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Modelling leaf dispersal and nutrient return in tree species mixtures

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ABSTRACT

Litter fall and the associated nutrient return are a significant supply of resources in forest ecosystems. In mixed stands both litter quantity and quality can change under different species compositions. Spatial heterogeneity inherent in mixed stands, defined by stand structure and the present species, will affect the litter composition around a tree of interest. Therefore spatially explicit information will be needed to determine how neighbourhood characteristics in a mixed stand have an effect on litter composition and nutrient return. Using a leaf dispersal model, we determined litter production and leaf shedding parameters of four different tree species. Results from this model indicated that the proportion of litter that originated from the neighbourhood was 86% and 77% at the local tree level for oak and beech respectively. Using this information we found that the presence of accompanying species birch or hornbeam had beneficial effects on local return of N, P, Ca, Mg and Mn. Return of K was optimal with only beech trees in the neighbourhood. These results could give an indication on how to use stand establishment, structure and management to optimize nutrient return.

1. Introduction

Mixed-species stands are being increasingly encouraged by forest management policies because of their expected benefits on productivity, stability and multifunctionality (Assmann, 1970; Bauhus et al., 2010; Gamfeldt et al., 2013; Kelty, 1992; Pawson et al., 2013). Through complementarity interactions, including facilitation and competitive reduction, mixed-species stands may be more productive than their corresponding monocultures (Forrester and Bauhus, 2016). The size of this complementarity effect may however vary strongly according to local site conditions and associated tree species in the mixture (Boyden et al., 2005; Condés et al., 2013; Forrester et al., 2013).

Hence, in nutrient-poor soils, mixing is predicted to increase complementarity if the species interactions improve availability, uptake, or use efficiency of limiting nutrients, assuming no other inherent or mixture-induced constraints (Forrester and Bauhus, 2016). A number of mechanisms may contribute to changes in the nutrient supply of mixtures compared to what would be expected in pure stands (Forrester and Bauhus, 2016; Richards et al., 2010; Rothe and Binkley, 2001). These mechanisms are related to changes in nutrient inputs through litter fall, weathering, atmospheric deposition or N_2 fixation. Additionally, nutrient outputs could be impacted through leaching, erosion or volatilization. Through annual returns, decomposition and mineralization, nutrient cycling as a whole will be affected (Augusto et al., 2002; Binkley and Giardina, 1998; Guckland et al., 2009; Knops et al., 2002; Richards et al., 2010).

Litter fall and associated nutrient return will be an essential factor for input in nutrient-poor ecosystems, which makes these mechanisms more sensitive to neighbourhood effects (Attiwill and Adams, 1993; Berg and McClaugherty, 2014; Bigelow and Canham, 2017; Richards et al., 2010). Increased nutrient supply in mixed-species stands compared to monocultures could be the result of mixing impacts on litter production, nutrient contents in litter fall and/or rates of litter decomposition. Differences in age, height and physiology can result in complementarity in the vertical canopy profile, resulting in higher canopy packing or canopy space filling and subsequent litter production (Jonckheere et al., 2004; Jucker et al., 2015; Pretzsch, 2014; Scherer-Lorenzen et al., 2007). Tree species diversity impacts on decomposition may result from the combination of (i) direct substrate-induced effects related to the combination of litter traits in the mixture, and (ii) indirect effects, arising from modified micro-environmental conditions (Hobbie et al., 2006; Joly et al., 2016; Jonard et al., 2008).

While a considerable amount of studies deal with the impact of tree species diversity on litter decomposition (Gartner and Cardon, 2004; Gessner et al., 2010; Hättenschwiler, 2005; Hättenschwiler et al., 2005;

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Richards et al., 2010), much less attention is given to the spatial redistribution of nutrients associated with leaf dispersal, yet the few available empirical studies show this might have an overwhelming impact on the supply of nutrients to target tree species or individual trees (Ferrari and Sugita, 1996; Gayer, 1886; Hoffmann, 1923; Mettin, 1986; Rothe, 1997; Stone, 1977).

The importance of this redistribution mechanism in supplying nutrients to specific individual trees in a mixture (target trees or species), will however strongly depend on stand structure, including vertical and horizontal patterns of tree arrangement, leaf shedding patterns and relative nutrient concentrations in the leaf litter fall of the component tree species. Under given wind conditions at the time of dispersal, mechanistic models of leaf dispersal show that height of release, crown size and leaf fall velocity are key tree characteristics affecting leaf dispersal. So, in addition to tree spatial arrangement, any difference in tree size distribution (diameter, height) and/or allometries between species, will strongly affect the dispersal pattern. Differences in leaf fall phenology between species may also shape contrasting leaf dispersal patterns due to different wind conditions and/or sheltering effects (Jonard et al., 2006).

On the other hand, nutrient concentrations in leaf litter fall may differ considerably between species growing on similar site conditions, as a result of different requirements, sources of uptake, allocation patterns and resorption efficiencies (Aerts, 1996; Augusto et al., 2002; Binkley, 1996; Killingbeck, 1996; Kooch et al., 2016). In particular, certain species are known to accumulate nutrients in their leaves, and are for that reason managed by forest practitioners as accompanying tree species. For instance, birch (*Betula pendula* Roth) and hornbeam (*Carpinus betulus* L.) frequently grow next to beech (*Fagus sylvatica* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.) trees in broadleaved stands growing on acid soils.

Here our focus is to quantify the local nutrient supply resulting from leaf litter fall in mixed-species stands. Low-elevation mixed broadleaved forests growing on acid soils were used as model ecosystems. In those forests, sessile oak and beech are the dominant species important for silviculture, while birch and hornbeam are accompanying species. We first calibrated an existing ballistic dispersal model (Jonard et al., 2006) for all four tree species from leaf litter traps spread over the stands. We then quantified the proportion of litter originated from the neighbourhood for the target oak and beech trees. Finally, we ran a series of simulations to further test the influence of contrasting neighbourhoods on litter fall and nutrient return at the local tree level.

We hypothesize that:

(i) species specific tree properties have major impacts on litter dispersal patterns
(ii) neighbouring trees have a strong influence on litter species composition at the individual tree level.
(iii) litter species composition strongly affects nutrient return at the individual tree level

The information gained from this study will be beneficial in understanding the driving factors of nutrient return in these mixed stands on poor acid soils. The use of a mechanistic model gives us the possibility to generalize our results, and possibly determine appropriate management strategies in mixed stands to optimize functioning and productivity.

2. Material and methods

2.1. Study area

We selected four different sites in the Belgian Ardennes in mixed broadleaved forests with one up to four species (sessile oak, beech, birch and hornbeam). To avoid large variations due to site conditions, all gradients were selected in mature stands on well drained brown acidic soils (USDA: Dystrochrepts). These sites had an elevation between 260 and 400 m a.s.l., with slopes not exceeding 5°. Since sessile oak and beech were the dominant species in these stands, we defined the areas in which to study leaf dispersal by selecting target trees of these two species. Selection was based on nearest neighbouring trees and their species composition. Detailed information of the different sites together with the distribution of target trees along the diversity gradient, can be found in Appendix A. In total we selected 47 oak target trees and 43 beech trees.

2.2. Litter sampling and analysis

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. A total of 180 litter traps were installed in September 2014 and fixed to the ground in order to avoid displacement by game. Litter traps were emptied in late December 2014, with only one trap that was damaged and unusable.

Litter was divided into species for each trap and dried at 65 °C for 48 h. This way we could determine total litter fall (g/m^2) and species proportions. For each species in every trap, leaves were ground and analysed for chemical composition. C and N concentration were measured using a Flash Analyzer and ICP (after wet digestion with HNO_3) was used to determine the concentrations of P, K, Ca, Mg and Mn. The species proportions allowed us to determine the total amount of nutrient return (in mg/m^2) in each trap.

2.3. Characterization of stand composition for use in the model

For a subset of 30 target trees (19 oak and 11 beech), which best represented the diversity gradient for oak and beech, we measured all trees (including the target tree) in a 30 m radius. Measurements were done from November 2014 to January 2015. Measured variables for every tree were circumference at 1.3 m height, crown projection area, total height, height of the crown base and height of maximum crown extension. A summary of all measured variables is included in the Supplementary information (Appendix B). The position of each tree and its crown projection area were measured using a FieldMap system (www.fieldmap.cz).

