RESEARCH ARTICLE

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Water use partitioning of native and non-native tree species in riparian ecosystems under contrasting climatic conditions

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Abstract

1. One of the suggested mechanisms behind the success of non-native plants in recipient ecosystems is competition avoidance with natives by means of different resource-use strategies, such as deeper water uptake under dry conditions.

2. We aimed at evaluating water source partitioning between native and non-native tree species coexisting in central Spain floodplains; determining the dependency on drought stress of such water sources use; and assessing if the reliance on deeper water sources relates with physiological and growth performance.

3. We assessed water uptake depth, leaf functional traits related to physiological performance and growth of native (*Populus alba*) and non-native trees (*Ailanthus altissima*, *Robinia pseudoacacia*) coexisting in riparian forests under different drought conditions (drier, intermediate and wetter). We analysed δ^2H and δ^{18}O isotopes in xylem water and in soil water from top, mid and deep soil depths and determined the contribution of each water source to overall plant xylem water. Leaf traits related with resource use and secondary growth were assessed for each species.

4. We found stronger differences between sites than between species, with all species taking more deep water in the driest site (~45% of the xylem water) than in the wettest (~15%). However, under drier conditions, species differences were significant for top-soil water use, with *R. pseudocacia* withdrawing more superficial water (~22%) than *A. altissima* (~8%). These results indicate stronger water partitioning under drier conditions. Non-native species showed a physiological strategy characterized by greater leaf N, water content, and enriched δ^{13}C and δ^{15}N values independently of the deep-water uptake. However, a positive relationship between deep soil water use and such strategy was found for *P. alba*.

5. We highlight that those native and non-native species differences were more evident regarding physiological performance at leaf level than for deep-water uptake or growth. Furthermore, our results suggest that differences in water sources used by coexisting species may increase under drier conditions.

KEYWORDS
drought, growth, niche segregation, non-native trees, physiological performance, riparian ecosystems, water isotopes

1 | INTRODUCTION

Biological invasions are clear and strong indicators of global change since they affect biodiversity and alter the environmental services in their new ranges (Castro-Díez et al., 2019, 2021; Vilà et al., 2011). This is due, in part, to the fact that many invasive species outperform the native (NT) ones, subsequently threatening the local biological diversity (Richardson & Pyšek, 2006).

Although many non-native (NNT) species are not able to survive and invade the new habitat, successful invaders tend to bear traits that allow for niche complementarity to reduce competition with natives (MacDougall et al., 2009). However, despite the increasing knowledge on the traits and strategies linked to successful plant invaders, the context dependency of the mechanisms behind invasive success limits our understanding of invasion events (Novoa et al., 2020). This is especially true in the case of adult tree species, which have been far less studied than other life stages and growth forms regarding the invasive process (but see Antunes et al., 2018; Porté et al., 2011). Therefore, more information of the mechanisms behind invasion success in adult trees is needed in particular contexts.

The success of invading trees does not only depend on the characteristics of the particular species, but also on their interaction with the biotic and abiotic environment of the receiving ecosystem (Castro-Díez et al., 2019). Therefore, changes in the environment associated with climate change are also expected to affect the invasive success of NNT trees. Changes that reduce the availability of resources, such as lower precipitation, higher temperatures and longer droughts, could favour NNT trees adapted to such conditions (Bellard et al., 2012; Bradley et al., 2010; Diez et al., 2012; González-Muñoz et al., 2015), especially if native ecosystems are highly stressed (e.g. riparian forests). Thus, an improved knowledge about how NNT tree species benefit and in which contexts will they benefit the most from these changes requires specific case studies addressing differences in resource use of NT and NNT species under contrasting conditions (see Funk & Vitousek, 2007).

Riparian ecosystems are highly vulnerable to invasion (Catford et al., 2011), and the impact that invasive species produce is particularly worrying given the numerous ecosystem services they provide: water purification, energy dissipation in floods or control of erosion, among others (Castro-Díez & Alonso, 2017). In these ecosystems, the reduction of flows not only due to climate change (through reduction of precipitation and decrease in water tables) but also due to anthropogenic uses (i.e. regulation or drift of flows for irrigation) can promote community shifts directly benefiting the existing NNT trees or indirectly reducing the competitive capacity and/or physiological performance of NT trees (Smith et al., 1998). For example, it has been acknowledged that invasive trees can alter water availability for human use (le Maitre et al., 2015; Ntshidi et al., 2018) and to have strong impacts on watershed hydrology and water balance (Cavaleri & Sack, 2010). Moreover, tree species with greater capacity to access deeper below-ground layers might have an advantage under more arid conditions compared to those relying on more superficial water (Pierret et al., 2016). However, few studies have compared the water pools accessed by coexisting tree species and their possible changes under distinct climate conditions (see Silvertown et al., 2015 for example), being especially scarce in invaded communities. This is due, among other reasons, to the fact that the study of water source partitioning and/or use usually requires complex methodologies to measure root-related traits. Nowadays, using isotopic techniques, it is possible to assess the differential water-use strategies of species that coexist in areas where water is or may become limiting (Antunes et al., 2018; Máguas et al., 2011; Saito et al., 2014).

Stable isotopes have been successfully used to evaluate the effects of invasive species on community functioning (McCue et al., 2020). The analysis of the isotopic composition of oxygen ($\delta^{18}O$) and hydrogen ($\delta^{2}H$) measured in the water extracted from woody tissues and the potential water sources allows us to study the depth from which the different species obtain water from (Brooks et al., 2010). As an example, under dry conditions, the water from the shallower soil horizons is more evaporated and enriched in the heavier isotopes of hydrogen and oxygen than the water from the deeper horizons, where the effect of evaporation is minimal (Filella & Peñuelas, 2004). Therefore, these techniques, together with functional traits, are very helpful to discern water-use strategies of coexisting species and to predict future changes in the structure, composition and functioning of NT communities in the presence of NNT species.

The main objective of this study is to determine water-use partitioning of three tree species coexisting in floodplains under contrasted climate conditions: the native (NT) *Populus alba* and the non-natives (NNT) *Robinia pseudoacacia* and *Ailanthus altissima*. The specific objectives are to (a) quantify the main sources of water—in terms of below-ground depth—used by the NT and NNT species; (b) test whether the water source used by each species is dependent on the drought stress experienced at each site; (c) determine whether the main water sources used by the trees are influenced by other intrinsic (tree size) and/or by extrinsic factors (size of the neighbours; distance to the river or canopy cover); and (d) assess whether the reliance on deeper soil layers is related to a better physiological and/or growth performance of the individuals.

Given that the study NNT species are not exclusively riparian trees, we hypothesize that they will rely more on deeper soil layers than NT trees. NT *P. alba* trees usually have more access to water in the floodplains and we expect them to be less flexible in adjusting to deeper water use under atypical water limitation. Under drier conditions—which promote shallow water evaporation—we expect that the water sources used by all species will shift towards deeper soil layers. By contrast, under wetter conditions, NT trees are expected to primarily rely on shallow water, while NNT ones may still rely on deeper water to avoid competition with natives. Thus, we expect higher partitioning among species under wetter conditions to minimize competition for water, in accordance with the expectation of more intense competition under less stressed conditions (Bertness & Callaway, 1994; Grime, 1973). Moreover, intrinsic (tree size) and extrinsic variables (such as basal area [BA] of neighbours, canopy cover and the distance to the river) might be important

variables explaining contrasting water sources use. Finally, we hypothesize that the ability to take water from deeper soil layers will enhance the trees' physiological and/or growth performance as it would balance the trees' water uptake with their losses.

2 | MATERIALS AND METHODS

2.1 | Study area and species

We identified three sites in central Spain along contrasting climatic conditions where the three target species coexist in riparian forests of the Henares river. These correspond to: a warm/dry site located in Mejorada del Campo (Madrid, 40°23′53.88″N; 3°30′32.86″W; 551 m a.s.l.); an intermediate site located in Guadalajara (Castilla la Mancha, 40°38′1.9″N; 3°11′10.6″W; 630 m a.s.l.) and a cold/wet site in Jadraque (Castilla la Mancha, 40°56′42.29 N; 2°56′27.04″W, 808 m a.s.l.). Hereafter, we refer to these sites as dry, intermediate and wet sites (DRY, INT and WET, respectively) but note that DRY and WET sites are also warmer and colder, respectively. The climate at all sites is continental Mediterranean, but they differ in mean annual temperatures and accumulated precipitation with mean temperatures of 15.28, 14.23 and 12.96°C, respectively, and annual precipitation of 364, 487 and 413 mm (period 2000–2020, Cruz-Alonso et al., 2022; Moreno & Hasenauer, 2016; Rammer et al., 2018). The drought period in this area usually lasts for 2–3 months during summer, being more pronounced at the DRY site compared to the WET one. The aridity index (P/PET, UNESCO, 1979) for the same period is 0.56, 0.63 and 0.67 in the DRY, INT and WET sites, respectively. At the three sites, soils are formed by limestone and quartzite gravels and polygenic pebbles, sands and silty-clay sands (floodplain, Mapa Geológico Español). We did not need any permission for the fieldwork.

