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Impact of interspecific interactions on the soil water uptake depth in a young temperate mixed species plantation

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SUMMARY

Interactions between tree species in forests can be beneficial to ecosystem functions and services related to the carbon and water cycles by improving for example transpiration and productivity. However, little is known on below- and above-ground processes leading to these positive effects. We tested whether stratification in soil water uptake depth occurred between four tree species in a 10-year-old temperate mixed species plantation during a dry summer. We selected dominant and co-dominant trees of European beech, Sessile oak, Douglas fir and Norway spruce in areas with varying species diversity, competition intensity, and where different plant functional types (broadleaf vs. conifer) were present. We applied a deuterium labelling approach that consisted of spraying labelled water to the soil surface to create a strong vertical gradient of the deuterium isotope composition in the soil water. The deuterium isotope composition of both the xylem sap and the soil water was measured before labelling, and then again three days after labelling, to estimate the soil water uptake depth using a simple modelling approach. We also sampled leaves and needles from selected trees to measure their carbon isotope composition (a proxy for water use efficiency) and total nitrogen content. At the end of the summer, we found differences in the soil water uptake depth between plant functional types but not within types: on average, coniferous species extracted water from deeper layers than did broadleaved species. Neither species diversity nor competition intensity had a detectable influence on soil water uptake depth, foliar water use efficiency or foliar nitrogen concentration in the species studied. However, when coexisting with an increasing proportion of conifers, beech extracted water from progressively deeper soil layers. We conclude that complementarity for water uptake could occur in this 10-year-old plantation because of inherent differences among functional groups (conifers and broadleaves). Furthermore, water uptake depth of beech was already influenced at this young development stage by interspecific interactions whereas no clear niche differentiation occurred for the other species. This finding does not preclude that plasticity-mediated responses to species interactions could increase as the plantation ages, leading to the coexistence of these species in adult forest stands.

1. Introduction

Current climate change models predict an increase in the intensity and frequency of drought events in central Europe in the coming decades (Christensen et al., 2007). Since one of the key drivers of wood production and sustainability of forest ecosystems is water availability (Breckle, 2002), the expected drier climatic conditions represent a serious threat to their productivity and resilience. To maintain high wood production rates in forest ecosystems in the future, we must elaborate new climate-smart management strategies that are able to counteract the effects of a drier climate on water availability for forest trees.

During the last few decades, accumulated evidence has brought to light beneficial effects of tree diversity on forest ecosystem

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Nomenclature

δ^2H_S	deuterium isotope composition of soil water (‰)	LMA	leaf mass per unit area (g m^{-2})
δ^2H_X	deuterium isotope composition of xylem water (‰)	N%	foliar nitrogen content (%)
$\delta^{13}C$	foliar carbon isotope composition (‰)	P	total daily precipitation (mm day^{-1})
ψ_{pd}	predawn leaf water potential (MPa)	PFT_C	percentage of conifer trees of the surrounding trees (%)
BA	cumulative basal area of the surrounding trees (cm^2)	REW	daily relative extractable soil water (unitless)
D_S	mean soil water uptake depth (cm)	R_G	total daily global radiation (MJ m^{-2})
H	Shannon biodiversity index (unitless)		

functions and services such as productivity (for a review see Scherer-Lorenzen, 2014). The degree to which resources are available for productivity depends on the capacity of a plant to exploit the resources available in the ecosystem – a capacity that can be enhanced by complementarity mechanisms. Indeed, while coexisting species compete with each other for resources, thereby influencing the structure and dynamics of the whole community. Complementarity in mixed species forests implies that co-occurring species exploit distinct ecological niches and can then use the available resources at different places or at different times (Loreau and Hector, 2001). The partitioning of ecological niches in mixed-species forests results either from inherent differences among species or from a differentiation that occurs in species ecological niches due to plasticity-mediated responses (Valverde-Barrantes et al., 2013). The consequence of this so-called niche stratification in mixed-species ecosystems is that during resource-limiting events or periods, competition for resources among species is lessened, and vital functions like transpiration and photosynthesis can be maintained at higher levels than in mono-specific situations.

