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# Spatio-temporal litterfall dynamics in a 60-year-old mixed deciduous forest

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## Abstract

• **Introduction** To increase our understanding of litterfall dynamics in mixed-species forests, seasonal and annual variations in litterfall mass and nutrient concentrations were assessed for a 60-year-old spontaneously developed forest dominated by silver birch (*Betula pendula* Roth), pedunculate oak (*Quercus robur* L.), and northern red oak (*Quercus rubra* L.) in Belgium.

• **Results** Total quantities and seasonal patterns of most litterfall fractions were similar over the 29-month study

period, but the species differed in start and duration of their leaf shedding period. The spatial distribution of litterfall persisted over the years for leaves, but not for total litterfall because of the varying spatial pattern of fallen twigs and reproductive structures. Consequently, predicting humus build-up based on short-term litterfall measurements may be difficult in mixed forests. Nutrient concentrations in leaf litter differed considerably between the species and throughout the year, but the seasonal pattern did not depend on the species. *Betula* returned significantly more nutrients to the soil per mass unit than *Quercus*, except for sodium.

• **Conclusion** As the present stand conditions only allow recruitment of *Q. rubra*, *Betula* is being outcompeted, which decreases the nutrient return to the soil and may negatively affect biogeochemical cycling.

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**Keywords** Nutrient cycling · Litterfall · *Quercus* · *Betula*

## 1 Introduction

Litterfall has frequently been studied (e.g., Bray and Gorham 1964; Reich et al. 2005) as it is a key component in the nutrient cycle of all plants. Together with nutrient resorption and foliar leaching (Luyssaert et al. 2005), litterfall and subsequent decomposition (Raimundo et al. 2008) are major pathways of nutrient return to plants. The relative importance of these pathways is nutrient-specific and can strongly differ between tree species, sites, and age of the trees (Binkley 1986). Generally, species on richer sites are postulated to return more nutrients to the soil, not because of lower nutrient retranslocation from senescing leaves, but rather because of higher leaf nutrient concentrations (Aerts 1996).

Still, tree species occupying the same site can differ conspicuously in nutrient return through litterfall (Muys et

al. 1992; Reich et al. 2005) and nutrient resorption (Lal et al. 2001), and therefore, each species exhibits a specific effect on the soil properties and the identity, abundance, and activities of diverse heterotrophic soil organisms (Muys et al. 1992; Reich et al. 2005). The species-specific effect of litter on the soil environment has often been attributed to differing decay rates and nutrient release because of differing carbon to nitrogen ratios (Cotrufo et al. 2000), lignin to nitrogen ratios (Hobbie et al. 2006), polyphenol concentrations (Osono and Takeda 2005), and leaf toughness (Perez-Harguindeguy et al. 2000). Litter Ca can also play a key role in litter decomposition (Hobbie et al. 2006) and soil properties (Reich et al. 2005).

In mixed-species forests, the local effect of litter on soil properties depends on the tree species involved and their relative contribution to the litter pool. It is known that the observed litter decomposition rates in mixed forests can substantially deviate from those expected from homogeneous forests (Hättenschwiler and Gasser 2005; Chapman and Koch 2007). For recalcitrant litter species, a significant acceleration of litter mass loss was noted with increasing litter diversity, while no such improvement was found for more rapidly decomposing species (Hättenschwiler and Gasser 2005). According to Chapman and Koch (2007), litter mixtures of more closely related plant species give rise to the most synergistic effects on litter dynamics, although this may be difficult to generalize.

Through the litterfall flux, trees also exert a physical control on the composition and abundance of the herb layer and tree regeneration (van Oijen et al. 2005). A thick litter stratum can obstruct plant establishment because of the low light intensity, the high humidity, and the occurrence of many pathogens (Sayer 2006). An altered litter layer composition also changes habitat structure, microclimatic conditions, and resource availability for macrofauna, mesofauna, and microbial communities, and, consequently, may significantly affect carbon and nutrient cycling (Hättenschwiler and Gasser 2005; Sayer 2006).

Understanding litterfall dynamics in mixed-species forests is a crucial step forwards in understanding nutrient dynamics and biogeochemical cycling because extrapolation of data from homogeneous plots is of limited use (Rothe and Binkley 2001). In this study, we aimed to assess seasonal and yearly variations in litterfall quality, quantity, and composition in a 60-year-old spontaneously developed deciduous forest in northern Belgium. During 29 months including three autumn periods, litterfall was measured in a 9.5-ha plot encompassing different levels of tree species mixtures of the indigenous silver birch (*Betula pendula* Roth) and pedunculate oak (*Quercus robur* L.), and the exotic northern red oak (*Q. rubra* L.). The research hypothesis is that the studied species differ in the timing and quality

of litterfall, which will lead to distinct horizontal and vertical spatial patterns in the composition of the humus layer in this mixed forest.

