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Depth distribution of soil water sourced by plants at the global scale: A new direct inference approach

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Abstract

The depth distribution of soil water contributions to plant water uptake is poorly known. Here we evaluate the main water sources used by plants at the global scale and the effect of climate and plant groups on water uptake variability and depth distribution. The global meta-analysis is based on isotope data (δ^2H and $\delta^{18}O$) extracted from 65 peer-reviewed papers published between 1990 and 2017.

We applied a new direct inference method to quantify the overlap between xylem water and soil water sources used by plants. The median overlap between xylem water and soil water at different depths varied between 28% and 100%, but they were generally >50%. The shallow (0-10 cm) soil water overlap with xylem water was largest in cold regions (100% ± 0%) and lowest at tropical sites (about 28%). Conversely, the median overlap between xylem water and deep soil water was largest in the arid and the tropical zones (>75%) and much smaller in the temperate and cold zones. Our results suggest that the isotopic composition of xylem water reflects mostly the signature of shallow soil water (<30 cm) in the cold and the temperate zones, whereas in the arid and the tropical zones, plants appear to exploit water in deeper soil layers. Our novel, simple statistically-based direct inference method performed well in determining these differences in water sources, and can be applied more widely to isotope-based plant water uptake studies.

KEYWORDS

climate, deuterium excess, direct inference; global scale, meta-analysis, soil water, stable isotopes, xylem water

1 | INTRODUCTION

Transpiration of terrestrial vegetation is a dominant force in the global water cycle, accounting for 60–80% of total evapotranspiration fluxes on land (Schlaepfer et al., 2014; Schlesinger & Jasechko, 2014). Transpiration is a major determinant of local microclimate and precipitation patterns and has a direct impact on water balance and streamflow regimes (Andréassian, 2004; Laurance, 2007). Given the important role of plant transpiration in the hydrological cycle, a more detailed understanding of plant water uptake and ecohydrological interactions between plants and soil water is crucial for developing effective land surface models and sustainable water use strategies.

The stable isotopes of hydrogen and oxygen (^{2}H and ^{18}O) are effective tools to determine the proportions of water sources to plant transpiration. Due to their conservative nature through soils and their occurrence in the water molecule, stable isotopes are increasingly used for tracing water fluxes in ecohydrological and other interdisciplinary studies (Penna et al., 2018; Scandellari & Penna, 2017). The quantification of the main water sources for plant transpiration on the basis of isotopic tracers is typically carried out through a graphical inference method (Brunel, Walker, & Kennett-Smith, 1995), two end-member mixing models (e.g., Thorburn & Walker, 1993), or statistically-based multisource mixing models (e.g., Schwendenmann, Pendall, Sanchez-Bragado, Kunert, & Hölscher, 2015). The graphical inference method defines the mean root water uptake depth as the soil depth where the isotopic composition of soil water is most similar to or equals the one of xylem water. Basically, this approach represents the plant root system as one unique root (Rothfuss & Javaux, 2017). IsoSource (Phillips & Gregg, 2003) is a widely used linear mixing model based on a mass balance equation (recent examples are Jia, Liu, Chen, & Yu, 2017; Zhu, Zhang, Gao, Qi, & Xu, 2016). Nowadays, statistical Bayesian mixing models such as SIAR (Parnell et al., 2013), MixSir, and MixSIAR (Moore & Semmens, 2008) are gaining popularity (e.g., Beyer, Hamutoko, Wanke, Gaj, & Koeniger, 2018). For a review and intercomparison of these methods, the reader is referred to Rothfuss and Javaux (2017). Bayesian isotope mixing models have the advantage of providing uncertainties of the estimated fractions of water sources and provide an optimal solution rather than a range of feasible solutions (Rothfuss & Javaux, 2017). However, a common underlying assumption of these approaches is that all water sources accessed by plant roots are adequately sampled and that the isotopic signature is conserved through the mixing processes. But in field studies, sampling all potential water sources is not always practical or possible, creating potential bias in the mixing model estimation of a given plant water source. Therefore, new methods that allow for robust quantification of water sources accessed by plants and that can be distinctly sampled are needed.

In many cases, the primary source of plant transpiration is soil water extracted from different depths by vegetation through roots (Asbjornsen et al., 2011; Gardner & Ehlig, 1963). Plants can access shallow and deep soil water, as well as groundwater with a tendency to prioritize the use of stable and continuous water sources (Zhao & Wang, 2018), at least in regions where some sources are continuously available. Several studies based on an isotope approach and focusing on the identification of different water sources accessed by plants have been conducted at individual sites in many regions of the world and on different plant species (e.g., to name a few recent studies, Allen, Kirchner, Braun, Siegwolf, & Goldsmith, 2019; Chi, Zhou, Yang, Li, & Zheng, 2019; Dubbert, Caldeira, Dubbert, & Werner, 2019; Evaristo et al., 2019; Nie et al., 2019; Oerter, Siebert, Bowling, & Bowen, 2019; Qiu et al., 2019). Recent meta-analyses assessed plant water sources across different biomes and plant species (Barbeta & Peñuelas, 2017; Evaristo, Jasechko, & McDonnell, 2015; Evaristo & McDonnell, 2017a, 2017b).

Despite these meta-analyses and the notable number of studies focusing on the quantification of water sources for tree transpiration in different parts of the world, knowledge on global scale estimates of soil water sources at different depths is still missing. Thus far, global meta-analyses have not quantified the depths of soil water contributions to plant water uptake. Indeed, the depth distribution (from the soil surface to the water table) is the key missing link to perhaps reconcile some of the disparity in results from different studies. Here we analyse isotope data extracted from 65 peer-reviewed papers published between 1990 and 2017. We propose a new direct inference method that can approximate the proportion of water sources to root water uptake even if one or more sources are missing. We use this new approach to evaluate the main water sources used by plants around the world and to quantify explicitly the depth distribution of soil water uptake and its relation to climate and plant groups.

Specifically, our work aims to answer the following questions:

1. To what extent does the isotopic composition of xylem water reflect that of soil water for different plant groups across the globe?
2. What is the depth distribution of this source water?
3. How does climate and plant groups control these patterns?

2 | MATERIALS AND METHODS

2.1 | Literature selection and data extraction

We based our global meta-analysis on isotope data extracted from 65 peer-reviewed papers (Data S1) published between 1990 and the end of 2017 that used both stable isotopes of water (δ^2H and δ^{18}O) for ecohydrological studies. We performed searches in Web of Science, Scopus, and Google Scholar using different combinations of the following keywords: "water uptake," "xylem," "soil water," "stable isotopes," "hydrogen," and "oxygen". Of the returned papers, we considered only those that reported both δ^{18}O and δ^2H data in soil water at different soil depths and in xylem water. Our returns included 25 and 37 of the 47 and 138 papers in Evaristo et al. (2015) and Evaristo and McDonnell (2017b), respectively, and 7 of the 35 papers examined in Barbeta and Peñuelas (2017).