2.4. Modelling litter biomass and nutrient return

Based on the measurements of the litter biomass and stand composition, we created a separate dataset for all four species, both the target (oak and beech) and accompanying species (birch and hornbeam). This dataset contained the litter biomass for that species in every trap in every site, with the measured trees of that species surrounding the tarp and their properties. For each species dataset, we determined a separate leaf dispersal model. We used a ballistic leaf dispersal model, as proposed in Jonard et al. (2006). This model calculates the litter production Q_j (in grams per year) of a single tree by an allometric equation:

$$Q_j = \alpha \times (R_j \times circ_j)^{\beta} \tag{1}$$

With α and β as model parameters, $circ_j$ the circumference of a tree j at 1.30 m height and R_j the crown-to-stem diameter ratio (calculated from the circumference and crown projection area). R_j was only included for oak ($R_j = 1$ for all other species) since its litter production is strongly dependent on its competitive status compared to the other species (Jonard et al., 2006). Tree-level litter production Q_j was then multiplied by the probability density of the litter shedding at a given position i. The probability density consists of a first part containing the frequency distribution of wind speeds, described by a Weibull distribution:

$$W(d_{ji}) = \frac{f}{h_{Mj}} \times \frac{\gamma_w}{\beta_{wji}} \times \left(\frac{d_{ji} \times f}{\beta_{wji} \times h_{Mj}}\right)^{\gamma_w - 1} \times \exp\left[-\left(\frac{d_{ji} \times f}{\beta_{wji} \times h_{Mj}}\right)^{\gamma_w}\right] \tag{2}$$

With h_{Mj} as the height of maximum crown extension and d_{ji} the distance between the tree *j* and shedding location *i*. Litter fall speed *f* is determined by collecting fresh litter from each site and dropping and timing the fall from a 3 m height in lab conditions (see Appendix C). Fall speeds were determined as 1.49, 1.24, 1.63 and 1.17 m/s for oak, beech, birch and hornbeam respectively. γ_w is a spreading parameter and β_{wji} a shape parameter as described by the following equation:

$$\beta_{wji} = \beta_{w0} + \beta_{w1} \times \cos(\vartheta_{ji} - \vartheta_d) \tag{3}$$

where β_{w0} and β_{w1} are model parameters and ϑ_d indicates the prevailing dispersal direction from north (in degrees). ϑ_{ji} is the clockwise angle between north and the direction formed by the tree *j* and the shedding location of the trap *i*.

This allows β_{wji} to vary as a function of direction. The second part of the probability density takes into account the distribution of different directions, described by a Von Mises distribution:

$$VM(\vartheta_{ji}) = \frac{1}{2 \times \pi \times I_0} \times \exp[\lambda \times \cos(\vartheta_{ji} - \vartheta_d)] \tag{4}$$

where λ is a parameter characterizing the dispersion around ϑ_d and I_0 is a normalization constant. By combining Eqs. (1), (2) and (4) and summing up the contributions of all trees, we end up with the final model:

$$q_i = \sum_j Q_j \times \frac{f}{h_{Mj}} \times \frac{\gamma_w}{\beta_{wji}} \times \left(\frac{d_{ji} \times f}{\beta_{wji} \times h_{Mj}}\right)^{\gamma_w - 1} \times \exp\left[-\left(\frac{d_{ji} \times f}{\beta_{wji} \times h_{Mj}}\right)^{\gamma_w}\right] \frac{1}{2 \times \pi \times I_0} \times \exp[\lambda \times \cos(\vartheta_{ji} - \vartheta_d)] \times \frac{180}{\pi \times d_{ji}} \tag{5}$$

In Eq. (5), the final term is added to express litter fall in grams per square meter per year instead of grams per square meter per degree per year. For full details on the leaf dispersal model, we refer to Jonard et al. (2006). The parameter set that needs to be estimated are α, β, β_{w0}, β_{w1}, γ_w, λ and ϑ_d. An initial set of parameters was chosen and Eq. (5) was optimized in a stepwise way using non-linear minimization. This method determined the best suited parameter set for each species, with their corresponding standard errors. We used the nlm-function and the R-software for all analyses (R Core Team, 2013).

2.5. Model validation and analysis

Model and parameter validation was done by comparing the predicted values with the observed values for each species separately. As a measure of fit, we performed an ordinary least squares regression between these values. We used the predicted values as the predictor variable and the observed values as the response variable (Piñeiro et al., 2008). Values were log-transformed to give all observations the appropriate weight and correct for heteroscedasticity. If the slope was not significantly different from 1 and the intercept not significantly different from 0, combined with a good R-squared, the prediction was deemed reliable.

To understand the drivers behind the variability in litter fall patterns, we carefully analysed the model outputs and ran simulations on the different parts of the model. Litter production of each species, as calculated by the allometric equation defined by parameters α and β (Eq. (1)), was compared between species. Using the Weibull distribution (Eq. (2)), we calculated the distances at which 9% up to 99% (in steps of 10%) of a tree's litter (with average height of maximum crown extension or each species) was dispersed. To further investigate how the probability of leaf shedding changes with distance, we studied the changes in probability density (as defined in Eq. (5)) for the dominant wind direction (downwind) for a fixed height of maximum crown extension per species (= 12.2 m). Finally, to indicate the changes in the shedding pattern with increasing tree height, we calculated the distance at which 99% of the tree's litter was dispersed, with the 1st quartile, average and 3rd quartile value of the height of maximum crown extension.

2.6. Contributions of neighbourhood

To quantify the contribution of neighbourhood trees to the leaf litter input and nutrient return, we performed an analysis at the target tree level. Around each target tree, we defined a 1 × 1 m grid of points around the subset of 30 target trees. For those grid points that were positioned within the crown projection area of the target tree, we determined litter composition using the leaf dispersal model. By removing the contribution of the target tree, we estimated the amount of litter fall originating only from neighbouring trees. We estimated the percentage P_N of neighbourhood litter q_N around a target tree by the following equation:

$$P_N = \frac{\sum_1^k q_{Nk}}{\sum_1^k q_{Tk}} \tag{6}$$

With q_{Nk} the amount of litter from the neighbourhood and q_{Tk} the total amount of litter, both at grid point *k*. Using this information, we can estimate nutrient return originating from the neighbourhood. First, we calculate nutrient return from the target tree (r_t , in mg/m^2). We observed that nutrient return at the trap level was dependent on total litter biomass (see Appendix D). Therefore we based nutrient return from the target tree on an average value for total litter mass (q_T,in g/m^2). The following formula is used for a given target species *t* (oak or beech), for the species average value of a given nutrient (*nut*, in mg/g):

$$r_t = (1 - P_N) \times q_T \times nut \tag{7}$$

Second, we determine the nutrient return by the neighbourhood (r_N, in mg/m^2), for a chosen species composition with proportions of litter for oak (p_{Loak}), beech (p_{Lbeech}), birch (p_{Lbirch}) and hornbeam ($p_{Lhornbeam}$):

$$r_N = P_N \times q_T \times (p_{Loak} \times nut_{oak} + p_{Lbeech} \times nut_{beech} + p_{Lbirch} \times nut_{birch} + p_{Lhornbeam} \times nut_{hornbeam}) \tag{8}$$

To see how the changes in litter species composition changes nutrient return (dr_t) between a pure stand and a mixed stand, we calculate the following ratio:

$$dr_t = \frac{r_t + r_N}{r_t + r_{Npure}} \tag{9}$$

With r_{Npure} being the r_N value where the proportion of the target species is 100%. We checked the ranges of the proportions in which each species was present in the litter trap, to have an indication of realistic litter mixtures (0–100% for the target species, 0–30% for birch and 0–60% for hornbeam). By changing proportions by 10%, we determined every possible mixture within these proportion ranges (Appendix H). By checking the range of dr_t, we get an indication of the range of change in nutrient return by changes in the neighbourhood.

3. Results

3.1. Composition of the litter traps

3.1.1. Litter fall

The larger part of the litter in the traps consists of oak leaves with the mass of beech leaves being significantly lower (see Table 1). Both accompanying species have an even lower contribution to the litter mass in the traps, with the lowest proportion made up of birch leaves.

Table 1
Minimum (min), mean with standard deviation (stdev) and maximum (max) of litter mass (in g/m^2 year) and species proportions (p_{Loak}, p_{Lbeech}, p_{Lbirch}, $p_{Lhornbeam}$) over all the traps. Litter mass differed significantly ($p < 0.05$) between all four species.

