Ann. For. Sci. 67 (2010) 110
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DOI: 10.1051/forest/2009089

Available online at:
www.afs-journal.org

Original article

Forest liming durably impact the communities of ectomycorrhizas and fungal epigeous fruiting bodies

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(Received 5 March 2009; accepted 6 July 2009)

Keywords:
mycorrhiza /
ecosystem management

Abstract

• Liming is a forestry practice used to counteract forest decline in acidic soils. It consists of direct Ca and Mg input to forest soil, which restores tree mineral nutrition, but also modifies microbial communities in soil. The aim of this study was to assess the effects of liming on both belowground (ectomycorrhizal root tips) and aboveground (epigeous sporocarps) fungal communities.

• Results showed that the modification of soil chemical properties (pH, and Ca-Mg contents versus total free Al and Fe concentrations) was a stronger factor of ECM community structuring than tree host. The species appearing in limed plots were ubiquist or known as good competitors and replaced acidophilic and stress species.

• At the sporocarp level, tree host was a stronger factor of community structuring than soil chemical properties associated with liming. On the whole, there was a shift in the community composition from a typical acidophilic forest fungal community of medium altitude in the untreated plots to a less typical one, with the reduced dominance of acidophilic fungi while many late-stage forest species appeared.

• We finally suggest a marker species (*Russula ochroleuca*) to assess both above and belowground effects of liming on ectomycorrhizal communities.

Mots-clés :
mycorhize /
management des écosystèmes

Résumé – Le chaulage forestier influence durablement les communautés d'ectomycorrhizes et de carpophores épigés.

• Le chaulage est une pratique forestière utilisée pour restaurer la nutrition minérale des arbres apparaissant sur sol acide. Il consiste en un apport direct de Ca et Mg au sol forestier, ce qui restaure la nutrition minérale de l'arbre, mais aussi modifie les communautés microbiennes du sol. Cette étude évalue les effets du chaulage sur les communautés fongiques hypogées (apex ectomycorrhiziens : « ECM ») et épigées (carpophores).

• Les résultats montrent que la modification des des propriétés chimiques du sol (pH et concentrations en Ca-Mg échangeables versus concentrations en Al et Fe échangeables) est un facteur de structuration de la communauté d'ECMs plus fort que l'arbre hôte. Les espèces qui sont apparues dans les placeaux chaulés sont ubiquistes ou compétitrices et ont remplacé des espèces acidophiles ou connues pour être associées à des conditions de stress.

• Concernant les carpophores, l'arbre hôte est un facteur de structuration de la communauté plus fort que les propriétés chimiques du sol associées au chaulage. Dans l'ensemble, on a observé une modification de la communauté fongique, passant d'une communauté typique de forêt acide de moyenne altitude dans les placeaux témoins vers une autre moins spécifique, caractérisée par une moindre dominance d'espèces acidophiles et l'apparition de nombreuses espèces de forêt mature.

• Nous suggérons enfin une espèce marqueur (*Russula ochroleuca*) qui permet d'évaluer facilement les effets du chaulage sur les communautés de champignons mycorrhiziens, aussi bien du point de vue des apex mycorrhiziens que des carpophores.

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Article published by EDP Sciences

1. INTRODUCTION

Symptoms of forest decline due to soil acidification have been reported in many forests of central Europe for the past 20 y (Ulrich, 1983). Spruce needle yellowing and beech defoliation were consequences of cation starvation due to free calcium and magnesium losses in acidic soils with low weathering rates. Liming (i.e. direct input of Ca and Mg in forest soils) proves to be efficient to restore tree mineral nutrition, and induces drastic and long-term changes in soil structure and chemical properties (Kreutzer, 1995). Calcareous amendments reduce the acidity of upper soil layers, increase cation exchange capacity and soil base saturation, especially in humus layers (Frank and Stuanes, 2003; Kreutzer, 1995; Renaud et al., 2000), and stimulates soil fauna (particularly earthworms) (Persson, 1988). Liming could also shift the humus type from mor to mull (Kreutzer, 1995).

Liming is now once again a topical subject for forest management as a tool to improve the production of wood biomass in nutrient-poor forest ecosystems. As this forest practice will be applied to large forest areas, ecological consequences of calcareous amendments are thus of critical importance. Renaud et al. (2000) showed increased plant species richness due to the apparition of meso-acidophilic to neutrophilic or nitrophilic species in limed spruce and fir forests. However, the abundance decrease of acidophilic species followed by appearance of widespread neutro- and nitrophilic ones could lead to a shift of patrimonial value of the ecosystem.

Because fungi are strongly influenced by soil organic matter and soil properties, the effect of liming on ectomycorrhizal (ECM) communities has already been surveyed. Liming enhanced sporocarp production of *Hygrophorus pustulatus* (Agerer et al., 1998) in spruce stands, and of *Lycoperdon gemmatum* in beech ones (Garbaye et al., 1979). Contrary to that, sporocarps of the acidophilic (but widespread) fungus *Russula ochroleuca* decreased in abundance in limed spruce stands (Agerer et al., 1998). In terms of ectomycorhizal root tips, very diverse effects of liming were recorded, probably because of site-dependant response to amendment. A promoting effect of liming on ECM root tip abundance was reported in oak plots (Bakker et al., 2000) and in the humic layers of a Norway spruce stand (Nowotny et al., 1998), but the opposite effect was observed in a mixed oak and beech forest (Blaise and Garbaye, 1983). Haug and Feger (1990) showed no significant effect of liming on relative frequency of mycorrhizal and non-mycorrhizal roots. When focusing on the relative abundances of certain ECM species, liming increased the abundance of ECMs of *Piceirhiza nigra* and *Tuber puberulum* in spruce forests (Qian et al., 1998). Investigation on the effects of liming on the exploration type of ECMs (according to Agerer, 2001) showed the reduced abundance of ECMs with abundant external mycelium (medium- and long-distance exploration types) in limed plots (Blaise and Garbaye, 1983). Nevertheless, most of the works performed to date, assessed effects of liming on a short time scale (less than 10 y) and without parallel survey of ECM root tips and the fruiting bodies (FB) of symbiotic and saprophytic fungal species.

Here, we addressed the hypothesis that, as for plants, liming shifts the ECM community structure from acidophilic to a more widespread and neutrophilic type. The aim of this paper is thus to evaluate the mid-term (i.e. 15 y) impact of liming on the structure of both belowground (mycorrhizal root tips) and aboveground (epigeous sporocarps) fungal communities and to relate it with soil chemical properties.

