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Nutrient return to the forest floor through litter and throughfall under 7 forest species after conversion from Norway spruce

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ABSTRACT

Tree species can influence nutrient return to the forest floor and nutrient cycling through the amount and chemical composition of throughfall and litter. We compared foliar nutrient concentrations, litter production, nutrient return and soil chemistry under 7 tree species planted on the same site after two generations of a Norway spruce (*Picea abies* (L.) KARST.) monoculture. Common alder (*Alnus glutinosa* (L.) GAERTN.), european beech (*Fagus sylvatica* L.), pedunculate oak (*Quercus robur* L.), silver birch (*Betula pendula* ROTH.), goat willow (*Salix caprea* L.) and rowan (*Sorbus aucuparia* L.) were planted within an experimental catchment on poor acid soil in south-eastern Belgium. Measurements were performed during one year, 11 years after planting. This study demonstrated that Ca, Mg, K and N concentrations in foliage and leaf litter are tree-species specific. Fresh foliage and foliar litter N concentrations were highest in alder and willow, while Ca, Mg and K concentrations were highest in rowan. Litter Ca concentrations were approximately twice in rowan than those of all other species. Differences in nutrient concentrations between foliage and leaf litter depended both on the element concerned and on tree species. The total average litterfall biomass ranged from 615 kg ha⁻¹ year⁻¹ under oak to 3122 kg ha⁻¹ year⁻¹ under rowan. Foliar litterfall represented above 85% for beech, spruce and oak, 70% for alder and willow and ca. 55% for birch and rowan. Reproductive parts formed 44% of total litterfall biomass under rowan. Ca, Mg, K and N return via throughfall, foliar litter and reproductive parts were higher under accompanying tree species (alder, birch, willow, rowan) than under the main commercial tree species (oak, beech, spruce). Total N return was in the order of 50 kg ha⁻¹ year⁻¹ under accompanying species, 33 kg ha⁻¹ year⁻¹ under spruce and near 20 kg ha⁻¹ year⁻¹ under beech and oak. Under rowan, total Ca, Mg, and K return to the forest floor through throughfall deposition, litterfall of leaves and reproductive parts amounted to 47, 9 and 66 kg ha⁻¹ year⁻¹, respectively. Compared to spruce, forest floor pH_{H2O} has increased by 0.4 unit under birch and rowan, and exchangeable Ca²⁺, Mg²⁺, K⁺ have increased about threefold under rowan. Planting rowan as accompanying species may therefore represent an interesting management option for improving forest floor chemistry on nutrient poor sites through Ca, Mg, and K nutrient return.

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1. Introduction

The forest canopy has a major influence on soil nutrient availability through the amount and chemical composition of litter and throughfall (Prescott, 2002; De Schrijver et al., 2007; Hansen et al., 2009). Tree species can further influence nutrient cycling through N₂ fixation, mineral weathering by root exudates, root uptake, soil processes, soil communities, and physical properties (Binkley and Giardina, 1998; Augusto et al., 2002; Aubert et al., 2010). Principles of sustainable forest management, such as the preservation of forests' biodiversity, productivity, soil and water resources, regeneration capacity, vitality, and carbon storage, as well as the adaptation of forest plantations to climate change, challenge previ-

ous management schemes, especially with regard to the choice of tree species. For example, the adaptation of forest management to climate change needs not only to consider species best suited to site characteristics, but also to future climatic conditions whilst maintaining/increasing the carbon sequestration potential (Ciais et al., 2008; Bolte et al., 2009). Furthermore, concerns about soil quality under coniferous monocultures (Augusto et al., 2002; Spiecker, 2003) have led to a shift in plantation strategies towards the use of native tree species adapted to local site conditions through the conversion of coniferous monocultures to broadleaved or mixed stands in several regions (Spiecker et al., 2004). Changes in species composition of plantation forests thus call for in-depth knowledge on the effects of tree species on ecosystem functioning when planted in monocultures and in mixtures (Richards et al., 2010).

Tree species differ in rooting depth and pattern, mycorrhizal associations, root transport and their ability of mobilising nutrients

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by secreting root exudates (Attiwill and Adams, 1993; Larcher, 2003), scavenging of atmospheric aerosol particles and canopy exchange (De Schrijver et al., 2007; Talkner et al., 2010). They influence nutrient return to the forest floor by both throughfall deposition (Lovett et al., 1996; Augusto et al., 2002; De Schrijver et al., 2008; Talkner et al., 2010) and litterfall (Binkley, 1995). Canopy characteristics including architecture, roughness and density, as well as nutrient status of the foliage influence the chemistry of throughfall (Michopoulos et al., 2007). Dry deposition is generally higher under conifers, as their canopy is more efficient in intercepting particles and cloud droplets than deciduous species (Erisman and Draaijers, 2003; de Vries et al., 2007). Throughfall deposition may thus be an important source of acidity and nutrients, but the relative importance of throughfall and litterfall have been rarely reported (Parker, 1983; Zimmermann et al., 2002). The efficiency of mineral nutrient uptake by roots and preferences for certain ions are inherent plant characteristics (Larcher, 2003; Reimann et al., 2007) leading to differences in leaf/needle and litter nutrient concentrations (Reimann et al., 2007). Such differences may explain changes in the properties of the upper soil, especially by so-called 'soil improving species' (Miller, 1984; Binkley, 1995). As trees are effective in taking up nutrients and redistributing them to the soil surface, afforestation or a change in vegetation can alter the bioavailability of mineral nutrients (Finzi et al., 1998; Jobbágy and Jackson, 2004; Vittori Antisari et al., 2013). Soil nutrient availability under tree species is often analysed through the lens of the influence of litter quality on litter decomposition rates (Reich et al., 2005; Hobbie et al., 2006; Jacob et al., 2009; Aponte et al., 2012). The rapid decomposition of high quality litter (low lignin/N or C/N ratio) during the initial stages (Melillo et al., 1982) has been previously used to explain differences in soil nutrient availability (see Dijkstra, 2003; Prescott, 2005 and references therein). While first-stage decomposition rates will determine the early rate of nutrient release, they are not likely to be related to the total amount of nutrients released. Indeed, high N concentrations will have a rate-retarding effect on litter decomposition at later stages and determine a limit value for mass loss, the 'maximum decomposition limit' (Berg, 2000). Consequently, it has been suggested that rather than decomposition rates it is litterfall mass, litter nutrient content and maximum decomposition limit that determine nutrient release (Prescott, 2002, 2005).

Several reviews showed that the quantity and quality of litterfall of different species differ at the global scale (Bray and Gorham, 1964; Vogt et al., 1986; Hobbie, 1992). While these data supply important information on the general patterns and controls of litterfall, such as climate (e.g. Berg and Meentemeyer, 2001; for conifers), they fail at providing information on the litterfall and nutrient return of different species when growing under similar conditions. In other, more local studies, the interpretation of tree species effects at different sites is often difficult due to possible pre-existing differences between the sites (Sariyildiz and Anderson, 2005; Berger et al., 2009). As some site-specific effects may be masked in large studies across environmental conditions (Berger et al., 2009; Hansen et al., 2009), common garden experiments and research on single sites allow evaluating tree species effects without environmental confounding factors (Binkley, 1995). In common garden experiments, tree species have been shown to influence soil N pools and dynamics (Finzi et al., 1998; Hobbie et al., 2007; Vesterdal et al., 2008), nutrient cycling and C turnover (Prescott, 2002; Vesterdal et al., 2012), soil acidity, fertility and earthworm abundance and diversity (Finzi et al., 1998; Reich et al., 2005), and litter decomposition (Hobbie et al., 2006). Most of these changes were mediated by a difference in litter quality, such as lignin, N and Ca concentrations. However, the majority of studies concern only main commercial tree species in mature stands (e.g. Binkley, 1995; Augusto et al., 2002) and surprisingly

little is known on the nutrient return to the forest floor of accompanying forest tree species in comparison to main commercial species (Reimann et al., 2007). Furthermore, data on nutrient return during early stand development are needed, as there is a distinct species effect on nutrient uptake at this stage (Miller, 1995), most likely to influence nutrient return to the forest floor. After canopy closure, nutrient requirements are mainly satisfied through retranslocation from older tissues (Miller, 1995; Ranger et al., 1997).