The study sites offered a unique opportunity to assess the different responses under contrasting climate conditions of coexisting tree species belonging to two categories: (a) non-native trees (NNT, the invasive *Ailanthus altissima* (Mill.) Swingle (RD630/2013) and the exotic *Robina pseudoacacia* L.); and (b) a native tree species (NT, *Populus alba* L.). The three species are deciduous and fast-growing pioneer trees. *P. alba* is native to the southern part of Eurasia and north Africa and is the dominant species in extended areas of the Henares river floodplains where precipitation ranges 300–1,000 mm with a short dry season (Lara et al., 1996). *A. altissima* is native to South East Asia and has a high tolerance to a wide range of environmental conditions (Kowarik & Säumel, 2007) but the native range of precipitations are between 400 and 1,400 mm, and this species tolerates a 4- to 8-month dry season. *R. pseudoacacia* is native to southeastern North America and it is a light-demanding pioneer tree able to grow in habitats spanning 700–2,000 mm with dry seasons not exceeding 4 months (CABI, 2021), although in the invaded range it is often found on direr climates, but associated with floodplains and river banks (Huntley, 1990).

During summer 2019, we sampled five adult trees per species and site, with similar diameter at breast height (dbh, Table S1). The location of each individual was recorded and the distance to the river was obtained with the IGN application (National Geographic Institute). All individuals were sampled as close as possible to avoid soil differences. We also calculated the total BA of the neighbour trees of each individual using the point cantered quarter method (Mitchell, 2015), which was used as a competition index accounting for neighbours with dbh >7.5 cm. Canopy cover (percentage of the sky covered by leaves) was calculated with the mobile application GLAMA (Tichý, 2014, 2016) using hemispheric photographs taken at breast height and 2-m distance to the north from the focal tree trunk. Measurements were taken at the peak of summer drought during 3 days with similar climate conditions (i.e. July 29th and 30th and August 3rd) after *c.* 1 month without rain to ensure that (a) the gradient in the composition of soil water isotopes was sufficiently contrasted to distinguish different depths (higher isotopic composition in top than in deep layers) and (b) water table was within its lowermost limit (maximizing possible differences in root water uptake).

2.2 | Xylem samples

Suberized xylem samples were obtained from 3-year-old sunlit twigs of about 10-cm long. The bark and phloem were removed as fast as possible to avoid contamination with phloem water, evaporation and consequent xylem water enrichment. The peeled xylem samples were placed in glass vials (airtight tubes, Duran GL-18, Duran Group GmbH) and sealed with a cap and parafilm. They were immediately introduced in dry ice and kept frozen until processing.

2.3 | Soil, river and well water samples

At the same time as we collected the xylem material, we also collected soil samples at different depths: 1–25 cm, 26–50 cm, 51–75 cm and 76–100 cm at each site (except at 76–100 cm at WET site; see Supporting Information 2). Two sampling points per site were selected to have two replicates for each soil depth and the mean value and SD were used for further statistical analysis. We also collected water from two close-by wells per site (sampled after bailing to remove stored casing water) and the river. Soil and water samples were rapidly sealed in glass vials with parafilm, introduced into a fridge with dry ice and kept frozen until processing.

2.4 | Xylem and soil water extraction

Xylem and soil water were extracted by cryogenic vacuum distillation (Dawson & Ehleringer, 1993) at the Department of Crop and Forest Sciences of the Universitat de Lleida (Spain). The extraction system consisted of 10 sample tubes connected with Ultra-TorrTM fittings (Swagelok Company) to 10 U-shaped collection tubes specifically designed for this system. Sample tubes were placed in a heated mineral oil bath (120°C) to evaporate water and the U-tubes

were cooled with liquid nitrogen to condense the water vapour. The extraction system is connected to a vacuum pump (model RV3; Edwards) to guarantee the flow of water vapour from the sample tubes to the collection tubes and to prevent contamination with atmospheric water vapour. The entire system maintains constant vacuum pressures of $c.$ 10^{-2} mbar. After an extraction time of 2 hr (soil) and 1.5 hr (xylem), trapped water was transferred into 2-ml vials and stored at 4°C until analysis.

2.5 | Water isotopic analyses

Water samples were analysed for ^2H and ^{18}O using IRIS analyses (Picarro L2130-i; Picarro Inc.) at the UdL (see Martín-Gómez et al., 2015 for further details). $\delta^{18}O$ and δ^2H values are expressed relative to Vienna Standard Mean Ocean Water (VSMOW) in per mil notation (‰; i.e. isotopic composition):

$$\delta^{18}O \text{ or } \delta^2H = \left(R_{sample} / R_{standard} - 1 \right) \times 1,000,$$

being R_{sample} and $R_{standard}$, heavy to light isotopic ratios ($^2H/H$ and $^{18}O/^{16}O$) of the sample and the standard, respectively.

Because residual organic contaminants in the distilled water can interfere with the IRIS analysis of plant and soil samples (Martín-Gómez et al., 2015), we checked for the presence of contaminants using Picarro Inc.'s ChemCorrect post-processing software v1.2.0.

2.6 | Secondary growth

Tree growth was measured for each individual as basal area increment of the last 5 years (BAI5). During the branch and leaf sampling, we further collected one stem core for tree growth determination. We used a 5 mm increment borer (Haglöf) at a height of 1.3 m trying to reach the pith. We followed standard dendrochronological techniques (Stokes & Smiley, 1968) to prepare the cores. These were dried, mounted, glued on wooden sticks and sanded with successively finer grades of sandpaper until optimal surface resolution allowed the annual rings to be distinguished under magnification. Annual radial increments were measured to the nearest 0.01 mm using CooRecorer and CDendro version 9.5 (Stockton Maxwell & Larsson, 2021). We estimated BAI5 as $BAI_5 = \pi (R_t^2 - R_{t-5}^2)$, where R_t is the radius of the stem, and R_{t-5} is the radius of the stem without the 5 outermost years. The radius of the stem, R_t, was computed by summing all tree rings. We further normalized this variable dividing it by its BA.

2.7 | Leaf traits related to main resources: Water, carbon and nutrients

Leaves from sun and shade exposures were collected (three for each exposure for *A. altissima* and *R. pseudoacacia* and six per exposure for *P. alba* given their smaller size). In the field, the leaves were weighted,

and chlorophyll content was determined with a Chlorophyll Meter SPAD-502Plus. Leaves were taken to the laboratory and oven-dried at 70°C during 48 hr. They were then weighted again to obtain the leaf dry mass and milled for further analyses. Foliage moisture content (FMC) was calculated as FMC = ([Fresh weight – Dry weight]/Dry weight) × 100. FMC has been related to stomatal regulation of water loss, water loss by cuticle and incomplete stomatal closure, to leaf water potentials and even to be affected by rooting depth (Nolan et al., 2020). Leaf traits measured in milled samples included leaf C and N percentages and isotope ratios ($\delta^{13}C$, $\delta^{15}N$). Carbon and nitrogen in the leaves were accounted for as they are important components of the leaf economics spectrum (Wright et al., 2004), related to biogeochemical cycles and carbon gain and allocation. We also evaluated leaf carbon isotope composition ($\delta^{13}C$) as a time-integrated functional response to environmental variations. The CO_2 supply at the site of carboxylation determines discrimination against $^{13}CO_2$ relative to $^{12}CO_2$ during photosynthesis (Farquhar & Richards, 1984). Thus, lower ^{13}C discrimination (enriched $\delta^{13}C$ values) could be driven by stomatal closure and/or higher photosynthesis capacity, which is very useful to compare species strategies under water limitations. Lastly, $\delta^{15}N$ in the leaf reflects the isotopic signature of N inputs to and losses from the system. Overall, there is fractioning of the heavy isotope during mineralization and nitrification, which means that organic N becomes enriched in ^{15}N whenever these rates are high (Lambers et al., 2008). However, many other factors are involved in the $\delta^{15}N$ signature, including rooting depth or the form of N that is utilized (see Schulze et al., 1994).

Dry samples of foliage were ground to a fine powder in a Retsch MM 200 (Haan, Germany). Powder (5±0.2 mg) was weighted into tin capsules and stable isotope ratio analysis was performed at the Stable Isotopes and Instrumental Analysis Facility, at the Faculdade de Ciências, Universidade de Lisboa—Portugal. $\delta^{13}C$ and $\delta^{15}N$ in the samples were determined by a continuous flow isotope mass spectrometry (Preston & Owens, 1983), on a Sercon Hydra 20–22 (Sercon) stable isotope ratio mass spectrometer, coupled to a EuroEA (EuroVector) elemental analyser for online sample preparation by Dumas combustion. $\delta^{15}N$ values are referred to air and $\delta^{13}C$ values are referred to Pee Dee Belemnite. The reference materials used were USGS-25, USGS-35, BCR-657 and IAEA-CH7 (Coleman & Meier-Augenstein, 2014); the laboratory standard used was Rice Flour. Uncertainty of the isotope ratio analysis was ≤0.1‰. The major mass signals of N and C were used to calculate total N and C abundances, using Wheat Flour Standard OAS (Elemental Microanalysis, UK, with 1.47%N, 39.53%C) as elemental composition reference materials.

2.8 | Quantification of water sources used by trees

To quantify the proportions of main water sources used by each species, we applied Bayesian mixing models using the MixSIAR Bayesian isotope mixing model (v 3.1; Stock & Semmens, 2016a). These Bayesian mixing models are commonly used in ecology for

estimating contributions to a mixture while accounting for variability for the data (Stock et al., 2018). In our study, we considered both the $\delta^{18}O$ and δ^2H isotopes despite some studies showing more negative δ^2H values in xylem than in water sources (Barbeta et al., 2021) because such isotopic offset was not found in our plots (see Figure S1). Moreover, all sampled water sources were sufficiently differentiated to distinguish between depths being more enriched in the top compared to deep soil layers.