2. MATERIAL AND METHODS

2.1. Study site

The experimental site of Humont (48° 00′ 00″ N, 6° 29′ 28″ E, Elevation: 570 m, Vosges mountains, North-Eastern France) consists in moderately declining stands of 35-year old Norway spruce (*Picea abies*) and 60-year-old beech (*Fagus sylvatica*). The liming treatment was carried out in part of these stands by helicopter in 1991 with 757 kg/ha of CaO and 380 kg/ha of MgO, as grounded dolomitic rock, which is a relatively low dose compared to most calcareous amendments in eastern europe. The allocrisol (typic dystrochrept, USDA, 1999) is formed on sandstone. Four blocks were defined, two under beech (B) and two under spruce (S); in each block a couple of plots (limed: L, and untreated: U) were defined, resulting in 8 plots of about 20 m × 20 m each. Fifteen years after the treatment, liming had resulted in a shift of the humus type from moder to oligomull, restored tree health, mineral nutrition and vegetation diversity and strongly increased earthworm colonisation (Renaud et al., 2000).

2.2. Soil analyses

The topsoil layers of five soil cores (8 cm in diameter, 20 cm deep) were taken in each plot in October 2006. The five cores were then pooled per plot, air-dried at ambient temperature during one week and sieved at 2 mm. We then measured, for each composite sample, the total contents of N, organic matter, pH, and concentrations of exchangeable Al^{3+}, Mg^{2+}, Fe^{3+}, Ca^{2+}, Mn^{2+}, K^{+} and Na^{+} (Thomas, 1982). Soil phosphorus contents were estimated using the Duchaufour method, consisting in a double acid and basic extraction, which solubilized both organic and mineral P components (Duchaufour and Bonneau, 1959).

2.3. Estimation of the ECM root tip community structure

Soil core sampling was carried out on October 2006 (before leaf fall, date 1), May 2007 (after bud break, date 2) and October 2007 (before leaf fall, date 3). At each date, ECM sampling was done in one of the two blocks for beech and spruce, in order to measure ECM community structure at least once for each treatment. Three soil cores (8 cm diameter, 15 cm deep, 750 cm^3) were randomly collected in each sampled plot for date 1. Twenty soil cores (4 cm diameter, 18 cm deep, 225 cm^3) were randomly collected in each sampled plot for date 2. Twenty soil cores of the same size were collected in each sampled plot for date 3 in a 5 × 4 grid (distance between two soil cores: 2.5 m). As the aim of this study was to estimate the effects of liming on ECM communities, the effect of season (spring vs. autumn) on community structure was not taken into account here,

and the spring 2007 sampling was considered as an independent time replicate. Considering that the ECM community structure is variable at a very small space scale (Dahlberg, 2001), three soil cores a few meters apart and thoroughly investigated took into account as much as variability in the ECM community than 20 smaller soil cores. The community structure obtained with the three sampling schemes was thus comparable.

Ectomycorrhizal morphotypes were then identified according to Agerer (1987–98). For each collected morphotype, seven tips were frozen at –80 °C and used, when possible, for extending the morphotype identification by DNA sequencing of the ITS region (Gardes and Bruns, 1993). Sequences were aligned using ITS sequences available in the NCBI (http://www.ncbi.nlm.nih.gov/) and UNITE (http://unite.ut.ee/) databases. The morphological description and the results of DNA identification of all morphotypes are given in the supplementary Table I.

Ectomycorrhizal tips of each species were exhaustively counted in soil cores at date 1. For the date 2 samples, roots were washed and homogeneously spread in a large Petri dish (20 cm diameter) containing tap water. Then ECM tips of each species were exhaustively counted in a 1/8 sector of the dish. For the sample date 3, roots were washed, homogeneously spread in the same type of Petri dish, and cut in small pieces (1 cm long). Root pieces were then randomly picked and ECMs counted until we reached 100 tips (Garbaye, 1990). For each date, values of abundance were then transformed into relative abundances by dividing the total number of ECM root tips belonging to a given species by the total number of root tips found in the plot. We then calculated the mean relative abundance of each species at the three sampling dates. We then compared the mean relative abundances of all species during the whole sampling campaign.

2.4. Counting of sporocarps

Only conspicuous, epigeous sporocarps were counted; hypogeous and hidden resupinate ones were ignored. At each date, fungal sporocarps were identified and counted in at least one block under spruce or beech, in order to measure sporocarp community structure at least one time for each block. Fruiting bodies were absent in May 2007, so the sampling date 2 was postponed to the beginning of July 2007 for sporocarp counting. In addition, we assessed the presence/absence of saprophytic species in each block. Areas from 1 600 m^2 to 3 200 m^2, equally distributed between treatments, were surveyed by the same two people, for up to 1 h per block, at each sampling date.

2.5. Statistics

The Shannon diversity index (H') was calculated as: $H' = -\sum((Ni/N) \times \log 2(Ni/N))$, and the Simpson's equitability index was calculated as: $D = \sum Ni(Ni-1)/(N(N-1))$, where Ni was the abundance of the species i and N the total number of individuals. Diversity indices (Shannon index, Simpson index) were then compared between limed and untreated plots for each tree host using a student t test.

Fungal communities structures in each treatment were compared using canonical correspondence analysis (CCA) based on soil analyses with relative abundances of the species (ECM root tips and sporocarps of ECM fungi) and presence/absence data (saprophytic species). Statistical calculations and representations were done using the R software (http://www.r-project.org) (Ihaka and Gentleman, 1996).

3. RESULTS

3.1. Description of the ECM fungal communities

Throughout the whole duration of the study, 40 morphotypes of ECM root tips were observed, and sporocarps of 52 species of ECM fungi and of 70 species of saprophytic fungi were found.

Concerning the ECM community, the most abundant morphotype was *Cenococcum geophilum*, always more abundant in the untreated plots (34 to 69% vs. 13 to 46% in the limed one, as seen in Tab. I). In the same way, *Russula ochroleuca* ECMs were almost absent in the limed plots (0.5% abundance in one spruce limed plot) but relatively abundant and present in all the untreated ones (1 to 11%). The limed plots were dominated by *Clavulina cristata* ECMs (except for SL-B one), under beech as well as under spruce, except in one replicate of the spruce limed plots. *Lactarius subdulcis* and *Tomentella sublilacina* were also found as codominant species in the beech limed plots. Ectomycorrhizae of *Xerocomus pruinatus* were found at low abundances but in all plots, whatever in limed or untreated ones. The ECM fungus *Laccaria amethystina* was not frequent but locally abundant in some beech plots.

