RESEARCH PAPER

Lack of effect of admixture proportion and tree density on water acquisition depth for European beech (*Fagus sylvatica* L.) and sycamore maple (*Acer pseudoplatanus* L.)

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Abstract

· *Key message* In a mixed, *Fagus sylvatica* L.-*Acer pseudoplatanus* L., young plantation, trees of both species absorbed water from superficial soil layers despite the presence of roots and water in deeper layers. Admixture proportion and tree density were weak predictors of water acquisition depth, as well as fine root vertical distribution, although it might be due to distinct periods of root and isotope investigations.

· *Context* Promoting mixed forests and reducing stand densities have been proposed as effective ways to maintain the productivity of temperate planted forest stands in a changing climate.

· *Aims* The objective of this study was to analyse how stand density and the degree of admixture of European beech and sycamore maple interactively influenced the water acquisition profile of individual trees.

· *Methods* We used a stable isotope (deuterium) approach to determine the profiles of soil water acquisition of both species in a 16-year-old plantation where trees had been planted along crossed gradients of tree density and species proportion. The profiles were then compared with the vertical distribution of fine root of these species in the plantation.

· *Results* All the target trees mostly absorbed soil water from the first few centimetres of soil despite homogenous vertical water availability and the fact that a great part of the fine root biomass was located below 10 cm. Admixture proportion and tree density had negligible effects on soil water acquisition depth.

· *Conclusion* No vertical differentiation of soil water acquisition between the two species was observed, suggesting that mixing these species does not promote reduction of belowground competition for resource acquisition. The vertical distribution of fine root may be a weak predictor of water acquisition depth.

Keywords Belowground competition · Fine root distribution · Niche differentiation · Stable isotope

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1 Introduction

Stand density and admixture both influence forest productivity (Forrester 2014; Liang et al. 2016). Indeed, stand density is the primary factor determining the intensity of inter-tree competition (Weiner and Freckleton 2010); tree mixture is known to affect facilitation and competition among individuals (Ammer 2016); the two processes have been shown to interact: at high stand densities, potential positive interactions in species-diverse ecosystems may be outweighed by resource competition, while little or no species interaction may occur at low densities (Forrester 2014). For these reasons, promoting mixed stands with a controlled density has been proposed as an adaptive management practise to ensure sustainable wood production under future climate conditions in temperate regions (Bravo-Oviedo et al. 2014; Park et al. 2014; Ammer 2016). However, it is not known how density and the degree of admixture in forest stands interactively influence resource acquisition by individual trees.

Fine root development and spatial distribution of roots are modified by the presence (identity, density) of neighbouring plants, even when soil resources are not limited (Cahill et al. 2010; Schmid et al. 2013, 2015). Stand density may thus influence the acquisition of soil resources, including water. In addition, the depth of water acquisition (D_{wa}) is a plastic trait in plants, which responds to both abiotic and biotic conditions such as water availability and the identity of the competitors (Grossiord et al. 2014; Fruleux et al. 2018; Bello et al. 2019; Brinkmann et al. 2019). In some cases, competition reduction among trees may emerge from the vertical or temporal differentiation of soil water sources among species or functional groups (Silvertown et al. 2015). Grossiord et al. (2014) found that the reduction of competition for water acquisition could occur when conifers and broadleaves are mixed because of contrasted water acquisition depth between the two functional groups. Recently, Bello et al. (2019) showed that sessile oak and Scots pine trees changed their water acquisition patterns in mixed stands relative to pure stands, leading to a partial vertical differentiation of soil water acquisition between the species in mixtures. Facilitation processes may also occur. For instance, water transfer from deep to shallow soil layers through the root system of a deep-rooted species ('Hydraulic lift') could provide a water supply for the surrounding shallow-rooted vegetation (Caldwell et al. 1998).

Depth of water acquisition by plants has been intensively investigated through the utilisation of stable isotopes (see Rothfuss and Javaux 2017 for a review). The capacity of a tree to extract water from a given soil volume is usually assumed to be linked to both the presence of available water and of fine roots in the volume. However, vertical distribution of fine roots and water acquisition profiles may diverge for two reasons. First, different types of fine roots show different capacities of water acquisition (Gambetta et al. 2013;

McCormack et al. 2015). Second, mycorrhizal fungal plant partners also contribute to water acquisition and transport, extending the soil volume explored by roots (Lehto and Zwiazek 2011). Thus, contrasted results in the literature make it impossible to conclude whether or not water uptake patterns correspond to the distribution of fine roots in woody species (Green and Clothier 1995; Midwood et al. 1998; Liu et al. 2011; Tang et al. 2018).