The input data of the MixSIAR model were the measured dual isotope values ($\delta^{18}O$ and δ^2H) of individual trees' stem xylem water (mixture raw data) and potential sources of water by site, considered to be soil water at different depths (0–25, 26–50, 51–75, 76–100 cm), river and well water. The discrimination values were set to zero for the two isotopes assuming no isotope fractionation during plant water uptake (Dawson & Ehleringer, 1991; Ehleringer & Dawson, 1992). Individual (tree level) effects were included in all analyses using raw tree tracer values together with mean and standard deviations of source tracer values (for each soil depth) by site. The Markov Chain Monte Carlo parameter was set to 'long' run length and the model was run for each tree dataset using the implemented process error option (Stock & Semmens, 2016b). Trace plots and the diagnostic tests Gelman–Rubin, Heidelberger–Welch and Geweke were used to determine the model convergence. The mean estimated proportions were used for further data analyses.

Aiming to lead to an easier interpretation of the water sources use, and more clearly indicate the primacy of certain water sources used by the species, we (posterior) reduced the sources to four main water sources. In this posteriori aggregation (Phillips et al., 2005), deeper soil layers (i.e. >75 cm) were merged, while keeping the contribution of top-soil and the two mid-layers, as they would indicate the use of deep roots, intermediate, shallow and very shallow roots. Mid-layers were not aggregated since they represented different water sources (isotopically separated and non-correlated in the diagnostic matrix of the mixing model). This resulted in the following four main water source categories, used for further statistical analyses: (a) Top: considering the uppermost soil water (from 0 to 25 cm); (b) Mid26: water from the intermediate soil profile from 26 to 50 cm; (c) Mid51: water from the intermediate soil profile from 51 to 75 cm soil depth; and (d) Deep: considering the deeper soil layers, summing the contribution of soil water below 75 cm, river and well water.

2.9 | Statistical analyses

Differences in water sources use between the study species and sites were evaluated with beta regression analyses for proportions (Cribari-Neto & Zeileis, 2010). To test for significant differences between sites and species, Tukey-adjusted comparisons were conducted. We also fitted a generalized linear mixed model using Template Model Builder with beta family (Brooks et al., 2017) to test for the effects of intrinsic (dbh) and extrinsic factors (distance to the river, canopy cover and BA of neighbouring trees) on water sources use using species as a random factor.

We performed a principal component analysis including all physiological variables (leaf $\delta^{13}C$, $\delta^{15}N$, N, C, FMC, chlorophyll content), dbh and growth (expressed as BAI5/BA). Nonparametric analyses of variance on Rank Aligned Transformed data were used to test the effects of site, species and their interaction on the scores of the first and second principal components (PC1 and PC2). We further used the PC scores to test whether the reliance on deep-water sources is related to plant physiological performance using Spearman's rank correlations (as the assumptions of normality and homoscedasticity were not observed). All analyses were performed using R software (R. 4.0.3 Statistical Computing).

3 | RESULTS

3.1 | Water sources used by the tree species at climate-contrasted sites

Analyses conducted to test for site and species effects on the contribution of top (from 0 to 25 cm), mid (from 26 to 50 cm and from 51 to 75 cm) and deep (>75 cm) water sources to xylem water indicated site differences for the sources used (Table 1, Figure 1). At the DRY site, all species took more water from deep sources (45% of the xylem water), followed by mid- (deep-mid 31%, shallower-mid 9%) and top ones (15%, Figure 1a). This pattern was different from that at the INT and WET sites (Figure 1b,c), where trees took most of the water from mid-layers (60% and 83%, respectively) compared with the deep (32% and 15%) and top ones (8% and 2% for INT and WET sites, respectively). Instead, species differences and the interaction site × species were

TABLE 1 Results from beta regression for proportion analyses testing site and species differences for Top, Mid26, Mid51 and Deep-water contribution to xylem water. See Figure 1 for further details on the species and site differences

	Pseudo R^2	F	p
Top	0.68		
site		24.45	<0.0001
sp		4.57	0.01
site×sp		4.09	0.003
Mid26	0.88		
site		299.926	<0.0001
sp		2.677	0.07
site×sp		2.119	0.08
Mid51	0.76		
site		77.056	<0.0001
sp		1.527	0.21
site×sp		1.907	0.11
Deep	0.86		
site		155.15	<0.0001
sp		2.41	0.09
site×sp		2.06	0.08
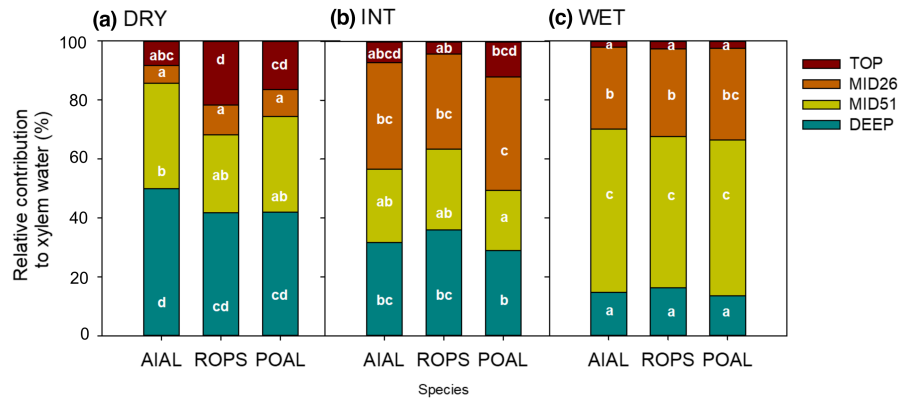
FIGURE 1 Relative contribution from different water sources to xylem water (%) at (a) DRY, (b) INT and (c) WET sites for each species (AIAL: *Ailanthus altissima*; ROPS: *Robinia pseudoacacia*; POAL: *Populus alba*). Different sources: Top (0–25 cm), Mid26 (26–75 cm); Mid51 (51–75 cm) and Deep (>75 cm) water sources are represented with different colours. Significant differences across sites and species are indicated with different letters. See Figure S2 and Table 1 for further details on species and site differences.

only found to be significant for the top-soil water source ($p = 0.003$, Table 1, Figure 1), although slight differences were also found for Mid26 and Deep layers ($0.05 < p < 0.1$, Table 1). Differences among species within sites were only found at the DRY site (Figure 1a). At the DRY site, *A. altissima* was the species taking less superficial water (~8%), and similar values were found at INT and WET for this species. *R. pseudoacacia* at DRY was the species showing the greatest top-soil water use (22%), which was significantly higher than the same species at INT and WET (Figure 1). Top water used by *P. alba* showed non-significant differences with the NNT species, but significantly lower values were found at the WET site compared to DRY and INT.

3.2 | Influence of other intrinsic and extrinsic factors on water sources use

Accounting for the possible influence of other intrinsic and extrinsic factors (apart from species and site effects) on the use of water sources by trees, we tested the proportion of Top, Mid26, Mid51 and Deep water use as a function of tree size (dbh), distance to the river, canopy cover and total BA of the neighbours. Sites had similar growth and competition-related variables, indicating a lack of confounding factors of the effects of site (BAI5/BA, $F = 0.35$; $p = 0.71$; Total BA, $F = 1.36$; $p = 0.27$). Our results pointed to canopy cover influencing the water use from the Top and Mid51-layer sources (Table 2). Results indicated a lower use of top soil water and a higher use of water from 51 to 75 cm layers when the canopy cover was higher (Table 2). Furthermore, total BA of the neighbour trees had a negative effect on Mid26-water use and a slight positive relationship for the deep-water use (Table 2).

3.3 | Relationship between deep-water sources use and trees' physiological and growth performance

The results of the principle component analyses, including all measured traits, revealed a first axis (PC1) mainly related to physiological

TABLE 2 Results from beta regression analyses considering the intrinsic variable (DBH) and the extrinsic ones [total basal area (BA) of the neighbours—T.BA (m^2 ha^{-1})]; distance to the river—D.river (m); and canopy cover—CC (%) for the proportions of Top, Mid26, Mid51 and Deep water sources use pooling all sites and species together

