



Seasonal variation in water uptake patterns of three plant species based on stable isotopes in the semi-arid Loess Plateau



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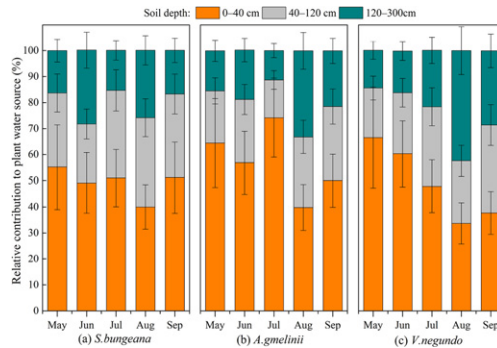
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HIGHLIGHTS

- Seasonal variations of water uptake pattern were determined by dual stable isotopes (δD and $\delta^{18}O$) and MixSIAR model.
- Soil water in the 0–120 cm depth contributed 75–80% to the total water uptake in the growing season.
- *Vitex negundo* displayed larger degree of ecological plasticity to switch water between shallow and deep soil layers.
- Functionally dimorphic root systems were related to flexible water uptake pattern.

GRAPHICAL ABSTRACT



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ABSTRACT

Water is a limiting factor and significant driving force for ecosystem processes in arid and semi-arid areas. Knowledge of plant water uptake pattern is indispensable for understanding soil–plant interactions and species coexistence. The ‘Grain for Green’ project that started in 1999 in the Loess Plateau of China has led to large scale vegetation change. However, little is known about the water uptake patterns of the main plant species that inhabit in this region. In this study, the seasonal variations in water uptake patterns of three representative plant species, *Stipa bungeana*, *Artemisia gmelinii* and *Vitex negundo*, that are widely distributed in the semi-arid area of the Loess Plateau, were identified by using dual stable isotopes of δ^2H and $\delta^{18}O$ in plant and soil water coupled with a Bayesian mixing model MixSIAR. The soil water at the 0–120 cm depth contributed $79.54 \pm 6.05\%$ and $79.94 \pm 8.81\%$ of the total water uptake of *S. bungeana* and *A. gmelinii*, respectively, in the growing season. The 0–40 cm soil contributed the most water in July ($74.20 \pm 15.20\%$), and the largest proportion of water ($33.10 \pm 15.20\%$) was derived from 120–300 cm soils in August for *A. gmelinii*. However, *V. negundo* obtained water predominantly from surface soil horizons (0–40 cm) and then switched to deep soil layers (120–300 cm) as the season progressed. This suggested that *V. negundo* has a greater degree of ecological plasticity as it could explore water sources from deeper soils as the water stress increased. This capacity can mainly be attributed to its functionally dimorphic root system. *V. negundo* may have a competitive advantage when encountering short-term drought. The ecological plasticity of plant water use needs to be considered in plant species selection and ecological management and restoration of the arid and semi-arid ecosystems in the Loess Plateau.

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1. Introduction

Water plays crucial roles in plant productivity and species diversity in both natural and anthropogenic ecosystems (Porporato et al., 2004), and determines the distribution and ecological functions of vegetation. Plants are able to obtain water from various sources over time, depending on species, growth forms and environment conditions (Dawson et al., 2002; Eggemeyer et al., 2009; Grossiord et al., 2017; Yang et al., 2015; Evaristo and McDonnell, 2017). The spatial and temporal variations in water sources absorbed by plants are referred to water uptake pattern. Plant water uptake plays an important role in understanding and modeling hydrological processes at the soil–vegetation–atmosphere interface (Chen et al., 2017; Sprenger et al., 2016; Vargas et al., 2017), and it provides critical insights into adaptive responses of plants to the changing environments (Dawson et al., 2002; Evaristo et al., 2016; Grossiord et al., 2017).

In arid and semi-arid ecosystems, soil moisture generated by precipitation is a limiting factor controlling vegetation structures and ecosystem processes (Gao et al., 2011; Moreno-de Las Heras et al., 2011). A healthy plant–soil ecosystem requires that water utilization by plants does not exceed the supply of soil water otherwise leads to water deficit (Chen et al., 2015). The capacity to adjust water use strategy along with the highly variable rainfall pattern and consequently soil water content is very critical for a plant to survive in these ecosystems (Wu et al., 2016; Grossiord et al., 2017). Plant derived the majority water from deep sources (e.g., deep soil water, groundwater) during the dry season while most water they used was derived from shallow sources supplied by upper soil layers during the wet season (Dawson and Pate, 1996; Asbjornsen et al., 2008). Multiple species living in the same habitat may have distinct water use patterns, making it possible for the species to coexist (Eggemeyer et al., 2009; Wu et al., 2016). This phenomenon may be attributed to hydrological niche segregation (Silvertown et al., 2015). Several studies showed that grass and herbs tended to continuously rely on water in the shallow soil layer across the growing season (Asbjornsen et al., 2008; Prechsl et al., 2015; Priyadarshini et al., 2016). In comparison, some studies showed that trees and shrubs tended to have the capacity to derive water sources from deeper soil layers (McCole and Stern, 2007; Wu et al., 2016). One of the reasons to explain the different water uptake patterns among varied plant functional types may relate to root morphology of plants. Some studies suggested that species with dimorphic roots have the capacity to switch water absorption zones between shallower and deeper soil layers (Dawson and Pate, 1996; Nie et al., 2010; Yang et al., 2015). The transposition capacity to absorb water sources from shallow to deep soil layers reflects plant ecological plasticity (Valladares et al., 2007). The greater ecological plasticity usually indicates a greater adaptation level to the environment. Therefore, a better understanding of plant water uptake patterns will improve our understanding of soil–plant interactions and guide ecosystem management practices in arid and semi-arid areas such as selection of plant species for ecological restoration (Jian et al., 2015; Lü et al., 2017; Sprenger et al., 2016).

