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Earthworm community characteristics during afforestation of abandoned chalk grasslands (Upper Normandy, France)

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Abstract

Earthworm biomass, density and species composition were assessed in different stages of secondary successions after a grazed chalk grassland was abandoned. Earthworm populations were abundant (an average of 51.2 to 130.2 g. m^{-2} and of 175.8 to 522.6 ind. m^{-2}) at all stages of succession. Grazing abandonment led to a rapid development of earthworm communities. Biomass and density reached their maximum in a recently ungrazed plot and decreased in a 44-year-old fallow. Density further increased, although biomass slightly decreased, with afforestation by deciduous species. Biomass and density were minimal under pine wood. Taxonomic richness (number of taxonomic units) remained unchanged during succession but species composition was deeply modified. Dynamics of earthworm communities seemed to be influenced by two environmental factors that were closely linked to two features of the vegetation: (i) the vertical structure of the vegetation (*i.e* the importance of herbaceous vegetation, litter and moss cover, and presence of trees), and (ii) the quality of the organic supply, depending on the nature of the vegetation (*i.e* herbaceous, coniferous or deciduous species).

Keywords: Earthworms, Lumbricidae, secondary successions, grazing, abandonment, chalk grasslands, woods, Upper Normandy, France.

Caractéristiques des communautés de vers de terre durant le boisement des pelouses calcicoles (Haute-Normandie, France).

Résumé

La biomasse, la densité et la composition spécifique des vers de terre a été évaluée dans différents stades d'une succession secondaire après l'abandon d'une pelouse calcicole pâturée. La biomasse et la densité des populations de vers de terre sont très élevée (51.2 à 130.2 g. m^{-2} et 175.8 à 522.6 ind. m^{-2} en moyenne) dans toutes les parcelles échantillonnées. L'abandon du pâturage conduit à un rapide développement des communautés de vers. La biomasse et la densité atteignent leur maximum dans une pelouse récemment mise en exclos, puis diminuent dans une pelouse abandonnée depuis 50 ans. La densité croit ensuite, alors que la biomasse diminue légèrement pendant l'installation du bois de feuillus. La densité et la biomasse sont minimales sous pinède. La richesse taxonomique (nombre d'unités taxonomiques) ne change pas pendant la succession, mais la composition spécifique varie de façon nette. La dynamique des communautés de vers de terre semblent être sous l'influence de deux facteurs environnementaux prépondérants, eux-mêmes étroitement liés à deux paramètres de la végétation : (i) la structure verticale de la végétation (importance de la couverture du sol par la végétation herbacée, la litière, les mousses, présence d'arbres) et (ii) la qualité des litières restituées, liée à la nature de la végétation (herbacée, conifères ou feuillus).

Mots-clés : Vers de terre, Lumbricidae, successions secondaires, pâturage, abandon, pelouses calcicoles, bois, Haute-Normandie, France.

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INTRODUCTION

Earthworms usually dominate soil macroinvertebrate communities in most terrestrial ecosystems of temperate latitudes (Lee, 1985). They help maintain soil physical and chemical properties by favouring the formation of stable water-resistant aggregates and participating in nutrient cycles (Zhang & Schrader, 1993; Lavelle, 1994).

In calcareous soils, earthworms participate in the maintenance of an active mull type of humus with rapid turnover, as they sustain high microbial populations (Scheu, 1990), and participate in the fragmentation and burying of fresh organic matter (Van der Drift, 1963; Hirschberger & Bauer, 1994a, b). In chalk grasslands, earthworms also play a role in vegetation dynamics because they influence in a selective way the composition of seed banks (Thompson *et al.*, 1994; Willems & Huijsmans, 1994).

Chalk grasslands in north-western Europe were traditionally used for sheep grazing. Since the end of the 1940s, this practice has been progressively abandoned and successional processes are leading to woodland extension and/or species-poor coarse grasslands (Willems & Bobbink, 1990). This general tendency has dramatic effects on calcicolous plant and faunal diversity, which are vulnerable to lack of grazing (Bobbink, 1987). The effects of various management options (*i.e* grazing, mowing, abandonment, etc.) on plant or epigeic invertebrates have been studied to support plans for conservation management (Morris, 1969; Wells, 1969; Sutherland & Hill, 1995). This study aimed to assess changes in density, biomass and specific richness of earthworm communities at different stages of post-pastoral secondary successions, and to identify the main factors responsible for this evolution. It is part of a program. carried out on chalk grasslands in Upper Normandy. France, that focuses on the ecology and on the main driving factors of biodiversity in these species-rich ecosystems (Dutoit & Alard, 1995; Dutoit *et al.*, 1997).

MATERIAL AND METHODS

Study sites

Sampling was done on calcareous slopes of the Seine Valley, Upper Normandy, North-West France (*fig.* 1). Mean annual precipitation of the area is 804 mm and mean temperature 9.9°C with low seasonal fluctuations (7.6°C on average). Freezing is infrequent (only 11 days during the sampling period) and probably does not often affect the soil layers. Soils are calcareous Rendzina, with neutral pH, aggregated structure, and highly active mull humus. The vegetation climax in the study area is the beech wood. Main soil and vegetation characteristics are summarised in *table* 1.

