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Review

Plant Water Use Strategy in Response to Spatial and Temporal Variation in Precipitation Patterns in China: A Stable Isotope Analysis

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Abstract: Spatial and temporal variation in precipitation patterns can directly alter the survival and growth of plants, yet in China there is no comprehensive and systematic strategy for plant use based on the effects of precipitation patterns. Here, we examined information from 93 published papers (368 plant species) on plant xylem water stable isotopes (δD and $\delta^{18}O$) in China. The results showed that: (1) The slope of the local meteoric water line (LMWL) gradually increased from inland areas to the coast, as a result of continental and seasonal effects. The correlation between δD and $\delta^{18}O$ in plant stem water is also well fitted and the correlation coefficients range from 0.78 to 0.89. With respect to the soil water line, the $\delta^{18}O$ values in relation to depth (0–100 cm) varied over time; (2) Plants' main water sources are largely affected by precipitation patterns. In general, plants prioritize the use of stable and continuous water sources, while they have a more variable water uptake strategy under drought conditions; (3) There are no spatial and temporal variations in the contribution of the main water source ($p > 0.05$) because plants maintain growth by shifting their use of water sources when resources are unreliable.

Keywords: stable isotope; local meteoric water line (LMWL); plant main water source (PMWS); contribution of plant main water source (CPMWS); China

1. Introduction

Vegetation plays an important role in global water cycles, and its survivorship and growth is essentially restricted by water resources. Stable isotope techniques have become one of the most powerful tools for understanding the relationship between plants and water sources. Precipitation is one of the key sources of water. Spatial distribution in the δD and $\delta^{18}O$ values of precipitation are commonly used in hydrologic studies [1]. Global meteoric water line observations in 1961 provided the foundation in this field [2]. Massive models based on spatial interpolation methods greatly boost accurate representation of stable isotopes in precipitation [3,4]. Furthermore, previous works have proved that latitude, altitude, amount of precipitation, and distance from coast are four major factors of variation in precipitation isotope ratios [5]. These driving forces, particularly uneven spatial distribution of precipitation, are extensively recognized as governing terrestrial biological activity, as a result of differing water use strategies [6,7]. In general, plants give priority to using stable and continuous water sources, although they can vary their water uptake strategy under special conditions. There is considerable research from all over the world showing how different plant species use water resources on the local scale. Flanagan and Ehleringer found that *Chrysothamnus nauseosus* (Pallas) Britt. derived its water primarily from groundwater, but the other three species (*Juniperus osteosperma* (Torr.)

Little, *Pinus edulis* Engelm., and *Artemisia tridentate* Nutt.) utilized precipitation and groundwater [8]. Xu et al. found that *Abies fargesii* Franch. Var. *faxoniana* (Rehder et E. H. Wilson) Tang S. Liu depends primarily and consistently on groundwater, while *Betula utilis* D. Don and *Bashania fangiana* (A. Camus) Keng f. prefer using rainwater, but always automatically convert to groundwater as the main source under water stressed conditions [9]. Rossatto et al. found that, in response to the groundwater level, vegetation at higher elevations extracted water from both shallow and deep soil layers and plants only rely on more superficial water at lower elevations [10]. Schwinning et al. found that all three of the species they examined (*Oryzopsis hymenoides, Gutierrezia sarothrae*, and *Ceratoides lanata*) took up deeper soil water under drought conditions and shallow soil water after a heavy rainfall event in summer in a cold desert ecosystem (Colorado Plateau) [11]. At a study site in the hyperarid Namib Desert, where mean annual precipitation is less than 12 mm, all of the trees are reliant on shallow soil water and groundwater from flood water infiltration [12]. In addition, fog water, karst water, and spring water can also be important supplementary water sources for plants [13–16]. The seasonality of precipitation patterns shapes species dynamics [17,18]. A series of studies have used δD and δ^{18}O to confirm seasonal shifts (dry/wet season) in water sources for plant growth [9,19–22]. Understanding the role of spatial and temporal variation in precipitation patterns on plant water use strategy is critical for accurately predicting the effects of climate change on terrestrial ecosystems worldwide, including this case study. However, on the national level, research into these questions has been not been comprehensive and systematic.

China is located in the East Asian monsoon climate zone, where precipitation has an uneven spatial and seasonal distribution [23]. Different environments have diverse precipitation patterns that are affected by many factors, such as elevation, latitude, and temperature. The 200 mm, 400 mm, and 800 mm precipitation isohyets divide the country into four regions: arid, semi-arid, semi-humid, and humid [24–26]. Regional divisions can help when examining the effects of spatial patterns of precipitation on plant water use strategies. Recently, hydrogen and oxygen stable isotope ratios of water within plants have been used to provide new information on vegetation water use strategies under natural conditions. In this study, plant xylem water stable isotope (δD and δ^{18}O) information from 93 published papers was examined. These papers were identified from the China National Knowledge Infrastructure (CNKI), Wanfang Data Knowledge Service Platform, and Web of Science databases. The references selected comprehensively and authentically cover the water use strategies of plants in the different regions of China. They represent 368 plant species (including the same plants in different habitats or of different ages), covering 229 species studied in the wet season and 139 in the dry season. The objectives of this study were: (1) to compare patterns of δD and δ^{18}O occurrence between precipitation, plant stem water, and soil water; (2) to identify regional and seasonal changes in the main water sources used by plants; (3) to analyze regional and seasonal changes in the contributions of the main water sources and the relationships between the main water sources and other water sources used by plants in China.

2. Materials and Methods

Rainfall data collection: the precipitation data were obtained from 2114 meteorological stations in the "Dataset of Monthly Surface Observation Values in Individual Years (1981–2010) in China" from the China Meteorological Data Service Center (CMDC) (which can be accessed at: http://data.cma.cn/en). Based on Kriging interpolation, precipitation data for China were divided into four categories: <200 mm, 200–400 mm, 400–800 mm, and >800 mm, representing arid, semi-arid, semi-humid, and humid regions, respectively. Rainwater isotope data for China were collected by the Global Network of Isotopes in Precipitation (GNIP) from International Atomic Energy Agency (IAEA/WMO, 2017). The GNIP Database can be accessed at: http://www.iaea.org/water. The hydrogen and oxygen stable isotope values for precipitation were obtained for each region in order to establish the equation of the local meteoric water line.

Plant xylem water stable isotope (δD and $\delta^{18}O$) data were collected from 93 published papers (listed and numbered in Appendix A except those that have been cited as references). The Chinese-language references were identified using the China National Knowledge Infrastructure (CNKI) and Wanfang Data Knowledge Service Platform databases, supported by the National Natural Science Foundation (NSFC), or state level publications such as Acta Ecologica Sinica, Journal of Applied Ecology, Journal of Natural Resources, Journal of Plant Ecology, and Scientia Silvae Sinicae. The English-language references were identified using the Web of Science. The references date from 2000 to 2017. They include papers on the analysis of plant water use strategy that mainly refer to plant water sources. After title/abstract screening and removal of duplicates, a total of 93 records remained and were included in the study; they were separated into four categories based on latitude and longitude of study area: arid region ($n = 28$), semi-arid region ($n = 19$), semi-humid region ($n = 23$), and humid region ($n = 23$).