	Estimate	SE	z value	Pr(>|z|)
(a) Top				
(Intercept)	0.15	0.89	0.17	0.87
DBH	−0.02	0.03	−0.57	0.57
T.BA	0.001	0.002	0.57	0.57
D.river	0.01	0.01	1.4	0.15
CC	−0.03	0.01	−3.15	0.002
(b) Mid26				
(Intercept)	−2.39	0.89	−2.68	0.01
DBH	0.02	0.03	0.93	0.35
T.BA	−0.005	0.002	−2.09	0.04
D.river	−0.006	0.01	−1.11	0.27
CC	0.01	0.01	1.29	0.20
(c) Mid51				
(Intercept)	−1.89	0.69	−2.75	0.01
DBH	−0.01	0.02	−0.28	0.78
T.BA	0.0004	0.002	0.24	0.81
D.river	0.01	0.004	1.64	0.10
CC	0.02	0.01	2.07	0.04
(d) Deep				
(Intercept)	0.47	0.74	0.63	0.53
DBH	−0.01	0.02	−0.56	0.58
T.BA	0.003	0.002	1.97	0.05
D.river	−0.01	0.004	−1.31	0.19
CC	−0.01	0.01	−1.52	0.13

performance (Figure 2). This axis accounted for 29.18% of the total variance with positive values representing individuals (mostly NNT trees) bearing higher leaf δ^{15}N, N, FMC and δ^{13}C, together with
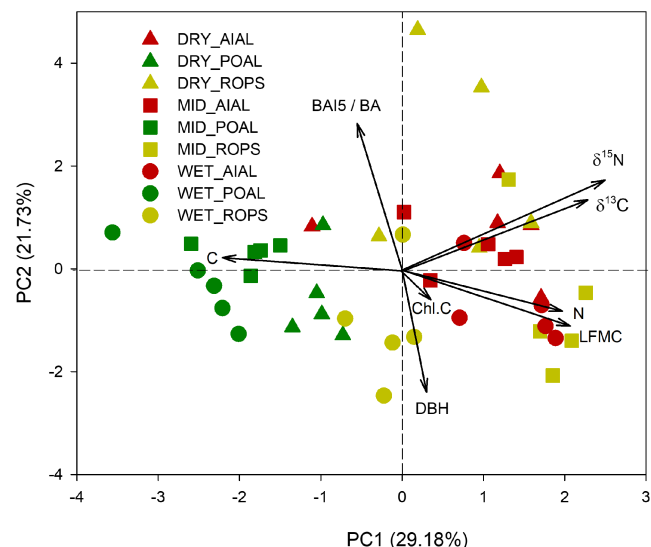
FIGURE 2 Results from principle component analyses (PCA) where all physiological and growth variables are grouped in the main two axis: PC1 accounting for 29.18% and PC2 accounting for 21.73% of the variance. Each individual is represented with different colours and symbols depending on the species and site. DBH (diameter at breast height), FMC (foliage moisture content), Chl.C (chlorophyll content), $\delta^{13}C$ (leaf carbon isotopes), $\delta^{15}N$ (leaf nitrogen isotopes), C (leaf carbon), N (leaf nitrogen) and normalized basal area increment for the last 5 years (BAI5/BA).

FIGURE 3 Relationships between Deep water source use (%) and (a) principal component (PC)1 (related to physiological performance) and (b) PC2 (related to growth performance). Different colours stand for species and symbols for site. Results from significant linear regressions are also shown.

lower leaf carbon percentages. PC1 showed significant differences across sites and species with significant effects of species-site interaction (Table S2; Figure S2). The species most positively related to this axis was the NNT *A. altissima*, while the NT *P. alba* was in the opposite direction with negative values indicating a higher percentage of carbon in the leaves and lower values of all other traits. *R. pseudoacacia* showed lower values of PC1 in WET than in INT and DRY, similar to the other NNT (*A. altissima*). On the contrary, *P. alba* had the lowest values of PC1 in the three sites with slightly greater values with higher water stress (Figure 2; Figure S2).

Instead, the second axis PC2 (21.73% of variance explained) was represented by growth performance, with higher values indicating greater BAI5/BA and lower DBH. Significant differences were found for the interactions between sites and species (Figure 2; Table S2; Figure S2), with highest values of PC2 being found for *R. pseudoacacia* in the DRY site (Figure 2; Figure S2) and the lowest values for all species in the WET site (except for *P. alba*, for which non-significant differences across sites were found).

We further conducted correlation analysis relating PC1 and PC2 separately for the three species with the deep-water uptake (%) to test for possible relationships between deeper water uptake and trees' performance. Results showed that higher PC1 values were positively related to greater deep-water uptake only for *P. alba* (Figure 3a). *A. altissima* showed high values of the physiological axis (PC1) independently of the deep-water source use ($r = -0.14$, $p = 0.61$), and *R. pseudoacacia* only showed a slight positive correlation between PC1 and proportion of deep-water uptake but it was
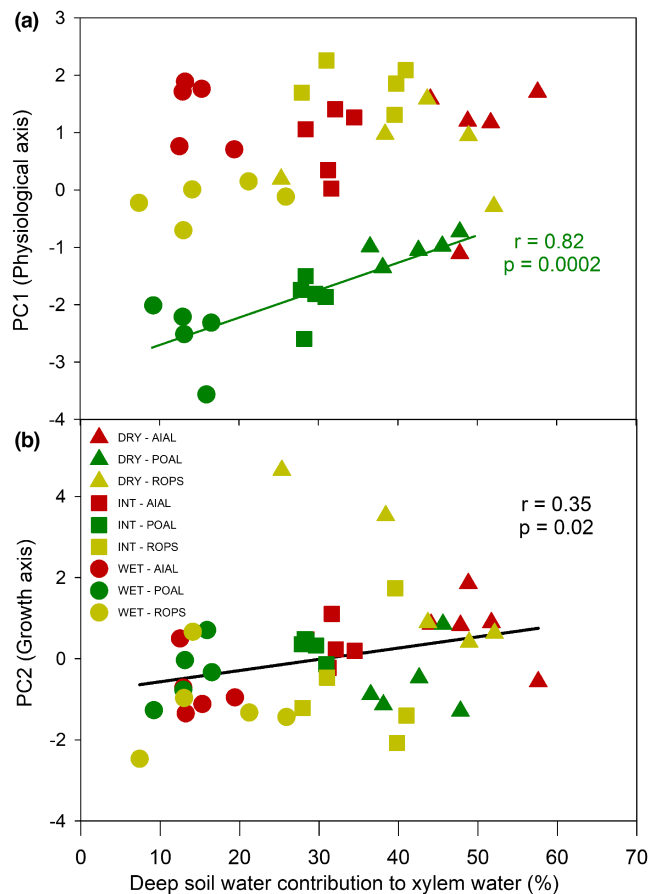
not significant ($r = 0.44$, $p = 0.09$). Considering the growth axis (PC2), we observed a positive, although slight, relationship with deep-soil water use (Figure 3b) for all species together.

4 | DISCUSSION

4.1 | Which are the main differences in the water sources used by the NT and NNT species at sites differing in drought stress?

We found that water use partitioning was more dependent on site than on species. In the DRY site, all species used more water from deep sources (45% of the xylem water), followed by the Mid51 layer (31%), while using less mid-shallow soil layers (26–50 cm, 9%), than in INT and WET sites. These results indicate that the three study species, independently of their identity and suite of traits, are able to shift sources and extract more deep water when soil water becomes scarce during the summer drought. Previous literature has shown deeper rooting depths in water-limited ecosystems (e.g. Barbeta & Peñuelas, 2017; Fan et al., 2017; Kozlowski & Pallardy, 2002; Leuschner et al., 2001; Schenk

& Jackson, 2002; Voltas et al., 2015). The advantages of having deep roots are evident under extended droughts, as trees can increase the ratio of root vs. above-ground biomass to increase whole plant water uptake, avoiding excessive drought stress and maintaining the plant's water status balance with water losses. Nonetheless, we hypothesized a deeper water uptake for NNT species as an efficient strategy to increase the amount of available water (Cavaleri et al., 2014) and to have access to resources unused by the NT species, allowing the non-natives to be more successful than the resident-dominant species. Instead, NNT species (i.e. *A. altissima* and *R. pseudoacacia*) did not take deeper water than the NT *P. alba* at either site. Our lack of difference in deep-water use among species could be explained since *P. alba*, despite being a riparian species, is well adapted to the strong seasonality of Mediterranean floodplains, where the water tables can be very deep during summer. Indeed, *P. alba* has been shown to be more drought tolerant than other coexisting NT tree species, such as *Salix alba* or *Populus nigra* (González et al., 2012), which could be linked to its formation of deeper roots. Thus, the three study species seem to be able to avoid low water potentials by developing deep tap roots as a mechanism for resisting soil water scarcity (see Brunner et al., 2015; Chaves et al., 2003; Hartmann, 2011) while still using some contributions of very shallow and occasional top-soil water.

Species differences in water use were only found for the top-layer at the DRY site, with *R. pseudoacacia* making use of a higher proportion of superficial water in the soil (especially compared to *A. altissima*). These species differences were not found at the other sites. This result contradicts our initial hypotheses of higher reliance of NT species on shallow water and of higher water partitioning in wetter conditions. However, it is in line with other studies suggesting higher resource partitioning among coexisting species where water is a limiting resource (e.g. Antunes et al., 2018; Lin et al., 1996; Silvertown et al., 2015; Weltzin & McPherson, 1997). Drier conditions would increase water stress between species that need to diversify the water uptake from other layers, including the uppermost ones from which it is more difficult to extract water and entails a higher risk of root cavitation (Sperry & Ikeda, 1997). Against our expectation of NNT species relying more on deeper soil layers than NT trees, *R. pseudoacacia* presumably develops lateral and shallow root spreads (DeGomez & Wagner, 2001), that are of great importance in water-limited environments to take advantage of shallow infiltration depths and occasional storms during the dry season in these systems (Dawson, 1996). Moreover, this species was also able to take as much deep water as the coexisting species, meaning that it successfully uses a dual root system that might confer this species with an efficient adaptive strategy for water and nutrient resource acquisition as found for typical Mediterranean species (David et al., 2013).

We initially expected more water partitioning (or hydrological niche segregation) under wetter conditions (see hypothesis in the introduction section). Some authors have pointed to those results, such as Xu et al. (2011) who found different water sources use when rainfall was available for three subalpine woody species, but the use of the same source under dry conditions. Instead, at the INT and WET sites, trees of all species took most of the water from mid-layers compared with the deep and top ones. These results support the idea that the majority of the roots are at the mid-soil layers taking most of the existing water at this middle range depth, when possible (e.g. Sánchez-Pérez et al., 2008), even being advantageous for more oxygenated conditions (Hahm et al., 2020). Thus, whenever there is enough available water, trees do not need to take it from deeper layers, where the investment in roots is costly, and the probability of oxygen limitation is higher.