Successional processes in chalk grasslands are complex and can be described as multi-directional (Dutoit & Alard, 1996). In our study, six sites were selected to represent different stages of the common successional sequence occurring in this ecosystem after grazing abandonment (*fig.* 2). The relevance of

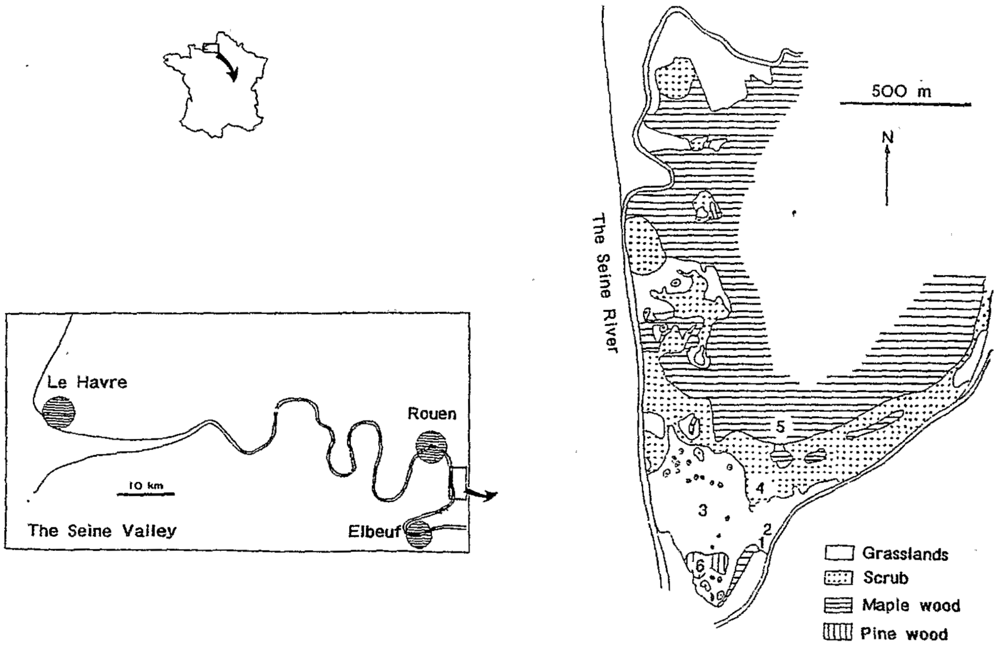

Figure 1. – Locality of study sites (1 = pasture; 2 = 2-year-old fallow; 3 = 44-year-old fallow; 4 = scrub; 5 = maple wood; 6 = pine wood).

Table 1. – Vegetation and soil characteristics of the six plots (C = carbon; O.M. = Organic Matter; CEC = Cation Exchange Capacity).

Plots (vegetation)	Moss (g/m2)	Herbaceous (g/m2)	Roots (g/m2)	Litter mass (g/m2)	Litter C:N ratio	Tree cover (%)
Grazed grassland	0	187	637	57	29	0
2-year-old fallow	0	573	838	93	35	0
44-year-old fallow	5	722	914	153	36	5
Scrub	137	16	593	228	27	90
Maple wood	27	75	533	304	22	100
Pine wood	323	231	914	264	57	70

Plots (0-15cm soil layer)	Clay (%)	Silt (%)	Sand (%)	Carbon (g/Kg)	O.M. (g/Kg)	CEC (Cmol/Kg)
Grazed grassland	37.4	48.9	13.7	39.2	67.4	10.1
2-year-old fallow	68.5	21.5	10.0	38.9	66.9	10.9
44-year-old fallow	74.1	22.5	3.4	54.1	93.1	16.6
Scrub	76.5	19.5	4.0	54.6	93.9	24.3
Maple wood	71.3	23.0	5.7	63.4	109.0	30.3
Pine wood	61.4	22.7	15.9	56.8	97.7	17.7

these choices have been discussed in the light of old aerial photographs (Dutoit & Alard, 1995). Obviously, none of these particular sites has been or is likely to go through all the described stages. Pine wood must be considered as an alternative late stage of the successional sequence, and certain stages (e.g. scrub vegetation) are not absolutely necessary steps for the development of the next stages. Thus, the set of plots cannot be considered to represent a true succession but rather, it represents an approximate (potential) successional sequence that emphasises the vertical changes that occur in the vegetation's structure. Despite this potential succession not being a true time series (*i.e* a chronosequence), it has been designed to reconstruct a tangible successional gradient (*i.e* afforestation process).

Site 1. A chalk grassland permanently grazed by sheep and horses for at least 6 years (pasture) with a high stocking rate (1.5 animal unit. ha^{-1}). Vegetation was an open short sward of small perennial herbs (e.g. *Festuca lemanii, Carex flacca* and *Lotus corniculatus*) with many bare areas.

Site 2. A chalk grassland formerly grazed, abandoned for 2 years (2-y. fallow). The vegetation consisted of a patchwork of perennial herbs (*Sesleria*