We excluded studies that did not report both isotopes or did not include soil water. Stable isotope data reported in the original papers were extracted either directly from tables or the text or through the data extraction tool Graph Data Extractor (Matthews, 2017) or obtained from digital repositories. The database includes isotope data from soil water (n = 5,328) and xylem water (n = 2,579) from 77 study sites (some papers reported data from more than one site, so the number of study sites is larger than the numbers of screened papers) belonging to four different climate zones of the world, according to Köppen classification (Peel, Finlayson, & McMahon, 2007; Figure 1; Table S1). For each paper, we collected additional information

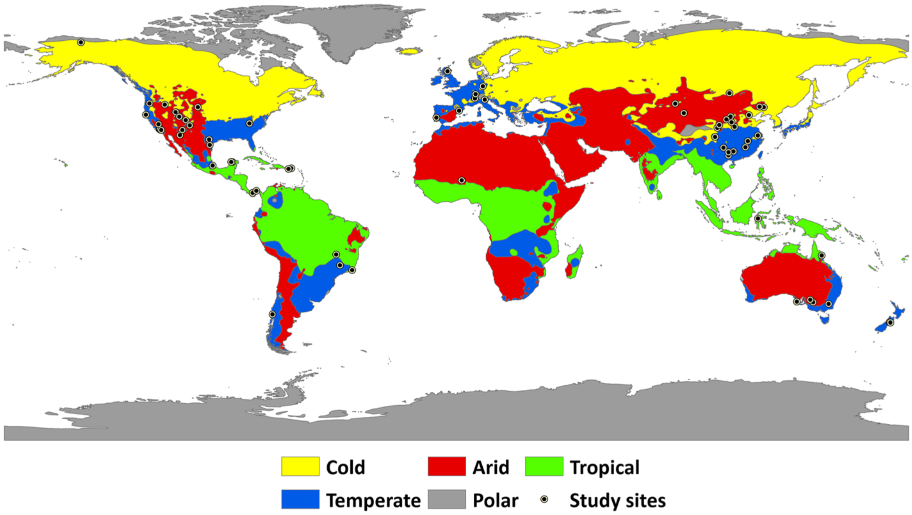

FIGURE 1 Köppen climate classification (Peel et al., 2007) for all study sites included in this global analysis

including the geographical coordinates of the study area, elevation, plant group or species, and soil depths reported by authors of the original papers. In case some of this information was missing, we obtained it through online resources. Coordinates were extracted via Google Earth, elevation via GPS Visualizer (Schneider, 2017), and the distinction between gymnosperms and angiosperms via The Plant List (2013).

To evaluate the effects of different environmental factors on the isotopic composition of soil and xylem water, we compiled the following information in a geographic information system environment: mean annual temperature (MAT) in degrees Celsius obtained from Esri ArcGIS online map derived from WorldClim Version 1.4 (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) for the period 1950–2000 (30 arc seconds or approx. 1 km at equator); global aridity index (United Nations Environment Programme, 1997) values extracted from a data set provided by Consortium for Spatial Information (Consultative Group on International Agricultural Research-Consortium for Spatial Information; Trabucco & Zomer, 2009) at 0.0083° spatial resolution. We chose to retrieve MAT and global aridity index values of the study sites from global databases because not all the papers reported all the characteristics, and we wanted to have a consistent database avoiding different classifications.

2.2 | Statistical tests and direct inference method

To compare xylem water and soil water samples from the four climate zones, we computed the deuterium-excess (d-excess) for each data point following Dansgaard (1964).

$$d-\text{excess} = \delta^2\text{H} - 8 \times \delta^{18}\text{O} \tag{1}$$

The d-excess is interpreted as an index for the characterization of non-equilibrium conditions during global evaporation–condensation processes. We used d-excess instead of line-conditioned excess (Landwehr & Coplen, 2006) because local meteoric water lines and/or the isotopic composition of local precipitation were not available for all the individual study sites. Therefore, for consistency in the data analysis, we computed d-excess.

All extracted isotopic data of soil and xylem waters were tested for normality and revealed that the data were not normally distributed (Shapiro–Wilk normality test; significance level at 0.01). All subsequent statistical analyses to compare samples were thus performed using non-parametric tests. These included the Mann–Whitney rank sum test (Hollander & Wolfe, 1999) to compare the isotopic values of xylem water and soil water within each climate zone, and the Kruskal–Wallis one-way analysis of variance test to assess differences in the isotopic composition of xylem and soil waters across the four climate zones, plant groups, and soil depths. Spearman rank correlation analyses were used to assess the strength of the correlation between MAT, elevation of the study sites and global aridity index with δ^{18}O, δ^2H and d-excess of soil water 2 and xylem water 3.

We quantified the contributions of water sources (i.e., soil water at different depths) to root water uptake at the global scale using a new isotope-based direct inference method. The only assumption underlying this method is that the isotopic signature of xylem water is conserved during the water uptake (i.e., no fractionation during transport) and reflects the contribution of the different water sources. For each study site, we plotted all the data in a dual-isotope space and drew ellipses on the basis of 99% confidence intervals (Friendly, Monette, & Fox, 2013) for each source (here the soil water at different depths) and xylem water (Figure 2), using the R function called *covEllipses* (Fox, Friendly, & Monette, 2018). For the determination of the ellipse parameters, we applied two algorithms to remove outliers, including the minimum volume ellipsoid (MVE; Van Aelst & Rousseeuw, 2009) and the minimum covariance determinant (MCD; Croux & Haesbroeck, 1999; Rousseeuw & Van Driessen, 1999), in order to provide information about the uncertainty of the estimates.

TABLE 1 Median d-excess (‰) of xylem water and soil water for different plant groups and soil water depths in different climate zones

Water type	Tropical	Arid	Temperate	Cold
Xylem water				
Angiosperms	4.3 (407)	−4.1 (196)	−1.4 (625)	−6.4 (395)
Gymnosperms	–	−16.7 (112)	0.5 (587)	−0.7 (197)
Soil water				
0–10 cm	6.1 (294)	−27.6 (39)	−2.7 (583)	−1.5 (236)
10–30 cm	8.9 (296)	−18.4 (70)	3.1 (387)	1.1 (393)
30–50 cm	9.4 (281)	−10.0 (54)	6.3 (511)	4.1 (231)
>50 cm	9.3 (323)	−2.6 (94)	7.6 (335)	4.4 (684)

Note. Number of samples are reported in parentheses.

