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Increased Groundwater Dependence of Riparian Vegetation in Response to Drought

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ABSTRACT

Riparian ecosystems in drylands face increasing risks from intensifying droughts, which lower water tables, reduce soil moisture and suppress streamflow—threatening vegetation and risking ecosystem collapse. Although riparian vegetation relies on subsurface water, the relative importance of groundwater versus rainfall-infiltrated soil moisture during drought remains unclear. As climate change prolongs drought severity, understanding how plants shift between water sources is key to predicting ecosystem resilience and guiding sustainable groundwater management. We conducted a stable isotope study along the Santa Clara River in southern California (2018–2020) during recovery from a severe (2012–2019) drought. We sampled $\delta^{18}O_p$ in plant xylem water from four native riparian woody species (*Salix exigua*, *S. laevigata*, *Populus trichocarpa*, *P. fremontii*) and the non-native grass *Arundo donax*. Shallow soil moisture and groundwater were sampled to characterize endmember $\delta^{18}O$ signatures. Isotope mixing models were developed to track shifts in water source contributions for each species over three growing seasons. Riparian plants showed opportunistic water use, relying on shallow soil moisture during wet periods and shifting to groundwater during droughts. Native taxa including *Populus* and *Salix* species increased groundwater use by up to 60% during drought, reflecting hydraulic flexibility and drought tolerance. In contrast, the invasive *A. donax* depended on shallow soil moisture for 64–86% of its water under all conditions. These findings underscore the importance of quantifying species- and site-specific groundwater use. Incorporating such ecological insights into groundwater sustainability planning will be critical for protecting riparian vegetation and maintaining ecosystem function in a changing climate.

1 | Introduction

Lowland riparian forests, despite their significant ecological importance, are among the most threatened forest types due to climate change (Bertrand et al. 2011; Dwire et al. 2018; Johnson et al. 2020; Loarie et al. 2009; Nakamura 2022), land conversion (Dodds et al. 2023; Gay et al. 2023; Zhang et al. 2023), flow regulation (Nagler et al. 2008) and unsustainable water extraction (Singer and Dunne 2004; Stella, Rodríguez-González, et al. 2013; Swanson and Bohlman 2021; Yang et al. 2022). These combined pressures intensify water stress in riparian forests, particularly in semi-arid regions, by reducing subsurface water availability, including shallow groundwater (Choat et al. 2012; Doughty et al. 2015; Evans et al. 2018; Jasechko et al. 2021; Posch et al. 2024; Quichimbo et al. 2020; Rohde, Biswas, et al. 2021; Stella, Riddle, et al. 2013; Warter et al. 2023). The decline in water availability has been shown to reduce the resilience of riparian vegetation to atmospheric drought and rising temperatures (Kibler et al. 2023; Posch et al. 2024; Williams et al. 2022), leading to widespread habitat degradation and biodiversity loss (Kløve, Ala-aho, et al. 2011; Kløve, Allan, et al. 2011; Li et al. 2024; Mologni et al. 2023; Stella, Riddle, et al. 2013; Stella and Bendix 2019). Although many riparian woodlands, particularly those dominated by *Salix* and *Populus*, are classified as groundwater-dependent ecosystems (GDEs), the extent to which they actually rely on groundwater versus rainfall-infiltrated soil moisture remains uncertain, especially under variable climatic conditions. Determining when, where and how riparian species shift between water sources is essential for evaluating their drought resilience and guiding sustainable groundwater management in dryland regions.

Recent severe droughts in California, such as the 2012–2019 event, caused prolonged water table recessions of several meters in many river basins, including the Santa Clara River (Downs et al. 2024; Jasechko et al. 2021; Williams et al. 2022). In addition to climate-driven drought, increased groundwater abstraction to support agricultural demands has further exacerbated these declines. As a result, riparian vegetation communities and other groundwater-dependent ecosystems (GDEs) are facing heightened stress (Eamus and Froend 2006; Kibler et al. 2021; Rohde, Biswas, et al. 2021; Rohde, Stella, et al. 2024; Rohde, Stella, et al. 2021). This challenge is particularly acute in basins where ecological, agricultural and urban needs compete for limited groundwater, often leading to legal and resource management conflicts. To address these pressures, California's Sustainable Groundwater Management Act (SGMA) requires local agencies to develop groundwater sustainability plans that account for all users, including ecosystems. However, it remains unclear how ecosystems should be represented in these plans, particularly given the limited understanding of species-specific groundwater reliance under changing hydrologic conditions (Rohde, Albano, et al. 2024; Rohde, Stella, et al. 2024; Stella and Bendix 2019).

In dryland GDEs, woody species primarily rely on two water sources: shallow soil moisture in the vadose zone, characterized by unsaturated fine-grained sediments, and groundwater in the phreatic zone, found below the water table in coarser-grained sediments that are associated with aquifers (Dawson and Ehleringer 1991; Singer et al. 2014, 2013). These sources fluctuate due to local rainfall, groundwater dynamics and broader climatic factors (Downs et al. 2024; Sargeant and Singer 2021). Groundwater table dynamics are influenced by lateral subsurface flow between the river and the aquifer, depending on whether the stream reach is gaining (receiving groundwater) or losing (discharging to groundwater), though these interactions are often complex and difficult to characterize (Quichimbo et al. 2020). Shallow soil moisture, controlled by precipitation, infiltration and evapotranspiration, may also be a key water resource for riparian species (Sargeant and Singer 2021; Singer et al. 2014).

Analysing the oxygen stable isotope composition ($\delta^{18}O$) of water in plant xylem in relation to these endmember sources provides an observational window into the contributions of soil moisture and groundwater to plant water uptake (Dawson et al. 2002; Ehleringer and Dawson 1992; Sargeant et al. 2019). Shallow soil water is generally enriched isotopically due to evapotranspiration (Gazis and Feng 2004; Hsieh et al. 1998; von Freyberg et al. 2020), whereas deep groundwater is generally depleted in $\delta^{18}O$ and remains relatively stable over space and time (Gat 1996). The distinct and locally defined $\delta^{18}O$ signatures of soil moisture and groundwater allow researchers to trace the relative use of each water source and gain insights into the groundwater dependence in riparian forest species over time and space (David et al. 2007; Dawson and Pate 1996; Sargeant et al. 2019; Sarris et al. 2013).

Plants rely on different water sources depending on species, rooting depth, functional traits and climate-controlled water availability (Stromberg and Patten 1990; Dawson and Ehleringer 1991; Sabathier et al. 2021; Sargeant and Singer 2021; Stromberg et al. 1996). Functional traits, such as rooting architecture and drought tolerance, play a significant role in determining plant water source preferences. Shallow-rooted species or those with limited access to groundwater are likely to use shallow soil water, whereas deep-rooted plants, especially phreatophytes, rely heavily on groundwater from an alluvial aquifer (Horton et al. 2001; Dawson and Pate 1996; Sun et al. 2016). Many phreatophytes develop dimorphic root systems, with shallow lateral roots for accessing surface water and deeper vertical roots for tapping groundwater (Bleby et al. 2010; Brooksbank et al. 2011; Burgess et al. 2000, 1998; David et al. 2013; Dawson and Pate 1996; Di et al. 2018; Pate et al. 1995). This dual-rooting strategy allows them to simultaneously use multiple water sources or switch sources depending on water availability and energetic demands. During wet seasons, shallow roots provide a less resistant pathway for water uptake, while deeper roots become critical during dry periods when accessing groundwater is more favourable as surface soils dry and water becomes harder to extract (Bleby et al. 2010). This flexibility in switching water sources enhances plant resilience to fluctuating water availability and supports survival in dynamic riparian environments (Liu et al. 2022; Penna et al. 2013; Singer et al. 2013). For example, Singer et al. (2013) found evidence that *Fraxinus excelsior* primarily used shallow soil moisture with limited capacity to switch to a deeper water source during severe drought conditions. In contrast, Snyder and Williams (2000) demonstrated that *Populus fremontii* predominantly used groundwater but increased its uptake of shallow soil moisture during summer rainy seasons when shallow water became available. These contrasting responses to drought highlight the importance of local hydrologic conditions, which fluctuate seasonally and are influenced by climate trends, in shaping plant water use strategies (Hultine et al. 2020). Understanding the climatic and hydrologic drivers of water source shifts is critical for predicting species-level drought tolerance and supporting groundwater management under a framework like California's SGMA. Identifying when and which species rely most on groundwater can help prioritize sensitive areas, guide monitoring efforts and inform the timing of restoration or pumping adjustments (Rohde, Albano, et al. 2024; Rohde et al. 2017).

