctuated with rainfall events in pure and

mixed plantations (Fig 2). The variation of normalized F_d for *H. rhamnoides* and *P. davidiana* in mixed

plantation was higher than the specific species in pure plantations, with corresponding CVs of 30.99%

and 34.88% in the mixed plantation, and 24.64% and 27.44% in pure plantations (Fig 2). The relative

295 response of water consumption to rainfall pulses was significantly influenced by both rainfall amount

and plant species ($P < 0.001$) (Fig 2, Table 1). Following large rainfall amounts (≥ 15.4 mm), the diurnal

variation of sap flow was significantly higher than the value before rainfall ($P < 0.05$) for *H. rhamnoides*

in pure plantation and for *P. davidiana* in both plantation types (Figs S3 and S4). The lowest rainfall

amount (7.9 mm) that significantly increased the diurnal variation of sap flow was observed for *H.*

300 *rhamnoides* in the mixed plantation (Fig S3). Furthermore, in response to rainfall pulses, the SF_R for *H.*

rhamnoides in pure (range 6.69 $\pm 1.22\%$ to 106.34 $\pm 4.7\%$) and mixed (range 2.23 $\pm 0.54\%$ to 190.89 $\pm$

15.49%) plantations was significantly higher ($P < 0.001$) than corresponding values for *P. davidiana*:

ranges 4.24 $\pm$ 0.52% to 60.28 $\pm$ 5.72% and 3.14 $\pm$ 0.53% to 83.04 $\pm$ 14.23% (Table 1). Mixed

afforestation significantly enhanced SF_R for both species ($P < 0.001$) (Table 1).

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Table 1. Repeated ANOVA (ANOVAR) parameters for the relative response of normalized sap flow

(SF_R) to rainfall pulses of *H. rhamnoides* and *P. davidiana* (n = 30).

	Variation source	*df*	*F*	*p*
	Rainfall	4	97.91	<0.001
Pure plantation	Species	1	121.13	<0.001
	Rainfall × Species	4	27.35	<0.001
	Rainfall	4	489.9	<0.001
Mixed plantation	Species	1	70.38	<0.001

		df		
	Rainfall $\times$ Species	4	249.17	<0.001
	Rainfall	4	42.63	<0.001
H. rhamnoides	Plantation type	1	337.09	<0.001
	Rainfall $\times$ Plantation type	4	215.43	<0.001
	Rainfall	4	10.05	<0.001
P. davidiana	Plantation type	1	32.36	<0.01
	Rainfall $\times$ Plantation type	4	19.12	<0.001

df = degree of freedom, Plantation type = pure and mixed plantation for each species. Pure and Mixed plantation indicate the result of SF_R for both species in different plantation types, respectively; *H. rhamnoides* and *P. davidiana* indicate the mixed afforestation effect on SF_R for these species.
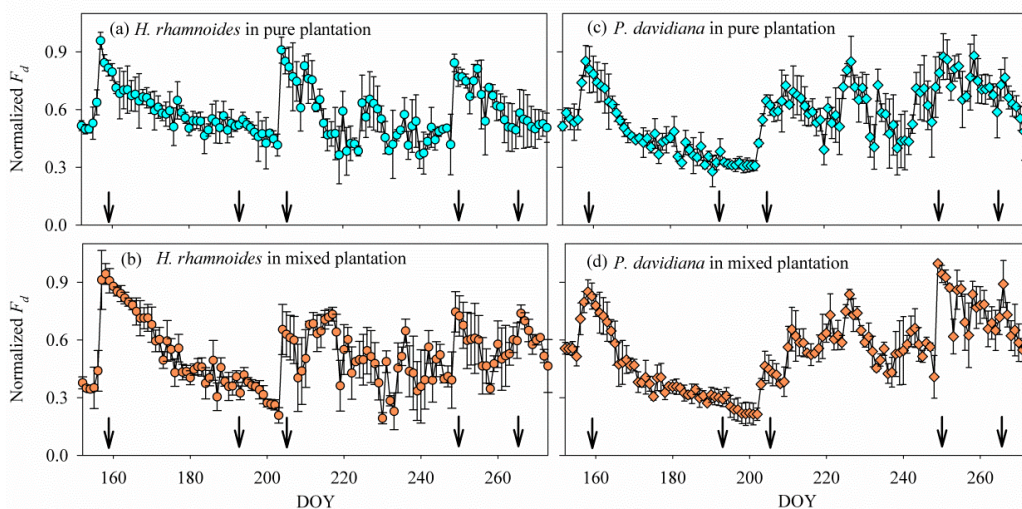

Figure 2. Variation in averaged ($\pm$ SD) daily normalized F_d for *H. rhamnoides* in (a) pure and (b) mixed plantations and for *P. davidiana* in (c) pure and (d) mixed plantations. Arrows indicate dates of sample collection: DOY 157–159 (6–8 June), DOY 194–196 (12 –14 July), DOY 204–206 (23–25 July), DOY 249–251 (6–8 September), and DOY 265–267 (22 –24 September).