Furthermore, the application of the two different methods for the detection of the outliers allowed for the analysis of the sensitivity of our results for a given algorithm. We then counted the number of xylem water samples falling in the intersection space (graphically overlapping) between the ellipse of the xylem water samples and the ellipses of the different potential water sources as follows:

$$\text{overlap}\,(\%) = \frac{n_{\text{water source}}}{n_{\text{total}} - n_{\text{out}}} \times 100, \tag{2}$$

where $n_{\text{water source}}$ represents the number of xylem water samples falling in the intersection space with a given water source, n_{total} represents the total number of xylem water samples, and n_{out} is the number of xylem water samples falling outside the xylem water ellipse (Figure 2). As the sample size for some study sites was small, we considered only those water sources with a minimum of four data points for the application of our inference method. We found that applying this method when less than four data points were available led to biased results compared with the ones obtained when more than four data points were available. This reduced the number of study sites from 77 to 56 for the computation of the overlap of soil water and xylem water. The key difference between this new isotope-based direct inference method and more commonly used mixing models is that the contributions here do not add up to one (or 100%) of the water uptake. Hence, the results do not provide proportional water use directly, but instead offer a more transparent approach towards similarities between different water sources and xylem water. As it eliminates issues with potentially unsampled water sources and the uncertainties associated with best-solution mixing models, comparisons between sites are therefore more straightforward.

TABLE 2 Spearman rank correlation coefficient for the relation between characteristics of the study sites and $\delta^{18}O$, $\delta^{2}H$, and d-excess of soil water (number of soil water samples = 5,328)

Characteristics	$\delta^{18}O$ (‰)	$\delta^{2}H$ (‰)	d-excess (‰)
MAT (°C)	0.58	0.67	0.16
Elevation (m a.s.l.)	−0.38	−0.49	−0.15
Global aridity index	0.17	0.31	0.36

Note. All the correlations are significant at the 0.001 significance level.

TABLE 3 Spearman rank correlation coefficient for the relation between characteristics of the study sites and $\delta^{18}O$, $\delta^{2}H$, and d-excess of xylem water (number of xylem water samples = 2,579)

Characteristics	$\delta^{18}O$ (‰)	$\delta^{2}H$ (‰)	d-excess (‰)
MAT (°C)	0.65	0.73	0.28
Elevation (m a.s.l.)	−0.39	−0.49	−0.27
Global aridity index	0.12	0.25	0.35

Note. All the correlations are significant at the 0.001 significance level.

3 | RESULTS

3.1 | Isotopic composition of xylem and soil waters in different climate zones

Soil and xylem waters had a large range of isotopic variability in all four climate zones (Figure 3). The median isotopic compositions of soil and xylem waters were enriched in heavy isotopes in the tropical zone ($\delta^{2}H$ = −34.7‰ [soil], −28.1‰ [xylem]; and $\delta^{18}O$ = −5.20‰ [soil], −3.88‰ [xylem]) and most depleted in the cold zone ($\delta^{2}H$ = −78.2‰ [soil], −95.6‰ [xylem]; and $\delta^{18}O$ = −10.27‰ [soil], −11.74‰ [xylem]; Table S2). Soil and xylem waters in the arid and the temperate zones had similar median isotopic compositions and intermediate between the tropical and the arid zones.

The isotopic composition of xylem water reflected that of soil water quite well in all climates, especially in the tropical zone (Figures 3 and S1).

Deviations of soil water from the global meteoric water line (GMWL) were particularly large in the arid zone, followed by the temperate and cold zones, and very small in the tropical zone. In addition, in the temperate and the arid zones, soil water was often more evaporated than xylem water, particularly for soil water samples that were very enriched in heavy isotopes (Figures 3 and S1). The deviation of soil water from the GMWL was related to the sampling depth, but there were differences across the climate zones (Figure 4). In the

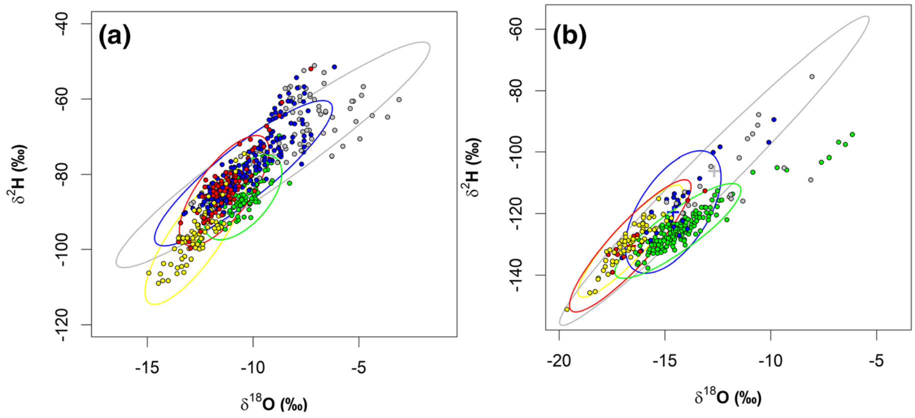

FIGURE 2 Examples of the computation of the degree of overlap between xylem water (green 99% confidence ellipse), 0–10-cm soil water (grey ellipse), 10–30-cm soil water (blue ellipse), 30–50-cm soil water (red ellipse), and >50-cm soil water (yellow ellipse) plotted in the dual-isotope space. Panel (a): xylem water, n = 93; 0–10 cm, n = 85; 10–30 cm, n = 160; 30–50 cm, n = 85; and >50 cm, n = 77; panel (b): xylem water, n = 137; 0–10 cm, n = 21; 10–30 cm, n = 24; 30–50 cm, n = 19; and >50 cm, n = 58

tropical zone, all the soil water samples plotted together along the GMWL, except for few samples of soil water at the 0–10-cm depth probably affected by evaporation (very low d-excess values). In the temperate and the cold zones, soil water sampled at 30–50- and >50-cm depths plotted together and quite close to the GMWL, whereas shallower soil water tended to deviate more from the GMWL. In the arid zone, the soil water sampled at >50-cm depth was the least affected by evaporation, whereas almost all the soil water from shallower layers plotted well below the GMWL (Figure 4). However, some discrepancies were observed due to the isotopic variability among the study sites.

We found a significant difference in the isotopic composition (for both isotopes) of soil water at different depths separately tested for the four climate zones (Kruskal–Wallis one-way analysis of variance test with significance level at 0.001 for both δ^2H and δ^{18}O).

3.2 | Overlap between xylem water and water sources

The dual-isotope plots highlighted the large overlap between the isotopic composition of soil water and xylem water across climate zones (Figures 3 and S1). The median overlap between xylem water and soil water at 0–10-cm depth decreased from the cold zone (100 ± 0%, representing median ± median absolute deviation, for the computations with both the MCD and MVE algorithms; Figure 5) to the temperate (58 ± 25% and 53 ± 20% for MCD and MVE, respectively), the arid (45 ± 16% for both MCD and MVE), and the tropical zone (28 ± 14% and 29 ± 14% for MCD and MVE, respectively). The median overlap between xylem and soil waters at 10–30 cm varied between 35 ± 17% using MCD (or 34 ± 16% for MVE) in the tropical zone and 84 ± 16% for MCD (85 ± 15% for MVE) in the temperate zone (Figure 5). The median overlap between xylem and soil waters at 30–50-cm depth was particularly large in the arid zone (96 ± 4% for MCD and 88 ± 4% for MVE), whereas the overlap between xylem and soil waters at >50-cm depth was the largest in the tropical zone (83 ± 8% for MCD and 77 ± 10% for MVE) followed by the arid climate (77 ± 2% for MCD and 77 ± 6% for MVE).

