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ORIGINAL PAPER

Nutrient supply at the local tree level in mixed forests of sessile oak and beech

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Abstract

In mixed-species forests, tree species composition can affect nutrient return through litter fall. This in turn is expected to have an effect on soil available nutrients, which could influence the nutrient status at the local tree level. Using ion-exchange resins, we estimated resin available soil nutrients at two depths beneath target trees of sessile oak and beech in the Belgian Ardennes. First we tested whether resin available nutrients were related to tree nutrition, using foliar nutrient concentrations as a proxy. In a second step, we tested whether local litter fall, through total nutrient return or litter species composition, affected resin available nutrients. In a final stage, we tested the impacts of local stand composition, as an integrated proxy of above- and belowground processes, and compared them to those of litter composition. With the exception of P for oak, nutrient supply was only poorly related to foliar nutrient concentrations for both target species. The effects of litter fall on nutrient supply were driven by litter species composition and not by total nutrient inputs. Litter composition and local stand composition effects were in close agreement. Our results show that nutrient supply to target trees in mixed-species stands is affected by local neighbourhoods, yet to a limited extent. Direct translation of resin available nutrients into foliar concentrations is probably hampered by complex capture patterns.

Keywords Forest nutrition · Nutrient return · Resin · Oak · Beech

Introduction

Tree species composition can affect the supply, capture and use efficiency of different resources like water, light or nutrients (Forrester and Bauhus 2016). Within mixed-species forests, it is therefore crucial to understand these different mechanisms. Changes in resource supply occur in different ways. Nutrient loss can be lower through changes in leaching or erosion (Richards et al. 2010). Nutrients may be added to the system through mineral weathering, throughfall deposition and litter fall (Binkley and Giardina 1998; Augusto et al. 2002; Guckland et al. 2009). Litter fall is an important factor, especially in nutrient-poor forest ecosystems (Attiwill and Adams 1993; Berg and McClaugherty 2014). In mixed forests, specific functional traits of different species have their effect on nutrient supply by influencing different soil properties (Ranger and Nys 1992; Binkley and Giardina 1998; Rothe and Binkley 2001; Augusto et al. 2002; Reich et al. 2005; Jandl et al. 2007; Hobbie 2015; Kooch et al. 2016). Species richness can result in a higher leaf litter production or a higher litter quality, with beneficial results for the chemical properties of the soil (Clark et al. 2001; Reich

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et al. 2005; Vesterdal et al. 2008; Guckland et al. 2009). Total litter production can be higher due to enhanced canopy packing or space filling due to the higher diversity (Jonckheere et al. 2004; Scherer-Lorenzen et al. 2007; Pretzsch 2014; Jucker et al. 2015). This complexity in the canopy is reflected on the forest floor, with a pronounced influence on forest floor quality (Prescott 2002; Marcos et al. 2010). The litter quality, affected by its species composition, has an effect on the soil organic matter, which in turn affects biological soil properties, such as communities of soil invertebrates and microorganisms (Garbeva et al. 2006; Ohta et al. 2014; Brunel et al. 2017). This will affect soil respiration, decomposition, mineralization, redistribution and immobilization of nutrients (Prescott 2005; Prescott and Vesterdal 2013; Yatso and Lilleskov 2016). Mixed leaf litter decomposition can show additive, synergistic or antagonistic effects, with a review summarizing that 50% of all litter mixtures showed a synergistic effect (Liu et al. 2003; Gartner and Cardon 2004; Hättenschwiler 2005; Hättenschwiler et al. 2005; Gessner et al. 2010; Richards et al. 2010). Next to initial litter quality, the decomposition rate can also change with variations in soil moisture, temperature and available carbon, due to species composition (Hobbie et al. 2006; Jonard et al. 2008).

Physical or anthropogenic disturbances have been reported to cause nutrient imbalances in forests in Europe (Reich and Frelich 2002; Jonard et al. 2014). This could result in lower productivity or even higher susceptibility to additional disturbances (Pearson and Palmer 2000; Loladze 2002; Ellsworth et al. 2004; Ainsworth and Rogers 2007; Lukac et al. 2010; Fischer et al. 2012). Mixed-species forests, which have often been observed to be more productive than monocultures, could possibly mitigate these imbalances through improved nutrition (Assmann 1970; Burkhart and Tham 1992; Kelty 1992; Frivold and Kolström 1999). The effect of mixtures on soil nutrient stock is often species specific, for example, soil exchangeable K (in mmol/kg) was shown to be lower under a beech-conifer mixture than under pure beech. However, K (in kg/ha) was higher when oak is mixed with hornbeam and lime (*Tilia cordata* and *Tilia platyphyllos*) instead of beech (Schmidt et al. 2015; Cremer and Prietzel 2017). In that last instance, available soil P (in kg/ha) was also found to be higher (Schmidt et al. 2015). Positive effects of ash litter fall were found on exchangeable Ca^{2+} and Mg^{2+} (in kg/ha) in a mixed deciduous forest (Langenbruch et al. 2012). Available soil P, Ca, Mg (in mg/kg) were also higher under *Alnus glutinosa* in a mixed forest stand in Iran, with higher available K under *Populus caspica* and *Ulmus minor* (Kooch et al. 2016).

Several studies use different methods and units to measure soil nutrient stock and available nutrients. Soil sampling and subsequent extraction of available elements or spectrometric methods are common, but are static and do not account for nutrient release and transport in the soil (Curtin et al. 1987; Abrams and Jarrel 1992). In addition, it may mobilize more nutrients than actually available for plants (Logan and Chaney 1983; Menon et al. 1988). Using ion-exchange resins overcomes this disadvantage while being used in situ, with minimal physical and chemical disturbance of the soil. Longer-term burial of ion-exchange resins in soil can provide information on the dynamics of nutrient supply, which can account for ion diffusion from greater distances, cation exchange and slow release of nutrients from mineralization (Skogley and Dobermann 1996; Qian and Schoenau 2002). A review on techniques for in situ soil water extraction indicated that the use of resins is recommended in studies where a small-scale point measurement of nutrient concentrations is needed, while indicating it is low-effort, low-maintenance, low-cost and feasible for a low temporal resolution of months (Weihermüller et al. 2007).