## 2 Material and methods

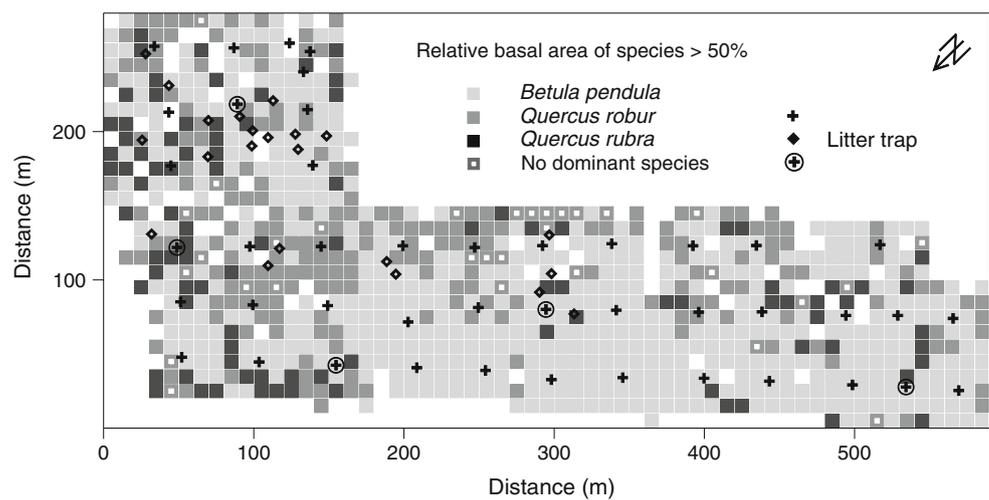
### 2.1 Site description

The research was performed in a mixed deciduous forest in Liedekerke (30 km west from Brussels) in the north of Belgium. The sandy loam soils of the study area are well drained and are classified as Albic Luvisols. Slope is less than 1% and the altitude is 25 m above sea level. Annual mean precipitation in the study years was 816 mm in 1998, 739 mm in 1999, and 787 mm in 2000, and annual mean temperature was 10.5°C, 11.0°C, and 11.1°C, respectively. The long-term (1980–2000) mean annual values are 754 mm and 10.2°C (data of the Royal Meteorological Institute of Belgium). The forest has a surface area of 55 ha in which a study plot of 9.5 ha was chosen. The study plot has been forested since at least 1780. Regular cutting and mowing between 1926 and 1940 resulted in the development of coppice and heathland. Subsequently, during the next 60 years, the vegetation developed spontaneously into a mixed deciduous forest, consisting of 15 intimately mixed deciduous tree species dominated by *B. pendula* and two *Quercus* species. In 2000, the mean basal area in the study area was 26.5 m<sup>2</sup> ha<sup>-1</sup>, of which *B. pendula* represented 56%, *Q. robur* 26%; *Q. rubra* 14%, and the remaining species 5% (Table 1). The absence of management in the studied forest allowed the development of a variety of tree species mixtures, ranging from intimate mixtures of individual trees to patches with one dominant species (Fig. 1). Thus, the study plot allowed examining spatio-temporal dynamics of litterfall in a mature mixed forest. The understory is dominated by *Rubus* spp. Due to the self-thinning of densely stocked and unmanaged *Betula* clusters and increasing competition with *Quercus* spp., the stand is experiencing a reduction in the stem number of *Betula* (Vanhellemont et al. 2009). The spatial distribution of leaf

**Table 1** Average stem number (ha<sup>-1</sup>), mean diameter at breast height (dbh, cm) and basal area (m<sup>2</sup> ha<sup>-1</sup>) of all trees with dbh>9.5 cm in 2000

Tree species	Stem number (ha <sup>-1</sup> )	Mean dbh (cm)	Basal area (m <sup>2</sup> ha <sup>-1</sup> )
<i>Betula pendula</i>	551	17.5	14.9
<i>Quercus robur</i>	134	23.2	6.8
<i>Quercus rubra</i>	38	32.5	3.6
Other species	47	16.6	1.2
Total	770	19.1	26.5

**Fig. 1** Map of the study area with dominant tree species, according to basal area, in 10×10 m grid cells and location of the litter traps. *Crosses* indicate traps placed in a grid of 40×40 m ( $n=44$ ), *diamonds* indicate traps distributed stratified randomly over a range of tree species mixtures ( $n=22$ ), and *circles* indicate traps used for chemical analysis ( $n=5$ )



litterfall mass in this stand has been modelled by Staelens et al. (2003, 2004).

## 2.2 Data collection

In the 9.5-ha study plot, all trees for which diameter at breast height (dbh, at 1.3 m) exceeded 9.5 cm were mapped and dbh was measured in January 2000. Litterfall was collected using 66 litter traps, which consisted of conical bags with a circular collecting surface of 0.2419 m<sup>2</sup>, supported at a height of 1 m above ground level. The traps were either placed in a grid of 40×40 m ( $n=44$ ) or distributed stratified randomly over a wide range of tree species mixtures ( $n=22$ ) (Fig. 1). Litterfall was collected from 3 August 1998 to 22 December 2000, weekly to monthly from August to December and at least every 2 months during the rest of the year. After collection, litter material was air dried and sorted into leaves, twigs, and branches (diameter <2 cm), and reproductive parts (flowers, fruits, and seeds). Leaves were separated by species for *Betula*, *Q. robur*, *Q. rubra*, and other species. All fractions were air dried, oven dried at 40°C for 48 h, and weighed to the nearest 0.1 g.

## 2.3 Chemical analysis

For chemical analysis, five litter traps were selected stratified randomly within five blocks of the study plot (Fig. 1). For each litter trap and for each litter fraction considered, collected litterfall was pooled into six samples per year. The first sample included the period from January to April (before leaf sprouting but including the shedding of bud scales and inflorescences); the second sample spanned the period May until June (young leaves and inflorescences); the third sample spanned the period July until September (before the main leaf litterfall peak). The last three samples included the main litterfall period of October (sample four), November (sample five), and December (sample six). During

periods with more than 5 g dry weight per litter fraction per trap, the content of the five traps was used separately; otherwise, their content was pooled into one bulk sample.