These results suggest that the isotopic composition of xylem water tends to be very similar to that of shallow soil water (0–10- and 10–30-cm depths) in the temperate and the cold zones, whereas in the arid and the tropical zones, the isotopic signature of xylem water reflects more the composition of deep soil water (30–50- and > 50-cm depths).

The median absolute deviations of the overlaps were quite variable across the climate zones and the water sources (Figure 5). They

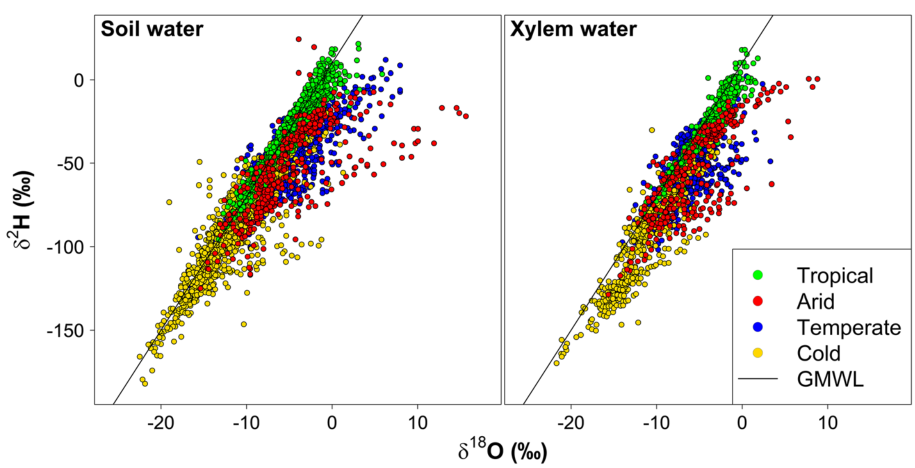

FIGURE 3 Dual-isotope plot of soil water (tropical, n = 1,284; arid, n = 383; temperate, n = 2,075; and cold, n = 1586) and xylem water (tropical, n = 442; arid, n = 308; temperate, n = 1,237; and cold, n = 592) samples in different climate zones according to Köppen climate classification

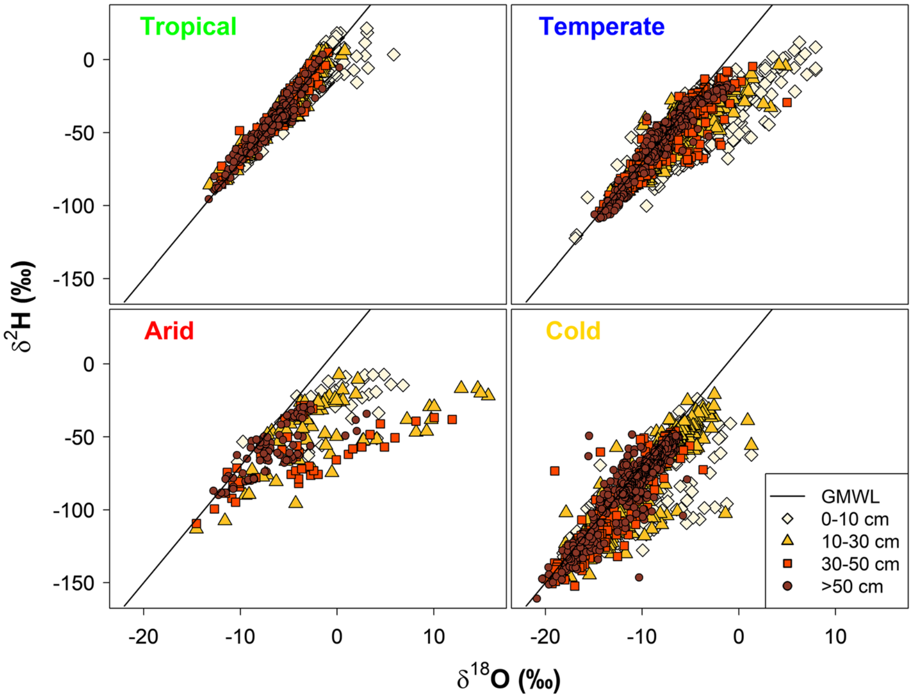

FIGURE 4 Dual-isotope plot of soil water at different depths in different climates, that is, tropical (0–10 cm, *n* = 294; 10–30 cm, *n* = 296; 30–50 cm, *n* = 281; and >50 cm, *n* = 323), arid (0–10 cm, *n* = 39; 10–30 cm, *n* = 70; 30–50 cm, *n* = 54; and >50 cm, *n* = 94), temperate (0–10 cm, *n* = 583; 10–30 cm, *n* = 387; 30–50 cm, *n* = 511; and >50 cm, *n* = 335), and cold zones (0–10 cm, *n* = 236; 10–30 cm, *n* = 393; 30–50 cm, *n* = 231; and >50 cm, *n* = 684)

were quite large especially in the cold zone, indicating a high variability in the overlap across the few study sites. However, the variability in the overlap across the study sites did not significantly affect the overall interpretation of the strong similarity in the isotopic composition of xylem water and soil water and the differences found across the climate zones. The differences in the overlaps between xylem water and soil water at different depths resulting from the application of the two algorithms (MCD and MVE) varied between −1% and + 1% for 61% of the cases, suggesting that there was a small sensitivity of the results to the choice of the algorithm used for detecting outliers and drawing the ellipses.

3.3 | Variability in the isotopic composition of xylem and soil waters among different climate zones

We found a significant difference in the isotopic composition (for both δ^2H and δ^{18}O) of xylem and soil waters across the four climate zones (Kruskal–Wallis one-way analysis of variance testwith significance level at 0.001 for both δ^2H and δ^{18}O of xylem water and soil water; Figure 3). The median d-excess of soil water increased (i.e., became less negative) with increasing soil depth in all climate zones (Table 1). Except for the tropical zone, the soil water at 0–10-cm depth had a negative median d-excess, whereas the deeper soil water had a positive median d-excess in all the climates but the arid zone. This indicates that evaporative fractionation processes were strongest in the arid zone, where even the median d-excess of soil water at >50-cm depth was negative and lower than the median d-excess of shallow soil water in the tropical and the cold zones (Table 1).