This study was conducted in a 16-year-old mixed plantation of European beech (*Fagus sylvatica* L.) and sycamore maple (*Acer pseudoplatanus* L.), which included a double gradient of tree density (number of trees per hectare) and species proportion (percentage of each species). In the plantation, Fruleux et al. (2018) studied the profiles of soil water acquisition of trees of both species for three different mixture levels (nearly pure conditions of beech and of maple, and an even mixture) at the highest plantation density during a summer drought. They showed that, on average, both species extracted water from deeper soil layers when they were in an even mixture relative to nearly pure conditions. However, the difference in water extraction depth was not linearly influenced by the mixture level, demonstrating a complex relation between mixture proportions and depth of water acquisition (D_{wa}). In our study, we performed a water labelling experiment during a wet summer in order to study the interactive effect of mixture and tree density levels on D_{wa}. We determined the water acquisition profiles of trees located along both tree density and species proportion gradients in the plantation and compared them to the fine root vertical distribution of the trees, estimated from soil data collected by Fruleux et al. (2018). Our hypotheses were that (1) the water extraction depth of each species would be affected by tree density and species mixture levels, and (2) vertical water acquisition profiles would be consistent with fine root vertical distribution patterns.

2 Material and methods

2.1 Study site

The plantation is located near Nancy in North-eastern France, in the Haye state forest (48° 38′ 17.18″ N, 6° 8′ 43.03″ E) and is described in Collet et al. (2014). Briefly, in November 1998, a total of 2014 1-year-old nursery-grown seedlings of either sycamore maple or European beech were planted on the central experimental plot (65 × 40 m) following a tree density-species mixture double-clinal design (Fig. 1). The first cline is a tree density gradient, where local tree density varies from 25,000 to 1500 trees ha^{-1}, according to an exponential function of the location on the x-axis. The second cline is a mixing gradient where the local proportion of the two species varies linearly with the location on the y-axis from pure beech to

Fig. 1 Map of the experimental plantation) showing the tree density (x-axis) and species mixture (y-axis) gradients of beech (*Fagus sylvatica* L.) and maple (*Acer pseudoplatanus* L.) in the Haye state forest in North-Eastern France. Each dot corresponds to a living tree (maple in black and beech in grey). Plain lines represent the external borders of the central zone where sampling was conducted. Black asterisks indicate target trees. Black squares and triangles indicate the locations of the soil sampling for isotope analyses 2 days before ($n = 3$) and 6 days after the labelling ($n = 4$), respectively
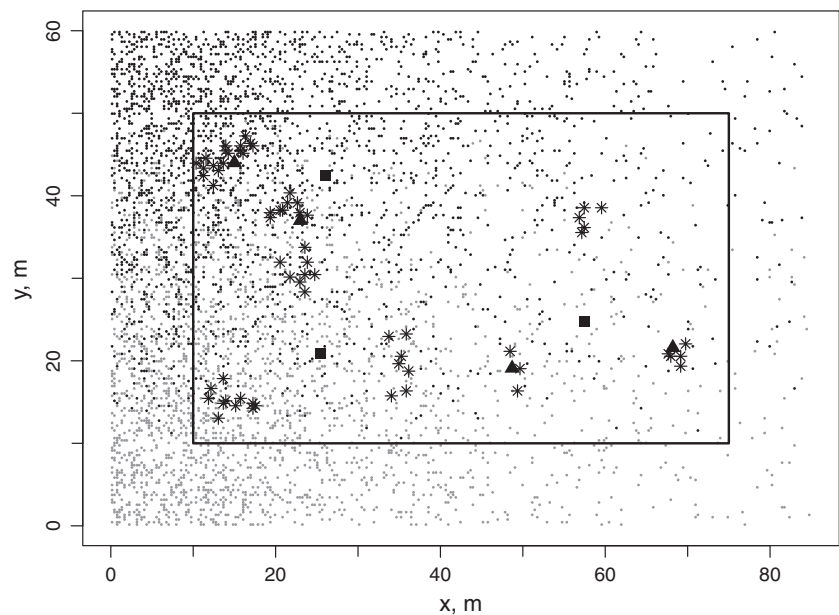
pure maple. Around this central zone, a 10-m-wide buffer zone was planted. The central zone and buffer zone have similar values of tree density and species mixture levels.

The 2014 summer was rather moist in North-Eastern France. Soil water content in the superficial soil layers was high (Fig. 2) and the predawn leaf water potential measured on the selected trees indicated an absence of water stress at the time of the isotope study (above -0.3 MPa, data not shown).

2.2 Selection of trees

The trees were selected according to the following criteria. In order to avoid any confounding effects caused by differing levels of light interception, we excluded all suppressed trees (i.e. neither dominant nor co-dominant). A competition index

Fig. 2 Mean gravimetric soil water content from five soil cores sampled throughout the plantation of the Haye state forest in North-Eastern France at the time of the isotope study in the 2014 summer (for a given depth, horizontal bars represent standard deviations for the five cores)

and an admixture proportion index were calculated for each selected tree, hereafter called 'target tree'. Trees in a 2.5 m radius around each target tree were considered for index calculation. We hypothesised that competition on a target tree would increase with (1) the diameter at breast height (Dbh) of the neighbouring trees, (2) their distance to the target tree and (3) the number of trees in the neighbourhood of the target tree. The Hegyi competition index for trees (H) fitted our assumptions and was calculated as (Contreras et al. 2011):

$$H = \sum_i \frac{d_i}{d \times dist_i},$$

where d_i is the Dbh of the ith neighbouring tree (cm), d the Dbh of the target tree (cm) and $dist_i$ the horizontal distance from the ith neighbouring tree to the target tree (m).

