



Changes in soil N mineralization and nitrification pathways along a mixed forest chronosequence

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ABSTRACT

Changes in soil N mineralization pathways occurring along a full rotation cycle have received little attention to date, while tree uptake for N may change during forest ageing. The aims of this study were (i) to characterize changes in potential net N mineralization and potential net nitrification within organic layers and the topsoil (organo-mineral horizon) along a 100-year chronosequence for a temperate oak–hornbeam forest and (ii) to reveal covariances between potential net N mineralization pathways and the properties of the humic epipedon (defined as the sum of organic layers and topsoil). For that purpose, a space-for-time substitution procedure and aerobic laboratory incubation method for 28 days at 28 °C in the dark were used. In addition, acetylene and captan were used to discriminate between autotrophic and heterotrophic (bacterial and/or fungal) nitrification. Several humic epipedon properties were determined, e.g. pH, exchangeable cation concentrations, effective cation exchange capacity, total C and N, dissolved organic C and N, fungal and microbial biomass N. Potential net N mineralization and nitrification pathways changed greatly along the mixed forest chronosequence. Potential net N mineralization in the organic layers increased with stand maturation whereas potential net nitrification in the topsoil decreased significantly. Selective inhibitors revealed changes in nitrification pathways along the chronosequence, i.e. potential net nitrification was autotrophic in the topsoil while it was mainly heterotrophic within the organic layers. In the organic layer, potential net nitrification was autotrophic at the onset of the chronosequence while it appeared heterotrophic during the aggradation phase and finally fungal in mature stands. A Co-Inertia Analysis was used to reveal covariances between N mineralization pathways and humic epipedon properties. The analysis showed two functional temporal shifts within N cycling along the chronosequence, one probably controlled by organic matter quality and high competition for available N resulting in the autotrophic *versus* heterotrophic nitrification shift in the organic layers and one mainly controlled by (i) fine organic matter abundance, allowing high N mineralization in the organic layers and (ii) acidity inhibited autotrophic nitrification in the topsoil.

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1. Introduction

Nitrogen (N) has long been recognized as one of the most limiting nutrients for forest ecosystem productivity (Duchaufour, 1989; Priha and Smolander, 1999). All species, both aboveground and belowground, are in intense competition for available N in forest ecosystems (Schimel and Bennett, 2004). In a low-N context, trees in association with mycorrhizal fungi possess the capacity to take up amino acids and other organic N compounds (Nasholm

et al., 1998, 2009). This could lead to a microbial N mineralization by-pass (Schimel and Bennett, 2004).

Since potential net N mineralization and nitrification represent great ecological indicators of forest ecosystem productivity (Reich et al., 1997; Robertson et al., 1999a,b), it is surprising that changes in soil N mineralization pathways along a full rotation cycle have received little attention to date (Idol et al., 2003; Welke and Hope, 2005). Changes in soil N cycling with forest ageing were usually studied with limited comparisons of two contrasted dynamic phases, e.g. young *versus* old stands (Coté et al., 2000; Fisk et al., 2002; Inagaki et al., 2004; Zeller et al., 2007). Consequently, the effects of intense tree growth phases on soil N cycling were not taken into account although N uptake by trees may increase during the aggradation phase (Brais et al., 1995). As a result, in earlier studies, N mineralization was often higher in older stands whereas nitrification was higher in younger ones (Brais et al., 1995; Coté

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et al., 2000; Idol et al., 2003; Zeller et al., 2007). However, these studies did not show one significant pattern of variation in N mineralization pathways. Therefore, it would be interesting to study N mineralization pathways along a complete forest rotation.

Among N transformations, nitrification, i.e. the conversion of ammonia to nitrate, plays an essential role for forest ecosystems (Hart et al., 1994; Persson and Wirén, 1995; Zhu and Carreiro, 1999). Chemolitho-autotrophic nitrification is carried out by ammonia-oxidizing bacteria and nitrite-oxidizing bacteria. Some heterotrophic bacteria and fungi possess the ability to produce nitrate from both organic and inorganic N (De Boer and Kowalchuk, 2001; Islam et al., 2007). In contrast to heterotrophic nitrification, autotrophic nitrification is the single process providing energy for carbon dioxide fixation and growth. Both heterotrophic nitrification, bacterial or fungal (Lang and Jagnow, 1986; Brierley and Wood, 2001), and autotrophic nitrification (Ste-Marie and Paré, 1999; Laverman et al., 2000) have been observed in forest soils. Autotrophic nitrification occurrence has been explained by hot-spots of ammonification or by pH-neutral micro-sites (De Boer and Kowalchuk, 2001).