	Oak	Beech	Birch	Hornbeam	Total	p_{Loak}	p_{Lbeech}	p_{Lbirch}	$p_{Lhornbeam}$
Min	3.86	0.00	0.00	0.00	48.67	0.02	0.00	0.00	0.00
Mean	***168.51***	***90.79***	***5.28***	***23.97***	***288.54***	***0.58***	***0.32***	***0.02***	***0.08***
± Stdev	± 75.94	± 75.56	± 9.74	± 33.37	± 59.58	± 0.23	± 0.26	± 0.04	± 0.12
Max	346.78	358.03	50.53	145.94	484.92	1.00	0.97	0.29	0.56

Table 2
Minimum (min), mean with standard deviation (stdev) and maximum (max) values of nutrient concentrations (in mg/g) in each species over all the traps. For a given element, tree species without common letters differ significantly ($p < 0.05$).

Species		C	N	P	K	Ca	Mg	Mn
Oak	Min	466.677	10.605	0.260	1.012	6.246	0.702	2.515
	Mean	^{b}***508.131***	^{a}***14.492***	^{a}***0.475***	^{a}***2.278***	^{c}***8.678***	^{b}***1.055***	^{a}***5.054***
	Stdev	± 11.250	± 1.610	± 0.127	± 0.835	± 1.330	± 0.223	± 1.073
	Max	539.285	19.825	0.810	4.396	12.692	1.591	7.997
Beech	Min	480.998	11.629	0.281	1.294	4.447	0.574	3.184
	Mean	^{b}***506.635***	^{b}***14.968***	^{b}***0.602***	^{b}***2.684***	^{b}***8.224***	^{a}***0.920***	^{b}***5.504***
	Stdev	± 10.981	± 1.500	± 0.177	± 1.003	± 1.843	± 0.204	± 1.189
	Max	536.349	18.454	1.286	5.421	14.051	1.507	8.748
Birch	Min	505.772	16.236	0.503	1.367	5.039	0.634	5.152
	Mean	^{c}***534.024***	^{d}***21.116***	^{c}***0.764***	^{a}***2.310***	^{a}***7.366***	^{a}***0.976***	^{c}***6.214***
	Stdev	± 17.789	± 2.778	± 0.147	± 0.985	± 1.529	± 0.216	± 1.098
	Max	592.999	27.906	1.142	4.794	11.547	1.347	9.109
Hornbeam	Min	457.115	13.486	0.575	1.409	5.039	0.750	3.744
	Mean	^{a}***500.042***	^{c}***18.244***	^{d}***0.825***	^{b}***2.620***	^{c}***8.866***	^{c}***1.286***	^{b}***5.730***
	Stdev	± 13.321	± 2.343	± 0.170	± 0.776	± 1.852	± 0.206	± 1.077
	Max	534.671	23.359	1.208	4.478	15.555	1.663	7.924

Using a two-sample *t*-test, we observed that the litter mass of all the different species was significantly different.

3.1.2. Nutrient concentrations

Looking at the target species we observe that, outside of C, the litter concentrations of every element were significantly different between oak and beech (see Table 2). Beech has the highest average concentration of K of all the species. For the other elements, the accompanying species show the highest average concentrations, with N and Mn in birch and P, Ca and Mg in hornbeam. Of these differences, only P in hornbeam was not significantly different from all other species.

3.2. Model parameterization and predictions

Using non-linear minimization, a set of model parameters and their standard error was determined (see Table 3). Their functions within the model can be found in the different equations under 2.4. Because non-linear minimization forced the calibration into an implausible parameter set for beech, the spreading parameter of the Weibull distribution (γ_w) was fixed to that of hornbeam (1.75) during calibration. This value was chosen due to the fact that the calibration for hornbeam gave the best results initially, and we used the parameter set of hornbeam as an initial parameter set for the calibration of beech.

In the ordinary least squares regression between predicted and observed values (see Table 4 and Appendix E), we observed that the slope is not significantly different from 1 and the intercept not significantly different from 0 for all species, considering the prediction for all species as reliable. The difference between predicted and observed values was smallest in oak ($R^2 = 0.867$), followed by hornbeam ($R^2 = 0.811$), birch and finally in beech. Beech and birch showed a higher variability represented in their lower R^2 value (0.651 and 0.678 respectively). When considering the total amount of litter biomass, we had to omit a low outlier which strongly influenced the regression. Its regression showed a slope significantly different from 1, an intercept significantly different from 0 and a low R^2 value (0.280), which indicates a less reliable prediction.

Table 3
Set of parameters, with their estimates and standard error (SE), obtained by non-linear minimization for each species for the leaf dispersal model. For beech, γ was fixed at 1.75 (see 3.2) so no SE could be calculated.

Parameter	Oak		Beech		Birch		Hornbeam	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
α	6.37	± 5.42	19925.88	± 2524.38	3131.62	± 979.17	16281.03	± 3809.47
β	2.36	± 0.25	1.98	± 0.23	1.06	± 0.67	1.48	± 0.32
β_{w0}	0.85	± 0.04	2.11	± 0.23	0.79	± 0.12	0.82	± 0.07
β_{w1}	0.22	± 0.06	1.68	± 0.37	0.67	± 0.14	0.76	± 0.09
γ	2.37	± 0.23	1.75	/	1.58	± 0.38	1.75	± 0.25
λ	0.66	± 0.21	0.08	± 0.22	0.19	± 0.53	0.29	± 0.26
ϑ_d	44.10	± 12.29	115.74	± 7.78	312.51	± 12.23	92.81	± 4.95

Table 4
Slope, intercept of OLS regression between the logarithms of predicted and observed litter fall values. R^2 only given for OLS regression. Significance of coefficients is indicated as $^{**}p < 0.05$ and $^{*}p < 0.1$. For the slope the significance indicates the difference from 1, for the intercept the difference from 0.

Species	Slope	Intercept	R^2
Oak	0.993	0.033	0.867
Beech	0.856	0.568	0.651
Birch	1.014	−0.026	0.678
Hornbeam	0.920	0.267	0.811
Total	**0.413	**3.338	0.280

3.3. *Drivers of litter fall dispersal*

3.3.1. *Litter production*

We calculated litter production (Eq. (1)) for the actual range of tree circumference present in the study area for each species (see Fig. 1). The crown-to-set diameter ratio (R_j) for oak was taken at 19.5, to assure comparability with Jonard et al. (2006). It must be noted that beech trees shed their leaves further than any other species, and the fixed 30 m radius was not sufficient for the model. In order to assure comparability between species and avoid an overestimation, the litter production parameters (α and β) for beech had to be corrected (see Appendix F). For a circumference smaller than 0.7 m, litter production is similar between beech and hornbeam. Litter production remains lower for oak than for beech over the full range of circumference. Birch shows the lowest production, with only a limited increase with larger circumference.

3.3.2. *Leaf shedding patterns*

The complete leaf shedding pattern of each tree was determined by calculating the distances at which 9% up to 99% of litter (in steps of 10%) was dispersed for each distance (see Fig. 2). As the percentage increases, the distances and surface of litter dispersal becomes larger, with the largest difference in surface between the 89% and 99% surface. All patterns show a clear preference for the dominant wind direction but the orientation of the shedding patterns varies across species, according to their main leaf dispersal direction ϑ_d (Table 3). Especially birch shows a different orientation from the other three species. Oak shows the shortest distances of leaf dispersal, with a more circular dispersal pattern. Apart from oak, all other species show an indentation in their leaf shedding pattern in the opposite of the dominant wind direction. For further investigation, the probability density of leaf shedding for each species in both the downwind and its opposite direction was determined (see Appendix G).

In the dominant wind direction, the probability density over distance (from Eq. (5)) can be compared between species with a fixed height of maximum crown extension h_M (Fig. 3). In this case, the probability for birch is highest close to the tree (higher than the other species). For oak, the probability density shows a peak further away from the trunk, at around 5 m. Beech shows to have lower probabilities overall for this one direction, however it does have a higher probability at further distances (between 25 and 30 m) compared to the other species. The probability of litter fall for oak and birch fell to zero within the 30 m radius around the target tree, however for hornbeam and beech the probability of litter fall was still greater than zero at 30 m from the target tree.

As height of maximum crown extension (h_M) increases, the dispersal distances also increase (see Fig. 4). Beech, with the furthest dispersal distances, shows the strongest increase in shedding area with increasing h_M. Albeit more limited than beech, birch and hornbeam both show dispersal beyond 30 m at higher h_M. Oak, at any height, remains within the 30 m radius for its litter dispersal.