The admixture proportion index (I_{mix}) was calculated as:
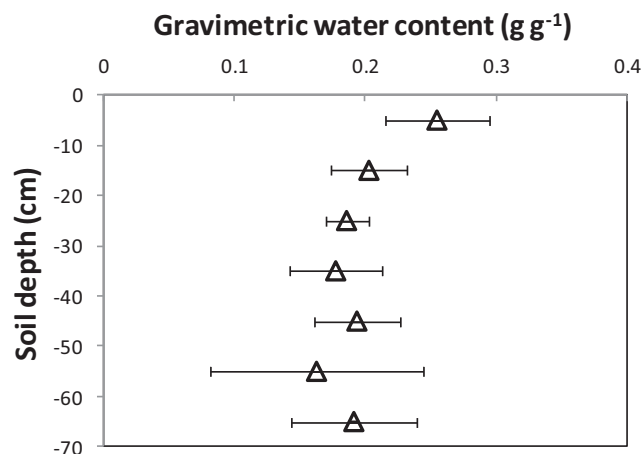
$$I_{mix} = \frac{\sum_i BA_{allos}}{\sum_i BA_{allos} + \sum_i BA_{cons}},$$

where BA_{allos} and BA_{cons} are the basal area of surrounding allospecific and conspecific trees, respectively.

We selected 32 beech trees and 33 maple trees distributed along the H and I_{mix} gradients (Fig. 1, Table 1, Fig. 6 in Appendix). Whenever possible, we selected trees located close to each other to reduce the total surface area to label with enriched deuterium (see Section 2.3). In the end, eight groups of trees were obtained, hereafter referred to as 'subplots' (Fig. 1).

2.3 Deuterium labelling

In summer 2014, a 1-m^2 grid pattern was laid out with pegs and strings in a 2-m radius around each target tree in order to facilitate water labelling. Coarse litter was removed from the

Table 1 Number of target trees (*N*), mean height (*Height*, m), mean diameter at breast height (*Dbh*, cm), mean Hegyi competition index (*H*) and mean mixture index (*I_{mix}*) with standard deviations of the mean for the studied species (beech: *Fagus sylvatica* L. and maple: *Acer pseudoplatanus* L.) in the Haye state forest in North-Eastern France. Letters indicate significant differences between species for each variable

Species	N	Height	Dbh	H	I_{mix}
Beech	32	9.4 ± 0.8 a	7.7 ± 2.4 a	10 ± 6 a	0.5 ± 0.3 a
Maple	33	9.8 ± 0.7 b	7.3 ± 2.6 a	11 ± 7 a	0.4 ± 0.2 a

forest floor before labelling. To create a vertical gradient in soil water deuterium isotope composition ($\delta^2 H$), each 1-m^2 was uniformly watered with 6 L of highly deuterium-enriched water. The $\delta^2 H$ of the prepared solution was 9500 ‰ and was obtained by mixing the water collected from a nearby pond ($\delta^2 H = -39.0$ ‰) with a highly concentrated deuterium solution (99.85 atom%, Eurisotop, France) in 1-m^3 plastic tanks. A total of 420 m^2 of soil were watered, corresponding to 2520 L of the solution.

2.4 Soil and branch sampling

Soil and branch samples were collected in July 2014, both 2 days before and 6 days after labelling. This time lapse allowed the labelled water to drain and a vertical gradient of $\delta^2 H$ to form (Grossiord et al. 2014). The pre-labelling sampling was done so that if a vertical gradient of soil water $\delta^2 H$ already naturally occurred in the plantation, we would be able to use it to analyse the xylem vs. soil water isotope composition data.

Xylem sap was collected from each target tree following Grossiord et al. (2014). We used a manual helical auger to collect soil samples. The soil cores were then split into four 20-cm-long sections for the pre-labelling sample collection ($n = 3$), and seven 10-cm-long sections for the post-labelling sample collection ($n = 4$, collected exclusively in the labelled area) (see Fig. 1 for the location of these soil cores). Soil and branch samples were stored at -20 °C until further processing.

2.5 Soil water acquisition depth

Water was extracted from the stem and soil samples and the $\delta^2 H$ was determined for each water sample, following the method in Grossiord et al. (2014). Graphical inference was used to make a preliminary identification of the main soil water acquisition depth by comparing soil water and xylem $\delta^2 H$; the method assumes that the main depth of soil water being used by a plant is the depth at which the soil water has a similar $\delta^2 H$ to the xylem water (Rothfuss and Javaux 2017). The fraction of water taken up by the trees according to source depth was then estimated with the Bayesian biotracer mixing

model MixSIAR (v3.1.7, 'MixSIAR' R package, Stock et al. 2018). We considered three soil water source depths: 0–10, 10–30 and 30–60 cm. Discrimination data was set to zero because there is no isotopic fractionation during water uptake by trees in temperate forests. We assessed model convergence with Gelman-Rubin and Geweke diagnostic tests. The median values (50% quartiles) were taken as the final predictions. Finally, we used the model developed by Romero-Saltos et al. (2005) and adapted by Stahl et al. (2013) to estimate the mean soil water uptake depth (D_{wa}, cm). D_{wa} was therefore treated as a quantitative variable in our statistical analyses.