Concerning sporocarps, *Russula ochroleuca*, *Laccaria amethystina* and *Inocybe napipes* were found in all the treatments, and *Russula ochroleuca* was the only species found in all the blocks (Tab. I). The fungal species *Amanita citrina* was the only species to be present only in untreated plots, whatever the tree host, and absent in limed ones. In the spruce untreated plot, the sporocarp community was dominated by *Russula ochroleuca* (51% of relative abundance, in mean between the two plots) and to a lesser extent *Hygrophorus olivaceoalbus* (24%). In spruce limed plots, the community was dominated by *Clavulina cristata* (46% in mean, but especially dominant in one replicate with 91% abundance), *Russula ochroleuca* (19%), and *Lactarius tabidus* (12%), but with large differencies between the two plots. *Amanita rubescens* and many other rare species (< 3% relative abundance: *Amanitopsis submembranacea, Cortinarius evernius, Elaphomyces muricatus, Lactarius helvus, Russula puellaris, Russula turci*) appeared in these limed spruce plots, while the abundance of the fungus *Xerocomus* was slightly repressed (from 2 to 5% in untreated plots vs. 1 to 2% in limed ones).

The consequences of liming under beech were less obvious because total abundances were not so high. In the untreated plots, the community was dominated by *Russula ochroleuca* (20% in mean between the two plots), *Russula fageticola* (17%) and *Cortinarius delibutus* (10%). In beech limed plots, the two latter species were absent and the community was dominated by *Laccaria laccata* (32%), *Russula ochroleuca* (13%) and *Russula cyanoxantha* (13%). We observed the apparition of *Clavulina cristata* and many *Amanita* and *Russula* species (*Amanita spissa, Amanita battarae, Amanita eliae, Russula heterophylla, Russula lilacea, Russula parazurea*); moreover, the relative abundance of other *Amanita* spp. (*Amanitopsis submembranacea*) and *Russula* spp. (*Russula brunneoviolacea*, *Russula cyanoxantha*) was

Table I. Relative abundance of ECM fungi in each of the 8 plots. S: spruce, B: Beech, U: untreated, L: limed, A: replicate A, B: replicate B. The intensity of the grey shading increases with higher values. The abbreviation name used for each species in Figures 1 and 2 is given in brackets in the first column.

	ECM root tips								Sporocarps							
Tree host	Beech				Spruce				Beech				Spruce			
Treatment	Limed		Untreated		Limed		Untreated		Limed		Untreated		Limed		Untreated	
Replicate	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Amanita battarrae (Amba)									6.45%							
Amanita citrina (Amci)											2.67%				1.05%	
Amanita crocea (Amcr)									3.23%							
Amanita eliae (Amel)									16.12%							
Amanita rubescens (Amru)	5.58%	0.36%	0.08%	1.49%							1.33%			3.60%		
Amanita sp. *(Amsp)*					0.35%			0.49%								
Amanita spissa (Amspi)										11.11%			0.46%			
Amanitopsis submembranacea (Amsub)									3.23%		1.33%			0.72%		
Boletus edulis (Boel)											1.33%					
Cantharella sp. *(Casp)*			0.04%													
Cantharellus cibarius (Caci)																0.64%
Cenococcum geophilum (Cege)	13.23%	26.03%	71.73%	34.07%	15.39%	45.75%	50.99%	69.59%								
Clavulina cristata (Clcr)	18.68%	17.97%	5.60%	8.43%	54.56%	3.28%	1.38%		3.23%				91.30%	0.72%	0.26%	
Cortinarius acutus (Coac)													0.46%		0.79%	
Cortinarius anomalus (Coan)		0.63%	0.80%				0.01%	0.24%								
Cortinarius argentatus (Coar)											1.33%					
Cortinarius delibutus (Code)											9.33%	11.11%				
Cortinarius evernius (Coer)														0.72%		
Cortinarius lebretonii (Coer)												11.11%	0.46%		1.31%	
Cortinarius sp. *(Cosp)*			0.14%	7.11%	0.66%		0.25%									
Dermocybe sp. *(Desp)*		0.24%	8.21%	1.21%												
Elaphomyces muricatus (Elmu)														2.16%		
Gomphidius glutinosus (Gogl)																2.55%
Hygrophorus olivaceoalbus (Hyol)			3.52%		0.02%	14.91%	3.18%						1.37%	15.11%	32.29%	15.92%
Hygrophorus pustulatus (Hypu)														5.76%		11.46%
Inocybe asterospora (Inas)												11.11%				
Inocybe lanuginosa (Inla)																0.64%
Inocybe napipes (Inna)									3.23%			11.11%	0.46%	0.72%	0.26%	
Inocybe petiginosa (Inpe)									3.23%							
Laccaria amethystina (Laam)	18.06%			12.02%					6.45%		1.33%	11.11%		6.47%	0.26%	
Laccaria laccata (Lala)									9.68%	55.56%	1.33%	11.11%				
Lactarius camphoratus (Laca)											2.67%				1.31%	14.01%
Lactarius helvus (Lahe)														2.88%		
Lactarius sp. *(Lasp)*			0.96%													
Lactarius sp.2 *(Lasp2)*			1.19%													
Lactarius sp.3 *(Lasp3)*					1.99%											
Lactarius sp.6 *(Lasp6)*		9.67%														
Lactarius subdulcis (Lasu)	11.60%	21.05%	1.45%	3.20%					3.23%		2.67%	11.11%				
Lactarius tabidus (Lata)					0.87%	4.68%	2.89%	1.12%			2.67%		0.46%	23.74%	2.10%	
Paxillus sp. *(Pasp)*				1.87%	0.83%		3.85%	0.39%								
Piceirhiza sp. *(Pisp)*					2.33%			1.20%								
Russula aeruginosa (Ruae)																2.55%
Russula brunneoviolacea (Rubr)									3.23%		1.33%					
Russula cyanoxantha (Rucy)	1.32%								25.79%		1.33%				0.52%	
Russula cyanoxantha var. pelteraui (Rucyp)											1.33%					
Russula densifolia (Rude)															0.26%	
Russula fageticola (Rufa)											33.34%					
Russula heterophylla (Ruhe)									3.23%							
Russula ionochlora (Ruio)															0.79%	
Russula lilacea (Ruli)									3.23%							
Russula nigricans (Runi)				2.81%								11.11%				
Russula ochroleuca (Ruoc)			2.32%	1.60%	0.54%		13.00%	4.81%	3.23%	22.22%	28.01%	11.11%	1.83%	35.25%	55.40%	46.50%
Russula parazurea (Rupa)										11.11%					0.26%	

Table I. Suite.