3.3 Variations in plant water sources

The soil water $\delta^{18}O$ and δD for pure *H. rhamnoides*, pure *P. davidiana*, and mixed plantations showed large vertical variation following small rainfall events ($\leq$ 7.9 mm), and exhibited relatively small

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vertical variations following large rainfall events (≥ 15.4 mm) (Fig S5). Generally, the isotopic values of soil water depleted from shallow to deep soil layers, and water isotopic values in shallow and middle soil layer were close to rainfall water in the three plantations following large rainfall events.

Although no significant difference in RUP was observed between *H. rhamnoides* (14.2 ± 7.81%) and

325   *P. davidiana* (12.43 ± 7.33%) in pure plantations (Fig 3, Table 2), the RUP was significantly higher for *H. rhamnoides* (19.17 ± 8.6%) than *P. davidiana* (14.59 ± 5.86%) in the mixed plantation ($P < 0.05$) (Table 2). In addition, *H. rhamnoides* mainly uptake water from the middle soil layer in pure and mixed plantations based on the MixSIR result, with corresponding average values of 36.27 ± 2.43% and 44.14 ± 3.06% (Fig 4). The water source for *P. davidiana* in pure and mixed plantations was mainly from the

330   deep and middle soil layers, respectively, with corresponding average values of 41.4 ± 15.18% and 40.17 ± 5.9%. In pure plantation, the water source from shallow and middle soil layers for *H. rhamnoides* was significantly higher than *P. davidiana*; however, the water source from the deep soil layer was significantly lower for the former species ($P < 0.05$) (Table 3). No significant differences in water sources from each soil layer were observed between these species in the mixed plantation (Table

335   3). In addition, mixed afforestation significantly enhanced RUP and decreased the deep soil water uptake proportion for *H. rhamnoides* and *P. davidiana* ($P < 0.05$) (Tables 2 and 3, Figs 3 and 4).
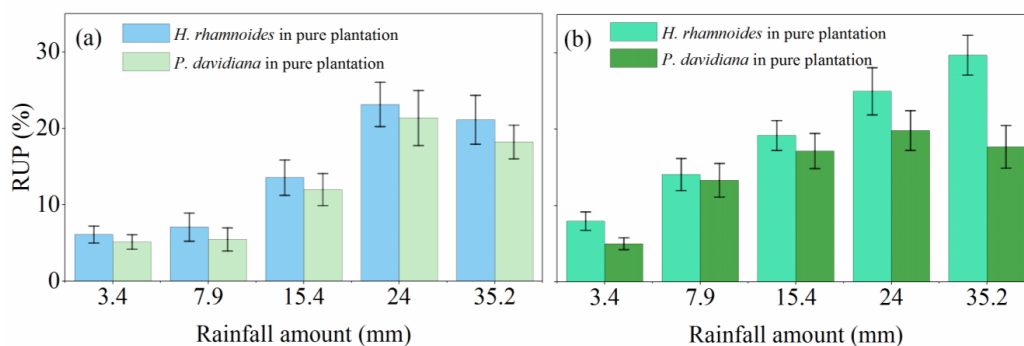