2.6 Determining fine root vertical proportions

Soil samples were collected 10 months after the labelling experiment (i.e. May 2015) by Fruleux et al. (2018), down to a depth of 60 cm at 92 locations in the plantation. From our field observations, fine roots were rarely found below a depth of 60 cm. For each location, fine root biomass was estimated in three soil sections (0–10, 10–30, 30–60 cm in depth, corresponding to the soil water source depths used in the MixSIAR model, see Section 2.5). To distinguish the species, we used the near infrared spectroscopy method that exploits the difference in biochemical composition of the fine roots from the two species (see Fruleux et al. 2018 for a precise description of the method). These data from the plantation were only used to estimate from a linear model the vertical distribution of the fine root biomass of each tree selected in this study as follows.

First, the proportion of beech and the competition level among trees around each of the 92 soil core locations were determined within a 2.5-m-radius neighbourhood area. The proportion of beech only was computed following the formula of I_{mix} (see Section 2.2). The competition at soil core locations cannot be quantified using the Heygi index as it has been designed for trees and requires the diameter at breast height of the focal tree. Instead, we used a different index, developed by Bréchet et al. (2011) for soil cores (I_c) as:

$$I_c = \sum_i BA_i \times \left(1 - \frac{dist_i}{2.5}\right),$$

where BA_i is the basal area of the *i*th neighbouring tree (m^2) and $dist_i$ is the horizontal distance from the *i*th neighbouring tree to the soil core location (m).

Second, we wrote a linear model to predict fine root biomass for each species (i.e. beech and maple) and for each soil section (i.e. 0–10, 10–30 and 30–60 cm) from the proportion of beech and the competition index.

Third, we calculated the proportion of beech and the competition index for each target tree location. In order to estimate the fine root biomass for each species and each soil section at the location of each target tree, these values were introduced into the corresponding linear model.

For each location, the predicted values for the fine root biomass of each species in each soil section (0–10, 10–30, 30–60 cm) were summed to obtain the total biomass of the species for the entire soil profile (0–60 cm). Then the fine root biomass of each species in each soil section was expressed as a proportion of the total biomass.

2.7 Statistical analyses

All statistical analyses were performed with the R software (R Development Core Team 2018). To analyse the effects of tree density and mixture on D_{wa} values, we performed multiple regression analyses with linear mixed-effects models ('lme' combined with 'anova.lme', 'nlme' package). The full models included H, $Imix$ and their interaction as explanatory variables. Interactions were removed as they were non-significant. Subplot was set as a random effect. For soil δ^2H, multiple comparisons between soil layers were performed with linear models ('lm' combined with 'anova'). For all analyses, when an effect was significant, we carried out multiple comparisons between treatments with Tukey contrasts ('glht', 'multcomp' package). Normality and homoscedasticity were graphically checked for all models. To compare the proportions of water extracted and the proportions of fine root biomass within each soil section and the two species, we verified normality with a Q-Q plot and homoscedasticity with a F test ('var.test'), then performed Student T tests ('t.test').

3 Results

3.1 Soil water and xylem water isotope composition

Before labelling, soil water δ^2H showed a significant decrease ($P < 0.001$) between the depths of 0–20 and 20–40 cm, from − 53 to − 76‰. There was no significant difference in soil water δ^2H between the depths of 20–40 and 40–60 cm ($P > 0.05$) (Fig. 3c). However, soil water δ^2H was significantly higher at 70 cm in depth than at 30 and 50 cm in depth (mean value: − 63 ‰, $P < 0.01$) (Fig. 3c). Xylem sap δ^2H had a mean value of − 66 ± 3‰ in both beech and maple (Fig. 3a). The C-shape of the vertical gradient prevented precise interpretation of the xylem water isotope data, since a given xylem value could potentially correspond to two soil depth values, highlighting the necessity of the labelling approach.

Labelling induced a strong increase in soil water δ^2H in the upper 30 cm of soil (Fig. 3d). The difference between the value at the depth of 0–10 cm (422 ‰) and the ones from the deeper layers was highly significant ($P < 0.001$) (Fig. 3d). However, below 10 cm in depth, soil water δ^2H was not significantly different among layers ($P > 0.05$) (Fig. 3d). The labelling successfully avoided the presence of a C-shape soil vertical gradient. The xylem sap δ^2H of the selected trees of both species was significantly enriched relative to pre-labelling values, with values ranging from 97 to 339‰ (Fig. 3b).

