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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

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A B S T R A C T

The purpose of this research was to compare soil chemistry, microbially mediated carbon (C) and nitrogen (N) transformations and microbial biomass in forest floors under European beech (*Fagus sylvatica* L.), sessile oak (*Quercus petraea* (Mattuschka) Lieblein), Norway spruce (*Picea abies* (L.) Karst) and Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) at four study sites. We measured soil chemical characteristics, net N mineralization, potential and relative nitrification, basal respiration, microbial and metabolic quotient and microbial biomass C and N under monoculture stands at all sites (one mixed stand). Tree species affected soil chemistry, microbial activities and biomass, but these effects varied between sites. Our results indicated that the effect of tree species on net N mineralization was likely to be mediated through their effect on soil microbial biomass, reflecting their influence on organic matter content and carbon availability. Differences in potential nitrification and relative nitrification might be related to the presence of ground vegetation through its influence on soil NH_4 and labile C availability. Our findings highlight the need to study the effects of tree species on microbial activities at several sites to elucidate complex N cycle interactions between tree species, ground vegetation, soil characteristics and microbial processes.

1. Introduction

At the beginning of the 19th century, plantation of Norway spruce and Scots pine for timber production was substantially increased in European forests (Zerbe, 2002). However, with the forest dieback symptoms observed during the 20th century, concerns were expressed with regard to the ecological and economical risks posed by coniferous monocultures (Augusto et al., 2002). Within the framework of sustainable forest management, additional concerns such as climate-induced dieback and other stress factors led to alternative forest management options, such as the conversion of coniferous monocultures into broadleaved or mixed forests, close to the potential natural vegetation of the site (Spiecker et al., 2004). However, in order to understand and anticipate how a change in species composition would affect ecosystem processes, a detailed knowledge of the effect of tree species on soil processes is necessary.

Nitrogen (N) is frequently the most limiting nutrient in forests (Prescott, 2002). Soil N transformations (ammonification, immobilization, nitrification) are microbially mediated processes which control the availability of N for plant uptake. Indeed, plants, heterotrophic microorganisms and ammonia oxidizers compete for inorganic N. Traditionally, heterotrophic microorganisms are assumed to be stronger competitors for inorganic N than plants (Hart and Firestone, 1991). More recently, it has been reported that plant roots and microorganisms are also able to use organic N (Schimel and Chapin, 1996) and that plants may be better competitors for N due to their root spreading facilities and the presence of mycorrhizae (Schimel and Bennett, 2004).

The effects of tree species on soil microbial processes are generally attributed to differences in quantity and quality of substrate input through litter and root exudates (Grayston et al., 1996; Augusto et al., 2002), their specific nutrition (Lipson and Näsholm, 2001), their influence on soil physical characteristics like soil structure and texture (Lavelle and Spain, 2001), pedoclimate (Canham et al., 1994) or on the development of an understory vegetation (Olsson and Falkengren-Grerup, 2003). Tree species may also influence input fluxes of nutrient and acidifying compounds in ecosystems, with greater deposition generally reported under conifers (De Schrijver et al., 2007). Although a number of studies report tree species effects on soil microbial activities, results are contradictory. Indeed, net N mineralization rates beneath

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coniferous compared to deciduous stands have been reported to be higher (Thomas and Prescott, 2000), similar (Zhong and Makeschin, 2006) or lower (Satti et al., 2003). C mineralization in soils beneath conifers has been reported as higher than (Brüggemann et al., 2005) or similar to (Thomas and Prescott, 2000) C mineralization in soils beneath deciduous species. However, most studies report results from measurements performed at one site only, or compare different study sites where environmental factors and pedology may interfere with the 'tree species effect' on microbial activities. Furthermore, most studies report only one microbial process, which renders interpretation of underlying mechanisms difficult.

Our study took place at four sites under four commercial tree species: European beech (*Fagus sylvatica* L.), sessile oak (*Quercus petraea* (Mattuschka) Lieblein), Norway spruce (*Picea abies* (L.) Karst) and Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco). We measured soil chemical characteristics (pH, organic matter, inorganic N, C/N ratio, exchangeable cations), net N mineralization, potential and relative nitrification, basal respiration, microbial biomass C and N, microbial and metabolic quotient in the forest floors. The aims of the present research were to: (1) investigate tree species effects on microbial biomass and C and N transformations in the forest floors; (2) explore the possibility of generalizing tree species effects across sites.

2. Materials and methods

2.1. Description of the study sites

This study was carried out at 3 Belgian sites: Chimay (50°01′N, 04°24′E), Hestreux (50°34′N, 06°01′E) and Vielsalm (50°18′N, 05°58′E) and at 1 site in the Grand-Duchy of Luxembourg: Rambrouch (49°49′N, 5°47′E). Elevation of these sites ranged from 340 to 460 m, with slopes below 3%, mean annual rainfall varied from 1000 to 1300 mm and mean annual temperature ranged from 7 °C to 8 °C. At each site, soil sampling was performed in neighbouring stands, located on the same geological parent material but covered with different tree species (Table 1). All stands were situated on acid brown soils (Cambisol (Dystric); IUSS Working Group WRB, 2006). The oak stand at Hestreux and the spruce stand at Rambrouch were characterised by an important cover of ground vegetation (80–90%). At Hestreux, the understory vegetation was dominated by *Molinia caerulea* (L.) Moench (50–75% coverage), *Deschampsia flexuosa* (L.) Trin. (5% coverage) and *Pteridium aquilinum* (L.) Kuhn (<5% coverage). At Rambrouch, understory vegetation was principally composed of *Vaccinium myrtillus* L. (75% coverage) and *D. flexuosa* (L.) Trin. (5% coverage).

2.2. Soil sampling and chemical analysis

Soils were sampled twice to account for potential differences in microbiological activities in response to environmental conditions (temperature, humidity) and phenological development of vegetation (affecting e.g. C availability through root exudation). Sampling times were April 2006, beginning of the growing season, and September 2006, end of the growing season. In April, four composite soil samples (10 cores, 4 cm diameter × variable depth (see Table 1), taken around each tree) were taken with a steel corer at 1 m from the base of the trunk from the upper organic horizon (L, F, H) under four randomly selected mature trees of each species represented at Chimay, Hestreux and Vielsalm (Table 1). In September, soil samples were collected at all sites (sampling beneath Douglas-fir was added at Vielsalm). In the mixed stand at Chimay, 10 cores for the composite samples were taken along a transect (8–10 m) between an oak and a beech tree. The moist field samples were sieved (4 mm) to remove stones, roots and coarse woody debris and were stored at 4 °C until analysis (less than 1 week). In September 2006, four composite mineral soil samples (three cores, 8 cm diameter × 40 cm depth) were taken at each site with a steel corer at 1.5 m from the base of the trunk under the same four trees as for organic horizons.