Figure 3. Variation in averaged (± SD) rainwater uptake proportion (RUP) for *H. rhamnoides* and *P. davidiana* in (a) pure and (b) mixed plantations after five rainfall events.
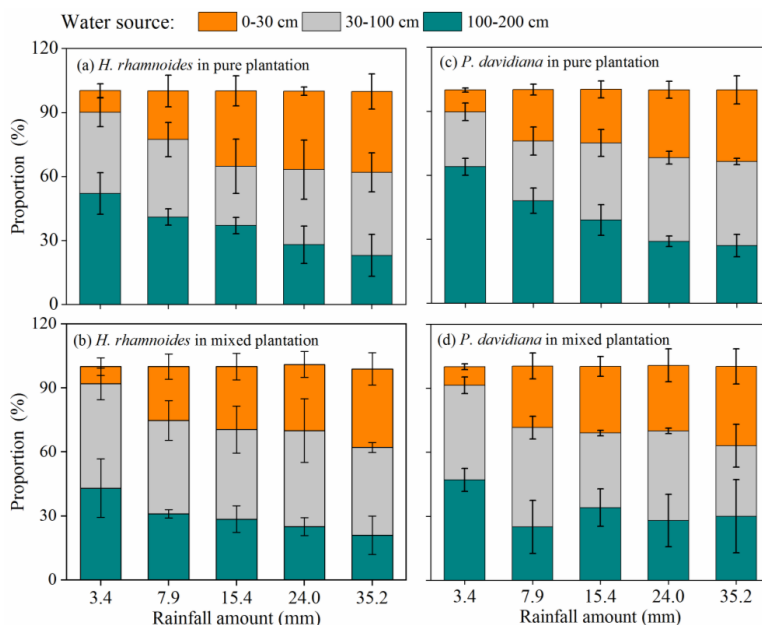
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Figure 4. Variation in averaged (± SD) plant water sources from three soil layers (0–30, 30–100, and 100–200 cm) for *H. rhamnoides* in (a) pure and (b) mixed plantations, and for *P. davidiana* in (c) pure and (d) mixed plantations after five rainfall events.

345

Table 2. Repeated ANOVA (ANOVAR) parameters for rainwater uptake proportion (RUP) for *H. rhamnoides* and *P. davidiana* (n = 30).

	Variation source	*df*	*F*	*p*
Pure Plantation	Rainfall	4	385.02	<0.01
	Species	1	21.02	<0.05
	Rainfall × Species	4	0.83	0.52
Mixed Plantation	Rainfall	4	17696.38	<0.01
	Species	1	4089.12	<0.01
	Rainfall × Species	4	1776.62	<0.01
H. rhamnoides	Rainfall	4	496.72	<0.01
	Plantation type	1	360.16	<0.01
	Rainfall × Plantation type	4	17.62	<0.01

	Rainfall	4	1969.3	<0.01
P. davidiana	Plantation type	1	54.83	<0.01
	Rainfall × Plantation type	4	208.06	<0.01

df = degree of freedom, Plantation type = pure and mixed plantation for each species. Pure and Mixed plantation indicate the result of SF_R for both species in different plantation types, respectively; *H. rhamnoides* and *P. davidiana* indicate the mixed afforestation effect on SF_R for these species.

Table 3. Repeated ANOVA (ANOVAR) parameters for relative water uptake proportion from shallow (0–30 cm), middle (30–100 cm), and deep (100–200 cm) soil layer for *H. rhamnoides* and *P. davidiana* (n = 30).

	Variation source	*df*	0-30cm		30-100cm		100-200cm	
			F	*p*	*F*	*p*	*F*	*p*
Pure Plantation	Rainfall	4	153.45	<0.01	145.04	<0.01	176.79	<0.01
	Species	1	8.69	<0.05	10.56	<0.05	11.08	<0.05
	Rainfall × Species	4	129.89	<0.01	112.46	<0.01	4.99	<0.01
Mixed Plantation	Rainfall	4	1.5	0.41	2.3	0.11	18.34	<0.01
	Species	1	2.2	0.21	1.48	0.29	3.9	0.12
	Rainfall × Species	4	0.9	0.48	2.41	0.09	1.9	0.16
H. rhamnoides	Rainfall	4	2.05	0.14	1.51	0.25	85.46	<0.01
	Plantation type	1	1.07	0.36	1.32	0.32	10.08	<0.05
	Rainfall × Plantation type	4	0.62	0.66	1.39	0.28	5.59	<0.01
P. davidiana	Rainfall	4	14.72	<0.01	71.59	<0.01	19.46	<0.01
	Plantation type	1	4.1	0.12	5.68	0.08	123.27	<0.01
	Rainfall × Plantation type	4	9.55	<0.01	85.29	<0.01	9.35	<0.01

df = degree of freedom, Plantation type = pure and mixed plantation for each species. Pure and Mixed plantation indicate the result of SF_R for both species in different plantation types, respectively; *H. rhamnoides* and *P. davidiana* indicate the mixed afforestation effect on water sources from different soil layers for these species.

3.4 Variations in plant leaf water potential

In response to rainfall pulses, *H. rhamnoides* exhibited higher CV for Ψ_{pd}, Ψ_m, and Ψ_{pd}–Ψ_m than

corresponding value for *P. davidiana* in both plantation types, except that *H. rhamnoides* exhibited

lower CVs for Ψ_{pd} than *P. davidiana* (12.99% and 18.33%, respectively) in the mixed plantation (Fig 5).