3.2 Water uptake depth

According to the graphical inference method, the xylem sap δ^2H values of both species were intermediate to the values of soil water δ^2H at the depths of 0–10 and 10–20 cm, indicating that both species absorbed water mainly from these two soil layers (Fig. 3b). Indeed, the MixSIAR model estimated that from 57 to 93% of the water absorbed by each target tree was from the 0–10-cm soil depth (Fig. 4). In agreement with the graphical inference and the MixSIAR model results, mean D_{wa} was − 14 ± 3 cm for beech and − 13 ± 3 cm for maple (Fig. 5). The difference in D_{wa} between the two species was not significant ($P > 0.05$).

3.3 Effects of admixture and tree density on water uptake depth

We tested whether admixture proportion and tree density influenced D_{wa} using the competition index H and the previously calculated admixture proportion index I_{mix}. A significant effect of H on D_{wa} was found for beech only (Table 2, Fig. 5a) with water uptake depth decreasing slightly with increasing competition. However, no effect of I_{mix} or of the interaction between H and I_{mix} was found for either species (Table 2, Fig. 5b).

### 3.4 Correspondence between water uptake and fine root biomass patterns

Water uptake by trees and their estimated fine root biomass decreased significantly with depth for the two species ($P < 0.001$); however, the decrease was less marked for the roots since almost the same proportion of fine root biomass ($\sim 40\%$) was present in the 0–10 cm and 10–30 cm depths (Fig. 4). For each species, a significant difference between the proportion of water extracted and the proportion of fine root biomass was found for all soil sections ($P < 0.001$), thus highlighting a lack of correspondence between the two traits (Fig. 4).

4 Discussion

4.1 Shallow water uptake by trees

In our study, all the target trees took up water mainly from the shallow soil layers (Figs. 3b, 4 and 5). Mean D_{wa} was low for both species and the measured values did not exceed 20 cm. This means that most of the water used for transpiration for both these

Fig. 3 Mean xylem water deuterium isotope composition for beech and maple **a** 2 days prior to labelling and **b** 6 days after labelling, and vertical profile of soil water deuterium isotope composition **c** 2 days prior to labelling, and **d** 6 days after labelling in the 2014 summer in the Haye state forest in North-Eastern France. Shaded coloured areas represent ranges of values between the first and the third quartile for the two species (beech: *Fagus sylvatica* L. and maple: *Acer pseudoplatanus* L.), making it possible to graphically infer the main soil water uptake depth from direct comparison of soil water and xylem sap deuterium isotope composition. Different letters indicate significant differences in deuterium isotope composition values among soil depth levels ($P < 0.05$). No significant difference in xylem water deuterium isotope composition was found between species ($P > 0.05$). Note that the x-axis of **a** and **c** differs from that of **b** and **d**. The dotted line on **b** and **d** serves as a benchmark for zero
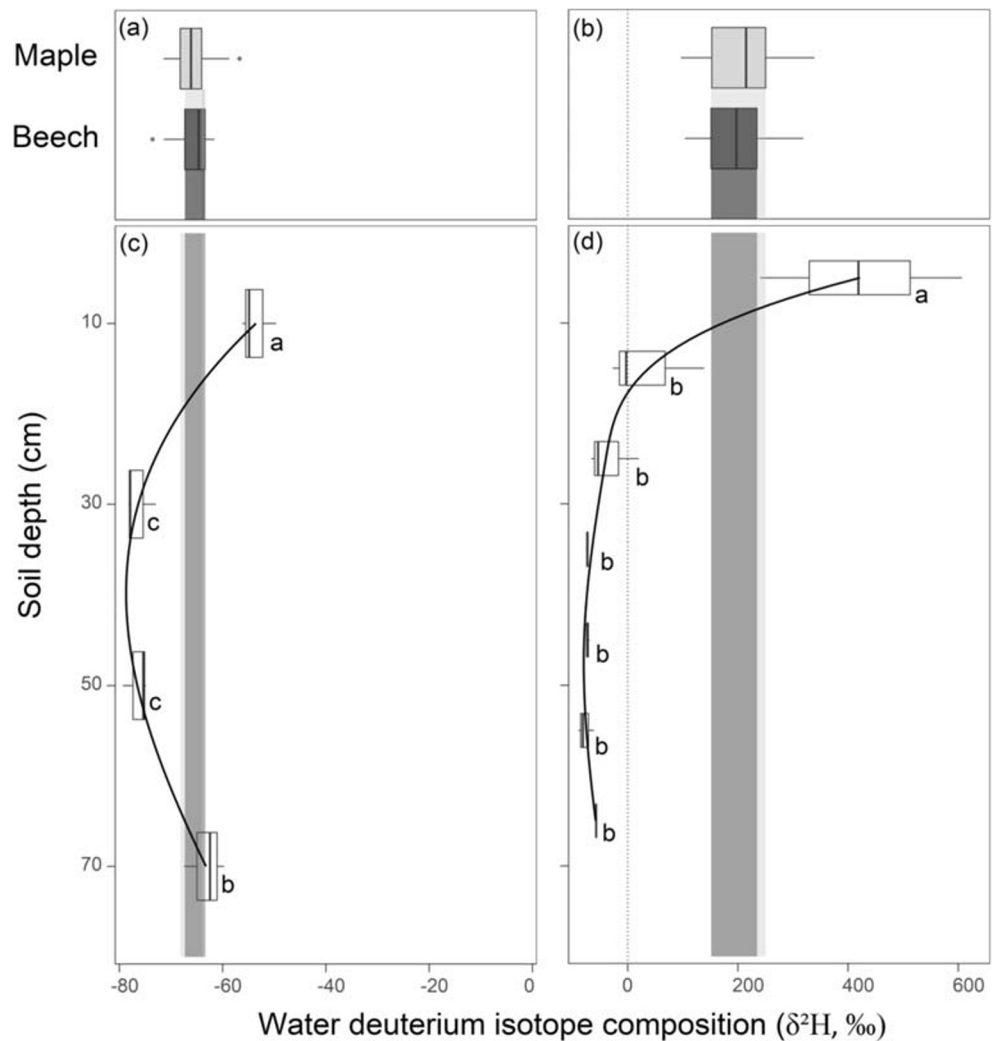