Soil moisture, pH and loss on ignition (LOI) were determined according to Allen (1989). The carbon content (C_{org}) was assumed to constitute 58% of loss on ignition (Allen, 1989). Both pH_{H_2O} and pH_{KCl} were measured, representing active and exchangeable acidity, respectively. Total C and N contents in soil samples were analysed using a C–N–S elemental analyser (Carlo Erba, Italy) on oven dried and ground sub-samples. NH_4-N was extracted with 1 M KCl (1:5, w:v) and analysed colorimetrically with a continuous flow analyser (AutoAnalyser3, BranLuebbe, Germany). Exchangeable cations (Al^{3+}, Ca^{2+}, Fe^{2+}, K^{+}, Mg^{2+}, Mn^{2+}, Na^{+}, Zn^{2+}) were extracted with 0.1 M $BaCl_2$ (1:5, w:v) (Hendershot and Duquette, 1986). Chemical analysis of the filtered (filter 595½, Whatman, Germany) and acidified $BaCl_2$ extracts (1% HNO_3 Suprapur) was performed using ICP-AESS (Varian, Australia). Mineral soil samples were analysed for total calcium content by ICP-AESS (Varian, Australia), after digestion with $H_2SO_4/HNO_3/HClO_4$ (Hossner, 1996).

2.3. Potential nitrification

Potential nitrification was determined using the 'shaken soil-slurry method' (Hart et al., 1994). This method involved shaking 10 g field moist, sieved soil in 100 ml solution (300 μM KH_2PO_4, 700 μM K_2HPO_4, 750 μM $(NH_4)_2SO_4$) on a rotary shaker (180 rev min^{-1}) at 25 °C in the dark. After 2, 6, 23, 26 and 29 h, homogenised sub-samples (15 ml) were taken, filtered (filter 595½, Whatman, Germany) and stored at −20 °C until analysis. NO_3-N concentrations were analysed colorimetrically with a continuous flow analyser (AutoAnalyser3, BranLuebbe, Germany). Nitrification rates were calculated by linear regression of nitrate concentrations over time (μg N g^{-1} d^{-1}).

2.4. Nitrogen mineralization

Net N mineralization was studied in aerobic laboratory incubation lasting 31 days at constant temperature (25 °C) in darkness and under field moisture (Hart et al., 1994). At the beginning and the end of the incubation, inorganic nitrogen was extracted with 1 M KCl solution (1:5, w:v) (Allen, 1989) and analysed colorimetrically using a continuous flow analyser (AutoAnalyser3, BranLuebbe, Germany). The net N mineralization rate (Nmin) was

Table 1
Site description.

Study site	Chimay	Hestreux	Vielsalm	Rambrouch
Tree species (depth of the forest floors)	Sessile oak (4 cm), European beech (6 cm), Mixed stand oak–beech (6 cm)	Sessile oak (3 cm), European beech (5 cm), Norway spruce (6 cm)	Sessile oak (4 cm), European beech (4 cm), Norway spruce (6 cm), Douglas-fir (5 cm)	Sessile oak (9 cm), European beech (5 cm), Norway spruce (4 cm), Douglas-fir (2 cm)
Geology	Shale and siltstone; Frasnien	Quartzite; Revinian	Phyllite or quartzo-phyllite; Salmian	Schist superior; Siegenian
History	Transformation of coppice into high forest	Transformation of heathland into coppice of broadleaves	Transformation of beech high forest into heathland and coppice	Beech high forest and mixed broadleaves (beech and oak)

calculated by dividing the net increase in inorganic N during the incubation period by the number of incubation days. Relative nitrification was expressed as the percentage of nitrogen produced as NO_3-N ([NO_3-N production/(NO_3-N+NH_4-N production)] × 100).

2.5. *Basal respiration, microbial biomass C and biomass N*

Basal respiration (BR) (CO_2 evolution without added substrate) was measured as CO_2 accumulation in the headspace (250 ml) of an amber bottle (Supelco, USA) from 20 g field moist soil, at 15 °C in the dark. Gas samples (4 ml) were taken at 0, 120, 150 and 180 min and analysed with an infrared absorption gas analyser (EGM-4, PPsystem, UK). Before measurements, soil samples were kept for 12 h at room temperature for equilibration (Lovell and Jarvis, 1998). The CO_2-C production rates were estimated by linear regression of CO_2-C against time ($\mu g\ g^{-1}\ h^{-1}$).

Soil microbial biomass C and N were determined by the chloroform fumigation extraction method (Beck et al., 1997), followed by 0.5 M K_2SO_4 extraction of both fumigated and unfumigated soils. Fumigations were carried out for a period of three days in vacuum desiccators with alcohol-free chloroform. Preliminary tests of incubation during 1, 3 or 5 days showed that an incubation time of 3 days was optimal for soil microbial biomass analyses (data not shown). Dissolved organic carbon in fumigated and unfumigated extracts was measured with a Total Organic Carbon analyser (Labtoc, Pollution and Process Monitoring limited, UK). Organic N in both extracts was measured with a continuous flow analyser equipped with a UV digestor (Autoanalyser3, BranLuebbe, Germany). Soil microbial biomass C and N were calculated by dividing the difference of total extract between fumigated and unfumigated samples with a conversion factor of 0.35 for biomass C (Sparling and West, 1990) and 0.54 for biomass N (Brookes et al., 1985). The metabolic quotient (qCO_2) represents the quantity of respired CO_2-C per unit of soil microbial biomass and was calculated by dividing basal respiration by soil microbial biomass C (Anderson and Domsch, 1990). The microbial quotient ($q$mic) represents the availability of soil C and was calculated by dividing microbial biomass C by C_{org} (Anderson and Domsch, 1990) with C_{org} = LOI/1.72 (Allen, 1989).

2.6. *Statistical analysis*

As multivariate ANOVA showed significant interactions, one-way ANOVA for unbalanced designs (proc GLM) was applied for analysing the effect of tree species on soil properties and microbial activities at each site and at each sampling time using the SAS program (SAS, SAS Institute Inc., 1985). Multiple comparisons of soil properties and microbial activities were performed by a Duncan's test ($\alpha = 0.05$). Chemical properties of deeper mineral soils of the different sites and under the different species were compared by a one-way ANOVA for unbalanced design (proc GLM, SAS, SAS Institute Inc., 1985). The relationships between variables were examined using Pearson's correlations.

3. Results

3.1. *Chemical characteristics of the mineral soil*

The mineral soil horizon was acidic at all stands with pH_{KCl} ranging from 3.4 to 4.2 (Table 2). Exchangeable cations ranged from 1.89 to 3.61 meq 100 g^{-1} and the sum of exchangeable base cations (SEB) ranged from 0.15 to 0.33 meq 100 g^{-1} across all stands. There were no significant differences in mineral soil chemistry under the different tree species within each site, except a lower pH_{KCl} under oak compared to beech and spruce at Hestreux ($F = 17.34$; $P < 0.0008$) and lower total calcium under oak compared to beech and beech–oak at Chimay ($F = 8.34$; $P < 0.0089$). Soils at Vielsalm and Hestreux showed significantly higher pH_{KCl} ($F = 40.04$; $P < 0.0001$) and total calcium content ($F = 77.75$; $P < 0.0001$), but lower exchangeable cations ($F = 9.17$; $P < 0.0001$) and sum of exchangeable base cations ($F = 14.05$; $P < 0.0001$) compared to soils at Rambrouch and Chimay.