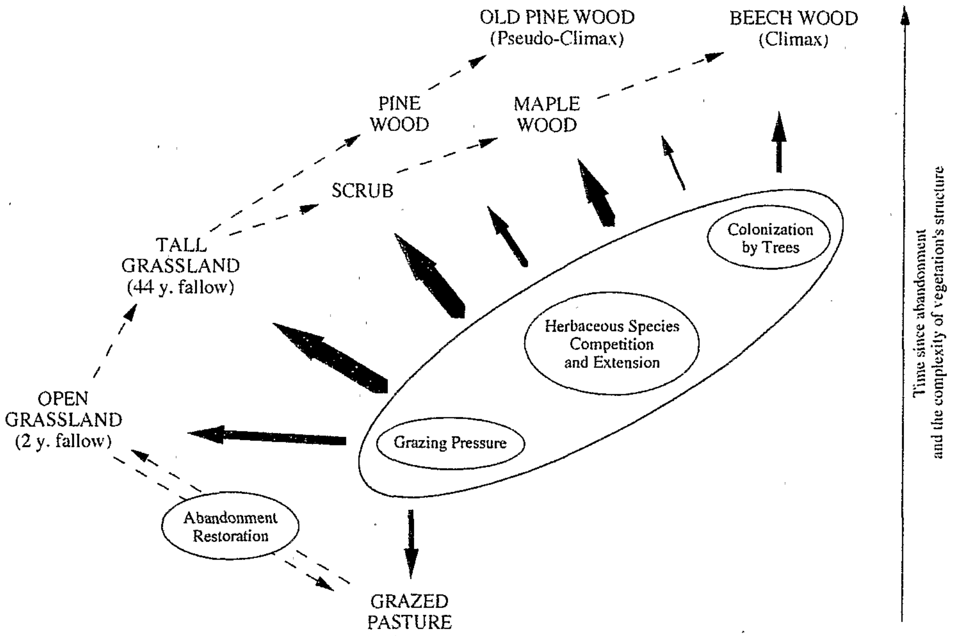

Figure 2. – Multi-directional post-pastoral dynamics after grazing cessation on the calcareous slopes of the Seine Valley, Upper Normandy, France, and some of their relevant biotic driving processes (ovals). Width of arrow corresponds to the relative importance of each successional stage in the study site. Dashed arrows represent one possible (potential) evolution of vegetation.

albicans and *Brachypodium pinnatum*) and bare ground.

Site 3. A tall grassland (*Brachypodium pinnatum* and *Sesleria albicans*) abandoned for 44 years (44-y. fallow) with scrub encroachment by *Rosa canina*, *Cornus sanguinea* and *Viburnum lantana*.

Site 4. A uniform 40-years-old scrub vegetation, dominated by *Crataegus monogyna* and *Cornus sanguinea*. *Viola hirta* and *Origanum vulgare* were the most common species of the herbaceous vegetation.

Site 5. A 40-year-old, naturally developed, deciduous wood dominated by *Acer pseudo platanus* and *Fraxinus excelsior* (maple wood). The scrub layer comprised mostly *Corylus avellana*, *Sambucus nigra* and *Crataegus monogyna*. The herbaceous vegetation was dominated by *Mercurialis perennis*.

Site 6. A 48-year-old, spontaneous, pine wood (*Pinus sylvestris*) with an important herbaceous cover (e.g. *Brachypodium pinatum*, *Sesleria albicans* and *Carex flacca*), probably developed from a tall grassland.

Sampling procedure

Two basic sampling methodologies were used: (i) hand sorting, according to Anderson & Ingram (1993) and (ii) formalin extraction, according to Baker & Lee (1993). A total of 30 samples were taken at each site. Every 2 months, from March 1994 to January 1995, five samples, 25 × 25 × 10 cm, were dug out with a spade. Soil monoliths were localized at mid-slope, at every 5 m, along a line whose direction was parallel to the slope and whose origin was chosen randomly. Each sample was carefully hand-sorted in a large plastic tray. Then, 2,5 L of 0.05% formalin were applied twice under the dug sample to expel

Table 2. – Mean annual density (ind. m^{-2}) and fresh biomass (g. m^{-2}) of 11 earthworm species collected in the six plots. Values in parentheses are standard error.

	Grasslands						**Scrub**		**Woods**			
	Grazed		2-year-old fallow		44-year-old fallow				Maple		Pine	
	Density	Biomass	Density	Biomass	Density	Biomass	Density	Biomass	Density	Biomass	Density	Biomass
Endogeics	**223.2 (25.5)**	**74.88 (11.17)**	**361.1 (25.6)**	**90.72 (12.04)**	**186.9 (17.2)**	**65.42 (8.18)**	**319.8 (26.7)**	**45.22 (4.19)**	**421.9 (27.9)**	**46.63 (3.86)**	**137.7 (13.2)**	**28.01 (3.58)**
Allolobophora chlorotica (SAVIGNY, 1826)	79.9 (12.3)	13.15 (2.31)	262.4 (21.5)	46.30 (7.32)	56.3 (8.5)	11.12 (2.27)	229.9 (24.6)	32.93 (3.96)	343.0 (20.5)	39.97 (3.33)	119.9 (16.3)	23.41 (3.50)
Allolobophora rosea (SAVIGNY, 1826)	13.4 (1.7)	0.94 (0.29)	-	-	15.4 (2.1)	2.28 (1.04)	22.3 (3.8)	3.21 (1.03)	52.3 (4.9)	5.02 (1.67)	13.3 (5.2)	1.55 (0.57)
Allolobophora muldali (OMODEO, 1956)	-	-	-	-	-	-	42.9 (4.7)	0.55 (0.23)	24.6 (8.7)	0.49 (0.24)	-	-
Allolobophora icterica (SAVIGNY, 1826)	-	-	2.6 (2.5)	0.93 (0.92)	38.4 (8.9)	15.60 (3.49)	22.3 (3.9)	7.46 (2.33)	-	-	-	-
Octolasiun cyaneum (SAVIGNY, 1826)	0.6 (0.5)	1.63 (1.56)	-	-	2.6 (2.8)	1.25 (1.21)	-	-	2.1 (2.0)	1.15 (1.20)	4.5 (2.7)	3.05 (2.11)
Aporrectodea caliginosa (SAVIGNY, 1826)	129.3 (17.8)	59.16 (11.38)	96.1 (14.3)	43.49 (7.94)	74.3 (9.2)	35.17 (6.46)	2.5 (2.3)	1.07 (1.12)	-	-	-	-
Anecics	**16.4 (3.7)**	**15.37 (4.06)**	**50.3 (7.9)**	**38.55 (7.62)**	**27.4 (4.3)**	**38.52 (6.82)**	**21.8 (4.1)**	**34.43 (9.51)**	**12.3 (3.0)**	**14.59 (5.73)**	**20.5 (3.8)**	**22.25 (4.53)**
Nicodrilus giardi (SAVIGNY, 1826)	3.6 (1.8)	3.82 (2.04)	18.1 (4.3)	13.81 (3.29)	18.2 (4.5)	30.75 (8.33)	10.2 (3.0)	22.17 (8.61)	10.4 (3.3)	14.45 (6.52)	9.7 (3.1)	14.00 (5.76)
Lumbricus terrestris (LINNE, 1758)	12.7 (4.0)	11.55 (4.46)	26.9 (5.5)	19.76 (5.89)	9.1 (2.9)	7.77 (3.86)	5.0 (2.0)	8.41 (4.53)	0.9 (0.5)	0.07 (0.04)	5.4 (2.2)	5.83 (3.74)
Lumbricus festivus (SAVIGNY, 1826)	-	-	5.3 (5.2)	4.98 (3.41)	-	-	6.6 (3.0)	3.85 (3.72)	0.9 (0.5)	0.07 (0.05)	5.4 (2.2)	2.42 (1.67)
Epigeics	**16.4 (8.8)**	**2.57 (1.80)**	**9.0 (2.7)**	**0.91 (0.33)**	**11.7 (3.9)**	**1.01 (0.39)**	**36.1 (18.4)**	**1.94 (1.02)**	**88.4 (9.9)**	**6.79 (1.33)**	**17.6 (5.4)**	**0.96 (0.31)**
Lumbricus castaneus (SAVIGNY, 1826)	16.4 (10.1)	2.57 (1.91)	9.0 (3.2)	0.91 (0.42)	11.7 (4.9)	1.01 (0.55)	36.1 (22.2)	1.94 (1.23)	88.4 (13.0)	6.79 (1.54)	11.4 (4.4)	0.55 (0.28)
Dendrobaena mammalis (SAVIGNY, 1826)	-	-	-	-	-	-	-	-	-	-	6.3 (2.6)	0.41 (0.22)
Total	**256.0 (27.8)**	**92.82 (14.30)**	**420.4 (35.5)**	**130.18 (17.15)**	**225.9 (20.7)**	**104.95 (11.27)**	**377.7 (41.1)**	**81.59 (11.71)**	**522.6 (36.8)**	**68.01 (7.13)**	**175.8 (14.2)**	**51.22 (6.66)**