In this study, we investigate groundwater reliance among dominant riparian plant species along the Santa Clara River, categorized into three functional groups: 1) native deep-rooted phreatophytes, including *Populus trichocarpa* and *P. fremontii* (POPU) and *Salix laevigata* (SALA); 2) a native rhizomatous shrub, *Salix exigua* (SAEX); and 3) a drought-tolerant invasive grass *A. donax* (ARDO). *A. donax* is widespread in the floodplain and a major competitor with riparian vegetation, often replacing native plants after flood scouring or prolonged drought (Lambert et al. 2010). Our study took place during the recovery period of a historically severe drought (2012–2019) along the Santa Clara River that caused significant groundwater table declines, reduced recharge and imposed severe hydrological stress on riparian ecosystems (Kibler et al. 2021; Rohde, Stella, et al. 2024; Williams et al. 2024). Although there is evidence of both riparian forest and grassland plant stress due to the drought from remote sensing analyses (Kibler et al. 2021; Warter et al. 2021), it is unknown how water availability to, and use by, riparian vegetation varied during the drought period. Here, we address three research questions: (1) To what extent do riparian plants with varying functional traits depend on groundwater versus shallow soil moisture? (2) Do riparian plants shift their water sources in response to seasonal and interannual drought conditions? (3) How do groundwater reliance and shifts in source water vary among different species?

2 | Methods

Between 2018 and 2020, we examined source water variability during the drought recovery period at three study sites along the Santa Clara River in southern California, United States, where water and plant conditions varied across the three sites. At each site over 3 years, we collected monthly samples during the growing season (April–October), including plant xylem water from 12 individual plants, and potential plant water sources from deep wells, shallow soil water at two depths, and surface water from the Santa Clara River, all for stable oxygen isotope analysis. In addition, soil moisture data at each site was collected hourly at three depths (approximately 20 cm, 60 cm and 100 cm). All data are publicly available in the Environmental Data Initiative repository (Kui and Kibler 2023).

2.1 | Study Site

The Santa Clara River is the largest free-flowing river in southern California. It flows 132 km from the Mojave Desert to the Pacific Ocean through urban, agricultural and undeveloped land in Los Angeles and Ventura Counties (Beller et al. 2016; Downs et al. 2013). The river comprises gaining and losing reaches and intermittent flows, with certain sections experiencing streamflow only during the rainy season (Downs et al. 2013). The river is divided into sub-basins bounded by converging bedrock structures that force groundwater toward the surface (Stillwater Sciences 2011). Within the Santa Clara River basin, there are six groundwater basins: Santa Clara River Valley East, Piru, Fillmore, Santa Paula, Mound and Oxnard. The study focused on three sites—Fillmore Cienega, Taylor and Hanson—with different climates and hydrogeological characteristics, which were selected to encompass a wide range of groundwater, soil moisture and plant conditions (Figure 1). These sites are within 40 km of the coast, where a strong gradient of coastal moisture and inland aridity exists along the river valley (Williams et al. 2022). The dominance of *Populus* species shifted along the river corridor. Upstream, Fillmore Cienega was dominated by *P. fremontii*, while downstream, Taylor had a mix of *P. fremontii* and *P. trichocarpa*, and Hanson was dominated by *P. trichocarpa*. In contrast, *S. laevigata* was present consistently across all sites along the river corridor. Previous research has provided time series data on groundwater levels at all study sites, indicating that the rate of groundwater decline was highest at Fillmore Cienega, followed by Taylor, and lowest at Hanson during the 2012–2019 California drought (Williams et al. 2022). As a result, Fillmore Cienega experienced widespread riparian plant stress and mortality, while the downstream sites, Taylor and Hanson, were less affected by drought stress (Kibler et al. 2021; Williams et al. 2022). The Santa Clara River is located in a Mediterranean climate, characterized by a wet rainy season in winter and spring and a dry season in summer and fall.

2.2 | Hydrology and Climate

Precipitation, potential evapotranspiration, groundwater elevation and soil moisture data were compiled to understand how hydroclimatic variables affected plant water uptake during the 2018–2020 sampling period. Daily precipitation data were retrieved from Ventura County Watershed Protection Hydrologic Data Server (https://vcwatershed.net/hydrodata/, Ventura County 2021). The meteorological station used (#171) was located at the Fillmore Fish Hatchery, approximately 500 m from our Fillmore Cienega site. Daily potential evapotranspiration (dPET) was retrieved from a global land surface database at 0.1° resolution, based on the Penman–Monteith method that characterizes the atmospheric evaporative demand using wind, solar radiation and temperature (Singer et al. 2021). The three study sites were located in three distinct grid cells for the dPET database.

Groundwater table level data, relative to the soil surface, were used to examine its influence on the plant xylem water. The United Water Conservation District collects the regional groundwater data, which is measured manually on a monthly basis. We selected one groundwater well located in each of the sites that had regular measurements between January 2018 and December 2020 (Figure 1). The wells were located within approximately 250 m of the river channel, with groundwater depths ranging from 0.5 to 8 m and well drilling depths between 21 and 186 m (United Water Conservation District 2016).

Soil moisture was measured at each site to determine shallow water availability to the plants and to evaluate how seasonal changes in soil water content influence isotopic signatures (i.e., low and/or declining soil moisture could result in enriched $\delta^{18}O$). Soil moisture data were collected by resistivity soil moisture sensors (Decagon Devices EC-5) connected to a

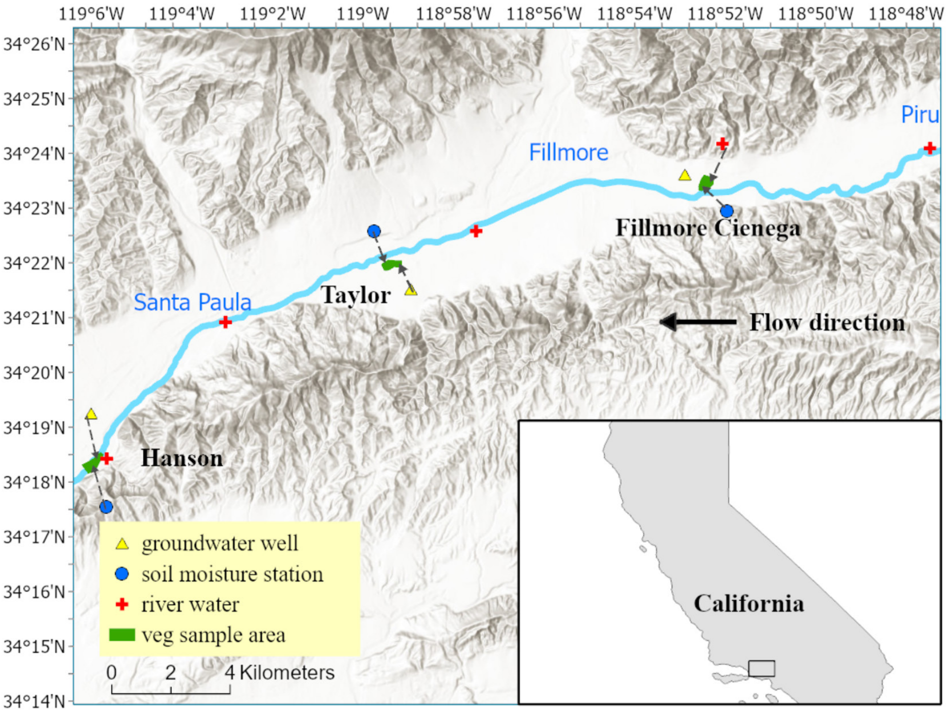

FIGURE 1 | Sampling locations along the Santa Clara River (depicted as a blue line). Nearby town names are shown in blue text. From April to October, approximately 36 plant xylem samples and six soil samples (collected at two depths) were taken monthly within vegetation sampling areas (green polygons). Additionally, three river water samples (red crosses) and three groundwater samples from deep wells (yellow triangles) were collected. Soil moisture was monitored at three stations (blue circles). All datasets are publicly available through the Environmental Data Initiative repository (Kui and Kibler 2023).