3.2. *Chemical characteristics of the organic layers*

All stands were located on highly acidic soils with pH_{H_2O} ranging from 3.7 to 4.3 (Table 3). A significant effect of tree species on soil pH_{H_2O} was observed at Hestreux only, where the soil was more acidic under spruce compared to beech and oak (both samplings). The pH_{KCl} varied between 2.7 and 3.2 across stands. An effect of tree species on pH_{KCl} was observed at all sites, except Hestreux. pH_{KCl} was significantly lower under spruce at Vielsalm and Rambrouch. We observed a lower pH_{KCl} under oak compared to beech at Chimay (September) and Rambrouch.

At Chimay, exchangeable soil NH_4-N was significantly lower under beech compared to oak and beech–oak (April), with no significant differences between stands at the other sites (Table 3). The influence of tree species on organic matter content (LOI) was observed at all sites except at Chimay (Table 3). LOI was highest under spruce at Hestreux (April), Vielsalm (April, not different from oak) and Rambrouch (September). At Vielsalm (September) and Rambrouch (September), LOI was higher under Douglas-fir compared to beech. A significant influence of tree species on moisture content was observed at Chimay (April), where moisture content was higher under oak than under beech and beech–oak, and at Rambrouch (September), where moisture content was highest under spruce and lowest under beech and Douglas-fir (Table 3).

Total nitrogen (N_{tot}) contents ranged from 0.46 to 0.96%. Within each site, tree species did not affect N_{tot} (Table 3). N_{tot} was significantly higher at Hestreux and Rambrouch compared to Vielsalm and Chimay (statistics not shown). At all sites, C/N ratios were higher under spruce and Douglas-fir compared to beech and oak (Table 3), whereas C/N ratios did not differ between sites (statistics not shown).

Effects of tree species on exchangeable cations in the forest floor were not consistent across sites and sampling times (Table 4). Exchangeable Ca^{2+} was low, ranging from 1.34 to 3.32 meq 100 g^{-1} across all stands, with no significant influence of tree species. Exchangeable K^+ was highest under oak at Hestreux and Vielsalm (April). At most sites (except Hestreux in April and Chimay in September), exchangeable Mg^{2+} was lowest under beech. Al^{3+} was higher under spruce and Douglas-fir at Vielsalm, whereas at Chimay, it was higher under oak compared to beech and beech–oak.

3.3. *N mineralization, relative nitrification and potential nitrification*

The net N mineralization rate (Nmin) ranged from 0.52 to 5.77 $\mu g\ N\ g^{-1}\ d^{-1}$ across stands and sampling times (Fig. 1a). Nmin was significantly higher at Hestreux compared to the other sites (statistics not shown). There was no consistent pattern of tree species effect across sites. Furthermore, at Chimay, species effect was dependent on sampling time. At this site, Nmin was significantly higher under oak compared to beech (both samplings) and beech–oak (April). At Hestreux, tree species had no significant effect on Nmin. At Vielsalm (April), Nmin was significantly higher under oak and beech than under spruce. In September, Nmin was higher under oak than under spruce and Douglas-fir. At Rambrouch (September), higher Nmin was observed under oak and spruce compared to Douglas-fir. At this site, Nmin beneath beech showed

Table 2
Chemical characteristics of the deep mineral soils (40 cm depth).

Site	Species	pH_{KCl}	Total Ca (mg 100 g^{-1})	Exchangeable cations (meq 100 g^{-1})	SEB (meq 100 g^{-1})
Chimay	Beech–oak	3.5 (0.04)a	67.2 (4.7)a	2.9 (0.2)a	0.31 (0.05)a
	Beech	3.4 (0.08)a	62.1 (2.1)a	3.4 (0.2)a	0.31 (0.02)a
	Oak	3.5 (0.07)a	45.2 (4.6)b	3.3 (0.3)a	0.29 (0.05)a
Hestreux	Beech	4.1 (0.04)a	143.3 (18.5)a	2.4 (0.2)a	0.18 (0.03)a
	Oak	3.9 (0.03)b	106.0 (3.6)a	3.1 (0.5)a	0.17 (0.03)a
	Spruce	4.2 (0.04)a	157.5 (15.4)a	2.1 (0.2)a	0.19 (0.02)a
Vielsalm	Beech	4.0 (0.08)a	123.1 (14.6)a	2.0 (0.2)a	0.19 (0.03)a
	Oak	4.1 (0.03)a	138.5 (7.3)a	1.9 (0.2)a	0.17 (0.02)a
	Spruce	4.0 (0.03)a	142.6 (4.7)a	2.3 (0.3)a	0.15 (0.03)a
	Douglas-fir	4.0 (0.07)a	146.4 (3.3)a	2.5 (0.4)a	0.25 (0.04)a
Rambrouch	Beech	3.8 (0.06)a	58.3 (1.6)a	2.8 (0.1)a	0.35 (0.04)a
	Oak	3.7 (0.03)a	46.6 (6.5)a	3.1 (0.2)a	0.32 (0.02)a
	Spruce	3.6 (0.11)a	51.0 (11.9)a	3.6 (0.6)a	0.30 (0.06)a
	Douglas-fir	3.7 (0.08)a	53.1 (6.2)a	3.3 (0.4)a	0.33 (0.07)a

Values are means (±SEM); $n = 4$. Exchangeable cations ($Al^{3+} + Ca^{2+} + Fe^{2+} + K^{+} + Mg^{2+} + Mn^{2+} + Na^{+} + Zn^{2+}$), SEB = sum of exchangeable base cations ($Mg^{2+} + Ca^{2+} + K^{+} + Na^{+}$). Different letters indicate significant differences between tree species at each site according to Duncan's test at $P < 0.05$.

an intermediate value. We observed a positive correlation between Nmin and moisture content ($P < 0.0001$, $R = 0.62$) and a negative correlation between Nmin and C/N ratio ($P < 0.01$, $R = -0.39$) (Table 5).

Relative nitrification (RN) ranged from 2 to 73% across all stands (Fig. 1b). Low RN (below 15%) was observed under oak–beech at Chimay (April), oak at Hestreux, spruce at Vielsalm (both samplings) and Rambrouch (September). At Chimay (April), RN was lower under beech–oak than under oak and beech. At Hestreux, RN was lower under oak compared to spruce (both samplings) and beech (September). At Vielsalm, RN was lower under spruce compared to beech and oak. At Rambrouch, RN was lower under spruce than under the other species. RN was positively correlated with potential nitrification ($P < 0.001$, $R = 0.55$) (Table 5).