Complementarity refers to above- and below-ground niche partitioning among species. Above-ground niche stratification in mixed-species forests is achieved because tree species have differing canopy structures; this leads to more efficient light interception in mixed stands than in monocultures (Kelty, 2006). This effect can promote plant photosynthesis and is therefore often cited as one of the main positive mechanisms underlying the higher productivity of mixed-species forested ecosystems (Forrester, 2014). However, higher photosynthesis rates necessarily induce higher transpiration rates in mixed-species communities. This might result in faster exhaustion of soil water levels, which in turn would be detrimental to community productivity. This negative effect can, however, be compensated for by below-ground niche stratification among species. Indeed, tree species also inherently differ in their rooting depth strategies. Some species typically restrict their roots to shallow soil layers while others develop a deep rooting system (e.g. Zapater et al., 2011). Furthermore, despite genetic constraints, plants display plasticity-mediated responses to neighbourhood interactions at below-ground level (e.g. Valverde-Barrantes et al., 2013); these diverging capacities of response to biotic interactions among species also contribute to partitioning in the below-ground space occupancy.

Many studies on rooting depth or root biomass distributions in mixed temperate forests have found evidence of below-ground niche stratification among species (Bolte and Villanuena, 2006; Hendriks and Bianchi, 1995). However, these vertical profiles do not precisely reflect the depth at which a given tree species is able to extract water under limiting soil water conditions. We must know the precise soil water uptake depth for the species coexisting in a given mixed stand to be able to clearly determine whether complementarity for water acquisition is actually occurring.

Assessing the stable isotope (deuterium or oxygen) composition of water in soil and plants is a powerful – and non-destructive – tool to help determine plant water acquisition patterns and complementarity in water use (Ehleringer and Dawson, 1992). Since roots do not fractionate against the heavier isotope (^{2}H or ^{18}O vs. ^{1}H and ^{16}O, respectively) during water uptake (Dawson and Ehleringer, 1993), the instantaneous isotope signature of water in the xylem reflects the mean isotope composition of water extracted from the soil. When a clear vertical gradient in soil water isotope composition exists, the comparison of plant (i.e. xylem) water isotope composition with that of soil water from different soil depths reveals the actual mean soil water uptake depth by a plant. Evaporation at the soil surface and precipitation with different isotopic composition both result in vertical isotope profiles that vary with soil depth (Ehleringer and Dawson, 1992). However, these processes do not always result in simple log-shaped vertical gradients (e.g. Bonal et al., 2000) and this can make interpreting the water uptake depth impossible. However, by applying highly isotopic enriched water onto the soil surface, we can create an artificial vertical gradient of soil water isotope signatures which allows us to accurately identify the depth of mean soil water uptake.

In this study, we followed such an approach. At the end of the 2013 summer in a 10-year-old plantation in central Germany with varying degrees of species mixture, we labelled the superficial soil layers with deuterium enriched water and then tested whether interspecific interactions influenced the soil water uptake depth for four temperate tree species – European beech, Sessile oak, Norway spruce and Douglas fir. We compared how the soil water uptake depth for these species varied according to species diversity, competition intensity and the presence of different plant functional types in their direct neighbourhood (i.e. surrounding trees). We further tested whether variation in soil water uptake depth were related to other functional traits that reflect both the competitive strength of a tree species and its access to soil resources. To do this, we analysed the effect of species interactions on foliar carbon isotope composition (i.e. a proxy for water use efficiency) and total nitrogen content.

2. Materials and methods

2.1. Site description

This study was conducted within the framework of the European FunDivEUROPE project, in a 10-year-old stand originally planted for a biodiversity experiment (BIOTREE-SIMPLEX site) (Scherer-Lorenzen et al., 2007) located near Kaltenborn in Thuringia, Germany (50.24°N, 07.00°E, 325 m a.s.l). The climate is Sub-Atlantic, with mean minimum temperatures of −2 °C and 16 °C during the winter and the summer and mean maximum values of 5 °C and 19 °C during the winter and summer (1997–2013 period). Mean annual precipitation is of 651 mm, rather equally distributed throughout the year. The bedrock, belonging to the lower Buntsandstein formation, consists of sandstone disrupted by some schist/clay layers. More detailed information about the