HOBO RX-3000 data logger (Onset Corporation). In May 2018, at each site, three soil sensors were installed near the edge of a tree canopy on the low floodplain by inserting them horizontally into the soil profile wall at depths of approximately 20 cm, 60 cm and 100 cm. The soil pit was backfilled to match the original bulk density. These sensors were programmed to log measurements every 5 min during the rainy season and every 30 min during the dry season from May 2018 to December 2020 (Figure 2).

2.3 | Source and Plant Xylem Water Sampling

We sampled potential water sources utilized by riparian plants, including river water, shallow soil moisture and groundwater, during the growing season (April to October) over 21 months. Each month, one river water sample was collected from the active channel near each site (see Figure 1 for locations), and one groundwater sample was taken from deep wells after purging standing water for 1–2 min to eliminate any enriched water stored in the well heads. Shallow soil moisture was collected in the soil samples at depths of 40 cm and 100 cm from randomly selected locations to capture isotopic variability and minimize disturbance.

We collected 12 plant xylem samples from each site, a total of 36 samples monthly from April through October each year ($n = 252$ samples). At each site, three individual plants of each species were selected to cover the local range of the topographic gradient. The two *Populus* species were grouped together because they have relatively similar morphologies, ecophysiology and water relations (Rood et al. 2003), and because sites varied in their distributions of *P. trichocarpa* and *P. fremontii*, with some sites containing one or both species, as well as their hybrids. For tall tree species, we used an increment borer (Haglöf Sweden AB, Långsele, Sweden) to obtain 2–3 cm of a tree xylem sample at 20–40 cm above the soil surface. For the shrubby species *S. exigua*, we collected non-photosynthetic tissue from stems 20–50 cm above the ground, as its stems function as the primary conduit for water transport from roots to leaves. For *A. donax*, we collected rhizome tissue, as its rhizomatous growth form relies on rhizomes as underground structures for both water storage and transport, making them the plant's primary water pathway. During the 3 years of sampling, we selected different but adjacent plants for *S. exigua*, and different rhizomes for *A. donax* to avoid detrimental damage to the individuals. Because *A. donax* is a rhizomatous plant, different rhizomes were likely from the same clone.

To minimize evaporative isotopic fractionation during sampling and handling, all samples (liquid and solid) were immediately sealed in plastic vials with cone caps and parafilm sealing to prevent evaporation, and kept in a cooler until they were moved to a freezer at the end of each sampling day, where they were stored until laboratory analysis.

2.4 | Sample Processing and Isotope Analysis

All samples were processed in the Center for Stable Isotope Biogeochemistry at the University of California, Berkeley, for

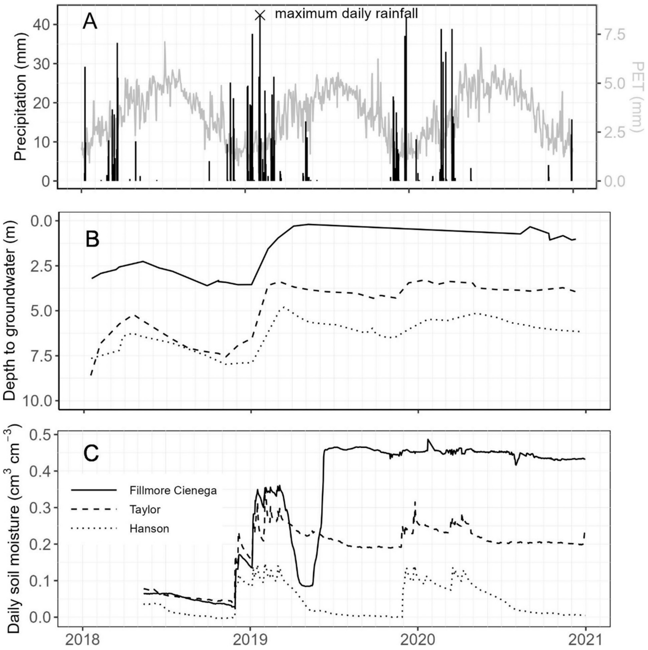

FIGURE 2 | Time series of (A) daily precipitation and PET; (B) depth to groundwater from wells at all three sites; and (C) soil moisture at 20 cm depth between Jan 2018 and Dec 2020. Precipitation data were collected next to the Fillmore Cienega site, with the maximum daily temperature during the sampling period annotated in the top panel. PET was the mean among three sites, and the locations for groundwater and soil moisture measurement are marked in Figure 1. The zero value on the y axis in panel B indicates the local ground surface at each well location. Site names and symbols are listed geographically from the most inland (Fillmore Cienega) to the coastal site (Hanson).

the determination of oxygen isotopic ratios. Water from the plant and soil samples was extracted using the cryogenic vacuum distillation method (West et al. 2006). To ensure the accuracy and reliability of our water extraction techniques, we subsampled the cores and compared the cryogenic method to a centrifugation extraction method, where water was extracted under pressures similar to those experienced by plants and soils in the field. For all *Populus* and *Salix* spp. samples, there were no significant differences in the oxygen isotope composition between the centrifuged samples (extracted at −1, −1.5 and −2 MPa) and the cryogenic method. In fact, other willow and poplar species from California and Colorado showed no significant differences in the oxygen isotope values using either method (Supplemental Table S1). These results demonstrate that either method yields consistent isotope compositions. We are therefore confident that our chosen method accurately reflects the water content and isotopic signatures in plant samples under field conditions.

Oxygen isotope ratios ($\delta^{18}O$) of water samples were then determined using one of two methods: (1) isotope ratio infrared spectroscopy using a L2140-i (Picarro Inc.) analyser for river and groundwater samples and (2) standard isotope ratio mass spectrometry in the continuous flow configuration using a Thermo Gas Bench II interfaced to a Thermo Delta V Plus mass spectrometer for extracted water samples from plants and soils. To ensure the compatibility of isotopic readings, we conducted comparison tests on a subset of samples using both methods. No significant differences were observed (Supplemental Table S2). In this study, we used $\delta^{18}O_p$ to represent oxygen isotopic values in plant xylem water, $\delta^{18}O_r$ for river water, $\delta^{18}O_g$ for groundwater and $\delta^{18}O_s$ for shallow soil moisture.