Mean values for potential nitrification (nitpot) ranged between 0.67 and 16.92 μg N g^{-1} d^{-1} across stands (Fig. 1c). Tree species had a significant influence on nitpot at all sites, except at Chimay. At Hestreux, nitpot was significantly lower under oak compared to beech and spruce in April, whereas it was significantly lower under oak and spruce compared to beech in September. At the other sites, effects of tree species were consistent for both sampling times. At Vielsalm, nitpot was significantly lower under spruce and Douglas-fir than under beech and oak. At Rambrouch, lower nitpot was observed under spruce and Douglas-fir than under beech and oak.

3.4. Respiration, metabolic and microbial quotient, microbial biomass C and N

Basal respiration (BR) ranged from 1.21 to 3.16 μg CO_2-C g^{-1} h^{-1} (Fig. 2c). Tree species did not influence BR at Chimay and Vielsalm. At Hestreux, BR was significantly higher under oak than under beech (both samplings) and under spruce than under beech (April). At Rambrouch, BR was significantly higher under spruce than under other species (Fig. 2c). We observed a positive correlation between BR and LOI ($P < 0.0001$, $R = 0.58$) (Table 5).

The microbial biomass C (MB-C) and N (MB-N) ranged from 1674 to 3169 μg g^{-1} and from 121 to 442 μg g^{-1}, respectively. Trees species influenced MB-C (Fig. 2a) and MB-N (Fig. 2b)

Table 3
Chemical characteristics of the forest floors.

Time of sampling	Site	Species	pH_{H_2O}	pH_{KCl}	NH4-N (mg g^{-1})	Organic matter (LOI, %)	Moisture (%)	N_{tot} (%)	C/N ratio
April 2006	Chimay	Beech–oak	4.2 (0.03)a	3.1 (0.01)a	10.3 (0.8)a	25.5 (0.6)a	44.2 (0.6)b	n.d.	n.d.
		Beech	4.2 (0.04)a	3.1 (0.04)a	4.6 (0.9)b	23.9 (1.2)a	42.2 (0.6)b	n.d.	n.d.
		Oak	4.1 (0.04)a	3.2 (0.01)a	14.3 (2.6)a	26.3 (0.5)a	48.2 (1.3)a	n.d.	n.d.
	Hestreux	Beech	4.2 (0.05)b	2.9 (0.03)a	14.7 (4.6)a	40.4 (2.5)b	57.2 (1.8)a	n.d.	n.d.
		Oak	4.3 (0.06)b	2.9 (0.02)a	33.4 (8.6)a	42.4 (1.2)b	60.0 (0.7)a	n.d.	n.d.
		Spruce	4.0 (0.01)a	2.8 (0.09)a	22.9 (2.7)a	51.6 (1.8)a	60.0 (0.4)a	n.d.	n.d.
	Vielsalm	Beech	4.0 (0.06)a	2.9 (0.06)b	11.7 (2.3)a	26.4 (1.8)b	47.7 (1.9)a	n.d.	n.d.
		Oak	4.1 (0.04)a	2.9 (0.07)b	11.3 (1.2)a	38.0 (3.1)a	55.7 (2.0)a	n.d.	n.d.
		Spruce	3.9 (0.04)a	2.7 (0.01)a	17.9 (3.9)a	37.6 (2.3)a	51.5 (2.7)a	n.d.	n.d.
September 2006	Chimay	Beech–oak	4.0 (0.03)a	2.9 (0.01)a	5.6 (3.6)a	21.6 (1.6)a	28.2 (0.9)a	0.50 (0.05)a	24.7 (2.0)a
		Beech	4.1 (0.03)a	3.0 (0.01)b	1.9 (0.7)a	18.4 (0.6)a	29.0 (1.8)a	0.46 (0.03)a	26.3 (0.9)a
		Oak	4.0 (0.04)a	2.9 (0.02)a	5.0 (1.4)a	22.1 (1.3)a	30.0 (1.1)a	0.56 (0.03)a	23.2 (0.8)a
	Hestreux	Beech	3.9 (0.05)b	2.9 (0.04)a	0.9 (0.7)a	37.3 (1.2)a	52.5 (0.5)a	0.93 (0.13)a	24.6 (0.8)b
		Oak	4.1 (0.01)b	2.8 (0.03)a	2.1 (1.9)a	39.8 (2.3)a	56.2 (1.0)a	0.96 (0.19)a	24.0 (0.5)b
		Spruce	3.8 (0.07)a	2.8 (0.11)a	0.0 (0.0)a	42.6 (1.9)a	52.2 (1.6)a	0.79 (0.05)a	29.2 (0.6)a
	Vielsalm	Beech	4.0 (0.03)a	2.9 (0.02)b	0.1 (0.02)a	25.1 (2.6)b	48.5 (2.4)a	0.59 (0.05)a	22 (1.9)b
		Oak	4.0 (0.08)a	2.8 (0.09)ab	3.00 (1.8)a	27.5 (2.7)ab	49.7 (2.4)a	0.66 (0.08)a	23.4 (0.4)b
		Spruce	3.9 (0.04)a	2.7 (0.01)a	11.4 (9.1)a	31.0 (1.1)ab	50.2 (0.9)a	0.66 (0.06)a	30.2 (0.3)a
		Douglas-fir	3.8 (0.07)a	2.8 (0.03)ab	0.0 (0.0)a	33.9 (1.3)a	46.5 (1.5)a	0.66 (0.06)a	27.7 (0.3)a
	Rambrouch	Beech	3.9 (0.05)a	3.1 (0.02)c	0.0 (0.0)a	31.1 (1.2)c	26.5 (1.0)c	0.72 (0.04)a	22.4 (0.4)b
		Oak	3.7 (0.08)a	2.9 (0.04)b	0.7 (0.7)a	38.2 (2.5)b	33.5 (1.5)b	0.81 (0.08)a	24.5 (0.2)b
		Spruce	3.7 (0.04)a	2.8 (0.03)a	1.6 (1.4)a	52.8 (1.2)a	37.0 (0.2)a	0.91 (0.05)a	29.4 (0.9)a
		Douglas-fir	3.7 (0.07)a	2.9 (0.03)b	2.4 (1.4)a	37.9 (0.5)b	26.5 (0.6)c	0.70 (0.02)a	28.4 (0.5)a

Values are means (±SEM); $n = 4$. LOI: loss on ignition, N_{tot}: total nitrogen. n.d.: not determined. Different letters indicate significant differences between tree species at each site according to Duncan's test at $P < 0.05$.

Table 4
Exchangeable cations (meq 100 g^{-1}) in forest floors.