We therefore used ion-exchange resins to determine resin available nutrients as an index of soil available nutrients at the local tree level in a four-species mixture along a diversity gradient in the Belgian Ardennes. Measurements around oak and beech target trees were made in two different soil layers, right below the organic horizon and in the upper mineral horizon. In the same sites, it has been observed that higher diversity has a positive effect on foliar nutrient concentrations in oak, mostly in relation to a higher diversity in the litter composition (Nickmans et al. 2015). We want to investigate the possible processes behind these observed effects and determine the role played by the distribution of available nutrients in mixed-forest stands. Therefore, our first hypothesis is that, at the target tree level, a (1) higher supply of nutrients in the soil results in higher foliar nutrient concentrations. We hypothesize that this higher availability of nutrients is a result of a (2) higher litter nutrient return and a (3) more diverse litter composition. Finally, we hypothesize that (4) a more diverse local stand composition, as an integrated proxy for above- and belowground processes at the local tree level, will have a positive effect on available nutrients.

Materials and methods

Study area

To be able to make observations at the local tree level, we selected target trees in mature stands of sessile oak and beech. In order to establish a tree diversity gradient, target trees were selected with surrounding trees from one up to four species (oak—*Quercus petraea* (Matt.) Liebl., beech—*Fagus sylvatica* L., birch—*Betula pendula* Roth—and hornbeam—*Carpinus betulus* L.). Selection was based on nearest neighbouring trees and their species composition. To avoid confounding factors due to contrasting site conditions, all target trees were selected on well-drained brown acidic soils (USDA: Dystrochrepts) formed on a loamy stony solifluction sheet in which the weathering products of the bedrock (lower devonian sandstone and schist) were mixed with added periglacial loess. The organic layers were shallow with a thickness between 1 and 5 cm. In the mineral layer, the average stone content was 17% (of the soil volume) in the first 10 cm. In order to best cover the range of the entire diversity gradient, target trees were selected in four different sites in broadleaved mixed-forest clusters in the Belgian Ardennes. These sites had an elevation between 260 and 400 m a.s.l., with slopes not exceeding 5°. Detailed information of the different sites, together with the distribution of target trees along the diversity gradient, can be found in Online Resource 1. In total, we selected 47 oak and 45 beech target trees.

Sampling

Resin available nutrients

Capsules were constructed out of PE tube (diameter 63 mm) and cut into rings of 1 cm thickness. These rings were filled with 34 g of wet Amberlite IRN-150 mixed-bed ion-exchange resin, and closed on both sides with nylon mesh cloth (250 µm) to allow for water percolation. Surrounding each target tree, capsules were placed at four positions at half the crown radius in the four cardinal directions. At each position, two capsules were placed, one just beneath the organic layer, and another at 5 cm below the border of the hemi-organic horizon. We sampled the upper soil horizons since tree species composition effects on nutrient supply are expected to be more pronounced there, especially in the shallow acidic soils of our study sites (Attiwill and Adams 1993; Finzi et al. 1998; Berg and McClaugherty 2014). Also, the majority of active fine roots are located in the topsoil, thereby giving preference to the nutrients available there (Weissen et al. 1990). Both capsules were placed with some horizontal distance to avoid influence of one capsule on the other.

All capsules were placed in March 2015, and recovered in November and December of the same year. Some capsules were lost due to recreation and game in the area (84% recovery rate). After recovery, capsules were placed in a plastic bag and stored at 2 °C. Capsules were washed with deionized water to remove excess soil particles. Afterwards the resins were collected in a plastic bottle with screw cap. For extraction, 100 ml of 4 N HCl was added to the resins and the bottle was shaken during 1 h. Afterwards, the 100 ml of extractant was recovered and refreshed by another 100 ml of 4 N HCl. This was repeated another two times, resulting in 400 ml extractant. By ICP spectrometry (Varian 720 E–S), the extractant was analysed to determine the concentration of Ca, K, Mg, Mn and total P (in mg/l). See Online Resource 2 for a detailed description of the resin capsule construction, placement and laboratory analysis. Concentrations in mg/l were converted to nutrient contents in mg/cm^2 by multiplying by the total amount of extractant and dividing by the contact surface area of the capsule (31.17 cm^2).

Foliar nutrient concentrations

By the use of a hunting gun, leaves of every target tree were sampled from the upper 1/3 part of the crown in July and August 2011. They were subsequently dried for 72 h at 65 °C and weighed. The elemental composition (Ca, K, Mg, Mn and P) was determined by ICP spectrometry after wet digestion with HNO$_3$.

Litter traps

Two perforated plastic boxes (size 60 × 40 cm, height 22 cm) were placed beneath each target tree, at a distance of half the crown radius, in the northeast and southwest orientation. They were installed in September 2014 and fixed to the ground in order to avoid displacement by game. Litter was collected in late December 2014. Traps of two target trees were lost, resulting in measurements for 43 target beech trees instead of 45. Litter from each trap was divided into species and dried at 65 °C for 48 h. This way we could determine total litter mass (L_{tot}, in g/m^2) and litter mass of each species i (L_i). Species proportions (p_{Li}) for each trap were determined by dividing L_i by L_{tot}.

For each species in every trap, leaves were ground and analysed for chemical composition. ICP after wet digestion with HNO$_3$ was used to determine the concentrations of Ca, K, Mg, Mn and P. The species proportions allowed us to determine for each species the total amount of nutrient return in mg/cm^2.

