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Spatio-temporal water uptake patterns of tree saplings are not altered by interspecific interaction in the early stage of a subtropical forest

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ABSTRACT

Complementary resource use has often been claimed to explain positive effects of plant diversity on ecosystem functioning, but the underlying mechanisms of complementarity have rarely been directly quantified in forest systems. The aim of this study was to characterize spatial and temporal water uptake of subtropical tree saplings, to assess the role of interspecific interaction on water uptake patterns and to quantify species niche breadth and overlap. Our experiment comprised two deciduous (*Castanea henryi*, *Quercus serrata*) and two evergreen tree species (*Elaeocarpus decipiens*, *Schima superba*) that were each planted in monoculture and 4-species mixture. We used deuterium-enriched water to trace seasonal water uptake from 5 cm and 20 cm soil depth. *Castanea* exploited predominantly the upper soil (74% of overall tracer uptake across treatments) whereas *Quercus* (50%), *Elaeocarpus* (57%) and *Schima* (62%) tended to use both soil layers more equally. Species identity had an overall significant effect on isotopic enrichment in stem water. There was no effect of species richness: niche breadth and overlap of single species was not affected by interspecific interactions in mixtures. Niche overlap between deciduous species was lowest (74%) whereas the two evergreen species had similar water uptake patterns (91%). According to our results, interspecific competition did not alter water uptake patterns of the studied species during the early phase of forest establishment. Thus, soil water uptake complementarity could only occur through inherent (fundamental) specific differences in water uptake niches based on sapling specialization, while phenotypic adjustments to interspecific interaction or neighbor diversity are less important.

1. Introduction

Water availability is one of the most important factors for plant productivity and nutrient cycling (Chapin et al., 2011). Moreover, seedling establishment and consequently tree species distribution and community organization are strongly affected by temporal and spatial variation in soil moisture at local and regional scales (Engelbrecht et al., 2007). Competition for belowground resources, including water and rooting space, is recognized as a major factor affecting tree growth and survival in dense seedling and sapling communities (Coomes and Grubb, 2000). However, little is known about the spatial and temporal patterns of water uptake by different species and whether water acquisition of individual trees is influenced by the diversity and composition of their local neighborhoods.

Trait divergence (Grime, 2006), e.g. interspecific differences in morphological traits, allow tree species to exploit soil water resources differently. Contrasting trait-mediated water exploitation strategies can promote complementary water uptake by hydrological niche differentiation (Silvertown et al., 2015). Generally, complementary resource acquisition has been recognized as important mechanism which can explain higher efficiency in

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uptake of limiting resources and thus increased biomass production in diverse plant species mixtures (Loreau and Hector, 2001; Cardinale et al., 2012) and lower vulnerability to drought because of more complete soil water utilization (Yang et al., 2011). This would also open management options to use complementary mixtures to improve adaptability to more severe and frequent droughts. Spatial complementarity exists when coexisting species use water resources from different soil layers (tap-rooted vs. lateral root system). For example, water uptake from different soil depths promotes species coexistence in savanna ecosystems (Weltzin and McPherson, 1997; Jackson et al., 1999; Rossatto et al., 2013) and tropical forests (Jackson et al., 1995; Meinzer et al., 1999; Stratton et al., 2000). Most studies have focused on spatial water partitioning whereas tree species differences in temporal water uptake have often been neglected. Temporal complementarity is a result of seasonal variation, e.g. timing of leaf flushing and senescence (Williams et al., 1997), or short-term variation, e.g. stomatal control (Oren et al., 1999; Pataki and Oren, 2003), in plant activity and water utilization among species. For example, in grassland ecosystems species with maximum root activity early in the year coexist with species that are most active in summer (Fitter, 1986; McKane et al., 1990). Thus, according to niche theory spatio-temporal resource partitioning promotes plant species coexistence as different species occupy different resource niches (Tilman, 1982).

Niche differentiation can occur due to inherent differences among species, i.e., different fundamental niche (the niche space occupied by a species under only conspecific competition), or due to phenotypic changes of resource uptake strategies in response to heterospecific neighbors, i.e. differences in realized niche space (the niche space occupied by a species under interspecific competition) (von Felten et al., 2009). Indeed, it has been shown that in the presence of interspecific competitors niche breadths and consequently niche overlap among species is smaller than niche breadth and overlap under conspecific competition (Silvertown et al., 1999; Silvertown, 2004; von Felten et al., 2009). As diverse plant communities should cover ultimately a larger total niche breadth, belowground resources should be exploited more efficiently by complementary resource use in species mixtures – an important mechanism leading to a positive biodiversity-ecosystem functioning relationship (Vandermeer, 1992; Loreau and Hector, 2001). Consequently, increasing plant diversity may also lead to enhanced community water uptake in comparison to monocultures, as shown for example in grassland (Verheyen et al., 2008), greenhouse model systems (De Boeck et al., 2006) and a tropical tree plantation (Kunert et al., 2012). Thereby, the hydrological niche of a plant species may depend on the composition or local diversity of the plant community.