The classification of the study sites on the basis of the global aridity index showed that xylem and soil waters in the most arid study sites had the most negative d-excess, suggesting the influence of relatively strong evaporation processes (Figure 6). An overall increasing trend in d-excess was observed for both xylem and soil waters from the arid and hyper-arid class to the humid class. Xylem water had lower d-excess than soil water in most of the global aridity index classes. However, for the arid and hyper-arid class, where sample size was smaller and variability generally larger, this pattern was not observed. Only in the humid class more than 50% of soil water and xylem water samples had positive d-excess values (Figure 6).

Both soil water (Table 2) and xylem water (Table 3) δ^2H and δ^{18}O values were strongly positively correlated with MAT. δ^2H and δ^{18}O of both xylem and soil waters also had a significant negative correlation with elevation of the study sites, 23 and a positive but weaker correlation with the global aridity index (Tables 2 and 3).

The d-excess of soil and xylem waters had the strongest positive correlation with the global aridity index (Tables 2 and 3), confirming that evaporative fractionation was stronger in the arid than the humid study sites. MAT and elevation also had significant correlations with d-excess of soil water (Table 2) and xylem water (Table 3), but they were weak particularly for soil water.

3.4 | Variability in the isotopic composition of xylem water for different plant groups

The isotopic compositions of xylem water in angiosperms and gymnosperms were similar in the cold zone (Mann–Whitney rank sum test significant at the 0.05 level for both δ^{18}O and δ^2H). We found a

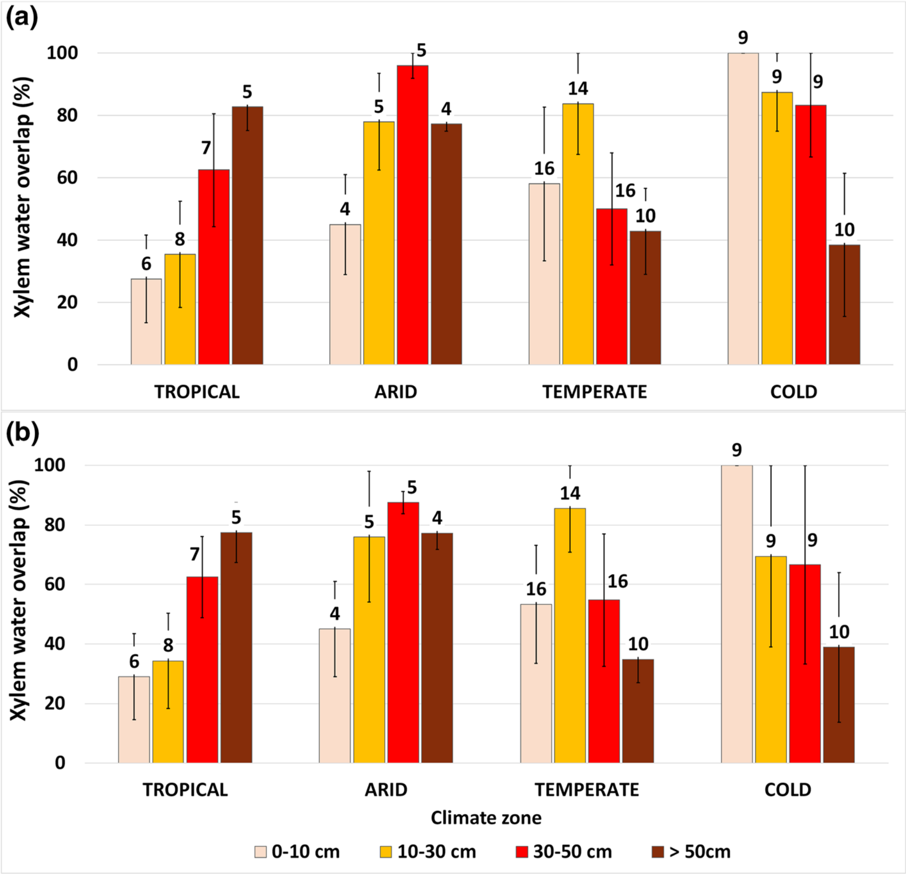

FIGURE 5 Median overlap (percentage) of xylem water with soil water at different depths (0–10, 10–30, 30–50, and >50 cm) in different climate zones. The number of samples considered for each climate zone is reported in Table S3. The number reported above each bar indicates the number of study sites. Error bars represent median absolute deviations. Robust covariance ellipses by using two methods for outliers detection: (A) minimum covariance determinant and (B) minimum volume ellipsoid

significant difference in the isotopic composition of xylem water of angiosperms and gymnosperms in the arid zone (Mann–Whitney rank sum test significant at the 0.001 level for both δ^2H and δ^{18}O) and the temperate zone (Mann–Whitney rank sum test significant at the 0.001 level for δ^{18}O and at 0.05 for δ^2H). The deviation of xylem water samples from the GMWL was evident and different for angiosperms and gymnosperms in the arid zone, whereas xylem water samples of angiosperms and gymnosperms plotted together and deviated similarly from the GMWL in the temperate and the cold zones (Figure 7).

The median d-excess was very negative for xylem water samples in the arid zone, with lower values for gymnosperms compared with angiosperms (Table 1). In the temperate zone, the median d-excess of xylem water was slightly lower for angiosperms than gymnosperms, whereas in the cold zone, stronger evaporation processes determined the lower median d-excess for angiosperms than gymnosperms. We found statistically significant differences in the d-excess of xylem water of angiosperms and gymnosperms in all the three climates (Mann–Whitney rank sum testsignificant at the 0.001 level in the arid and the temperate zones, and at 0.01 in the cold zone). Our choice in grouping of plants did not allow for exploring their role in the tropics as all the samples contained data for angiosperms only (Figure 7; Table 1).

4 | DISCUSSION

4.1 | Xylem water isotopic composition reflects soil water uptake from different depths across the globe

Dual-isotope plots (Figure 3) and the direct inference approach (Figure 5) revealed a strong overlap of xylem water and soil water isotopic composition across climate zones. This implies that trees and shrubs across the globe obtain most of their water from soil water. It has to be noted that our findings might be slightly biased towards soil water uptake as groundwater data were not considered in our study5. However, our findings are in line with previous studies and meta-

