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Import and release of nutrients during the first five years of plant litter decomposition

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ABSTRACT

During the initial stages of leaf and needle litter decomposition, microorganisms face nitrogen (N) and phosphorus (P) scarcity since plant litter is very N- and P-poor compared to microbial biomass. The processes that microorganisms use to cope with the unfavorable stoichiometry, such as transport of nutrients into decomposing litter, are still not fully understood.

The aim of the study was to explore the import and release of nutrients (N, P, K, Mn, Ca, and Mg) into and from decomposing Norway spruce (*Picea abies* Karst) and Scots pine (*Pinus silvestris* L.) needle litter. For this purpose, we conducted a paired-stand litterbag study at eight temperate and boreal forest sites in Sweden that each have a spruce and a pine stand, over a period of five years.

The mass of N in decomposing spruce and pine needle litter increased during the first 172 and 356 days, on average by 19% and 30%, respectively, compared to the initial masses of the element in the litter. The mass of P in pine litter increased during the first 526 days of decomposition, on average by 48%. Net release of N from spruce litter, relative to the initial N amount, only began after 895 days of decomposition. Net release of N and P from pine litter, relative to the initial amounts of the elements, started only after 1097 days. In contrast, K, Mn, Ca, and Mg were released right from the beginning of the decomposition process.

The results show that N and P import into decomposing plant litter is a quantitatively important process in temperate and boreal coniferous forests during the first stage of litter decomposition when N and P concentrations are low. Nutrient import alleviates stoichiometric imbalance between the microbial biomass and the litter and likely contributes to microbial nutrient acquisition.

1. Introduction

The organic layer of forest soils is a challenging environment for microbial life since microorganisms face substrates with very low nitrogen (N) and phosphorus (P) concentrations, and thus high C:N and C:P ratios, compared to their own biomass (Zechmeister-Boltenstern et al., 2015; Spohn, 2020). Soil microbial biomass has relatively constrained molar C:N and C:P ratios across different soils and ecosystems (Cleveland and Liptzin, 2007; Xu et al., 2013) equaling 8 and 42, respectively, on a global average (Xu et al., 2013). In contrast, the molar foliage litter C:N ratio is 58 in temperate broadleaf forests and 87 in temperate coniferous forests, on a global average, while the molar foliage litter C:P ratio is 1702 in temperate broadleaf forests and 2352 in temperate coniferous forests (McGroddy et al., 2004). More specifically, the molar C:N ratio of foliage is 47 for Scots pine (*Pinus silvestris* L.) and 41 for Norway spruce (*Picea abies* Karst), on a European average (Cools et al., 2014). The N and P concentrations of plant litter tend to increase during decomposition due to the loss of C (mostly in the form of CO_2 but also DOC), leading to decreases in the C:N and C:P ratios (Blair, 1988; Berg and McClaugherty, 2020). Thus, it can be expected that N and P scarcity, or limitation, occurs mostly in the beginning of the decomposition process.

There are different ways in which microorganisms can cope with the unfavorable C:N:P stoichiometry (Mooshammer et al., 2014; Spohn, 2015, 2016; Manzoni et al., 2021). To a very limited extent, microorganisms can increase their biomass C:N and C:P ratios, and this might be more important in the organic layer than in mineral soil, as indicated by the less constrained microbial biomass element ratios in organic layers compared to mineral soil (Fanin et al., 2013; Heuck et al., 2015; Zederer et al., 2017). Further, microorganisms can increase their respiration rate

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(Spohn and Chodak, 2015; Spohn, 2015) or the rate at which they release incompletely decomposed organic C as dissolved organic carbon (DOC) (Hessen and Anderson, 2008), which allows them to dispose of C. The change in the respiration rate or C excretion rate leads to a decrease in the microbial C use efficiency, if not associated with a similar increase in the gross growth rate (Sinsabaugh et al., 2013; Spohn et al., 2016a). Next, microorganisms can increase their N use efficiency (Mooshammer et al., 2014). They can also increase the residence time of N or P in their biomass by reducing N and P losses and increasing nutrient resorption from senescing hyphae, which decreases the microbial need to take up N and P (Spohn and Widdig, 2017; Čapek et al., 2021). Moreover, microorganisms likely selectively feed on fractions of the soil organic matter (SOM) that match more closely their nutritional needs, which also leads to a larger return on the investment of exoenzyme release as compared to more nutrient-poor fractions (Arsuffi and Suberkropp, 1989; Hood et al., 2014). This means that microorganisms proliferate more strongly in locations that are stoichiometrically closer to their nutritional demands, and they might more intensively colonize these patches if they can move, as in the case of fungi and mobile bacteria (Bending and Read, 1995; Leake et al., 2001). In addition, diazotroph microorganisms in decomposing plant detritus can fix N_2 from the air (Rinne et al., 2017). Finally, mostly fungi (Wells et al., 1990; Wells and Boddy, 1995; Frey et al., 2003; Boberg et al., 2014) but also microfauna, insects, and mobile prokaryotes (Filipiak, 2018) can transport nutrients from nutrient-enriched spots in soil to N- and P-poor microsites, which they colonize to take up easily-available organic carbon there. In addition, litter can be enriched with nutrients from canopy throughfall and faeces of canopy-inhabiting phyllophageous insects (Joergensen and Meyer, 1990). Transport of N and P into decomposing litter, has been shown for pine needles (Staaf and Berg, 1982; Fahey, 1983; Berg, 1988; Yavitt and Fahey, 1986), while results about N and P import into the litter of other tree species is rather scarce (for exceptions see Berg and McClaugherty, 1989; Osono and Takeda, 2001). Given the small number of studies about nutrient import into decomposing plant litter, also the magnitude of the process is still not well known.

In contrast to N and P, other nutrients such as potassium (K), manganese (Mn), calcium (Ca), and magnesium (Mg) are less strongly retained in litter (Berg and Staaf, 1980; Staaf and Berg 1982; Berg and McClaugherty, 2020). Particularly K, but also Mg and Ca are quickly leached out of decomposing plant litter (Osono and Takeda, 2004).