Characterization of stand composition

From November 2014 to January 2015, dendrometric measurements were done in a radius of 18 m surrounding the target tree. Basal area (BA) and crown projection area (CPA) of all trees were measured using a field map data collector (www.fieldmap.cz) and summed to determine local density (BA$_{\text{tot}}$ and CPA$_{\text{tot}}$). Species proportions were calculated as follows:

$$p_{Xi} = {}^{X_i}\!/_{X_{\text{tot}}}$$

With p as the proportion, X indicating BA or CPA and i indicating the species. Using these proportions, diversity was calculated using the Shannon–Weaver diversity index:

$$SW_x = -\sum p_{Xi} * \ln\left(p_{Xi}\right)$$

Which, following Jost (2006), was rescaled using the following equation:

$$\mathrm{div}_X = \exp\left(SW_X\right)$$

Data analysis

Our data were divided over four sites and two different soil layers. As a first exploratory analysis, we tested the effect of site, layer and their interaction using a two-way ANOVA. Both the effects of site and layer showed to be significant for all nutrients which is why we chose to separate the analyses of the two layers (see Online Resource 3). To address the variability between sites, we used mixed model comparison (Burnham and Anderson 2002). For this method, we calculated a null model where only the effect of the site on the response variable in question is included (as a random factor). We then added the explanatory variable, whose effects we wanted to test, to the model and observed whether it improved. To quantify this improvement we determined whether the Akaike information criterion (AIC) decreased significantly when compared to the null model by ANOVA. Detailed inspection of these significant models gives more information on the sign and magnitude of these effects. The significance of the model coefficients was tested by the Satterthwaite approximation and a likelihood ratio test (Satterthwaite 1941; Luke 2017). It is possible that a model had a significant decrease in AIC, without having a significant coefficient. The decrease in AIC gives an indication of which model better represents the data, but it gives no measure of the overall fit of this better model. An explanatory variable has a distinguishable effect when including it in the model shows both a significant decrease in AIC and a significant coefficient for that variable.

Depending on the resolution of the different measurements, model comparison was applied on different scales. The first analysis was at the level of the target tree, since only one measurement of foliar nutrient concentrations was made. Resin available nutrients of all four positions around the target tree were therefore averaged per layer. The analyses concerning litter quality and composition were done at the litter trap level. For the resin available nutrients, an average value of the north and east position and of the south and west position was taken, in order to link them with the values in the northeast and southwest litter trap, respectively. At the trap level, we first tested the effect of litter quality as represented by the litter nutrient content (in mg/cm^2). Secondly, we tested different models studying the effect of litter composition, more specifically its species proportions and diversity.

The final part of the analysis was at the capsule level, where the effect of the surrounding stand composition was tested. We determined that the best distribution of stand composition diversity was based on crown projection area within a 13 m radius around the capsules (see Online Resource 4). At the capsule level, the analysis included an additional step. First it tested whether local density (BA$_{tot}$ or CPA$_{tot}$) showed an effect. If so, local density was included further in the modelling. However, for our data no significant effects of local density were found, so only the effects of species proportions and diversity (based on CPA) were modelled. This allowed us to compare the effects of litter and local stand composition directly, without interference of stand density effects.

Results

Exploratory analysis

Resin available nutrients

On average, resin available nutrient content was higher for the capsules in the mineral soil than in the organic soil, except for P (see Table 1). Differences in resin available nutrients at the different sites can be found in Online Resource 5. A principal component analysis of the resin available nutrients (see Online Resource 6) indicated a correlation of all different nutrients alongside the first principal component, which explained 61.7% of the variance in the organic and 67.4% in the mineral layer. Mainly Ca, Mg and Mn were correlated (more in the organic capsules), with P showing the biggest difference (see Online Resource 6).

Table 1 Minimum (min), mean with standard deviation (SD) and maximum (max) values of resin available nutrient content in the organic and mineral layers (in mg/cm^2) across all sites and target tree species

Layer	Ca	K	Mg	Mn	P
Organic					
Min	0.006	0.023	0.004	0.010	0.001
Mean ± SD	0.251 ± 0.158	0.290 ± 0.161	0.057 ± 0.034	0.098 ± 0.061	0.006 ± 0.005
Max	0.703	0.744	0.156	0.279	0.020
Mineral					
Min	0.009	0.012	0.003	0.002	< 0.001
Mean ± SD	0.312 ± 0.224	0.351 ± 0.238	0.091 ± 0.069	0.126 ± 0.094	0.005 ± 0.003
Max	1.012	1.057	0.280	0.387	0.014

Table 2 Minimum (min), mean with standard deviation (SD) and maximum (max) values of foliar nutrient concentrations (mg/g) of both target species

Target species	Ca	K	Mg	Mn	P
Oak $n = 45$					
Min	2.487	4.038	0.334	1.555	0.753
Mean ± SD	5.166^{a} ± 1.446	6.829^{a} ± 1.605	0.801^{a} ± 0.298	3.069^{a} ± 0.941	1.100^{a} ± 0.170
Max	8.129	11.049	1.414	5.965	1.480
Beech $n = 43$					
Min	2.759	4.668	0.693	1.591	0.737
Mean ± SD	4.716^{a} ± 1.019	6.934^{a} ± 1.156	1.067^{a} ± 0.225	2.837^{a} ± 0.784	1.248^{a} ± 0.249
Max	6.669	10.446	1.696	4.227	2.223

Means without common letters were significantly different between species ($p < 0.05$)

Table 3 Minimum (min), mean with standard deviation (SD) and maximum (max) values of nutrient contents (mg/cm^2) and litter mass (g/m^2) of each species (L_{oak}, L_{beech}, L_{birch}, $L_{hornbeam}$) in the litter traps

	Ca	K	Mg	Mn	P	L_{oak}	L_{beech}	L_{birch}	$L_{hornbeam}$
Min	0.041	0.017	0.006	0.029	0.005	3.861	3.444	0.944	1.361
Mean ± SD	0.242 ± 0.069	0.069 ± 0.030	0.030 ± 0.010	0.149 ± 0.043	0.016 ± 0.006	169.776 ± 74.798	95.327 ± 72.747	11.163 ± 11.695	39.164 ± 35.347
Max	0.465	0.202	0.067	0.255	0.053	346.778	358.028	50.528	145.944

Foliar nutrient concentrations

Comparing the foliar nutrient concentrations between the different target trees, we observed significantly higher concentrations of Mg and P in beech. Other nutrient concentrations were not significantly different between species (see Table 2).

Litter nutrient content

In the different litter traps, we observed that oak is the most dominant species based on litter mass. Birch leaves are represented the least (see Table 3). More detailed data on the nutrient content in the different litter traps is available in Online Resource 7.

Modelling analysis

Relation resin available nutrients—foliar nutrient concentrations

Direct relationships between resin available nutrients and foliar nutrient concentrations were limited, with only an effect of P underneath the organic layer on foliar P concentration in oak (Table 4). In beech, a significant effect of K in the organic soil and of Mn in both organic and mineral soil was found, however, without significant coefficients.