Stable isotope analyses have been used effectively to determine the reliance of a species on shallow, middle, and deep soil water, groundwater, river water, spring water, fog water, karst water, and seawater [27–31]. Suberized twigs from plants and different depths of soil samples were selected for the stable isotope ratio measurements in the respective source papers. In this study, the plant potential water sources were also defined following the original definitions in the respective source papers. Groundwater was defined as a saturated region of the water. Spring water referred to deep water, but it was treated as an individual potential water source. Karst water was defined as water stored in the epikarst zone. It is difficult to compare the contribution of soil water because different papers have their own definitions of shallow soil water, middle soil water, and deep soil water. We exploit the cluster analysis method to normalize the soil classification based on variations of $\delta^{18}O$ values for the four regions. "Minor water sources" include river water, spring water, fog water, karst water, and seawater, because they are usually not the main water sources used by vegetation and play complementary roles. Water sources used by plants were divided into five categories: shallow soil water, middle soil water, deep soil water, precipitation, groundwater and minor water sources.

The significance of groundwater receives wider attention and plants tend to take dissimilar groundwater use strategies in different regions [32]. Therefore, the contribution of groundwater deserves special consideration and we defined it as the number of samples out of a population of plant samples reported to have groundwater contributing to xylem water in each region [33].

The effects of seasonality and region were tested with factorial ANOVAs and Student's t test. These analyses were conducted using SPSS 18.0 (International Business Machines Corporation (IBM), New York City, NY, USA). Maps were created using ArcMap 10.2 (Environmental Systems Research Institute (ESRI), Redlands, CA, USA).

3. Results and Discussion

3.1. The Relationship between δD and $\delta^{18}O$

3.1.1. Meteoric Water Line

In theory, variations in $\delta^{18}O$ and δD under equilibrium fractionation conditions can be described using the equation for the global meteoric water line, which has a slope of 8 (Global Meteoric Water Line (GMWL) $\delta D = 8\,\delta^{18}O + 10$) [2]. The slope for specific conditions depends upon factors like the humidity, the temperature, the wind speed, and the turbulence in the water. The intercept (=deuterium excess) of the precipitation line at the source area reflects the rate of evaporation [5], to some degree, representing the climate and regional characteristics. It can also provide a reference for inferring plant water sources. Zheng et al. first used the least squares method to establish the Chinese meteoric water line ($\delta D = 7.9\,\delta^{18}O + 8.2$) in 1983 [34]. The slope is close to 8. While China is a vast country with complex terrain, all rainfall cannot be expected to lie along the Global Meteoric Water Line, and regional or local meteoric water lines are required that can represent the real natural conditions. Here we used data from the CMDC and GNIP Database to determine the regional meteoric water line equations for four regions of China (Table 1): the arid region (δD = 6.231 δ^{18}O − 0.458), semi-arid region (δD = 7.283 δ^{18}O − 1.457), semi-humid region (δD = 7.652 δ^{18}O + 5.34), and humid region (δD = 8.067 δ^{18}O + 12.304). The continental effect, seasonal effect, as well as particular geographical location influences the slope.

The arid and semi-arid regions are located in northwestern China and in the hinterland of the Eurasian continent and are affected by a cold northwesterly airflow in winter. Airflow from the southwestern Indian Ocean is blocked by the Qinghai-Tibet Plateau in summer. This means that there is little annual precipitation and intense evaporation, which results in a local meteoric water line with a lower slope, and a more negative intercept. Compared with the semi-arid region, the slope of the equation for the arid region deviates greatly from the normal value (Table 1). Based on the Chinese Network of Isotopes in Precipitation, the study by Liu et al. showed that raindrops suffered re-evaporation whilst falling, and the precipitation vapor was mixed with some local recycled water vapor in Northwest China (local meteoric water line (LMWL), δD = 7.05 δ^{18}O − 2.17, n = 50) [35]. Other studies suggest a slope range from 6.01 to 7.56 [36–39] for the arid and semi-arid regions of China. The humid and semi-humid regions are affected by an eastern monsoon climate and controlled by high-pressure over Siberia, with strong cold air activity and less precipitation in winter, then with the warm moist air of the Pacific bringing abundant rainfall in summer [40]. Because of an obvious continental effect, the slopes of the meteoric water lines for the humid and semi-humid regions are higher than elsewhere and are in the range of 7.6 to 8. Specifically, the slope for the humid region is 8.02, which is slightly higher than in the GMWL. Also, there are some similar results from previous research. For example, Zhang et al. established a local meteoric water line for Southwest China (δD = 7.99 δ^{18}O + 7.46, r^2 = 0.99, n = 70) [41]; Wu et al. established a LMWL for Sichuan Province (δD = 7.96 δ^{18}O + 8.67, r^2 = 0.97, n = 68) [42]; and Liu et al. established a LMWL for Yunnan Province (δD = 7.53 δ^{18}O + 1.42, r^2 = 0.97, n = 92) [43]. There is a trend in that heavy isotopes in precipitation are gradually depleted from coast to inland regions [40].

From the arid, semi-arid, semi-humid, and humid regions, average values for δ^{18}O and δD in precipitation were observed to vary from −22.75‰ and −19.94‰, −16.37‰ and −6.77‰, −173.60‰ and −146.66‰, and −119.92‰ and −42.29‰, respectively. The results showed that δ^{18}O and δD values for precipitation were reduced with increasing distance from the ocean. In particular, stable isotopes (δD and δ^{18}O) on the Tibetan Plateau exhibited the lowest values (−243.11‰ for δD and −32.51‰ for δ^{18}O), while values were highest in the humid region (−6.81‰ for δD and 0.19‰ for δ^{18}O) because of latitude and elevation effects (Appendix B Figures A1 and A2). Tian et al. found that δ^{18}O in precipitation at Xixiabangma on the Tibetan Plateau showed an obvious altitude effect [44]. Liu et al. established a model of the quantitative relationship between δ^{18}O in precipitation and latitude and altitude ($\delta^{18}O_{ppt}$ = − 0.0176 LAT^2 + 1.1195 LAT − 0.0016 ALT − 23.7553) [45].

Table 1. The relationship between δD and δ^{18}O values for precipitation and plant stem water.

Region	Equation	R^2	N	Range of δD (‰)	Range of δ^{18}O (‰)
GMWL	δD = 8 δ^{18}O + 10		400		
LMWL of China	δD = 7.9 δ^{18}O + 8.2	0.977	107		
LMWL of A	δD = 6.231 δ^{18}O − 0.458	0.859	10,397	−212~−43.6	−30.79~−8.56
LMWL of S-A	δD = 7.283 δ^{18}O − 1.457	0.995	4888	−238.5~−75	−32.5~−11.4
LMWL of S-H	δD = 7.652 δ^{18}O + 5.34	0.993	9079	−219.5~−29.9	−30.2~−5.0
LMWL of H	δD = 8.067 δ^{18}O + 12.304	0.989	9240	−251.5~8.1	−32.23~0.13
PSWL of A	δD =5.189 δ^{18}O − 26.909	0.791	23	−92~−18.36	−13~+3.2
PSWL of S-A	δD =7.088 δ^{18}O − 16.539	0.781	34	−98~−40	−11~−2.3
PSWL of S-H	δD =6.117 δ^{18}O − 21.386	0.814	30	−88~−32	−11.5~−2.3
PSWL of H	δD =7.596 δ^{18}O − 5.773	0.89	43	−94~−21.5	−10.9~−2

GMWL: Global Meteoric Water Line; LMWL: Local Meteoric Water Line; PSWL: Plant Stem Water Line; A: Arid region; S-A: Semi-arid region; S-H: Semi-humid region; H: Humid region. N represents the number of samples.