Litter was ground by means of a Culatti mill and dried at 70°C before analysis of the total nitrogen (N) concentration using a modified Kjeldahl method. Samples were digested by nitric acid (HNO<sub>3</sub>; 65%) and perchloric acid (HClO<sub>4</sub>; 70%) in a 5:1 ratio and analyzed for K, Ca, Mg, Na, and Fe by means of flame atomic absorption spectrophotometry. P was determined colorimetrically in the same digestion by the molybdate method (Scheel 1936). The quality of the chemical analyses was checked by including method blanks, certified reference samples (CRM 100), and inter-laboratory tests. The coefficient of variation of repeated measurements of CRM 100 samples was smaller than 5%, and the recovery was higher than 95% for all certified elements.

## 2.4 Statistical analysis

The mass of the different litterfall fractions was compared between the study years (1998, 1999, and 2000) with paired samples *t* tests ( $n=66$  traps). The inter-annual variability of the litterfall fraction mass, i.e., the temporal stability of the spatial pattern, was studied by means of Pearson correlation coefficients between the litterfall in different years. Missing leaf litterfall of January to July 1998 was not accounted for because less than 3% of the annual leaf fall occurred from January to July in 1999 and 2000. Branches, reproductive structures, and total litterfall were only compared between 1999 and 2000 because the lack of data before August 1998 biased the 1998 results of these fractions.

For each fraction, litterfall mass and nutrient concentration per period of the year ( $n=6$ , cf. 2.3) were used to calculate annual mass-weighted mean nutrient concentrations, by summing the products of litterfall mass and nutrient concentration per period and dividing this sum by

the annual litterfall mass. General linear model repeated measures analyses were performed on these annual mean nutrient concentrations ( $n=5$  traps) with “year” as within-subjects factor and “tree species” as between-subjects factors. As data collected on adjacent sampling dates are auto-correlated, and so the circularity (or sphericity) condition for repeated measures analysis is usually not met, the MANOVA approach (based on Pillai's test statistic) was adopted for analyzing the within-subjects effects (O'Brien and Kaiser 1985). Tree species were divided into homogeneous groups by means of the Scheffé post hoc test (Neter et al. 1996). All statistical analyses were performed with SPSS for Window 15.0. A level of  $p < 0.05$  was chosen as the minimum for significance.

### 3 Results

#### 3.1 Litterfall mass

Mean annual litterfall mass was  $5.5 \text{ t ha}^{-1}$  (Table 2), of which leaves represented 67%, twigs 23%, and reproductive structures 10%. Leaf litterfall (LLF) mass of *Betula* was significantly higher in 1999 compared to both other years ( $p < 0.001$ ), while in 1998, the LLF mass of *Q. robur* was significantly lower ( $p < 0.001$ ) compared to the two subsequent years. The total LLF mass was highest ( $p < 0.001$ ) in 1999. For the other litterfall fractions, no significant mass differences between 1999 and 2000 were found. The order of the mean annual LLF mass of the three main species (*B. pendula* > *Q. robur* > *Q. rubra*) corresponded to the species order of stem number and basal

area (Table 1), even though both *Quercus* species contributed more LLF per unit basal area than *Betula*.

The coefficients of variation of the mean annual LLF mass of the three main species (Table 2) reflect the variety of species mixtures in the study area (Fig. 1). The LLF mass of *Betula* had the lowest spatial variation coefficient (49%) because this species is most evenly distributed over the area, while *Q. rubra* had the highest spatial variation (81%) because the distribution of this species is more clustered (Fig. 1). The variation coefficient of the total LLF mass (13%) was much lower than for the species-specific LLF and indicates an only moderate impact of species mixture on the spatial distribution of the total LLF. For 40% of the litter traps, *Betula* contributed more than half of the total LLF mass, while *Q. robur* and *Q. rubra* dominated the LLF for only 12% and 5% of the traps, respectively.

Over the study period, the seasonal pattern of litterfall was relatively stable. All species lost a minor quantity of leaves during spring and summer, but the start and duration of the active leaf shedding period differed clearly between species (Fig. 2). *Betula* LLF started in August and continued until November. Before the first of November, 90% of the *Betula* leaves had fallen, and from August to mid-October, *Betula* represented the major part of the LLF mass. Both *Quercus* species started shedding leaves at the beginning of October. About 60% of all *Q. rubra* litter fell in October, and the shedding ended in the middle of November. From mid-October to mid-November, *Q. rubra* dominated LLF. Around 60% of all leaf litter fell from *Q. robur* fell in November and the shedding ended in mid-December (Fig. 2). From mid-November to the end of December, the majority of the LLF consisted of *Q. robur*.

**Table 2** Annual mean  $\pm$  standard deviation ( $X \pm \text{SD}$ ) and coefficient of variation (CV) of the mass ( $\text{g m}^{-2} \text{ yr}^{-1}$ ) of different litter fractions for 66 litter traps in two or three measuring years