Compared with *P. davidiana*, *H. rhamnoides* exhibited significantly positive Ψ_{pd} in pure plantation,

negative Ψ_m in the mixed plantation, and larger $\Psi_{pd}-\Psi_m$ in both plantation types (P < 0.05) (Table 4).

365   Meanwhile, mixed afforestation significantly reduced the Ψ_m and increased the Ψ_{pd} for *H. rhamnoides*

and *P. davidiana* (P < 0.05), respectively, and significantly increased $\Psi_{pd}-\Psi_m$ for both species (Table 4).
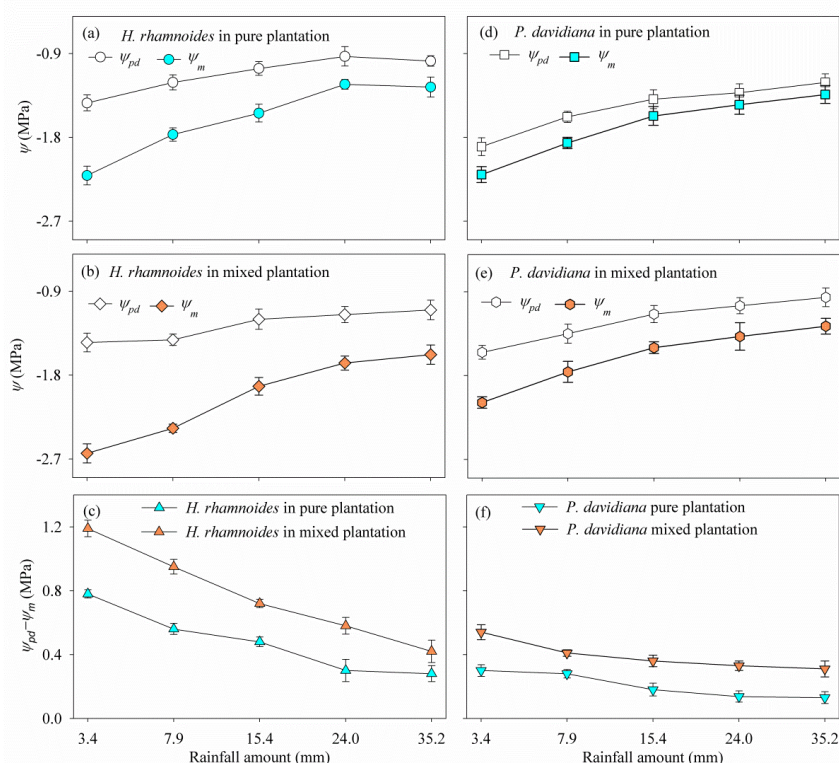

Figure 5. Variation in averaged (± SD) plant predawn (Ψ_{pd}), midday leaf water potential (Ψ_m), and leaf

water potential gradient ($\Psi_{pd}-\Psi_m$) for (a–c) *H. rhamnoides* and (d–f) *P. davidiana* in both plantation

370   types after five rainfall events.

Table 4. Repeated ANOVA (ANOVAR) parameters for predawn (Ψ_{pd}), midday leaf water potential (Ψ_m),

and leaf water potential gradient ($\Psi_{pd}-\Psi_m$) for *H. rhamnoides* and *P. davidiana* (n = 30).

	Variation source	df	Ψ_{pd}		Ψ_m		$\Psi_{pd}-\Psi_m$	
			F	p	F	p	F	p
Pure Plantation	Rainfall	4	4.02	<0.05	24.44	<0.01	47.88	<0.01

		df	F	P	F	P	F	P
	Species	1	182.74	<0.01	4.9	<0.05	969.97	<0.01
	Rainfall ×Species	4	3.24	<0.05	2.08	0.13	18.68	<0.01
	Rainfall	4	0.66	0.63	25.54	<0.01	82.49	<0.01
Mixed Plantation	Species	1	0.12	0.75	127.3	<0.01	3420.1	<0.01
	Rainfall ×Species	4	1.8	0.18	3.7	<0.05	35.92	<0.01
	Rainfall	4	7.14	<0.01	19.64	<0.01	3.59	<0.05
H. rhamnoides	Plantation type	1	27.05	<0.01	496.66	<0.01	1278.96	<0.01
	Rainfall ×Plantation type	4	1.69	0.202	3.32	<0.05	6.66	<0.01
	Rainfall	4	30.78	<0.01	12.39	<0.01	7.38	<0.01
P. davidiana	Plantation type	1	792.77	<0.01	2.97	0.16	634.12	<0.01
	Rainfall ×Plantation type	4	3.8	<0.05	0.09	0.98	3.83	<0.05

df = degree of freedom, Plantation type = pure and mixed plantation for each species. Pure and Mixed plantation indicate the result of SF_R for both species in different plantation types, respectively; *H. rhamnoides* and *P. davidiana* indicate the mixed afforestation effect on leaf water potential for these species.