	ECM root tips								Sporocarps							
Tree host	Beech				Spruce				Beech				Spruce			
Treatment	Limed		Untreated		Limed		Untreated		Limed		Untreated		Limed		Untreated	
Replicate	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Russula puellaris (Rupu)														0.72%		
Russula risigalina (Ruri)									3.23%							
Russula sp. 2 *(Rusp2)*							0.21%									
Russula turci (Rutu)													0.46%			
Russula vesca (Ruve)													0.91%			0.64%
Russula violeipes (Ruvi)															0.26%	
Sebacina epigaea (Seep)	1.50%			0.88%												
Tomentella sp. *(Tosp)*	11.72%			7.00%												
Tomentella sp. 2 *(Tosp2)*				1.98%				5.54%								
Tomentella sublilacina (Tosu)	14.48%	15.56%	0.05%	7.94%	4.70%		1.00%									
Tricholoma saponaceum (Trsa)											1.33%					
Tricholoma sp. *(Trsp)*						14.26%										
Tylopilus felleus (Tyfe)															0.26%	
UECM sp.*1 (UE1)*					6.99%	6.35%	12.79%	7.11%								
UECM sp.10 *(UE10)*																
UECM sp.11 *(UE11)*						5.27%										
UECM sp.12 *(UE12)*						0.27%										
UECM sp.13 *(UE13)*						0.81%										
UECM sp.14 *(UE14)*						0.16%										
UECM sp.15 *(UE15)*		1.81%														
UECM sp.2*(UE2)*					2.71%		0.85%	6.84%								
UECM sp.5*(UE5)*			0.15%													
UECM sp.6*(UE6)*							0.90%									
UECM sp.7*(UE 7)*			2.73%													
UECM sp.8*(UE8)*							1.12%									
UECM sp.9*(UE9)*							0.28%									
Xerocomus badius (Xeba)													1.83%	1.44%	2.10%	5.10%
Xerocomus chrysenteron (Xech)											5.33%					
Xerocomus ferrugineus (Xefe)															0.26%	
Xerocomus pruinatus (Xepr)	3.82%	6.67%	1.01%	8.38%	8.07%	4.25%	7.29%	2.67%							0.26%	
Diversity (Shannon index)	1.82	2.08	1.19	2.20	1.58	1.70	1.68	1.19	1.15	2.44	2.06	2.20	0.45	1.88	1.18	1.61
Equitability (Simpson index)	0.82	0.86	0.47	0.84	0.66	0.74	0.70	0.50	0.62	0.88	0.79	0.89	0.16	0.79	0.58	0.72

promoted by liming. Oppositely, the abundance of *Lactarius subdulcis* and *Inocybe napipes* was higher in the untreated plots, while many *Cortinarius* spp. (*Cortinarius delibutus, Cortinarius lebretonii, Cortinarius argentatus*) were absent in the limed plots. There was no significant effect of liming on ECM or FB diversity (Shannon index) or equitability (Simpson index) (Tab. I).

Clavulina cristata was a dominant species of both below–(ECM root tips) and aboveground (sporocarps) communities, showing its high fructification rate, contrary to *Lactarius subdulcis*, dominant in terms of ECM root tips but without any fructification in the limed beech plots.

3.2. Canonical analysis-ECM root tips

Results of a CCA based on relative abundances of ECM root tips showed a strong opposition between limed and untreated plots (Fig. 1). The first canonical component (33% of the total variance, *x* axis) strongly opposed exchangeable Mn^{2+}, Ca^{2+} and Mg^{2+}contensts, and pH, to Al^{3+}, N, C and

Table II. Chemical properties of the topsoil in the 8 sampling plots. Concentrations in C, N and available P are given in $g\,kg^{-1}$. Concentrations in exchangeable H^+, Al^{3+}, Ca^{2+}, Fe^{3+}, Mg^{2+}, Mn^{2+}, K^+ and Na^+ are given in $cmol+\,kg^{-1}$. The available P has been measured using the method of Duchaufour and Bonneau (1959).

Code	SU-A	SU-B	SL-A	SL-B	BU-AB	U-B	BL-A	BL-B
N	4.89	3.80	4.83	4.56	3.86	4.28	4.17	3.07
C/N	21.10	20.80	19.90	21.00	16.40	15.80	18.70	17.50
C	103.00	79.10	95.90	96.00	63.40	67.60	78.10	53.70
pH	4.24	4.01	4.27	4.38	4.16	4.02	4.60	4.53
H+	1.44	1.16	1.00	0.76	0.76	0.84	0.76	0.80
Al3+	8.10	8.91	6.74	8.39	6.95	8.20	4.86	5.22
Ca2+	0.80	0.37	0.93	0.82	0.15	0.20	3.57	1.57
Fe3+	0.14	0.22	0.10	0.07	0.09	0.11	0.02	0.02
Mg2+	0.44	0.25	0.44	0.39	0.24	0.22	0.96	0.47
Mn2+	0.18	0.10	0.24	0.05	0.06	0.14	0.44	0.43
K+	0.41	0.29	0.39	0.27	0.30	0.35	0.41	0.29
Na+	0.05	0.04	0.04	0.04	0.04	0.03	0.05	0.03
P2O5	0.17	0.17	0.19	0.22	0.27	0.23	0.19	0.20

Table III. Distribution and code name (for Fig. 3) of the 70 species of saprophytic fungi found in the study.