deep burying species. Earthworms were killed in 70° alcohol and kept in 5% formalin before weighing and counting.

Herbaceous plants and moss cover were determined, using 50 × 50 cm quadrats; litter using 25 × 25 cm quadrats; and herbaceous root biomass with a 10 cm diameter and 12 cm depth cylinder. Samples were dried at 75°C for 24 h before weighing. Soil analyses were carried out, using the standards methods recommended by Alleen *et al.* (1974). The percentage of tree cover was estimated, using aerial photographs of the sites.

Data processing

Earthworms were identified according to Bouché (1972) and grouped into three ecological categories (*i.e* epigeics, endogeics and anecics). Differences in mean density and biomass were tested, using the parametric Fisher test (see Appendix).

Two multivariate analysis were performed, using Mac Mul and Graph Mu softwares for Macintosh (Thioulouse, 1990): (i) a principal component analysis (PCA), including 22 environmental variables (*i.e* vegetation characteristics and soil physical and chemical properties), performed to identify the main environmental factors responsible for ecological gradients along successions; (ii) a correspondence analysis (CA), using the three earthworm ecological categories, with a view to describing changes in earthworm communities. Biomass and density of individual species were projected as additional variables on the two first axes of the CA to judge the field covered by the species.

RESULTS

Species composition

Eleven earthworm species were identified in the whole sampling area (*table* 2). Four species were found in all plots (*i.e Allolobophora chlorotica, Nicodrilus giardi* (=*Aporrectodea terrestris*), *Lumbricus terrestris* and *Lumbricus castaneus*). However, some species showed preferences for one or some stages of succession: *Allolobophora muldali, L. castaneus.* and *Allolobophora rosea* for scrub and maple wood; *Dendrobaena mammalis* for pine wood; *Allolobophora icterica* for scrub and 44-y. fallow; *L. terrestris* and *Aporrectodea caliginosa* for the three grasslands.

Biomass and density

Biomass was moderate in the pasture, reaching a maximum in the ungrazed plot, and decreasing during succession. This pattern occurred in endogeic and anecic species (*fig.* 3*a*, *table* 2). In general, biomass was largely dominated by endogeic (*A. chlorotica, A. caliginosa* and *A. icterica*) and anecic (*L. terrestris* and *N. giardi*) species in all stages of succession, whereas epigeics (principally *L. castaneus*) significantly increased in the pasture, scrub and woods (*fig.* 4).

Density was high in the 2-y. fallow compared with the pasture (*fig.* 3*b*, *table* 2). It decreased in the 44-y. fallow, and reached a maximum in the maple wood and a minimum in the pine wood. Anecic density was highest in the ungrazed plot and decreased during afforestation. Endogeic species (*A. caliginosa* in the grasslands, *A. chlorotica* in the scrub and wooded plots) were dominant in density in all plots and particularly abundant in the 44-y. fallow and maple wood. In the pasture, scrub and wooded plots, epigeic species (mostly *L. castaneus*) were also of some importance (*fig.* 4).

Environmental factors

The two multivariate analyses revealed that two factors were responsible for 91.70% (PCA, *fig.* 5) and 96.2% (CA, *fig.* 6) of the total variance observed.