The aim of the study was to explore the import and release of nutrients during the first five years of decomposition of spruce and pine needle litter. For this purpose, we determined nutrient (N, P, K, Mn, Ca, and Mg) import and release from decomposing spruce and pine needle litter at eight temperate and boreal forest sites in Sweden that each have paired stands of Norway spruce and Scots pine, over a period of five years, using litterbags. We hypothesized that external N and P is imported into the decomposing spruce and pine needle litter during the first years of needle litter decomposition, whereas K, Mn, Ca, and Mg are continuously released from needle litter from the start of the decomposition process. This study is unique since it has a paired-site design with two tree species, it is replicated at eight sites over five years, and provides not only data on changes in mass loss during decomposition but also changes in nutrient contents over time. In contrast, most previous litter decomposition studies considered fewer sites over a shorter period of time, did not have a paired-site design and many only provide data on mass loss but not on changes in the nutrient contents.

2. Material and methods

2.1. Site description

Decomposition was studied at eight sites that have both a Norway spruce (*Picea abies*) and a Scots pine (*Pinus sylvestris*) stand and that were chosen because they have contrasting properties (Table 1). The sites are located in south and central Sweden between 56°N and 63°N, thus

Table 1
Basic characteristics of the eight temperate and boreal forest sites that each have paired stands of Norway spruce and Scots pine.

Site	Site name	**Latitude (N)**	**Longitude (E)**	**Altitude (m)**	**MAP (mm)**	**MAT (°C)**	Soil order	Texture	Humus form	Under- story	Stand	**Basal area (m^2 ha^{-1})**	**Stand age (years)**	Canopy cover
1	Dimbo	59°07′	15°44′	70	560	5.5	Podzol	Fine sand-medium sand	Moder	Grasses and herbs	Spruce	29.9	54	0.8
											Pine	27.8	54	0.8
2	Grensholm	58°33′	15°51′	58	520	6.1	Eutric Cambisol	Clay	Mull	Tall herbs and grasses	Spruce	33.8	54	0.9
											Pine	28.1	58	0.8
3	Mästocka	56°36′	13°15′	135	1070	6.8	Podzol	Sandy till	Mor	Blueberry	Spruce	34.6	53	0.9
											Pine	20.0	57	0.6
4	Kungs-Husby	59°31′	17°16′	30	470	5.2	Eutric Cambisol	Clay	Mull	Grasses and blueberry	Spruce	28.9	57	0.8
											Pine	31.0	53	0.9
5	Remningstorp	58°28′	13°39′	128	530	5.6	Podzol	Gravelly sand	Moder/Mull-like moder	Blueberry	Spruce	25.3	58	0.7
											Pine	23.0	61	0.6
6	Tomta	59°49′	16°33′	63	550	5.1	Podzol	Clay	Mor	Grasses and blueberry	Spruce	40.0	55	1.0
											Pine	32.8	53	1.0
7	Tveten	58°06′	13°17′	170	675	5.5	Podzol	Sandy till	Mor	No understory	Spruce	21.9	55	0.6
											Pine	23.8	59	0.6
8	Västbyn	63°13′	14°28′	325	460	2.1	Dystric Cambisol	Clayey till	Mor	Blueberry	Spruce	27.5	71	0.7
											Pine	36.0	71	1.0

covering temperate and boreal forest. Mean annual precipitation (MAP) at the eight sites ranged from 460 mm to 1070 mm, and the mean annual temperature (MAT) varied between 2.1 °C and 6.8 °C. The average stand age was 58 ± 6 years (Table 1). The forests did not receive fertilizer. Atmospheric N deposition at the sites was very likely never higher than 4 kg^{-1} ha^{-1} yr^{-1} (Spohn and Stendahl, 2022).

2.2. Litter-bag study and chemical analyses

Litter was collected in the autumn by gently shaking the limbs of the trees and collecting the needles on spread-out tarpaulins. Green needles were removed by hand. Litter was air-dried, and stored dry at room temperature. Before weighing, the needles were equilibrated to a constant moisture level (5–8 ± 0.5%) by drying them at room temperature for about one month. Exact dry mass was determined as the average of 25 replicate samples that were dried to a constant mass at 85 °C. Litterbags, measuring 8 × 8 cm, excluding a 1 cm-wide edge, were made of polyester net with a mesh size of about 1.0 × 1.0 mm for pine needles and about 1.0 × 0.5 mm for spruce needles. We adapted the bags mesh sizes to the size of the needles with the intention to have as wide mesh sizes as possible. The 2–5 cm long and paired Scots pine needles did not easily go through a 1 × 1 mm net, whereas a net with 2 × 2 mm mesh more readily allowed needles to pass. In contrast, the needles of Norway spruce were single and thinner than those of Scots pine and passed readily through a 1 × 1 mm mesh, but not through a net with 1 × 0.5 mm mesh. The litterbags' different mesh sizes do not prevent the main decomposers from entering the bags since decomposition in these forest systems is almost exclusively conducted by fungi and bacteria but not by soil animals (Persson et al., 1980). In a previous two-year study incubating Scots pine litter, it was confirmed that there was no difference in the decomposition rate between the bags with different mesh sizes (1.0 × 1.0 mm and 1.0 × 0.5 mm) (Berg, unpublished).

Exactly 1.00 g of needles was placed in each litterbag. The bags were deployed on the top of the litter layer at the site and stand from which the litter originated at 25 randomly located plots per stand (each measuring 1 × 1 m) and fastened using 15-cm long pegs of stainless steel. At regular intervals during five years, 25 litterbags, one from each plot, were collected and carefully cleaned. Dry mass loss was determined by drying the samples to a constant mass at 85 °C, and the 25 samples from each stand were merged to obtain one composite sample. Subsequently, nutrient concentrations were analyzed as follows. After a wet oxidation in H_2SO_4, total N was analyzed using a semi-micro Kjeldahl procedure (Nihlgård, 1972). Samples were digested for 48 h in a 2.5:1 (v/v) mixture of nitric and perchloric acid for the analysis of P, K, Mn, Ca, and Mg. Phosphorus was determined colorimetrically by a method including molybdenum blue (John, 1970). Potassium, Mn, Ca, and Mg were determined by atomic absorption spectrometry (PerkinElmer 603) according to Pawluk (1967). The litter decomposition study was conducted from 1979 to 1984.