species was absorbed from the shallowest soil layer, as we already found under dry conditions in the same plantation (Fruleux et al. 2018). These results are also consistent with previous findings for European beech, with shallow water acquisition depths (< 0.5-m depth) even during a drought period (Zapater et al. 2011; Meissner et al. 2012; Grossiord et al. 2014; Goisser et al. 2016). Similarly, Brinkmann et al. (2019) showed that the D_{wa} of European beech and sycamore maple always remained above 0.6-m depth, even though these two species were able to shift their water uptake to deeper soil layers when water availability decreased in the topsoil. Other studies showed that the roots of mature beech trees are able to reach much deeper horizons (several meters) to extract water (Packham et al. 2012), and a small amount of deep roots have been found to strongly contribute to water acquisition during severe drought periods (Maeght et al. 2013; Pierret et al. 2016).

While a consistent pattern between the vertical distribution of fine root biomass and water acquisition depth has been found for herbaceous and shrub species (Liu et al. 2011;

Bing et al. 2016), a distinct pattern has been found for tree species (Green and Clothier 1995; Midwood et al. 1998; Tang et al. 2018). In our study, 60% of the fine root biomass was below 10 cm, but only 20% of the soil water used by the studied trees was extracted in these horizons (Fig. 4). This lack of consistency between fine root distribution and water extraction depth was not the result of contrasting water availability among soil layers as our study was conducted during a moist summer with wet soils. However, the possibility still remains that this inconsistency was due to the shallowest soil layer being slightly moister than the deeper soil layers (Fig. 2). Fine roots may also exhibit differences in water uptake capacity among soil depths. Indeed, the fine root morphology, anatomy and water flow resistance do vary with depth in woody species (McElrone et al. 2004; Wang et al. 2015). However, no such information is available for sycamore maple, and the xylem anatomical and hydraulic properties of beech fine roots were not significantly influenced by soil depth in the study conducted by Kirfel et al. (2017). Studies focusing on water