The first factor of the PCA accounts for 75.8% of the environmental variance and clearly separates plots

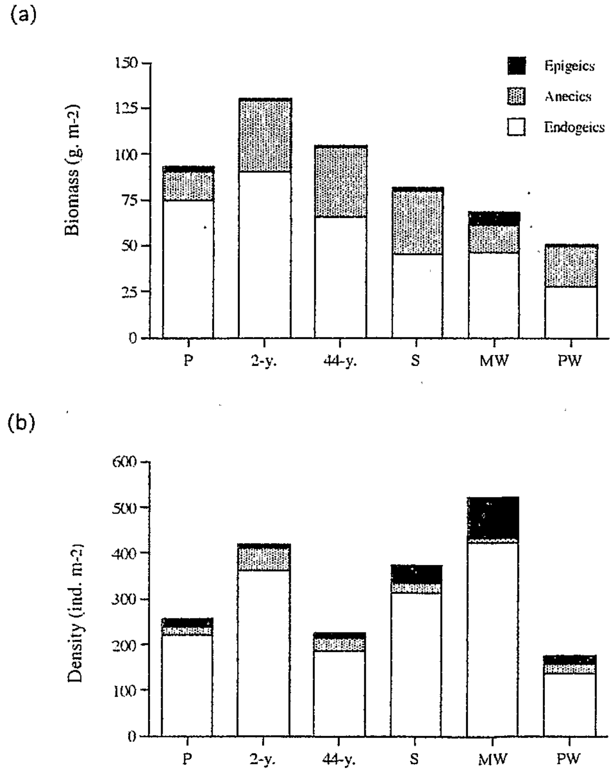

Figure 3. – Mean annual fresh biomass (a) and density (b) of earthworms in the six plots (P = pasture; 2-y. = 2-year-old fallow; 44-y. = 44-year-old fallow; S = scrub; MW = maple wood; PW = pine wood).

with high herbaceous biomass from plots with dense tree cover. The second factor of the PCA (15.9% of the variance) separates pine wood and fallows from pasture and maple wood, and is mostly related to litter quality (*i.e* C:N ratio) (*fig.* 5). The first factor of the CA (*fig.* 6) accounts for 63.3% of the variance in the community structure and opposes maple wood and pasture, with a significant presence of epigeic (*L. castaneus*) and few endogeic species (*A. muldali* and *A. rosea*), to fallows and pine wood, with a significant presence of anecic (*L. festivus* and *N. giardi*), large endogeic (*A. icterica*) and epigeic (*D. mammalis*) species. The second factor of the CA explains 32.9% of the variance and ordinates plots in a similar way as does the PCA for environmental variables. It mostly separates open herbaceous vegetation plots, where communities were exclusively dominated by endogeic (*A. caliginosa*) and anecic (*L. terrestris*) species, from wooded plots, with more diversified populations.

Ordination of plots in relation to these factors are similar for the two analyses and these factors can thus be identified as environmental gradients in the PCA and as the response of soil macrofaunal communities in the CA. The first gradient is defined as the effect of the vegetation structure (factor II of PCA and factor I of CA), which determines the diversity of microhabitats and life conditions for earthworm populations. The second gradient is assumed to represent the effect of the quality of the above-ground litter (factor I of PCA and factor II of CA), which principally depends on the nature of the vegetation and on the presence of domestic herbivores.

DISCUSSION

Earthworms are the major component of soil macrofauna of the calcareous hillsides of Upper Normandy. In all the plots, they represented more than 73% of the total macrofauna biomass (Decaëns *et al.*, 1997). Density and biomass of Lumbricidae are higher (fallows and pine wood) or equivalent (pasture and maple wood) with other data available for comparable vegetation types (*table* 3). These values can be explained by the presence of optimal soil conditions for all the collected species, *i.e* neutral pH, eubiotic conditions and high level of Ca in our plots (Bouché, 1972).

Two major environmental factors seem to determine the evolution of earthworm populations: (i) the effect of the vegetation structure and (ii) the

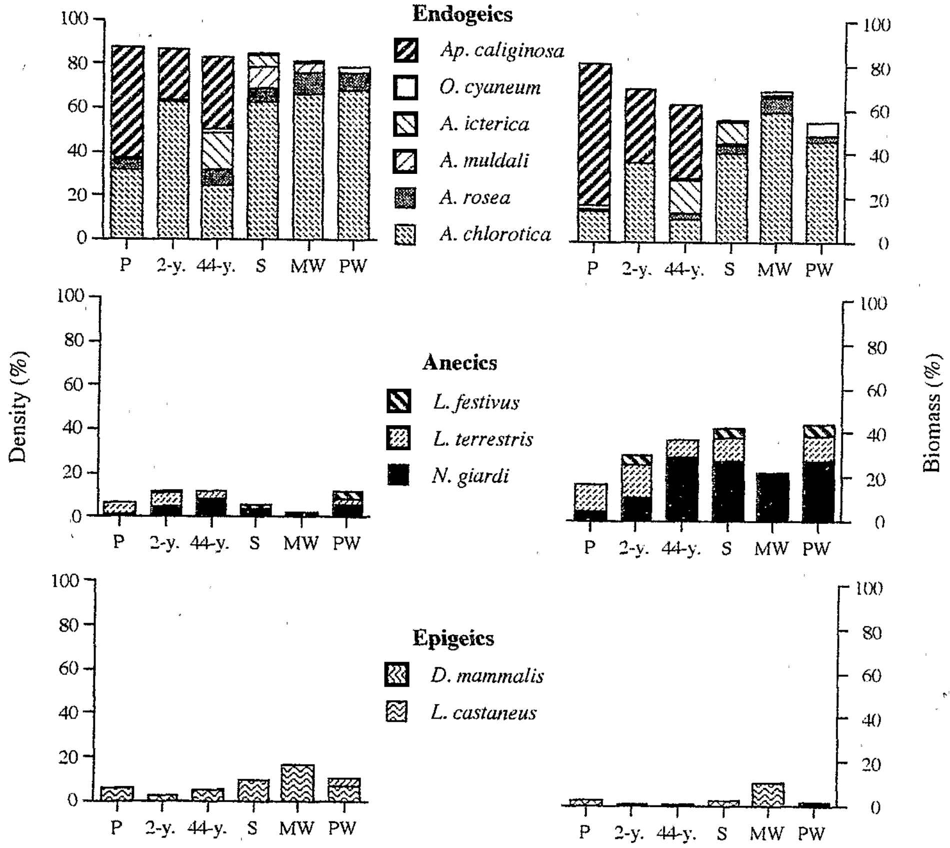

Figure 4. – Relative contributions to biomass and density of 11 earthworm species recorded in the six plots (Abbreviations for post-pastoral successions as in *figure* 3).