Besides pH, several factors controlling the internal N cycle are likely to vary along stand maturation (Brais et al., 1995). These include humidity and temperature (Knoepp et al., 2000), forest stand composition and structure (Aubert et al., 2005), composition of vegetation (Schaffers and Sykora, 2000), organic matter quantity and quality—for instance, the C/N ratio (Priha and Smolander, 1999), lignin quantity (Hättenschwiler et al., 2005), or dissolved organic N and C availability (Strauss and Lamberti, 2002).

The aims of the present study were thus (i) to characterize changes in potential net N mineralization and potential net nitrification pathways within the organic layers and the topsoil along a 100-year chronosequence of oak–hornbeam even-aged high forest and (ii) to reveal covariances between potential net N mineralization pathways and the properties (i.e. chemical and microbial soil parameters) of the humic epipedon (defined as the sum of organic layers and the topsoil).

In the light of previous work (Idol et al., 2003; Zeller et al., 2007), we tested the hypotheses that (1) potential net N mineralization and nitrification within the humic epipedon would change along the mixed oak–hornbeam chronosequence, (2) potential net nitrification would be autotrophic within young stands versus heterotrophic within mature ones.

2. Materials and methods

2.1. Study site

The sites were located in the Montargis National Forest (France, the Center region, 4091 ha). The climate is of the oceanic type with a mean annual rainfall and temperature of about 647 mm and 10.9 °C, respectively (Chevalier, 2003). The vegetation belongs to Quercus-Fagetea sylvaticae (Rameau, 1997; Bardat et al., 1999). We used the space-for-time substitution procedure to empirically reconstitute an even-aged forest chronosequence (Pickett, 1989). Within the Montargis forest, we selected twelve stands (Table 1) among the stands set of Ponge and Chevalier (2006). The stands were representative of four silvicultural phases (SP), i.e. 21–27 years old (SP20), 41–42 years old (SP40), 73–75 years old (SP75) and 99 years old (SP100). The stands are managed as an even-aged mesoacidic mixed oak–hornbeam forest (*Quercus petraea* Lieblein, *Carpinus betulus* L.) by the French Forestry Service (ONF). In order to retain a reasonable signal-to-noise ratio, all stands were located on the same bedrock with similar topography, situated on a plateau and selected among Ponge and Chevalier (2006) stands growing on more than 70 cm of loess as parent materials. All soils were LUVISOLS according to the world reference base (FAO, 1998).

Table 1
Stand characteristics.

Characteristics	Silvicultural phases											
	SP20			SP40			SP75			SP100		
	1	2	3	1	2	3	1	2	3	1	2	3
Stand age (years in 2006) ^a	27	21	24	41	42	42	73	75	75	99	99	99
Last year thinning	-	-	-	1999	2002	2004	1998	1999	1999	2000	2000	2000
Area (ha)	15.6	13.4	14.2	22.1	16.4	19.4	13.6	15	13.4	25.2	25.7	25.7
Longitude (WGS84)	2°48'57"E	2°48'45"E	2°48'47"E	2°48'14"E	2°47'12"E	2°46'46"E	2°47'17"E	2°47'11"E	2°46'45"E	2°47'25"E	2°47'16"E	2°47'21"E
Latitude (WGS84)	48°1'23'N	48°1'13'N	48°1'12'N	48°1'32'N	48°1'14'N	48°1'15'N	48°0'54'N	48°1'10'N	48°1'11'N	48°0'53'N	48°0'50'N	48°0'50'N
Altitude (m.a.s.l.)	123	122	121	122	119	116	115	118	115	116	114	114
% Oak (G/ha)	95	90	83	99	89	66	65	64	66	56	78	71
% Hornbeam (G/ha)	5	10	17	1	9	11	34	24	29	36	8	29
Oak/Hornbeam leaves ratio ^b	11	19	20	20	12	24	4	9	8	7	8	14
Humus forms ^c	M to O	M	M	M	M	M	M	M	M to O	M to O	O to H	O to E
Vertical sequence ^d	OLn	OLn	OLn	OLn	OLn	OLn	OLn	OLn	OLn	OLn	OLn	OLn
	OLv	(OLv)	(OLv)	(OLv)	(OLv)	(OLv)	(OLv)	(OLv)	(OLv)	OLv	OLv	OLv
	A	A	A	A	A	A	A	A	A	(OF)	OF	OF
										A	A	(OH)
												A

^a According to the Office National des Forêts (1996).

^b Oak:hornbeam leaves ratio in the organic layers.

^c With O: Oligomull; M: Mesomull; H: Hemimoder; E: Eumoder according to AFES (1998).

^d With OLn: unmodified leaf less than one year old, OLv: unmodified leaf more than one year old, OF: coarse plant fragment with fine organic matter (FOM), OH: more than 70% FOM, A: organic-mineral horizon according to AFES (1998).

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