Fig. 4 Mean proportions of water extracted (square) and of proportions of fine root biomass (circle) for each soil section for maple (*Acer pseudoplatanus* L.) (**a**) and beech (*Fagus sylvatica* L.) (**b**) in the Haye state forest in North-Eastern France. Standard deviations are represented by horizontal bars
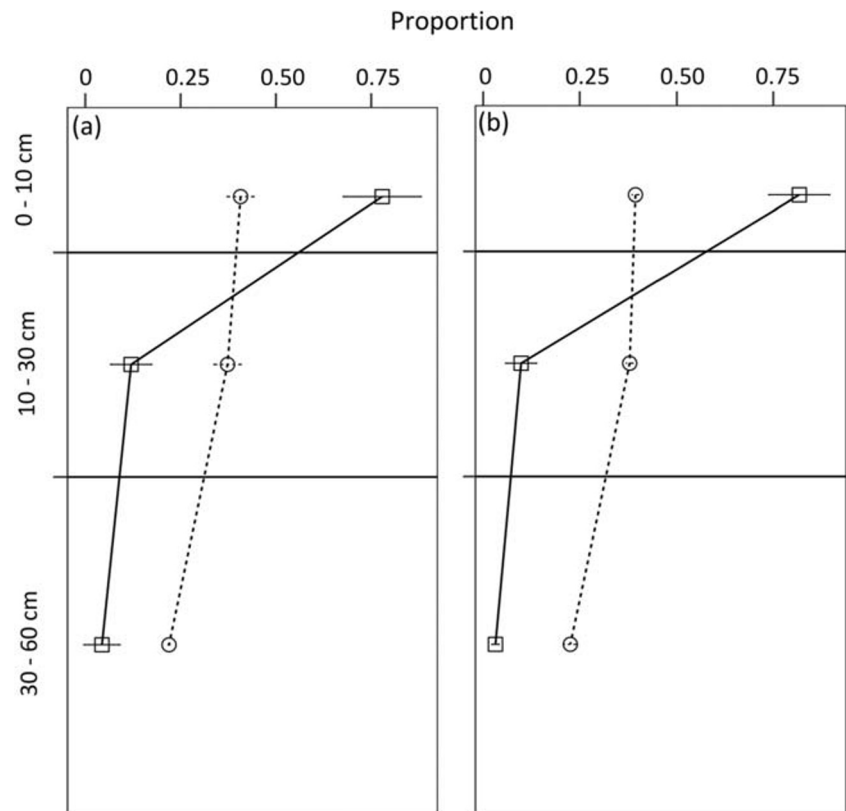
uptake capacity of fine roots with soil depth are therefore needed to better understand these patterns. The lack of correlation between fine root biomass and water source depth could also be explained by the role of associated mycorrhizal fungi in water acquisition (Lehto and Zwiazek 2011). Finally, as fine roots were collected 10 months after the deuterium labelling experiment, the vertical distribution of fine roots may be different to the one present at that time.
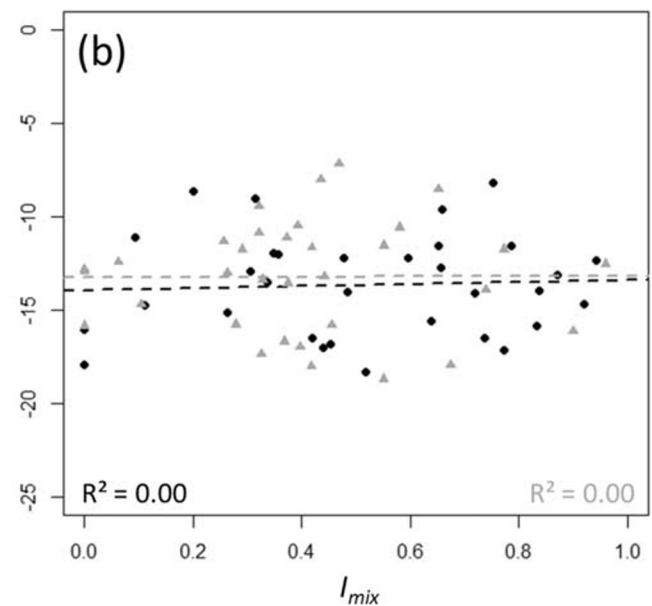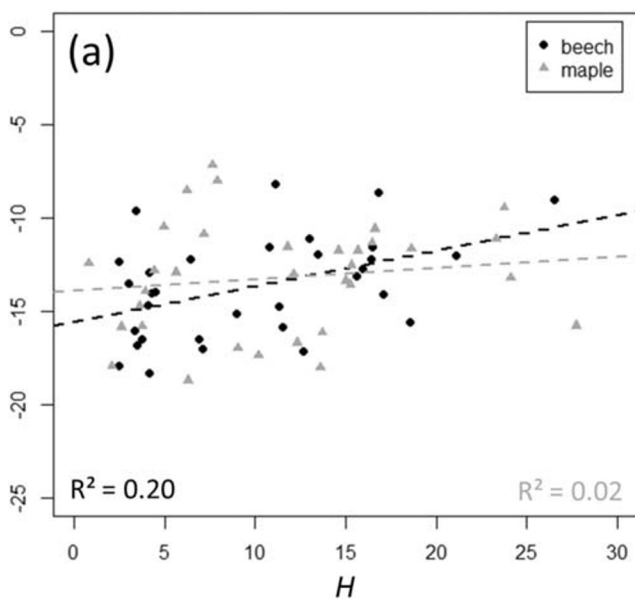
Fig. 5 Soil water uptake depth (D_{wa}, cm) of beech (*Fagus sylvatica* L., in black) and maple (*Acer pseudoplatanus* L., in grey) trees in relation to **a** the Hegyi competition index (H) and **b** a mixture index (I_{mix}) calculated for each target tree in the Haye state forest in North-Eastern France. Dotted lines represent regression lines

Table 2 The influence of the Hegyi competition index (H) the mixture index (I_{mix}) and their interaction on the soil water uptake depth (D_{wa}, cm) of beech (*Fagus sylvatica* L.) and maple (*Acer pseudoplatanus* L.) trees in the Haye state forest in North-Eastern France were tested with linear mixed-effects models. Models without the interaction were also computed, as the interaction was not significant

	df	dendf	F value	P value	sig
D_{wa} of beech					
H	1	23	6.356	0.019	*
I_{mix}	1	23	0.113	0.740	
$H:I_{mix}$	1	23	1.647	0.212	
D_{wa} of beech					
H	1	24	5.725	0.024	*
I_{mix}	1	24	0.056	0.814	
D_{wa} of maple					
H	1	23	0.717	0.406	
I_{mix}	1	23	0.059	0.810	
$H:I_{mix}$	1	23	0.118	0.734	
D_{wa} of maple					
H	1	24	0.765	0.390	
I_{mix}	1	24	0.054	0.820	

Shown are degrees of freedom (df), denominator degrees of freedom (dendf), F value, P value and significance level (*$P < 0.05$)