2.5 | Statistical Analysis

To understand the relationships between groundwater fluctuations, shallow soil moisture, PET and plant water isotopic signals, we constructed linear mixed-effects models with plant xylem $\delta^{18}O_p$ as the response variable and site and species as random factors. The predictive variables included soil moisture from the top 20 cm, depth to groundwater and PET, all of which were averaged over the 7 days preceding the sampling date. The groundwater data at Fillmore Cienega were recorded monthly and we interpolated the 7-day averaging using a linear method between the two adjacent months. Soil moisture, PET and depth to groundwater were measured at a single location at each site, and the complexity of underground soil texture and bedrock structure made it impossible to precisely estimate soil moisture and groundwater depth at individual plant locations. To address this limitation and enable meaningful comparisons of effect sizes, all variables were standardized into z-scores. This transformation converts variables to a relative scale instead of absolute values, enabling direct comparison of their influence on $\delta^{18}O_p$ regardless of differing units or magnitudes. We compared eight models (see Table 1) incorporating different combinations of predictor variables using Akaike information criterion corrected for small sample sizes (AIC_c), including a null model with only the random factors (Burnham and Anderson 2004). We evaluated multicollinearity using the variance inflation factor (VIF) for models with multiple predictors and found no evidence of inflation (VIF < 2.1). We also calculated Akaike weights for each model, as well as the cumulative weights for the ranked models. The best model was the one with the lowest AIC_c value, reflecting its relative likelihood compared to the other candidate models (Burnham and Anderson 2004). However, because model selection uncertainty is common in ecological data, we also identified a set of 'top models'—those with ΔAICc values less than 4 and a cumulative Akaike weight < 0.99—to account for competing models with similar empirical support. This approach provides a more robust inference by recognizing that multiple models may explain the data nearly equally well (Burnham and Anderson 2004; Richards 2005).

To examine whether $\delta^{18}O$ values were distinct among three source waters (river, groundwater and shallow soil moisture), we constructed a linear mixed-effects model with year and site as random factors using the *lmer()* function. The models were fitted using restricted maximum likelihood (REML) and *p* values derived using the 'Kenward–Roger' approximations because this method produced acceptable type 1 error rates for smaller samples (Luke 2017). We also tested the pairwise differences of least squares mean for source water types using the *difflsmeans()* function to understand whether $\delta^{18}O$ values differed between every pair of source waters (see results in Table 2). The same test and procedure were also applied to linear mixed-effects model testing the differences in plant xylem

TABLE 1 | Model comparison for the linear mixed-effects models testing the effects of depth to groundwater (dtw), soil moisture (sm) and potential evapotranspiration (pet) on plant xylem oxygen isotope values $\delta^{18}O_p$. All candidate models tested are included with their estimated parameter coefficients and AIC model selection criteria. All predictors were z-score transformed so that the effect sizes could be compared to determine which variables have the greatest influence on $\delta^{18}O_p$ values. Coefficients in bold indicate significance at α level <0.05. Model selection criteria include number of parameters (k), difference between a given model's Akaike information criterion (AIC_c) and the lowest AIC_c among all candidate models (ΔAIC_c), Akaike weight (w) and cumulative Akaike weight ($\sum$**w**).

		Estimated coefficients					
Formula	**k**	**dtw**	**pet**	**sm**	**ΔAIC_c**	**w**	**$\sum$w**
$\delta^{18}O_p \sim \mathrm{dtw} + (1 \mid \mathrm{site}) + (1 \mid \mathrm{species})$	5	**1.42**			0	0.55	0.54
$\delta^{18}O_p \sim \mathrm{dtw} + \mathrm{pet} + (1 \mid \mathrm{site}) + (1 \mid \mathrm{species})$	6	**1.41**	−0.02		2.05	0.20	0.74
$\delta^{18}O_p \sim \mathrm{dtw} + \mathrm{sm} + (1 \mid \mathrm{site}) + (1 \mid \mathrm{species})$	6	**1.44**		0.02	2.1	0.19	0.93
$\delta^{18}O_p \sim \mathrm{dtw} + \mathrm{pet} + \mathrm{sm} + (1 \mid \mathrm{site}) + (1 \mid \mathrm{species})$	7	**1.43**	−0.02	0.02	4.16	0.07	1
$\delta^{18}O_p \sim \mathrm{sm} + (1 \mid \mathrm{site}) + (1 \mid \mathrm{species})$	5			**−0.61**	35.29	<0.01	1
$\delta^{18}O_p \sim \mathrm{pet} + \mathrm{sm} + (1 \mid \mathrm{site}) + (1 \mid \mathrm{species})$	6		−0.06	**−0.59**	36.87	<0.01	1
$\delta^{18}O_p \sim \mathrm{pet} + (1 \mid \mathrm{site}) + (1 \mid \mathrm{species})$	5		−0.16		65.16	<0.01	1
$\delta^{18}O_p \sim (1 \mid \mathrm{site}) + (1 \mid \mathrm{species})$	4				66.11	0.00	1

TABLE 2 | Pairwise comparisons of least squares means were performed using a linear mixed-effects model to test whether $\delta^{18}O$ values differed among three source waters: shallow soil moisture $\delta^{18}O_s$, groundwater $\delta^{18}O_g$ and river water $\delta^{18}O_r$. The lower value represents the lower bound of the 95% confidence interval, and the upper value represents the upper bound of 95% confidence interval.

	Estimate	Std. error	df	*t* Value	Lower	Upper	Pr(>|t|)
$\delta^{18}O_r - \delta^{18}O_s$	−1.69	0.31	305	−5.49	−2.30	−1.09	<0.01
$\delta^{18}O_r - \delta^{18}O_g$	0.63	0.32	305	1.94	−0.01	1.26	0.053
$\delta^{18}O_s - \delta^{18}O_g$	2.32	0.29	304	7.94	1.75	2.90	<0.01

TABLE 3 | Pairwise comparisons of least squares means were conducted following a linear mixed-effects model, with site and the sample event number included as random factors to account for repeated surveys and to test whether $\delta^{18}O_p$ values differed among four species: *Arundo donax* (ARDO), a mix of two *Populus* species, *Populus trichocarpa* and *P. fremontii* (POPU), *Salix laevigata* (SALA) and *Salix exigua* (SAEX). The lower value represents the lower bound of the 95% confidence interval, and the upper value represents the upper bound.

	Estimate	Std. error	df	t Value	Lower	Upper	Pr(>|t|)
ARDO - POPU	1.16	0.16	682	7.19	0.84	1.47	<0.001
ARDO - SALA	1.23	0.17	686	7.33	0.9	1.56	<0.001
ARDO - SAEX	1.85	0.16	683	11.42	1.53	2.17	<0.001
POPU - SALA	0.08	0.17	686	0.45	−0.25	0.41	0.65
POPU - SAEX	0.7	0.16	682	4.27	0.38	1.02	<0.001
SALA - SAEX	0.62	0.17	686	3.64	0.29	0.95	<0.001

$\delta^{18}O_p$ values among species, with site and sampling event as random factors to account for temporal and spatial variance (see results in Table 3). All linear mixed models and post hoc tests described above were constructed using the R-package *lmerTest* (Luke 2017).

The proportional contributions of endmember sources to plant water use were estimated using Bayesian isotope mixing models in the R-package *MixSIAR* (Stock et al. 2018). The following three models were developed:

1. The 'year model' included species and year as fixed effects to determine differences in source water use between years, which varied hydrologically between drought and wet conditions.
2. The 'season model' included species and season as fixed effects to examine the seasonal variability in water usage.
3. The 'site model' included species and site as fixed effects to quantify the water usage among three sites under a range of drought conditions.

For all models, plant xylem $\delta^{18}O_p$ was considered as the dependent variable, and the independent variables were the mean and standard error of the $\delta^{18}O$ from shallow soil moisture and groundwater sources. These source values were grouped by year (for the year model), season (for the season model), or by site (for the site model). In the 'season model', we defined April–June as spring and July–October as summer, representing the wetter and drier periods of the growing season, respectively. The 'shallow soil moisture' source was derived from pooled $\delta^{18}O_s$ measurements at 40 cm and 100 cm depths, while the groundwater source reflected deeper water below the vadose zone. This approach allowed us to represent general shallow and deep water sources while accounting for variation across space and time. Endmember $\delta^{18}O$ data used in models were restricted to the period of collection overlapping with $\delta^{18}O_p$ data. We parameterized the model assuming that no $\delta^{18}O_p$ fractionation occurred during root water uptake, in accordance with well-supported evidence from prior studies (Ehleringer and Dawson 1992). The Markov chain Monte Carlo run option was set to 'long' (chain length = 300,000, burn = 200,000, thin = 100, chains = 3) for all models to ensure convergence based on Gelman Rubin and Geweke diagnostic tests (Stock et al. 2018). Models were run using residual × process error structure with the uninformative prior setting. All data analyses were performed in R version 4.3.0 (R Core Team 2023).