Table 3. – Fresh biomass (g. m^{-2}), density (g. m^{-2}) and specific richness of earthworm populations in different vegetation types (N = number of species; 1 = hand sorting; 2 = chemical repellents; 3 = combination of 1 and 2; 4 = washing and sieving).

Vegetation type	Locality	N	Density	Biomass	Methodology	Authors
Grazed grasslands						
Sown pasture	Sweden	5 to 7	109	59	2	Nordström and Rundgren, 1973
Sown pasture	Wales	7	646	149	1	Reynoldson, 1966
Sown pasture	France	9 to 14	288	125	4	Bouché, 1977
Natural grassland	*France*	*7*	*255*	*93*	*1, 2*	*This study*
Abandoned grasslands						
Natural grasslands	Romania	-	5 to 100	1 to 20	1	Gruia, 1969
Natural grasslands	Wales	7	22	8	1	Reynoldson, 1966
Natural grassland	*France*	*7 to 8*	*226 to 420*	*105 to 130*	*1, 2*	*This study*
Woods						
Ash wood	Sweden	9 to 10	122 to 209	63 to 89	1	Nordstöm and Rundgren, 1973
Maple wood	*France*	*8*	*523*	*68*	*1, 2*	*This study*
Maple wood	England	10 to 11	447 to 532	145 to 148	1, 3	Cuendet, 1984
Beech wood	Germany	11	205	11	1, 2, 3	Schaefer and Schauermann, 1990
Beech wood	Belgium	1 to 5	1 to 103	1 to 22	1, 2, 3	David et al., 1993
Beech wood	Germany	6	233 to 260	13 to 20	1	Scheu, 1992
Beech wood	England	6 to 10	21 to 174	2 to 52	1, 3	Cuendet, 1984
Pine wood	Sweden	3 to 4	19 to 105	2 to 10	2	Nordstöm and Rundgren, 1973
Pine wood	*France*	*8*	*176*	*51*	*1, 2*	*This study*

effect of the quality of litter brought to the soil. As far as our study is concerned, no direct relationships were found between other soil properties and earthworm populations. Main soil properties at these stages of succession do not significantly vary and no relationships were found with Lumbricidae communities. However, soil parameters are expected to influence earthworms in later stages, especially soil acidification in the maturing pine wood.

In the grasslands, the absence of tree cover, which can buffer adverse micro-climatic conditions occurring in the superficial soil layers (*i.e* summer

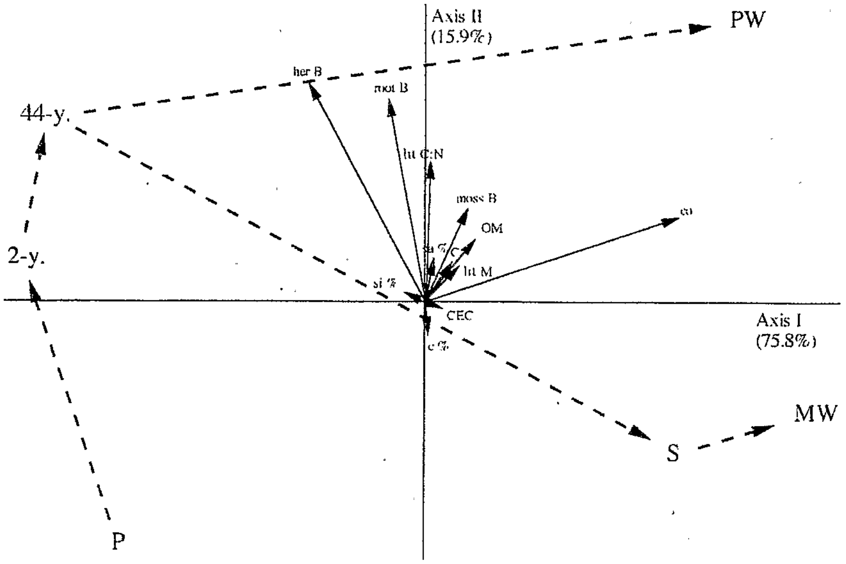

Figure 5. – Ordination of environmental variables and plots in relation to the first two factors extracted from the PCA (abbreviations as in *figure* 3; dotted lines represent the potential evolution of the vegetation during the succession).

Abbreviation: herb B: Herbaceous biomass; moss B: Moss biomass; root B: Root biomass; lit M: Litter mass; co: Tree and shrub cover; lit C:N: Litter C:N ratio; c%: Clay content; si%: Silt content; sa%: Sandy content; C: Organic carbon; OM: Organic matter; CEC: Cation exchange capacity.

