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Effects of neighbourhood identity and diversity on the foliar nutrition of sessile oak and beech

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ABSTRACT

Nutrient imbalances, caused by changing environmental conditions or site conditions, can negatively affect productivity and tree vigour. Mixing could possibly mitigate these effects by influencing foliar nutrition. Therefore we investigated foliar nutrition of sessile oak and beech surrounded by one to three other tree species in broadleaved temperate forests in the Belgian Ardennes. Neighbourhood was determined by measuring basal area, crown projection area and litter proportions for 82 oak trees and 44 beech trees. Using linear mixed models, the hypothesis was tested whether neighbourhood identity (i.e. the presence of a particular species) or diversity (i.e. the number of species present) had a positive effect on foliar nutrition. We found that there was a general positive effect of mixing, although it proved difficult to completely separate the identity effect from the diversity effect. In oak, litter affected Ca, K and P the strongest. Aboveground interactions were also involved, especially for Mg and both ratios (N/P and N/Mg), and for Ca and P in beech. The effects on N nutrition turned out to be difficult to separate from other sources, which also influenced the observed effects for the ratios. Generally it can be concluded that mixing had a positive effect on foliar nutrition, indicating its potential as a measure to mitigate nutrient imbalances, especially in oak stands.

1. Introduction

Forest trees experience changes in foliar nutrient concentrations due to human disturbances and climate change (Reich and Frelich, 2002). Analyzing the nutrient concentrations in foliar tissues can therefore give an indication of the nutritional status of forest trees and additionally assess the site conditions and tree vigour (Marschner, 1995; Ewald, 2005; Mellert et al., 2008). Nutrient imbalances are known to result in a lower productivity and higher sensitivity to additional stress factors such as storms, frost or insect damage (Pearson and Palmer, 2000; Loladze, 2002; Ellsworth et al., 2004; Ainsworth and Rogers, 2007; Lukac et al., 2010; Fischer et al., 2012). In Europe, broadleaved forests are showing a temporal pattern of an increase in foliar nitrogen (N) and a decrease in foliar phosphorus (P), calcium (Ca), magnesium (Mg) and potassium (K) concentrations (Duquesnay et al., 2000; Flückiger and Braun, 1998; Jonard et al., 2014; Luyssaert et al., 2004; Mellert et al., 2004; Thelin et al., 1998). A possible measure to mitigate nutrient imbalances is to create and/or maintain mixed species forests.

Most studies on mixed species forests are focused on productivity. They often observe that mixed species forests are more productive than monocultures (Assmann, 1970; Kelty, 1992). For near-natural mixed stands of oak and beech, performance proved to be superior in the long term, with an exceeded biomass productivity of up to 30% compared to their corresponding pure stands (Kölling and Zimmermann, 2007; Manthey and Leuschner, 2007; Pretzsch et al., 2012, 2013). The beneficial effects of mixing have often been at least partly attributed to an improved nutrition, due to changes in resource availability (Burkhart and Tham, 1992; Frivold and Kolström, 1999; Kelty, 1992). These changes are a result of a more beneficial combination of plant traits (Kelty, 1992). Morphological traits, like crown size or fine root biomass, are closely correlated with resource acquisition, tree fitness and competition and therefore important for productivity. For example, Dieler and Pretzsch (2013) found that beech trees have a higher crown extension when surrounded by oak. Leuschner et al. (2001) found that beech fine roots are more abundant and grow faster in a mixture with oak than in a pure stand. Next to resource acquisition, different tree species also affect the inputs in the soil nutrient supply through differences in litter quality and decomposition rates (Wardle et al., 1997; McTiernan et al., 1997; Binkley and Giardina, 1998; Rothe and Binkley, 2001;

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Richards et al., 2010). For example, decomposition of oak and beech leaf litter, respectively, increased and decreased in mixtures of both species (Jonard et al., 2008).

As opposed to studies of productivity, there have been few studies that compare foliar nutrient concentrations for species in mixtures (Rothe and Binkley, 2001). It remains difficult to draw general conclusions, since different mixtures have their own specific characteristics and responses, depending on species traits, stand composition and site characteristics (Jones et al., 2005). In studies on the admixing of broadleaved trees to conifer stands, foliar concentrations of N, P, K, Ca and Mg in conifers were generally similar between mixed and pure stands (Neft and Stangl, 1985; Heinsdorf, 1997; Rothe et al., 2003). A meta-analysis of different mixtures in plantations showed no trend in foliar N for a species grown in mixtures (without N-fixers) compared to pure stands (Richards et al., 2010). There are, however, studies which showed an increase in foliar nutrient concentrations. For example, *Picea abies* needles improved in P and K nutrition when mixed with beech, birch or oak (Thelin et al., 2002). Similar results were found in a two-species mixture with birch, but with similar foliar concentrations for N, Ca and Mg when compared to pure stands (Brandtberg, 2001).