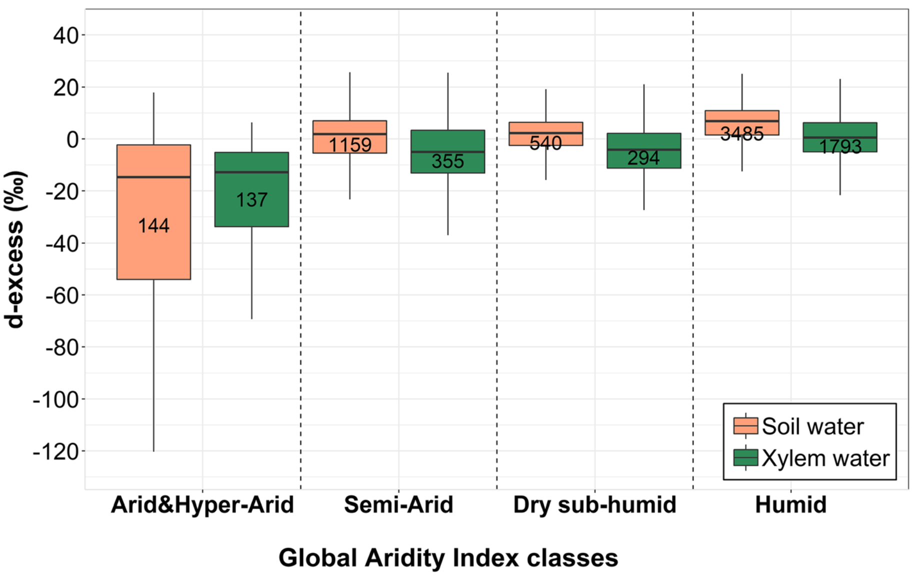

FIGURE 6 Boxplots of soil water and xylem water deuterium-excess (d-excess) grouped as a function of global aridity index classes (aridity index; United Nations Environment Programme, 1997; aridity index values increase for more humid conditions and decrease with more arid conditions). Boxes represent the 25th and 75th percentiles, and whiskers indicate the minimum and maximum values excluding the outliers. The number inside each box indicates the sample size. The horizontal solid line within boxes represents the median

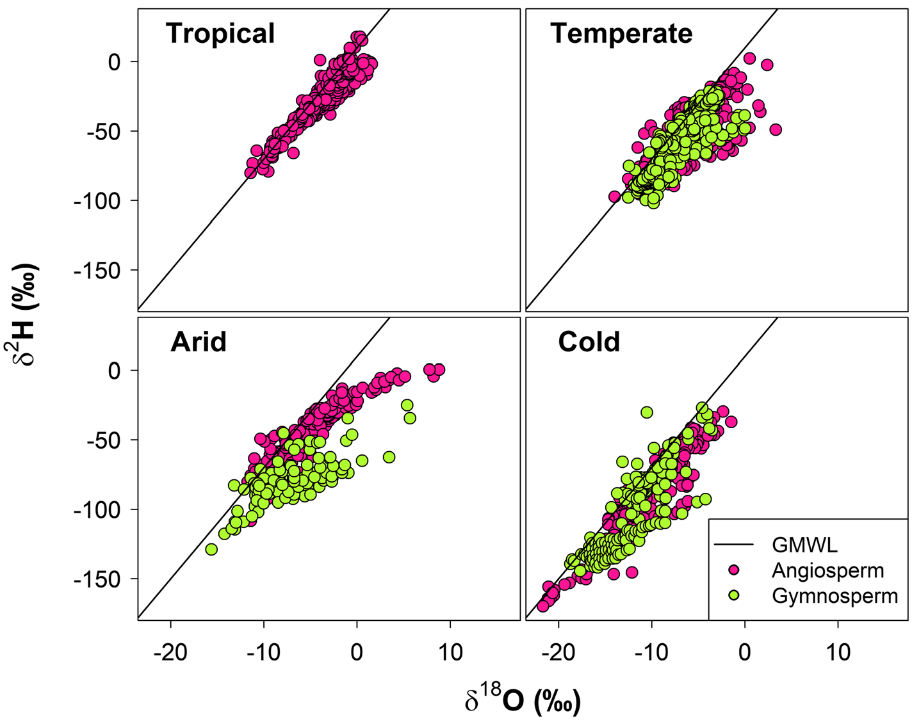

FIGURE 7 Dual-isotope plot of xylem water for different plant groups in the different climate zones. Tropical zone, angiosperms: n = 407; temperate zone, angiosperms: n = 625; gymnosperms: n = 587; arid zone, angiosperms: n = 196; gymnosperms: n = 112; cold zone, angiosperms: n = 395; and gymnosperms: n = 197

analyses showing that trees across most climate zones predominantly rely on soil water (Bowling, Schulze, & Hall, 2017; Brooks, Barnard, Coulombe, & McDonnell, 2010; Evaristo et al., 2019; Geris, Tetzlaff, McDonnell, & Soulsby, 2017; Grossiord et al., 2016; Gu et al., 2015; Rose, Graham, & Parker, 2003; Rossatto, de Carvalho Ramos Silva, Villalobos-Vega, Sternberg, & Franco, 2012; Wei, Fang, Liu, Zhao, & Li, 2013; Yang & Fu, 2017).

Our results also suggest that trees take up most of their water from the upper soil layers (here 0–50 cm; Figure 5). Despite strong fluctuations in soil water availability, several studies have shown that trees obtain a considerable proportion of water from shallower soil layers (Barnard et al., 2010), although the extent of this proportion is highly variable depending on tree species, soil type, and environmental conditions. The reliance on water from upper soil layers has been related to higher nutrient availability (Goldsmith et al., 2012; Schwendenmann et al., 2015) and root biomass (February & Higgins, 2010; Jobbágy & Jackson, 2001) in these soil layers and rehydration of upper soil due to hydraulic lift under dry conditions (Caldwell, Dawson, & Richards, 1998). To minimize energy use, plants are likely to extract water from soil layers with highest rooting density assuming the soil is uniformly wet (Adiku, Rose, Braddock, & Ozier-Lafontaine, 2000) and at the highest available water potential (i.e., easiest to withdraw; Gardner, 1960). Moreover, plants can often take up relatively “new” water (Sprenger et al., 2019) although some recent studies showed that water transpired from trees during summer originated from rain that fell during the previous winter (Allen et al., 2019; Brinkmann et al., 2018).

In line with other studies, our findings also show that plants extract water from multiple soil layers (Figure 5; Asbjornsen, Shepherd, Helmers, & Mora, 2008; Le Roux, Bariac, & Mariotti, 1995; Schwendenmann et al., 2015). Water uptake from deeper soil layers (here below 50 cm) is often reported from arid/semiarid regions (Evaristo & McDonnell, 2017b) but is also found in areas characterized by pronounced dry seasons (Barbeta & Peñuelas, 2017). For example, deep rooting (Davidson et al., 2011; Markewitz, Devine, Davidson, Brando, & Nepstad, 2010) and deep soil water extraction in tropical forests are important mechanisms to sustain growth during the dry season (Restrepo-Coupe et al., 2013; Wu et al., 2016). A number of studies suggest that deep root systems are not restricted to trees and shrubs in arid/semiarid and seasonally dry forests (e.g., Pierret et al., 2016). Thus the role of deep root water uptake across ecosystems may have been underestimated (Pierret et al., 2016). Studies have shown that in very deep soil, some trees can develop deep roots that may access “old” waters (Sprenger et al., 2019; Zhang et al., 2017).