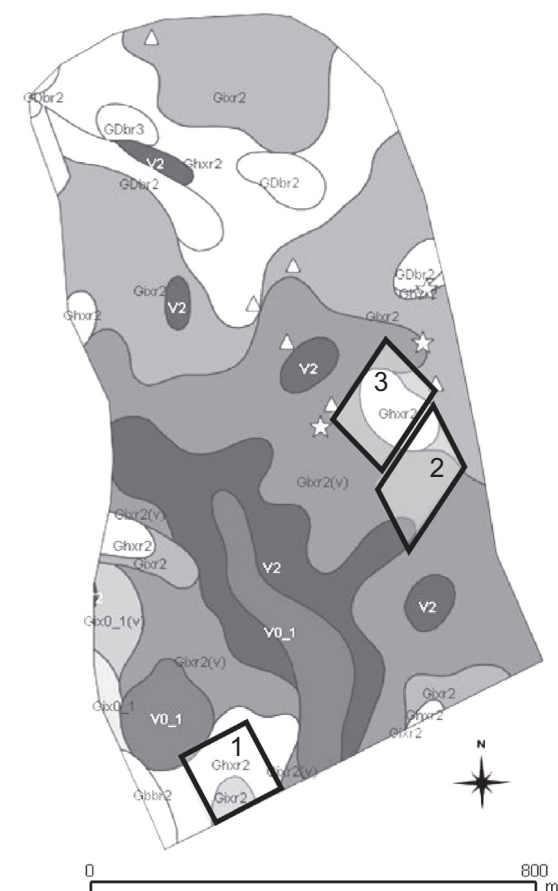
The general objective of this study was to examine the potential of three main commercial (spruce, oak, beech) and four accompanying (birch, rowan, willow, alder) temperate forest tree species to improve forest floor chemistry through nutrient return in throughfall and litterfall in the absence of environmental confounding factors. The study was performed on an acid, nutrient-poor site after two generations of Norway spruce monoculture, showing forest decline symptoms and Mg deficiencies (Weissen et al., 1990). We used a common garden experiment, where 6 tree species were planted in a replicated block design (in addition to spontaneous regenerated Norway spruce), to explore, 11 year after planting: (1) nutrient concentrations in fresh foliage and litter fractions, (2) biomass of litterfall fractions, (3) nutrient return to the forest floor (throughfall and litterfall), and (4) forest floor chemistry.

2. Materials and methods

2.1. Study site and experimental design

The study was conducted within the 81-ha experimental catchment 'Robinette' (50°33'N, 6°04'E; 470–530 m above sea level), located in the 'Hertogenwald' (literally the 'Duke's forest') in the 'Ardenne' natural region of south-eastern Belgium. The climate in the study area is characterised by a mean annual temperature of 7 °C and a mean annual precipitation of 1300 mm (Buldgen, 1984). The geological formation consists of quartzites, quartzophyllades and phyllades belonging to the Quaternary Period, covered by eolian loess loam (Buldgen, 1984). The soils in the catchment are classified as Cambisols (Dystric) (IUSS, 2006). They are characterised by moder to dysmoder humus type and a base saturation of 10–15% in the mineral soil horizons (Delecour, 1978). According to the soil map of Belgium (Legrain et al., 2011), 74% of the catchment area is covered by stony loamy soils ('G'; more than 5% gravel) with moderately poor to poor drainage ('h' and 'i'), 21% by peaty soils ('V'; more than 30% organic matter) and the remaining 5% are stony soils with good drainage (Fig. 1).

In 1996, the second generation Norway spruce (*Picea abies* (L.) KARST.) monoculture was clearcut and, in 1998, 3 fenced plots of 2 ha were installed on Gh or Gi soils (Fig. 1). Within these three fenced plots, common alder (*Alnus glutinosa* (L.) GAERTN.), pedunculate oak (*Quercus robur* L.), silver birch (*Betula pendula* ROTH.), goat willow (*Salix caprea* L.) and rowan (*Sorbus aucuparia* L.) were planted in alternate rows, spaced by 2.5 m. These species are suitable for the site, according to climate, soil hydrological and trophic conditions (Weissen et al., 1994). European beech (*Fagus sylvatica* L.) is not well adapted to the hydrological conditions of the soil at this site, but, according to general practice in the area, one row was planted for ornamental reasons alongside the forest path in plot 1 (Fig. 1). Alder, rowan, birch and oak were also planted within the catchment (with individual protections against deer damage). Norway spruce was not planted, but spontaneous regeneration resulted in thickets across the catchment, with trees in the same age class as planted deciduous species. We sampled within the 3 fenced plots and under spruce trees located in the thickets across the catchment (Fig. 1). Measurements were performed un-



Legend:

- 1, 2, 3 fenced plots: fresh foliage, throughfall and litterfall under planted deciduous species
- 1 fenced plot: soil sampling under planted deciduous species
- △ fresh foliage, throughfall, litterfall and soil sampling under spruce thickets
- ☆ fresh foliage, throughfall and litterfall sampling under spruce thickets

Fig. 1. Map of the Robinette experimental site and sampling locations. Grey tones and letters indicate soil types according to the soil map of Belgium.

der the canopy of individual trees and prior to crown closure, so interactions among tree species are considered to be negligible.

2.2. Stand characteristics

Height, density and stem circumference of live trees (>2 m height) were measured in April 2010 within five randomly located 0.04 ha subplots (20 m × 20 m) in each of the 3 fenced plots (McIntire and Fortin, 2006) and within ca. 10 × 10 m areas of the nine Norway spruce plots situated across the catchment.

2.3. Fresh foliage nutrient contents

Fresh leaves and needles were sampled in August 2009. Nine deciduous trees per species were randomly selected within the fenced plots (3 trees per species per plot). All 9 beech trees were located within the row of beech located in plot 1. Nine spruce trees

were selected across the catchment ($n = 9$) (Fig. 1). Alder, birch, rowan, willow, oak and beech leaves were collected by hand around the tree from the upper half and the outer canopy (leaves developed in full light) of the tree (Rautio et al., 2010). Spruce needles were sampled from 3 branches detached from the upper half and the outer canopy around each selected tree. For each branch, current-year needles (spruce0), 1-year-old needles (spruce1) and 2-year-old needles (spruce2) were sampled. All samples were placed in paper bags and transported to the laboratory. They were dried to a constant weight (70 °C, 24 h), ground with an electronic grinder (Culatti, Model DFH-48, 1 mm mesh size) and stored in pillboxes until analysis. Samples were digested with the sulphuric acid–hydrogen peroxide procedure (Allen, 1989). Concentrations of Ca, Mg, and K were determined using ICP-AES (Varian, Australia). Total C and N contents were determined by dry combustion using a C–N–S elemental analyser (Carlo Erba, Italy).

2.4. Litterfall

Litterfall was collected monthly, from June 2009 to May 2010, with circular litter traps (0.4 m²). The traps consisted of 1 mm nylon mesh netting attached to a plastic hoop, raised 1 m above the ground with 3 wooden poles (Pitman et al., 2010). Nine litter traps were installed under nine, randomly selected, deciduous trees per species (alder, birch, rowan, willow) within the fenced plots (3 trees per species per plot). For beech, all 9 litter traps were installed within the row of beech located in 1 plot. Litter traps were installed under 9 spruce trees across the catchment (Fig. 1).

Litter from species other than the target tree was removed (representing less than 5%) and litterfall was divided into three fractions: leaves/needles, twigs, reproductive parts (flowers, seeds and fruits), dried to constant weight (70 °C, 24 h), weighed and pooled to constitute an annual sample. Well mixed subsamples were ground with an electronic grinder (Culatti, Model DFH-48, 1 mm mesh size) and stored in pillboxes until analysis. Leaves/needles and reproductive parts fractions were chemically analysed as describe above.

2.5. Throughfall

Throughfall was collected monthly from June 2009 to May 2010. Collectors consisted of polyethylene funnels, 10 cm diameter, placed at 1 m height and connected by a black polyethylene tube to a polyethylene bottle placed below the ground. A nylon mesh (mesh size 1 mm) was placed in the neck of the funnels to avoid contamination.

Throughfall collectors were placed under the same trees than those for litterfall sampling. Under spruce, throughfall was sampled with 5 collectors (contents pooled), installed in the 9 plots across the catchment ($n = 9$). Under alder, birch, rowan, willow, and oak throughfall was sampled under the 9 randomly selected trees of each species in the fenced plots (3 trees per species per plot). Throughfall samples of the three collectors under each species in each fenced plot were pooled ($n = 3$). Under beech, all 9 collectors were installed within the row of beech located in 1 plot and pooled by groups of 3 ($n = 3$).

Throughfall pH was measured with a glass electrode (WTW, pH-Electrode SenTix 41). Samples were filtered (filter 615^{1/4} Machery-Nagel, Germany) and stored at 4 °C until analyses. NO₃⁻-N concentrations were determined using High Performance Liquid Chromatography (HPLC, Hitachi). Cations (Ca²⁺, Mg²⁺, K⁺) were analysed using ICP-AES (Varian, Australia). NH₄⁺-N and dissolved organic nitrogen (DON) were analysed colorimetrically with a continuous flow analyser equipped with an UV digester (AutoAnalyzer3, Bran-Luebbe, Germany). Dissolved organic carbon (DOC) was measured

with a Total Organic Carbon analyser (Labtoc, Pollution and Process Monitoring Limited, UK).