2.3. Data analysis

We modeled the mass loss of litter as a function of time using an asymptotic concave function (Michaelis-Menten model). The model has been used previously for other datasets to describe changes in soil pools over time (McMahon et al., 2010; Spohn et al., 2016b).

$$MassLoss = MassLoss_{Max} \bullet \frac{Time}{k_M + Time} \quad \text{(Eq. 1)}$$

$MassLoss_{Max}$ is the maximum mass loss, and k_M equals the time at which mass loss equals half of $MassLoss_{Max}$. We modeled the mass loss as a function of time based on Eq. (1) using the nls function in R (version 4.1.1, R Core Team, 2021). We calculated the masses of elements in the litterbags (in g) by multiplying the litter mass (in kg) with the respective litter element concentrations (in g kg^{-1}). Based on this, we calculated changes (in %) in the masses of elements (N, P, K, Mn, Ca, and Mg) in the litterbags relative to their initial masses contained in 1.00 g of needle litter. We tested whether differences between the initial masses of N and P in the litterbags and the masses of N and P in the litterbags at the time when the mean of the N and P amounts was highest were statistically significant using Welch Two Sample *t*-test, where $P = 0.05$ was considered as the threshold of significance. In addition, we tested if there was a significant correlation between the mass loss of the litter at the end of the experiment and a) the mean annual temperature at the site, b) the initial N concentration of the litter or c) the initial P concentration of the litter, whereby $P = 0.05$ was considered as the threshold of significance. All data analyses were conducted using R (version 4.1.1, R Core Team, 2021).

3. Results

Mass loss of litter derived from the same tree species during the five years followed a similar pattern across the eight study sites (Fig. 1a–d and data in Appendix A), despite contrasting climate and soil characteristics (Table 1). Pine needle litter decomposed initially faster than spruce needle litter, but after 1830 days, similar percentages of the mass had been lost from the litters of both tree species (78.7 ± 5.7% and 76 ± 3.3%, respectively) (Fig. 1a–d, Table 2). The k_M values that indicate the time of half the maximal decomposition equaled 895 days for spruce and 429 days for pine (Fig. 1c and d). $MassLoss_{Max}$ was overestimated by the model for spruce litter, likely because the rate of mass loss of litter was still relatively high in the fifth year of decomposition for spruce litter, in contrast to pine litter (Fig. 1a and c). The mass loss of the litter at the end of the experiment was not significantly correlated with the initial N or P concentrations of the litter ($P > 0.05$). However, the mass loss of pine litter, but not of spruce litter, at the end of the experiment was significantly and positively correlated with the mean annual temperature of the sites ($R^2 = 0.60$, $P < 0.05$).

The mass of N in decomposing spruce litter (in litter bags that contained initially 1.00 g needle litter) increased during the first 172 days, on average by 19% compared to the initial mass of the element (Fig. 1e). The mass of N in decomposing pine litter increased during the first 365 days, on average by 30% compared to the initial mass of the element (Fig. 1f, Table 2). The mass of P in decomposing pine litter increased during the first 526 days, on average by 48% (Fig. 1h). In contrast, for spruce litter, P import was only observed at site 3 (Fig. 1g) where the initial litter P concentration of the spruce litter was as low as the initial P concentration of the pine litter. Net release of N, relative to the initial mass of N in the litter, only occurred after 895 days from spruce litter (Fig. 1e, Table 2). In pine litter, net release of N and P relative to their initial amounts was observed only after 1097 days (Fig. 1f and h, Table 2). Only 25 and 24% of the masses of N and P were lost after 1830 days of decomposition from pine litter (relative to the initial masses of N and P in 1.00 g of litter). For spruce litter the losses of N and P during 1830 days were larger (32.5 and 64.5% of the initial masses, respectively) (Table 2).

The concentrations of N (in g kg^{-1}) in the plant litter increased strongly during the first 526 days of decomposition by a factor of up to 2.8, i.e., 280% (Fig. 2a and b). Similarly, also the P concentration in the pine litter increased strongly during the first 526 days of decomposition in a similar magnitude as the N concentration (Fig. 2c). In contrast, in the spruce litter, the P concentration changed less and not consistently (Fig. 2c). Most molar N:P ratios of the litter during the five years of decomposition were in the range of 30–40, and there was no substantial change in the N:P ratio of the decomposing spruce and pine litter over time (Fig. 2e and f).

In contrast to N and P, we observed a net release of K, Mn, Ca, and Mg since the beginning of the decomposition process (Fig. 3, Table 2). The relative mass loss of Mn (relative to the initial Mn mass in 1.0 g of litter, in %) was smaller than the relative mass loss of needle litter throughout the decomposition process (Table 2). The relative decreases in the masses of Mg and K (in %) in spruce litter were larger than the relative