3.4. *Contribution of neighbourhood at target tree level*

3.4.1. *Litter fall*

We determined the percentage of litter fall at the target tree level, originating from only the neighbouring trees. Around oak trees, the minimum, mean and maximum values were 74%, 86% and 98% respectively. For beech trees this was 62%, 77% and 95%. Using a *t*-test, we found that values for beech were significantly lower ($p < 0.05$).

3.4.2. *Nutrient return*

For every possible litter species composition (reported in Appendix H) we calculated the difference in nutrient return between a mixed and

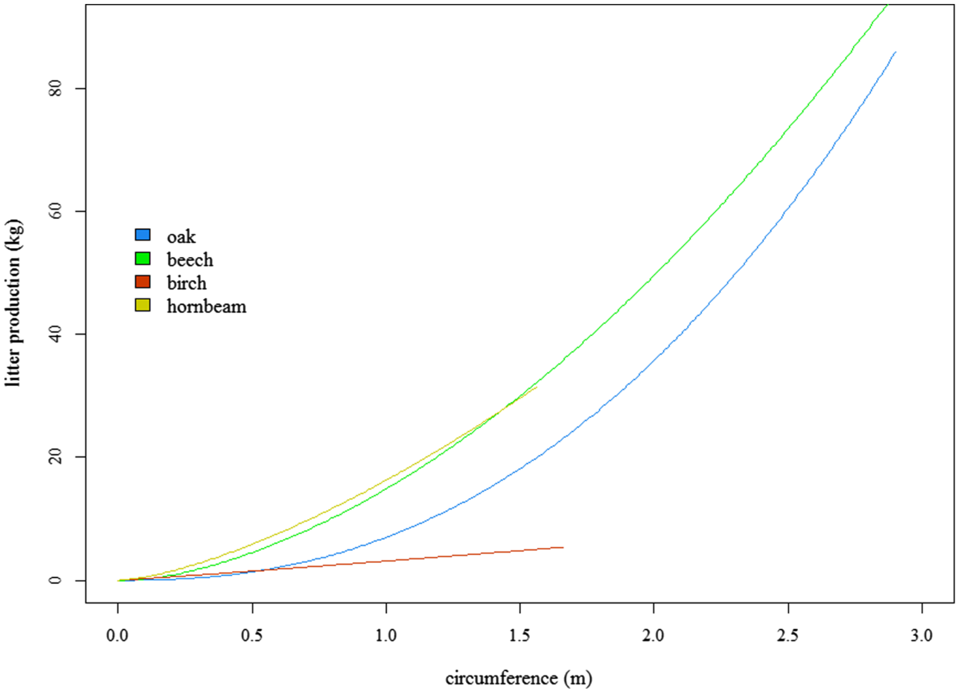

Fig. 1. Litter production based on circumference (circ), as calculated using the α and β parameters. R of oak was taken at 19.5 (cfr Jonard et al., 2006).

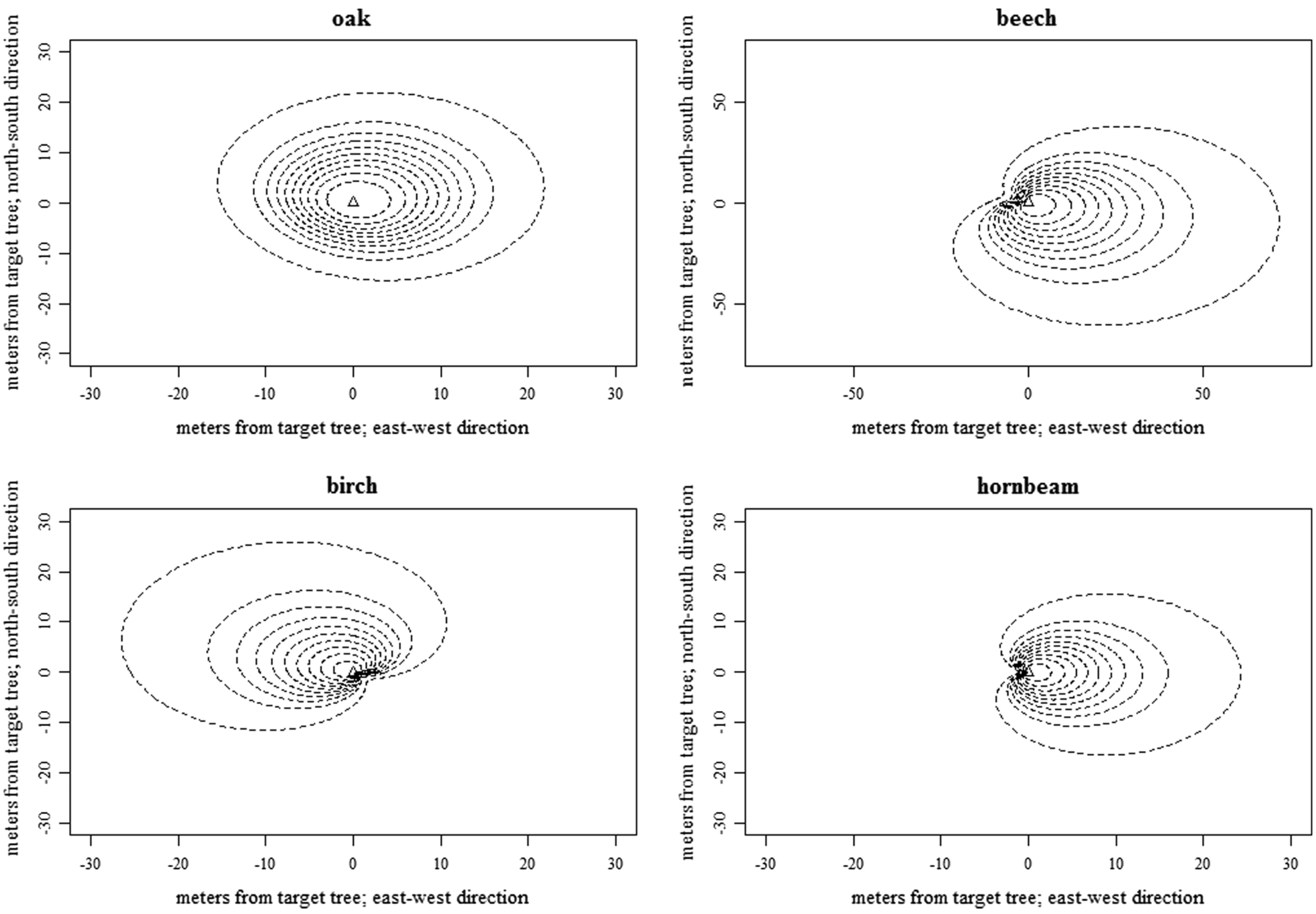

Fig. 2. Shedding surfaces of the different species for which 9 up to 99% (in steps of 10%) of leaf litter is dispersed. Average values for h_{Mj} are used for each species (oak = 16.9 m; beech = 10.1 m; birch = 12.4 m; hornbeam = 7.5 m; Tabel E2).

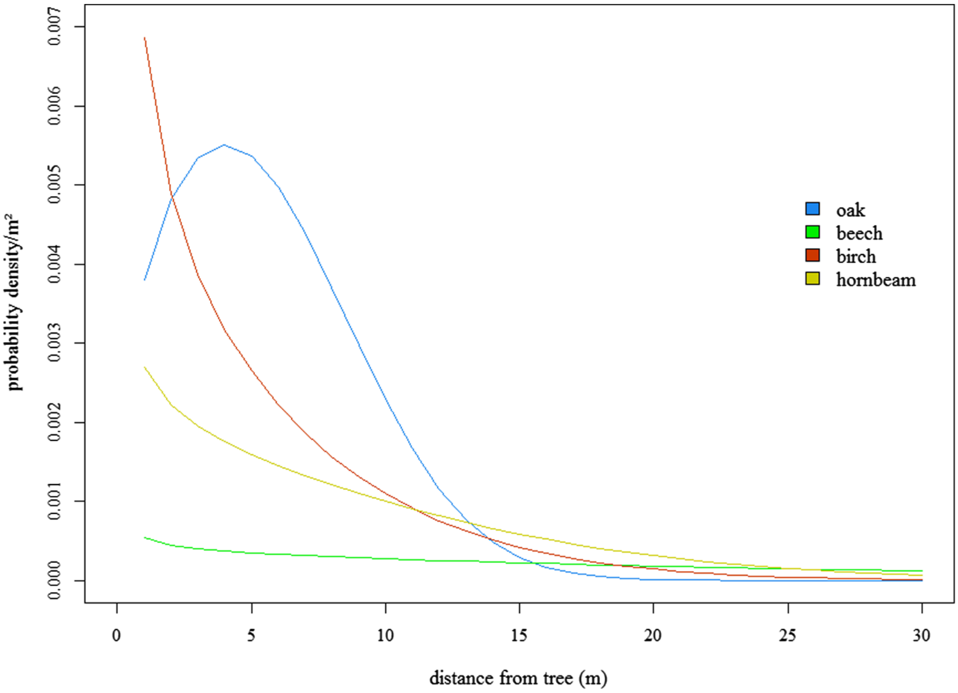

Fig. 3. Relation between the distance from a given position and the probability density per m^2 of a leaf ending up at that position, as described by the dispersal model in Eq. (5) (only in the downwind direction, dominant wind direction θ_d for each species). For comparison, h_{Mj} is fixed at 12.2 m for each species.