Relation resin available nutrients—litter composition

Using model comparison, we found no relation between litter nutrient content and available nutrients (see Online Resource 9). Looking at the species composition and the diversity of the litter, some nutrients showed significant effects (Table 5). We observed that, for the organic capsules, the highest

Table 4 ΔAIC between null model (only effect of site) and model including resin available nutrients, studying their effect on foliar nutrient concentrations (in mg/g)

Layer	Nutrient	Oak		Beech	
		ΔAIC	Sign	ΔAIC	Sign
Organic	Ca	−5.749		−4.553	
	K	−0.151		−5.221	
	Mg	−3.441		−5.843	
	Mn	−5.712		**2.482****	(+)
	P	**6.135****	++	−4.879	
Mineral	Ca	−5.761		−5.838	
	K	−1.532		**11.492*****	(+)
	Mg	−4.058		−2.472	
	Mn	−5.143		**4.565****	(+)
	P	−2.909		−2.584	

Positive values indicate a significant improvement (*$p < 0.1$, **$p < 0.05$, ***$p < 0.01$) upon the null model. Sign indicates a positive or negative relation and the significance of the coefficient of the model (++$p < 0.05$, +$p < 0.1$, (+)not significant using Satterthwaite approximation and LRT). Detailed information on the significant models can be found in Online Resource 8

Bold values are positive values which show a significant difference ($p < 0.1$) in AIC from the null model

Table 5 ΔAIC between the null model (only effect of site) and a model including litter and stand composition variables (p_L = proportion of litter mass of oak, beech, birch or hornbeam; div_L = diversity based on litter composition; p_C = proportion of crown projection area of oak, beech, birch or hornbeam; div_C = diversity based on crown projection area), studying their effect on resin available nutrients

Layer	Nutrient	p_{Loak}		p_{Lbeech}		p_{Lbirch}		$p_{\text{Lhornbeam}}$		div_L	
		ΔAIC	Sign	ΔAIC	Sign	ΔAIC	Sign	ΔAIC	Sign	ΔAIC	Sign
Organic	Ca	−5.812		−2.014		**8.077*****	(+)	**0.652***	(+)	0.229	
	K	−4.364		−3.965		−4.625		−1.118		−2.224	
	Mg	−7.741		−1.900		**3.278****	(+)	−0.589		−2.535	
	Mn	−4.102		**0.767***	(−)	−0.269		**4.327****	(+)	−3.217	
	P	−1.920		−1.946		−5.634		−5.922		−6.593	
Mineral	Ca	−1.478		−1.291		−5.182		−0.485		**3.589****	(+)
	K	−4.093		−3.571		−3.822		**0.262***	(+)	**15.882*****	++
	Mg	−4.689		−5.859		−4.545		**3.740****	(+)	**16.806*****	++
	Mn	−5.890		−5.500		−4.141		**3.476****	(+)	**8.955*****	+
	P	−5.388		−5.014		−3.014		−5.739		−5.321	

Layer	Nutrient	p_{Coak}		p_{Cbeech}		p_{Cbirch}		$p_{\text{Chornbeam}}$		div_C	
Organic	Ca	−5.345		−3.895		−1.913		−5.119		−1.935	
	K	−2.347		−3.557		−5.206		−2.520		−4.519	
	Mg	−5.012		−4.454		−0.217		−3.613		−3.968	
	Mn	−4.950		**2.252****	(−)	−4.476		−0.033		−5.583	
	P	−5.231		−4.270		−5.796		−5.391		−3.878	
Mineral	Ca	**1.753***	–	−1.214		−5.486		**1.851****	(+)	**5.614*****	(+)
	K	**0.486***	–	−5.834		−5.527		−0.310		**4.847****	(+)
	Mg	**2.274****	–	−5.820		−4.272		**4.890****	(+)	**16.380*****	++
	Mn	−5.448		−2.837		−3.521		−2.432		**0.691***	+
	P	−1.704		−5.654		−3.796		−0.512		−3.761	

Positive values indicate a significant decrease in AIC (*$p < 0.1$, **$p < 0.05$, ***$p < 0.01$) upon the null model. Sign indicates a positive or negative relation with each explanatory variable and the significance of the coefficient of the model (++/−− $p < 0.05$, +/− $p < 0.1$, (+)/(−) not significant using Satterthwaite approximation and LRT). Detailed information on the significant models can be found in Online Resource 8

Bold values are positive values which show a significant difference ($p < 0.1$) in AIC from the null model

improvement in AIC was for the effect of the proportion of birch on Ca. However, looking at the models in detail, the coefficients were shown to be not significant. Significant effects with significant coefficients in the mineral layer were mostly of diversity, as observed for K, Mg and Mn.

Relation resin available nutrients—local stand composition

At the level of each capsule, we observed limited relationships between local stand composition and resin available nutrients in the organic layer (Table 5). Beneath the organic layer, Mn showed a significant improvement in AIC with a higher proportion of beech, but without a significant coefficient. In the mineral layer, we observed a positive diversity effect for Ca, K, Mg and Mn, with only significant coefficients for Mg and Mn. The proportion of oak had a significant negative effect on Ca, K and Mg, with significant coefficients. Conversely, the proportion of hornbeam showed a significant improvement in AIC for Ca and Mg, but without significant coefficients. Diversity showed positive effects, significant for Ca, K, Mg and Mn. However, only the coefficients for the latter two were significant.

Discussion

We studied the effects of species mixtures on resin available nutrients. After checking whether they had a direct effect on foliar nutrient concentrations, we tested whether diversity had an effect on resin available nutrients in the organic or mineral soil, through litter nutrient return and local stand composition. The several aspects we studied, coinciding with the different hypotheses, are described below.

Effects of resin available nutrients on foliar nutrient concentrations

Direct effects of the resin available nutrients on the foliar nutrient concentrations were limited, opposed to our hypothesis (Table 4). The only element for which a comparable result was found was P, where foliar P in oak increased significantly with increasing P content beneath the organic layer. This is comparable to the results from a foliar nutrient study in the same sites, which revealed positive effects of diversity on foliar nutrient concentrations in oak. Using a similar modelling approach, it gave the best model for P when diversity was based on litter. However, the same was found for Ca, K and Mg, of which no effects are found here (Nickmans et al. 2015). For beech, no connections with the foliar nutrient study were found. There will probably be other factors, possibly related to nutrient capture or use efficiency in beech trees, which can influence the effects of litter diversity on foliar nutrient concentrations (Forrester and Bauhus 2016).