Species name	Code in Figure 3	Beech				Spruce			
		Limed		Untreated		Limed		Untreated	
		A	B	A	B	A	B	A	B
Armillaria mellea	Ar me				X				
Ascocoryne sarcoides	As sa				X				
Baeospora myosura	Ba my	X		X					
Bisporella citrina	Bi ci		X						
Calocera cornea	Ca co	X							
Calocera viscosa	Ca vi	X		X			X		
Clitocybe metachroa	Cl me			X					
Collybia butyracea	Co bu	X	X	X					
Collybia distorta	Co di			X					
Collybia peronata	Co pe			X					
Coltrichia perennis	Col pe			X					
Cordyceps capitata	Co ca		X						
Coriolus versicolor	Co ve			X					
Coprinus micaceus	Co mi			X					
Creopus gelatinosus	Cr ge			X					
Crepidotus cesatii	Cr ce		X						
Cystoderma jasonis	Cy ja	X							
Dacrymyces stillatus	Da st				X				
Ditiola pezizaeformis	Di pe				X				
Flammulaster limulatoides	Fl li			X					
Fomes fomentarius	Fo fo			X	X	X			
Fomitopsis pinicola	Fo pi	X		X	X				
Fuligo septica	Fu se	X							
Galerina hypnorum	Ga hy	X							
Ganoderma lipsiense	Ga li				X				
Gymnopilus hybridus	Gy hy		X						
Hypholoma dispersum	Hy di		X						
Hypholoma fasciculare	Hy fa		X	X	X				
Hypholoma marginatum	Hy ma		X						
Hypholoma sublateritium	Hy su		X		X				
Hypoxylon fragiforme	Hy fr				X				
Hypoxylon sp.	Hy sp			X	X				
Kuehneromyces mutabilis	Ku mu			X	X	X	X		
Marasmiellus ramealis	Ma ra	X		X		X	X		
Marasmius alliaceus	Ma al			X	X				
Megacollybia platyphylla	Me pl			X	X	X	X		
Microomphale perforans	Mi pe	X	X	X	X				
Mycena filopes	My fi			X	X	X	X		
Mycena galericulata	My ga		X	X	X	X	X		
Mycena galopus	My gp	X		X			X		
Mycena leptophylla	My le	X							
Mycena pura	My pu		X						
Oligoporus caesius	Ol ca	X							
Oligoporus subcaesius	Ol su			X	X				
Oligoporus tephroleucus	Ol tp			X					
Oudemansiella mucida	Ou mu				X				
Oudemansiella radicata	Ou ra	X		X		X	X		X
Oxyporus laetomarginatus	Ox la	X							
Panellus stipticus	Pa st			X	X				
Pholiota flammans	Ph fl		X		X				
Pholiota lenta	Ph le			X					
Pholiota limonella	Ph li				X				
Physosporus nitreus	Ph ni				X				
Plicatura crispa	Pl cr			X					

Table III. Suite.

Species name	Code in Figure 3	Beech				Spruce			
		Limed		Untreated		Limed		Untreated	
		A	B	A	B	A	B	A	B
Plicaturopsis faginea	Pl fa				X				
Pseudohydnum gelatinosum	Ps ge		X		X				
Rickenella fibula	Ri fi				X				
Schizopora paradoxa	Sc pa				X				
Stereum hirsutum	St hi			X	X	X	X		
Strobilurus esculentus	St es	X							
Strobilurus tenacellus	St te	X							
Trametes gibbosa	Tr gi				X				
Trametes versicolor	Tr ve			X		X	X		
Tremella foliacea	Tr fo		X						
Tyromyces stipticus	Ty st		X						
Ustulina deusta	Us de				X				
Xylaria hypoxylon	Xy hy		X	X	X				
Xylaria polymorpha	Xy po		X	X	X				

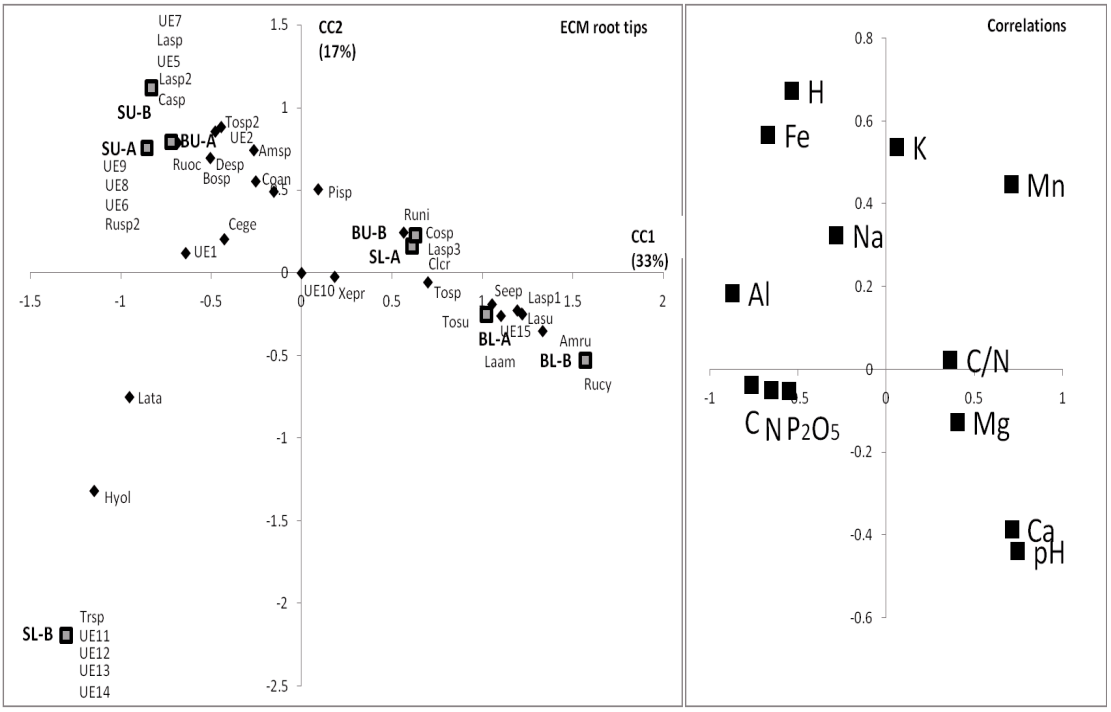

Figure 1. Canonical analysis based on the relative abundance of ECM root tips in each plot. Correlations: correlation circle between soil nutrient contents. ECM root tips: projection of the species and the 8 investigated plots on the plan of the two first canonical components. The first component (CC1) explained 33% of the total variance, and the second one (CC2) 17% (total: 50%). S: spruce, B: Beech, U: untreated, L: limed, A: replicate A, B: replicate B. The name of each species is abbreviated according to Table I.