4.2 | Climate has first-order effect on the isotopic compositions of xylem and soil waters

The observed major control exerted by climate on the isotopic composition of xylem and soil water confirmed several ecological studies across different regions (see Werner et al., 2012 and references therein). The climate control was evident via climate zone grouping (Figures 3–5) and exploring variations in isotopic signatures with climate-related proxies including aridity index (Figure 6), MAT (Figure S2), and elevation (Tables 2 and 3; Figures S2 and S3). Stable water isotope composition of precipitation is strongly related to altitude, temperature, and other climate factors (Dansgaard, 1964; Gat, 1996). Therefore, to some extent, the relative differences between isotopic signatures in the various climates found in xylem water and soil water samples reflected those in precipitation. The d-excess values for soil and xylem waters both decreased as a function of aridity index values, whereby most negative d-excess values were found in the arid climate zone whereas least negative or even positive values were found in humid regions (Figure 623). High potential evapotranspiration, relatively low soil water content (Allison, Barnes, & Hughes, 1983), and low relative humidity (Cappa, Hendricks, DePaolo, & Cohen, 2003; Gibson, Birks, & Edwards, 2008) are all factors that enhance non-equilibrium fractionation during evaporation and are typically most pronounced for arid regions.

The evaporation front in the soil profile was also markedly different between climate zones and again most distinct for the arid regions. Our results showed that overall, deep (>50 cm) soil water was less deviated from the GMWL (Figure 4). The d-excess profile changes with depth were most marked in the arid, then temperate and cold zone, whereas little variations were found for the tropical zone (Table 1). Using data from 25 sites across the world, Sprenger, Leistert, Gimbel, and Weiler (2016) revealed that the evaporative fractionation effects were generally limited to the upper 30 cm of the soil, but that effect was climate dependent. Deep progression fronts up to 2–3 m have been reported for sites in arid climates (e.g., Beyer et al., 2018; Singleton, Sonnenthal, Conrad, DePaolo, & Gee, 2004), whereas in tropical climates, a clear vertical gradient in the soil water isotopic signal is usually only observed under pronounced dry seasons (Querejeta, Estrada-Medina, Allen, & Jiménez-Osornio, 2007). In tropical regions, the high humidity (Goller et al., 2005; Good, Noone, & Bowen, 2015) and typically dense vegetation cover (Dubbert, Cuntz, Piayda, Maguás, & Werner, 2013) can both contribute to relatively low soil evaporation.

Xylem water in the arid and cold zones had lower d-excess values (Table 1). This is consistent with Bertrand et al. (2014), Yang and Fu (2017), and Zhu, Wang, Mao, Zheng, and Xu (2014) and values reported for the tropical and temperate zone (Goldsmith et al., 2012; Hervé-Fernández et al., 2016; Rosado, De Mattos, & Sternberg, 2013). The patterns between climate zones largely reflect those found in the soil water and indicate more fractionation with aridity. However, the result for the cold zone is quite different, with a more extreme difference between the soil and xylem water found in this region. As observed elsewhere and across climate zones (e.g., Evaristo et al., 2015), soil water often shows more fractionated isotope signatures than xylem water, with xylem water reflecting water uptake from a blend of sources. However, in our analyses for the cold climate zone, none of the soil water depths showed similarly strong negative median d-excess values as the xylem water (Table 1). In addition to possible improper sampling, that is, not sampling the right water pool (Penna et al., 2018), one explanation could be that plant source water in cold regions might not be adequately represented by the soil water samples alone or that soil water in cold climates is recharged by (non-fractionated, and isotopically light) snowmelt. Isotope signatures in soil and xylem water always reflect the combined effects of source variation, mixing, and fractionation (Benettin et al., 2018). By pooling all soil water across depths and plant water across groups, some of the patterns may have also come out more extreme than as for a per-site comparison of samples across soil depth and plant groups.

4.3 | Effect of plant groups on isotopic composition of xylem water

We found significantly higher xylem water δ^2H and δ^{18}O values in angiosperms than gymnosperms in the arid zone (Figure 7). The most enriched xylem water across all studies was measured in *Guiera senegalensis*, a perennial woody shrub found across the Sahel (Brunel, Walker, Dighton, & Monteny, 1997). Xylem water of *Guiera senegalensis* was often higher than the highest soil water δ^2H and δ^{18}O values (Brunel et al., 1997). Evaporative enrichment of xylem water has been associated with leaflessness (Ellsworth & Sternberg, 2015; Phillips & Ehleringer, 1995) and periods of limited sap flow (Martín-Gómez, Serrano, & Ferrio, 2017), which may partly explain higher xylem water δ^2H and δ^{18}O values in angiosperms across the arid zone.

Furthermore, differences in plant functional traits between angiosperms and gymnosperms (e.g., photosynthetic capacity, leaf phenology, transpiration rate, hydraulic capacity, water use efficiency, and rooting pattern; Augusto, Davies, Delzon, & De Schrijver, 2014; Cernusak, Winter, Aranda, & Turner, 2008) may contribute to differences in xylem water isotopic composition. For example, angiosperms tend to have higher leaf transpiration rates (Hetherington & Woodward, 2003) and are less drought resistant than gymnosperms (Choat et al., 2012). To meet the water demand, plants in arid systems sometimes rely on water from upper soil layers that is characterized by higher $\delta^{18}O$ and $\delta^{2}H$ values due to high evaporation especially during summer (Rose et al., 2003; West, Hultine, Burtch, & Ehleringer, 2007).

However, most studies showed that water isotope composition and water uptake patterns tend to be species- and ecosystem-specific (e.g., Asbjornsen et al., 2008; Goldstein et al., 2008; Phillips & Ehleringer, 1995; Weltzin & McPherson, 1997; Williams & Ehleringer, 2000). For example, various gymnosperms growing in a woodland in southern Utah showed differences in their water uptake. *Pinus edulis* acquired water from both shallow and deep water sources, whereas the shrub *Juniperus osteosperma* used shallow water when water was available in the spring and shifted to deeper sources for the remainder of the growing season, and *Pinus taeda* obtained water predominantly from the upper soil profile (Retzlaff, Blaisdell, & Topa, 2001; West et al., 2007).

4.4 | Limitations of the study

Our findings can be considered statistically robust due to the large number of samples (>5,000 for soil water and >2,500 for xylem water; Table S2) and of plant species (>170) included in this meta-analysis. Nevertheless, we acknowledge some limitations that may impact the interpretation of the results. First, the study sites are unevenly distributed among the four climatic zones, with the highest number in the temperate zone and the smallest number in the tropical zone. Hence, areas characterized by particular climatic conditions within the arid, tropical, and cold zones are underrepresented, and more studies would be necessary to include in order to make the global analysis of plant water uptake more generalizable.