3 | Results

The 3-year sampling period (2018–2020) spanned the drought recovery period of the extended California drought (2012–2019). The year 2018 was classified as a 'dry' year, while 2019 and 2020 were considered 'wet' years with increased precipitation and soil moisture (Figure 2). Consistent with expectations, $\delta^{18}O_s$ (Figure 3) and $\delta^{18}O_p$ (Figure 4) were more depleted during the wet years compared to the dry year. At the site level, $\delta^{18}O_p$ was generally more enriched than the groundwater signal (Figure 4), suggesting that plants did not rely exclusively on groundwater. However, water source reliance varied in both degree and pattern among the four riparian species.

3.1 | Hydrology and Climate

Substantial rainfall in early 2017 provided some drought relief from the peak drought period of 2013–2016; however, a relatively dry winter in 2017–2018 prolonged drought conditions into the summer of 2018 (Kibler et al. 2021). Additional rainfall in late 2018 and early 2019 ended the drought. During this period, precipitation in the Santa Clara River watershed was sufficient to recharge the soil and groundwater, which caused an increase in soil moisture content and groundwater table level (Figure 2). The precipitation was largely concentrated in late winter and early spring each year (Figure 2A), with the maximum daily rainfall of ~ 42 mm occurring in early 2019. The dPET fluctuated between 1.4 and 7 mm day^{-1}, with the peaks occurring consistently in summer and fall. In response to increased rainfall, groundwater levels recharged gradually in 2018 and more substantially in 2019, subsequently maintaining a consistently shallow water table for the remainder of the study period (Figure 2B).

Soil moisture was consistently low across sites in 2018 (dry year), but seasonal and site differences became more apparent

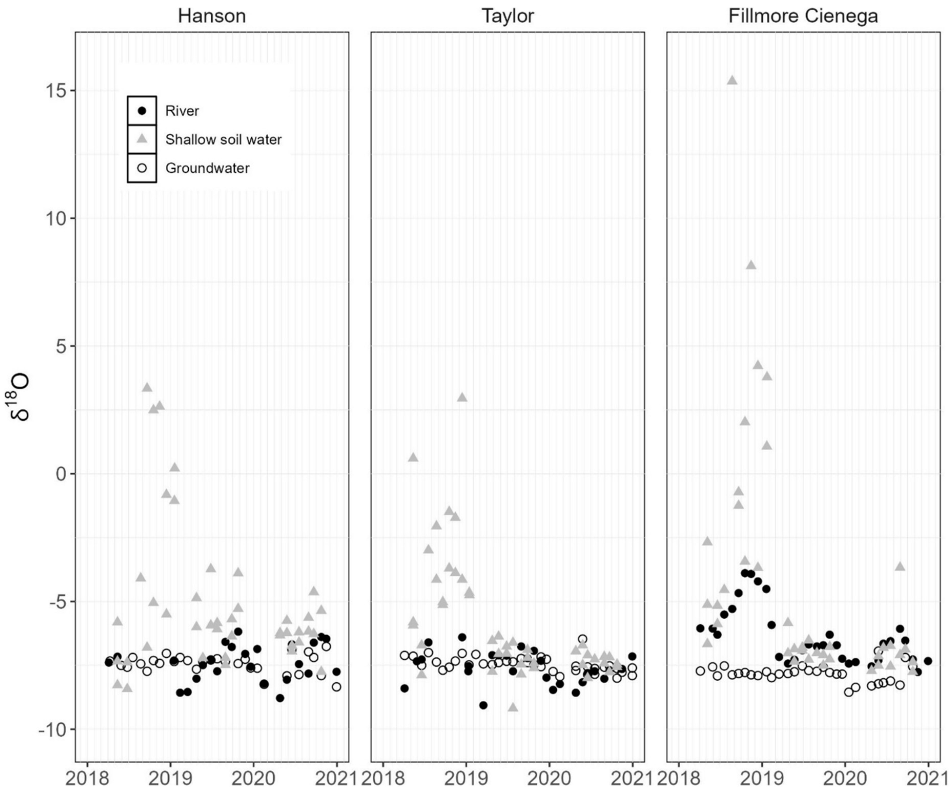

FIGURE 3 | Time-series of $\delta^{18}O$ for source waters at each site: river, shallow soil moisture and groundwater. Sites are oriented from most downstream (Hanson) to upstream (Fillmore Cienega).

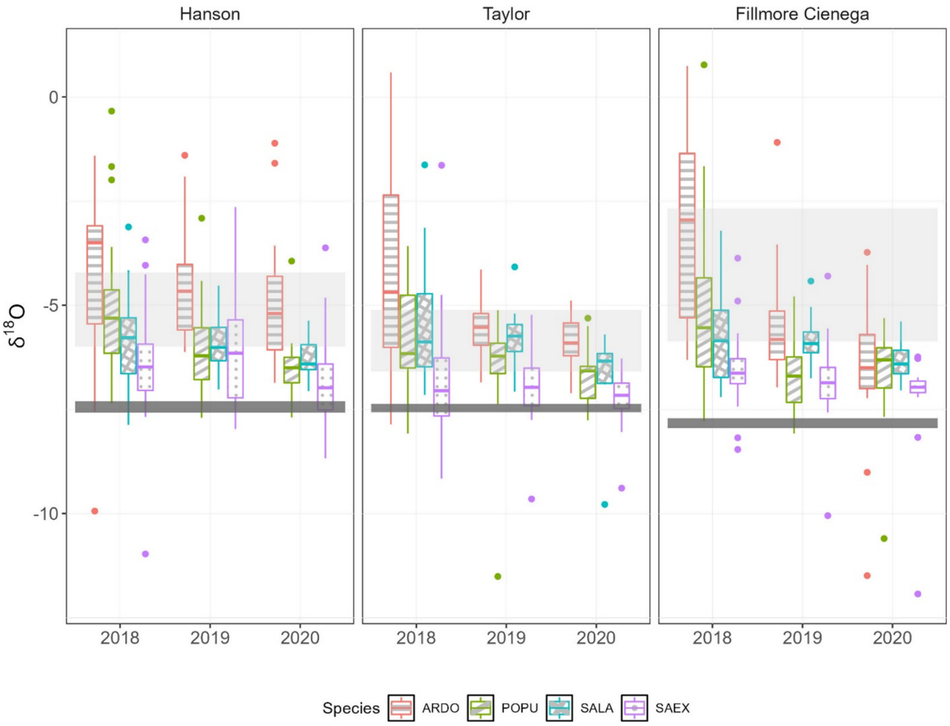

FIGURE 4 | Boxplots showing plant xylem water $\delta^{18}O_p$ values for dominant riparian species in each of the sampling years. Species include *Arundo donax* (ARDO), a mix of two *Populus* species, *Populus trichocarpa* and *P. fremontii* (POPU), *Salix laevigata* (SALA) and *Salix exigua* (SAEX). As references, the darker grey bands show the 95% CI of the groundwater $\delta^{18}O_g$ at the given site and lighter grey bands span the 95% CI for the shallow soil moisture $\delta^{18}O_s$ values.

with the return of wetter conditions. At Fillmore Cienega, the most upstream site, soil moisture in the top 20 cm soil profile was extremely low in the first sampling year (April—October in 2018), with an average moisture of $0.05\,cm^3\,cm^{-3} \pm 0.01\,cm^3\,cm^{-3}$ (STD) for the whole growing season. Following rainfall in early 2019, soil moisture remained high and close to saturation ($> 0.4\,cm^3\,cm^{-3}$), and stable in the topsoil profile throughout the 2019 and 2020 growing seasons (Figure 2C). During this period, we also observed saturated conditions and pooled water in certain areas of the floodplains where plant sampling occurred. A similar temporal pattern was observed at the two downstream sites, where soil moisture was low in 2018, with growing season averages of $0.057\,cm^3\,cm^{-3} \pm 0.01\,cm^3\,cm^{-3}$ (STD) at Taylor and $0.01\,cm^3\,cm^{-3} \pm 0.01\,cm^3\,cm^{-3}$ (STD) at Hanson. In the subsequent years, soil moisture at these sites displayed consistent seasonal patterns: increasing during the rainy season, declining in early spring and remaining low through summer and fall (Figure 2C).