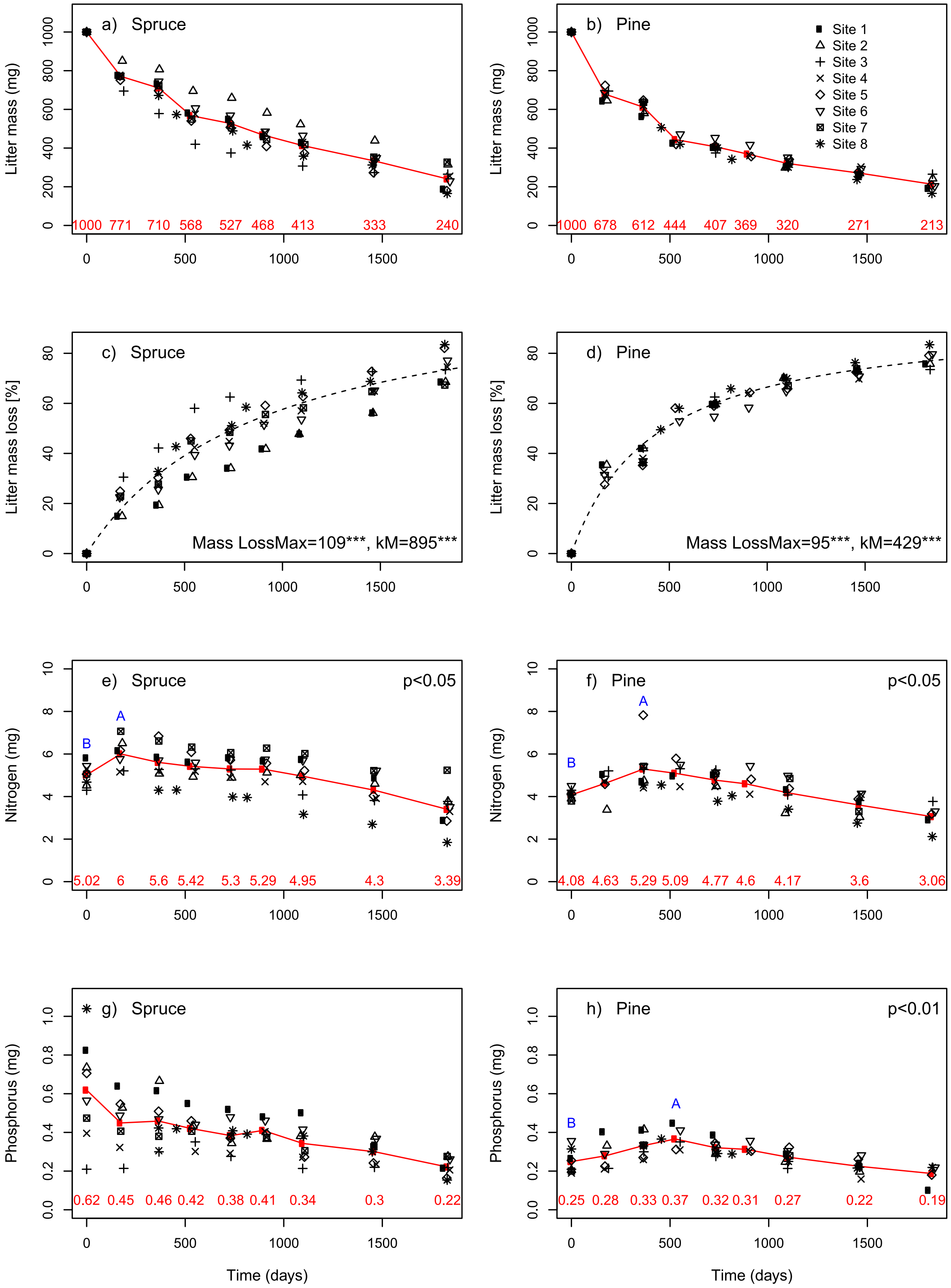

Fig. 1. Remaining mass (a and b) and accumulated mass loss (c and d) of needle litter as well as masses of nitrogen (e and f) and phosphorus (g and h) in spruce and pine needle litter (in litter bags that contained initially 1.00 g needle litter) as a function of time during decomposition. Red dots and red numbers indicate the arithmetic means. Stars in panels c and d indicate the level of significance of the model parameters, whereby *** stands for P < 0.001. Different blue capital letter in panels e, f, and h indicate significant differences tested between the initial masses of N and P in the litterbags and the masses of N and P in the litterbags at the time when the mean was highest. The level of significance of this difference is indicated in the top right corner of each panel. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 2

Change (in %) in the masses of elements (N, P, K, Mn, Ca, and Mg) in Norway spruce and Scots pine needle litter after a given number of days of decomposition, relative to their initial masses contained in 1.00 g of needle litter. In addition, the change in mass of spruce and pine needle litter relative to litter mass at day 0 is given. Negative changes in element masses indicate a net release of nutrients from litter compared to day 0, whereas positive changes indicate a net import of nutrients into the decomposing litter as compared to day 0.

Element	Spruce						Pine					
	Change day 173 (%)	Change day 365 (%)	Change day 528 (%)	Change day 895 (%)	Change day 1097 (%)	Change day 1830 (%)	Change day 173 (%)	Change day 365 (%)	Change day 528 (%)	Change day 895 (%)	Change day 1097 (%)	Change day 1830 (%)
N	+19.5	+11.6	+8.0	+5.4	−1.4	−32.5	+13.5	+29.7	+24.8	+12.7	+2.2	−25.0
P	−27.4	−25.8	−32.3	−33.9	−45.2	−64.5	+12.0	+32.0	+48.0	+24.0	+8.0	−24.0
K	−59.8	−62.1	−60.9	−69.0	−75.3	−85.1	−35.8	−35.8	−22.2	−39.5	−58.0	−75.3
Mn	−45.5	−39.2	−45.9	−37.8	−45.0	−52.3	−57.5	−56.7	−61.7	−55.8	−64.2	−68.3
Ca	−17.0	−8.1	−25.6	−32.6	−47.9	−76.4	−14.6	−27.1	−51.6	−61.7	−76.0	−86.7
Mg	−28.7	−40.6	−61.4	−70.3	−73.3	−80.2	−34.0	−52.8	−64.2	−56.6	−60.4	−75.5
Needle litter	−22.9	−29.0	−43.2	−53.2	−58.7	−76.0	−32.2	−39.0	−55.6	−63.1	−68.0	−78.7

decrease in the mass of spruce litter throughout the decomposition process (Table 2). With respect to pine litter, this was only true for Mg, while the mass of K decreased more slowly than the mass of the needle litter (Fig. 3; Table 2). The initial Ca concentrations in spruce litter varied strongly among the sites but were on average more than twice as high as in pine litter, while the relative losses of Ca were larger in pine than in spruce litter (Fig. 3g and h; Table 2).

4. Discussion

Here we show that N was imported into decomposing spruce and pine needle litter during the first 172 and 365 days of decomposition, respectively. Further, P was imported into pine litter during the first 526 days of decomposition, and the average import of P relative to the initial amount (48%) was larger than for N (30%). At site 3, where the initial litter P concentration was low, P import into the decomposing spruce litter also occurred (Fig. 1g), which suggests that P import was largely affected by the litter P concentration. Import of N and P likely occurred predominantly during the first months of decomposition because of the low N and P concentrations during this stage of decomposition (Fig. 2a–d). The imported nutrients are most likely derived from nutrient-rich parts of the mineral soil or litter layer, and are transported by fungi, mobile prokaryotes, soil microfauna, and insects (Wells et al., 1990; Wells and Boddy, 1995; Frey et al., 2003; Filipiak, 2018). It might also be that N enters the litter through N_2 fixation (Rinne et al., 2017). However, given that N and P in pine needle litter showed similar dynamics, transport of N together with P seems more likely. The transport of N and P into litter results mostly from the colonization of the litter by fungi, i.e. movement of biomass, and the senescence of N- and P-rich biomass of fungi in the colonized litter (Osono and Takeda, 2001). In addition, transport of N through an established fungal mycelium and release of N-rich exoenzymes may contribute to the enrichment of litter with N (Sinsabaugh et al., 2002). Through heavily colonizing the litter and supplementing it with N- and P-rich necromass, fungi create an organic matter pool that is stoichiometrically less dissimilar to their own biomass than the plant litter.