2.6. Forest floor sampling and analyses

Forest floor (Of and Oh, <10 cm thick) was sampled beneath the canopy of 6, randomly selected, trees of each species in the fenced plot 1 and under 6 spruce trees located in the catchment. The 6 soil sampling locations were chosen randomly out of the 9 throughfall/litterfall sampling plots for each species. Each sample was a composite of 5 subsamples taken with a corer (8.2 cm diameter) at 1 m distance around each selected tree. Samples were sieved (4 mm) and stored at 4 °C before analysis (within one week of sampling). Soil pH was measured in distilled water and 1 M KCl with a glass electrode (WTW, pH-Electrode SenTix 41) in a soil suspension (1:1; v:v). Exchangeable cations (Ca^{2+} , Mg^{2+} , K^{+}) were extracted using 0.1 M BaCl_2 (Hendershot and Duquette, 1986). Chemical analysis of the filtered (Machery-Nagel 615^{1/4}, Germany) BaCl_2 extracts were performed using ICP-AES (Varian, Australia). Soil C and N contents were measured with a C–N–S elemental analyser (Carlo Erba, Italy) on oven dried and ground subsamples. The dry mass of the sample was calculated by weight loss after drying 3–5 g of soil at 105 °C to constant weight.

2.7. Data analyses

Data collected for individual trees were extrapolated to the hectare scale for each tree species separately. Annual throughfall fluxes were calculated for each sample by summing monthly fluxes, obtained by multiplying monthly throughfall or bulk volume by element concentration. Annual potential nutrient return to the forest floor from foliar litterfall and reproductive parts was calculated by multiplying element concentrations with the quan-

tity of the litter fraction for each litter trap. Foliage to leaf litter ratios were calculated from mean element concentrations in each species.

Effects of tree species were analysed by two-way analysis of variance, with plot as a block factor. As a block effect was not pronounced (alder and rowan smaller in plot 2), one-way analysis of variance was performed to evaluate the differences between the tree species investigated in foliage and litterfall nutrient contents, litterfall quantity and potential nutrient return to the forest floor (proc GLM, SAS 9.2; SAS Institute Inc., Cary, NC, USA). Differences in forest floor chemistry were also analysed with one-way ANOVA. In case of significant differences, means were separated by Duncan's multiple range test. Results are reported as significant when $P < 0.05$.

3. Results

3.1. Stand characteristics

Mean height, circumference and density for young spruce thickets (natural regeneration) across the catchment were 4 m, 16.7 cm and 6028 trees ha^{-1} respectively (Table 1). Whereas tree height and circumference were in the same range than those of the other species, the density of spruce thickets was much higher than that of deciduous species planted in the three fenced plots (no significant difference between the three plots). Within plots 1 and 2, tree density did not differ between the deciduous species. In plot 3, birch density was significantly higher compared to oak and willow.

Within all plots (Table 1), birch trees were largest with mean (across plots) height and circumference of 6.6 m and 29 cm, respectively. In plot 1, alder were also larger (height: 5.9 m) than other species, except rowan. Birch trees had a higher circumfer-

Table 1

Mean (SE; $n = 5$) tree height, tree density and circumference at 130 cm of planted (1998) tree species in three fenced plots and spruce regeneration in thickets ($n = 9$) within the catchment in 2010. Number of trees measured per plot (minimum–maximum number measured in 5 subplots).

Stand characteristics	Species	Catchment	Plot 1		Plot 2		Plot 3	
Height (m)	Alder	4 (0.3)	6.0 (0.7) a	A	3.4 (0.2) b	B	4.5 (0.4) b	AB
	Birch		6.7 (0.4) a	A	6.4 (0.2) a	A	6.6 (0.3) a	A
	Beech		6.3 (0.4)					
	Oak		3.7 (0.2) b	A	3.2 (0.3) b	A	3.8 (0.1) b	A
	Willow		3.4 (0.2) b	A	3.2 (0.1) b	A	3.7 (0.0) b	A
	Rowan		5.2 (0.4) ab	A	3.9 (0.2) b	B	5.1 (0.2) ab	A
	Spruce							
Tree density (stems ha^{-1})	Alder	6028 (2161)	270 (44) a	A	135 (37) a	A	185 (52) ab	A
	Birch		260 (71) a	A	125 (26) a	A	305 (63) a	A
	Beech		n.d.*					
	Oak		130 (48) a	A	30 (18) a	A	40 (26) b	A
	Willow		140 (38) a	A	70 (46) a	A	80 (58) b	A
	Rowan		165 (27) a	A	180 (65) a	A	200 (64) ab	A
	Spruce							
C_{130} (cm)	Alder	16.7 (1.8)	23.6 (4.3) a	A	15.3 (1.5) b	A	23.9 (4.1) ab	A
	Birch		24.3 (2.1) a	A	31.7 (2.2) a	A	31.2 (3.1) a	A
	Beech		21.1 (2.5)					
	Oak		13.9 (1.3) a	A	15.9 (3.6) b	A	11.5 (0.8) b	A
	Willow		n.d.		n.d.		n.d.	
	Rowan		19.3 (1.0) a	A	18.1 (1.1) b	A	19.2 (0.8) ab	A
	Spruce							
Number of trees	Alder	197 (20–27)	54 (7–16)		27 (2–9)		37 (1–12)	
	Birch		52 (5–21)		25 (2–7)		61 (9–21)	
	Beech		13					
	Oak		26 (1–10)		0–4 (6)		8 (0–5)	
	Willow		28 (2–8)		0–10 (14)		16 (0–12)	
	Rowan		33 (4–10)		2–16 (36)		40 (1–11)	
	Spruce							

Different small letters in each column denote significant differences among tree species ($P < 0.05$). Different capital letters in each row denote significant differences among plots ($P < 0.05$).

* n.d.: Not determined.

ence than some other species in plots 2 and 3. The circumference of the other tree species was similar in the three plots.

3.2. Fresh foliage and litter nutrient contents

Fresh foliar N, Ca, Mg and K concentrations differed significantly between the seven tree species growing on the same site (Table 2). N concentrations were three times higher in alder and willow than in spruce ($P < 0.05$), while they were intermediate in the other species. Ca, Mg and K concentrations were highest in fresh foliage of rowan and lowest in spruce needles. Alder and willow also had higher K concentrations in fresh foliage than the other species. Ca concentrations in spruce significantly increased by 146% from current-year needles to 2-year-old needles (Table 3). Mg and K concentrations did not differ significantly in spruce needles of different age classes.

Foliar litter C/N ratio was significantly higher for beech and spruce (ca. 50) than for willow and alder (ca. 25) (Table 2), whereas N concentrations were highest in alder and willow. Foliar litter Ca concentrations were approximately twice in rowan (20 mg g⁻¹) than all other tree species. Foliar litter Ca concentrations of beech were also significantly higher than the concentrations of most other species (except rowan and oak). Mg foliar litter concentrations were also highest in rowan, followed by birch and alder. K concentrations in foliar litter ranged from 2.8 (spruce) to 9.0 (willow) mg g⁻¹ in the different species.

Differences in nutrient concentrations between fresh foliage and leaf litter depended both on the element concerned and on tree species (Table 2). N and K concentrations decreased substantially during senescence for all species, except for spruce and oak, respectively. In spruce needles, N concentrations were higher in leaf litter compared to the fresh foliage. K concentrations in oak leaves and litter were comparable. Calcium concentrations increased after leaf abscission for all species, except for rowan (ratio = 1). Mg concentrations in leaf litter decreased for alder, birch, beech and rowan, but increased for willow and spruce and were comparable for oak.

3.3. Litterfall

The mean total litterfall biomass flux was highest under rowan (3122 kg ha⁻¹ yr⁻¹) and birch, lowest under beech, spruce and oak (615 kg ha⁻¹ yr⁻¹) and intermediate under alder and willow

(Table 4). Foliar litterfall biomass was significantly lower under oak and beech (544 and 646 kg ha⁻¹ year⁻¹, respectively) than under the other tree species. Mean annual litter return as branches/twigs was highest under birch (651 kg ha⁻¹ year⁻¹) and alder, followed by willow and lowest under oak, beech, rowan and spruce (7.5 kg ha⁻¹ year⁻¹). Reproductive parts of litterfall biomass ranged from 0.0 (oak) to 1493 (rowan) kg ha⁻¹ year⁻¹. Willow, birch and alder showed intermediate values for litter return in form of reproductive parts (388–597 kg ha⁻¹ year⁻¹).

Foliar litterfall represented above 85% of total litterfall for the main forestry species beech, spruce and oak. Foliar litterfall of alder and willow represented ca. 70% of total litterfall biomass, the remaining fractions being branches/twigs and reproductive parts, in equal proportions. For birch and rowan, foliar litterfall represented ca. 55% of total litterfall biomass, the remaining fractions being branches/twigs and reproductive parts, in equal proportions under birch and mainly reproductive parts (44%) under rowan.

3.4. Nutrient return in throughfall and litterfall

Throughfall water fluxes were significantly lower, by ca. 50%, under spruce compared to the other tree species (Table 5). A comparison of annual nutrient fluxes via throughfall, foliage litter and reproductive parts among tree species indicated significant differences ($P < 0.05$) for most considered elements, except throughfall NH₄⁺-N, DON and total N (Tables 5 and 6).