3.2 | Hydrologic Influences on Plant $\delta^{18}O$

The linear mixed-effects model testing the effects of hydrological conditions on plant xylem $\delta^{18}O_p$ indicated that soil moisture, PET and depth to groundwater were all important drivers for plant water source selection (Table 1). All three variables were in the subset of top models (those with cumulative Akaike weight < 0.99). In the single-variable models examining each in dependent variable separately, the estimated standardized coefficients for soil moisture, PET and depth to groundwater were −0.61, −0.16 and 1.42, respectively (Table 1). These standardized coefficients represented the change in $\delta^{18}O_p$ for a one standard deviation increase in each predictor variable (with z-score transformed), with no other predictors in the model. Specifically, the coefficient for depth to groundwater (1.42) was approximately nine times larger than that for PET (−0.16) and about two times larger than that for soil moisture (0.61). This indicated that depth to groundwater was the most influential factor affecting plant water source selection, followed by shallow soil moisture and PET. The positive relationship between depth to groundwater and $\delta^{18}O_p$ showed that as groundwater levels declined, plants' $\delta^{18}O_p$ became more enriched, reflecting reduced root access to groundwater. The negative relationships between PET and $\delta^{18}O_p$ indicated that as PET increased (e.g., throughout the summer), plants' δ18O became more depleted, reflecting greater reliance on groundwater.

3.3 | Stable Isotope Analysis for Source Waters and Plant Xylem Water

The $\delta^{18}O$ of the three potential water sources (river, groundwater and shallow soil moisture) ranged from −9.18 to 15.36‰ (Figure 3). The linear mixed-effects model and the post hoc tests suggest that the soil moisture water $\delta^{18}O_s$ (−5.1 ± 3.6‰, mean ± SD) differed significantly from the river $\delta^{18}O_r$ (−7.1 ± 1.0‰) and groundwater $\delta^{18}O_g$ (−7.6 ± 0.4‰) whereas the river water and groundwater were more isotopically similar (Table 2). This pattern is also shown in Figure 3, where $\delta^{18}O_r$ was mostly in the range of the groundwater $\delta^{18}O_g$ in wetter years (i.e., 2019 and 2020), indicating some degree of connectivity. Based on these patterns, we used shallow soil moisture and groundwater as the two distinct endmember sources in the MixSIAR models.

The seasonal pattern of $\delta^{18}O$ values in shallow soil moisture and river water was consistent, showing depletion during winter and spring and enrichment during late summer and early fall (Figure 3). At Fillmore Cienega, shallow soil moisture exhibited more pronounced seasonal variations compared to river water and groundwater, with the strongest enrichment observed in the summer of 2018. During this period, the most enriched shallow soil moisture signal was 15.3‰, while the river water peaked at −3.89‰, coinciding with the lowest recorded groundwater table and soil moisture content during the study period (Figure 2). Following the rise in groundwater levels in the spring of 2019, the river $\delta^{18}O_r$ values became more depleted and closely aligned with the groundwater signal (Figure 3). Notably, at the site level, $\delta^{18}O_r$ values at Taylor and Hanson (the two downstream sites) were relatively stable and similar to the groundwater signal, suggesting stronger groundwater contributions in these downstream reaches, likely due to the bedrock structure that elevates the groundwater table. In contrast, the upstream Fillmore Cienega site showed consistently more enriched $\delta^{18}O_r$ relative to groundwater, $\delta^{18}O_g$, indicating greater separation between surface and groundwater at that location. As we expected, the isotopic signal from the groundwater across the basin had the least fluctuation over the 3 years (Figure 3) among all source waters, ranging between −6.47 and −8.55‰.

Plant xylem tissue $\delta^{18}O_p$ ranged from −19.3 to 1.44‰ (Figure 4). The plant tissue analysis (linear mixed-effects model followed by pairwise comparison) indicated that $\delta^{18}O_p$ was significantly more enriched for *A. donax* (−4.9 ± 2.2‰) compared to native riparian woody species (Table 3), a pattern consistent across all years (Figure 4). In addition, the standard deviation of *A. donax* $\delta^{18}O_p$ across all years was approximately 1.4 times greater than the woody species, consistent with the greater variability of $\delta^{18}O_s$, which together suggests shallow soil moisture was the main water source for *A. donax*. For native woody species, $\delta^{18}O_p$ was similar between *Populus* spp. (−6.1 ± 1.6‰) and *S. laevigata* (−6.0 ± 1.5‰), but was significantly more depleted for *S. exigua* (−6.8 ± 1.5‰) (Figure 4; Table 3), suggesting a higher proportional use of groundwater.

3.4 | Mixing Model for Determining Source δ^{18}O

Results from isotope mixing models revealed that, regardless of functional type, riparian tree species relied on groundwater during the drought, but made advantageous use of shallow soil moisture when it was available (Figure 5). In 2019 and 2020 when rainfall was high, the native trees derived ≥ 65% of their water from shallow soil moisture, compared to ≥ 88% for *A. donax*. In the dry year, 2018, the model estimated that shallow soil water accounted for 29–38% of the source water for native trees compared to 62% for *A. donax*. The use of shallow soil moisture decreased by 55–62% for native trees and by 36% for *A. donax* between the wet (2019) and dry (2018) years, highlighting a sizeable shift in water sources from shallow soil moisture to groundwater during drier conditions.

We observed clear seasonal patterns in water source use, with all species relying more heavily on groundwater during summer in contrast to spring (Figure 5B). This shift was inversely related to the availability of shallow soil moisture throughout the growing season (Figure 2C, see sites Taylor and Hanson). Facultative phreatophytes used approximately 20% groundwater in spring, increasing to ~ 47% in summer and early fall. In comparison, *S. exigua* acted more like an obligate phreatophyte, showing a more pronounced shift with groundwater use increasing from 44% in spring to 74% in summer, reflecting a 30% increase in reliance on deeper water sources. In contrast, the drought-tolerant *A. donax* exhibited a smaller change, using only 7% groundwater in spring and 20% in summer, demonstrating its consistent use of shallow soil moisture year-round.

The source water consumption patterns differed systematically among the three sites (Figure 5C), with all species showing the highest proportion of groundwater use at Fillmore Cienega (22–60% among all species at the site). This was notably higher compared to the two downstream sites, Hanson (15–49%) and Taylor (10–36%), where proportional groundwater uptake was similar, and soil moisture values were slightly lower during 2019 and 2020 (Figure 2). Despite these site-specific differences, a consistent pattern of source water use was observed across species: *A. donax* was the most dependent on shallow soil moisture (78–90% across sites), while *S. exigua* exhibited the lowest dependence (40–64%, Figure 5C).

4 | Discussion

Our findings highlight the capacity of riparian vegetation in dryland ecosystems to adjust water use strategies in response to changing hydrologic conditions. This flexibility, shifting between shallow soil moisture and groundwater, plays a critical role in maintaining plant function and ecosystem stability under increasing climate variability. However, not all species exhibit the same degree of plasticity. Species-specific traits such as rooting depth, life history characteristics and physiological adaptations shape their responses to water stress, influencing riparian community resilience. Our study illustrates how native phreatophytes and invasive species differ in water source use during and after extreme drought in the Santa Clara River basin. These findings can inform restoration strategies by identifying which species are more likely to persist under future drought scenarios and which areas may serve as hydrologic refugia for maintaining riparian habitat.