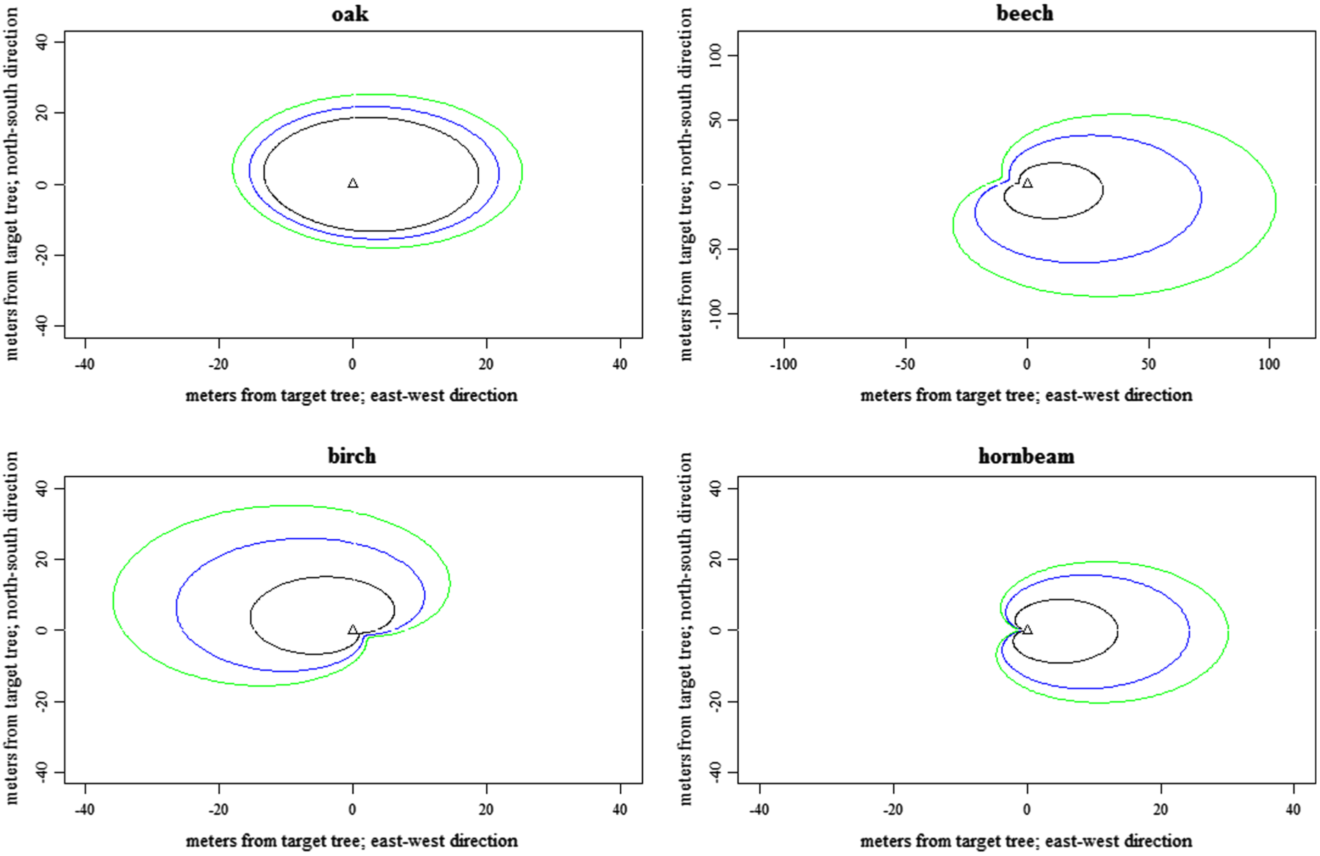

Fig. 4. Shedding surfaces of the different species for which 99% of litter is dispersed, based on a selected value for h_M. Black lines indicate distances for 1st quartile of the h_{Mj} (oak = 14.6 m, beech = 4.4 m, birch = 7.2 m, hornbeam = 4.2 m). Blue lines indicate distances for average h_{Mj} (oak = 16.9, beech = 10.1, birch = 12.4, hornbeam = 7.5). Green lines indicate distances for 3rd quartile of the h_{Mj} (oak = 19.6, beech = 14.4, birch = 16.8, hornbeam = 9.3).

pure stand (dr_t), for both target species and every element (see Fig. 5). Looking at the range of differences in nutrient return, we observe that for target oak trees all mixtures for N, P, K and Mn have values above 1. The same can be said for Mg around target beech trees. Most of the other elements always have their mean value above 1, except for Ca with oak and K with beech. C shows values around 1 for both target species. Comparing the species proportions of the litter mixtures that had maximum differences in nutrient return between pure and mixed stands (Table 5), it must be noted that surprisingly the highest scoring litter mixtures were the same for both target species. We observe that K content only benefits from beech in the mixture, whereas for all the other nutrients birch, hornbeam or both were present in their maximum proportion.

4. Discussion

We wanted to study whether tree species mixture had an effect on litter fall and nutrient return, by using an existing leaf dispersal model (Jonard et al., 2006). We expanded this model for a four species mixture and used the parameters to determine individual species properties important for leaf dispersal, together with information on the effects of stand structure on the dispersal of litter and associated nutrient input. Below we will discuss these results.

4.1. Prediction of litter fall

The best litter fall prediction is for oak, probably due to the fact that it is the dominant species in our study area and present around almost every target tree (even beech). The combined number of beech and hornbeam trees in all the 30 m radius measurements is almost comparable around the different target trees (356 and 355 individual trees respectively, see Appendix B). However, the prediction for beech is less reliable than that of hornbeam, probably due to the larger shedding distance which extended outside of the 30 m radius. Birch is also the least represented species surrounding the target trees. The calibration of the model will probably be more reliable when a species covers more of the entire range of possible litter biomass in a trap (0–100% of litter biomass). Birch leaves are very light, which results in a limited range in litter mass. Oak, due to its dominancy, has a much larger range of values (see Table 1). This explains both the less reliable prediction for birch and the best prediction for oak, which are respectively the least and the most represented over the entire range of values. Looking at total litter mass, the prediction is less reliable when compared to the single-species predictions. Total litter mass has higher values and a limited standard deviation overall, resulting in an expected less reliable prediction (see Table 1). Also, this value is a combination of the single-species predictions and can therefore incorporate errors of different single-species predictions. Based on our results, the prediction of total litter fall results is a slight underestimation of the actual observed values (see Table 4 and Appendix E).

4.2. Drivers of litter fall deposition

4.2.1. Litter production

Litter production of the target species is comparable to the results of oak and beech in Jonard et al. (2006). For trees with a smaller circumference, hornbeam continues to have the highest litter production (see Fig. 1). At around 1.44 m circumference the higher production shifts towards beech, which remains to have the highest litter production when tree circumference is higher.