Time of sampling	Site	Species	Al^{3+}	Ca^{2+}	Fe^{2+}	K^{+}	Mg^{2+}	Mn^{2+}	Zn^{2+}
April 2006	Chimay	Beech–oak	4.45 (0.15)b	2.05 (0.19)a	0.05 (0.01)a	0.14 (0.01)a	0.39 (0.02)a	0.45 (0.04)a	0.02 (0.01)a
		Beech	4.65 (0.37)b	1.90 (0.20)a	0.05 (0.01)a	0.14 (0.01)a	0.30 (0.03)b	0.46 (0.05)a	0.02 (0.01)a
		Oak	5.76 (0.19)a	1.51 (0.21)a	0.07 (0.01)a	0.18 (0.02)a	0.42 (0.03)a	0.50 (0.03)a	0.02 (0.01)a
	Hestreux	Beech	7.88 (0.29)a	1.78 (0.39)a	0.09 (0.01)a	0.23 (0.03)b	0.46 (0.07)a	0.16 (0.02)b	0.07 (0.01)b
		Oak	5.61 (0.87)a	2.03 (0.3)a	0.06 (0.01)a	0.34 (0.01)a	0.89 (0.11)a	0.06 (0.01)b	0.12 (0.01)a
		Spruce	8.89 (2.06)a	2.63 (0.78)a	0.11 (0.02)a	0.15 (0.02)c	0.58 (0.15)a	0.42 (0.01)a	0.08 (0.01)b
	Vielsalm	Beech	4.43 (0.29)b	1.78 (0.37)a	0.10 (0.02)a	0.13 (0.01)b	0.41 (0.05)b	0.35 (0.05)b	0.03 (0.01)a
		Oak	4.21 (0.46)b	3.32 (0.59)a	0.08 (0.01)a	0.25 (0.03)a	0.68 (0.09)a	0.61 (0.08)a	0.05 (0.01)a
		Spruce	7.25 (0.55)a	1.82 (0.25)a	0.15 (0.02)a	0.12 (0.02)b	0.69 (0.08)a	0.20 (0.04)b	0.05 (0.01)a
September 2006	Chimay	Beech–oak	5.05 (0.47)ab	1.90 (0.48)a	0.03 (0.01)a	0.12 (0.03)a	0.37 (0.04)a	0.35 (0.09)a	0.02 (0.01)a
		Beech	4.24 (0.32)b	2.28 (0.34)a	0.02 (0.01)a	0.13 (0.02)a	0.36 (0.06)a	0.50 (0.06)a	0.02 (0.01)a
		Oak	5.66 (0.15)a	1.34 (0.30)a	0.04 (0.01)a	0.12 (0.03)a	0.37 0.05)a	0.35 (0.04)a	0.02 (0.01)a
	Hestreux	Beech	8.55 (0.67)a	1.51 (0.17)a	0.04 (0.01)a	0.10 (0.01)b	0.43 (0.02)b	0.14 (0.02)b	0.07 (0.01)b
		Oak	5.95 (0.74)a	1.73 (0.34)a	0.05 (0.01)a	0.18 (0.02)a	0.81 (0.11)a	0.06 (0.01)b	0.11 (0.01)a
		Spruce	9.21 (1.54)a	1.75 (0.33)a	0.05 (0.01)a	0.07 (0.01)b	0.40 (0.08)b	0.29 (0.04)a	0.05 (0.01)b
	Vielsalm	Beech	4.41 (0.36)b	1.88 (0.45)a	0.04 (0.01)b	0.09 (0.02)a	0.45 (0.02)bc	0.39 (0.09)a	0.03 (0.01)a
		Oak	5.20 (0.35)b	1.73 (0.52)a	0.04 (0.01)b	0.09 (0.01)a	0.41 (0.08)c	0.36 (0.07)a	0.11 (0.07)a
		Spruce	6.69 (0.38)a	1.50 (0.15)a	0.05 (0.01)ab	0.11 (0.02)a	0.62 (0.06)ab	0.20 (0.03)a	0.04 (0.01)a
		Douglas-fir	6.78 (0.14)a	2.17 (0.17)a	0.06 (0.01)a	0.03 (0.01)a	0.67 (0.05)a	0.32 (0.04)a	0.05 (0.01)a
	Rambrouch	Beech	8.22 (0.30)a	1.83 (0.40)a	0.04 (0.01)a	0.08 (0.02)a	0.54 (0.04)b	0.26 (0.01)b	0.02 (0.01)c
		Oak	7.98 (0.11)a	2.25 (0.28)a	0.05 (0.01)a	0.11 (0.02)a	0.61 (0.06)b	0.60 (0.07)a	0.03 (0.01)bc
		Spruce	8.47 (0.45)a	3.07 (0.35)a	0.05 (0.01)a	0.10 (0.01)a	0.89 (0.05)a	0.34 (0.03)b	0.07 (0.01)a
		Douglas-fir	8.24 (0.45)a	2.19 (0.37)a	0.05 (0.01)a	0.06 (0.01)a	0.66 (0.04)b	0.38 (0.08)b	0.04 (0.01)b

Values are means (±SEM); $n = 4$. Different letters indicate significant differences between tree species at each site according to Duncan's test at $P < 0.05$.

differently according to sites and sampling times. At Chimay and Vielsalm (April), the MB-C was highest under oak compared to other stands whereas no differences appeared in September. At Hestreux, tree species did not influence MB-C. At Rambrouch, highest MB-C was observed under spruce. In April, MB-N was higher under oak than under other species at all sites. In September, this difference was only observed at Hestreux. At Rambrouch, MB-N under spruce was significantly higher than under other species. We observed a positive relationship between MB-C and BR ($P < 0.0001$, $R = 0.62$) and a positive correlation between MB-C and LOI ($P < 0.0001$, $R = 0.46$). MB-C ($P < 0.0001$, $R = 0.40$) and MB-N ($P < 0.0001$, $R = 0.58$) were positively correlated with Nmin (Table 5).

The metabolic quotient ($q\mathrm{CO_2}$) ranged from 0.54 to 1.27 µg $\mathrm{CO_2}$-C mg MB-C^{-1} h^{-1}. The $q\mathrm{CO_2}$ was significantly higher under spruce at Hestreux (April) and Rambrouch. No effect of tree species on $q\mathrm{CO_2}$ was observed at the other sites (Fig. 2d).

The microbial quotient ($q$mic) ranged from 0.84 to 2.22% (Fig. 2e). At Chimay (April), $q$mic was lower under beech compared to oak and beech–oak. At Hestreux (April) and Vielsalm, $q$mic was lowest under spruce and Douglas-fir (September). We observed a negative correlation between $q\mathrm{CO_2}$ and $q$mic ($P < 0.0001$, $R = -0.41$). No correlation was observed between basal respiration and $q$mic ($P = 0.22$, $R = -0.11$) (Table 5).

4. Discussion

4.1. Chemical characterisation of the study sites

One difficulty in studying the influence of tree species on soil chemical and microbial characteristics is linked to the selection of comparable study sites. Indeed, the effect of tree species may be masked by the pedology of the site, variability between sites and former occupation (Binkley and Valentine, 1991). In our study, stands under different species at each site present similar geology, rainfall, temperature, slope and site history. Furthermore, based on the analyses of total Ca, pH, exchangeable cations and sum of exchangeable base cations of deeper mineral soil layer (40–50 cm), suggested by Berger et al. (2006) as indicators for the selection of comparable study sites, we consider that the various stands selected on each site are comparable. Differences in soil chemistry and microbial activities in the forest floors are therefore assumed to reflect the effect of tree species.