If species mixtures have a positive effect on nutrient concentrations, they could act as a buffer against possible nutrient deficiencies resulting from changing environmental conditions or inherent site conditions. To our knowledge, there have been no studies dealing with the impact of mixture on tree nutrition in temperate broadleaved forests, excluding studies with N-fixing trees or shrubs (Binkley et al., 1992; Forrester et al., 2007; Oakley et al., 2006; Sayyad et al., 2006). Therefore this study focuses on the foliar nutrient contents (N, P, K, Ca, Mg, N/P, N/Mg) of sessile oak (*Quercus petraea* (Mattuschka) Liebl.) and beech (*Fagus sylvatica* L.) in the Belgian Ardennes, surrounded by up to three other tree species. We hypothesized that:

– The identity of the species surrounding the target trees influenced their foliar nutrition.
– A higher diversity in neighbouring species had a positive effect on foliar nutrition.

2. Materials and methods

2.1. Selection and characterization of the target trees

In order to establish a diversity gradient, target trees of oak and beech with surrounding trees from one up to four species (oak, beech, birch – *Betula pendula* Roth – and hornbeam – *Carpinus betulus* L.) had to be selected. To avoid large variations due to site conditions, these gradients were selected in mature stands on well drained brown acidic soils (USDA: Dystrochrepts). Four different sites were found in broadleaved mixed-forest clusters in the Belgian Ardennes (Table 1).

Target trees were selected based on the nearest neighbouring trees and their species composition. Table 2 indicates how the target trees were distributed over the diversity gradient, with an indication of the present species (target tree and nearest neighbours). For oak 82 target trees were selected, and 44 for beech. After the target trees were selected, they were characterized by measuring their basal area at 1.3 m height (BA_t) and crown projection area (CPA_t).

2.2. Characterization of the neighbourhood

2.2.1. Sampling

The neighbourhood was characterized using two different approaches. The first approach determined the presence and size of the neighbouring species, by measuring the BA (at 1.3 m height) of all trees in a 15 m radius. CPA was only measured for the nearest neighbours, in order to determine a relation between BA and CPA for all species. These relations were included in the Supplementary information A. Based on this relation, the CPA for all the trees in a 15 m radius could be determined. These values were summed to indicate the local tree density surrounding the target tree (BA_{tot} and CPA_{tot}). Additionally, the BA and CPA for every different species in the 15 m radius was determined (BA_i/CPA_i for species *i*).

A second approach was to look at leaf litter composition, since it plays an important role as an input in the nutrient cycle. Litter was sampled at four different positions (N, S, E, W) around each target tree. The sampling distance from the tree was determined by calculating the mean radius (R_0) of the crown from the CPA_t measurement. At these positions, fresh foliar litter (OL_N, age < 1 year) was collected from a surface of 0.25 m^2 (0.5 m $*$ 0.5 m) in the fall of 2011. The litter was dried for 72 h at 65 °C and the total dry mass of litter (L_{tot}) for every target tree was determined. Afterwards the leaves were sorted per species and weighed again (L_i for species *i*).

2.2.2. Expression of neighbourhood

Using the species specific values (BA_i, CPA_i, L_i), species identity variables were calculated as a proportion of each species *i* ($P_{X\text{-}i}$):

$$P_{X\text{-}i} = X_i / X_{tot}$$

With *X* indicating the source of the data, being BA, CPA or L. These values were used to express species identity effects, being effects of the presence, size or litter proportion of a specific species.

Additionally, neighbourhood diversity was determined using a Shannon–Weaver diversity index (SW_X):

$$SW_X = -\Sigma P_{X\text{-}i} * \ln(P_{X\text{-}i})$$

With *X* indicating the source of the data (BA, CPA or L) and $P_{X\text{-}i}$ being the proportions for each species, as calculated for the species identity effect. In order to express this index as a true species diversity variable, conform Jost (2006), it was rescaled using the following equation:

Table 1
Selected characteristics of the four studied sites.

Location		Topography			Species composition	
Administrative forest area	Coordinates	Elevation (m)	Slope (°)	Orientation	Tree species richness	Species in mixture
Marche-en-Famenne	50°27′N 5°6′E	400	5	South-east	3	Oak–beech–birch
Libin	50°06′N 5°1′E	360	5	North	4	Oak–beech–birch–hornbeam
Nassogne	50°06′N 5°3′E	260–300	0	–	4	Oak–beech–birch–hornbeam
Couvin	50°02′N 4°44′E	300	5	East	4	Oak–beech–birch–hornbeam