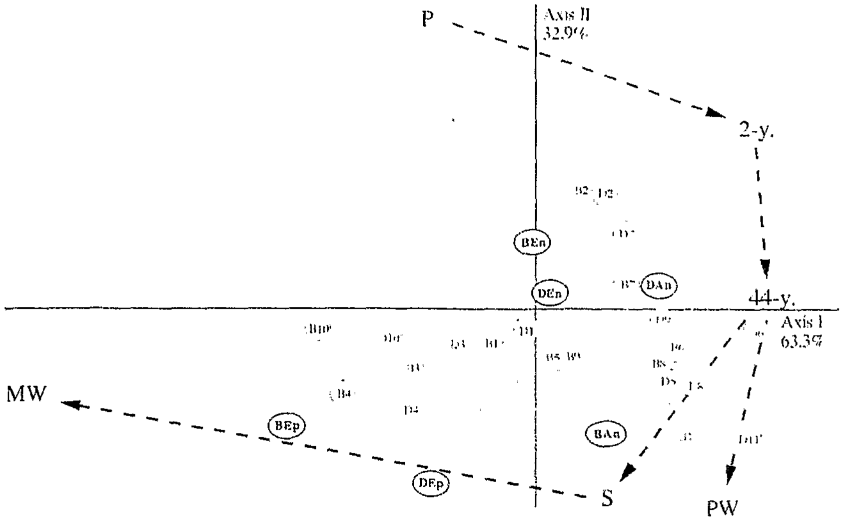

Figure 6. – Ordination of ecological categories and plots in relation to the first two factors extracted from the CA. (Abbreviations as in *figure* 3; dotted lines represent the potential evolution of vegetation during succession).

D = density; B = biomass; Ep = Epigeic species; An = Anecic species; En = Endogeic species; 1 = *Allolobophora chlorotica*; 2 = *Aporrectodea caliginosa*; 3 = *Allolobophora rosea*; 4 = *Allolobophora muldali*; 5 = *Octalasium cyaneum*; 6 = *Allolobophora icterica*; 7 = *Lumbricus terrestris*; 8 = *Lumbricus festivus*; 9 = *Nicodrilus giardi*; 10 = *Lumbricus castaneus*; 11 = *Dendrobaena mammalis*.

drought and extreme temperatures), leads to the predominance of adapted species such as the endogeic *A. caliginosa*, a preferential species of juvenile stages of successions (Pizl, 1992; Scheu, 1992). In the pasture, the dominance in biomass of endogeic species probably results from the high level of primary production of the pasture (Hutchinson & King, 1980) and from high root quality (*i.e* C:N ratio), because of the presence of domestic herbivores (Seastedt *et al.*, 1988). The return to soil of important amounts of animal dung with low C:N ratio may explain the presence of relatively high populations of the occasional coprophagous L. castaneus (Bouché, 1977).

The increase in density and biomass observed during the first 2 years after abandonment is certainly related to a modification in the vegetation structure. The growth of herbaceous cover and the accumulation of an insulating litter layer are expected to effectively improve the suitability of the environment for earthworms (Scheu, 1992).

In the 44-y. fallow, biomass and density were low, compared with later stages. Scheu (1992) explains this phenomenon as a decrease in primary productivity during succession. Another explanation is the accumulation of energy supply in the form of a non-palatable litter layer (Bobbink & Willems, 1993).

Development of scrub and, later, of the deciduous arboreous vegetation, leads to important modifications in earthworm communities. The accumulation of a dead leaf layer with a low C:N ratio provides both a specific habitat and a high quality food substrate for epigeic species. Litter and shade protect the soil from adverse microclimatic conditions and allow the colonization of the superficial soil layers (0-5 cm) (Lee, 1985; Scheu, 1992). The increased number of endogeic earthworms in the maple wood (mostly *A. chlorotica*), may result from the build-up of a mineral soil, rich in humus, that provides an adequate and permanent food supply for these species (Scheu, 1992). Density and biomass of anecic species (especially *L. terrestris*) significantly decreased in the maple wood. Scheu (1992) has observed the same evolution in an ash-dominated wood. This may be related to the lack of a permanent litter layer throughout the year.

In the pine wood, the low biomass and density, compared with the maple wood, can be explained by the difference in the quality of litter between the two plots. Pine needles have a lower nutrient value than maple or *Mercurialis* leaves (*table* 2). The influence of quality (*i.e* litter C:N ratio and presence of polyphenolic substances) of the food substrate for Lumbricidae populations has, moreover, been mentioned by various authors (Watkin & Wheeler, 1966; Nordstrom & Rundgreen, 1973; Cuendet, 1984, Muys *et al.*, 1992).

According to these authors, a possible evolution of earthworm populations in the woods would be a decline of earthworm populations in both sites, because of the leaf nitrogen content of the different tree species. The maple wood, during the next years, will change into a beech wood (*i.e* the climax). Beech leaves are considered to have very low palatability (Cuendet, 1984), and the resulting decrease in resource quality will lead to a slight decrease of biomass and density. Average values of earthworm communities in beech woods on limestone generally do not exceed

205 ind. m^{-2} and 52 g. m^{-2} (*table* 3). In the case of the pine wood, the decrease in communities should be more spectacular. Maturation of the vegetation should effectively lead to a disappearance of the herbaceous cover and soil acidification. These factors, added to the low quality of litter, should lead to a large decrease, not only in biomass and density, but also in species richness of communities (see *table* 3).

CONCLUSION

The importance of other soil macroinvertebrate groups (such as Diplopoda, Gastropoda or Isopoda) in advanced stages of successions has been pointed out by Schaefer & Schauermann (1990), David *et al.* (1993) and Decaëns *et al.* (1997). Other studies should not focus just on earthworms, but should take into account the role of the whole macrofauna in the functioning of the soil system and its modifications during secondary successions.