4.2 | Are the main water sources used by the trees influenced by other intrinsic and extrinsic factors?

Apart from the environmental effect found, we explored other factors that could influence water sources use among the study species. We found, regardless of the species, lower top-water use with greater canopy cover. Furthermore, adult trees tended to use more mid-layer water (from 51 to 75 cm) whenever the canopy cover was higher. Although one could argue that canopy cover is directly related to competition, it only had a slight relationship with total BA ($r = 0.25$, $p = 0.09$), which was used in this study as a competition index among adult trees. Consequently, this effect of canopy cover might not be related to competition with coexisting adults but to water uptake niche segregation between adults and coexisting small trees and shrubs in the understorey (e.g. Ivanov et al., 2012), not captured by total BA. Because canopy cover was measured at 1.3 m, this variable included not only the uppermost canopy cover, but also the cover from shrubs and small trees that are greater than 1.3 m but lower than 7.5 cm of dbh (not measured by the total BA of neighbours). Thus, we suggest that adult trees change their water sources driven by both, climate and understorey pressure to avoid competition in the uppermost soil layers. These results agree with other studies reporting that the understory vegetation accounts for a high fraction of the total transpiration in Mediterranean riparian ecosystems (Nadal-Sala et al., 2017; Roberts, 1983). Our results further pointed to total BA of the neighbours being more important for mid- (26–51 cm) and deep-water uptake than the distance to the river or tree size. These results are in accordance with adult tree competition reducing the water uptake from 26 to 51 cm soil layers and leading to deeper water withdrawal (Schenk, 2006). Other studies have also suggested competition for water driving to deeper water uptake, as plant responses to competition are similar to those for water shortage in the soil (Nambiar & Sands, 1993). However, in the present study, this effect was only slightly significant, and thus we would need further samples to be able to affirm this relationship as a general pattern.

4.3 | Does the reliance on deeper water sources have an impact on NT or NNT species' physiological and growth performance?

Regarding the set of functional leaf traits, our results indicate that the NNT trees are characterized by lower leaf carbon in a trade-off with

high nitrogen contents; fast nitrogen cycling and acquisition from different sources (as denoted by high $\delta^{15}N$ values, Craine et al., 2015); high leaf water content, which can further be related to higher leaf water potentials (Nolan et al., 2020) and also enriched $\delta^{13}C$ values, suggesting that NNT trees may present a stronger stomatal control relative to photosynthesis (*A*) compared to the NT trees higher *A* relative to stomatal conductance (g_s) or a combination of both factors. Such physiological performance of the NNT trees suggests an acquisitive strategy regarding nutrient uptake, as frequently reported for invasive species (Funk et al., 2016; Leishman et al., 2007; van Kleunen et al., 2010). The NNT *R. pseudoacacia* is a species that, apart from being N-fixing through *Rhizobium* symbiosis (Ferrari & Wall, 2007), has both arbuscular mycorrhizae (AM) and especially ectomycorrhizae (ECM), which explains the high values of N in the leaves and the high value of $\delta^{15}N$ (Högberg, 1990). Concerning *A. altissima*, we also found high values of $\delta^{15}N$ which might not be explained through the ECM, as this species only has AM (Huebner et al., 2007). Thus, we speculate that the high $\delta^{15}N$ values in *A. altissima* leaves could be due to a higher amount of rapidly degradable litter under these individuals (González-Muñoz et al., 2013) compared to *P. alba*. For the later species, the high C and lignin content (González-Muñoz et al., 2013) might reduce the leaf turnover, thus decreasing leaf $\delta^{15}N$ and N content despite having AM and ECM (Werner et al., 2018).

Since carbon isotope ratios ($\delta^{13}C$) in C3 plants are expected to represent a proxy for stomatal limitations to photosynthetic activity (Farquhar et al., 1989) integrated over long time intervals (from the budburst until leaf maturation), the higher values of $\delta^{13}C$ for the NNT compared to NT species could be due to stomatal regulation of the former species avoiding water losses through stomatal control as an early response to water deficits in the study locations. This strategy would allow the maintenance of the leaf water status (as denoted by high leaf water content) at a level that does not impair metabolic processes, such as C gain. In line with these results, Trifilò et al. (2004) reported *A. altissima* promptly closing stomata under severe drought. In a phenological study with the same species in a comparable riparian ecosystem, Castro-Díez et al. (2014) observed that the three species started to grow at a similar date, but *A. altissima* arrested growth significantly earlier than *R. pseudoacacia* and *P. alba*. Thus, we conjecture that *A. altissima* avoids drought stress during summer regulating the stomata but experiences high g_s and photosynthesis earlier in the growing season (i.e. during shorter periods). In this way, the overall enriched leaf $\delta^{13}C$ values would reflect both the high photosynthesis during spring and the stomatal closure during the summer. This hypothesis would also be in line with higher leaf nitrogen concentrations for the NNT species and thus photosynthetic capacity during short periods (see Manzoni et al., 2015). Furthermore, the NNT species studied, and especially *R. pseudoacacia*, have also been shown to have high leaf plasticity (Ranney et al., 1990) such as leaf abscission during drought. Despite being generally considered a drought-resistant species, previous studies have identified *R. pseudoacacia* being limited by water supply (Vítková et al., 2015) or displaying decreases in photosynthetic rates and increased water-use

efficiency because of stomatal limitation (Wang et al., 2007). Furthermore, it has been shown to present the lowest transpiration values per BA unit compared to coexisting Mediterranean riparian species (Nadal-Sala et al., 2017). Contrary to the NNTs, the NT species *P. alba* was characterized by higher carbon content in the leaves together with lower N content, lower N contribution from different sources, lower leaf water content and lower $\delta^{13}C$. This would mean that the NT species has, in general, higher stomatal conductance relative to photosynthesis than NNT species and thus, higher water loss, but it could also mean *P. alba* bearing lower photosynthetic rates than the NNTs. Thus, gas exchange data (in particular c_i/c_a) or leaf $\delta^{18}O$ isotopic composition would be needed to confirm if these observed changes are driven mostly by g_s or by *A*. Interestingly, *P. alba* was the only species showing a significant increase in the physiological axis (PC1) with higher deep-water uptake, which suggests that the ability to explore deep soil layers for this species can increase its resource acquisitive performance during dry spells, increase leaf water and even be related to a higher stomatal control or to greater photosynthetic capacity. Species adapted to drought tend to invest more biomass into roots to optimize water uptake while minimizing water loss from transpiration, which could be the case for *P. alba* (i.e. increased root-to-shoot ratio as shown for other *Populus* species by Bogeat-Triboulot et al., 2007). The positive relationship between deep-soil water use and a higher PC1 for *P. alba* was mainly due to the water stress gradient, with higher values of the physiological axis and contribution to xylem water from deep layers being found at the DRY site. Thus, we hypothesize that in drier sites *P. alba* invests more carbon in the roots to have a deeper water uptake and have an additional stomatal control or higher photosynthetic capacity, which would allow for a better performance in terms of resource acquisition and/or leaf water status. Still, we must take into account that the patterns of C and N acquisition, water status and the trade-offs involved are not fully explained and thus species' overall strategies are still not completely defined.

Several studies have shown NNT species to have faster growth than their native counterparts (e.g. Grotkopp et al., 2002; van Kleunen et al., 2010), but this was not found in our study (see also Daehler, 2003). Instead, higher growth (BAI during the last 5 years) was found for individuals that used deeper water in the soil regardless the species. Although the relationship between growth and deep-water use was not strong ($r = 0.35$; $p = 0.02$), this result agrees with a better growth performance of the individuals using deeper water, as suggested by other studies (Christina et al., 2017; Pierret et al., 2016). While investing in root biomass could imply a lower carbon allocation in photosynthetic and shoot tissues (Weinstein et al., 1991), we might also reason that allocation of carbon to deep roots could overcompensate the costs (particularly if it allows reaching a reliable water table) finally resulting in a positive carbon increment over the long term (Ivanov et al., 2012). Very few studies, to the best of our knowledge, have related growth performance and water sources use in adult individuals. Thus, further studies relating the physiological, growth and water uptake depth of adult NT and

NNT trees would certainly help to better understand the differences and similarities in their performance.

5 | CONCLUSIONS

We have addressed the water use from different sources of NNT and NT trees coexisting in riparian forests and its possible relationship with tree growth and physiological performance under contrasting climate conditions. We found all species taking deeper water in the driest site while maintaining their physiological status suggesting that the three study species are able to avoid water stress. Water partitioning among species was only found on the superficial layers in the DRY site, which agrees with hydrological niche segregation under drier conditions. At dry conditions, *R. pseudoacacia* was the species withdrawing more superficial water (~22%) than the others, exploring both deep and shallow water (i.e. making use of a dual root system). NNT species showed a physiological strategy characterized by greater leaf N, water content, $\delta^{13}C$ and $\delta^{15}N$ independently of the deep-water uptake. A positive relationship between deep-soil water uses and physiological performance was only found for *P. alba*. We highlight that NT and NNT species differences were more evident regarding leaf functional traits than for deep-water uptake or growth. Overall, *R. pseudoacacia* seems to have a higher capacity to efficiently use distinct water sources, which is a plastic response that might provide this NNT species with a higher advantage under climatic changes in Mediterranean riparian ecosystems. Furthermore, our results indicate that the water sources used by coexisting riparian species might be more partitioned under drier conditions.