Under the 7 tree species, Ca return to the forest floor occurred in the range of 6.1–9.8 kg ha⁻¹ year⁻¹ as throughfall deposition, 6.2–32.3 kg ha⁻¹ year⁻¹ in form of leaf litter and 0–5.6 kg ha⁻¹ year⁻¹ as reproductive parts (Table 5). Throughfall Ca²⁺ deposition was

Table 3

Mean (SE; $n = 9$) foliage nutrient concentrations in needles of different ages. Spruce0 = current year needles; Spruce1 = 1 year old needles; Spruce2 = 2 year old needles.

Needle age class	Macro-elements (mg g ⁻¹)		
	Ca	Mg	K
Spruce0	2.77 c (0.19)	0.62 a (0.04)	6.76 a (0.48)
Spruce1	5.67 b (0.24)	0.68 a (0.05)	6.27 a (0.40)
Spruce2	6.81 a (0.37)	0.59 a (0.06)	5.66 a (0.33)

Different letters indicate significant differences between age classes ($P < 0.05$).

Table 2

Mean (SE; $n = 9$) fresh foliage and foliar litter nutrient concentrations (mg g⁻¹). Ratio of concentrations in fresh foliage and foliar litter (fresh foliage/foliar litter): values greater than 1 indicate higher concentrations in fresh foliage; values below 1 indicate higher concentrations in foliar litter.

Species	Fresh foliage (mg g ⁻¹)				Foliar litter (mg g ⁻¹)					Fresh foliage/foliar litter			
	N	Ca	Mg	K	C/N	N	Ca	Mg	K	N	Ca	Mg	K
Alder	28.4 a (1.5)	7.23 b (2.02)	2.02 b (0.21)	13.42 a (0.54)	23.71 d (1.82)	22.67 a (1.56)	8.90 c (1.13)	1.79 b (0.15)	5.11 c (0.34)	1.25	0.81	1.13	2.63
Birch	21.2 bc (0.9)	7.60 b (0.68)	2.10 b (0.10)	10.94 b (0.61)	39.56 c (2.55)	13.06 b (0.74)	10.20 c (0.93)	1.83 b (0.06)	5.18 c (0.42)	1.56	0.75	1.15	2.11
Beech	22.8 bc (0.9)	6.49 b (0.38)	1.22 c (0.14)	9.36 b (0.63)	55.63 a (4.40)	9.21 c (0.68)	14.07 b (1.38)	0.71 d (0.10)	4.24 cd (0.54)	2.48	0.46	1.72	2.21
Oak	20.7 c (1.4)	6.24 b (0.47)	1.69 b (0.13)	9.41 b (0.86)	41.76 bc (3.96)	12.92 b (1.09)	11.56 bc (1.38)	1.40 c (0.09)	3.54 de (0.46)	1.60	0.64	1.06	1.05
Willow	25.2 ab (0.9)	6.53 b (0.77)	1.73 b (0.21)	13.57 a (0.89)	26.17 d (0.55)	20.15 a (0.43)	9.78 c (0.65)	1.59 bc (0.09)	8.95 a (0.71)	1.25	0.33	0.72	1.81
Rowan	18.9 c (0.6)	12.16 a (0.45)	3.46 a (0.13)	14.56 a (0.92)	40.31 bc (2.44)	13.09 b (0.93)	19.61 a (1.66)	2.41 a (0.13)	7.50 b (0.46)	1.44	1.05	2.47	4.11
Spruce	9.1 d (0.5)	2.77 c (0.19)	0.62 d (0.04)	6.76 c (0.48)	49.52 ab (4.49)	10.59 bc (0.79)	9.48 c (0.61)	0.82 d (0.06)	2.76 e (0.36)	0.86	0.29	0.76	2.45

Different letters indicate significant differences between species ($P < 0.05$).

Table 4
Mean (SE; $n = 9$) annual quantities and percentages of litterfall fractions.

Species	Quantities (kg ha ⁻¹ year ⁻¹)				Litterfall fractions (%)		
	Total litterfall	Foliar litter	Branches/twigs	Reproductive parts	Foliar litter	Branches/twigs	Reproductive parts
Alder	2213.2 b (334.2)	1401.6 a (164.6)	423.7 ab (169.5)	387.9 bc (77.3)	67.7 cd (5.1)	15.7 ab (4.2)	16.7 bc (2.3)
Birch	2845.0 ab (187.8)	1596.5 a (162.6)	651.0 a (141.1)	597.4 b (86.7)	56.4 d (4.5)	22.2 a (4.6)	21.4 b (2.9)
Beech	752.3 c (115.6)	645.9 b (101.6)	28.1 c (19.1)	78.3 c (10.5)	85.9 ab (2.3)	2.8 cd (1.9)	11.3 cd (1.2)
Oak	614.9 c (101.3)	544.1 b (97.9)	70.8 c (11.8)	0.0 c (0.0)	85.2 ab (4.9)	14.8 ab (4.9)	0.0 e (0.0)
Willow	2113.8 b (222.3)	1624.3 a (180.3)	229.1 bc (31.1)	260.3 bc (67.9)	76.9 bc (1.8)	11.0 bc (1.0)	12.1 cd (2.4)
Rowan	3122.2 a (362.0)	1593.8 a (177.7)	35.6 c (8.3)	1492.9 a (343.4)	55.3 d (6.9)	1.2 d (0.3)	43.5 a (6.7)
Spruce	1261.2 c (279.5)	1198.7 a (273.2)	7.5 c (1.9)	55.0 c (7.9)	94.1 a (1.1)	0.6 d (0.1)	5.3 de (1.1)

Different letters indicate significant differences between species ($P < 0.05$).

Table 5
Mean yearly throughfall volume (SE; $n = 9$ spruce, $n = 3$ deciduous), annual nutrient return in throughfall and in two litter fractions (SE; $n = 9$; kg ha⁻¹ year⁻¹). Total = sum of throughfall deposition and fluxes of foliar litter and reproductive parts.

Species	Throughfall Volume (mm year ⁻¹)	Ca (kg ha ⁻¹ year ⁻¹)				Mg (kg ha ⁻¹ year ⁻¹)				K (kg ha ⁻¹ year ⁻¹)			
		Throughfall	Foliar litter	Litter: Reproductive parts	Total	Throughfall	Foliar litter	Litter: Reproductive parts	Total	Throughfall	Foliar litter	Litter: Reproductive parts	Total
Alder	887.78 a (35.30)	8.08 ab (0.55)	12.94 bc (3.18)	1.52 bc (0.39)	22.5	2.16 ab (0.13)	2.50 b (0.39)	0.44 bc (0.10)	5.1	19.78 b (2.39)	7.25 c (1.06)	1.47 b (0.40)	28.5
Birch	1038.41 a (17.46)	9.80 a (1.80)	16.62 b (2.91)	2.53 b (0.54)	28.9	2.98 a (0.43)	2.94 b (0.36)	0.68 b (0.12)	6.6	27.37 a (3.79)	8.49 bc (1.32)	2.71 b (0.51)	38.6
Beech	916.03 a (14.89)	6.91 ab (0.50)	9.03 bc (1.61)	0.55 c (0.12)	16.5	1.59 b (0.13)	0.49 c (0.11)	0.05 c (0.01)	2.1	12.32 c (0.92)	2.99 d (0.70)	0.14 b (0.03)	15.5
Oak	1066.04 a (14.31)	9.32 a (0.46)	6.17 c (1.41)	0 c (0)	15.5	2.14 ab (0.17)	0.75 c (0.15)	0 c (0)	2.9	16.36 bc (2.81)	2.18 d (0.60)	0 b (0)	18.5
Willow	981.50 a (112.24)	7.80 ab (1.06)	15.30 bc (1.34)	1.33 bc (0.23)	24.4	1.85 b (0.20)	2.55 b (0.28)	0.26 bc (0.06)	4.7	29.54 a (1.36)	14.74 a (1.99)	2.71 b (1.12)	47.0
Rowan	1013.11 a (45.53)	9.36 a (0.70)	32.33 a (5.67)	5.55 a (1.06)	47.3	2.58 ab (0.15)	3.86 a (0.47)	2.11 a (0.47)	8.6	33.47 a (2.51)	11.74 ab (1.32)	20.49 a (4.87)	65.6
Spruce	525.61 b (57.58)	6.10 b (0.67)	11.72 bc (2.94)	0.19 c (0.03)	18.0	1.96 b (0.26)	1.08 c (0.29)	0.03 c (0.01)	3.1	17.62 bc (1.24)	3.71 d (1.12)	0.01 b (0.02)	21.34

Different letters indicate significant differences between species ($P < 0.05$).

significantly higher under birch, oak and rowan, compared to spruce. Ca return as leaf litter and reproductive parts was at the least twice as much under rowan compared to the other tree species. Three groups could be distinguished for the total Ca return (sum of throughfall deposition and fluxes of foliar litter and reproductive parts): highest return was observed under rowan (47.3 kg ha⁻¹ year⁻¹), followed by alder, birch and willow (22.5–28.9 kg ha⁻¹ year⁻¹), and lowest return under beech, oak and spruce (15.5–18 kg ha⁻¹ year⁻¹). Throughfall formed 20% (rowan)–60% (oak) of total annual Ca return.