P_2O_5 contents (Fig. 1, Correlations). Predictions of canonical coordinates also showed the differentiation between limed and untreated plots following the first canonical component for beech and (ii) a differentiation between a limed plot (SL-A) and the other spruce ones (Fig. 1, ECM root tips). The correspondence analysis (CA) based on ECM root tip relative abundances revealed the opposition between species found in SL-A and both limed beech plots (*Russula cyanoxantha, Tomentella sublilacina, Amanita rubescens, Clavulina cristata, Lactarius subdulcis*) against those found in SL-B and all untreated plots (*Cantharellus* sp., UECM spp. 1 to 9, *Russula ochroleuca, Cenococcum geophilum*) (Fig. 1, ECM root tips). The second canonical component (17% of the total variance, *y* axis) was not strongly correlated with one environmental variable: it was to some extent correlated with available soil Na^+, K^+, H^+ and Fe^{3+} concentrations. The second canonical component also predicted an opposition between limed (especially SL-B) and untreated plots; the CA also showed a distinct group of

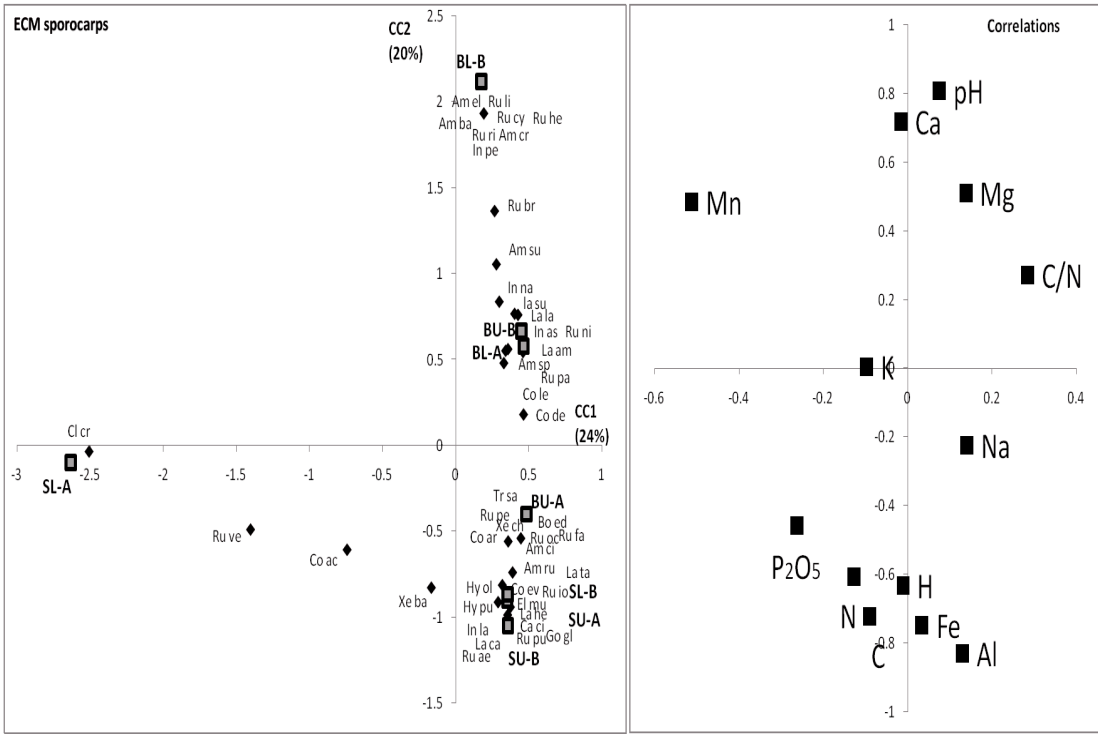

Figure 2. Canonical analysis based on the relative abundance of sporocarps of ECM species in each plot. Correlations: correlation circle between soil nutrient contents. ECM root tips: projection of the species and the 8 investigated plots on the plan of the two first canonical components. The first component (CC1) explained 24% of the total variance, and the second one (CC2) 20% (total: 44%). S: spruce, B: Beech, U: untreated, L: limed, A: replicate A, B: replicate B. The name of each species is abbreviated according to Table I.

species close to the SL-B plot (*Hygrophorus olivaceoalbus, Tricholoma* sp., UECM spp. 11 to 14, *Lactarius tabidus*).

3.3. Canonical analysis-Sporocarps of ECM fungi

Results of a CCA based on relative abundances of ECM sporocarps clearly isolated SL-A and BL-A plots. The first canonical component (24% of the total variance, *x* axis) was positively correlated to concentrations in soil available K and negatively correlated with soil P concentration (Fig. 2, Correlations). Predictions of first canonical coordinate isolated clearly the SL-A plot from the other ones (Fig. 2, ECM sporocarps). The correspondence analysis (CA) based on sporocarp abundances also isolated species found in SL-A plot (particularly *Clavulina cristata*, and to a lesser extent *Russula vesca* and *Cortinarius acutus*). The second canonical component (20% of the total variance, *y* axis) strongly opposed pH, exchangeable Mn, Ca and Mg concentrations, to Na, Al, H, C and N contents (Fig. 2, Correlations). Even if BU-B was close to BL-A, predictions with the second canonical coordinate gradually isolated the beech limed plots from the untreated ones (Fig. 2, ECM sporocarps). The CA also distinguished species found only in the limed beech plots (*Amanita battarae, Amanita crocea, Amanita eliae, Amanitopsis submembranacea, Inocybe petiginosa*, *Russula cyanoxantha, Russula heterophylla, Russula lilacea, Russula risigalina*) (Fig. 2, sporocarps). The species and plot ordination appeared as a horseshoe, showing that the sampled plots were probably distributed along an environmental gradient (Ramette, 2007).

3.4. Canonical analysis-Sporocarps of saprophytic fungi

The first canonical component (22% of the total variance, *x* axis) isolated the spruce plots from beech ones, and was correlated with pH, Ca^{2+} and Mn^{2+}, and negatively correlated with Al^{3+} (Fig. 3, Correlation). The second canonical component (19% of the total variance, *y* axis) was correlated with K and negatively correlated with soil P contents. Nevertheless, prediction of canonical components showed no distinction between limed and untreated plots. There was a clear block effect for spruce.