Import of N has previously been reported mostly for pine litter (Staaf and Berg, 1982; Fahey, 1983; Yavitt and Fahey, 1986; Berg and McClaugherty, 1989). Here we show that N is also imported into spruce needle litter during the first stage of decomposition. In accordance with Fahey (1983) who studied nutrient dynamics in decomposing Lodgepole pine (*Pinus contorta* Douglas) needle litter in Wyoming, USA, we found higher P than N import into pine litter. The percentage of increase in both N and P observed in the present study was a little larger than the one observed by Fahey (1983) who reported increases in N by about 10% and increases in P by about 15%. However, it might be that Fahey (1983) missed the time point of maximal net N and P import due to the coarser temporal resolution of the study. Similarly, Osono and Takeda (2001) reported that the mass of N increased by 40% and the mass of P by 50% in Japanese beech (*Fagus crenata* Blume) litter during the first two years of decomposition. The higher import of P than of N into pine needle litter is also in accordance with Staaf and Berg (1982) who investigated decomposition of Scots pine needle litter at a site in central Sweden and found that the mass of P relative to the initial P mass increased by almost 70% during the first two years of decomposition.

Our results show that N and P import into decomposing plant litter is a quantitatively important process that substantially enriches the litter with N and P. Therefore, the process of N and P transport into decomposing litter should be considered in studies of the stoichiometric imbalance between microbial biomass and soil, and the process should also be included in microbial decomposition models (Manzoni et al., 2021). The enrichment of the plant litter with N- and P-rich microbial necromass is likely beneficial for microbial N and P acquisition, because the enrichment renders the litter stoichiometrically more similar to the microbial biomass. It could be speculated that the import of nutrients slows down the decomposition process because it decreases the necessity for microorganisms to mine the litter for nutrients (Craine et al., 2007). Yet, given the faster decomposition (Fig. 1c and d) and the higher P concentration (Fig. 2c and d) of spruce litter compared to pine litter, this speculation about nutrient mining is unlikely true.

The total net loss of N from spruce and pine needle litter during 1830 days (5 years) was small (33 and 25%, respectively) compared to the loss of litter mass (76 and 79%, respectively) as well as the loss of other elements, such as K and Mg, indicating that N is strongly retained in the litter. The reason for this is most likely that microbial biomass is very N-rich (the global mean of the microbial biomass C:N ratio equals 6, Xu et al., 2013), and microorganisms, including fungi, incorporate a large part of the N derived from the needles into their biomass which retains N in decomposing litter. The same applies to P in pine litter as pine litter only released on average 24% of its initial P. In contrast, spruce litter released on average 65% of its initial P during the first five years of decomposition, and the reason for this is very likely the higher P concentration of the spruce litter at the beginning of the decomposition process.

The smaller relative loss of Mn as compared to the relative mass loss of needle litter throughout the decomposition process (Table 2) indicates that Mn was also preferentially retained, particularly in spruce litter, albeit less strongly than N in spruce litter and N and P in pine litter. The reason for the retention of Mn might be that Mn is needed for the oxidative decomposition of organic compounds through the lignin-degrading enzyme manganese peroxidase produced by white-rot fungi (Perez and Jeffries, 1992). This interpretation is supported by strong Mn enrichment in decomposing dead wood (Blanchette, 1984) and foliage litter (Pinzari et al., 2018). The differences in the time during which individual elements are retained in the decomposing litter, likely also strongly affect the transit time of the elements in the entire forest