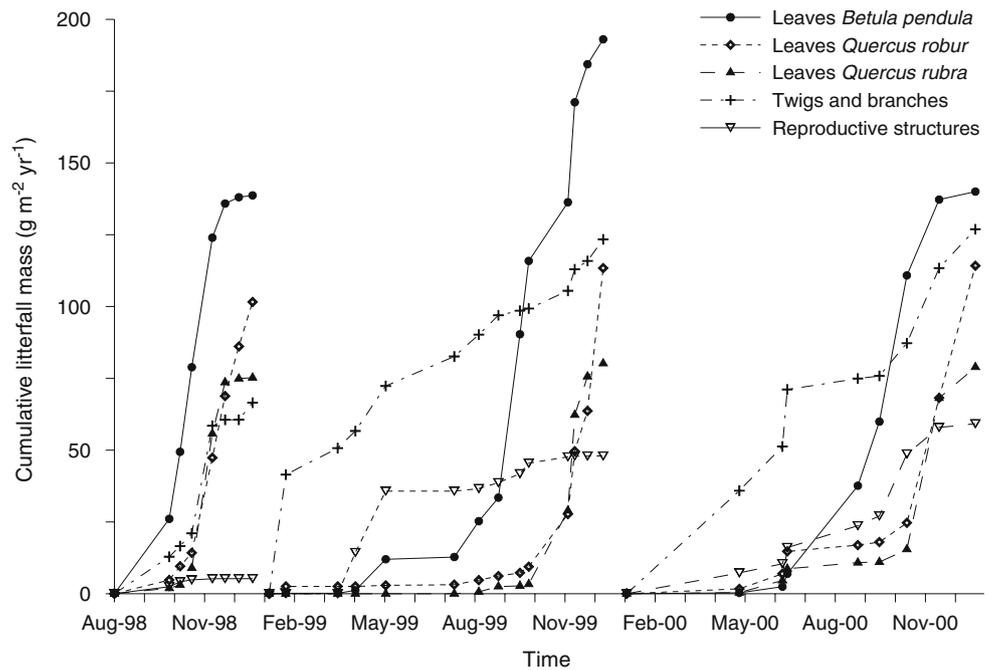
Litterfall fraction	1998		1999		2000		Mean*	
	$X \pm \text{SD}$	CV	$X \pm \text{SD}$	CV	$X \pm \text{SD}$	CV	$X \pm \text{SD}$	CV
Leaves								
<i>Betula pendula</i>	139 <sup>a</sup> ±71	48	193 <sup>b</sup> ±87	48	140 <sup>a</sup> ±79	56	159±78	49
<i>Quercus robur</i>	102 <sup>a</sup> ±72	71	112 <sup>b</sup> ±78	69	115 <sup>b</sup> ±79	69	110±74	68
<i>Quercus rubra</i>	75 <sup>a</sup> ±64	86	80 <sup>a</sup> ±71	88	77 <sup>a</sup> ±60	77	76±62	81
Other species	7 <sup>a</sup> ±12	164	10 <sup>a</sup> ±14	139	13 <sup>a</sup> ±15	120	10±13	129
Total	323 <sup>a</sup> ±49	15	396 <sup>b</sup> ±58	15	345 <sup>a</sup> ±56	16	355±46	13
Twigs and branches <sup>†</sup>	–	–	123 <sup>a</sup> ±71	58	126 <sup>a</sup> ±74	58	125±50	40
Reproductive structures	–	–	48 <sup>a</sup> ±31	65	59 <sup>a</sup> ±67	113	54±40	75
Total	–	–	568 <sup>a</sup> ±102	18	531 <sup>a</sup> ±111	21	551±86	16

Different letters within a row indicate significantly different ( $p < 0.01$ ) means between years

\*Mean of 1998–2000, except for twigs and branches, reproductive structures, and total litterfall (mean of 1999–2000) because the lack of data before August 1998 biased the 1998 results of these fractions

<sup>†</sup> Diameter < 2 cm

**Fig. 2** Cumulative mass ( $\text{g m}^{-2} \text{ yr}^{-1}$ ) of different litterfall fractions from August 1998 to December 2000



Twigs and branches were shed throughout the year, but the highest quantities were observed during the leafless period. *Betula* twigs in particular fell during storms and in periods of frost (data not shown). From January to July, twigs dominated the litter input. Reproductive structures had a first peak in spring (April) caused by the shedding of inflorescences; with a second peak in September–October due to the shedding of acorns.

The spatial pattern of the LLF mass of individual tree species was stable over time, with high and significant ( $p < 0.001$ ) Pearson correlations between the study years (Fig. 3). For the total LLF mass, however, the correlation coefficients were much lower ( $r = 0.51$  for comparison of 1998 and 1999;  $r = 0.53$  for 1998–2000; and  $r = 0.64$  for 1999–2000;  $p < 0.001$  for all pairs of years). The spatial distribution of fallen twigs and branches ( $p = 0.45$ ), reproductive structures ( $r = 0.30$ ,  $p = 0.02$ ), and, consequently, total annual litterfall ( $r = 0.26$ ,  $p = 0.04$ ) was more variable between 1999 and 2000.