4.2 Lack of effects from admixture and tree density

For forest ecosystems, the existing literature on the effect of mixture proportion on tree D_{wa} is scarce and has provided contrasting results. Indeed, some studies comparing water uptake patterns of tree species in monospecific and species diverse stands found no significant effect of the presence of allospecific trees (Schwendenmann et al. 2015; Goisser et al. 2016; Trogisch et al. 2016). Other studies found only slight effects. For instance, Meissner et al. (2012) showed that the soil water uptake of ash trees was more homogeneously distributed throughout the soil depth in mixtures than in monospecific conditions. However, in the same study, the vertical soil water uptake of European beech and lime trees did not vary with the identity of neighbouring trees. Grossiord et al. (2014) studied the D_{wa} of four temperate tree species arranged in different mixtures, only the D_{wa} of beech was slightly influenced by its close neighbours and only when these ones were conifers. Finally, some studies carried out during summer drought periods showed deeper water extraction by trees in even mixtures (Fruleux et al. 2018; Bello et al. 2019). The mixture proportion had no effect on D_{wa} in this study, in contrast with previous results in the same plantation (Fruleux et al. 2018). The major difference between the two studies was soil water condition (wet in 2014 and dry in 2015). The lack of correspondence between fine roots and extraction depth we observed was therefore probably related to soil water conditions and thus confirms the major impact of abiotic conditions

on D_{wa} patterns in mixed forests. Particularly, as mixed stands are often more productive than monospecific ones, they also tend to transpire more, leading to drier superficial soil layers (Forrester 2017). This situation may induce deeper soil water uptake during drought events or uptake depth may remain the same if the superficial horizons remain wet enough, as in 2014.

Interestingly, we found that tree density had a slight effect on D_{wa} for beech trees, but not for maples. Beech roots tended to extract water from shallower soil layers when tree density was high. This might be due to increased competition for resource acquisition. Beech root systems are known for their plasticity and exert strong pressure on the root systems of competing trees species (Leuschner et al. 2001; Rewald and Leuschner 2009), particularly in the shallow soil layers that directly receive rainfall and hold nutrients from litter decomposition. However, the amplitude of the change in the D_{wa} of beech trees was less than 10 cm along the density gradient; this amplitude is small and should not be over-interpreted. For maple, the absence of any tree density effect on water extraction depth suggests either weaker root plasticity or a low sensitivity to belowground competition.

4.3 Absence of vertical differentiation for soil water acquisition

Competition reduction through the vertical differentiation of soil water acquisition among species is thought to be a major process allowing species to coexist in mixed forests (Silvertown et al. 2015). In our study, D_{wa} was very similar between the two species, whatever the tree density or species mixture level (Fig. 5). This result is consistent with the patterns found in the same plantation under dry conditions (Fruleux et al. 2018), showing that both species took up water from similar soil layers during both a dry and a wet summer. We clearly show that in this young beech and maple plantation, competition for soil resources is not reduced through vertical differentiation. Neither the identity of competing trees nor the stem density in the immediate surroundings of the target tree was a key factor in modifying water acquisition depth for the two species.

5 Conclusions

In the studied plantation, soil water acquisition depth of both beech and maple was shallow. As previously found for other tree species, fine root vertical distribution might be a poor predictor of the vertical water uptake pattern for these species. In contrast to our expectations, we found no admixture effect on soil water extraction depth for these species; and the degree of competition among trees (i.e. tree density) had only a slight effect on soil water acquisition depth for beech, and none for

maple. Even though species composition and tree density are two important factors that influence forest tree growth and resistance to disturbance, the precise mechanisms that drive these patterns remain rather unclear. We demonstrate here that species composition and tree density levels promoted no reduction in belowground competition for resource acquisition in this plantation and that belowground resource acquisition did not seem to be a major mechanism. Yet, the plantation is still rather young (16 years old) and vertical soil water uptake profiles may vary throughout the growing season and with stand age. Further work analysing seasonal and inter-annual variations in D_{wa} is therefore needed and should include both spring and autumn periods when spatial niche differentiation might occur.

Data availability The datasets generated and/or analysed during the current study are available from the corresponding author on reasonable request.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

Appendix
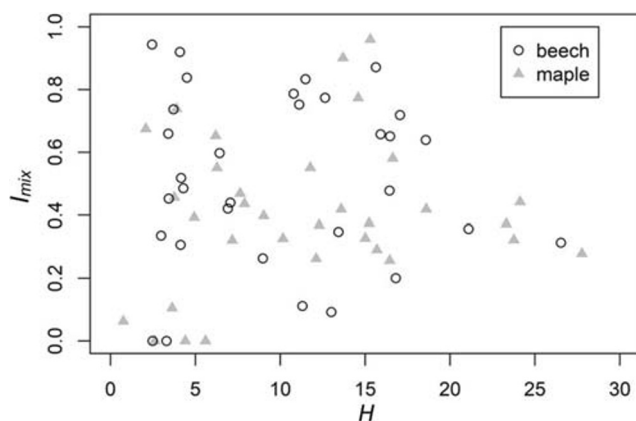
Fig. 6 Mixture index (I_{mix}) as a function of the Hegyi competition index (H) for each target tree (beech: *Fagus sylvatica* L. or maple: *Acer pseudoplatanus* L.) in the Haye state forest in North-Eastern France

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