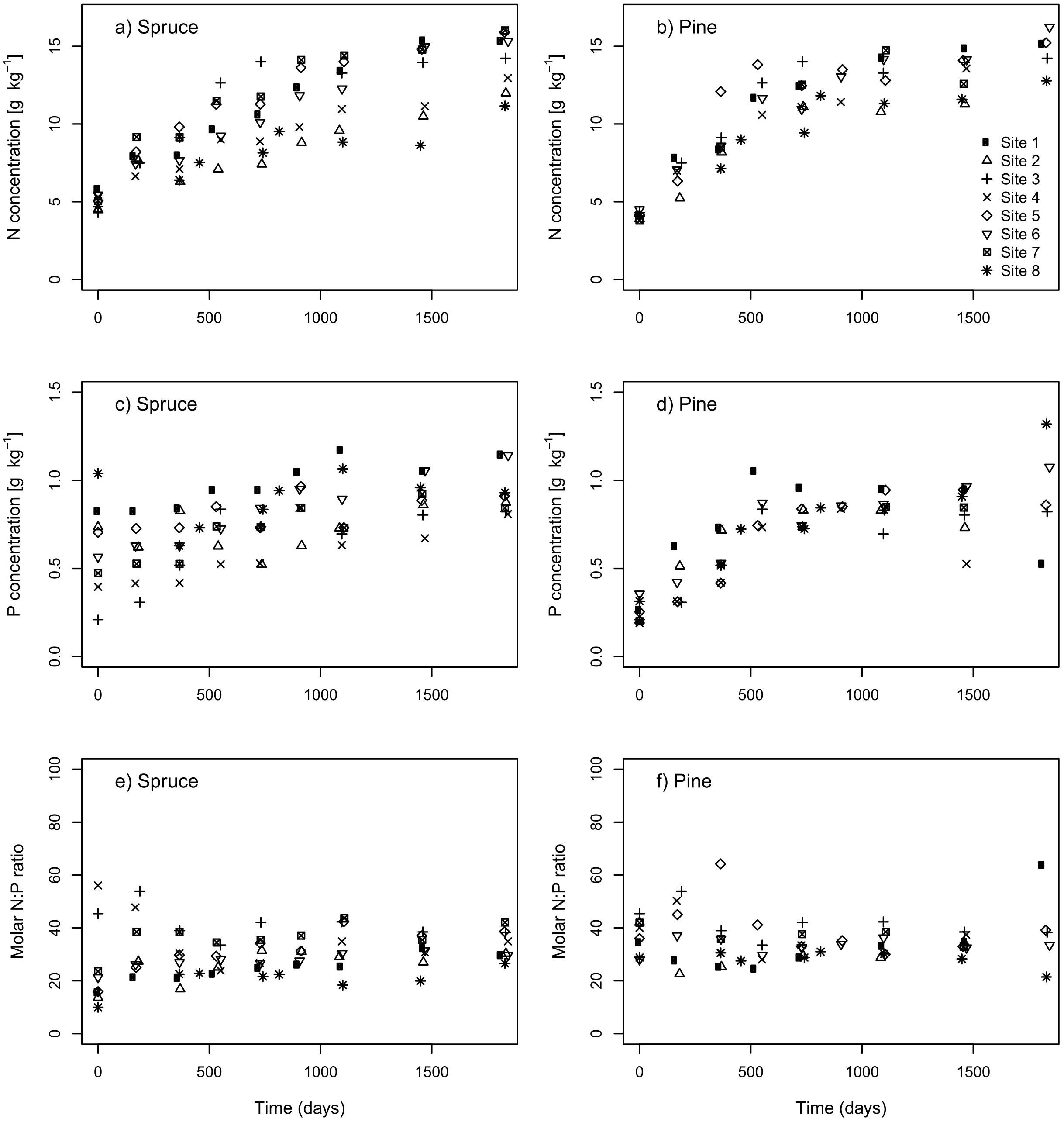

Fig. 2. Nitrogen concentrations (a and b), phosphorus concentration (c and d), and the molar N:P ratios (e and f) of spruce and pine needle litter as a function of time of decomposition.

ecosystem (Spohn and Sierra, 2018).

Our study shows that pine needle litter decomposed initially faster than spruce needle litter (see k_M value in Fig. 1c and d which was more than two times larger for spruce than for pine) which could be due to differences in organic matter quality among spruce and pine litter or due to the higher P concentration of the spruce litter (Fig. 2c). Yet, after five years, the accumulated mass losses of the two litter types were very similar. Notably, mass loss of litter derived from the same tree species during the five years followed a similar pattern across all eight sites (Fig. 1a–d), despite contrasting climate and site characteristics (Table 1). The similar mass loss of the litter derived from one tree species at the contrasting sites, and the differences in decomposition among spruce and pine litter indicate that litter characteristics are more important for the decomposition process than site characteristics (within similar climate zones and biomes). This finding is in contrast to recent reviews about mineral soil (Schmidt et al., 2011; Dungait et al., 2012), which state that organic matter quality plays a subordinate role for the decomposition process. In this context, our results suggest that, in contrast to the mineral soil, in the organic layer, the decomposition process is largely controlled by organic matter quality, at least if only similar climate zones and biomes are considered.

In conclusion, our study shows that substantial N and P import into decomposing needle litter takes place during the initial stages of decomposition. The import of N and P into the N- and P-poor litter alleviates a stoichiometric imbalance between the microbial biomass and the litter during initial decomposition when the N and P concentrations of the litter are low, and thus likely contributes to microbial nutrient acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial

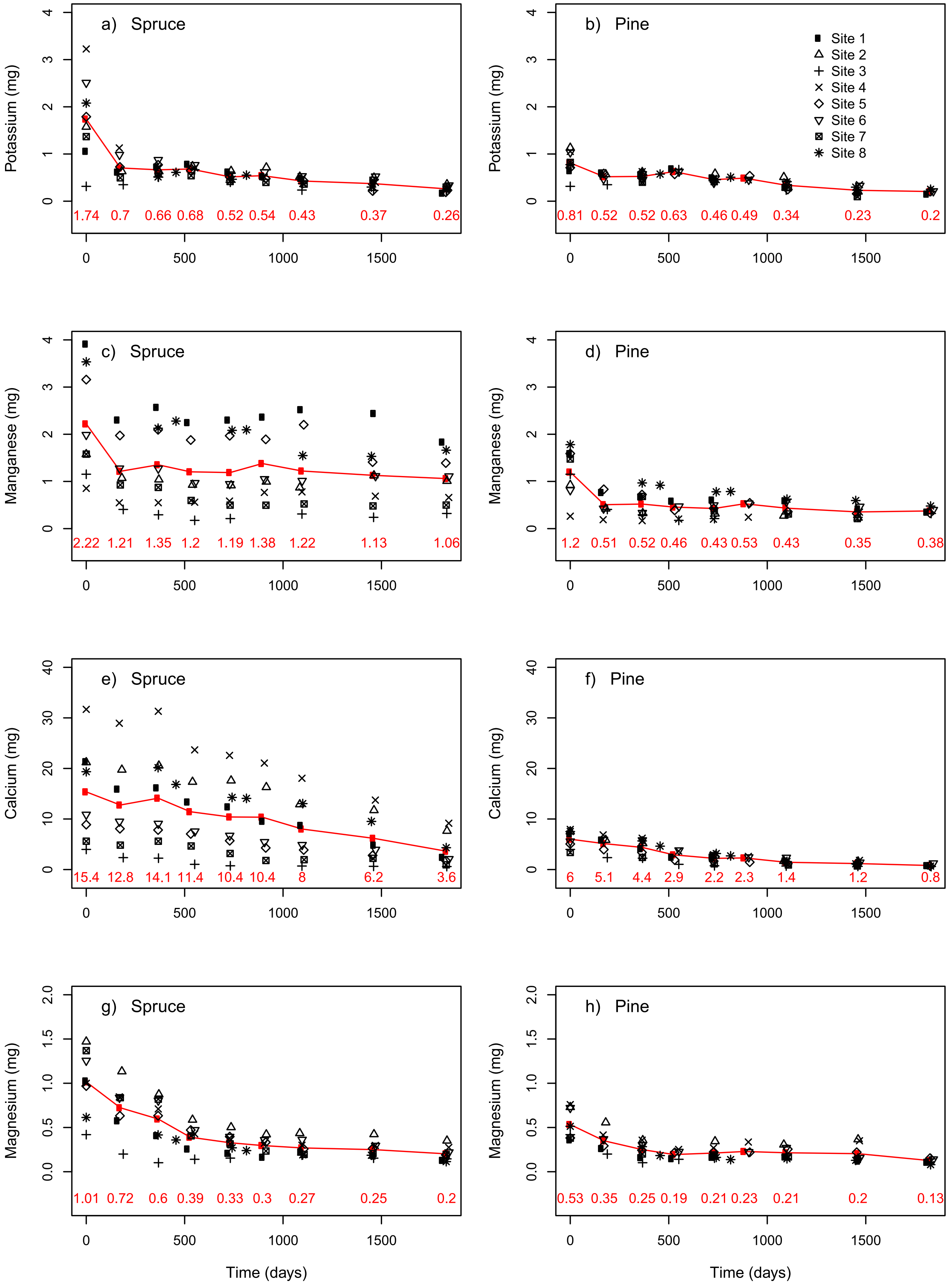

Fig. 3. Remaining mass of potassium (a and b), manganese (c and d), calcium (e and f), and magnesium (g and h) in decomposing spruce and pine needle litter (in litterbags that contained initially 1.00 g needle litter) as a function of time. Red dots and red numbers indicate the arithmetic means. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data of this study can be found in Appendix A.