4. DISCUSSION

There was an inversion in the environmental variables associated with the two main canonical components between ECMs and fruiting bodies. Soil parameters relevant with the effect of liming (increased Ca^{2+}, Mg^{2+}, pH, and decreased Al^{3+}, total N and total C) were correlated with the first canonical component for ECMs and with the second one for fruiting

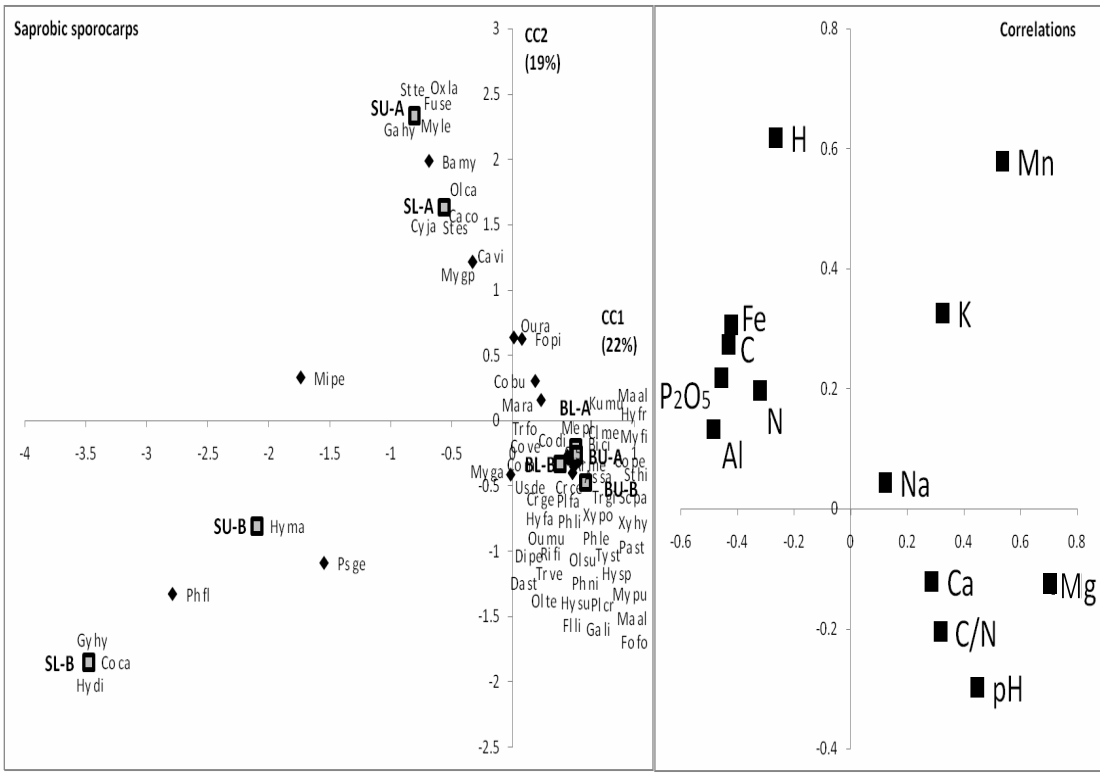

Figure 3. Canonical analysis based on the presence/absence of sporocarps of saprophytic species in each plot. Correlations: correlation circle between soil nutrient contents. ECM root tips: projection of the species and the 8 investigated plots on the plan of the two first canonical components. The first component (CC1) explained 22% of the total variance, and the second one (CC2) 19% (total: 41%). S: spruce, B: Beech, U: untreated, L: limed, A: replicate A, B: replicate B. The name of each species is abbreviated with the first two letters of its genus name, followed by a space and the first two letters of its species name (see also supplementary Tab. II).

bodies. In contrast, increased exchangeable K^+ content and decreased in available P content were both correlated with the first canonical component for fruiting bodies and with the second one for ECMs, meaning that liming was a stronger factor of community structuring than tree host for ECMs, but not for sporocarps.

Concerning ECMs, there were many common species between spruce and beech plots. Among them, two ECM species were particularly repressed by liming: the most abundant ECM species in the overall community (*Cenococcum geophilum*), and another frequent ECM species (*Russula ochroleuca*). *Cenococcum geophilum* has often been reported as the dominant species of the ECM community (Baier et al., 2006; Courty et al., 2005; Dickie and Reich, 2005; Tedersoo et al., 2003). Generally a strong dominance of *Cenococcum geophilum* ECMs is reported in stressed forest stands, which is consistent with the status of moderate decline of the forest studied here. Acidophilic morphotypes as *Russula ochroleuca* were also repressed in limed plots. A similar decrease of abundance of this ECM in a liming experiment has already been reported (Qian et al., 1998). In contrast, liming also promoted relative abundance of the two ECM morphotypes *Clavulina cristata* and *Tomentella sublilacina* in both spruce and beech plots. These two species have often been found in surveys of ECM root tips and are considered as ubiquist (Buée et al., 2005; Frey et al., 2004; Köljalg et al., 2000; Taylor and Bruns, 1999; Tedersoo et al., 2006). Moreover, *Tomentella sublilacina* is an excellent competitor in mature forests (Taylor and Bruns, 1999). Liming also promoted relative abundance of the beech-specific and widespread ECM fungus *Lactarius subdulcis* (Courty et al., 2005). The main consequences of liming on ECM communities have therefore been the shift from *Cenococcum geophilum* and acidophilic species (i.e. and *Russula ochroleuca*) to a community dominated by ubiquist and highly competitive species. It is probable that the presence of these ubiquist species was due to the emergence of more nutrient-rich ecological niches in the limed areas, characterized by increased pH and contents of exchangeable Ca and Mg, as observed on our sample site.

Community structuring of ECM fruiting bodies appeared more distinct between spruce and beech. Opposition between the SL-A plot and all the other ones was a prominent factor of community structuring. This plot was characterized by the very high abundance of *Clavulina cristata* and by a slight reduction of the abundance of *Xerocomus badius*, a mesoacidophilic fungus (Köttke et al., 1998). A possible "genet effect" (presence in one plot only because of a limited genet size) for *Clavulina cristata* is unlikely, because its sporocarps covered almost all the limed plot, and were nearly absent from the untreated one.

The second factor of sporocarp community structuring gradually opposed beech limed and untreated plots; the limed plot coordinates were correlated with parameters characteristic of limed soils (exchangeable Ca and Mg, pH). Moreover, we observed that the 3 acidophilic species *Amanita citrina, Cortinarius delibutus* and *Russula fageticola* (in order of decreasing acidophilic optimum) were absent in the limed plots. The two latter ones were codominant species of the beech untreated plots, but none of the 3 species were found as ECM root tips. The relative abundance of *Russula ochroleuca* sporocarps also clearly decreased in the limed spruce plots, as observed by Agerer et al. (1998). As in the spruce limed plots, the abundance of an ubiquist fungus (*Laccaria laccata*) was also promoted by liming in beech. Nevertheless, acidophilic species as *Russula brunneoviolacea* also occurred in beech limed plots, showing that underlying soil acidity remained even after liming.