Effects of litter quality and litter species composition on resin available nutrients

Logically we expected that with higher litter nutrient content, the resin available nutrients in the soil would increase through nutrient return. However, our results did not support this hypothesis (see Online Resource 9). Since resin capsules are non-discriminative in their source of the nutrients, other sources could have possibly contributed to the observed resin available nutrients (e.g. throughfall, deposition, weathering, root turnover, root exudates,…), complicating their relation with litter nutrient content. Furthermore, interference from other mechanisms could result in nonadditive mixing effects (Bigelow and Canham 2017). For example, temporal differences in nutrient release from litter could change soil availability of nutrients. K and Mg are usually lost rapidly from litter and Ca shows rapid loss through leaching (Kucera 1959; Stachurski and Zimka 1975; McLaughlin and Wimmer 1999; Osman 2013). Mn has been shown to have similar mobility to N, which suggests it is immobilized in the early phases of decomposition with mineralization at a later stage (Melillo et al. 1989; Prescott 2005; Xu et al. 2006).

We did observe significant effects of litter species composition, not its nutrient content, on nutrient availability (Table 5). For the resin available nutrients beneath the organic soil layer, we observed limited effects of species proportions on Ca, Mg and Mn (only based on AIC). These species effects are, however, not a logical result of the higher litter nutrient content of the present species (see Online Resource 7). Next to their positive effects on resin available nutrients, the effects of the proportion of hornbeam on Ca and birch on Mg were also found in the corresponding foliar nutrients. However, they were always accompanied by additional effects of other species or diversity which are absent here (Nickmans et al. 2015). In the mineral layer, we found expected significant diversity effects, also reflected in the significance of their coefficients (except for Ca). The observed effects appear to be limited in magnitude, shown by their low coefficient values (see Online Resource 8). By contrast, it is, however, surprising that no effect of litter nutrient content or composition on P was found, especially since it was the only resin available nutrient beneath the organic layer which was significantly related to on foliar nutrient concentrations (Table 4). P concentrations in the soil solution (which was measured by the resin capsules) are small, since P is strongly bound to the solid phase of soils. This could explain the absence of a litter diversity effect on available P (Parfitt 1979; Achat et al. 2009). Being strongly bound to the soil could also make the temporal resolution of supply and release more complex, which would make the relations between resin available nutrients, litter nutrient content and foliar nutrient concentrations less straightforward.

Species composition effects suggest that mechanisms other than nutrient input through litterfall (see Table 5) are at play. One of these mechanisms could be changes in decomposition rate, which could be affected by a changing litter composition (Liu et al. 2003; Gartner and Cardon 2004; Hättenschwiler 2005; Hättenschwiler et al. 2005; Gessner et al. 2010; Richards et al. 2010). Oak and beech litter are considered low-quality and decomposition rates can improve by the addition of high-quality litter of for example birch (Setiawan et al. 2016). This would explain why the effects of birch or hornbeam, although not significant, were positive where that of beech was negative (see Table 5).

There are several hypotheses on how these synergistic non-additive effects occur. First off, lignin content is an indicator of litter quality which is negatively correlated with decomposition (Meentemeyer 1978; Melillo et al. 1982; Aerts 1997). Hornbeam for example has a lower lignin content (Hobbie et al. 2006) which could change the overall lignin content of a litter mixture, possibly influencing its decomposition rate. Next to that, changes in the soil microclimate could also have a positive influence, as found for a higher mean annual soil temperature (Hobbie et al. 2006; Jonard et al. 2008). The thickness of the forest floor can also have an effect, with higher cellulose mass loss observed in its deeper layers (Piene and Van Cleve 1978; Binkley 1984). Conditions for decomposition can be more favourable at depth since accumulated organic matter can maintain a higher water content, due to less evaporation and runoff combined with higher infiltration (Virzo De Santo et al. 1993; Schume et al. 2004; Ilek et al. 2015). Jonard et al. (2008) stated that this would explain a higher decomposition rate in beech stands, an effect which was not clearly found in our results. The thickness of the organic layer in our study sites is rather small (around 1–5 cm), which could limit these effects.

Changes in the biological properties in the soil can also affect decomposition rates. Nutrient transfer via fungal hyphae could be one possibility, together with positive effects on soil macro- and microfauna abundance (Hättenschwiler 2005). Different litter compositions can influence soil organic matter, which in turn affects biological soil properties such as communities of invertebrates or microorganisms (Garbeva et al. 2006; Ohta et al. 2014; Brunel et al. 2017). For a litter mixture of oak and beech, it was found that the decomposition rate of oak was higher in the mixture, possibly attributed to microorganisms benefitting from a higher P concentration in leaf litter (Jonard et al. 2008). Litter dynamics could also be influenced by its nutrient content, with higher Ca content showing a positive effect on the abundance of earthworms (Hobbie et al. 2006).

Effects of local stand composition on resin available nutrients

In the organic soil layer, only the proportion of beech in the neighbourhood showed a negative effect on Mn content. This was also found in the litter, but with lower ΔAIC, which suggests that the effect found in the litter is a possible remnant of a stand composition effect. Higher canopy cover could result in temperature decreases in the ground climate, affecting decomposition rates (Hobbie et al. 2006; Jonard et al. 2008). Beech trees had the highest crown projection area of all species in these stands, which could explain their negative species effect (Nickmans et al. 2018, submitted). If this was the case, however, it remains surprising that there are no effects found on the other nutrients. Following a similar mechanism, we would expect that higher diversity will have a negative effect due to higher canopy packing and space filling (Pretzsch 2014; Jucker et al. 2015). However, the observed diversity effects were only for the mineral capsules and positive. We can therefore argue that the nutrients in the mineral soil are affected through other factors than solely by the soil microclimate.