Mg return to the forest floor was in the range of 1.6–3 kg ha⁻¹ year⁻¹ for throughfall, 0.5–3.9 kg ha⁻¹ year⁻¹ for foliar litter and

0–2.1 kg ha⁻¹ year⁻¹ for reproductive parts. Throughfall Mg²⁺ deposition was highest under birch and lowest under spruce, beech and willow. Mg return as leaf litter and reproductive parts was highest under rowan. As for Ca, three groups could be distinguished for the total Mg return: highest return was observed under rowan (8.3 kg ha⁻¹ year⁻¹), followed by alder, birch and willow (5.1–6.6 kg ha⁻¹ year⁻¹), and lowest return under beech, oak and spruce (2.9–3.1 kg ha⁻¹ year⁻¹). Mg return in throughfall was 30% (rowan)–76% (beech) of the total annual nutrient return.

K return to the forest floor was in the range of 12.3–33.5 kg ha⁻¹ year⁻¹ for throughfall, 2.2–14.7 kg ha⁻¹ year⁻¹ for foliar litter and 0–20.5 kg ha⁻¹ year⁻¹ for reproductive parts. Highest

Table 6

Mean yearly annual nitrogen return in throughfall (SE; $n = 9$ spruce, $n = 3$ deciduous; $\text{kg ha}^{-1} \text{ year}^{-1}$) and in two litter fractions (SE; $n = 9$; $\text{kg ha}^{-1} \text{ year}^{-1}$). DON = dissolved organic nitrogen. Total N return: sum of organic and inorganic throughfall deposition, fluxes of foliar litter and reproductive parts.

	Throughfall				Litter		Total N return N
	$\text{NO}_3^- \text{-N}$	$\text{NH}_4^+ \text{-N}$	DON	Total N throughfall	Foliar litter N	Litter: reproductive parts N	
Alder	2.80 b (0.55)	5.96 a (1.24)	5.30 a (0.52)	13.94 a (1.37)	33.42 a (6.09)	9.58 b (2.18)	57.1
Birch	4.90 ab (1.19)	6.67 a (1.67)	6.35 a (0.73)	17.27 a (3.11)	20.70 b (2.50)	10.11 b (1.62)	48.8
Beech	3.80 b (0.16)	4.33 a (0.52)	4.30 a (0.31)	12.11 a (0.69)	5.80 c (0.87)	1.07 c (0.18)	19.3
Oak	3.52 b (0.57)	6.07 a (1.39)	5.58 a (0.50)	15.16 a (1.69)	7.56 c (1.83)	0 c (0)	22.8
Willow	3.36 b (0.63)	4.55 a (0.70)	5.46 a (0.45)	13.32 a (1.36)	32.52 a (3.46)	5.59 bc (1.21)	52.6
Rowan	3.25 b (0.49)	3.76 a (0.48)	5.37 a (0.07)	12.02 a (0.88)	20.27 b (1.86)	18.45 a (4.36)	51.3
Spruce	8.27 a (1.19)	6.53 a (1.06)	3.96 a (0.36)	18.76 a (2.33)	13.75 bc (3.82)	0.64 c (0.11)	33.0

Different letters indicate significant differences between species ($P < 0.05$).

K^+ throughfall deposition occurred under birch, willow and rowan. Leaf litter K return was highest under willow, whereas rowan showed highest K return in form of reproductive parts. The same 3 classes as before can be distinguished for K return with highest return under rowan ($65.6 \text{ kg ha}^{-1} \text{ year}^{-1}$), followed by alder, birch and willow ($28.5\text{--}47 \text{ kg ha}^{-1} \text{ year}^{-1}$), and lowest return under beech, oak and spruce ($15.5\text{--}21.3 \text{ kg ha}^{-1} \text{ year}^{-1}$). K nutrient return was composed by 51% (rowan)–88% (oak) of throughfall.

N deposition via throughfall occurred in the forms of nitrate, ammonium and dissolved organic nitrogen (Table 6). $\text{NO}_3^- \text{-N}$ deposition was significantly higher under spruce ($8.3 \text{ kg ha}^{-1} \text{ year}^{-1}$), whereas $\text{NH}_4^+ \text{-N}$, DON and total N deposition did not differ among species. Total N deposition in throughfall ranged between 12–19 $\text{kg ha}^{-1} \text{ year}^{-1}$, with DON contributing by 21% under spruce and by 36–45% under the other species. N return to the forest floor was in the range of 5.8–33.4 $\text{kg ha}^{-1} \text{ year}^{-1}$ for foliar litter and 0–19 $\text{kg ha}^{-1} \text{ year}^{-1}$ for reproductive parts. Foliar litter deposition was highest under alder and willow ($33 \text{ kg ha}^{-1} \text{ year}^{-1}$), followed by birch and rowan ($20 \text{ kg ha}^{-1} \text{ year}^{-1}$), and lowest under beech, oak and spruce. N return through reproductive parts was at least double under rowan compared to the other species. Total N return to the forest floor ranged from 19–33 $\text{kg ha}^{-1} \text{ year}^{-1}$ under beech, oak and spruce, and was around 50 $\text{kg ha}^{-1} \text{ year}^{-1}$ under alder, birch, willow and rowan. Throughfall formed 24% (alder)–66% (oak) of total annual nutrient return for N.

3.5. Forest floor chemistry

The mean pH measured in H_2O and KCl ranged from 3.5 to 3.9 and from 2.9 to 3.2 under the different species (Table 7). $\text{pH}_{\text{H}_2\text{O}}$ was significantly increased by 0.4 units under birch and rowan, compared to spruce and beech. Soil pH_{KCl} under willow, birch, rowan and alder was significantly higher (0.2 units) than under spruce and oak. Soil C/N ratio was highest under beech (29) and lowest under alder (22). Exchangeable Ca^{2+} , Mg^{2+} , K^+ were significantly higher under rowan, with increases of 212%, 189%, 168%, respectively, compared to spruce.

4. Discussion

We studied nutrient return to the forest floor under 3 commercial and 4 accompanying forest tree species planted within an experimental catchment after 2 generations of Norway spruce monoculture. Our results demonstrate that tree species can improve forest floor nutrient availability, 11 years only since conversion from a second-generation Norway spruce plantation. Rowan showed high nutrient improvement capacities, with exchangeable Ca, Mg, and K concentrations increased by factors of 1.4–2.3, 1.7–2.7, 1.5–3.8, respectively, compared to the other investigated deciduous species, and by a factor of 3, 2.8, and 2.5 compared to

Table 7

Forest floor pH, C/N ratio and exchangeable Ca^{2+} , Mg^{2+} and K^+ (means, SE; $n = 6$).

Soil characteristic	Alder	Birch	Beech	Oak	Willow	Rowan	Spruce
pH (H_2O)	3.64 abc (0.08)	3.91 c (0.05)	3.49 a (0.11)	3.60 ab (0.08)	3.84 bc (0.11)	3.90 c (0.03)	3.54 ab (0.06)
pH (KCl)	3.10 bc (0.08)	3.13 bc (0.06)	2.96 ab (0.06)	2.89 a (0.03)	3.22 c (0.07)	3.11 bc (0.06)	2.86 a (0.04)
C/N	21.69 c (0.31)	24.03 bc (1.05)	28.94 a (1.01)	25.54 b (1.02)	24.76 bc (0.74)	23.58 bc (2.91)	26.44 ab (1.93)
Ca^{2+} (mg kg^{-1})	1416.63 c (246.82)	1766.86 bc (330.13)	1876.88 bc (287.82)	2364.99 b (237.35)	1608.38 bc (329.11)	3311.24 a (396.36)	1061.15 c (127.74)
Mg^{2+} (mg kg^{-1})	160.78 b (26.24)	259.70 b (60.15)	203.47 b (62.21)	233.61 b (37.70)	176.94 b (44.25)	436.38 a (48.54)	150.71 b (18.33)
K^+ (mg kg^{-1})	186.39 c (28.84)	376.55 b (46.38)	153.02 c (47.39)	181.82 c (23.44)	283.62 bc (52.78)	581.19 a (65.67)	217.08 c (42.80)

Different letters indicate significant differences between species ($P < 0.05$).