3.1.2. Plant Stem Water Line

Plants take up water from the soil, and soil water is recharged by rainfall. δD and $\delta^{18}O$ values of plant stem water tend to differ according to water source acquisition across the soil-plant-atmosphere continuum because there is no isotopic fractionation during water uptake by terrestrial plants except for salt-excluding plant species [46,47].

The range of isotopic values (δD and $\delta^{18}O$) in precipitation is greater than in the stem water in vegetation (Table 1) because the range of soil water is reduced by the mixing of precipitation water. The plant study sites are relatively scattered, and the meteorological station that collected rainfall data can be difficult to accurately match to study sites. In general, δD and $\delta^{18}O$ values for plant stem water are relatively large and are mainly distributed in the upper part of the isotopic values for precipitation due to evaporation affecting both rain and the soil surface (Figure 1).

The study found that the correlation between δD and $\delta^{18}O$ in plant stem water is well established for the four regions of China: the arid region ($\delta D = 5.1890\ \delta^{18}O - 26.909$), semi-arid region ($\delta D = 7.0879\ \delta^{18}O - 16.539$), semi-humid region ($\delta D = 6.1168\ \delta^{18}O - 21.386$), and humid region ($\delta D = 7.5962\ \delta^{18}O - 5.7731$) (Figure 1). The results of Least Significant Difference (LSD) tests showed that δD differs between the arid region and the other regions ($p < 0.05$). As for $\delta^{18}O$, there is also a significant difference between the arid region and the other regions ($p < 0.01$). The results are because of severe evaporation in the arid region. In general, the slope of the Plant Stem Water Line (PSWL) increases gradually from the arid region, to the semi-humid region, to the semi-arid region, to the humid region. Notably, the slope for the semi-humid region was less steep than that for the semi-arid region, which may be related to water sources accessed by plants.

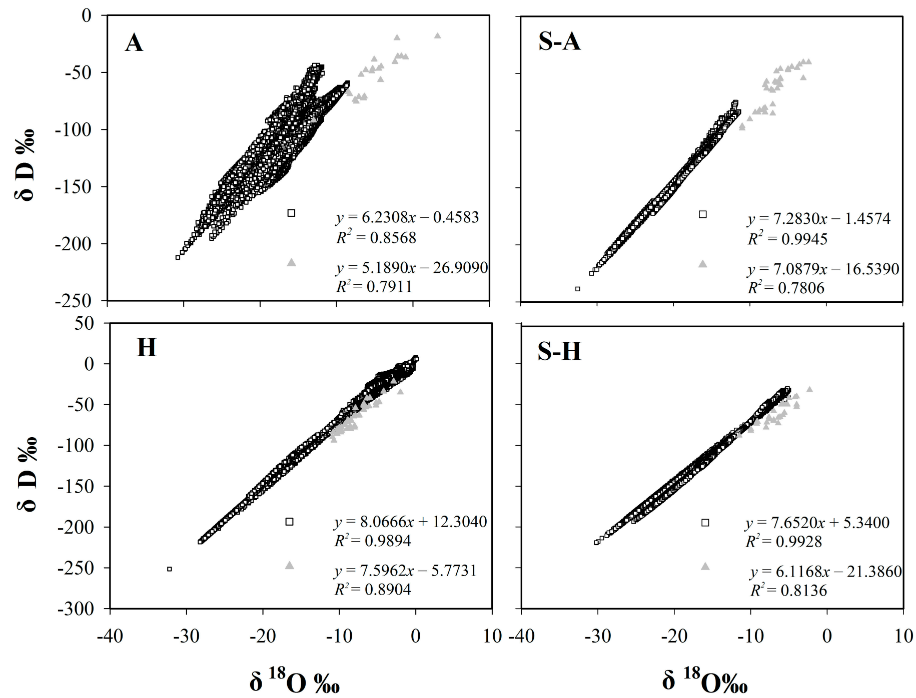

Figure 1. The relationship between δD and $\delta^{18}O$ values for precipitation and plant stem water. The hollow squares represent isotopic values for precipitation, the solid triangles represent isotopic values for plant stem water. A: Arid region; S-A: Semi-arid region; S-H: Semi-humid region; H: Humid region.

3.1.3. Soil Water Line

The $\delta^{18}O$ values by depth (0–100 cm) varied with time (Figure 2). In the top 20 cm of the soil profile, $\delta^{18}O$ showed a high variation for all regions ($p < 0.05$), and the coefficients of variation were −0.10,

−0.10, −1.00, and 0.41 for the humid region, semi-humid region, semi-arid region, and arid region, respectively, due to the combined impact of summer precipitation and soil evaporation. There was also an increasing trend during the year, with average $\delta^{18}O$ values of −6.50‰, −3.47‰, −1.45‰, and −1.29‰, respectively. At a depth of 20–80 cm, $\delta^{18}O$ had relatively low values compared with the top soil layer (0–20 cm) and the coefficients of variation were −0.03, −0.12, −0.16, and −0.39, respectively, for the four regions. The values remained relatively constant in deep soil layers (below 80 cm), with coefficients of variation of −0.03, −0.06, −0.03, and −0.04, respectively, for the four regions. The $\delta^{18}O$ values varied greatly with the seasons, ranging from −8.68‰ to 0.01‰ in the wet season, and from −7.59‰ to 3.33‰ in the dry season. Average isotopic values in the arid region were at the highest level, ranging from −3.18‰ (in the wet season) to 0.22‰ (in the dry season). Average isotopic values in the semi-arid region and the semi-humid region were intermediate, varying from −6.14‰ (in the wet season) to −4.24‰ (in the dry season) in the semi-arid region and from −6.47‰ (in the wet season) to −4.83‰ (in the dry season) in the semi-humid region. Average isotopic values in the humid region were at the lowest level, ranging from −7.80‰ (in the wet season) to −7.04‰ (in the dry season). Owing to high evaporative demand, precipitation during the dry season freely evaporated from the soil surface, bringing about decreased infiltration and shallower soil water penetration, which was short-lived, especially in the arid region.