For the mineral capsules, the significant models with the proportions of certain species always had a lower ΔAIC than those with diversity. Looking at the correlations between the different species identity and diversity variables (see Online Resource 10), we observed that these identity effects could be a remnant of the diversity effect. For example, a higher diversity will often result in a lower proportion of oak since it is so dominant in our stands. This could result in a positive diversity effect being shown as a negative effect of the proportion of oak. Significance of the coefficients for the diversity effects remained the same except for K. Based on the difference in ΔAIC, the model based on litter composition was better for K and Mn. For Mg, the difference between the two models was smaller, which was also found for the diversity effect on foliar nutrient concentrations (Nickmans et al. 2015). For these nutrients, we can argue that stand composition is to a certain degree linked to litter composition, which could explain its effect. However, for Ca, the model based on stand composition gives the largest ΔAIC, so the litter effect is probably a proxy of the stand composition effect. Foliar leaching of Ca has been shown to be higher in late successional species and dependent on total leaf area (McLaughlin and Wimmer 1999). This could change the supply of Ca to the soil considerably, depending on higher canopy packing with higher diversity. It could also explain the limited (no significant coefficient) effect of hornbeam on Ca. Since the ΔAIC did not differ strongly, we could argue that the effects of both litter and stand composition play a role in their own way. The interaction between the different mechanisms makes a clear distinction of effects difficult.

Conclusion

Outside of an effect of P underneath the organic layer, we observed no effects of resin available nutrients on foliar nutrient concentrations, which was in contrast to our hypothesis. We did, however, observe that effects on nutrient supply, although limited, are not driven by both total nutrient return and litter species composition as hypothesized, but mainly by litter species composition alone. Neighbourhood composition of the forest stand was shown to have comparable effects, indicating its possible use as a proxy for litter species composition while possibly incorporating additional nutrient-supply processes besides litter fall. Alltogether, these findings pinpoint the importance of other factors such as decomposition and nutrient capture in our sites. Although additional research on these factors is needed, the knowledge from this study can inform some decisions regarding management of these types of forests. For the same sites, it has been shown that a large percentage of litter at the local tree level (86% for oak, 77% for beech) originated from the neighbourhood (Nickmans et al. 2018, submitted). Choices made regarding stand composition can therefore strongly influence litter composition at the local tree level. As shown, this will affect soil availability of K, Mg and Mn and to some extent Ca, which in turn could ameliorate foliar nutrient concentrations and possibly mitigate nutrient imbalances. For this type of mixed forest, this knowledge can have practical silvicultural implications, in order to achieve a more desireable litter decomposition. It could inform choices made for specific management strategies, such as planting schemes for afforestation, species selection or tree selection in thinning.

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References

Abrams MM, Jarrel WM (1992) Bioavailability index for phosphorus using ion exchange resin impregnated membranes. Soil Sci Soc Am J 56:1532–1537

Achat DL, Bakker MR, Augusto L et al (2009) Evaluation of the phosphorus status of P-deficient podzols in temperate pine stands: combining isotopic dilution and extraction methods. Biogeochemistry 92:183–200. https://doi.org/10.1007/s10533-008-9283-7

Aerts R (1997) Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. Oikos 79:439–449

Ainsworth EA, Rogers A (2007) The response of photosynthesis and stomatal conductance to rising [CO2]: mechanisms and environmental interactions. Plant Cell Environ 30:70–258. https://doi.org/10.1111/j.1365-3040.2007.01641.x

Assmann E (1970) The principles of forest yield study: studies in the organic production, structure, increment, and yield of forest stands. Pergamon Press, Oxford

Attiwill PM, Adams MA (1993) Tansley nutrient review No. 50. Nutrient cycling in forests. New Phytol 124:561–582

Augusto L, Ranger J, Binkley D, Rothe A (2002) Impact of several common tree species of European temperate forests on soil fertility. Ann For Sci 59:233–253. https://doi.org/10.1051/forest

Berg B, McClaugherty C (2014) Plant litter, 3rd edn. Springer, Berlin

Bigelow S, Canham C (2017) Neighborhood-scale analyses of non-additive species effects on cation concentrations in forest soils. Ecosystems 1–13:1351–1363. https://doi.org/10.1007/s10021-017-0116-1

Binkley D (1984) Does forest removal increase rates of decomposition and nitrogen release? For Ecol Manag 8:229–233. https://doi.org/10.1016/0378-1127(84)90055-0

Binkley D, Giardina C (1998) Why do tree species affect soils? The warp and woof of tree-soil interactions. Biogeochemistry 42:89–106

Brunel C, Gros R, Ziarelli F, Farnet Da Silva AM (2017) Additive or non-additive effect of mixing oak in pine stands on soil properties depends on the tree species in Mediterranean forests. Sci Total Environ 590–591:676–685. https://doi.org/10.1016/j.scitotenv.2017.03.023

Burkhart HE, Tham A (1992) Predictions from growth and yield models of the performance of mixed species stands. In: Cannell MGR, Malcolm DC, Robertson PA (eds) The ecology of mixed-species stands of trees, British Ec. Blackwell Scientific Publications, Oxford, pp 21–34

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, second. Springer, Berlin

Clark DA, Brown S, Kicklighter DW et al (2001) Net primary production in tropical forests: an evaluation and synthesis of existing field data. Ecol Appl 11:371–384. https://doi.org/10.2307/3060895

Cremer M, Prietzel J (2017) Soil acidity and exchangeable base cation stocks under pure and mixed stands of European beech, Douglas fir and Norway spruce. Plant Soil 415:393–405. https://doi.org/10.1007/s11104-017-3177-1

Curtin D, Syers JK, Smillie GW (1987) The importance of exchangeable cations and resin-sink characteristics in the release of soil phosphorus. J Soil Sci 38:711–716

Ellsworth DS, Reich PB, Naumburg ES et al (2004) Photosynthesis, carboxylation and leaf nitrogen responses of 16 species to elevated pCO2 across four free-air CO2 enrichment experiments in forest, grassland and desert. Glob Chang Biol 10:2121–2138

Finzi AC, Canham CD, Van Breemen N (1998) Canopy tree soil interactions within temperate forests: species effects on pH and cations. Ecol Appl 8:447–454. https://doi.org/10.2307/2641084

Fischer R, Waldner P, Carnicer J, et al (2012) The condition of forests in Europe. 2012 executive report. Hamburg