DATA AVAILABILITY STATEMENT
Data available from the Zenodo repository https://doi.org/10.5281/zenodo.5596622 (Granda et al., 2022).

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REFERENCES

Antunes, C., Díaz-Barradas, M. C., Zunzunegui, M., Vieira, S., & Máguas, C. (2018). Water source partitioning among plant functional types in a semi-arid dune ecosystem. *Journal of Vegetation Science*, 29(4), 671–683. https://doi.org/10.1111/jvs.12647

Barbeta, A., Gimeno, T. E., Clavé, L., Fréjaville, B., Jones, S. P., Delvigne, C., Wingate, L., & Ogée, J. (2021). An explanation for the isotopic offset between soil and stem water in a temperate tree species. *New Phytologist*, 227(3), 766–779. https://doi.org/10.1111/nph.16564

Barbeta, A., & Peñuelas, J. (2017). Increasing carbon discrimination rates and depth of water uptake favor the growth of Mediterranean evergreen trees in the ecotone with temperate deciduous forests. *Global Change Biology*, 23(12), 5054–5068. https://doi.org/10.1111/gcb.13770

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, 15, 365–377. https://doi.org/10.1111/j.1461-0248.2011.01736.x

Bertness, M. D., & Callaway, R. (1994). Positive interactions in communities. *Trends in Ecology & Evolution*, 9(5), 191–193.

Bogeat-Triboulot, M. B., Brosché, M., Renaut, J., Jouve, L., le Thiec, D., Fayyaz, P., Vinocur, B., Witters, E., Laukens, K., Teichmann, T., Altman, A., Hausman, J. F., Polle, A., Kangasjärvi, J., & Dreyer, E. (2007). Gradual soil water depletion results in reversible changes of gene expression, protein profiles, ecophysiology, and growth performance in *Populus euphratica*, a poplar growing in arid regions. *Plant Physiology*, 143(2), 876–892. https://doi.org/10.1104/pp.106.088708

Bradley, B. A., Wilcove, D. S., & Oppenheimer, M. (2010). Climate change increases risk of plant invasion in the Eastern United States. *Biological Invasions*, 12, 1855–1872. https://doi.org/10.1007/s10530-009-9597-y

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9(2), 378–400.

Brooks, R. J., Barnard, H. R., Coulombe, R., & McDonnell, J. J. (2010). Ecohydrologic separation of water between trees and streams in a Mediterranean climate. *Nature Geoscience*, 3(2), 100–104. https://doi.org/10.1038/ngeo722

Brunner, I., Herzog, C., Dawes, M. A., Arend, M., & Sperisen, C. (2015). How tree roots respond to drought. *Frontiers in Plant Science*, 6, 547. https://doi.org/10.3389/fpls.2015.00547

CABI. (2021). *Invasive species compendium*. CAB International Retrieved from http://www.cabi.org/isc

Castro-Díez, P., & Alonso, Á. (2017). Effects of non-native riparian plants in riparian and fluvial ecosystems: A review for the Iberian Peninsula. *Limnetica*, *36*(2), 525–541. https://doi.org/10.23818/limn.36.19

Castro-Díez, P., Alonso, Á., Saldaña, A., & Granda, E. (2021). Widespread non-native trees on regulating ecosystem services. *Science of The Total Environment*, *778*, 146141. https://doi.org/10.1016/j.scitotenv.2021.146141

Castro-Díez, P., Valle, G., González-Muñoz, N., & Alonso, Á. (2014). Can the life-history strategy explain the success of the exotic trees *Ailanthus altissima* and *Robinia pseudoacacia* in Iberian floodplain forests? *PLoS ONE*, *9*(6), 30–32. https://doi.org/10.1371/journal.pone.0100254

Castro-Díez, P., Vaz, A. S., Silva, J. S., van Loo, M., Alonso, Á., Aponte, C., Bayón, Á., Bellingham, P. J., Chiuffo, M. C., DiManno, N., Julian, K., Kandert, S., la Porta, N., Marchante, H., Maule, H. G., Mayfield, M. M., Metcalfe, D., Monteverdi, M. C., Núñez, M. A., ... Godoy, O. (2019). Global effects of non-native tree species on multiple ecosystem services. *Biological Reviews*, *94*(4), 1477–1501. https://doi.org/10.1111/brv.12511

Catford, J. A., Downes, B. J., Gippel, C. J., & Vesk, P. A. (2011). Flow regulation reduces native plant cover and facilitates exotic invasion in riparian wetlands. *Journal of Applied Ecology*, *48*(2), 432–442. https://doi.org/10.1111/j.1365-2664.2010.01945.x

Cavaleri, M. A., Ostertag, R., Cordell, S., & Sack, L. (2014). Native trees show conservative water use relative to invasive trees: Results from a removal experiment in a Hawaiian wet forest. *Conservation Physiology*, *2*(1), 1–14. https://doi.org/10.1093/conphys/cou016

Cavaleri, M. A., & Sack, L. (2010). Comparative water use of native and invasive plants at multiple scales: A global meta-analysis. *Ecology*, *91*(9), 2705–2715. https://doi.org/10.1890/09-0582.1

Chaves, M. M., Maroco, J. P., & Pereira, J. S. (2003). Understanding plant responses to drought-from genes to the whole plant. *Functional Plant Biology*, *30*, 239–264.

Christina, M., Nouvellon, Y., Laclau, J. P., Stape, J. L., Bouillet, J. P., Lambais, G. R., & le Maire, G. (2017). Importance of deep water uptake in tropical eucalypt forest. *Functional Ecology*, *31*(2), 509–519. https://doi.org/10.1111/1365-2435.12727

Coleman, M., & Meier-Augenstein, W. (2014). Ignoring IUPAC guidelines for measurement and reporting of stable isotope abundance values affects us all. *Rapid Communications in Mass Spectrometry*, *28*(17), 1953–1955. https://doi.org/10.1002/rcm.6971

Craine, J. M., Brookshire, E. N. J., Cramer, M. D., Hasselquist, N. J., Koba, K., Marin-Spiotta, E., & Wang, L. (2015). Ecological interpretations of nitrogen isotope ratios of terrestrial plants and soils. *Plant and Soil*, *396*(1–2), 1–26. https://doi.org/10.1007/s11104-015-2542-1

Cribari-Neto, F., & Zeileis, A. (2010). Beta regression in R. *Journal of Statistical Software*, *34*(2), 1–24. https://doi.org/10.18637/jss.v034.i02

Cruz-Alonso, V., Rodríguez-Sánchez, F., Pucher, C., Ruiz-Benito, P., Astigarraga, J., Neumann, M., & Ratcliffe, S. (2022). *easyclimate: Easy access to high-resolution daily climate data for Europe*. Retrieved from https://github.com/VeruGHub/easyclimate

Daehler, C. C. (2003). Performance comparisons of co-occurring native and alien invasive plants: Implications for conservation and restoration. *Annual Review of Ecology, Evolution, and Systematics*, *34*, 183–211. https://doi.org/10.1146/annurev.ecolsys.34.011802.132403

David, T. S., Pinto, C. A., Nadezhdina, N., Kurz-Besson, C., Henriques, M. O., Quilhó, T., Cermak, J., Chaves, M. M., Pereira, J. S., & David, J. S. (2013). Root functioning, tree water use and hydraulic redistribution in *Quercus suber* trees: A modeling approach based on root sap flow. *Forest Ecology and Management*, *307*, 136–146. https://doi.org/10.1016/j.foreco.2013.07.012

Dawson, T. E. (1996). Determining water use by trees and forests from isotopic, energy balance and transpiration analyses: The roles of tree size and hydraulic lift. *Tree Physiology*, *16*(1–2), 263–272. https://doi.org/10.1093/treephys/16.1-2.263

Dawson, T. E., & Ehleringer, J. R. (1991). Streamside trees that do not use stream water. *Nature*, *350*, 335–337. https://doi.org/10.1038/350335a0

Dawson, T. E., & Ehleringer, J. R. (1993). Isotopic enrichment of water in the 'woody' tissues of plants: Implications for plant water source, water uptake, and other studies which use the stable isotopic composition of cellulose. *Geochimica et Cosmochimica Acta*, *57*(14), 3487–3492. https://doi.org/10.1016/0016-7037(93)90554-A

DeGomez, T., & Wagner, M. R. (2001). Culture and use of black locust. *HortTechnology*, *11*(2), 279–288. https://doi.org/10.21273/hortech.11.2.279

Diez, J. M., D'Antonio, C. M., Dukes, J. S., Grosholz, E. D., Olden, J. D., Sorte, C. J. B., Blumenthal, D. M., Bradley, B. A., Early, R., Ibáñez, I., Jones, S. J., Lawler, J. J., & Miller, L. P. (2012). Will extreme climatic events facilitate biological invasions? *Frontiers in Ecology and the Environment*, *10*(5), 249–257.

Ehleringer, J. R., & Dawson, T. E. (1992). Water uptake by plants: Perspectives from stable isotope composition. *Plant, Cell and Environment*, *15*, 1073–1082.

Fan, Y., Miguez-Macho, G., Jobbágy, E. G., Jackson, R. B., & Otero-Casal, C. (2017). Hydrologic regulation of plant rooting depth. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(40), 10572–10577. https://doi.org/10.1073/pnas.1712381114

Farquhar, G. D., Ehleringer, J. R., & Hubick, K. T. (1989). Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology*, *40*, 503–537. https://doi.org/10.1146/annurev.pp.40.060189.002443

Farquhar, G. D., & Richards, R. (1984). Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. *Australian Journal of Plant Physiology*, *11*, 539–552.