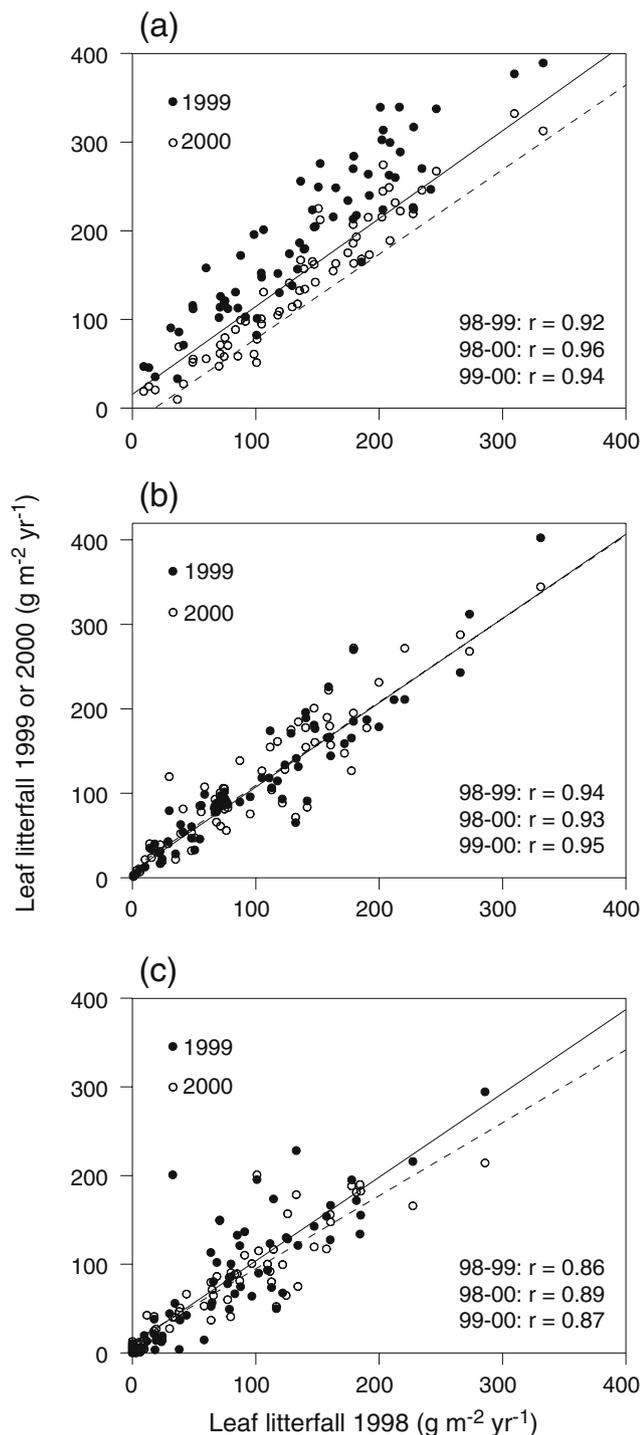
### 3.2 Nutrients in litterfall

Mean concentrations of Mg and K in the LLF of *Betula* and *Q. robur* were higher in May–June than in April (Fig. 4). For *Q. robur* LLF, N and P concentrations were also higher in the period May–June compared to the period January–April, while for *Betula*, the N and P concentrations were highest in January–April. For the *Q. rubra* LLF, this comparison could not be made because no leaves fell before April. During the main litterfall period (October to December), the concentrations of N, P, Mg, and K in LLF decreased over time (Fig. 4). Ca concentrations in the LLF

of the three species decreased from the period January–April to May–June, after which they showed an upward trend that stagnated or decreased slightly in December (Fig. 4). Na concentrations in LLF showed a similar pattern to Ca but increased more clearly from October to December. Concentrations of Fe in LLF peaked in the period January–April after which they remained stable.

Compared to leaves, twigs generally had lower nutrient concentrations that stayed rather constant throughout the year. For most elements, concentrations in twigs were of the same magnitude as in leaves of *Q. rubra* in December. Averaged over the study area and for the years 1999–2000, twigs accounted for 12% (K) to 19% (Ca and Fe) of the total nutrient flux to the forest floor in litterfall. Reproductive structures represented two different fractions: inflorescences dominating in April and in July–September and fruits (mostly acorns) dominating from October to December. Inflorescences were very rich in N, P, Mg, Ca, and Fe, but poor in K, whereas fruits had high K concentrations and low concentrations of other nutrients. Averaged over the study area and for 1999–2000, reproductive structures contributed 6% (Na, Ca) to 17% (Fe) of the total nutrient flux in litterfall. On average, leaves accounted for 72–78% of the total nutrient flux in litterfall, except for Fe (64%).

The annual mass-weighted mean nutrient concentrations in LLF were significantly ( $p < 0.022$ ) influenced by the measuring year for all elements other than Mg ( $p = 0.59$ ) and Fe ( $p = 0.058$ ). The most notable differences in LLF concentrations between years were observed for N, P, K, and Na (Table 3); however, without clear pattern for the different tree species. For example, the N concentration in LLF of *Betula* was lowest in 1998 and highest in 2000,



**Fig. 3** Relationship between leaf litterfall mass ( $n=66$ ) in the measuring years for **a** *Betula pendula*, **b** *Quercus robur*, and **c** *Q. rubra*. The lines show the linear regressions between 1998 and 1999 (full line) and between 1998 and 2000 (dashed line), the lines of which overlap in **b**. All Pearson correlation coefficients ( $r$ ) are significant at  $p<0.001$

while for both *Quercus* species, it was lowest in 1999. In addition to differences between years, the annual nutrient concentrations differed significantly ( $p<0.001$ ) between the tree species, except for Na ( $p=0.30$ ): fallen *Betula* leaves