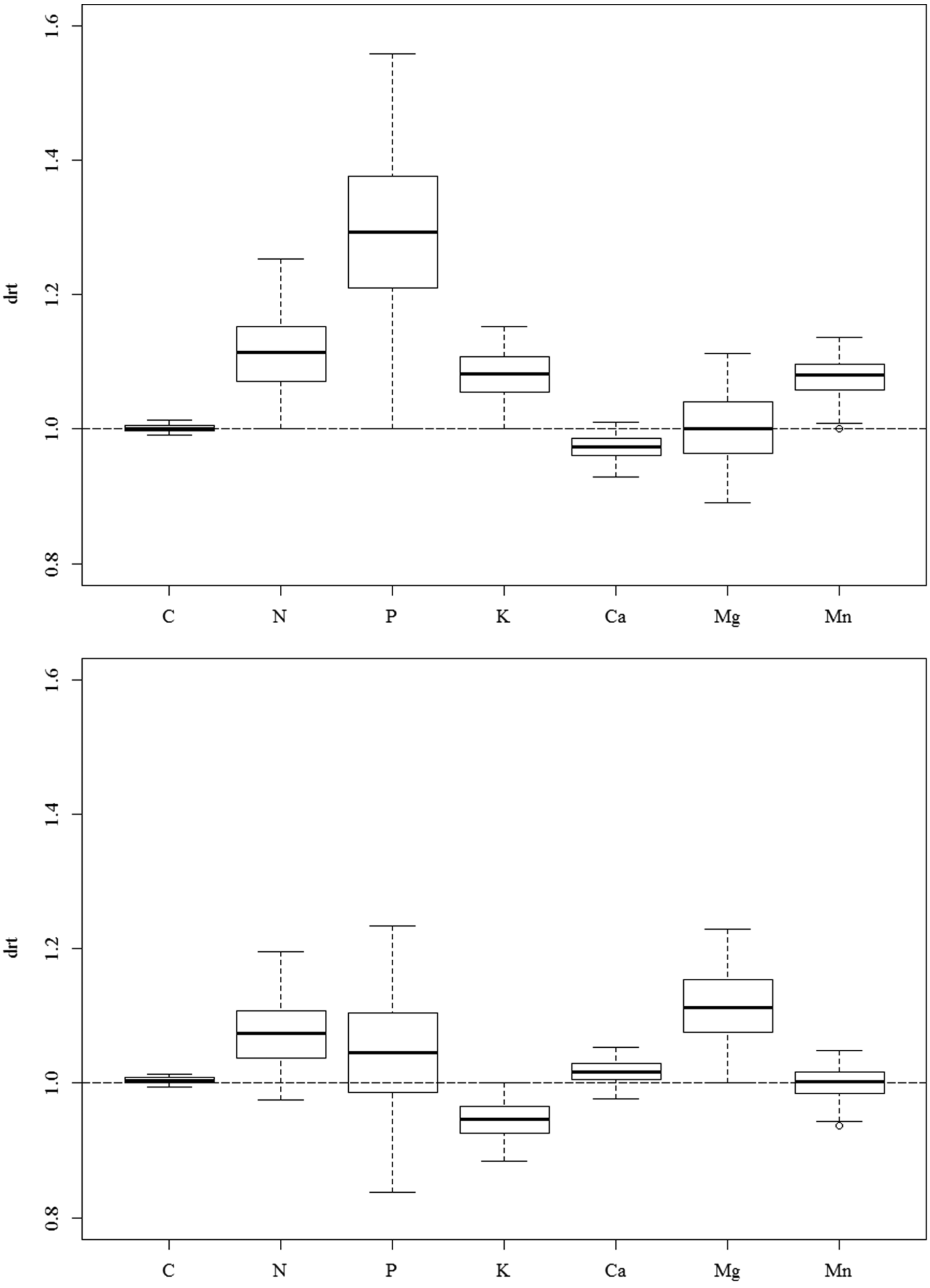

Fig. 5. Boxplot of dr_t for the different elements for target species oak (above) and beech (below). dr_t is the ratio between the nutrient inputs under a target tree (oak or beech) for a selected litter species composition (Appendix H) and nutrient inputs of a reference neighbourhood consisting of only the target species (see Eq. (9)). The dotted line indicates value 1 (=no difference from pure situation).

Table 5
Maximum values of dr_t for both target species, with the corresponding litter mixture. Tested ranges of proportions were 0–100% for the target species, 0–30% for birch and 0–60% for hornbeam (see Appendix H).

Nutrient	Maximum dr_t		Proportion of species			
	Oak	Beech	Oak	Beech	Birch	Hornbeam
C	1.01	1.01	0.70	0.00	0.30	0.00
N	1.25	1.20	0.10	0.00	0.30	0.60
P	1.56	1.23	0.10	0.00	0.30	0.60
K	1.15	1.00	0.00	1.00	0.00	0.00
Ca	1.01	1.05	0.40	0.00	0.00	0.60
Mg	1.11	1.23	0.40	0.00	0.00	0.60
Mn	1.14	1.05	0.10	0.00	0.30	0.60

As shade-tolerant species, beech and hornbeam have deeper crowns with more leaves and a larger foliage area (Canham et al., 1994; Chapman and Gower, 1991; Lusk and Contreras, 1999). Considering all measured trees (see Appendix B), both species show a lower mean height of the crown base compared to the other species. On average beech trees have the largest crown projection areas and the deepest crowns (difference between height and crown base height) of all species. Oak and birch trees, being more light demanding species, will have leaves on the outside of the crown and a lower foliage area. In birch trees we observe smaller crowns (see Appendix B). Their leaves are also smaller and lighter, only contributing around 3% to the total amount of litter production at the trap level (see Table 1). However, even with litter production for oak being lower than that of beech and hornbeam, it still has the largest contribution to total litter mass due to its dominance in the study area.

Litter production in itself can be dependent on neighbourhood. In mixed stands, both hornbeam and beech show increased productivity with higher neighbourhood diversity (Ratcliffe et al., 2015). When mixed with a more light demanding species (like oak), it has been observed that beech trees have a larger plasticity in crown morphology, resulting in higher crown extensions (Dieler and Pretzsch, 2013; Valladares et al., 2002). This could result in more dense and vertically layered canopies in these mixtures (Jucker et al., 2015; Kelty, 2006; Morin et al., 2011; Pretzsch, 2014). Since hornbeam is also a shade-tolerant species, we expect the same mechanisms apply. A higher production of beech could also impede the crown development and litter production of more light demanding species like oak. This difference in crown development is taken into account in the model for oak (through the parameter R), where for beech this was deemed not necessary (Jonard et al., 2006). A study showed that birch trees had smaller crowns in a mixed forest with pedunculate (*Quercus robur* L.) and red oak (*Quercus rubra* L.). They found a slightly higher litter production of birch compared to our study, however with a smaller size range of trees (Staelens et al., 2003). Birch trees are known to have an apical dominance which results in lengthier leader shoots in the crown top (Maillette, 1982). Growing with intraspecific neighbours, they tend to invest less in number and size of branches (Lintunen and Kaitaniemi, 2010), which is in agreement with the limited increase in litter production with higher circumference (Fig. 1).

4.2.2. Shedding patterns

The furthest dispersal was, logically, in the dominant wind direction as determined in the model (ϑ_d). We used the quartile values for height of maximum crown extension (h_M) of each species, in order to have a representative range of dispersal for our study area (Figs. 2 and 4). With increasing h_M, dispersal distances logically increase (Fig. 4). Beech shows the strongest increase in dispersal distance with increasing h_M. Dispersal distances for birch can be longer than for hornbeam since they are on average taller trees. Oak trees show the smallest effect of h_M on dispersal distance, which is expected given the more balanced contributions of different wind directions. Considering the pattern of leaf dispersal in only the dominant wind direction (Fig. 3), oak showed the highest probability of leaf shedding at a certain distance from the tree. This is in agreement with the preferential distribution of leaves in the outer part of the crown in oak trees. The other species show their highest probability closest to the tree trunk, also indicated by the indentation in their shedding patterns in the opposite of the dominant direction (which is absent for oak, see Fig. 2). Combined with a higher leaf fall velocity than the other species, this could explain why the dispersal distance for oak remains lower than for the other species, since a large part of the litter is already dispersed at this distance from the target tree. Following this reasoning, the dispersal distance of birch leaves should be the lowest due to its higher leaf fall velocity. However, our field observations showed that oak trees tend to shed branches with several leaves attached. This would result in even higher leaf fall velocities and lower dispersal distances than those measured for a single leaf.