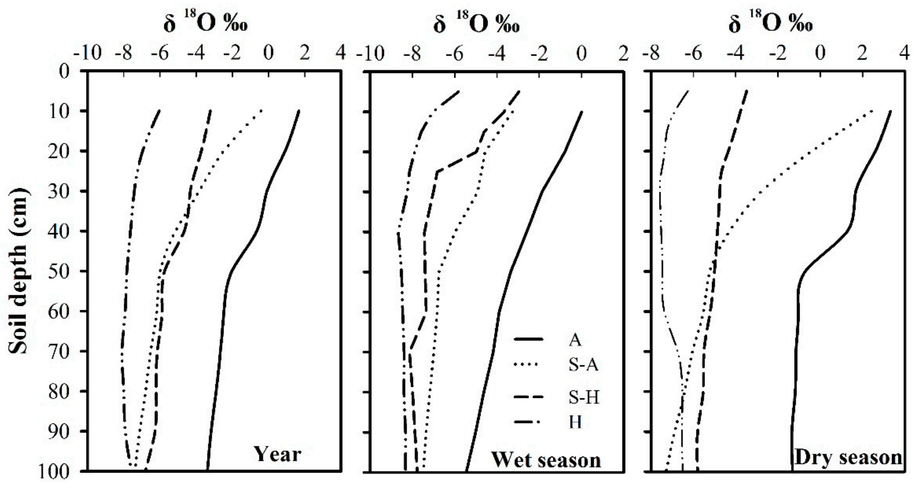

Figure 2. Seasonal dynamics of the $\delta^{18}O$ values in soil water (0–100 cm). A: Arid region; S-A: Semi-arid region; S-H: Semi-humid region; H: Humid region.

There was obvious change in $\delta^{18}O$ values with depth. In general, shallow soil water was the most unstable zone and the $\delta^{18}O$ values had high variation; the middle soil water had lower $\delta^{18}O$ values than the shallow soil water and limited changes with depth; the deep soil water had relatively stable $\delta^{18}O$ values within the soil profile. Soil water needed to be classified into different layers for effective analysis of any variations. Cluster analysis can provide preliminary soil groupings based upon the squared Euclidean distance. The variations of $\delta^{18}O$ values make each soil layer (0–100 cm) produce different squared Euclidean distances so that they were clustered into different groups. For example (Figure 3a), when the squared Euclidean distance is equal to 5, the soil layers were divided into five groups: 10 cm, 20 cm, 30–40 cm, 50–80 cm, and 90–100 cm. By analogy, when the squared Euclidean distance is equal to 10, the soil layers were divided into three layers: 10 cm, 20–40 cm, and 50–100 cm. Intense evaporation made the classification of data for the soil surface fragmented. A series of studies were conducted on a small scale and provided references for soil classification [13,25,48–57]. Combing previous studies and the results of cluster analysis allowed for valid and reliable soil classification (Table 2).

Table 2. The results of our soil classification.

Region	Previous Studies			The Preliminary Results of Cluster Analysis		Final Results
	Author	Location	Classification/cm	Classification/cm	SED	Reclassification/cm
A	Dai et al. (2015) Zhou et al. (2017) Zhang et al. (2017)	Gurbantonggut Desert Badain Jaran Desert Heihe River Basin	0–40, 40–100, 100–300, 0–50, 50–150, 150–300 0–30, 30–80, 80–200	0–10, 10–20, 20–40, 40–80, 80–100	5	0–40, 40–100, >100
S-A	Yang et al. (2011) Wu et al. (2016) Zhu et al. (2014)	Inner Mongolia Tibet Plateau Ningxia plain	0–20, 20–40, >40 0–30, 30–60, 60–120 0–40, 40–140, 140–200	0–10, 20–30, 30–60, 60–100	2.5	0–30, 30–60, >60
S-H	Liu et al. (2017) He et al. (2016) Lv et al. (2016)	Huabei plain Huabei plain Loess plateau	0–20, 20–60, 60–100 0–30, 30–100 0–10, 10–40, 40–80, 80–120	0–10, 10–20, 20–60, 60–100	5	0–20, 20–60, >60
H	Rong et al. (2014) Gu et al. (2015) Yang et al. (2015)	karst area karst area Jitai Basin	0–10, >10 0–5, 5–30, 30–50, 50–90 0–20, 20–50, 50–100	0–5, 5–10, 10–40, 40–100	5	0–10, 10–40, >40

SED: Squared Euclidean distance; A: Arid region; S-A: Semi-arid region; S-H: Semi-humid region; H: Humid region. In the semi-arid region, $\delta^{18}O$ values are relatively stable compared to the other regions so that squared Euclidean distances were separated into classes using a value of 2.5.

In the arid region, soil water could be divided into three layers: shallow soil water (0–40 cm), middle soil water (40–100 cm), and deep soil water (>100 cm). In the semi-arid region, it was divided into: shallow soil water (0–30 cm), middle soil water (30–60 cm), and deep soil water (>60 cm). In the semi-humid region, the classification was shallow soil water (0–20 cm), middle soil water (20–60 cm), and deep soil water (>60 cm). There are some specific formations that create different conditions, for example, Karst areas are found in the humid region and are characterized by shallow soils and exposed rocks with poor stability [58,59]. Rainfall flows underground rapidly and little infiltration occurs, which causes the loss of surface water and desiccation [60]. Karst areas is a typical shallow soil area [61] and there have been many plant water source studies undertaken there. To date, most research studies were carried out in karst areas in the humid region, so they involved relatively shallow soils, with the classification: shallow soil water (0–10 cm), middle soil water (10–40 cm), and deep soil water (>40 cm). In general, the results of soil classification were slightly different from previous studies because here we combined many published papers on a regional scale, while previous research has focused on the local scale. Our overview not only reveals variations in isotopic values of soil profiles, but also provides a standard for measuring soil water sources of different plants in the same region.

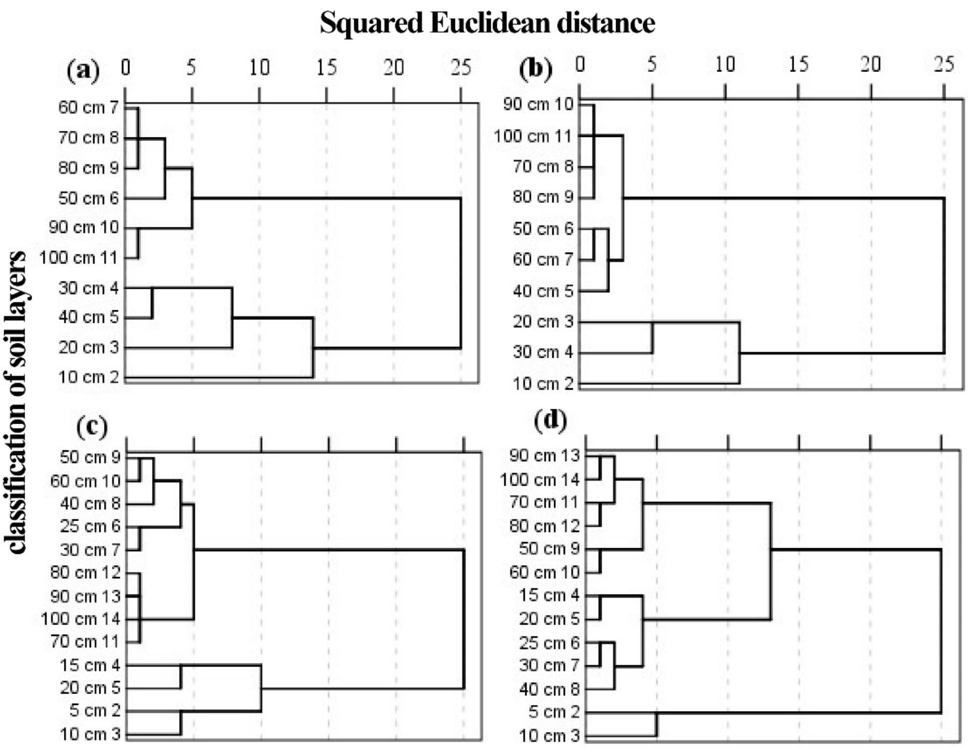

Figure 3. Soil cluster analysis using $\delta^{18}O$ values. *x*-axis, Squared Euclidean distance; *y*-axis, Soil depth (0–100 cm); (**a**) Arid region; (**b**) Semi-arid region; (**c**) Semi-humid region; (**d**) Humid region. The length of the black line represents the size of squared Euclidean distance, the nodes represent soil layers that have the nearest distance and were clustered into one group.