Acknowledgment

The litterbag study was designed and conducted by Maj-Britt Johansson (†) at the Swedish University of Agricultural Sciences.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2022.108878.

References

Arsuffi, T.L., Suberkropp, K., 1989. Selective feeding by shredders on leaf-colonizing stream fungi: comparison of macroinvertebrate taxa. Oecologia 79, 30–37.

Bending, G.D., Read, D.J., 1995. The structure and function of the vegetative mycelium of ectomycorrhizal plants: V. Foraging behaviour and translocation of nutrients from exploited litter. New Phytologist 130, 401–409.

Berg, B., 1988. Dynamics of nitrogen (^{15}N) in decomposing Scots pine (*Pinus sylvestris*) needle litter. Long-term decomposition in a Scots pine forest. VI. Canadian Journal of Botany 66, 1539–1546.

Berg, B., McClaugherty, C., 1989. Nitrogen and phosphorus release from decomposing litter in relation to the disappearance of lignin. Canadian Journal of Botany 67, 1148–1156.

Berg, B., McClaugherty, C., 2020. Plant Litter: Decomposition, Humus Formation, Carbon Sequestration. Springer Nature.

Berg, B., Staaf, H., 1980. Decomposition rate and chemical changes of Scots pine needle litter. I. Influence of stand age. Ecological Bulletins 32, 363–372.

Blair, J.M., 1988. Nitrogen, sulfur and phosphorus dynamics in decomposing deciduous leaf litter in the southern Appalachians. Soil Biology and Biochemistry 20, 693–701.

Blanchette, R.A., 1984. Manganese accumulation in wood decayed by white rot fungi. Phytopathology 74, 725–730.

Boberg, J.B., Finlay, R.D., Stenlid, J., Ekblad, A., Lindahl, B.D., 2014. Nitrogen and carbon reallocation in fungal mycelia during decomposition of boreal forest litter. PLoS One 9, e92897.

Čapek, P., Choma, M., Tahovská, K., Kaňa, J., Kopáček, J., Šantrůčková, H., 2021. Coupling the resource stoichiometry and microbial biomass turnover to predict nutrient mineralization and immobilization in soil. Geoderma 385, 114884.

Cleveland, C.C., Liptzin, D., 2007. C: N: P stoichiometry in soil: is there a "Redfield ratio" for the microbial biomass? Biogeochemistry 85, 235–252.

Cools, N., Vesterdal, L., De Vos, B., Vanguelova, E., Hansen, K., 2014. Tree species is the major factor explaining C: N ratios in European forest soils. Forest Ecology and Management 311, 3–16.

Craine, J.M., Morrow, C., Fierer, N., 2007. Microbial nitrogen limitation increases decomposition. Ecology 88, 2105–2113.

Dungait, J.A., Hopkins, D.W., Gregory, A.S., Whitmore, A.P., 2012. Soil organic matter turnover is governed by accessibility not recalcitrance. Global Change Biology 18, 1781–1796.

Fahey, T.J., 1983. Nutrient dynamics of aboveground detritus in lodgepole pine Pinus contorta ssp. latifolia ecosystems, southeastern Wyoming. Ecological Monographs 53, 51–72.

Fanin, N., Fromin, N., Buatois, B., Hättenschwiler, S., 2013. An experimental test of the hypothesis of non-homeostatic consumer stoichiometry in a plant litter–microbe system. Ecology Letters 166, 764–772.

Filipiak, M., 2018. Nutrient dynamics in decomposing dead wood in the context of wood eater requirements: the ecological stoichiometry of saproxylophagous insects. In: Ulyshen, M. (Ed.), Saproxylic Insects. Springer, Cham, pp. 429–469.

Frey, S.D., Six, J., Elliott, E.T., 2003. Reciprocal transfer of carbon and nitrogen by decomposer fungi at the soil–litter interface. Soil Biology and Biochemistry 35, 1001–1004.

Hessen, D.O., Anderson, T.R., 2008. Excess carbon in aquatic organisms and ecosystems: physiological, ecological, and evolutionary implications. Limnology & Oceanography 53, 1685–1696.

Heuck, C., Weig, A., Spohn, M., 2015. Soil microbial biomass C: N: P stoichiometry and microbial use of organic phosphorus. Soil Biology and Biochemistry 85, 119–129.

Hood, J.M., McNeely, C., Finlay, J.C., Sterner, R.W., 2014. Selective feeding determines patterns of nutrient release by stream invertebrates. Freshwater Science 33, 1093–1107.

Joergensen, R.G., Meyer, B., 1990. Nutrient changes in decomposing beech leaf litter assessed using a solution flux approach. Journal of Soil Science 41, 279–293.

John, M.K., 1970. Colorimetric determination of phosphorus in soil and plant materials with ascorbic acid. Soil Science 109, 214–220.

Leake, J.R., Donnelly, D.P., Saunders, E.M., Boddy, L., Read, D.J., 2001. Rates and quantities of carbon flux to ectomycorrhizal mycelium following ^{14}C pulse labeling of Pinus sylvestris seedlings: effects of litter patches and interaction with a wood-decomposer fungus. Tree Physiology 21, 71–82.

Manzoni, S., Chakrawal, A., Spohn, M., Lindahl, B.D., 2021. Modeling microbial adaptations to nutrient limitation during litter decomposition. Frontiers in Forests and Global Change 4, 686945.

McGroddy, M.E., Daufresne, T., Hedin, L.O., 2004. Scaling of C:N:P stoichiometry in forests worldwide: implications of terrestrial Redfield-type ratios. Ecology 85, 2390–2401.