Ferrari, A. E., & Wall, L. G. (2007). Nodulation and growth of black locust (*Robinia pseudoacacia*) on a desurfaced soil inoculated with a local Rhizobium isolate. *Biology and Fertility of Soils*, *43*(4), 471–477. https://doi.org/10.1007/s00374-006-0125-2

Filella, I., & Peñuelas, J. (2004). Indications of hydraulic lift by Pinus halepensis and its effects on the water relations of neighbour shrubs. *Biologia Plantarum*, *47*(2), 209–2014.

Funk, J. L., Standish, R. J., Stock, W. D., & Valladares, F. (2016). Plant functional traits of dominant native and invasive species in mediterranean- climate ecosystems. *Ecology*, *97*(1), 75–83. https://doi.org/10.1890/15-0974.1

Funk, J. L., & Vitousek, P. M. (2007). Resource-use efficiency and plant invasion in low-resource systems. *Nature*, *446*(7139), 1079–1081. https://doi.org/10.1038/nature05719

González, E., González-Sanchis, M., Comín, F. A., & Muller, E. (2012). Hydrologic thresholds for riparian forest conservation in a regulated large Mediterranean river. *River Research and Applications*, *28*(1), 71–80. https://doi.org/10.1002/rra.1436

González-Muñoz, N., Castro-Díez, P., & Parker, I. M. (2013). Differences in nitrogen use strategies between native and exotic tree species: Predicting impacts on invaded ecosystems. *Plant and Soil*, *363*(1–2), 319–329. https://doi.org/10.1007/s11104-012-1329-x

González-Muñoz, N., Linares, J. C., Castro-Díez, P., & Sass-Klaassen, U. (2015). Contrasting secondary growth and water-use efficiency patterns in native and exotic trees co-occurring in inner Spain riparian forests. *Forest Systems*, *24*(1), 1–10. https://doi.org/10.5424/fs/2015241-06586

Granda, E., Antunes, C., Máguas, C., & Castro-Díez, P. (2022). Data from: Water use partitioning of native and non-native tree species in riparian ecosystems under contrasting climatic conditions. *Zenodo*, https://doi.org/10.5281/zenodo.5596622

Grime, J. P. (1973). Competitive exclusion in herbaceous vegetation. *Nature*, *242*(5396), 344–347. https://doi.org/10.1038/242344a0

Grotkopp, E., Rejmánek, M., & Rost, T. L. (2002). Toward a causal explanation of plant invasiveness: Seedling growth and life-history strategies of 29 pine (Pinus) species. *The American Naturalist*, *159*(4), 396–419. https://doi.org/10.1086/338995

Hahm, W. J., Rempe, D. M., Dralle, D. N., Dawson, T. E., & Dietrich, W. E. (2020). Oak transpiration drawn from the weathered bedrock vadose zone in the summer dry season. *Water Resources Research*, *56*(11), 1–24. https://doi.org/10.1029/2020WR027419

Hartmann, H. (2011). Will a 385 million year-struggle for light become a struggle for water and for carbon? – How trees may cope with more frequent climate change-type drought events. *Global Change Biology*, *17*(1), 642–655. https://doi.org/10.1111/j.1365-2486.2010.02248.x

Högberg, P. (1990). ^{15}N natural abundance as a possible marker of the ectomycorrhizal habit of trees in mixed African woodlands. *New Phytologist*, *115*(3), 483–486. https://doi.org/10.1111/j.1469-8137.1990.tb00474.x

Huebner, C. D., McQuattie, C., & Rebbeck, J. (2007). Mycorrhizal associations in Ailanthus altissima (Simaroubaceae) from forested and non-forested sites. *Journal of the Torrey Botanical Society*, *134*(1), 27–33. https://doi.org/10.3159/1095-5674(2007)134[27:MAIAAS]2.0.CO;2

Huntley, J. C. (1990). *Robinia pseudoacacia* L. Black locust. In R. M. Burns, B. H. Honkala, & Silvics of North America (Eds.), *Agriculture handbook no. 654. Forest service* (Vols. 2, hardwoods, pp. 755–761). United States Department of Agriculture.

Ivanov, V. Y., Hutyra, L. R., Wofsy, S. C., Munger, J. W., Saleska, S. R., de Oliveira, R. C., & de Camargo, P. B. (2012). Root niche separation can explain avoidance of seasonal drought stress and vulnerability of overstory trees to extended drought in a mature Amazonian forest. *Water Resources Research*, *48*(12), 1–21. https://doi.org/10.1029/2012WR011972

Kowarik, I., & Säumel, I. (2007). Biological flora of Central Europe: *Ailanthus altissima* (Mill.) Swingle. *Perspectives in Plant Ecology, Evolution and Systematics*, *8*(4), 207–237. https://doi.org/10.1016/j.ppees.2007.03.002

Kozlowski, T. T., & Pallardy, S. G. (2002). Acclimation and adaptive responses of woody plants to environmental stresses. *Botanical Review*, *68*(2), 270–334. https://doi.org/10.1663/0006-8101(2002)068[0270:AAAROW]2.0.CO;2

Lambers, H., Chapin, F. S., & Pons, T. L. (2008). Plant water relations. In *Plant physiological ecology* (pp. 163–223). Springer New York. https://doi.org/10.1007/978-0-387-78341-3_5

Lara, F., Garilleti, R., & Ramírez, P. (1996). *Estudio de la vegetación de los ríos carpetanos de la cuenca del Jarama (CEDEX)*. Centro de Estudios de Técnicas Aplicadas.

le Maitre, D. C., Gush, M. B., & Dzikiti, S. (2015). Impacts of invading alien plant species on water flows at stand and catchment scales. *AoB Plants*, *7*(1), plv043. https://doi.org/10.1093/aobpla/plv043

Leishman, M. R., Haslehurst, T., Ares, A., & Baruch, Z. (2007). Leaf trait relationships of native and invasive plants: Community- and global-scale comparisons. *New Phytologist*, *176*(3), 635–643. https://doi.org/10.1111/j.1469-8137.2007.02189.x

Leuschner, C., Backes, K., Hertel, D., Schipka, F., Schmitt, U., Terborg, O., & Runge, M. (2001). Drought responses at leaf, stem and fine root levels of competitive *Fagus sylvatica* L. and *Quercus petraea* (Matt.) Liebl. trees in dry and wet years. *Forest Ecology and Management*, *149*(1–3), 33–46. https://doi.org/10.1016/s0378-1127(00)00543-0

Lin, G., Phillips, S. L., & Ehleringer, J. R. (1996). Monosoonal precipitation responses of shrubs in a cold desert community on the Colorado Plateau. *Oecologia*, *106*(1), 8–17. https://doi.org/10.1007/BF00334402

MacDougall, A. S., Gilbert, B., & Levine, J. M. (2009). Plant invasions and the niche. *Journal of Ecology*, *97*(4), 609–615. https://doi.org/10.1111/j.1365-2745.2009.01514.x

Máguas, C., Rascher, K. G., Martins-Loução, A., Carvalho, P., Pinho, P., Ramos, M., Correia, O., & Werner, C. (2011). Responses of woody species to spatial and temporal ground water changes in coastal sand dune systems. *Biogeosciences*, *8*(12), 3823–3832. https://doi.org/10.5194/bg-8-3823-2011

Manzoni, S., Vico, G., Thompson, S., Beyer, F., & Weih, M. (2015). Contrasting leaf phenological strategies optimize carbon gain under droughts of different duration. *Advances in Water Resources*, *84*, 37–51. https://doi.org/10.1016/j.advwatres.2015.08.001

Martín-Gómez, P., Barbeta, A., Voltas, J., Peñuelas, J., Dennis, K., Palacio, S., Dawson, T. E., & Ferrio, J. P. (2015). Isotope-ratio infrared spectroscopy: A reliable tool for the investigation of plant-water sources? *New Phytologist*, *207*(3), 914–927. https://doi.org/10.1111/nph.13376

McCue, M. D., Javal, M., Clusella-Trullas, S., le Roux, J. J., Jackson, M. C., Ellis, A. G., Richardson, D. M., Valentine, A. J., & Terblanche, J. S. (2020). Using stable isotope analysis to answer fundamental questions in invasion ecology: Progress and prospects. *Methods in Ecology and Evolution*, *11*(2), 196–214. https://doi.org/10.1111/2041-210X.13327

Mitchell, K. (2015). *Quantitative analysis by the point-centered quarter method*. Retrieved from http://people.hws.edu/Mitchell/PCQM.pdf

Moreno, A., & Hasenauer, H. (2016). Spatial downscaling of European climate data. *International Journal of Climatology*, *36*(3), 1444–1458. https://doi.org/10.1002/joc.4436

Nadal-Sala, D., Sabaté, S., Sánchez-Costa, E., Poblador, S., Sabater, F., & Gracia, C. (2017). Growth and water use performance of four co-occurring riparian tree species in a Mediterranean riparian forest. *Forest Ecology and Management*, *396*(April 2017), 132–142. https://doi.org/10.1016/j.foreco.2017.04.021

Nambiar, E. K. S., & Sands, R. (1993). Competition for water and nutrients in forests. *Canadian Journal of Forest Research*, *23*(10), 1955–1968. https://doi.org/10.1139/x93-247

Nolan, R. H., Blackman, C. J., de Dios, V. R., Choat, B., Medlyn, B. E., Li, X., Bradstock, R. A., & Boer, M. M. (2020). Linking forest flammability and plant vulnerability to drought. *Forests*, *11*(7), 1–16. https://doi.org/10.3390/F11070779

Novoa, A., Richardson, D. M., Pyšek, P., Meyerson, L. A., Bacher, S., Canavan, S., Catford, J. A., Čuda, J., Essl, F., Foxcroft, L. C., Genovesi, P., Hirsch, H., Hui, C., Jackson, M. C., Kueffer, C., le Roux, J. J., Measey, J., Mohanty, N. P., Moodley, D., … Wilson, J. R. U. (2020). Invasion syndromes: A systematic approach for predicting biological invasions and facilitating effective management. *Biological Invasions*, *22*(5), 1801–1820. https://doi.org/10.1007/s10530-020-02220-w

Ntshidi, Z., Gush, M., Dzikiti, S., & le Maitre, D. (2018). Characterising the water use and hydraulic properties of riparian tree invasions: A case study of *Populus canescens* in South Africa. *Water SA*, *44*, 328–337. https://doi.org/10.4314/wsa.v44i2.18

Phillips, D. L., Newsome, S. D., & Gregg, J. W. (2005). Combining sources in stable isotope mixing models: Alternative methods. *Oecologia*, *144*, 520–527.