4.2. Influence of tree species on soil chemistry of the forest floors

At two sites, we found higher exchangeable acidity under spruce compared to beech and oak. Higher acidity under spruce than under deciduous trees has been frequently reported in the topsoil (e.g. Augusto et al., 2002) and may be related to the influence of litter and surface roots (Pritchett and Fisher, 1987) and the higher interception of potentially acidic atmospheric pollutants under conifers (De Schrijver et al., 2007). In contrast to results reported by others (Ranger et al., 1995; Takahashi, 1997), exchangeable calcium was not affected by tree species in our study. This could be explained by the high acidity of our sites, buffering the effect of tree species on exchangeable calcium.

4.3. Influence of tree species on net N mineralization and microbial biomass

Our results showed a clear effect of tree species on net N mineralization, but the observed effect was not consistent across study sites. Higher net N mineralization rates observed under oak and beech compared to spruce and Douglas-fir at Vielsalm were consistent with higher N mineralization under deciduous species compared to coniferous species reported in the literature (e.g. Côté et al., 2000). This difference is generally attributed to the better quality (lower C/N or lignin/N ratios) of deciduous litter (Scott and Binkley, 1997) and supported by the lower C/N ratios in the forest floors measured under the deciduous species at our sites. However, we observed highest N mineralization under spruce at Rambrouch and no differences in N mineralization between conifers and deciduous trees at Hestreux. N mineralization rates in forest floors represent late stage decomposition, when initially chemically different litter has been transformed into relatively uniform soil organic matter, as stated by the decay filter hypothesis (Melillo et al., 1989). At this decomposition stage, main controlling factors reported are climate (temperature, moisture), soil texture, total N pool and new sources of labile C (Melillo et al., 1989; Prescott, 2005).

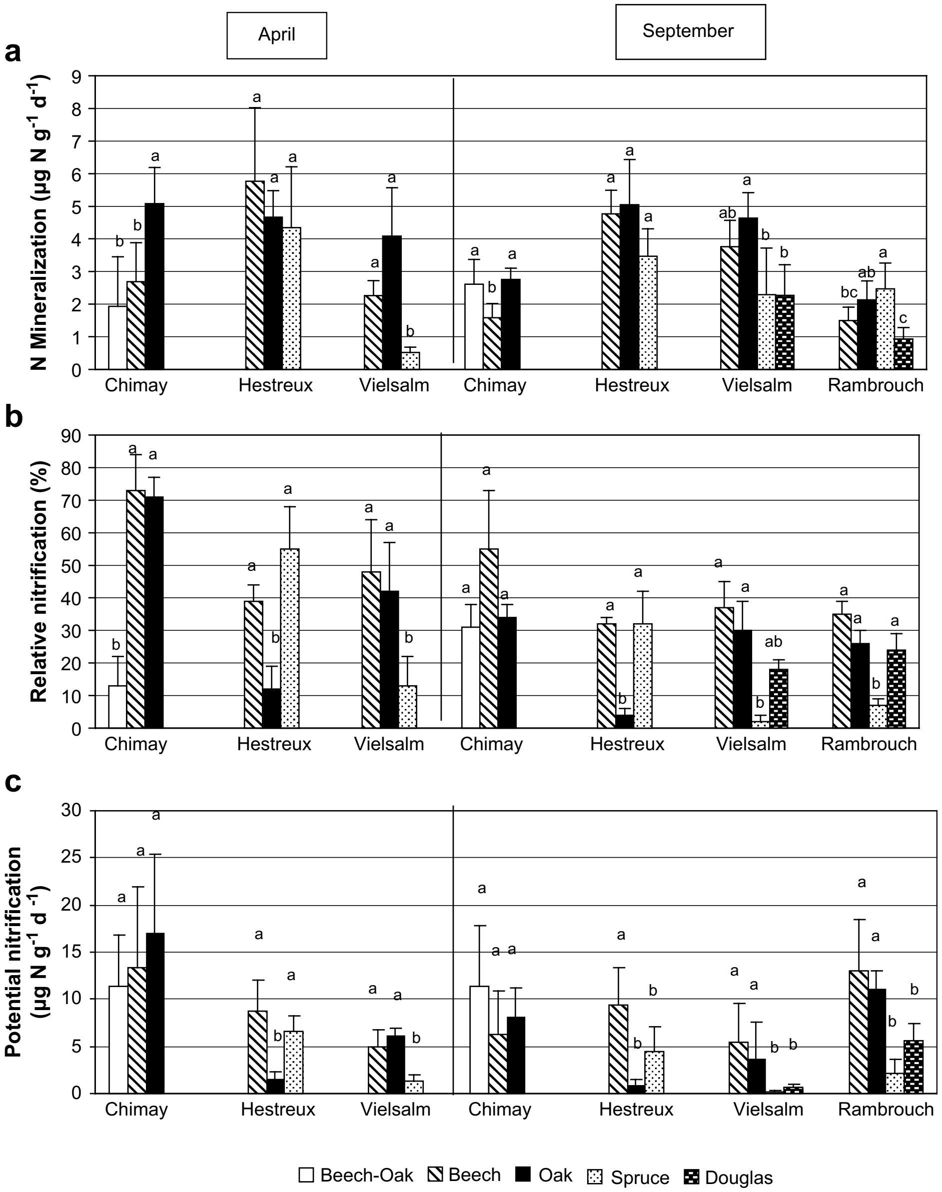

Fig. 1. Effect of tree species at 3–4 sites on (a) net N mineralization, (b) relative nitrification and (c) potential nitrification for forest floors sampled in April and September 2006. Different letters indicate significant differences between species at each site and sampling time (one-way ANOVA; Duncan's test, $P < 0.05$). Data are averages $n = 4$ (±SEM).

None of these factors, except labile C (not measured), were different under the tree species within our sites and therefore cannot account for the observed differences in N mineralization. The availability of labile C may be evaluated by the ratio of microbial carbon to organic carbon (*q*mic) (Anderson and Domsch, 1990), higher ratios resulting from the diversity of organic matter input and/or through a more efficient microbial community. However, as *q*mic represents a fraction of total organic matter content, the latter has to be considered in the interpretation of N mineralization rates, which are expressed per gram of soil. For example, lower labile C availability (lower *q*mic) at Hestreux was offset by higher organic matter content, resulting in similar microbial biomass C and N mineralization rates under the tree species studied at this site. Similarly, higher N mineralization under spruce at Rambrouch might be explained by the high organic matter content under this stand, although *q*mic was not different between the species studied.