Forrester DI, Bauhus J (2016) A review of processes behind diversity—productivity relationships in forests. Curr For Rep 2:45–61. https://doi.org/10.1007/s40725-016-0031-2

Frivold LH, Kolström T (1999) Yield and treatment of mixed stands of boreal tree species in Fennoscandia. In: Olsthoorn AFM, Bartelink HH, Gardiner JJ et al (eds) Management of mixed-species forest: silviculture and economics. Institute for Forestry and Nature Research, Wageningen, pp 98–117

Garbeva P, Postma J, van Veen JA, van Elsas JD (2006) Effects of agronomical measures on the microbial diversity of soils as related to the suppression of soil-borne plant pathogens. Environ Microbiol 8:233–246. https://doi.org/10.1023/A:1016393915414

Gartner TB, Cardon ZG (2004) Decomposition dynamics in mixed-species leaf litter. Oikos 104:230–246

Gessner MO, Swan CM, Dang CK et al (2010) Diversity meets decomposition. Trends Ecol Evol 25:372–380. https://doi.org/10.1016/j.tree.2010.01.010

Guckland A, Jacob M, Flessa H et al (2009) Acidity, nutrient stocks, and organic-matter content in soils of a temperate deciduous forest with different abundance of European beech (*Fagus sylvatica* L.). J Plant Nutr Soil Sci 172:500–511. https://doi.org/10.1002/jpln.200800072

Hättenschwiler S (2005) Effects of tree species diversity on litter quality and decomposition. In: Scherer-Lorenzen M, Körner C, Schulze E-D (eds) Forest diversity and function. Temperate and boreal systems, ecological. Springer, Berlin, pp 149–164

Hättenschwiler S, Tiunov AV, Scheu S (2005) Biodiversity and litter decomposition in terrestrial ecosystems. Annu Rev Ecol Evol Syst 36:191–218

Hobbie SE (2015) Plant species effects on nutrient cycling: revisiting litter feedbacks. Trends Ecol Evol 30:357–363. https://doi.org/10.1016/j.tree.2015.03.015

Hobbie SE, Reich PB, Oleksyn J et al (2006) Tree species effects on decomposition and forest floor dynamics in a common garden. Ecology 87:2288–2297

Ilek A, Kucza J, Szostek M (2015) The effect of stand species composition on water storage capacity of the organic layers of forest soils. Eur J For Res 134:187–197. https://doi.org/10.1007/s10342-014-0842-2

Jandl R, Lindner M, Vesterdal L et al (2007) How strongly can forest management influence soil carbon sequestration? Geoderma 137:253–268. https://doi.org/10.1016/j.geoderma.2006.09.003

Jonard M, Andre F, Ponette Q (2008) Tree species mediated effects on leaf litter dynamics in pure and mixed stands of oak and beech. Can J For Res 38:528–538

Jonard M, Fürst A, Verstraeten A et al (2014) Tree mineral nutrition is deteriorating in Europe. Glob Chang Biol 21:418–430. https://doi.org/10.1111/gcb.12657

Jonckheere I, Fleck S, Nackaerts K et al (2004) Review of methods for in situ leaf area index determination Part I. Theories, sensors and hemispherical photography. Agric For Meteorol 121:19–35. https://doi.org/10.1016/j.agrformet.2003.08.027

Jost L (2006) Entropy and diversity. Oikos 113:363–375

Jucker T, Bouriaud O, Coomes DA (2015) Crown plasticity enables trees to optimize canopy packing in mixed-species forests. Funct Ecol 29:1078–1086. https://doi.org/10.1111/1365-2435.12428

Kelty MJ (1992) Comparative productivity of monocultures and mixed-species stands. In: Kelty MJ, Larson BC, Oliver CD (eds) The ecology and silviculture of mixed-species forests, forestry. S. Kluwer Academic Publishers, Dordrecht, pp 125–142

Kooch Y, Tarighat FS, Hosseini SM (2016) Tree species effects on soil chemical, biochemical and biological features in mixed Caspian lowland forests. Trees 31:863–872. https://doi.org/10.1007/s00468-016-1511-5

Kucera CL (1959) Weathering characteristics of deciduous leaf litter. Ecology 40:485–487

Langenbruch C, Helfrich M, Flessa H (2012) Effects of beech (*Fagus sylvatica*), ash (*Fraxinus excelsior*) and lime (*Tilia spec.*) on soil chemical properties in a mixed deciduous forest. Plant Soil 352:389–403. https://doi.org/10.1007/s11104-011-1004-7

Liu W, Fox JED, Xu Z (2003) Litterfall and nutrient dynamics in a montane moist evergreen broad-leaved forest in Ailao Mountains, SW China. Plant Ecol 164:157–170

Logan TJ, Chaney RL (1983) Metals. In: Page AL, Gleason TL, Smith JE et al (eds) Utilization of municipal wastewater and sludges on land. University of California, Riverside, pp 235–326

Loladze I (2002) Rising atmospheric CO2 and human nutrition: toward globally imbalanced plant stoichiometry? Trends Ecol Evol 17:457–461. https://doi.org/10.1016/S0169-5347(02)02587-9

Lukac M, Calfapietra C, Lagomarsino A, Loreto F (2010) Global climate change and tree nutrition: effects of elevated CO2 and temperature. Tree Physiol 30:20–1209

Luke SG (2017) Evaluating significance in linear mixed-effects models in R. Behav Res Methods 49:1494–1502. https://doi.org/10.3758/s13428-016-0809-y

Marcos E, Calvo L, Marcos JA et al (2010) Tree effects on the chemical topsoil features of oak, beech and pine forests. Eur J For Res 129:25–30. https://doi.org/10.1007/s10342-008-0248-0

McLaughlin SB, Wimmer R (1999) Tansley review No. 104 calcium physiology and terrestrial ecosystem processes. New Phytol 142:373–417

Meentemeyer V (1978) Macroclimate and Lignin control of litter decomposition rates. Ecology 59:465–472. https://doi.org/10.1890/08-2294.1

Melillo JM, Aber JD, Muratore JF (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63:621–626. https://doi.org/10.2307/1936780