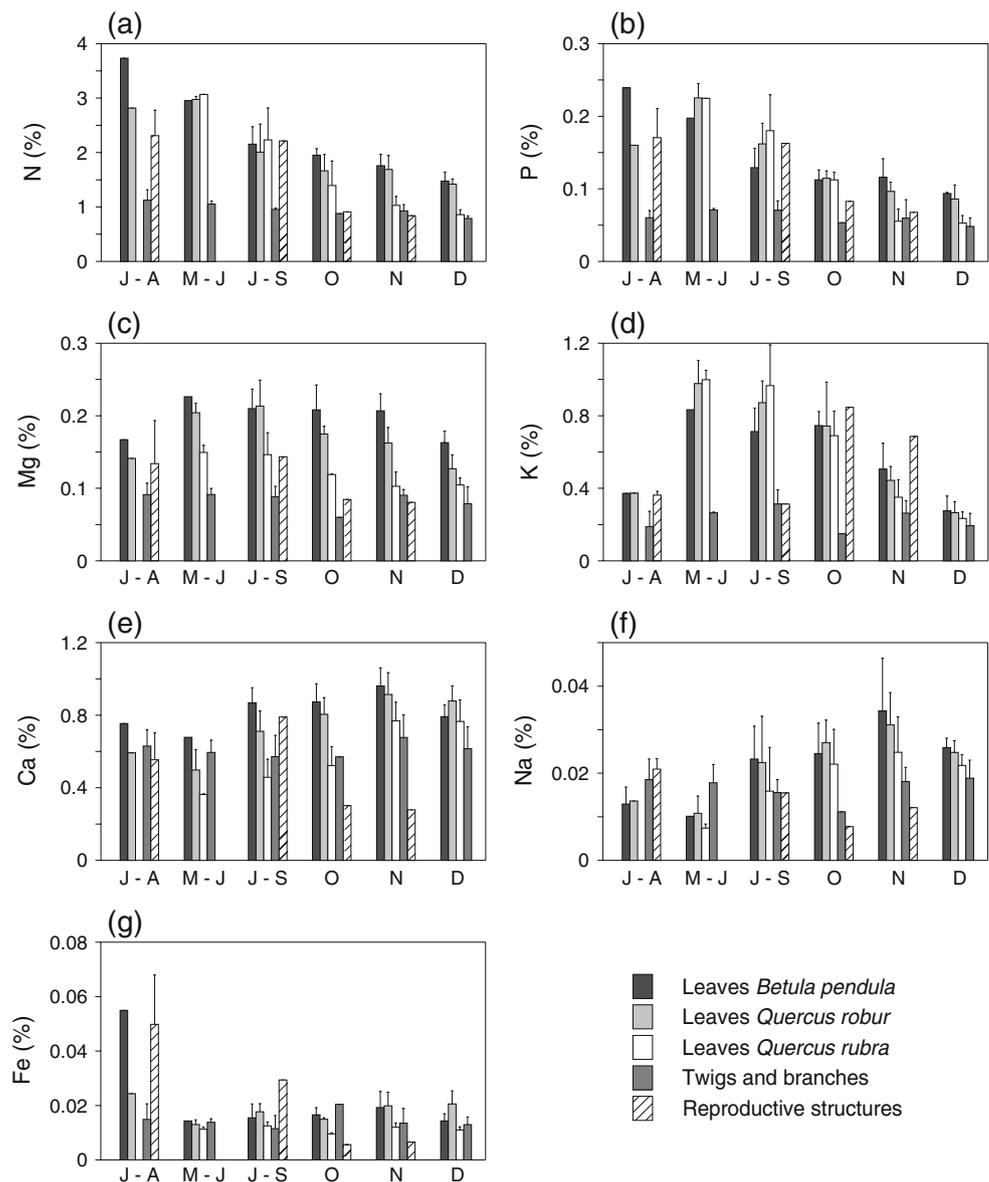
had the highest overall nutrient concentrations per mass unit and *Q. rubra* leaves the lowest (Table 3). Furthermore, for N, P, and Mg, the annual concentrations in fallen leaves of *Q. robur* were significantly higher than in *Q. rubra* leaves. The tree species' effect on the annual mass-weighted mean LLF concentrations was significantly ( $p<0.05$ ) influenced by the year, except for Ca ( $p=0.38$ ). Relative standard deviations of the mass-weighted mean nutrient concentrations in LLF were generally lower than 10% of the mean (Table 3).

The seasonal evolution of nutrient concentrations in the actual LLF at the forest floor depends on the combination of the species-specific nutrient concentrations and shedding periods. This is shown for the mass-weighted concentration of N and Ca, as two representative example nutrients, in three theoretical LLF mixtures that are representative for different parts of the study stand, with 70% of the annual LLF mass contributed by one of the three main species and 15% by the two other species (Fig. 5). The first half of the year is not included because of the negligible leaf shedding in that period (<3% of the annual LLF). For N, the three mixtures differed most in the mass-weighted concentration in October and November, while this held true for Ca in July–September and October.

#### 4 Discussion

The mean annual litterfall mass ( $5.5 \text{ t ha}^{-1}$ ) of the studied 60-year-old spontaneously developed mixed deciduous forest was relatively high for a temperate deciduous woodland, though not exceptional. For an uneven-aged forest (115–160 years) and a mixed 80-year-old forest in the south of Belgium, litterfall masses of  $5.6$  and  $5.3 \text{ t ha}^{-1} \text{ year}^{-1}$  were reported, respectively (Duvigneaud and Denayer–De Smet 1971). For 25 forests in the north of Belgium, litterfall varied from  $2.5$  to  $6.5 \text{ t ha}^{-1} \text{ year}^{-1}$  (Muys 1993). Lonsdale (1988) and Nihlgard (1970) reported an average contribution of leaves to the total litterfall mass of 67% and 64%, respectively, which is comparable with our data (67%). Other studies, for young forests in particular, reported a higher share of foliage in the total litterfall mass (Bray and Gorham 1964; Pedersen and Bille-Hansen 1999). In a time sequence of *Fagus sylvatica* forest development, Lebret et al. (2001) found a decrease in the share of leaves from thicket stage (89%) to mature forest (69%), a trend which is also described by Binkley (1986). In our study area, the share of twigs and branches (23%) is high compared with the studies of Bray and Gorham (1964; 12–15%) and Lebret et al. (2001; 8–13%). This can be explained by (a) the typical “swaying” of *Betula* trees, which results in branch damage and fall, and (b) the present forest development stage, which is characterized

**Fig. 4** Temporal course (six periods within the year, averaged over the measuring years) of nutrient concentrations (%) in different litterfall fractions. Vertical lines indicate standard deviations ( $n=3$ )



by a heavy reduction in the stem number of *Betula* (Vanhellemont et al. 2009) due to self-thinning of the densely stocked and unmanaged *Betula* clusters and increasing competition with *Quercus*.