3.2. Plant Main Water Source

Water available to plants comes from precipitation, soil water, groundwater, and so on. Precipitation falling in the wet season has a markedly different effect on soil water than during the dry season. In general, precipitation in the rainy season accounts for 70–80% of annual precipitation in most of China [27,62–64]. The timing and magnitude of rainfall has significant implications for the water uptake of plants [6,65].

Here, we have summarized the seasonal variation trends for the main water sources for plants in the four regions of China (Figures 4 and 5). The proportions were obtained from the number of samples for each main water source from all the samples in each region. In the wet season, trees would favor the use of deep soil water (34.3%) and groundwater (31.5%) in the arid region (Figure 6a), as their root systems give them better access to water that has infiltrated more deeply. Shallow soil water is the main water source for vegetation in the semi-arid region (62.6%) and semi-humid region (72.7%). Annual precipitation is more than 800 mm in the humid region, and shallow soil water (35%) and precipitation (32.5%) are the main water sources for plants in this region. In the dry season (Figure 6b), one of the major challenges facing vegetation in water-limited arid ecosystems is the discontinuous nature of water availability [66]. In the arid region, plants can efficiently utilize shallow soil water (54.2%), deep soil water (20.8%), and groundwater (20.8%) to avoid drought stress. In the semi-arid region, plants consistently use various water sources: shallow soil water (26.9%), middle soil water (19.2%), deep soil water (34.6%), and groundwater (19.2%). In the semi-humid region, plants rely on shallow soil water (43.5%), middle soil water (26.1%), and deep soil water (17.4%). In the humid region, plants rely on shallow soil water (25.8%), deep soil water (31.8%), and precipitation (16.6%).

Plants have strong adaptability to the environment, using diverse water sources in particular geographical situations (Figure 7). Riparian forests tend to use river water in arid and semi-arid regions. For example, Li et al. found that the riparian tree species *Populus eupheratica* used more stream water (68%) in the lower reaches of the Heihe River, especially during the discharge period [67]. Zhu et al. found that the water use patterns of plants varied over time. At the beginning of the growing season, four plants (*Sympegma regelii* Bunge, *Ceratoides latens* (J. F. Gmel.) Reveal et Holmgren, *Calligonum mongolicum* Turcz., and *Ephedra przewalskii* Stapf) in Golmud used a mixture of both precipitation and groundwater; in the mid-to-late period of the growing season, *Sympegma regelii* Bunge took up shallow soil water, while the three other plants species extracted from deep soil water and groundwater [68]. Xing et al. found that *Salsola abrotanoides* Bge. used river water preferentially over precipitation in the Qaidam Basin [38]. In contrast, Dawson and Ehleringer published a landmark paper demonstrating that mature streamside riparian trees in a semi-arid dry mountain catchment made use of water from deeper strata rather than stream water, and only small streamside individuals appeared to use stream water [69]. Recently, Bowling et al. revisited this study and found that neither groundwater nor stream water matched the δD and $\delta^{18}O$ values of xylem water because of the "two water worlds" hypothesis [70]. In the semi-humid region, one of the water sources for plants is spring water. Trees growing in the Beijing mountain area are often located on rocky outcrops, and Liu et al. found that the tree species *Platycladus orientalis* (L.) Franco predominantly utilized natural spring water (57.8%) and the tree species *Quercus variabilis* Bl. primarily extracted water from natural springs (40.5%) and middle soil water (25.9%) [71]. Sun et al. found that *Quercus variabilis* Bl. also used spring water (19.6%) during the dry season in the south-facing area of the Taihang Mountains [72]. In the humid region, plants also used minor water sources (karst water, spring water, fog, river water, and seawater), which accounted for 10.6% of the total water usage. The humid region (Southwest China) is home to one of the largest karst areas in the world [73]. The high proportion of bedrock outcrops makes spring water and karst water common supplementary water sources for plants [13,18,31,74]. In addition, Fu et al. found that the proportion of fog water contributing to xylem water ranged from 15.8% (*Cleistanthus sumatranus* (Miq.) Muell. Arg.) to 41.3% (*Combretum latifolium* Bl.) [14]. Zhan et al. found that approximately 16% of the water sources of plants originated from fog in the northern Dongting lake area [75]. Huang et al. found that indigenous mangrove species (*Kandelia obovata, aegiceras corniculatum, and Avicennia marina*) used groundwater and seawater in coastal shelterbelt forests of southeast China [29].