Melillo JM, Aber JD, Linkins AE et al (1989) Carbon and nitrogen dynamics along the decay continuum: plant litter to soil organic matter. Plant Soil 115:189–198. https://doi.org/10.1007/BF02202587

Menon RG, Hammond LL, Sissingh H (1988) Determination of plant-available phosphorus by iron-impregnated filter paper (Pi) soil test. Soil Sci Soc Am J 53:110–115

Nickmans H, Verheyen K, Guiz J et al (2015) Effects of neighbourhood identity and diversity on the foliar nutrition of sessile oak and beech. For Ecol Manag 335:108–117. https://doi.org/10.1016/j.foreco.2014.09.025

Nickmans H, Jonard M, Verheyen K, Ponette Q (2018) Modelling leaf dispersal and nutrient return in tree species mixtures (submitted)

Ohta T, Niwa S, Agetsuma N, Hiura T (2014) Calcium concentration in leaf litter alters the community composition of soil invertebrates in warm-temperate forests. Pedobiologia (Jena) 57:257–262. https://doi.org/10.1016/j.pedobi.2014.07.003

Osman KT (2013) Forest soils. Springer, Berlin

Parfitt RL (1979) Anion adsorption by soil and soil material. Adv Agron 30:1–50

Pearson PN, Palmer MR (2000) Atmospheric carbon dioxide concentrations over the past 60 million years. Nature 406:695–699

Piene H, Van Cleve K (1978) Weight loss of litter and cellulose bags in a thinned white spruce forest in interior Alaska. Can J For Res 8:42–46

Prescott CE (2002) The influence of the forest canopy on nutrient cycling. Tree Physiol 22:1193–1200. https://doi.org/10.1093/treephys/22.15-16.1193

Prescott CE (2005) Do rates of litter decomposition tell us anything we really need to know? For Ecol Manag 220:66–74

Prescott CE, Vesterdal L (2013) Tree species effects on soils in temperate and boreal forests: emerging themes and research needs. For Ecol Manag 309:1–3. https://doi.org/10.1016/j.foreco.2013.06.042

Pretzsch H (2014) Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. For Ecol Manag 327:251–264. https://doi.org/10.1016/j.foreco.2014.04.027

Qian P, Schoenau JJ (2002) Practical applications of ion exchange resins in agricultural and environmental soil research. Can J For Res 82:9–21

Ranger J, Nys C (1992) Effects of spruce plantation (*Picea abies Karst.*) On the soil function of a previous broad-leaved ecosystem: analytical and experimental investigations. In: Teller A, Mathy P, Jeffers J (eds) Responses of forest ecosystems to environmental changes. Elsevier, London, pp 784–785

Reich PB, Frelich L (2002) Temperate Deciduous Forests. In: Mooney HA, Canadell JG, Munn T (eds) Encyclopedia of global environmental change, vol 2. The earth system: biological and ecological dimensions of global environmental change. Wiley, Chichester, pp 565–569

Reich PB, Oleksyn J, Modrzynski J et al (2005) Linking litter calcium, earthworms and soil properties: a common garden test with 14 tree species. Ecol Lett 8:811–818. https://doi.org/10.1111/j.1461-0248.2005.00779.x

Richards AE, Forrester DI, Bauhus J, Scherer-Lorenzen M (2010) The influence of mixed tree plantations on the nutrition of individual species: a review. Tree Physiol 30:208–1192. https://doi.org/10.1093/treephys/tpq035

Rothe A, Binkley D (2001) Nutritional interactions in mixed species forests: a synthesis. Can J For Res 31:1855–1870

Satterthwaite FE (1941) Synthesis of variance. Psychometrika 6:309–316. https://doi.org/10.1007/BF02288586

Scherer-Lorenzen M, Luis Bonilla J, Potvin C (2007) Tree species richness affects litter production and decomposition rates in a tropical biodiversity experiment. Oikos 116:2108–2124

Schmidt M, Veldkamp E, Corre MD (2015) Tree species diversity effects on productivity, soil nutrient availability and nutrient response efficiency in a temperate deciduous forest. For Ecol Manag 338:114–123. https://doi.org/10.1016/j.foreco.2014.11.021

Schume H, Jost G, Hager H (2004) Soil water depletion and recharge patterns in mixed and pure forest stands of European beech and Norway spruce. J Hydrol 289:258–274. https://doi.org/10.1016/j.jhydrol.2003.11.036

Setiawan NN, Vanhellemont M, De Schrijver A et al (2016) Mixing effects on litter decomposition rates in a young tree diversity experiment. Acta Oecol 70:79–86. https://doi.org/10.1016/j.actao.2015.12.003

Skogley EO, Dobermann A (1996) Synthetic ion-exchange resins: soil and environmental studies. J Environ Qual 25:13–24

Stachurski A, Zimka JR (1975) Leaf fall and the rate of litter decay in some forest habitats. Ekol Pol 23:103–108

Vesterdal L, Schmidt IK, Callesen I et al (2008) Carbon and nitrogen in forest floor and mineral soil under six common European tree species. For Ecol Manag 255:35–48. https://doi.org/10.1016/j.foreco.2007.08.015

Virzo De Santo A, Berg B, Rutigliano FA et al (1993) Factors regulating early-stage decomposition of needle litters in five different coniferous forests. Soil Biol Biochem 25:1423–1433

Weihermüller L, Siemens J, Deurer M et al (2007) In situ soil water extraction: a review. J Environ Qual 36:48–1735. https://doi.org/10.2134/jeq2007.0218

Weissen F, Hambuckers A, Van Praag HJ, Remacle J (1990) A decennial control of N-cycle in the Belgian Ardenne forest ecosystems. Plant Soil 128:59–66. https://doi.org/10.1007/BF00009396

Xu X, Shibata H, Enoki T (2006) Decomposition patterns of leaf litter of seven common canopy species in a subtropical forest: dynamics of mineral nutrients. J For Res 17:1–6. https://doi.org/10.1007/s11104-004-8069-5

Yatso KN, Lilleskov EA (2016) Effects of tree leaf litter, deer fecal pellets, and soil properties on growth of an introduced earthworm (*Lumbricus terrestris*): implications for invasion dynamics. Soil Biol Biochem 94:181–190. https://doi.org/10.1016/j.soilbio.2015.11.030