For trees of the same height, as shown in Fig. 3, beech and hornbeam show higher probabilities at a further distance in accordance with their slower leaf fall velocities. The even higher dispersal distance of beech is probably due to other factors outside of tree height or leaf fall velocity. Field observations showed that beech trees shed their leaves later in the sampling period than other species, which is also found in literature (Berkley, 1931; Otto and Nilsson, 1981). Marcescence occurs in hornbeam and oak as well, but this was not observed in the field (Berkley, 1931; Otto and Nilsson, 1981). Later shedding of beech leaves could diminish sheltering effects by neighbouring trees (which have already lost their leaves), possibly explaining the further dispersal. Temporal variability in leaf shedding could also explain the contrasting dominant wind direction for birch (312° from north) compared to the other species (between 44° and 115° from north). In a mixed deciduous forest of two types of oak and birch, it was indicated that birch trees shed their leaves earlier than oak trees (Staelens et al., 2011). In addition, birch occupies the higher strata of the canopy (second highest average height of maximum crown extension) which would make its crown more susceptible to wind or short wind gusts. If this earlier shedding or wind gust occurred during an interval of different wind direction, this would explain the difference with the other species. Oak, being the tallest species, could also have lower sheltering effects. However, short wind gusts would only stimulate branch shedding (as discussed above), which would not lead to further dispersal distances.

The interactions between the different species add to the complexity of leaf shedding in the mixed stands. However, our model gives us an indication of the differences between the present species. Additional complexity could make the model more accurate but would result in a model which could not be generalized easily.

4.3. Contribution of neighbourhood trees to litter fall and nutrient return

Around the target tree there is a high percentage of litter originating from neighbouring trees. Looking at the integrated value per target tree (P_t), percentages are above 60% for all target trees. While high, the percentage in beech is still significantly lower than in oak. One possible factor could be the fact that the crown of a beech tree is more extended and has an overall higher litter production, strongly influencing litter directly underneath it. We also observed that the peak of dispersal for oak is further away from the stem, which could explain the lower influence it has close to the target tree. To determine which neighbouring trees affect the target tree level, we have to look at the leaf shedding patterns. Due to the direction of leaf dispersal, a fixed radius could take into account trees which would have no effect on litter fall for a given position (for example west of a hornbeam tree). Conversely, the influence of trees with longer dispersal distances just outside the fixed radius could be overlooked. This could explain why, in the same study area, diversity of litter and diversity based on stand composition were correlated but the effects of litter species composition showed stronger effects on foliar concentrations (Nickmans et al., 2015).

Due to the high percentage of litter originating from neighbouring trees, litter quality at the target tree level could be heavily impacted by the choice of surrounding tree species. Every increased proportion of another species is shown to be beneficial for N, P, K and Mn litter content around oak. Beneficial effects are mostly linked with the accompanying species (see Table 5). When looking at the mixtures in detail (Appendix H), the presence of hornbeam is important for Ca in combination with a low proportion of beech (around 20%). Mg content also benefits from birch and beech, although for beech only up to a certain level (around 60%).

If the target species is beech, Mg content always improves when adding different species. Next to the importance of the accompanying species, oak shows beneficial effects for N, P and Mn, but mostly for Mg and Ca. Looking at the mixtures in detail, the presence of oak has to remain lower ($< 50\%$) to benefit P and Mn, where Ca benefits from a good balance between oak and the accompanying species. N content is negatively affected when birch is absent and the proportion of hornbeam drops to 10% or lower. For K, the most optimal situation is a pure stand of beech (100%). These different effects are logically related to the differences in litter nutrient content between species (see Table 2). If the mixture would consist of species with more contrasting nutrient concentrations, these effects could become even more pronounced.

Some of these results coincide with what we found for the effects of litter diversity on foliar nutrient concentrations and soil available nutrients in the same study area. In both studies the litter sampling was done in the same way and for foliar nutrient concentrations it was observed that higher litter diversity had positive effects on N, P, K, Mg and Ca in oak. These were linked with significant effects of one or more of the neighbouring species (Nickmans et al., 2015). However, no effect of beech was found for foliar K, which is surprising due to its strong effect on K return. Similar positive effects of litter diversity were found on available Ca, K, Mg and Mn in the soil, partly explaining the effect on the foliar nutrient concentrations in oak (Nickmans et al., 2018). In target beech trees, the N concentration was positively influenced by the presence of oak in the litter. Other effects on foliar nutrient concentrations were limited in beech, which could have been due to the lower percentage originating from the neighbourhood, but also since more mixtures had negative effects (Nickmans et al., 2015). Given the beneficial effects of a mixed neighbourhood on Mg return, we would expect positive effects on foliar Mg. However, effects of local density and target tree size were also found for foliar Mg in beech trees, resulting in additional factors which could interact with litter composition effects (Nickmans et al., 2015). This complexity could mask the relation between litter composition and foliar nutrient concentrations.

5. Conclusions and recommendations

The use of a dispersal model allowed us to predict and understand spatial patterns of litter fall in mixed-species stands. It clearly demonstrated the importance of the neighbouring trees and how the redistribution of their litter had a major contribution to the nutrient supply at the individual (target) tree level, in particular the positive effect of accompanying species in acidic nutrient-poor forest stands. Litter mixtures showed a higher initial nutrient content when they consisted of the highest possible proportions of accompanying species.

At this point, our approach on nutrient return is an approximation based on average litter nutrient concentrations. As discussed above, neighbourhood can already have an effect on initial foliar nutrient concentrations. Next to that, other factors will play an additional role in the redistribution of other elements. For example, different shedding periods can change resident time of litter in the traps. K, Mg, Ca and Na are normally rapidly released from litter, which could affect their average nutrient concentrations in the traps (Kucera, 1959; McLaughlin and Wimmer, 1999; Osman, 2013; Stachurski and Zimka, 1975). Also, subsequent processes of decomposition, redistribution and capture of nutrients will have an additional influence on tree nutrition. Additional research and insights on how these different factors interact could make for an even more accurate indication of the effects of litter distribution on nutrient return.

Our results could give relevant guidelines on how to optimize stand structure and mitigate nutrient imbalances. With information on dominant wind directions, it could help in determining placement of beneficial species relative to trees of interest. For example, based on our sampling period, we could indicate that structurally hornbeams should be positioned west from the trees of interest. Our results could also contribute to choices in thinning and management. Safeguarding hornbeam or birch trees during thinning could mitigate certain nutrient deficiencies, for example Mg or P (which have been shown to be deficient in our study area). Although simplified, it shows that this would have practical implications for stand establishment and management.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.01.001.

References

Aerts, R., 1996. Nutrient resorption from senescing leaves of perennials : are there general patterns ? J. Ecol. 84, 597–608.

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, P.M., Adams, M.A., 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.

Bauhus, J., Pokorny, B., van der Meer, P.J., Kanowski, P.J., Kanninen, M., 2010. Ecosystem goods and services – the key for sustainable plantations. In: Bauhus, J., van der Meer, P.J., Kanninen, M. (Eds.), Ecosystem Goods and Services from Plantation Forests. Earthscan, London, UK, pp. 205–227.

Berg, B., McClaugherty, C., 2014. Plant Litter Decomposition, Humus Formation, Carbon Sequestration, third ed. Springer, Berlin, Heidelberg.

Berkley, E.E., 1931. Marcescent leaves of certain species of quercus. Bot. Gaz. 92, 85–93.

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

Binkley, D., 1996. The influence of tree species on forest soils: processes and patterns. In: Mead, D.J., Cornforth, I.S. (Eds.), Proceeding of Tree Species and Soil Workshop. Agronomy Society of New Zealand Special Publication #10. Lincoln University Press, Canterbury, NZ, pp. 1–33.

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

Boyden, S., Binkley, D.A.N., Senock, R., 2005. Competition and facilitation between eucalyptus and nitrogen-fixing falcataria in relation to soil fertility. Ecology 86, 992–1001.

Canham, C.D., Finzi, A.C., Pacala, S.W., Burbank, D.H., 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. Can. J. For. Res. 24, 337–349.

Chapman, J.W., Gower, S.T., 1991. Aboveground production and canopy dynamics in sugar maple and red oak trees. Can. J. For. Res. 21, 1533–1543.

Condés, S., Del Rio, M., Sterba, H., 2013. Mixing effect on volume growth of *Fagus sylvatica* and *Pinus sylvestris* is modulated by stand density. For. Ecol. Manage. 292, 86–95. https://doi.org/10.1016/j.foreco.2012.12.013.