3.5 Influence of water sources and $\Psi_{pd}-\Psi_m$ on plant water consumption

The SF_R significantly increased with increasing RUP and decreasing $\Psi_{pd}-\Psi_m$ for *H. rhamnoides* ($P < 0.01$) in both plantation types (Fig 6). Meanwhile, SF_R significantly increased with decreasing $\Psi_{pd}-\Psi_m$ for *P. davidiana* in both plantation types ($P < 0.05$). However, a significant relationship between SF_R and RUP was observed for *P. davidiana* in the mixed ($P < 0.05$) but not in pure plantations (Fig 6). Furthermore, SF_R significantly increased with decreasing water uptake proportion from the deep soil layer for *H. rhamnoides* in both plantation types and *P. davidiana* in mixed plantation ($P < 0.05$) (Table S3). No significant relationship was observed between SF_R and water uptake proportion from shallow or middle soil layers for both species in both plantation types.

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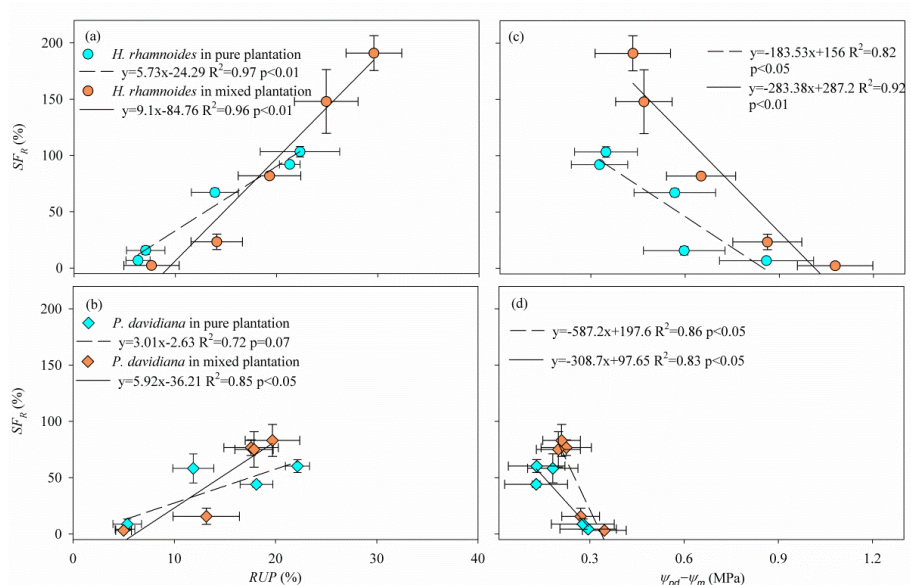Sciences
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Figure 6. Relationship of (a, b) rainwater uptake proportion (RUP) and (c, d) leaf water potential gradient ($\Psi_{pd}-\Psi_m$) with relative response of normalized F_d (SF_R) for *H. rhamnoides* and *P. davidiana* in both plantation types.

4 Discussion

4.1 Rainwater uptake enhances water consumption for *H. rhamnoides* but not *P. davidiana* in pure plantations

Rainwater is the only replenished soil water source in the studied region, because plants cannot uptake ground water of approximately 100 m depth below the surface (Wu et al., 2021). Small rainfall events generally only wet the soil surface and may evaporate before plant root uptake (Zhao and Liu, 2010). However, large rainfall events are most likely recharge soil moisture and enhance the metabolic activity of plant fine roots (Hudson et al., 2018), thus enhancing plant water uptake. Similar to *Salix psammophila* and *Caragana korshinskii* in the studied region (Zhao et al., 2021), both *H. rhamnoides* and *P. davidiana* exhibited plasticity in water sources in pure plantations (Fig 4), with *H. rhamnoides* exhibiting the greater plasticity. In pure plantations, the obviously lower SWC at all soil depths (Fig 1) and large water uptake proportion from the deep soil layer (Fig 4) after 3.4 mm of rainfall for these two species, suggested that this rainfall amount did not relieve the drought caused by 36 days (DOY 157–

405   192) of no rainfall. The RUP for *H. rhamnoides* but not *P. davidiana* significantly increased following

an increase in rainfall amount ($P < 0.05$) (Fig S6), indicating that water uptake was more sensitive to

rainfall for *H. rhamnoides*. This may be mainly due to the greater proportions of fine root surface area

distributed in the shallow soil layer for *H. rhamnoides* ($40.85 \pm 3.14\%$) compared to *P. davidiana*

($21.94 \pm 2.3\%$) (Fig S2).