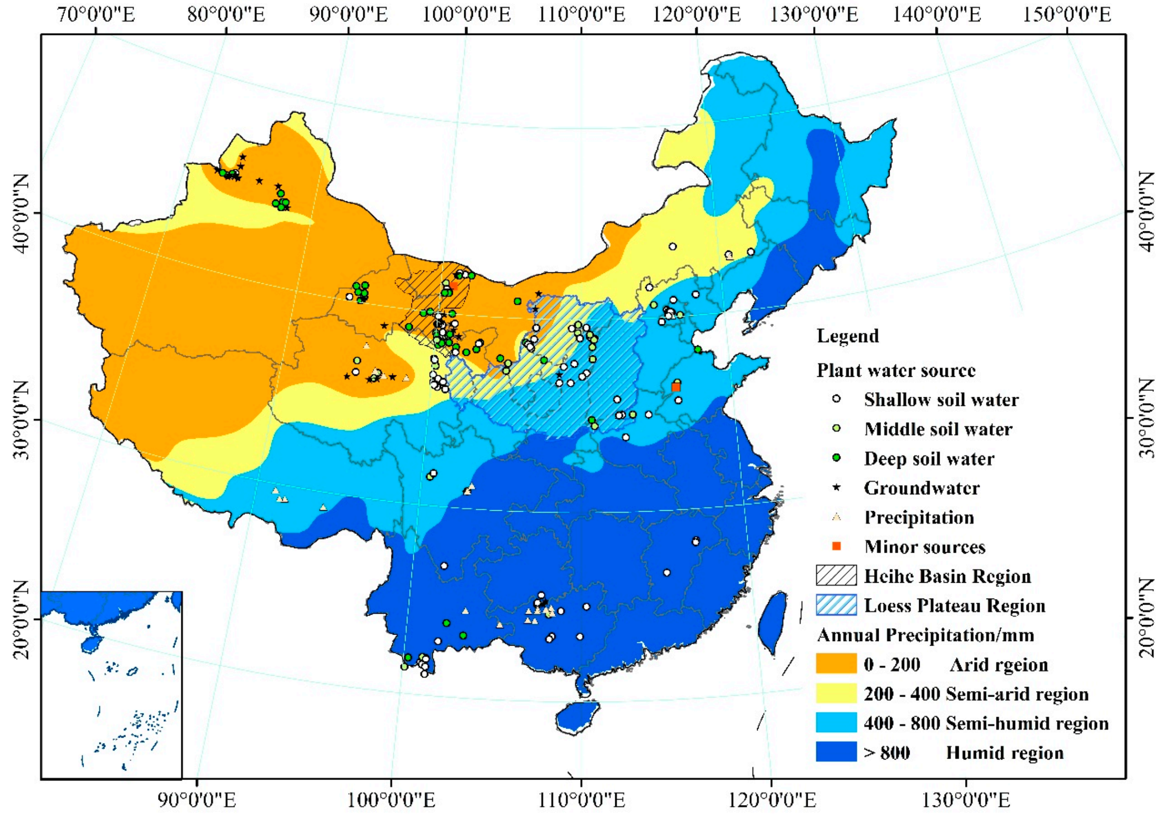

Figure 4. Plants' main water sources in the wet season.

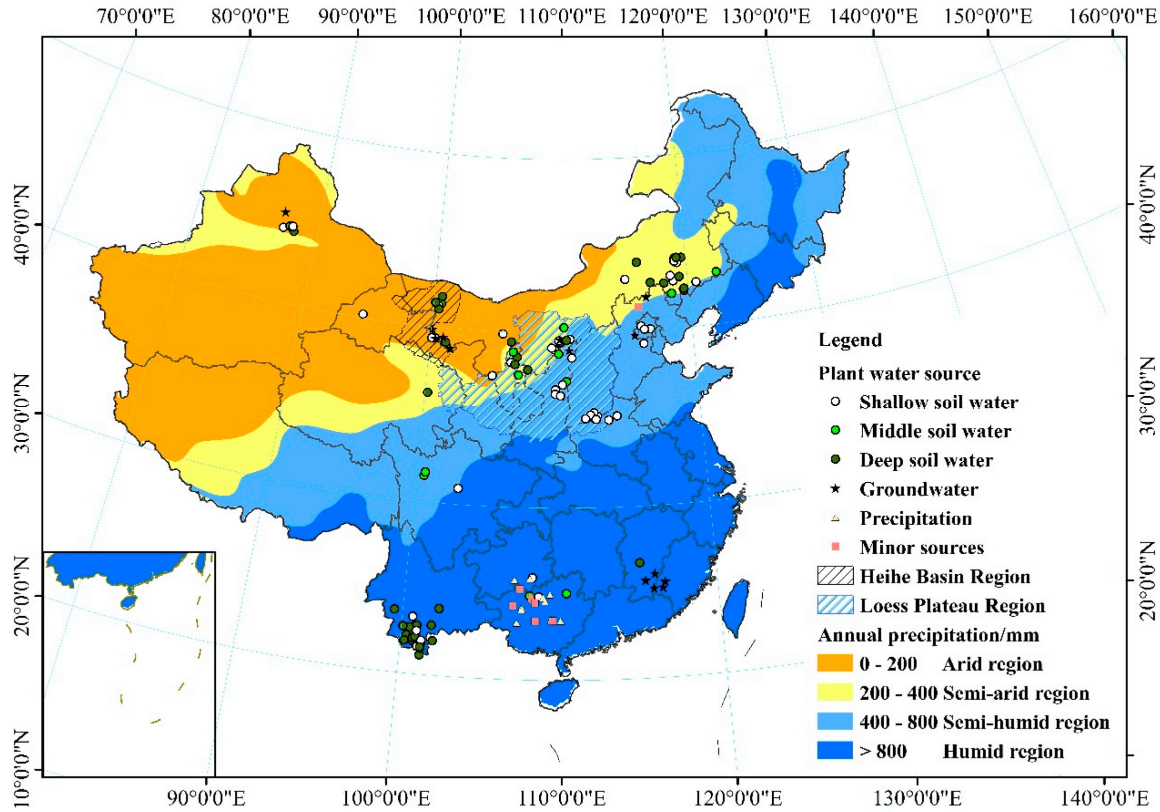

Figure 5. Plants' main water sources in the dry season.

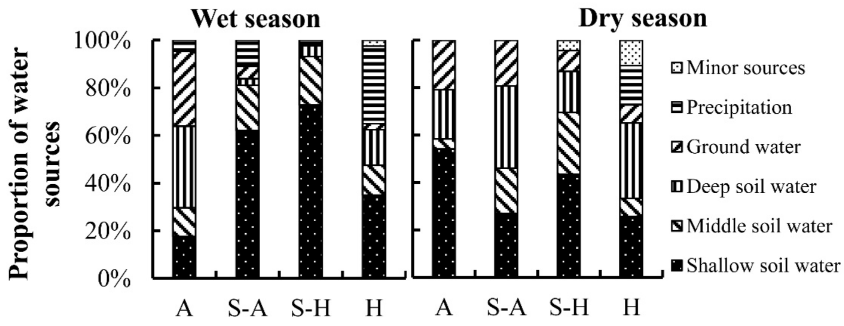

Figure 6. Seasonal changes in the proportion of plant water sources. A: Arid region; S-A: Semi-arid region; S-H: Semi-humid region; H: humid region.

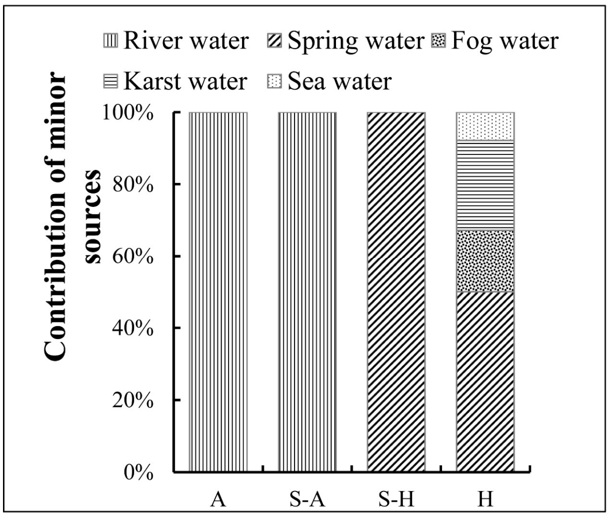

Figure 7. Contribution of minor water sources. A: Arid region; S-A: Semi-arid region; S-H: Semi-humid region; H: humid region.