Dieler, J., Pretzsch, H., 2013. Morphological plasticity of European beech (*Fagus sylvatica* L.) in pure and mixed-species stands. For. Ecol. Manage. 295, 97–108.

Ferrari, J.B., Sugita, S., 1996. A spatially explicit model of leaf litterfall in hemlock–hardwood forests. Can. J. For. Res. 26, 1905–1913.

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

Forrester, D.I., Kohnle, U., Albrecht, A.T., Bauhus, J., 2013. Complementarity in mixed-species stands of Abies alba and Picea abies varies with climate, site quality and stand density. For. Ecol. Manage. 304, 233–242. https://doi.org/10.1016/j.foreco.2013.04.038.

Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M.C., Fröberg, M., Stendahl, J., Philipson, C.D., Mikusiński, G., Andersson, E., Westerlund, B., Andrén, H., Moberg, F., Moen, J., Bengtsson, J., 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. Nat. Commun. 4, 1340. https://doi.org/10.1038/ncomms2328.

Gartner, T.B., Cardon, Z.G., 2004. Decomposition dynamics in mixed-species leaf litter. Oikos 104, 230–246.

Gayer, K., 1886. Der gemischte Wald, seine Begründung und Pflege insbesondere durch Horst- und Gruppenwirtschaft. Paul Parey Verlag, Berlin.

Gessner, M.O., Swan, C.M., Dang, C.K., McKie, B.G., Bardgett, R.D., Wall, D.H., Hättenschwiler, S., 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., Thomas, F.M., Leuschner, C., 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. Springer, Berlin, pp. 149–164.

Hättenschwiler, S., Tiunov, A.V., Scheu, S., 2005. Biodiversity and litter decomposition in terrestrial ecosystems. Annu. Rev. Ecol. Evol. Syst. 36, 191–218.

Hobbie, S.E., Reich, P.B., Oleksyn, J., Ogdahl, M., Zytkowiak, R., Hale, C.M., Karolewski, P., 2006. Tree species effects on decomposition and forest floor dynamics in a common garden. Ecology 87, 2288–2297.

Hoffmann, F., 1923. Mischungen von Buchen mit Nadelholz, insbes. mit der Fichte und Tanne. Allg. Forst- und Jagdzeitung 99, 273–281.

Joly, F.X., Fromin, N., Kiikkilä, O., Hättenschwiler, S., 2016. Diversity of leaf litter leachates from temperate forest trees and its consequences for soil microbial activity. Biogeochemistry 129, 373–388. https://doi.org/10.1007/s10533-016-0239-z.

Jonard, M., Andre, F., Ponette, Q., 2006. Modeling leaf dispersal in mixed hardwood forests using a ballistic approach. Ecology 87, 2306–2318.

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.

Jonckheere, I., Fleck, S., Nackaerts, K., Muys, B., Coppin, P., Weiss, M., Baret, F., 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.

Jucker, T., Bouriaud, O., Coomes, D.A., 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, M.J., 1992. Comparative productivity of monocultures and mixed-species stands. In: Kelty, M.J., Larson, B.C., Oliver, C.D. (Eds.), The Ecology and Silviculture of Mixed-Species Forests. Kluwer Academic Publishers, Dordrecht, Boston, London, pp. 125–142.

Kelty, M.J., 2006. The role of species mixtures in plantation forestry. For. Ecol. Manage. 233, 195–204. https://doi.org/10.1016/j.foreco.2006.05.011.

Killingbeck, K.T., 1996. Nutrients in senesced leaves: keys to the search for potential resorption and resorption proficiency. Ecology 77, 1716–1727.

Knops, J.M.H., Bradley, K.L., Wedin, D.A., 2002. Mechanisms of plant species impacts on ecosystem nitrogen cycling. Ecol. Lett. 5, 454–466. https://doi.org/10.1046/j.1461-0248.2002.00332.x.

Kooch, Y., Tarighat, F.S., Hosseini, S.M., 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, C.L., 1959. Weathering characteristics of deciduous leaf litter. Ecology 40, 485–487.

Lintunen, A., Kaitaniemi, P., 2010. Responses of crown architecture in Betula pendula to competition are dependent on the species of neighbouring trees. Trees – Struct. Funct. 24, 411–424. https://doi.org/10.1007/s00468-010-0409-x.

Lusk, C.H., Contreras, O., 1999. Foliage area and crown nitrogen turnover in temperate rain forest juvenile trees of differing shade tolerance. J. Ecol. 87, 973–983. https://doi.org/10.1046/j.1365-2745.1999.00408.x.

Maillette, L., 1982. Structural dynamics of silver birch. I. The fates of buds. J. Appl. Ecol. 19, 203–218.

McLaughlin, S.B., Wimmer, R., 1999. Tansley Review No . 104 Calcium physiology and terrestrial ecosystem processes. New P 142, pp. 373–417.

Mettin, C., 1986. Inwieweit ist Laubstreu eine ökologische und ökonomische Hilfe in Nadelholzbeständen? Allg. Forstzeitung 37, 918–922.

Morin, X., Fahse, L., Scherer-Lorenzen, M., Bugmann, H., 2011. Tree species richness promotes productivity in temperate forests through strong complementarity between species. Ecol. Lett. 14, 1211–1219.

Nickmans, H., Titeux, H., Ponette, Q., Verheyen, K., 2018. Nutrient supply at the local tree level in mixed forests of sessile oak and beech. Eur. J. For. Res. 137, 807–817. https://doi.org/10.1007/s10342-018-1141-0.

Nickmans, H., Verheyen, K., Guiz, J., Jonard, M., Ponette, Q., 2015. Effects of neighbourhood identity and diversity on the foliar nutrition of sessile oak and beech. For. Ecol. Manage. 335, 108–117. https://doi.org/10.1016/j.foreco.2014.09.025.

Osman, K.T., 2013. Forest Soils. Springer.

Otto, C., Nilsson, L.M., 1981. Why Do beech and oak trees retain leaves until spring ? Oikos 37, 387–390.

Pawson, S.M., Brin, A., Brockerhoff, E.G., Lamb, D., Payn, T.W., Paquette, A., Parrotta, J.A., 2013. Plantation forests, climate change and biodiversity. Biodivers. Conserv. 22, 1203–1227. https://doi.org/10.1007/s10531-013-0458-8.

Piñeiro, G., Perelman, S., Guerschman, J.P., Paruelo, J.M., 2008. How to evaluate models: observed vs. predicted or predicted vs. observed? Ecol. Modell. 216, 316–322. https://doi.org/10.1016/j.ecolmodel.2008.05.006.

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

Ratcliffe, S., Holzwarth, F., Nadrowski, K., Levick, S., Wirth, C., 2015. Tree neighbourhood matters – tree species composition drives diversity-productivity patterns in a near-natural beech forest. For. Ecol. Manage. 335, 225–234. https://doi.org/10.1016/j.foreco.2014.09.032.

Richards, A.E., Forrester, D.I., Bauhus, J., Scherer-Lorenzen, M., 2010. The influence of mixed tree plantations on the nutrition of individual species: a review. Tree Physiol. 30, 1192–1208. https://doi.org/10.1093/treephys/tpq035.

Rothe, A., 1997. Influence of tree species composition on rooting patterns, hydrology, elemental turnover, and growth in a mixed spruce–beech stand in Southern Germany (Höglwald). Forstl Forschungsberichte München 163.

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

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.

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

Staelens, J., Nachtergale, L., De Schrijver, A., Vanhellemont, M., Wuyts, K., Verheyen, K., 2011. Spatio-temporal litterfall dynamics in a 60-year-old mixed deciduous forest. Ann. For. Sci. 68, 89–98. https://doi.org/10.1007/s13595-011-0010-5.

Staelens, J., Nachtergale, L., Luyssaert, S., Lust, N., 2003. A model of wind-influenced leaf litterfall in a mixed hardwood forest. Can. J. For. Res. 33, 201–209. https://doi.org/10.1139/x02-174.

Stone, D.M., 1977. Leaf dispersal in a pole-size maple stand. Can. J. For. Res. 7, 189–192.

Team, R.C., 2013. R: A language and environment for statistical computing.

Valladares, F., Manuel, J., Aranda, I., Balaguer, L., Dizengremel, P., Manrique, E., Dreyer, E., 2002. The greater seedling high-light tolerance of Quercus robur over *Fagus sylvatica* is linked to a greater physiological plasticity. Trees 16, 395–403.