The quantities of most litterfall fractions were relatively constant between years, although for *Betula* leaves, a remarkably high mass was observed in the second measuring year. It is known that annual litterfall can vary considerably, and part of this variation has been related to differing weather conditions for coniferous species (Starr et al. 2005; Saarsalmi et al. 2007). Furthermore, fluctuations in litter quantity exceeding 10% have been reported in case of insect infestations (Pedersen and Bille-Hansen 1999), mast years (Lebret et al. 2001), or exceptional climatologic conditions such as frost, storm damage, dry or wet periods (Knutson 1997; Pedersen and Bille-Hansen 1999). Clima-

tologic conditions may explain the higher values for *Betula* leaves in 1999, but the study period is too short to derive sound conclusions. Also for *Q. robur*, significant differences in leaf litter mass were noted between years, with a slightly lower value in 1998. These small differences can hardly be considered exceptional, and yearly differences of the same magnitude have also been observed in other studies (Le Dantec et al. 2000; Lebret et al. 2001). For all litterfall fractions, seasonal patterns were stable over the measured years, but the temporal patterns differed considerably between the different fractions (species-specific leaves, twigs, and reproductive structures). The three species differed with respect to start and duration of the leaf shedding period, and consequently, the litterfall mass and fraction of each tree species changed over the autumn period.

**Table 3** Annual mass-weighted mean±standard deviation ( $\bar{X}\pm\text{SD}$ ) of the nutrient concentrations ( $\text{g kg}^{-1}$ ) of the different litterfall fractions for five litter traps

Litter fraction	Year	N	P	Mg	K	Ca	Na	Fe
Leaves <i>Betula pendula</i>	1998	17.7±0.7	1.04±0.10	1.90±0.14	5.87±0.30	8.79±0.38	0.34±0.02	0.16±0.02
	1999	19.8±1.0	1.25±0.08	2.14±0.19	7.09±0.62	9.63±0.37	0.24±0.03	0.22±0.03
	2000	20.9±0.6	1.27±0.16	2.15±0.17	6.20±0.42	8.46±0.59	0.25±0.03	0.17±0.02
<i>Quercus robur</i>	1998	17.8±1.0	1.07±0.16	1.53±0.17	3.67±0.28	9.11±0.93	0.24±0.01	0.14±0.04
	1999	14.4±1.3	0.93±0.14	1.53±0.13	4.51±0.18	8.72±0.75	0.25±0.01	0.15±0.05
	2000	17.4±0.7	0.97±0.12	1.51±0.20	4.03±0.37	8.36±1.11	0.33±0.01	0.11±0.02
<i>Quercus rubra</i>	1998	11.2±1.0	0.57±0.08	1.16±0.11	3.52±0.52	7.65±0.92	0.33±0.06	0.12±0.02
	1999	8.8±1.0	0.52±0.09	0.92±0.22	3.71±1.31	7.52±1.28	0.17±0.03	0.12±0.03
	2000	13.6±1.6	0.85±0.21	1.06±0.17	4.29±0.53	6.88±0.85	0.26±0.11	0.11±0.01
Twigs and branches <sup>a</sup>	1999	10.9±1.7	0.61±0.10	0.97±0.10	2.61±0.74	6.35±0.97	0.18±0.04	0.15±0.04
	2000	9.5±1.5	0.62±0.12	0.83±0.09	2.21±0.69	6.19±0.87	0.17±0.05	0.14±0.03
Reproductive structures	1999	22.0±3.0	1.57±0.39	1.44±0.51	4.51±0.16	5.64±1.25	0.17±0.02	0.41±0.09
	2000	13.7±1.9	1.10±0.15	1.00±0.14	5.93±0.80	4.47±0.60	0.12±0.02	0.15±0.02