4.1 | Riparian Plants Are Opportunistic in Using a Combination of Water Sources

Riparian plants exhibit opportunistic water use, predominantly relying on shallow soil moisture when water availability is high, while shifting to groundwater during drought or dry seasons. This dynamic water-use strategy is somewhat expected, as riparian plants are adept at simultaneously accessing multiple water sources within this hydrologically dynamic environment, depending on which type of water source is the most readily available and energetically efficient to uptake (Glenn and Nagler 2005). For most riparian species, root systems are typically denser within the top meter of soil (Jackson et al. 1996; Tumber-Dávila et al. 2022), making shallow soil moisture a more utilized water source when conditions allow. Native plants sourced 60–90% of their water from shallow soil moisture during

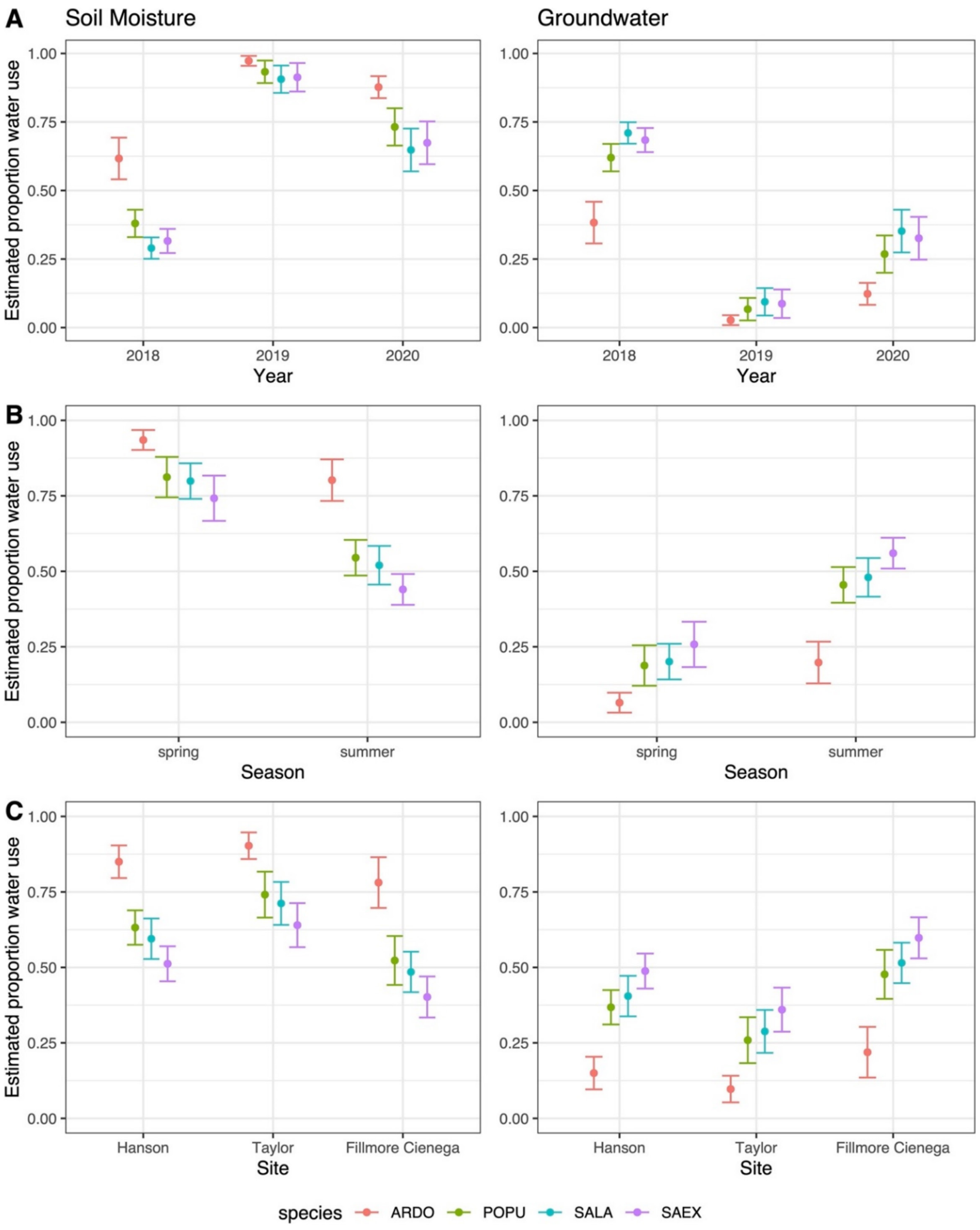

FIGURE 5 | Results of MixSIAR model estimates for the proportion of shallow soil moisture (left column) versus groundwater (right column) used by each species, grouped by (A) year, (B) season and (C) site. Error bars display standard deviation. Species names are abbreviated where ARDO is *Arundo donax*, POPU is a combination of *Populus trichocarpa* and *P. fremontii*, SALA is *Salix laevigata*, SAEX is *Salix exigua*.

the wet years of 2019 and 2020. This pattern indicates that even for riparian species, accessing shallow soil moisture during wet periods is an efficient and productive strategy. Winter precipitation during these wet years was stored in the soil and lasted well into the following summer, providing the majority of water uptake by plants during the subsequent dry season.

Although riparian plants consistently used a greater proportion of shallow soil moisture, they were able to shift their water source as needed. For instance, native *Populus* and *Salix* trees demonstrated the ability to increase groundwater use by ~ 60% during droughts. This adaptability underscores the resilient structural and hydraulic traits, such as deep, well-developed root systems and xylem capable of maintaining water transport under low water potentials, which enable these species to access deeper water sources during periods of surface water scarcity (Hultine et al. 2020). These traits are critical for drought survival, allowing plants to maintain physiological function and delay or avoid hydraulic failure, and may confer a competitive advantage in increasingly water-limited riparian systems. Similar trends have been observed for various *Populus* spp. and *Salix* spp. (Bailey et al. 2022; Singer et al. 2013; Snyder and Williams 2000; Williams et al. 2024), *Eucalyptus camaldulensis* (Pettit and Froend 2018) and *Quercus robur* (Pinto et al. 2014). These shifts not only emphasize the critical role of groundwater as a fallback resource during dry seasons or prolonged droughts but also illustrate its complementary relationship with shallow soil moisture in supporting plant water needs (Sargeant and Singer 2016; Singer et al. 2014), and serving as a key driver in sustaining groundwater-dependent ecosystems.

4.2 | Spatial and Temporal Influences on Source Water Use

Seasonal, interannual and site-specific factors strongly influenced the source water use of riparian plants. Variations in local groundwater table depth, as well as differences in water availability across seasons and years, played critical roles in shaping plant water sources. Spatial variability in groundwater use was closely linked to local groundwater table depth and shallow soil moisture. Species at Fillmore Cienega exhibited the highest groundwater use (22–60%, mean values among species) likely due to the shallower groundwater table and the presence of saturated soil conditions, a phenomenon unique to this site. This easy water accessibility would be expected to enable facultative phreatophytes to efficiently utilize both shallow soil water and groundwater, which can maximize their overall water uptake (Bleby et al. 2010; Dawson and Pate 1996). Groundwater consumption was lower at the downstream sites, ranging 15–49% at Hanson and 10–36% at Taylor, where groundwater tables were deeper than at Fillmore Cienega and showed no signs of saturated shallow soil conditions. Despite these conditions, most species continued to rely heavily on shallow soil moisture, even in dry periods. At Hanson, soil moisture during the 2019 and 2020 growing seasons—particularly in late summer and fall—may have approached the wilting point (< 5%), based on regional estimates (Warter et al. 2021). Yet, plants still appeared to source approximately 60% of their water from shallow layers. This is somewhat surprising and may suggest that water uptake was occurring below our soil measurement depth, possibly from soil layers deeper than 1 m, where rain-infiltrated moisture could mix with groundwater via the capillary fringe. Given the spatial heterogeneity and complexity of subsurface water dynamics, future research would benefit from finer-scale hydrologic monitoring within the root zone to better capture plant-accessible moisture.