Water sources utilized by plants can be determined by many methods, such as root system excavation (Xu and Li, 2006), sap flow techniques (Delzon and Loustau, 2005), electrical resistivity (Mares et al., 2016), GIS tools (Howard and Merrifield, 2010), radioactive tracer tritium (Zhang et al., 2017). Although these methods could determine plant water sources in some extent, stable isotope technique provides an effective, powerful and nondestructive approach for identifying and partitioning the different potential water sources used by plants (Ma and Song, 2016; Geris et al., 2017; Hardanto et al., 2017; Rothfuss and Javaux, 2017). Previous studies have proven that no isotopic fractionation of water occurs during water absorption by roots and transportation along the root–shoot conduit before transpiration starts in terrestrial plants (Brunel et al., 1995; Dawson et al., 2002; Ehleringer and Dawson, 1992), except for some coastal wetland species (Lin and Sternber, 1993) and woody xerophytes (Ellsworth and Williams,

2007), for which isotope fractionation occurs for hydrogen but not for oxygen during plant water uptake. Evaristo et al. (2017) reported that plant water sources quantification methods should consider the possible effects of hydrogen isotope fractionation. Nevertheless, the stable isotopes of $\delta^2\text{H}$ and $\delta^{18}\text{O}$ in water still can be used to determine water uptake patterns (Ehleringer et al., 1991; Li et al., 2007; Moreno-Gutiérrez et al., 2015; Swaffer et al., 2014; Yang and Fu, 2017). Although previous studies on water uptake patterns have been conducted in various ecosystems (Eggemeyer et al., 2009; Liu et al., 2010; Schwendenmann et al., 2015), there are still uncertainties regarding plant water uptake patterns (Eggemeyer et al., 2009; Yang et al., 2015). Only soil samples of 0–100 cm depths were collected and extracted as the main soil water sources in most studies (Meißner et al., 2012; Prechsl et al., 2015; Yang et al., 2015). This may underestimate the proportional contribution of soil water to plant water sources and correspondingly overestimate that of other water sources (e.g., spring, ground water, fog), particularly for shrubs and trees with deeper roots. Therefore, including deep soil sampling is necessary to improve the accuracy of water uptake quantification from varied sources and understanding of plant–water interactions (Querejeta et al., 2007; Wu et al., 2014).

The 'Grain for Green' project that was implemented in the Chinese Loess Plateau in 1999 is the largest vegetation restoration project in the world (Chen et al., 2015). Trade-offs between vegetation recovery and water depletion has attracted extensive attention (Chen et al., 2015; Jian et al., 2015; Wang et al., 2010). Unsuitable species selection for vegetation restoration leads to soil desiccation, vegetation degradation and difficulties in renewal and reforestation (Chen et al., 2008; Jian et al., 2015; Wang et al., 2010). Although some studies explored soil water migration (Yang and Fu, 2017) and plant water use strategy for natural and planted shrub (Lü et al., 2017), the difference between species and seasonal variations of water uptake pattern remain poorly understood in this region.

In this study, we examined the ecological plasticity of three plant species, *Stipa bungeana* (herb), *Artemisia gmelinii* (subshrub) and *Vitex negundo* (shrub) in terms of the water uptake patterns across the vertical soil profile during the growing seasons by using the isotopic technique. We hypothesized that the three species have different ecological plasticity in plant water uptake. The objectives of this study were to: (i) investigate the isotopic compositions of soil water and their vertical gradients along the soil profile, (ii) quantify the seasonal variations in water uptake patterns and identify their differences among the three species.

2. Materials and methods

2.1. Study area

This study was conducted in the Yangjuangou catchment in the central region of the Loess Plateau in Shanxi Province, China (36°42'45" N, 109°31'45" E). This catchment is a typical Loess hilly and gully region with a total area of 2.02 km². The elevation is between 1050 and 1298 m, and the slope gradients range from 10 to 30° (Liu et al., 2012). This area is influenced by the semi-arid continental climate. The annual average precipitation and air temperature from 1960 to 2016 were 537 mm and 10 °C, respectively (Fig. 1). Approximately 80% of the precipitation is concentrated between May and September, with large inter-annual variability. The growing season for most plant species starts in late April and ends by early October. Droughts frequently occur in spring and early summer because there is little precipitation during this period (Liu et al., 2012; Wang et al., 2012). The soil in the study area was loessial soil with the texture of silty loam, consisting of 25% clay (<0.002 mm), 55% silt (0.002–0.05 mm) and 20% sand (>0.05 mm) (Li et al., 2003). The soil is vulnerable to erosion because of weak resistance. The soil in the study area was derived from loess, and the soil depth is usually 50–200 m depending on the topography

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