Second, coexisting plant species may have different eco-hydrological niches that we were not able to adequately represent in this study, other than simply separating angiosperms from gymnosperms. Similarly, different species, or even the same species but of different age, size, and/or growing in diverse environmental conditions, are likely characterized by different root depths that might reach different soil depths and access different water sources, therefore hampering an equal comparison in the analysis of plant water uptake (e.g., Bargués Tobella et al., 2017). However, the large sample size of our study may make the general pattern reasonably valid.

Third, most papers did not collect samples of soil and xylem waters at the same time or did not specify the collection time: this limits the assessment of the possible differences between the isotopic composition of xylem water and of its potential water sources in the light of the lag time between root water absorption and transport to the leaves, which can take days to weeks or even months (e.g., Allen et al., 2019; Brinkmann et al., 2018). However, given the large number of samples taken from different species and different climate regions, these possible differences are likely smoothed out.

Fourth, some issues intrinsic in meta-analyses, particularly at the global scale, exist, and they can limit more vigorous comparison of results. Of particular importance is the adoption of different sampling protocols for xylem water (e.g., samples collected from twigs or from the stem or from wood cores) and soil material (e.g., Goldsmith et al., 2019 showed heterogeneity of isotopic signal due to spatial variability of soil water samples) and different water extraction methods both for xylem water and soil water (Table 4). Several studies have reported that different water extraction techniques can return different isotopic composition from the same sample (see the comprehensive review by Millar, Pratt, Schneider, & McDonnell, 2018 for plant water samples and comments in Penna et al., 2018), and that even the same technique carried out in different laboratories can have a strong impact in determining the isotopic composition of soil water (Orlowski et al., 2018). Therefore, uncertainties associated to the different water extraction techniques can possibly impact our findings. However, this uncertainty is difficult to quantify due to the variety of extraction methods (Table 4) and settings reported in the collected papers, and the lack, in many papers, of any information on the uncertainty related to the application of the extraction method, and, more in general, the lack of a common procedure. With these conditions, it is almost impossible to incorporate a reliable uncertainty estimate into the algorithms used in our direct inference approach (Figures 2 and 5). Moreover, there might be other factors that could affect the isotopic composition of soil water and that we were not able to consider, often because this information is not reported in the reviewed papers. For instance, nutrients tend to be concentrated in the upper soil and can lead to temporally plastic root water uptake behaviour and hence variations in the isotopic composition of xylem water even in plants with access to groundwater (Dubbert et al., 2019). Organic matter can prevent or reduce soil evaporation and increase water retention (Ankenbauer & Loheide, 2017; Saxton & Rawls, 2006; Schoonover & Crim, 2015) and influence fractionation effect of soil water as well as soil microbial respiration (Stoll, 2014).

Finally, we must note that differences exist in the estimates of soil water uptake reported in the original studies included in the database and the estimates derived from our analysis. Differences are not surprising due to intrinsic uncertainty in the different methods applied. The mixing models typically used in the papers we analysed (e.g., IsoSource and MixSIAR) are based on the assumption that all water sources accessed by plant roots are adequately sampled and that the tracer signature is conserved through the mixing processes. However, in field studies, sampling all potential water sources is not always practical or possible, creating potential bias in the mixing model estimation of plant water source. The direct inference method we proposed here is a simple statistically-based method that we applied to compare all data included in the global database. On the basis of its assumptions, this approach has the advantage to quantitatively assess the contribution of each of the identified water sources

TABLE 4 Percentage of papers on the basis of water extraction techniques

Extraction technique	No. of papers	Percentage (%) of papers	No. of samples per climate zone[a]			
			Tropical	Arid	Temperate	Cold
Azeotropic distillation	8	12.1	0	187	257	200
Cryogenic vacuum distillation	56	84.8	1,726	504	2,937	1,724
Liquid-vapour equilibration	1	1.5	0	0	0	254
Pressure chamber	1	1.5	0	0	86	0

[a]The number of samples reported in the table are the sum of both xylem water and soil water samples.

even if one or more sources are missing. However, this approach relies on the assumption that no fractionation occurs at the soil–root interface or within plant woody tissues that is being increasingly questioned (Barbeta et al., 2019). Hence, these results should be used with caution, and extended analyses on various plant species and in different climatic contexts are needed to further test this method and to evaluate the differences compared with widely used mixing model results.

5 | CONCLUDING REMARKS AND HOW TO MOVE FORWARD

Previous global meta-analyses studies have assessed the relative contributions of soil water and groundwater used by various plant species, but have not yet provided estimates of soil water depth contributions to water uptake. As far as we know, this is the first study that evaluated the main water sources used by plants globally and explored the effect of climate and plant groups on water uptake variability. Our meta-analysis was based on the extraction of isotopic data (both δ^2H and δ^{18}O) from 65 peer-reviewed papers published between 1990 and the end of 2017. The database included isotopic compositions of soil water and xylem water from 77 study sites belonging to four climate zones (i.e., tropical, arid, temperate, and cold zones).

The analysis of dual-isotope plots showed that there was a wide overlap between the isotopic composition of xylem water with that of soil water, indicating soil water as the main water source for plant transpiration. We developed and applied a new direct inference method to quantitatively assess the overlapping proportions between xylem water and water sources potentially exploited by plants. The median overlaps between xylem and soil waters at different depths were generally above 50%. We also found that climate acts as the main driver of the isotopic composition of soil water. Our results suggest that the isotopic composition of xylem water tends to be very similar to that of shallow soil water (0–10- and 10–30-cm depths) in the temperate and the cold zones, whereas in the arid and the tropical zones, the isotopic signature of xylem water reflects more the composition of deep soil water (30–50- and >50-cm depths)

The proposed new direct inference method to quantify overlaps between xylem water and various water sources has a high potential due to its intrinsic ease of application and because it is an information-based method that can be used to determine the main water sources used by plants for transpiration. However, future research should aim at testing the new direct inference method across more study sites and comparing it with other methods (e.g., Bayesian mixing models) for the quantification of the contribution of water sources to transpiration.

Finally, our research suggests that further ecohydrological research should be performed in tropical and arid zones because of the few studies published in these regions so far. Collection of soil water samples at different depths to connect in time and space to corresponding xylem water samples is urgently needed to build a more robust data set for future analysis of transport processes within the soil–plant–atmosphere continuum.

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AUTHOR CONTRIBUTIONS

D. P., G. Z., and M. B. suggested the main objective and the meta-analysis approach. D. P. proposed the direct inference method and developed it with G. Z.. A. A. performed the literature search, compiled the database, and did the data analyses. J. G. and L. S. contributed to refining the objectives and data analyses, and L. S. provided additional data. A. A., G. Z., D. P., L. S., and J. G. wrote the manuscript, and J. J. M. and M. B. edited and revised it.

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SUPPORTING INFORMATION

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