Earthworm communities during afforestation of grasslands principally respond to two environmental gradients that are closely bound with vegetation evolution. The evolution of the structure (*i.e* the development of the herbaceous vegetation and, later, the formation of the wood) and nature (*i.e* whether coniferous or deciduous) of the vegetation determines the diversity of micro-habitats and life conditions for earthworm populations. This hypothesis agrees with Scheu (1992), who concluded that earthworms first react to the availability of preferred micro-habitats during secondary successions. Babel *et al.* (1992) also demonstrated that the diversity of vegetation cover is a critical determinant in the diversity of other functional groups. This pattern of response has been described by Lavelle (1996) in his hypothesis of "Nested Biodiversities", according to which diversity in plant communities determines below-ground diversity in the following order: plant diversity — ecosystem engineers (*sensus* Stork & Eggleton, 1992; Lavelle, 1996) — litter transformers (meso-fauna) — micro-fauna → micro-flora. In the case of secondary successions, it would now be of great interest to describe the links existing between the diversity of ecosystem engineers (here earthworms) and the community structure of smaller invertebrates and micro-organisms.

Overall, specific richness remains unchanged along the succession, but species composition evolves markedly. As mentioned by Scheu (1992) and Pizl (1992), major modifications appear in epigeic populations, which seem more sensitive to disturbances in their environment. Small earthworms (mostly epigeic and small endogeic species) are generally considered as r-selected (Bouché, 1977; Lee, 1985), that is, they increase in number during successions. This contrasts with the general theory of succession, according to which the maturation of vegetation leads to an increase in K-selected species (Scheu, 1992). The r-selection was presumably caused by the formation of the litter layer, which represented a new habitat for adapted species. Hence, experimental studies should focus on the evolution of the micro-habitat diversity and its relationships with the population dynamics of *Lumbricidae*.

Further research is also needed to understand the dynamics of populations in shifting environments and processes of colonization of new habitats by soil fauna. From this viewpoint, spatial (*i.e* patch dynamics) and temporal patterns of faunal changes induced by modifications in vegetation, especially at the transition from one successional stage to another, should give us valuable information. The question of whether soil fauna either are passive actors in vegetation dynamics or play a catalytic and/or active role in successional processes is central to this research.

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Appendix. – Summary of the parametric Fisher PLSD test of significant differences between the six plots.

P = grazed grassland; 2-y = ungrazed grassland; 44-y = abandoned grassland; S = Scrub; MW = maple wood; PW = pine wood
"x > y" means that y is less than x with P < 0.05; "x >> y" with P < 0.01; "x >>> y" with P < 0.001; NS = no significant

Ecological category	Species	Response variable	P(F)	Result of the fisher PLSD test
Endogeic		Density	< 0.001	MW >>> 2-y >>> P, 44-y, PW; S >>> PW; MW >> P, S; 2-y > S > 44-y > PW; S > P
		Biomass	< 0.001	P >>> PW; 2-y >>> S, MW, PW; P >> S, MW; 44-y >> PW; 2-y > 44-y
	Allolobophora chlorotica	Density	< 0.001	MW >>> P, 44-y, S, PW; 2-y, S >>> 44-y; 2-y, S >> P; 2-y, S > PW
		Biomass	< 0.001	MW >>> 2-y >>> P, 44-y; MW, 2-y > PW > 44-y; S >>> 44-y; S > P
	Allolobophora rosea	Density	< 0.001	MW >>> P, 2-y, 44-y, S, PW; S > 2-y
		Biomass	< 0.001	MW >>> 2-y; MW >> P, PW; S >> 2-y; MW > 44-y
	Allolobophora muldali	Density	< 0.001	S >>> P, 2-y, 44-y, PW; MW > P, 2-y, 44-y, PW
		Biomass	< 0.001	S >>> P, 2-y, 44-y, PW; MW >> P, 2-y, 44-y, PW
	Allolobophora icterica	Density	< 0.001	44-y >>> P, 2-y, MW, PW; S > P, 2-y, MW, PW
		Biomass	< 0.001	44-y >>> P, 2-y, MW, PW; S > P, MW, PW
	Octalasium cyaneum	Density	NS (P= 0.6306)	No significant differences
		Biomass	NS (P= 0.5719)	No significant differences
	Aporrectodea caliginosa	Density	< 0.001	P >>> 44-y, S, MW, PW; P >> 2-y >>> S, MW, PW; 44-y > S, MW, PW
		Biomass	< 0.001	P >>> 44-y, S, MW, PW; P >> 2-y >> S, MW, PW; 44-y >> S, MW, PW
Anecic		Density	< 0.001	2-y >>> P, S, MW, PW; 2-y >> 44-y >> P, MW; 44-y > S
		Biomass	< 0.01	2-y, 44-y >> P, MW; S > P, MW
	Nicodrilus giardi	Density	< 0.01	2-y >>> P; 2-y >> S, MW, PW; 44-y >> P, PW
		Biomass	< 0.01	S >> P, 2-y; 44-y >> 2-y, P; 2-y >> P; 44-y > S, MW > PW
	Lumbricus terrestris	Density	< 0.001	2-y >>> P, 44-y, S, MW, PW
		Biomass	< 0.001	2-y >>> P, 44-y, S, MW, PW; 44-y > MW
	Lumbricus festivus	Density	NS (P= 0.4023)	No significant differences
		Biomass	NS (P= 0.5238)	No significant differences
Epigeic		Density	< 0.001	MW >>> P, 2-y, 44-y, PW
		Biomass	< 0.001	MW >>> P, 2-y, 44-y, PW; MW > S
	Lumbricus castaneus	Density	< 0.001	MW >>> P, 2-y, 44-y, S, PW
		Biomass	< 0.001	MW >>> 2-y, 44-y, PW; MW >> S, P
	Dendrobaena mammalis	Density	< 0.001	PW >>> P, 2-y, 44-y, S, MW
		Biomass	< 0.01	PW >> P, 2-y, 44-y, S, MW
Total earthworm population		Density	< 0.001	MW > 2-y >>> P, 44-y, PW; MW >>> S >> P, 44-y, P > PW
		Biomass	< 0.001	2-y >>> MW, PW; 2-y >> S; 44-y >> PW; 2-y > P > PW; 44-y > MW