Whereas previous studies have often addressed water uptake related to tree species identity (e.g. Xu et al., 2011; Yang et al., 2015), water uptake strategies of coexisting tree species planted at different levels of diversity have been scarcely elucidated. The humid subtropics represent a global hotspots of woody plant diversity, particularly in Southeast China with similar proportions of evergreen and deciduous tree species (Wang et al., 2007; Bruelheide et al., 2011). But despite the high tree diversity little is known about species coexistence related to spatial and temporal resource partitioning in the humid subtropics (Nie et al., 2011). In particular, the importance of niche differentiation for species coexistence during forest regeneration with tree saplings as the demographic bottleneck is still poorly understood (Rother et al., 2013). Thus, there is a fundamental need to measure directly resource partitioning to evaluate the importance of resource niche differentiation for recruitment success (Clark et al., 1999). Therefore, we focus on tree saplings as trees at early developmental stage are usually most vulnerable to low water availability because of their shallow root system and low non-structural carbohydrate reserves (Niinemets, 2010; Anderegg and Anderegg, 2013; O'Brien et al., 2014).

To reveal belowground multidimensional resource use, i.e. the spatial and temporal uptake of different nutrients and water, stable isotopes have become a powerful tool as they allow tracing of the flow of elements in biological systems (Adams and Grierson, 2001). In particular, stable isotopes allow the direct testing of resource partitioning, while considering root activity, instead of relying on indirect methods such as comparing biomass production or root depth in monoculture and mixture (Bachmann et al., 2015). Because in terrestrial plants no fractionation commonly occurs during water uptake and transport in stem vessels, the isotopic signature of xylem water reflects the isotopic signature of the plant water source, which can be used to infer soil water uptake patterns (Ehleringer and Dawson, 1992; Dawson et al., 2002). Often the natural abundance of deuterium (^{2}H or D) or oxygen-18 (^{18}O) is used to elucidate water uptake from different soil depths or rain events as well as water partitioning among plant individuals or growth forms (Jackson et al., 1995; Meinzer et al., 1999; Meißner et al., 2012; Rossatto et al., 2013; Bertrand et al., 2014). If only weak or no natural isotopic soil gradients exist, application of enriched tracer solutions, e.g. D_2O, by injection into the soil matrix (Plamboeck et al., 1999) or surface irrigation (Moreira et al., 2000; Sternberg et al., 2002) is best suited to trace water uptake from distinct soil layers. Although the deuterium tracer technique is not aimed at determining absolute plant water use (i.e., it does quantify on its own the total amount of water transpired by the plant), it allows identifying the relative differences in water uptake among species (Schwendenmann et al., 2010). However, most studies that have adopted the tracer injection technique considered only one soil layer and point of time.

Using the tracer injection technique, we examined spatial and seasonal water uptake patterns of four tree species at sapling stage in monoculture (fundamental niche) and mixture (realized niche) in subtropical East China. Based on phenology and natural abundance we selected two deciduous (*Castanea henryi*, *Quercus serrata*) and two evergreen (*Eleaocarpus decipiens*, *Schima superba*) species from the local species pool. We hypothesized that (i) spatial and temporal water uptake patterns of tree saplings are related to species identity and phenology and that (ii) interspecific competition induces adaptive shifts in water uptake patterns of individual species. Finally, we aimed at determining the hydrological resource-based niche breadth, as well as niche overlap between species, to identify those species combinations offering high potential for complementary water resource use.

2. Methods

2.1. Study site

This study was carried out in Jiangxi Province, Southeast China (N29°06.293 E117°55.286). The prevalent climate is subtropical with distinct seasonality: a hot-humid season from April to September and a cool-dry season from October to March (Geißler et al., 2012). Mean annual temperature is 16.7 °C and mean annual precipitation is 1821 mm (Yang et al., 2013) most of which (about 80%) occurs between March and September. The region belongs to the subtropical evergreen broadleaved forest belt, one of the most important and diverse vegetation formations of eastern Asia (Richardson, 1990; Wang et al., 2007). The regional mid-subtropical forest is characterized by a high diversity of woody plant species. For example, 159 tree species from 49 families have been identified in a nearby 24 ha plot (Legendre et al., 2009). Evergreen species are dominant in terms of number of individuals but