The positive correlation between microbial biomass C and N mineralization might be explained by the role played by microbial extracellular enzymes in the depolymerisation of N-containing polymers to dissolved organic nitrogen (Chapin et al., 2002; Schimel and Bennett, 2004). This is also supported by positive correlations reported between microbial biomass and exoenzyme activities (Rejmánková and Sirová, 2007) and microbial biomass, urease enzyme activity and N mineralization (Hackl et al., 2004). The depolymerisation would be the initial rate-limiting step of N mineralization (Chapin et al., 2002), which is controlled by the same factors as those controlling decomposition, namely quality and quantity of the organic matter, microbial community composition and environmental factors regulating microbial activity (Swift et al., 1979).

4.4. Influence of tree species on potential and relative nitrification

As net N mineralization rates are the result of gross N mineralization and N immobilization, their interpretation is sometimes difficult. In our study, potential nitrification rates reflect the maximum rate of nitrification and are equivalent to gross rates, as water and nutrient limitations, as well as nitrate immobilization

Table 5

Pearson's correlation coefficients of environmental variables and biogeochemical and microbial variables.

	LOI	pH_{H_2O}	pH_{KCl}	NH_4-N	Moisture	N_{tot}	C/N	Nmin	nitpot	RN	BR	MB-C	MB-N	qCO_2
pH_{H_2O}	0.533^{***}													
pH_{KCl}	0.413^{***}	0.437^{***}												
NH_4-N	0.273^{*}	-0.368^{***}	0.103^{NS}											
Moisture	0.468^{***}	-0.269^{*}	0.358^{**}	0.491^{***}										
N_{tot}	0.737^{***}	0.344^{NS}	0.344^{NS}	-0.136^{NS}	0.404^{*}									
C/N	0.448^{*}	0.446^{*}	0.447^{*}	0.141^{NS}	0.014^{NS}	0.092^{NS}								
Nmin	0.252^{NS}	-0.278^{*}	0.054^{NS}	0.229^{NS}	0.620^{***}	0.424^{*}	-0.390^{*}							
nitpot	-0.244^{NS}	-0.134^{NS}	-0.608^{***}	-0.039^{NS}	-0.215^{NS}	0.065^{NS}	-0.333^{NS}	-0.015^{NS}						
RN	-0.241^{NS}	-0.206^{NS}	-0.444^{***}	0.054^{NS}	0.15^{NS}	-0.267^{NS}	-0.266	0.144^{NS}	0.548^{***}					
BR	0.582^{***}	-0.102^{NS}	0.328^{*}	0.413^{***}	0.609^{***}	0.449^{**}	0.161^{NS}	0.455^{***}	-0.326^{*}	-0.278^{NS}				
MB-C	0.458^{***}	-0.016^{NS}	0.165^{NS}	0.178^{NS}	0.297^{NS}	0.377^{NS}	-0.321^{NS}	0.397^{***}	-0.102^{NS}	-0.177^{NS}	0.622^{***}			
MB-N	0.266^{NS}	0.498^{***}	0.103^{NS}	0.602^{***}	0.615^{***}	0.452^{**}	0.262^{NS}	0.581^{***}	0.056^{NS}	0.028^{NS}	0.600^{***}	0.504^{***}		
qCO_2	0.257^{NS}	-0.094^{NS}	0.292^{*}	0.298^{*}	0.481^{***}	0.031^{NS}	0.706^{NS}	0.187^{NS}	-0.341^{*}	-0.197^{NS}	0.630^{***}	0.222^{*}	-0.192^{NS}	
$q$mic	-0.655^{***}	-0.406^{***}	-0.434^{***}	-0.123^{NS}	-0.323^{*}	-0.449^{**}	-0.268^{NS}	-0.001^{NS}	0.192^{NS}	0.165^{NS}	-0.115^{NS}	0.066^{NS}	0.311^{*}	-0.417^{***}

*,** and *** designate significant differences at $P < 0.01$, 0.001, and 0.0001, respectively. NS indicates that the correlation is not significant. LOI: loss on ignition ($n = 92$), N_{tot}: total nitrogen ($n = 55$), C/N: C/N ratio ($n = 55$), Nmin: net nitrogen mineralization ($n = 91$), nitpot: potential nitrification ($n = 88$), RN: relative nitrification ($n = 91$); BR: basal respiration ($n = 92$), MB-N: microbial biomass N, MB-C: microbial biomass C ($n = 92$).

and denitrification are eliminated in the shaken soil-slurry method (Hart et al., 1994). As nitrifiers depend on the nitrification process for energy, this measurement can be used as an index of the size of the ammonia oxidizer community in a soil sample (Hart et al., 1994). In addition, relative nitrification (the percentage of nitrogen mineralized which is nitrified) may give insight into factors that regulate nitrification independently of mineralization (Robertson, 1982).

In the literature, different processes have been suggested to explain tree species effects on nitrification in soils, namely microclimate (moisture, temperature), ammonification, C/N ratio of litter and organic matter, pH, essential nutrients (such as phosphorus), production of inhibitory compounds, competition for ammonium by ground vegetation and N immobilization by heterotrophs (Robertson, 1982; Howard and Howard, 1991; Nugroho et al., 2007). Traditionally, a C/N ratio of 25–27 is considered to be a threshold below which net nitrification and nitrate leaching may take place (Gundersen and Rasmussen, 1990). However, Robertson (1982) has shown relative nitrification over a wide range of C/N ratios and Carnol et al. (1997) observed nitrate leaching at sites with high C/N ratios. In our study, relative nitrification was also observed above a C/N ratio of 25 and was not correlated to forest floor C/N ratios, indicating that the C/N ratio of the forest floor was not a good indicator of the potential impact of tree species on nitrification.

We showed a clear effect of tree species on relative and potential nitrification, consistent for both samplings, but not across sites. For example, lower potential nitrification was observed under spruce and Douglas-fir at Vielsalm and at Rambrouch, but, at Hestreux, potential nitrification was lowest under oak. The lower potential nitrification observed under spruce and Douglas-fir at Vielsalm and Rambrouch could be due to the higher inhibitory capacity and organic acid content reported for coniferous litter (Wedraogo et al., 1993; Strobel et al., 1999). Lower potential nitrification under spruce and Douglas-fir at Vielsalm could also be due to lower net N mineralization observed at these two stands.

Within sites, we observed a good correspondence between potential nitrification and relative nitrification under the tree species studied (except for Chimay), indicating that the population size of nitrifying bacteria controls the influence of tree species on nitrification rates. Two stands (spruce in Rambrouch and oak in Hestreux) were characterised by the presence of abundant ground vegetation, potentially limiting the size of the nitrifier population by competition with plants and heterotrophs (Kaye and Hart, 1997). This competition may take place through ammonium uptake by the vegetation (Olsson and Falkengren-Grerup, 2003) and/or increased N immobilization by heterotroph microorganisms due to increased C availability through root exudates (Landi et al., 2006). In this study, higher N immobilization is supported by the higher microbial N content measured at both stands with abundant ground vegetation.