Pierret, A., Maeght, J. L., Clément, C., Montoroi, J. P., Hartmann, C., & Gonkhamdee, S. (2016). Understanding deep roots and their functions in ecosystems: An advocacy for more unconventional research. *Annals of Botany*, *118*(4), 621–635. https://doi.org/10.1093/aob/mcw130

Porté, A. J., Lamarque, L. J., Lortie, C. J., Michalet, R., & Delzon, S. (2011). Invasive Acer negundo outperforms native species in non-limiting resource environments due to its higher phenotypic plasticity. *BMC Ecology*, *11*(1), 28. https://doi.org/10.1186/1472-6785-11-28

Preston, T., & Owens, N. J. P. (1983). Interfacing an automatic elemental analyser with an isotope ratio mass spectrometer: The potential for fully automated total nitrogen and nitrogen-15 analysis. *The Analyst*, *108*(1289), 971–977. https://doi.org/10.1039/an9830800971

Rammer, W., Pucher, C., & Neumann, M. (2018). *Description, evaluation and validation of downscaled daily climate data version 2*. Retrieved from ftp://palantir.boku.ac.at/Public/ClimateData

Ranney, T. G., Whitlow, T. H., & Bassuk, N. L. (1990). Response of five temperate deciduous tree species to water stress. *Tree Physiology*, 6(4), 439–448. https://doi.org/10.1093/treephys/6.4.439

Richardson, D. M., & Pyšek, P. (2006). Plant invasions: Merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography*, 30(3), 409–431. https://doi.org/10.1191/0309133306pp490pr

Roberts, J. (1983). Foerest transpiration: A conservative hydrological process? *Journal of Hydrology*, 66, 133–141.

Saito, T. S., Sukumo, M. T., Lbasit, M., Yasuda, H., Kawai, T., Matsuo, N., Inosako, K., Acharya, K., Babiker, A. E., Hamd, A. A., & Nawata, H. (2014). Estimation of water sources of invasive tree species in arid environments by oxygen stable isotope analysis. *Journal of Arid Land Studies*, 32, 29–32.

Sánchez-Pérez, J. M., Lucot, E., Bariac, T., & Trémolières, M. (2008). Water uptake by trees in a riparian hardwood forest (Rhine floodplain, France). *Hydrological Processes*, 22(3), 366–375. https://doi.org/10.1002/hyp.6604

Schenk, H. J. (2006). Root competition: Beyond resource depletion. *Journal of Ecology*, 94(4), 725–739. https://doi.org/10.1111/j.1365-2745.2006.01124.x

Schenk, H. J., & Jackson, R. B. (2002). Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology*, 90(3), 480–494. https://doi.org/10.1046/j.1365-2745.2002.00682.x

Schulze, E., Kelliher, F. M., Korner, C., Lloyd, J., & Leuning, R. (1994). Relationships among maximum stomatal conductance, ecosystem surface conductance, carbon assimilation rate, and plant nitrogen nutrition: A global ecology scaling exercise. *Annual Review of Ecology and Systematics*, 25(1), 629–662. https://doi.org/10.1146/annurev.es.25.110194.003213

Silvertown, J., Araya, Y., & Gowing, D. (2015). Hydrological niches in terrestrial plant communities: A review. *Journal of Ecology*, 103(1), 93–108. https://doi.org/10.1111/1365-2745.12332

Smith, S. D., Devitt, D. A., Sala, A., Cleverly, J. R., & Busch, D. E. (1998). Water relations of riparian plants from warm desert regions. *Wetlands*, 18(4), 687–696.

Sperry, J. S., & Ikeda, T. (1997). Xylem cavitation in roots and stems of Douglas-fir and white fir. *Tree Physiology*, 17(4), 275–280. https://doi.org/10.1093/treephys/17.4.275

Stock, B. C., Jackson, A. L., Ward, E. J., Parnell, A. C., Phillips, D. L., & Semmens, B. X. (2018). Analyzing mixing systems using a new generation of Bayesian tracer mixing models. *PeerJ*, 6, e5096. https://doi.org/10.7717/peerj.5096

Stock, B. C., & Semmens, B. X. (2016a). MixSIAR GUI user manual. Version 3.1. https://github.com/brianstock/MixSIAR

Stock, B. C., & Semmens, B. X. (2016b). Unifying error structures in commonly used biotracer mixing models. *Ecology*, 97(10), 2562–2569. https://doi.org/10.1002/ecy.1517

Stockton Maxwell, R., & Larsson, L.-A. (2021). Measuring tree-ring widths using the CooRecorder software application. *Dendrochronologia*, 67, 125841. https://doi.org/10.17632/r3v7236kkz.1

Stokes, M. A., & Smiley, T. L. (1968). *An introduction to tree ring dating.* University Chicago Press.

Tichý, L. (2014). *GLAMA-gap light analysis mobile application.* Department of Botany and Zoology.

Tichý, L. (2016). Field test of canopy cover estimation by hemispherical photographs taken with a smartphone. *Journal of Vegetation Science*, 27(2), 427–435. https://doi.org/10.1111/jvs.12350

Trifilò, P., Raimondo, F., Nardini, A., lo Gullo, M. A., & Salleo, S. (2004). Drought resistance of *Ailanthus altissima*: Root hydraulics and water relations. *Tree Physiology*, 24(1), 107–114. https://doi.org/10.1093/treephys/24.1.107

UNESCO. (1979). *Aridity definition (UN documents).* United Nations Educational, Scientific and Cultural Organization.

van Kleunen, M., Weber, E., & Fischer, M. (2010). A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters*, 13(2), 235–245. https://doi.org/10.1111/j.1461-0248.2009.01418.x

Vilà, M., Espinar, J. L., Hejda, M., Hulme, P. E., Jarošík, V., Maron, J. L., Pergl, J., Schaffner, U., Sun, Y., & Pyšek, P. (2011). Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, 14, 702–708. https://doi.org/10.1111/j.1461-0248.2011.01628.x

Vítková, M., Tonika, J., & Müllerová, J. (2015). Black locust-Successful invader of a wide range of soil conditions. *Science of The Total Environment*, 505, 315–328. https://doi.org/10.1016/j.scitotenv.2014.09.104

Voltas, J., Lucabaugh, D., Chambel, M. R., & Ferrio, J. P. (2015). Intraspecific variation in the use of water sources by the circum-Mediterranean conifer Pinus halepensis. *New Phytologist*, 208(4), 1031–1041. https://doi.org/10.1111/nph.13569

Wang, M. C., Wang, J. X., Shi, Q. H., & Zhang, J. S. (2007). Photosynthesis and water use efficiency of Platycladus orientalis and Robinia pseudoacacia saplings under steady soil water stress during different stages of their annual growth period. *Journal of Integrative Plant Biology*, 49(10), 1470–1477. https://doi.org/10.1111/j.1672-9072.2007.00561.x

Weinstein, D. A., Beloin, R. M., & Yanai, R. D. (1991). Modeling changes in red spruce carbon balance and allocation in response to interacting ozone and nutrient stresses. *Tree Physiology*, 9(1–2), 127–146. https://doi.org/10.1093/treephys/9.1-2.127

Weltzin, J. F., & McPherson, G. R. (1997). Spatial and temporal soil moisture resource partitioning by trees and grasses in a temperate savanna, Arizona, USA. *Oecologia*, 112(2), 156–164. https://doi.org/10.1007/s004420050295

Werner, G. D. A., Cornelissen, J. H. C., Cornwell, W. K., Soudzilovskaia, N. A., Kattge, J., West, S. A., & Toby Kiers, E. (2018). Symbiont switching and alternative resource acquisition strategies drive mutualism breakdown. *Proceedings of the National Academy of Sciences of the United States of America*, 115(20), 5229–5234. https://doi.org/10.1073/pnas.1721629115

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., … Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, 428(6985), 821–827. https://doi.org/10.1038/nature02403

Xu, Q., Li, H., Chen, J., Cheng, X., Liu, S., & An, S. (2011). Water use patterns of three species in subalpine forest, Southwest China: The deuterium isotope approach. *Ecohydrology*, 4(2), 236–244. https://doi.org/10.1002/eco.179

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