410   Rainwater uptake does not permit water consumption increase after rainfall pulses especially in

semiarid and arid environments (Dai et al., 2020; Grossiord et al., 2017; West et al., 2007), and the

influence of water potential gradient ($\Psi_{pd}-\Psi_m$) on plant water consumption should also be considered

(Hudson et al., 2018; Kumagai and Porporato, 2012). For example, although *Juniperus osteosperma*, a

deep rooted plant species, could uptake rainwater after large events in the west of the United States, the

415   sap flux did not increase with increasing rainfall amount (West et al., 2007). The synchronization

between rainwater uptake and water consumption for *J. osteosperma* was mainly attributed to the

uptake of rainwater by plant being unable to reverse the cavitation in its roots and stems (Grossiord et

al., 2017; West et al., 2007). Our previous investigations in the studied region indicated that *P.

davidiana* is relatively more vulnerable to cavitation than *H. rhamnoides*, with water potential at 50%

420   loss of conductivity of -1.15 MPa (Zhang et al., 2013) and -1.49 MPa (Dang et al., 2017), respectively,

based on stem vulnerability curves. Being less vulnerable to stem cavitation allowed *H. rhamnoides* to

experience a significantly lower Ψ_m and larger $\Psi_{pd}-\Psi_m$ compared with *P. davidiana* in response to soil

water conditions after rainfall pulses. The large $\Psi_{pd}-\Psi_m$ for *H. rhamnoides* was consistent with the high

SF_R and CVs of normalized sap flow, indicating that this species exhibited a rainfall sensitive

425   mechanism. The relative constant $\Psi_{pd}-\Psi_m$ for *P. davidiana* was consistent with the relatively small SF_R

and CVs of normalized sap flow, indicating that this species exhibited a rainfall insensitive mechanism.

Furthermore, after rainfall events, the SF_R for *H. rhamnoides* but not for *P. davidiana* significantly

increased following rainfall amount increases ($P < 0.05$) (Fig S6), also indicating that water

consumption was more sensitive to rainfall for *H. rhamnoides*.

430   The SF_R was significantly influenced by RUP and $\Psi_{pd}-\Psi_m$ for *H. rhamnoides* in the pure plantation,

indicating that rainwater uptake and leaf physiological adjustment enhanced its plant water use (Figs 6

and 7). However, the SF_R was only significantly influenced by $\Psi_{pd}-\Psi_m$ for *P. davidiana* (Fig 7),

suggesting that its water use was mainly constrained by plant physiological characteristics. The ET_0

represents the atmospheric evaporative demand, and has been observed to influence plant water

consumption in water limited (Li et al., 2021) and non-water limited regions (Iida et al., 2016).

However, in the present study, neither ET_0 after rainfall nor relative response of ET_0 significantly

influenced SF_R for either species in pure plantations (Table S4). The influence of plant physiological

characteristics (i.e. $\Psi_{pd}-\Psi_m$) on SF_R for both species, may partially contribute to the lack of atmosphere

evaporative demand effect on plant water consumption in the studied region, although these species