The lower relative nitrification observed under beech–oak (both samplings) and under oak (September) at Chimay could not be explained by a low number of nitrifiers, as the potential nitrification was of the same order of magnitude under the three stands (oak, beech and mixed). Although it is generally understood that microorganisms preferentially use ammonium, different studies (Rice and Tiedje, 1989; Stark and Hart, 1997) have shown that nitrate immobilization could be an important process in forest ecosystems. Stark and Hart (1997) attributed a poor relation between net and gross nitrification rates to nitrate immobilization, which would occur in forest soils with high C availability or with rapid turnover of the microbial biomass. Direct measurements of nitrate immobilization at Chimay would however be needed to support this hypothesis.

4.5. *Tree species and carbon mineralization*

Some authors observed no effect of tree species on basal respiration (Priha et al., 1999; Welke and Hope, 2005), whereas others revealed higher respiration under spruce compared to beech, birch, oak, larch and pine (Brüggemann et al., 2005; Menyailo et al., 2002). In this study, an influence of tree species on basal respiration was observed at Hestreux and Rambrouch only. At Hestreux, under spruce, higher respiration might be due to the lower substrate quality (lower $q$mic), resulting in a lower C use efficiency (higher qCO_2) (Anderson and Domsch, 1990), combined with a higher organic matter content. Under oak, increased carbon availability, via a broader range of substrates (Grayston et al., 1996) through root exudates of the ground vegetation and good yield efficiency (high $q$mic, low qCO_2) would increase respiration. At Rambrouch, higher basal respiration under spruce would be the result of low quality litter (high qCO_2), high organic matter content and increased root exudates through ground vegetation ($q$mic similar for all stands at this site). The potential effect of root exudates is supported by results of Menyailo et al. (2002) and Vance and Chapin (2001), reporting the control of respiration by easily available C and increased respiration after addition of low molecular weight organic carbon, respectively.

In conclusion, our work confirmed that tree species have an effect on net N mineralization, relative and potential nitrification, basal respiration and microbial biomass. This effect depended on

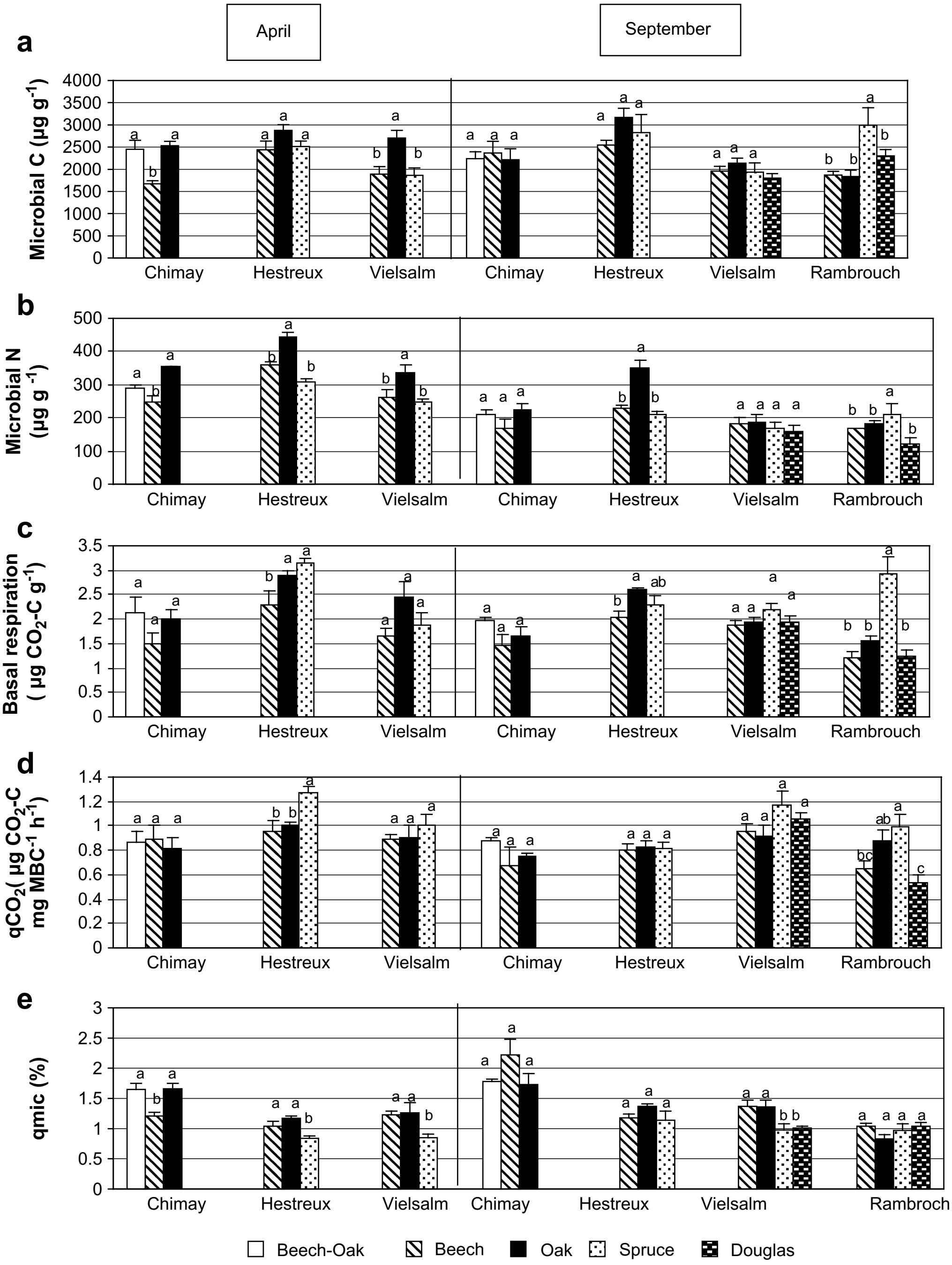

Fig. 2. Effect of tree species at 3–4 sites on (a) microbial biomass C (MB-C), (b) microbial biomass N (MB-N), (c) basal respiration (BR), (d) metabolic quotient (qCO_2) and (e) microbial quotient ($q$mic) for forest floors sampled in April and September 2006. Different letters indicate significant differences between species at each site and sampling time (one-way ANOVA; Duncan's test, $P < 0.05$). Data are averages $n = 4$ (±SEM).

the study site, demonstrating that the impact of tree species on C and N transformations in the forest floors cannot be generalized across sites. Some tree species effects were not consistent for samplings in spring and autumn, indicating that the sampling time has also to be considered carefully when evaluating tree species effects and that several samplings across the season should be considered. The effect of tree species on net N mineralization is likely to be mediated through their effect on soil microbial biomass, reflecting their influence on organic matter content and carbon availability. Differences in potential and relative nitrification might be related to the presence of ground vegetation through its influence on NH_4 and labile C availability. Detailed process-related studies are thus necessary to elucidate complex N cycle interactions between tree species, ground vegetation, soil characteristics and microbial processes.

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