McMahon, S.M., Parker, G.G., Miller, D.R., 2010. Evidence for a recent increase in forest growth. Proceedings of the National Academy of Sciences 107, 3611–3615.

Mooshammer, M., Wanek, W., Hämmerle, I., Fuchslueger, L., Hofhansl, F., Knoltsch, A., Schnecker, J., Takriti, M., Watzka, M., Wild, B., Keiblinger, K., Zechmeister-Boltenstern, S., Richter, A., 2014. Adjustment of microbial nitrogen use efficiency to carbon: nitrogen imbalances regulates soil nitrogen cycling. Nature Communications 5, 1–7.

Nihlgård, B., 1972. Plant biomass, primary production and distribution of chemical elements in a beech and a planted spruce forest in South Sweden. Oikos 23, 69–81.

Osono, T., Takeda, H., 2001. Organic chemical and nutrient dynamics in decomposing beech leaf litter in relation to fungal ingrowth and succession during 3-year decomposition processes in a cool temperate deciduous forest in Japan. Ecological Research 16, 649–670.

Osono, T., Takeda, H., 2004. Potassium, calcium, and magnesium dynamics during litter decomposition in a cool temperate forest. Journal of Forest Research 9, 23–31.

Pawluk, S., 1967. Soil analysis by atomic absorption spectrophotometry. Atomic Absorption Newsletter 6, 53–56.

Perez, J., Jeffries, T.W., 1992. Roles of manganese and organic acid chelators in regulating lignin degradation and biosynthesis of peroxidases by Phanerochaete chrysosporium. Applied and Environmental Microbiology 58, 2402–2409.

Persson, T., Bååth, E., Clarholm, M., Lundkvist, H., Söderström, B.E., Sohlenius, B., 1980. Trophic structure, biomass dynamics and carbon metabolism of soil organisms in a Scots pine forest. Ecological Bulletins 32, 419–459.

Pinzari, F., Cuadros, J., Migliore, M., Napoli, R., Najorka, J., 2018. Manganese translocation and concentration on Quercus cerris decomposing leaf and wood litter by an ascomycetous fungus: an active process with ecosystem consequences? FEMS Microbiology Ecology 94, 111.

R Core Team, 2021. A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Austria, Vienna.

Rinne, K.T., Rajala, T., Peltoniemi, K., Chen, J., Smolander, A., Mäkipää, R., 2017. Accumulation rates and sources of external nitrogen in decaying wood in a Norway spruce dominated forest. Functional Ecology 31, 530–541.

Schmidt, M.W., Torn, M.S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I.A., et al., 2011. Persistence of soil organic matter as an ecosystem property. Nature 478, 49–56.

Sinsabaugh, R.L., Carreiro, M.M., Repert, D.A., 2002. Allocation of extracellular enzymatic activity in relation to litter composition, N deposition, and mass loss. Biogeochemistry 60, 1–24.

Sinsabaugh, R.L., Manzoni, S., Moorhead, D.L., Richter, A., 2013. Carbon use efficiency of microbial communities: stoichiometry, methodology and modelling. Ecology Letters 16, 930–939.

Spohn, M., 2015. Microbial respiration per unit microbial biomass depends on litter layer carbon-to-nitrogen ratio. Biogeosciences 12, 817–823.

Spohn, M., 2016. Element cycling as driven by stoichiometric homeostasis of soil microorganisms. Basic and Applied Ecology 17, 471–478.

Spohn, M., 2020. Increasing the organic carbon stocks in mineral soils sequesters large amounts of phosphorus. Global Change Biology 26, 4169–4177.

Spohn, M., Chodak, M., 2015. Microbial respiration per unit biomass increases with carbon-to-nutrient ratios in forest soils. Soil Biology and Biochemistry 81, 128–133.

Spohn, M., Klaus, K., Wanek, W., Richter, A., 2016a. Microbial carbon use efficiency and biomass turnover times depending on soil depth–Implications for carbon cycling. Soil Biology and Biochemistry 96, 74–81.

Spohn, M., Novák, T.J., Incze, J., Giani, L., 2016b. Dynamics of soil carbon, nitrogen, and phosphorus in calcareous soils after land-use abandonment–A chronosequence study. Plant and Soil 401, 185–196.

Spohn, M., Sierra, C.A., 2018. How long do elements cycle in terrestrial ecosystems? Biogeochemistry 139, 69–83.

Spohn, M., Stendahl, J., 2022. Carbon, nitrogen, and phosphorus stoichiometry of organic matter in Swedish forest soils and its relationship with climate, tree species, and soil texture. Biogeosciences 19, 2171–2186.

Spohn, M., Widdig, M., 2017. Turnover of carbon and phosphorus in the microbial biomass depending on phosphorus availability. Soil Biology and Biochemistry 113, 53–59.

Staaf, H., Berg, B., 1982. Accumulation and release of plant nutrients in decomposing Scots pine needle litter. Long-term decomposition in a Scots pine forest II. Canadian Journal of Botany 60, 1561–1568.

Wells, J.M., Boddy, L., 1995. Phosphorus translocation by saprotrophic basidiomycete mycelial cord systems on the floor of a mixed deciduous woodland. Mycological Research 99, 977–980.

Wells, J.M., Hughes, C., Boddy, L., 1990. The fate of soil-derived phosphorus in mycelial cord systems of Phanerochaete velutina and Phallus impudicus. New Phytologist 114, 595–606.

Xu, X., Thornton, P.E., Post, W.M., 2013. A global analysis of soil microbial biomass carbon, nitrogen and phosphorus in terrestrial ecosystems. Global Ecology and Biogeography 22, 737–749.

Yavitt, J.B., Fahey, T.J., 1986. Litter decay and leaching from the forest floor in Pinus contorta lodgepole pine ecosystems. Journal of Ecology 525–545.

Zechmeister-Boltenstern, S., Keiblinger, K.M., Mooshammer, M., Peñuelas, J., Richter, A., Sardans, J., Wanek, W., 2015. The application of ecological stoichiometry to plant–microbial–soil organic matter transformations. Ecological Monographs 85, 133–155.

Zederer, D.P., Talkner, U., Spohn, M., Joergensen, R.G., 2017. Microbial biomass phosphorus and C/N/P stoichiometry in forest floor and A horizons as affected by tree species. Soil Biology and Biochemistry 111, 166–175.