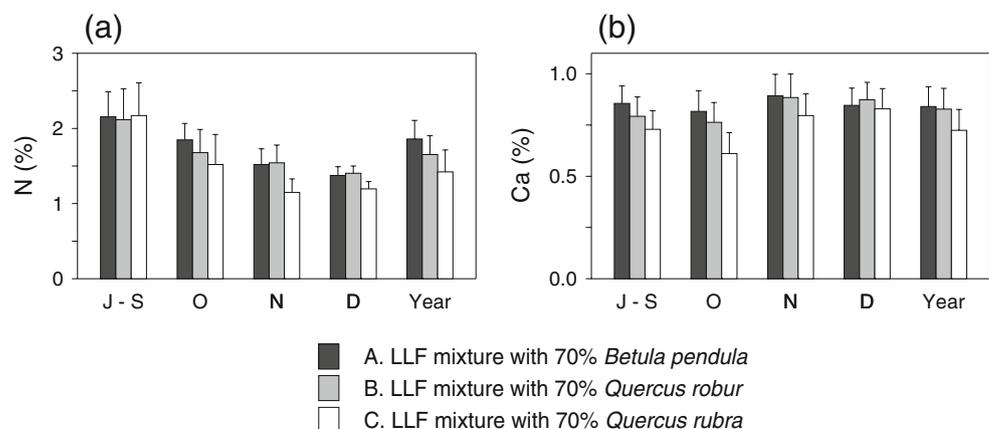
<sup>a</sup> Diameter < 2 cm

Because of the relatively low spatial variation in total leaf litterfall, the spatial heterogeneity in leaf fall in this mixed forest was mainly related to the relative contribution of each species to the total leaf fall. The spatial pattern of leaf litterfall for each tree species persisted over the study period, while the spatial distribution of falling twigs and branches was more random. Similarly, high temporal variation of annual twig fall has been found before (Bray and Gorham 1964; Lebret et al. 2001). Fall of branches is a local phenomenon of great importance for the total litterfall mass, and consequently, the spatial distribution of total litterfall was variable between the measuring years. Therefore, predicting humus build-up using litterfall measurements of a few measuring years might be difficult in the present development stage of the studied forest type. Besides variations in the horizontal distribution, the litter layer is characterized by a vertical gradient determined by the main leaf shedding periods, with *Betula* leaves at the bottom, covered by a mixture of species with domi-

nance of first *Betula* and then *Q. rubra*, and on top a layer of *Q. robur* leaves. Such diversity in litter composition will affect the temporal and spatial distribution of microclimatic conditions and litter composition, which is very important for the distribution of the decomposer community (Sayer 2006). Further redistribution of fallen leaves on the forest floor is likely small because of the absence of slopes in the study stand, moisture surplus in winter, decreased wind velocities due to the dense and evergreen understory of *Rubus* spp., and fungal mycelia binding fresh litter to the forest floor.

Per mass unit, the lowest amount of nutrients was returned to the forest floor by *Q. rubra* leaves because of the lower concentrations of Mg, Ca, and Na during the entire year and because of the lower concentrations of N and P during the autumn months. The K and P concentrations in *Q. rubra* leaves corresponded to those found by Côté and Fyles (1994), while N concentrations were about 50% higher and Ca and Mg about 50% and 100% lower,

**Fig. 5** Temporal course (July–September, October, November, December, and annual mass-weighted mean, averaged over the measuring years) of **a** N and **b** Ca concentrations (%) in three theoretical leaf litterfall mixtures of *Betula pendula*, *Quercus robur*, and *Q. rubra* (with an annual contribution to the LLF mass of 70% by one species and of 15% by the two other species each). Vertical lines indicate standard deviations ( $n=3$ )



respectively. Besides differences in soil characteristics, the lower concentration of Mg may be due to the high atmospheric N deposition in the studied region since excess  $\text{NH}_4^+$  in soil solution hinders or impedes  $\text{Mg}^{2+}$  consumption by roots (Marschner 1995). For all nutrients except for Na, *Betula* returned significantly more nutrients to the soil per mass unit leaf litter compared with the two *Quercus* species. An important proportion of *Betula* leaf litter already fell during summer and early autumn when the nutrient concentrations were high, and during the main leaf shedding period from October to December, the nutrient concentrations of *Betula* litter were also higher than the other two species. Compared with data presented by Côté and Fyles (1994) on *Betula papyrifera* Marsch. and *Betula alleghaniensis* Britton, the N concentrations were again much higher and the Ca and Mg concentrations much lower at our study site. A comparison of the two *Quercus* species showed that *Q. robur*'s weighted mean leaf nutrient concentrations were significantly higher compared to *Q. rubra*, except for Na and Ca. Similarly, Reich et al. (2005) found higher leaf nutrient concentrations in both *B. pendula* and *Q. robur* compared to *Q. rubra*.

Although considerable differences in leaf litterfall nutrient concentrations were found between the studied tree species throughout the year, the overall seasonal pattern was species-independent. In general, after a peak in May–June, concentrations of N, P, K, and Mg decreased steadily, probably due to carbohydrate accumulation and leaching. For deciduous forests, it is well documented that, during autumn, N and P, and to a lesser degree K and Mg, are recycled from the senescing leaves (Lal et al. 2001). We can thus suppose that in the period before abscission, resorption and leaching were responsible for the major part of the decrease in nutrient concentrations. The concentrations of Ca and Na, which are two relatively immobile elements in leaves, were lowest in May–June during the period of leaf expansion, after which they continuously increased till November.

Without severe competition of late-successional species (e.g., *Acer* spp., *F. sylvatica*), the present stand conditions allow recruitment of *Q. rubra* only (Gordon et al. 1995). *Quercus rubra* will gradually become the most important species of the mixture in the next decades since its physiological capacity to regenerate and survive beneath a closed or semi-closed canopy goes together with its higher competitive strength. As *Betula* is outcompeted by *Quercus* in the study area (Vanhellemont et al. 2009), the major input of *Betula* leaf litter and the amount of nutrients returning through leaf litterfall will decrease, and the seasonal evolution of the nutrient input will change (Fig. 5). The nutrient input by twigs and reproductive structures will change too because a higher share of dead *Betula* branches accompanies the reduction of *Betula* leaf

litterfall. Given the significantly higher nutrient concentrations, particularly of Ca, in *Betula* litter compared to *Quercus* leaves and twigs, the importance of *Betula* litter as a more rapidly decomposing admixture will continue to decrease. This is expected to have profound effects on the forest floor decomposition rate, the abundance and diversity of soil fauna, and the soil fertility. Consequently, the present study indicates the importance of considering potential differences in the litterfall quality of tree species. Forest management can affect the horizontal and vertical redistribution of nutrients in the humus layer of mixed deciduous forests.

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