spruce. Although rowan has long been considered as a 'soil improving species', surprisingly little data have been published on available nutrients under this species (Emmer et al., 1998). We found only 2 papers investigating soil recovery under spontaneous birch and rowan regenerations in the organic horizon of former spruce stands. In the regeneration plots, 20 years after windthrow in the upper Solling (NW-Germany), increased total P, K, and Mg contents were observed compared to the mature spruce stand (Zerbe and Meiwes, 2000) and 20–50 years after forest dieback or clearcut in the Krkonoše mountains (Czech Republic), exchangeable K, Ca and Mg were higher under the pioneers, compared to the 40–120 year-old spruce stands (Emmer et al., 1998). The similarity in soil chemistry under beech, oak and spruce is in line with a comparative study of mature spruce, beech, oak and Douglas-fir stands at four sites, showing that exchangeable calcium in the forest floor was not affected by these tree species (Malchair and Carnol, 2009). Also, a similar effect of beech relative to spruce was found in the mineral topsoil after afforestation of former agricultural land (Hagen-Thorn et al., 2004). In contrast to literature data, we did not find increased acidification under alder (Van Miegroet and Cole, 1984; Hart et al., 1997) or a difference in pH under oak and beech compared to spruce (Augusto et al., 2002). In our experiment, plantations were established on initially very acid soils, so that changes in pH under the main tree species may take longer to develop than the 11 years since plantation. Furthermore, acidity due to increased nitrification under alder (data not shown) might be buffered by cation exchange, a hypothesis supported by the low exchangeable cation concentrations under alder. Decreased soil acidity in the forest floor under pioneer species (alder, willow, birch and rowan) is consistent with previous reports for birch and rowan compared to spruce (Emmer et al., 1998), Douglas fir (Welke and Hope, 2005) and pine-spruce stands (Kanerva and Smolander, 2007). In contrast to these studies, we compared soil chemistry under young trees of the same age, confirming that the early soil improving capacities of birch and rowan offer good possibilities for restoration management.

Fresh foliar nutrient concentrations differed between the 7 tree species growing at the same site, confirming that the chemical foliar composition depends not only on site but also on species (Hobbie, 1992). As expected, we found highest leaf N concentrations in the N₂-fixing alder (Hansen and Dawson, 1982). Highest Ca, Mg and K concentrations in fresh leaves of rowan may be explained by plant physiological characteristics leading to better exploitation of soil resources from the total pool of available nutrients (Attiwill and Adams, 1993; Larcher, 2003). There were several indications of nutrient deficiencies in the commercial tree species in this experiment. Indeed, according to threshold values summarised by Jonard et al. (2009), N, Ca and Mg concentrations in fresh spruce foliage were below the deficiency level, and K concentrations within the critical level. Also the new foliar nutrient thresholds, compiled by Mellert and Göttlein (2012), classify N concentrations of spruce needles in our study in the extreme deficiency range, Ca and Mg in the latent deficiency range, and K in the central normal range. N nutrition of oak was in the critical range (Jonard et al., 2009), and Ca nutrition of oak was in the deficiency range (Mellert and Göttlein, 2012). Nutrient concentrations of the other reported elements for oak and beech were in the normal or optimal ranges. Threshold values published by Mellert and Göttlein (2012), compiled data from young and old stands, while data summarised by Jonard et al. (2009) were established for mature trees. However, as foliar nutrient concentrations decrease with tree age (DeBell and Radwan, 1984), nutrient deficiency for the major elements is very likely to occur at our site.

Retranslocation, the nutrient recovery from senescent tissues, especially foliage, is an important species-specific mechanism for the conservation of nutrients within the tree (Mahendrapa

et al., 1986; Miller, 1995). We observed N translocation for all species (20–60% of leaf N before abscission), except spruce. The high N translocation in beech (60%) was in the same range as values reported for low-fertility soils (Sariyildiz and Anderson, 2005) and for afforested agricultural land (Hagen-Thorn et al., 2006). Increased Ca concentration in litter relative to leaves might be explained by Ca retention in combination with decreased K concentrations due to leaching of K and simple sugars after autolysis of the cells during senescence (Sariyildiz and Anderson, 2005). Differences in fresh foliage nutrient concentrations and retranslocation resulted in high concentrations in foliar litter of alder (N), willow (N, K), rowan (Ca, Mg, K), and birch (Mg), relative to the other species. Nutrient concentrations in foliar litter are generally considered to be higher for deciduous species compared to conifers (Augusto et al., 2002), which was confirmed in our study. The higher litter nutrient contents observed in this study are consistent with the measured changes in soil chemistry. Better soil nutrient availability is often thought to be related to faster initial decomposition rates, due to lower litter C/N (Taylor et al., 1989; Zhang et al., 2008). However, soil nutrient enrichment in our study was highest under rowan rather than under species with lowest litter C/N ratios (alder, willow). This could be explained by the rate-retarding effect of high litter N concentrations on later decomposition stages, leading to a lower total mass loss (Berg, 2000) and consequently lower nutrient release. Thus, despite initially different decomposition rates, mass loss of numerous species tend to converge on the longer scale (12 y) (Prescott, 2010), so that nutrient enrichment of the soil would mainly be determined by litter biomass and nutrient content (see below).

Total annual litterfall was up to three times higher under accompanying species than that of the main forestry species. Higher litter biomass of pioneer species in our study reflects their rapid growth and canopy development. This is part of the inherent characteristics of these species, which, in addition to high litter quality, enable nutrient return to the forest floor early during stand development. Differences in throughfall volume (526–1066 mm year⁻¹), litterfall quantities (615–3122 kg ha⁻¹ year⁻¹), as well as litter and throughfall nutrient concentrations, resulted in diverging nutrient return to the forest floor under the 7 species. The fraction of nutrient return to the soil by throughfall was higher under commercial tree species, compared to pioneers, representing 83–88 vs 51–71% for K, 42–60 vs 20–36% for Ca, 63–76 vs 30–45% for Mg, and 57–66 vs 23–35% for N. In contrast, higher nutrient return by litterfall relative to throughfall has been reported under chesnut in Switzerland (Zimmermann et al., 2002). Total Ca, Mg, K and N return via throughfall, foliar litter and reproductive parts was higher under accompanying tree species (alder, birch, willow, rowan) than under the commercial tree species (oak, beech, spruce). Total N return was in the order of 50 kg ha⁻¹ year⁻¹ under accompanying species, 33 kg ha⁻¹ year⁻¹ under spruce and near 20 kg ha⁻¹ year⁻¹ under beech and oak. Under rowan, total deposition was highest, amounting to 47, 9 and 66 kg ha⁻¹ year⁻¹ for Ca, Mg, and K, respectively. The threefold increase in soil exchangeable Ca²⁺, Mg²⁺, and K⁺ may thus be related to the high return of these nutrients under rowan.

Assessment of the long-term potential of rowan to increase soil nutrient availability and extrapolation to forest management plans would require some further information. Data through stand development on the forest floor, mineral weathering, exchangeable cation pools, the mineral soil layer, and the evolution of litter biomass and chemical composition with stand age would allow evaluating the proportion of pioneer species needed for a sufficient improvement in soil quality. Furthermore, in the longer term, soil Ca enrichment through tree species may have a profound effect on soil acidity, along with earthworm abundance and diversity, as has been reported 30 years after afforestation of a previous pine

forest (Reich et al., 2005). Although litter input is likely to increase with stand age, especially during the rapid growth phase of trees (Lebet et al., 2001; Welke and Hope, 2005; Trap et al., 2011), the difference between species is likely to decrease with time, as in closed-canopy temperate forests, the amount of litterfall is only slightly influenced by species (Augusto et al., 2002) and tree density (Bray and Gorham, 1964). The variation of foliar nutrient concentrations with age depend on the species; for example, nutrient concentrations of alder have been reported to decrease with tree age (DeBell and Radwan, 1984), while concentrations in birch increased (Ovington and Madgwick, 1959). Although differences between species in nutrient return to the forest floor might evolve during stand development, differences are most important for soil fertility during early stages. Indeed, at this stage trees rely mostly on soil for their nutrient requirements (Miller, 1995), so that soil enrichment is particularly important during early stand development for avoiding deficiency symptoms.

Our study allows strong inference for the individual tree species effects (Hurlbert, 1984), as species were subjected to identical site conditions, including land use history, climate, rainfall composition and geology. Indeed, within sites, tree species effects can be important (Malchair and Carnol, 2009) and most relevant for forest management. However, results cannot be extrapolated to other environmental conditions and across large geographical regions (Binkley, 2008). Both large scale approaches and replicated experiments at plot or catchment scale provide useful and complementary information on forest ecology, keeping a balance between generalisation and specificity (Kim et al., 2009; Minocha et al., 2010; Sridevi et al., 2012). This study improves our understanding of the effects of individual tree species on nutrient return, necessary for the mechanistic explanation of nutrient cycling in other studies, such as mixed species stands (Nadrowski et al., 2010; Richards et al., 2010).

In conclusion, our data suggest that differences in total nutrient return via throughfall and litterfall under tree species influence the availability of nutrients in the forest floor, 11 years after conversion from a Norway spruce plantation. Tree-species specific Ca, Mg, K and N concentrations in foliage and leaf litter, as well as distinct throughfall deposition and litterfall biomass, resulted in higher Ca, Mg, K, and N return under accompanying tree species (alder, birch, willow, rowan) than under the main commercial tree species (oak, beech, spruce). Under rowan, high throughfall, litterfall biomass, and litterfall Ca, Mg and K concentrations resulted in highest nutrient return to the forest floor and higher exchangeable Ca, Mg, and K in the forest floor. Planting rowan as accompanying species may therefore represent an interesting management option for improving soil chemistry on nutrient poor sites through Ca and Mg nutrient return.