Some places in the overall limed area showed recolonization by *Sphagnum* species, showing a probable local soil re-acidification, often localized in hollows. It was the case in the SL-B plot, the fungal community of which was very close to that of the untreated plots. Moreover, we found in this plot very acidophilic species such as *Lactarius helvus*, in this plot. This means that the effect of liming on fungal communities is not uniform, probably because of the heterogeneous distribution of liming material in the soil, or by differences of soil drainage. The uneven distribution of some fungal species among the sampling plots (such as *Clavulina cristata*) may also be due to spatial soil heterogeneity in nutrient distribution, which is expected to significantly vary at a 5 m scale in forest soils (Gallardo, 2003). The SL-A plot, showing a strong dominance of *Clavulina cristata* in both ECM and sporocarp communities, presented high concentrations of exchangeable Mn: this might reflect preference of this ECM fungus to Mn-rich soils. It is also likely that, knowing that ECM fungi vary a lot in niche size preference (Toljander et al., 2006), earthworm bioturbation after liming decreases the micro-scale soil heterogeneity, and thus destroys potential niches for fungi of less ecological amplitude. The bacterial communities, which are also affected by liming (Bäckman et al., 2003), could also indirectly elicit or repress some fungal species and thus influence fungal community structure.

The relative abundance of *Russula ochroleuca* sporocarps was affected by liming, as well as its fruiting behaviour. The sporocarps were widespread all over the 4 untreated plots, whereas they were always restricted to the base of trees in the limed ones, where most of the acidity occurs through stem flow. This suggests *Russula ochroleuca* as a good marker species of above and belowground effects of liming on ECM communities, using its ECM root tip relative abundance in several limed and untreated soils cores, and the position of its fruiting bodies in whole untreated and limed plots. This could be a quick and useful tool for foresters, because ECM root tips of *Russula ochroleuca* are frequent and easy to identify (pale yellow surface covered with bright yellow dots), as well as its sporocarps. Moreover, the spatial repartition of this species shows that local acidity can occur even in the limed plots and thus the soil spatial heterogeneity observed here can highly influence fungal community structure. A similar liming-induced reduction of the abundance of acidophilic species at the profit of ubiquist, neutrophilic or competitive ones was observed on forest ground vegetation (Hallbäcken and Zhang, 1998) and mosses (Dulière et al., 2000). In the same way, high-dose liming decreased germination of acidophilic plant species (such as *Vaccinium myrtillus*) but increased germination of widespread ones (*Primula veris, Senecio sylvaticus*) (Olsson and Kellner, 2002). Nevertheless, liming did not have any significant effect on sporocarp and ECM community diversity (Shannon index) and equitability (Simpson index), even while the ECM diversity (Shannon index) had a tendency to decrease in limed plots. These results strongly tend to highlight the trivialization of all the communities after liming, due to the establishment of more nutrient-rich, and thus less selective, ecological niches.

Finally, among the environmental factors studied here, tree host was the most important for controlling the presence/absence of sporocarps of saprophytic fungal species. This has been mentioned in the literature for most of the lignin degrading basidiomycete species (Osono, 2007). Nevertheless, one non-specific species (*Clitocybe nebularis*) was present only in limed plots; other *Clitocybe* spp. and *Collybia* spp., known as unspecific to a tree host (Osono, 2007), were not affected by liming. The presence of many saprophytic fungi could be affected by interactions with other soil microbes (Osono, 2007), C/N ratio (Lindahl et al., 2007), litter thickness (Yamashita and Hijii, 2006) or earthworm presence (Osono, 2007). Even if all these factors were more or less influenced by liming, we did not observe a specific pattern of saprophytic fungi community structure in the limed plots. We did not observe a significant reduction of fungal diversity (Shannon index and Simpson index) in plots where N concentration increased.

Some other soil factors that can affect sporocarp production were not studied here; they could have interfered with liming for structuring fungal communities. For example, soil humidity is a major factor of fungal fructification (Bonet et al., 2008; Kawakami et al., 2004), as well as soil temperature (Li, 1979), or CO_2 concentration (Dahlberg and Van Etten, 1982). The age of the root system sampled can also be of critical importance for evaluating the ECM community structure (Gibson and Deacon, 1988). Finally, fungal species differ in their distribution: some occur in a very patchy way, whereas other ones can be solitary. This is true for sporocarps as well as for ECM root tips. The sampling strategy used here may overestimate the abundance of these patchy species compared to solitary ones. All these concerns, as well as the longer lifespan of a mycorrhiza (one week to one month) compared to that of a sporocarp (one day to one week), makes sporocarp survey more sensitive to climate than ECM community description. This can be a reason why the ECM communities studied here appear more sensitive to liming than sporocarp ones.

In conclusion, liming influenced very differently the structure of the communities of ECM root tips and sporocarps of symbiotic and saprophytic fungi. This forest practice had no obvious effect on saprophytic communities, but reduced the abundance of some acidophilic and meso acidophilic fruiting bodies of symbiotic fungi. This is compensated by the

increased abundance of ubiquist species (*Clavulina cristata* and in a lesser extent *Laccaria laccata*). Finally, the same effect of liming (replacement of acidophilic and stress species by ubiquist and highly competitive ones) was observed in ECM root tip communities, and it was the main factor of community structuring, whatever the tree host. The appearance of ubiquist fungi was correlated with the development of new ecological niches, characterized by higher pH and exchangeable Ca^{2+}, Mg^{2+} and Mn^{2+} concentrations. Nevertheless, the re-acidification of limed plots was observed in some depressed areas. These results show that, as for plants, liming leads to the trivialization of symbiotic fungal communities, even 15 y after the treatment.

Acknowledgements: We thank Pr. C. Nys for providing the experimental site of Humont and for his expertise about liming, and the *Office National des Forêts* for allowing us to sample roots in the experimental plots. We also thank Dr. B. Marçais for useful comments on statistical analyses, and Dr P. Frey-Klett for very useful discussion about the results. The PhD scholarship of the first author was partly supported by the Lorraine Region. Part of this work has been funded by the Agence Nationale de la Recherche (contract FUNDIV, ANR-06-BDIV-006-01).

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