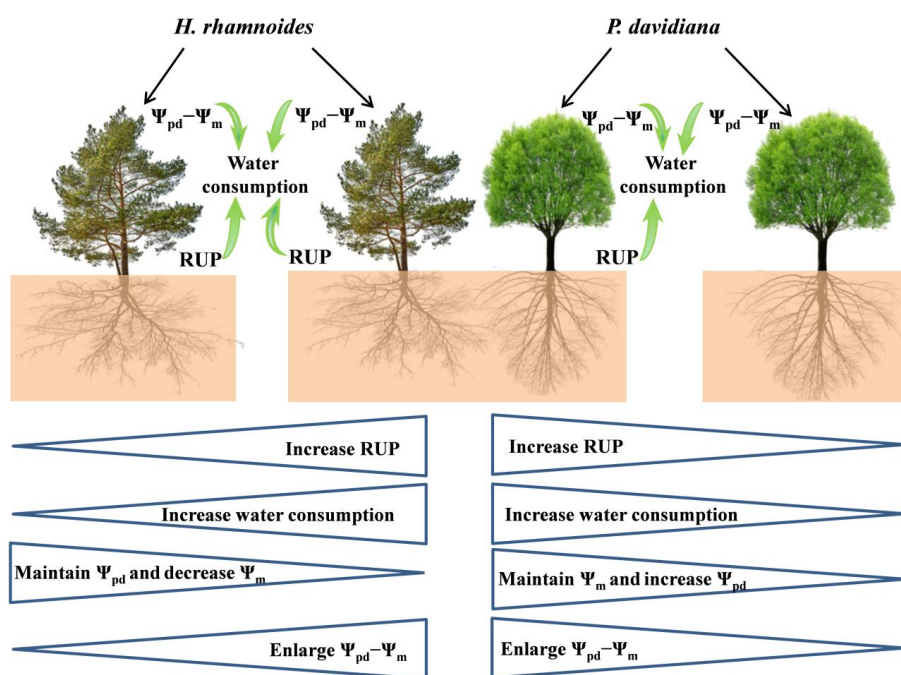exhibited different rainfall pulse sensitivity.

Figure 7. Schematic of rainwater uptake, leaf water potential gradient, and plant water consumption for

H. rhamnoides and *P. davidiana* in both plantation types. Both rainwater uptake proportion (RUP) and

leaf water potential gradient ($\Psi_{pd}-\Psi_m$) enhanced plant water consumption after rainfall pulses for *H.*

rhamnoides in pure and mixed plantations, and for *P. davidiana* in mixed plantation. However, $\Psi_{pd}-\Psi_m$

rather than RUP significantly influenced plant water consumption after rainfall pulses for *P. davidiana*

in the pure plantation. Mixed afforestation effect of these parameters for each species are indicated at

the bottom half of the schematic, with "increase", "decrease" or "enlarge" indicating a significant

difference (P < 0.05) for a species between pure and mixed plantations. Mixed afforestation

450   significantly enhanced RUP and plant water consumption, decreased Ψ_m, and enlarged $\Psi_{pd}-\Psi_m$ for *H.*

rhamnoides, and also significantly enhanced the RUP and water consumption, increased Ψ_{pd}, and

enlarged $\Psi_{pd}-\Psi_m$ for *P. davidiana*.

4.2 Rainwater uptake enhances water consumption for coexisting species in mixed plantation

455   Spatial water resource partitioning is considered one of the essential plant strategies to maintain

coexistence in mixed plantations, especially in semiarid and arid regions (Munoz-Villers et al., 2020;

Silvertown et al., 2015; Yang et al., 2020). However, water source competition has widely been

observed among coexisting plant species according to the literature surveys by Silvertown et al. (2015)

and Tang et al. (2018), regardless of annual average rainfall amount. In the present study, the

460   non-significant differences in xylem $\delta^{18}O$ and δD (P > 0.05) and plant water sources for the three soil

layers (Table 3, Fig 4) indicated water competition between these species in the mixed plantation,

although the RUP was significantly higher for *H. rhamnoides* (Table 2).

Generally, two types of adaptation can be adopted by plants to cope with resource competition:

increased competition ability or minimized competition interactions (West et al., 2007). Consistent with

465   the first adaptation type, mixed afforestation enhanced the RUP for *H. rhamnoides* and *P. davidiana*

(Figs 3 and 7, Table 2). Although mixed afforestation did not significantly alter the Ψ_{pd} and Ψ_m for *H.*

rhamnoides and *P. davidiana*, respectively, significantly negative Ψ_m and positive Ψ_{pd} were observed for

corresponding species (P < 0.01) (Table 4). Mixed afforestation significant increased Ψ_{pd} for *P.*

davidiana, possibly due to the advantage of access to soil moisture recharged by rainwater through an

470   increased root surface area in the shallow soil layer for this species in the mixed plantation (Fig S2).

Thus, plant physiological (Ψ_m) and root morphological adjustments were adopted by *H. rhamnoides* and

P. davidiana in the mixed plantation, respectively, to significantly enlarge $\Psi_{pd}-\Psi_m$ and increase RUP

(Fig 7). Similar to the result in pure plantations, no significant relationship between SF_R and ET_0 after

rainfall and relative response of ET_0 was observed for these species in the mixed plantation (Table S4).

475 This result also confirmed the influence of physiological or morphological factors on water consumption for these species in the mixed plantation in response to rainfall pulses.