The ability to access groundwater determines species' groundwater use and accessibility is related with spatial and temporal distribution of groundwater. The average contributions of groundwater in the wet season and the dry season were 10.7% and 8.9%, respectively, although the seasonal variation was not significant ($p > 0.05$). The percentages of samples that have groundwater contribution to xylem water out of the total samples in the arid region, semi-arid region, semi-humid region, and humid region were 56.8%, 27.0%, 28.4%, and 6.6%, respectively. The average contributions of groundwater from the arid region, semi-arid region, semi-humid region, and humid region were 23.3%, 7.0%, 4.4%, and 3.7%, respectively (Figure 8). There is a high variation between the former and the latter because the number of samples with groundwater contributions was high, but per sample the contribution of groundwater was relatively low. In summary, the contribution of groundwater is positively related to the degree of drought. This is consistent with the point of view presented by Evaristo and McDonnell [33].

In particular, the Loess Plateau is located in the semi-arid and semi-humid regions, which have less precipitation and poor water resources. Soil water status is worse because of the presence of soil dry layers [76]. The results reveal that 43.9% of the samples from the Loess Plateau had some groundwater in the xylem water, and these tended to be from the northern Loess Plateau (Figure 5). Whether groundwater was used by plants depended on the complex topography of the sites on the Loess Plateau. The central and southern Loess Plateau is a hill and gully area where the soil layers are deep—up to more than 80 m. It is difficult for plants to access groundwater. In the rainy season and the dry season on the Loess Plateau, plants are dependent on soil water from different layers.

In the northern part of the Loess Plateau, in the Mu Us Desert, groundwater level is low and plants can absorb water from the saturated zone [77].

The Heihe River basin is the second largest inland river basin in the arid and semi-arid regions of northwest China. It is a classic area for studying oases and desertification [78]. Plants here mainly used deep soil water and groundwater through the year. From the Heihe River Basin, 67.7% of the xylem water samples contained a contribution from groundwater, mainly samples from the lower reaches of the Heihe River Basin (Figure 5).

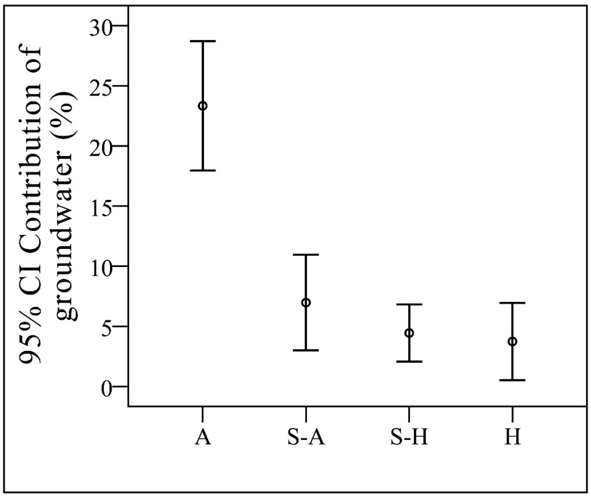

Figure 8. Contribution of groundwater. CI: Confidence Interval; A: Arid region; S-A: Semi-arid region; S-H: Semi-humid region; H: humid region.

3.3. Contribution of the Plant Main Water Source

The contribution of the plant main water source (CPMWS) values were 56.3% in the wet season and 57.6% in the dry season, and there was no significant seasonal difference ($p > 0.05$). In the dry season, the average CPMWS values were 60.3%, 56.0%, 55.3%, and 56.0%, respectively, from the arid region, semi-arid region, semi-humid region, and humid region, and there was no significant regional difference ($p > 0.05$). In the wet season, the average CPMWS values were 60.8%, 55.9%, 56.6%, and 59.6% from the arid region, semi-arid region, semi-humid region, and humid region, and there was also no significant regional difference ($p > 0.05$). Although the average CPMWS values had no significant seasonal or regional differences, the main water sources of plants differed in both the wet and the dry seasons.

In the arid region, the main water sources for plants in the dry season were shallow soil water, deep soil water, and groundwater; their median CPMWS values were 69.1%, 56.0%, and 63.5%, respectively (Figure 9). In the wet season, in contrast, shallow soil water had a low CPMWS value of 51.3%. Deep soil water and groundwater made high contributions and their median CPMWS values were 68.8% and 69.3%, respectively. In the semi-arid region, the median CPMWS values of shallow soil water, middle soil water, deep soil water, and groundwater in the dry season were 62.0%, 56.0%, 47.1%, and 55.5%, respectively. Compared with the dry season, the median CPMWS of shallow soil water decreased to 53.0%, the median CPMWS of middle soil water increased to 63.5%, and the combination of deep water and groundwater was 47.5% in the wet season. In the semi-humid region, the CPMWS of shallow and middle soil water showed an increasing trend, and the CPMWS of the combination of deep water and groundwater exhibited a decreasing trend from the dry season to the wet season. The values for shallow soil water, middle soil water, and the combination of deep soil water and groundwater were 61%, 60.5%, and 37.5% in the dry season. The values for shallow soil water, middle soil water, and the combination of deep soil water and groundwater were 54.2%, 56.4%, and 44.0% in the wet season. In the humid region, shallow soil water and middle soil water exhibited relatively large differences from 57.6% and 51% in the dry season to 51.6% and 62.6% in the wet season, respectively. In some special cases, precipitation made the highest contribution: 84.8% (dry season) and 87.9% (wet season) in karst areas, where rainfall was treated as a potential water source for plants growing on outcrops, as they can use rainfall stored in crevices/cracks directly [79]. For example, Nie et al. found that in the dry season, five species (*Radermachera sinica* (Hance) Hemsl., *Sterculia euosma* W. W. Smith, *Schefflera octophylla* (Lour.) Harms, *Alchornea trewioides* (Benth.) Muell. Arg, *Celtis biondii* Pamp.) utilized both recent and previous rainfall, in percentages ranging from 89.1% to 100% [80].

In general, soil water was the main water source for plants and shallow soil water made the highest contributions. CPMWS is closely related to available water sources for plants. Due to the occurrences of facilitative and competitive interactions, different plants alleviate water stress by switching their utilization of water sources. In the dry savannas, Walter [81] proposed a two-layer hypothesis that relies on vertical niche partitioning, and it has been proposed that shallowly-rooted grasses use water only from the subsurface layers. On the contrary, deeply-rooted woody trees primarily depend on subsoil water below the grass roots [81]. The roots offer powerful evidence for testing this hypothesis [82]. Deeply-rooted perennials showed a complete dependence on summer precipitation. Shallowly-rooted herbaceous utilized both summer precipitation and winter-spring precipitation in the desert of southern Utah [83]. Moreover, Ward et al. found that this assumption is not only suitable for the dry savannas, but is also suitable for some mesic areas [84].