Temporally, riparian plants relied primarily on shallow soil water during wetter seasons, such as spring, and wet years, including 2019 and 2020. However, during dry summer and fall months, as well as in the drought year of 2018, groundwater use increased substantially. All species in our study increased groundwater uptake to offset declining soil water availability, with native species showing a 28% rise compared to 14% for *A. donax* from spring to summer, and a 60% increase compared to 36% for *A. donax* during the dry year relative to wetter years. These patterns align with studies in other ecosystems (David et al. 2007; Dawson and Pate 1996; Sarris et al. 2013; Scott et al. 2008), collectively highlighting the dynamic interplay between seasonal water availability and plant water strategies—essential for resilience in semi-arid regions like southern California, where variable precipitation and prolonged droughts impose frequent water stress.

4.3 | Species Varied in Their Dependence on Groundwater

Riparian species exhibited notable variation in their reliance on groundwater, shaped by their adaptive strategies. Native riparian woody vegetation, such as *Populus* and *Salix*, demonstrated higher groundwater use across varying hydrological conditions compared to the invasive *A. donax*, which predominantly depended on shallow soil moisture. The dependence on groundwater increased for all species during drought.

Deep-rooted species, such as *Populus* and *Salix*, exhibited flexibility in water source use, particularly during drought periods. Our results suggest native trees might rely on deep taproots to access stable groundwater as shallow soil moisture becomes scarce. This behaviour is consistent with that of facultative phreatophytes, such as *Tamarix ramosissima*, which can readily use shallow soil moisture when available but switch to groundwater during droughts (Busch et al. 1992; Sun et al. 2016). Investing in deep root systems has been identified as a key adaptive strategy for drought tolerance in riparian woody species (Hultine et al. 2020; Rood et al. 2011). Similar plasticity is seen in other deep-rooted species in semi-arid regions, such as Mediterranean pines, which rely more on deeper water sources during prolonged droughts (Sarris et al. 2013). However, rapid groundwater recession beyond rooting depth or seedling growth rates can limit ecological function and threaten species persistence (Stella et al. 2010; Williams et al. 2022).

Shrub species have shallower root systems than trees (Schenk and Jackson 2002) and thus are generally expected to rely more heavily on shallow soil moisture. However, the native shrub *S. exigua* showed the highest groundwater dependence among all species studied, including *Populus* and *Salix* trees. Snyder and Williams (2000) conducted water isotopic research along the

San Pedro River in southeastern Arizona and discovered that a similar willow species, *Salix gooddingii*, did not take up water from upper soil layers during the summer rainy period, but instead used only groundwater, even at an ephemeral stream site where depth to groundwater exceeded 4 m. In contrast, the same study showed that cottonwoods are somewhat more flexible and capable of using shallow soil water when available (Snyder and Williams 2000) Although there were differences in baseline groundwater consumption, with *S. exigua* relying more heavily on groundwater during the wet season (34%) compared to native tree species (20%), the seasonal increase in groundwater uptake during the dry season was consistent across all native species, rising by approximately 28%. This suggests that native species (*Populus* and *Salix*) exhibit comparable sensitivity to seasonal declines in soil moisture, as they adapt to water stress by increasing their reliance on groundwater. On a broader scale, a recent remote-sensing analysis in California found that willow-dominated riparian thickets and cottonwood stands alike exhibit declining canopy greenness (NDVI) as groundwater depth increases, reflecting parallel water stress responses in both vegetation types (Rohde, Stella, et al. 2021). These findings highlight the functional convergence between native riparian shrubs and trees in their groundwater dependence, reinforcing the importance of considering both groups in groundwater management and conservation planning.

The invasive *A. donax* exhibited a contrasting strategy, heavily relying on shallow soil moisture across seasons and hydrological conditions. These findings align with studies by Moore et al. (2016) that showed *A. donax* predominantly used surface soil water recharged by winter/spring flooding while the proportion of groundwater consumed was only 32%. The relatively limited reliance of *A. donax* on groundwater reflects its shallow rooting structure and architecture adapted to efficiently utilize shallow soil moisture. Most of its roots are concentrated in the upper 50 cm of the soil profile, with few roots extending beyond 95 cm (Stover et al. 2018), precluding its use of deeper groundwater. This shallow rooting strategy is complemented by an interconnected rhizome network, facilitating rapid water transport among neighbouring ramets (Kui et al. 2013; Moore et al. 2016). Additionally, *A. donax* possesses drought-resilient xylem architecture, enabling it to lower water demand through strategies such as leaf drop and biomass reduction (Haworth et al. 2017; Pompeiano et al. 2017). These adaptations provide a competitive advantage in environments with limited groundwater availability, potentially allowing *A. donax* to outcompete native species under future drought scenarios (Lambert et al. 2014; Mann et al. 2013). This displacement may force native species to increase their reliance on groundwater, intensifying competition with human water demands and placing greater pressure on this vital resource. This presents a significant knowledge gap, warranting further research to better understand the long-term impacts of *A. donax* on groundwater dynamics and the resilience of native riparian species under increasing drought conditions.

4.4 | Management Implications

Given projections of increasing drought severity and frequency in southern California (Cayan et al. 2008; Diffenbaugh et al. 2015), declining groundwater levels intensify stress on these species, as observed during the 2012–2019 drought along the Santa Clara River corridor, where mortality and canopy dieback were widespread (Kibler et al. 2021; Williams et al. 2024). Without sustainable groundwater management, riparian ecosystems are likely to experience reduced biodiversity, weakened ecological resilience and impaired ecosystem services. California's 2014 Sustainable Groundwater Management Act provides a regulatory framework to address these challenges by requiring local agencies to identify and protect GDEs. Our results, supported by previous research, show that both native riparian trees and shrubs—especially *S. exigua*—are highly sensitive to groundwater declines and rely heavily on groundwater during dry periods. Maintaining shallow groundwater levels throughout the growing season is essential to prevent vegetation dieback and habitat degradation.

In basins like the Santa Clara River, where natural flow regimes remain relatively intact but agricultural groundwater demand is high, managed flow releases or targeted aquifer recharge during the dry season could help support riparian vegetation. Late summer and fall, when surface soil moisture is lowest, may be the most effective period for such interventions. Importantly, while increased groundwater availability can enhance the survival of native species, its effect on invasive species like *A. donax* may be limited, given their shallow rooting and reliance on surface moisture. These findings underscore the value of incorporating species-specific water use strategies into SGMA implementation to better guide restoration, prioritize monitoring and improve long-term groundwater sustainability planning in California's dryland basins.

Author Contributions

L.K. led fieldwork and data collection, conducted statistical analysis and drafted the manuscript. J.W. contributed to statistical analysis, reviewed relevant literature and assisted with manuscript editing. M.B.S. and J.C.S. conceived the study, provided statistical guidance and contributed to placing the case study in a broader context. C.L.K. assisted with study design, field instrumentation and fieldwork. T.E.D. performed isotope analyses and contributed to data interpretation. M.M.R. coordinated site access and permitting, and provided input on the management implications of the manuscript. A.M.L. assisted with fieldwork and data interpretation. D.A.R. contributed to manuscript editing. All authors reviewed and approved the final version of the manuscript.

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Data Availability Statement

The data that support the findings of this study are openly available in Environmental Data Initiative at https://edirepository.org/, data package DOI: 10.6073/pasta/98b1154256c7f7547c6a0e2b6e191560.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.