Furthermore, consistent with the second adaptation type, mixed afforestation significantly decreased the water uptake proportion from the deep soil layer for these species (Table 3). The increasing rainfall amount significantly decreased water source proportion from deep soil layer (P<0.05) for *H.*

480 *rhamnoides* and *P. davidiana* in the mixed plantation (Table S3), with the corresponding values decreasing from $43.13 \pm 13.74\%$ and $47.07 \pm 5.39\%$ (both after 3.4 mm), respectively, to $21.54 \pm 8.9\%$ (after 35.2 mm) and $28.66 \pm 12.26\%$ (after 24 mm) (Fig 4). Thus, both increased rainwater uptake and decreased water source competition from the deep soil layer were adopted by these species in the mixed plantation to minimize water sources competition under water limited conditions.

485

4.3 Implications for plantation species and type selection based on rainwater uptake and consumption

Rainwater uptake by plant and water consumption response to rainfall pulses may influence plant physiological process and the water cycle (Meier et al., 2018; Zhao et al., 2021). In pure plantations, *H.*

490 *rhamnoides* rather than *P. davidiana* showed rainwater uptake advantage due to the large $\Psi_{pd}-\Psi_m$ for the former species, although both species exhibited plasticity in water sources. The excessive water uptake from the deep soil may desiccate deep soil (Wu et al., 2021), weakening plant resilience to drought stress and thus plant community sustainability in this Loess Plateau region (Song et al., 2018; Zhao et al., 2021). Whether rainwater uptake can reduce plant water uptake from deep soil layers is

495 essential for plantation adaptation (West et al., 2012; Wu et al., 2021). In the present study, the proportion of water sources from deep soil layers was significantly decreased with increased rainfall amount for these species in both pure and mixed plantations (P < 0.05), except for *P. davidiana* in pure plantation. Physiological (e.g., Ψ_m) and morphological (fine root distribution) adjustments were observed for *H. rhamnoides* and *P. davidiana* in the mixed plantation, respectively, to enlarge $\Psi_{pd}-\Psi_m$

500 and enhance the rainwater uptake and water consumption (Tables 1 and 2; Fig 7). Mixed afforestation also significantly decreased the deep soil water uptake proportion for both species (Table 3).

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Furthermore, mixed afforestation increased the total biomass of *H. rhamnoides* and *P. davidiana* that calculated through the allometric equation indicated in Zhou et al (2018) and Tang et al (2019) (Table S5). Thus, rainfall pulse sensitive species in pure plantation, and plant species in mixed plantation that

505   can adopt physiological or morphological adjustment to enhance rainwater uptake and reduce excessive water uptake from deep soil layers, should be more considered for use in the studied region.

5 Conclusions

The influence of water sources and $\Psi_{pd}-\Psi_m$ on water consumption in response to rainfall pulse was

510   determined for *H. rhamnoides* and *P. davidiana* in the semiarid Loess Plateau region. In pure plantations, the SF_R was significantly influenced by RUP and $\Psi_{pd}-\Psi_m$ for *H. rhamnoides*, but the SF_R was only significantly influenced by $\Psi_{pd}-\Psi_m$ for *P. davidiana*. Meanwhile, the lower value $\Psi_{pd}-\Psi_m$ was consistent with the high SF_R for *H. rhamnoides*, and the higher value $\Psi_{pd}-\Psi_m$ was consistent with the low SF_R for *P. davidiana*, in response to rainfall pulses. Thus, *H. rhamnoides* and *P. davidiana* exhibited

515   sensitive and insensitive response to rainfall pulses, respectively. Furthermore, mixed afforestation enhanced the rainwater uptake and water consumption for both species. Significantly lower plant Ψ_m and increased fine root surface area were adopted by *H. rhamnoides* and *P. davidiana* in the mixed plantation, respectively, to enlarge $\Psi_{pd}-\Psi_m$ and enhance rainwater uptake and decrease water source competition from the deep soil layer. The SF_R was significantly influenced by RUP and $\Psi_{pd}-\Psi_m$ for

520   both species in the mixed plantation, and rainwater uptake enhanced plant water consumption in the mixed plantation regardless of species sensitivity to rainfall pulses.

Data availability

The data that support the findings of this study are available from the corresponding author upon

525   request.

Author contribution

YKT designed the study, performed the statistical analyses and wrote the original manuscript draft.

LNW and YQY performed the experiments and collected the data. DXL collected the data.

530

Declaration of Competing Interest

The authors declare that they have no conflict of interest.

Acknowledgement

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