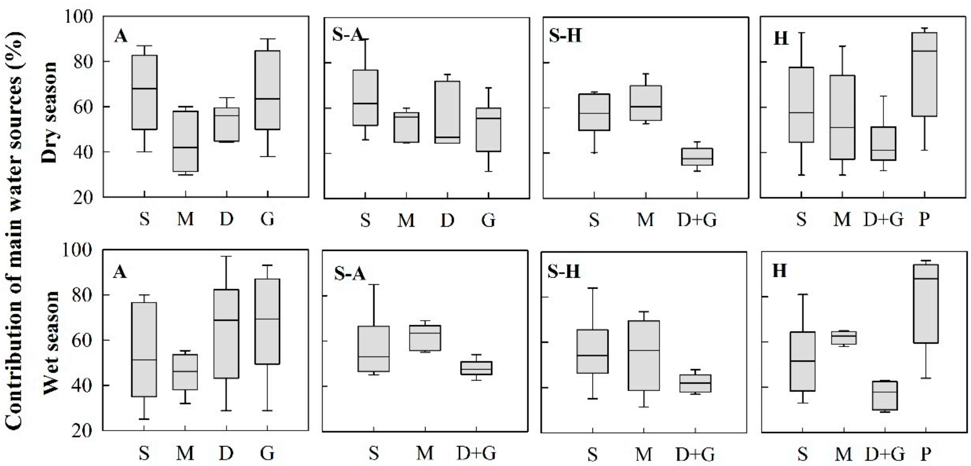

Figure 9. Contribution of the plant main water source. A: Arid region; S-A: Semi-arid region; S-H: Semi-humid region; H: humid region; S: Shallow soil water; M: Middle soil water; D: Deep soil water; G: Groundwater; P: Precipitation; D + G: Combination of deep soil water and groundwater. Deep soil water and groundwater were classified as a group because of the small number of samples for groundwater.

4. Conclusions

Influenced by continental and seasonal effects, the slope of the LMWL gradually increased from the arid region, to the semi-arid region, to the semi-humid region, to the humid region (6.231, 7.283, 7.652, and 8.067, respectively) in China. For each region, the ranges of isotopic values (δD and $\delta^{18}O$) in vegetation are mainly distributed in the upper part of the LMWL because evaporation affects both rainfall and the soil surface. With respect to the soil water line, the $\delta^{18}O$ values by depth (0–100 cm) varied with time, especially for the top soil layer.

Soil water availability for plants is affected by seasonal rainfall patterns. In the wet season, plants favor deep soil water and groundwater in the arid region. Shallow soil water is the main water source for vegetation in the semi-arid region and semi-humid region. In the humid region, shallow soil water and precipitation are the main water sources for plants. In the dry season, in water-limited arid ecosystems, plants can efficiently utilize shallow soil water, deep soil water, and groundwater to avoid drought stress. In the semi-arid region, plants consistently use various water sources: shallow soil water, middle soil water, deep soil water, and groundwater. In the humid region, plants rely on shallow soil water, deep soil water, and precipitation.

Soil water was the main water source for plants, and shallow soil water made the highest contributions. The contribution of plant main water source (CPMWS) values exhibited no significant seasonal or regional difference, although there were seasonal differences in specific water sources. These figures are closely related to available water sources for plants. Plants maintain their growth via shifting their utilization of water sources when there is water source instability, with both facilitative and competitive interactions occurring.

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Author Contributions: Y.Z. and L.W. designed the study. Y.Z. compiled the data set and conducted the statistical analyses. Y.Z. and L.W. wrote the manuscript.

Conflicts of Interest: The authors have no conflicts of interest to declare.

Appendix A

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Appendix B

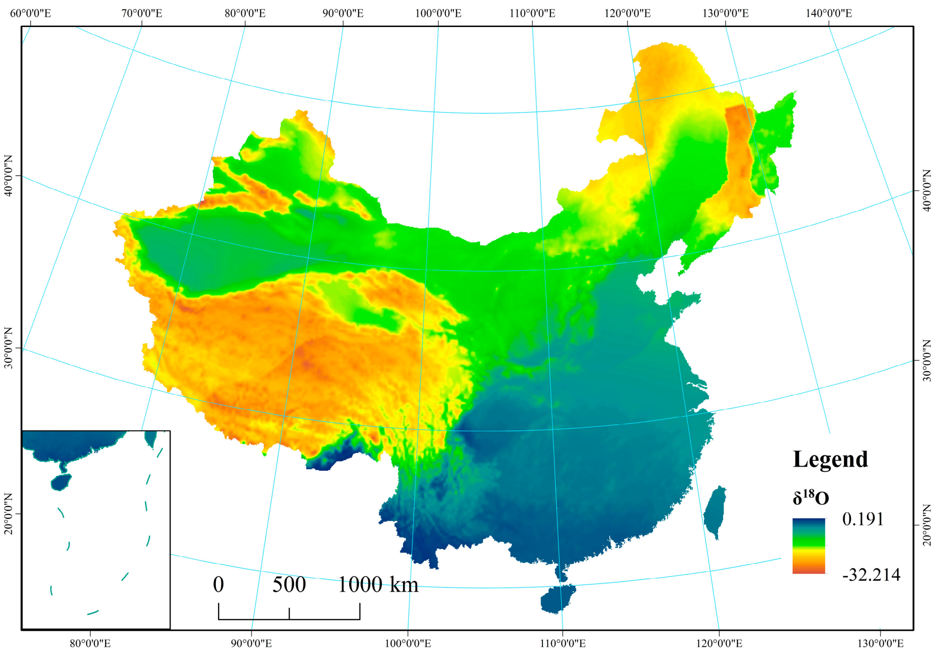

Figure A1. Spatial distribution of $\delta^{18}O$ in precipitation across China.

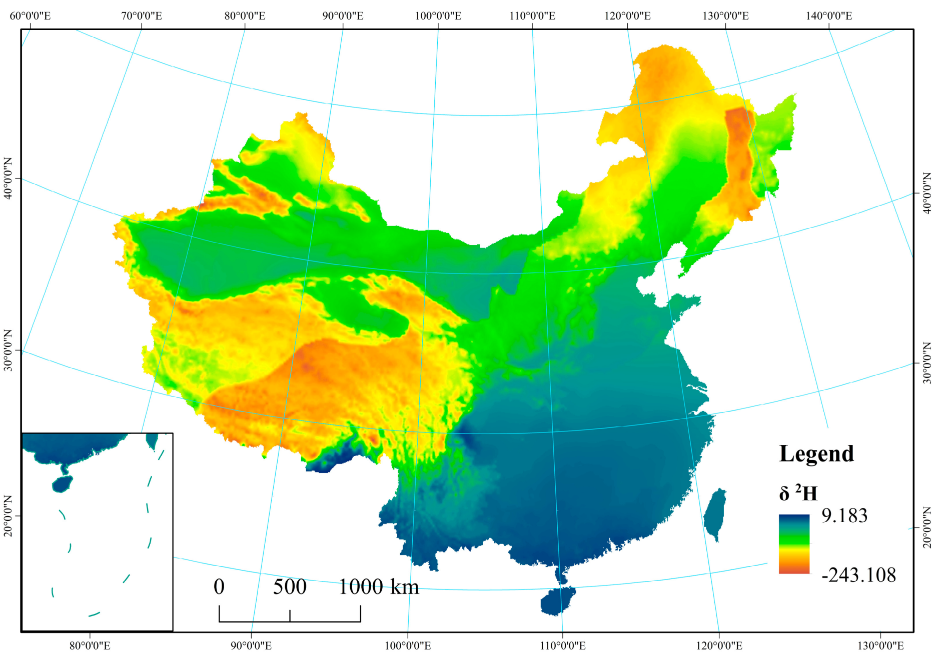

Figure A2. Spatial distribution of $\delta^{2}H$ in precipitation across China.

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