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References

Allen, S.E., 1989. Chemical Analysis of Ecological Materials, second ed. Blackwell Scientific Publication, London.

- Aponte, C., García, L.V., Marañón, T., 2012. Tree species effect on litter decomposition and nutrient release in mediterranean oak forests changes over time. *Ecosystems*, 1–15.
- Attiwill, P.M., Adams, M.A., 1993. Nutrient cycling in forests. *New Phytol.* 124, 561–582.
- Aubert, M., Margerie, P., Trap, J., Bureau, F., 2010. Aboveground-belowground relationships in temperate forests: plant litter composes and microbiota orchestrates. *For. Ecol. Manage.* 259, 563–572.
- 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.
- Berg, B., 2000. Litter decomposition and organic matter turnover in northern forest soils. *For. Ecol. Manage.* 133, 13–22.
- Berg, B., Meentemeyer, V., 2001. Litter fall in some European coniferous forests as dependent on climate: a synthesis. *Can. J. For. Res.* 31, 292–301.
- Berger, T.W., Untersteiner, H., Topf, M., Neubauer, C., 2009. Nutrient fluxes in pure and mixed stands of spruce (*Picea abies*) and beech (*Fagus sylvatica*). *Plant Soil* 322, 317–342.
- Binkley, D., 1995. The influence of tree species on forest soils: processes and patterns. In: Mead, D.J., Cornforth, I.S. (Eds.), *Proceedings of the Trees and Soil Workshop Agronomy Society of New Zealand Special Publication #10*. Lincoln University Press, Canterbury, pp. 1–33.
- Binkley, D., 2008. Three key points in the design of forest experiments. *For. Ecol. Manage.* 255, 2022–2023.
- Binkley, D., Giardina, C., 1998. Why do tree species affect soils? The warp and woof of tree–soil interactions. *Biogeochemistry* 42, 89–106.
- Bolte, A., Ammer, C., Löf, M., Madsen, P., Nabuurs, G.J., Schall, P., Spathelf, P., Rock, J., 2009. Adaptive forest management in central Europe: climate change impacts, strategies and integrative concept. *Scand. J. Forest Res.* 24, 473–482.
- Bray, J.R., Gorham, E., 1964. Litter production in forests of the world. *Adv. Ecol. Res.* 2, 101–157.
- Buldgen, P., 1984. Etude écosystémique de deux bassins versants boisés en Haute-Ardenne. PhD thesis, Département de Botanique. ULg, Liège, p. 218.
- Ciais, P., Schelhaas, M.J., Zaehle, S., Piao, S.L., Cescatti, A., Liski, J., Luyssaert, S., Le-Maire, G., Schulze, E.D., Bouriaud, O., Freibauer, A., Valentini, R., Nabuurs, G.J., 2008. Carbon accumulation in European forests. *Nat. Geosci.* 1, 425–429.
- De Schrijver, A., Geudens, G., Augusto, L., Staelens, J., Mertens, J., Wuyts, K., Verheyen, K., 2007. The effect of forest type on throughfall deposition and seepage flux: a review. *Oecologia* 153, 663–674.
- De Schrijver, A., Staelens, J., Wuyts, K., Van Hoydonck, G., Janssen, N., Mertens, J., Gielis, L., Geudens, G., Augusto, L., Verheyen, K., 2008. Effect of vegetation type on throughfall deposition and seepage flux. *Environ. Pollut.* 153, 295–303.
- de Vries, W., van der Salm, C., Reinds, G.J., Erisman, J.W., 2007. Element fluxes through European forest ecosystems and their relationships with stand and site characteristics. *Environ. Pollut.* 148, 501–513.
- DeBell, D.S., Radwan, M.A., 1984. Foliar chemical concentrations in red alder stands of various ages. *Plant Soil* 77, 391–394.
- Delecour, F., 1978. Facteurs édaphiques et productivité forestière. *Pédologie* 28, 271–284.
- Dijkstra, F.A., 2003. Calcium mineralization in the forest floor and surface soil beneath different tree species in the northeastern US. *For. Ecol. Manage.* 175, 185–194.
- Emmer, I.M., Fanta, J., Kobus, A.T., Kooijman, A., Sevink, J., 1998. Reversing borealization as a means to restore biodiversity in Central-European mountain forests – an example from the Krkonose Mountains, Czech Republic. *Biodivers. Conserv.* 7, 229–247.
- Erisman, J.W., Draaijers, G., 2003. Deposition to forests in Europe: most important factors influencing dry deposition and models used for generalisation. *Environ. Pollut.* 124, 379–388.
- Finzi, A.C., Van Breemen, N., Canham, C.D., 1998. Canopy tree–soil interactions within temperate forests: species effects on soil carbon and nitrogen. *Ecol. Appl.* 8, 440–446.
- Hagen-Thorn, A., Callesen, I., Armolaitis, K., Nihlgård, B., 2004. The impact of six European tree species on the chemistry of mineral topsoil in forest plantations on former agricultural land. *For. Ecol. Manage.* 195, 373–384.
- Hagen-Thorn, A., Varnagiryte, I., Nihlgård, B., Armolaitis, K., 2006. Autumn nutrient resorption and losses in four deciduous forest tree species. *For. Ecol. Manage.* 228, 33–39.
- Hansen, E.A., Dawson, J.O., 1982. Effect of *Alnus glutinosa* on hybrid populus height growth in a short-rotation intensively cultured plantation. *Forest Sci.* 28, 49–59.
- Hansen, K., Vesterdal, L., Schmidt, I.K., Gundersen, P., Sevel, L., Bastrup-Birk, A., Pedersen, L.B., Bille-Hansen, J., 2009. Litterfall and nutrient return in five tree species in a common garden experiment. *For. Ecol. Manage.* 257, 2133–2144.
- Hart, S.C., Binkley, D., Perry, D.A., 1997. Influence of red alder on soil nitrogen transformations in two conifer forests of contrasting productivity. *Soil Biol. Biochem.* 29, 1111–1123.
- Hendershot, W.H., Duquette, M., 1986. A simple barium-chloride method for determining cation-exchange capacity and exchangeable cations. *Soil Sci. Soc. Am. J.* 50, 605–608.
- Hobbie, S.E., 1992. Effects of plant species on nutrient cycling. *Trends Ecol. Evol.* 7, 336–339.
- Hobbie, S.E., Reich, P.B., Oleksyn, J., Ogdahl, M., Zytowski, R., Hale, C., Karolewski, P., 2006. Tree species effects on decomposition and forest floor dynamics in a common garden. *Ecology* 87, 2288–2297.
- Hobbie, S.E., Ogdahl, M., Chorover, J., Chadwick, O.A., Oleksyn, J., Zytowski, R., Reich, P.B., 2007. Tree species effects on soil organic matter dynamics: the role of soil cation composition. *Ecosystems* 10, 999–1018.

- Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monograph* 54, 187–211.
- IUSS, 2006. World Reference Base for Soil Resources 2006: A Framework for International Classification, Correlation and Communication. World Soil Resources Reports.
- Jacob, M., Weland, N., Platner, C., Schaefer, M., Leuschner, C., Thomas, F.M., 2009. Nutrient release from decomposing leaf litter of temperate deciduous forest trees along a gradient of increasing tree species diversity. *Soil Biol. Biochem.* 41, 2122–2130.
- Jobbágy, E.G., Jackson, R.B., 2004. The uplift of soil nutrients by plants: biogeochemical consequences across scales. *Ecology* 85, 2380–2389.
- Jonard, M., Andre, F., Dambrine, E., Ponette, Q., Ulrich, E., 2009. Temporal trends in the foliar nutritional status of the French, Walloon and Luxembourg broad-leaved plots of forest monitoring. *Ann. For. Sci.* 66, 412–421.
- Kanerva, S., Smolander, A., 2007. Microbial activities in forest floor layers under silver birch, Norway spruce and Scots pine. *Soil Biol. Biochem.* 39, 1459–1467.
- Kim, C., Son, Y., Lee, W.K., Jeong, J., Noh, N.J., 2009. Influences of forest tending works on carbon distribution and cycling in a *Pinus densiflora* S. et Z. stand in Korea. *For. Ecol. Manage.* 257, 1420–1426.
- Larcher, W., 2003. *Physiological Plant Ecology: Ecophysiology and Stress Physiology of Functional Groups*, third ed. Springer, Berlin.
- Lebre, M., Nys, C., Forgeard, F., 2001. Litter production in an Atlantic beech (*Fagus sylvatica* L.) time sequence. *Ann. For. Sci.* 58, 755–768.
- Legrain, X., Renneson, M., Genot, V., Demarcin, P., Liénard, A., Bock, L., Colinet, G., 2011. Cartographie des sols en Belgique: aperçu historique et présentation des travaux actuels de valorisation et de révision de la Carte Numérique des Sols de Wallonie. *BASE* 15, 647–656.
- Lovett, G.M., Nolan, S.S., Driscoll, C.T., Fahey, T.J., 1996. Factors regulating throughfall flux in a new New-Hampshire forested landscape. *Can. J. Forest Res.* 26, 2134–2144.
- Mahendrapa, M.K., Foster, N.W., Weetman, G.F., Krause, H.H., 1986. Nutrient cycling and availability in forest soils. *Can. J. Soil Sci.* 66, 547–572.
- Malchair, S., Carnol, M., 2009. Microbial biomass and C and N transformations in forest floors under European beech, sessile oak, Norway spruce and Douglas-fir at four temperate forest sites. *Soil Biol. Biochem.* 41, 831–839.
- McIntire, E.J.B., Fortin, M.J., 2006. Structure and function of wildfire and mountain pine beetle forest boundaries. *Ecography* 29, 309–318.
- Melillo, J.M., Aber, J.D., Muratore, J.F., 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63, 621–626.
- Mellert, K.H., Göttlein, A., 2012. Comparison of new foliar nutrient thresholds derived from van den Burg's literature compilation with established central European references. *Eur. J. For. Res.* 131, 1461–1472.
- Michopoulos, P., Baloutsos, G., Economou, A., Samara, C., Thomaidis, N.S., Grigoratos, T., 2007. Nutrient cycling and foliar status in an urban pine forest in Athens, Greece. *Plant Soil* 294, 31–39.
- Miller, H.G., 1984. Nutrient cycles in birchwoods. *Proc. Roy. Soc. Edinb. B: Biol.* 85, 83–96.
- Miller, H.G., 1995. The influence of stand development on nutrient demand, growth and allocation. *Plant Soil* 168–169, 225–232.
- Minocha, R., Long, S., Thangavel, P., Minocha, S.C., Eagar, C., Driscoll, C.T., 2010. Elevation dependent sensitivity of northern hardwoods to Ca addition at Hubbard Brook Experimental Forest, NH, USA. *For. Ecol. Manage.* 260, 2115–2124.
- Nadrowski, K., Wirth, C., Scherer-Lorenzen, M., 2010. Is forest diversity driving ecosystem function and service? *Curr. Opin. Env. Sust.* 2, 75–79.
- Ovington, J.D., Madgwick, H.A.I., 1959. The growth and composition of natural stands of birch. *Plant Soil* 10, 389–400.
- Parker, G.G., 1983. Throughfall and stemflow in the forest nutrient cycle. In: MacFadyen, A., Ford, E.D. (Eds.), *Advances in Ecological Research*. Academic Press, pp. 57–133.
- Pitman, R., Bastrup-Birk, A., Breda, N., Rautio, P., 2010. Part XIII. Sampling and Analysis of Litterfall. In: *Manual on Methods and Criteria for Harmonized Sampling, Assessment, Monitoring and Analysis of the Effects of Air Pollution on Forests*. UNECE ICP Forests Programme Co-ordinating Centre, Hamburg, p. 16.
- Prescott, C.E., 2002. The influence of the forest canopy on nutrient cycling. *Tree Physiol.* 22, 1193–1200.
- Prescott, C.E., 2005. Do rates of litter decomposition tell us anything we really need to know? *For. Ecol. Manage.* 220, 66–74.
- Prescott, C., 2010. Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils? *Biogeochemistry* 101, 133–149.
- Ranger, J., Marques, R., Colin-Belgrand, M., 1997. Nutrient dynamics during the development of a Douglas-fir (*Pseudotsuga menziesii* Mirb.) stand. *Acta Oecol.* 18, 73–90.
- Rautio, P., Fürst, A., Stefan, K., Raito, H., Bartels, U., 2010. Part XII. Sampling and Analysis of Needles and Leaves. In: *Manual on Methods and Criteria for Harmonized Sampling, Assessment, Monitoring and Analysis of the Effects of Air Pollution on Forests*. ICP Forests Programme Co-ordinating Centre, Hamburg, p. 19.
- Reich, P.B., Oleksyn, J., Modrzynski, J., Mrozinski, P., Hobbie, S.E., Eissenstat, D.M., Chorover, J., Chadwick, O.A., Hale, C.M., Tjoelker, M.G., 2005. Linking litter calcium, earthworms and soil properties: a common garden test with 14 tree species. *Ecol. Lett.* 8, 811–818.
- Reimann, C., Arnoldussen, A., Boyd, R., Finne, T.E., Koller, F., Nordgulen, O., Englmaier, P., 2007. Element contents in leaves of four plant species (birch, mountain ash, fern and spruce) along anthropogenic and geogenic concentration gradients. *Sci. Total Environ.* 377, 416–433.
- 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.
- Sariyildiz, T., Anderson, J.M., 2005. Variation in the chemical composition of green leaves and leaf litters from three deciduous tree species growing on different soil types. *For. Ecol. Manage.* 210, 303–319.
- Spiecker, H., 2003. Silvicultural management in maintaining biodiversity and resistance of forests in Europe-temperate zone. *J. Environ. Manage.* 67, 55–65.
- Spiecker, H., Hansen, J., Klimo, E., Skovsgaard, J.P., Sterba, H., Teuffel, K.v. (Eds.), 2004. *Norway Spruce Conversion – Options and Consequences*, Leiden, Boston.
- Sridevi, G., Minocha, R., Turlapati, S.A., Goldfarb, K.C., Brodie, E.L., Tisa, L.S., Minocha, S.C., 2012. Soil bacterial communities of a calcium-supplemented and a reference watershed at the Hubbard Brook Experimental Forest (HBEF), New Hampshire USA. *Fems Microbiol. Ecol.* 79, 728–740.
- Talkner, U., Kramer, I., Holscher, D., Beese, F.O., 2010. Deposition and canopy exchange processes in central-German beech forests differing in tree species diversity. *Plant Soil* 336, 405–420.
- Taylor, B.R., Parkinson, D., Parsons, W.F.J., 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. *Ecology* 70, 97–104.
- Trap, J., Bureau, F., Brethes, A., Jabiol, B., Ponge, J.F., Chauvat, M., Decaëns, T., Aubert, M., 2011. Does moder development along a pure beech (*Fagus sylvatica* L.) chronosequence result from changes in litter production or in decomposition rates? *Soil Biol. Biochem.* 43, 1490–1497.
- Van Miegroet, H., Cole, D.W., 1984. The impact of nitrification on soil acidification and cation leaching in a red alder ecosystem. *J. Env. Qual.* 13, 586–590.
- Vesterdal, L., Schmidt, I.K., Callesen, I., Nilsson, L.O., Gundersen, P., 2008. Carbon and nitrogen in forest floor and mineral soil under six common European tree species. *For. Ecol. Manage.* 255, 35–48.
- Vesterdal, L., Elberling, B., Christiansen, J.R., Callesen, I., Schmidt, I.K., 2012. Soil respiration and rates of soil carbon turnover differ among six common European tree species. *For. Ecol. Manage.* 264, 185–196.
- Vittori Antisari, L., Falsone, G., Carbone, S., Vianello, G., 2013. Short-term effects of above- and belowground detritus of world forests. In: MacFadyen, A., Ford, E.D. (Eds.), *Advances in Ecological Research*. Academic Press, pp. 303–377.
- Weissen, F., Hambuckers, A., Van Praag, H.J., Remacle, J., 1990. A decennial control of N-cycle in the Belgian Ardenne forest ecosystems. *Plant Soil* 128, 59–66.
- Weissen, F., Bronchart, L., Piret, A., 1994. Guide de boisement des stations forestières de Wallonie. Namur, Belgique, p. 175.
- Welke, S.E., Hope, G.D., 2005. Influences of stand composition and age on forest floor processes and chemistry in pure and mixed stands of Douglas-fir and paper birch in interior British Columbia. *For. Ecol. Manage.* 219, 29–42.
- Zerbe, S., Meiwes, K.J., 2000. Zum Einfluss von Weichlaubhölzern auf Vegetation und Auflagehumus von Fichtenforsten - Untersuchungen in einem zwei Jahrzehnte alten Birken-Ebereschen-Vorwald im Hoch-Solling [On the influence of softwoods on vegetation and organic layer of spruce stands - Investigations in a two decades old birch-rowan forest in the upper Solling (Niedersachsen/NW-Germany)]. *Forstwiss. Centralbl.* 119, 1–19.
- Zhang, D., Hui, D., Luo, Y., Zhou, G., 2008. Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. *J. Plant Ecol.* 1, 85–93.
- Zimmermann, S., Braun, S., Conedera, M., Blaser, P., 2002. Macronutrient inputs by litterfall as opposed to atmospheric deposition into two contrasting chestnut forest stands in southern Switzerland. *For. Ecol. Manage.* 161, 289–302.