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Horizons and Humus Forms in Beech Forests of the Belgian Ardennes

Jean-François Ponge*

ABSTRACT

Forest soil organic horizons are named on the basis of visual observations made directly in the field, thus this is often subjective. To find more objective bases for their classification, humus form horizons in 13 beech stands (*Fagus sylvatica* Ehrh.) were compared. Test sites were located in the Belgian Ardennes (western Europe), which encompasses a wide range of ecological conditions. I used a semi-quantitative micromorphological method for the description of horizons, and a multivariate method for data analysis. These methods helped to discern objective discontinuities among Oi, Oe, and Oa horizons, adding new criteria for their characterization, such as the root system of trees. Within these horizons, transitions between sub-horizons are gradual and thus do not lie on clear-cut criteria. The transition between Oa and A horizons was also gradual. The composition of Oa and A horizons varies according to humus form. The vertical distribution of soil organisms and their vertical movements were considered the origin of discontinuous and continuous processes taking part in the transition from one horizon to another. The observation of horizons under a dissecting microscope may help to find more reliable bases for their nomenclature, even without the use of costly soil sections.

SINCE THE PIONEERING WORK of Müller (1889), who described two basic humus forms, mull and torf, beneath Danish beech forests, on the basis of microscopic observations, there have been many attempts to classify humus profiles in forest soils. Different horizons or sub-horizons are generally recognized within the O (Brady, 1984) or Ao (Duchaufour, 1997) horizons. Although discrepancies concerning the terminology of these strata exist, three main strata are recognized, Oi (entire leaves), Oe (fragmented leaves), and Oa (holorganic fecal pellets). Differences in the development of these horizons, together with structure and chemical properties of the underlying A horizon, allow recognition of three main humus forms, now called mull, moder, and mor (Klinka et al., 1981; Delecour, 1983; Green et al., 1993; Brêthes et al., 1995; Jabiol et al., 1994, 1995).

The mor humus form, together with dysmoder (moder with a thick H stratum), has been also called raw humus (Kubišna, 1953; Delecour, 1980). The recognition of biological processes taking place in the development of humus profiles (Hartmann, 1965; Zachariae, 1965; Bal, 1982) suggested that some features, such as compaction of the soil matrix, deposition of fecal pellets, skeletonization of leaves or tunneling of needles, are the direct result of soil faunal activity. Thus, as for most biological processes, the transition from one horizon to another should be considered discontinuous because of tolerance limits and food and habitat preferences of soil organisms.

Characterization of organic horizons and humus forms on the basis of morphological features is common; however, the existence of clear-cut changes between one horizon and another has been poorly demonstrated through quantitative or semi-quantitative morphological data. Federer (1982) pointed out that simple remeasurements of thickness of forest soil horizons may lead to false conclusions if done by two individuals. Discrepancies between field and laboratory observable features of horizons have been reported (Bernier et al., 1993). This may indicate that some morphological criteria used for the definition of organic horizons are inadequate or difficult to employ with accuracy in the field. This is particularly true for the transition from Oa to A horizons and for subdivisions which have been recognized within Oi and Oe horizons (Babel, 1971).

In the present study, my purpose was to determine whether the transition from one organic horizon to another is a continuous or, rather, a step-by-step process, with sharp delineations in horizon properties. In doing so, I addressed the question as to whether horizons exhibit true emergent properties and have not been created by soil scientists for classification purposes only.

MATERIAL AND METHODS

Nomenclature

Comparable organic horizons have several different names depending on the taxonomic system in use. The commonly

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Table 1. Main features of the 13 studied sites. Phytosociological types according to Thill et al. (1988). Soil types according to FAO-UNESCO classification (Driessen and Dudal 1991). Humus forms according to Brêthes et al. (1995).

Site	Altitude	Phytosociological type	Soil type	Humus form
	m			
1	370	Luzulo-Fagetum festucetosum	Dystric cambisol	Dysmull
3	465	Luzulo-Fagetum festucetosum	Dystric cambisol	Eumoder
4	500	Luzulo-Fagetum typicum	Dystric cambisol	Dysmoder
5	505	Luzulo-Fagetum vaccinietosum	Dystric cambisol	Eumoder to dysmoder
16	445	Luzulo-Fagetum vaccinietosum	Dystric cambisol	Eumoder
17	430	Luzulo-Fagetum typicum	Dystric cambisol	Hemimoder to eumoder
22	400	Luzulo-Fagetum typicum	Gleyic cambisol	Eumoder to dysmoder
24	390	Luzulo-Fagetum festucetosum	Dystric cambisol	Dysmull to dysmoder
26	430	Luzulo-Fagetum vaccinietosum	Leptic podzol	Dysmoder
28	375	Luzulo-Fagetum festucetosum	Dystric cambisol	Amphimull to eumoder
40	385	Luzulo-Fagetum vaccinietosum	Ferric podzol	Dysmoder
100	350	Melico-Fagetum festucetosum	Dystric cambisol	Oligomull to dysmull
307	380	Luzulo-Fagetum vaccinietosum	Leptic podzol	Amphimull

used nomenclature of Brêthes et al. (1995) corresponds to USDA nomenclature as follows: OL equals Oi, OF equals Oe, and OH equals Oa. These horizons correspond to L, F, and H horizons, respectively, recognized by Hesselmann (1926) and later refined by Babel (1971).

The classification of humus forms by Brêthes et al. (1995) was used in this study. It is not based on a strong relationship between the features O and A horizon, as this is the case in other classifications. For instance, a crumbly A horizon (typical of mull) may coexist with a thick O horizon (typical of moder). Some humus forms, such as hemimoder and amphimull, were described by other authors as mull-moder (Duchaufour, 1997) or mull-like moder (Kubiřna, 1953; Delecour, 1980, 1983). A hemimoder means a moder humus form (A horizon with organic matter juxtaposed to mineral matter) without any Oa

horizon. An amphimull means a mull humus form (A horizon with organo-mineral assemblages) with a distinct Oa horizon.

The nomenclature of soil types used in this study followed the FAO-UNESCO classification (Driessen and Dudal, 1991). Cambisols and podzols correspond to Inceptisols and Spodosols, respectively, in USDA Soil Taxonomy (Brady, 1984). Nomenclature of plant species followed Rameau et al. (1989).

Study Sites

Thirteen mature beech stands were selected in the Belgian Ardennes, covering a wide range of humus forms (Table 1). Beech (*Fagus sylvatica* L.) forests were chosen because of their wide distribution and the need for a wide range of environmental conditions, in particular soil and climate, without

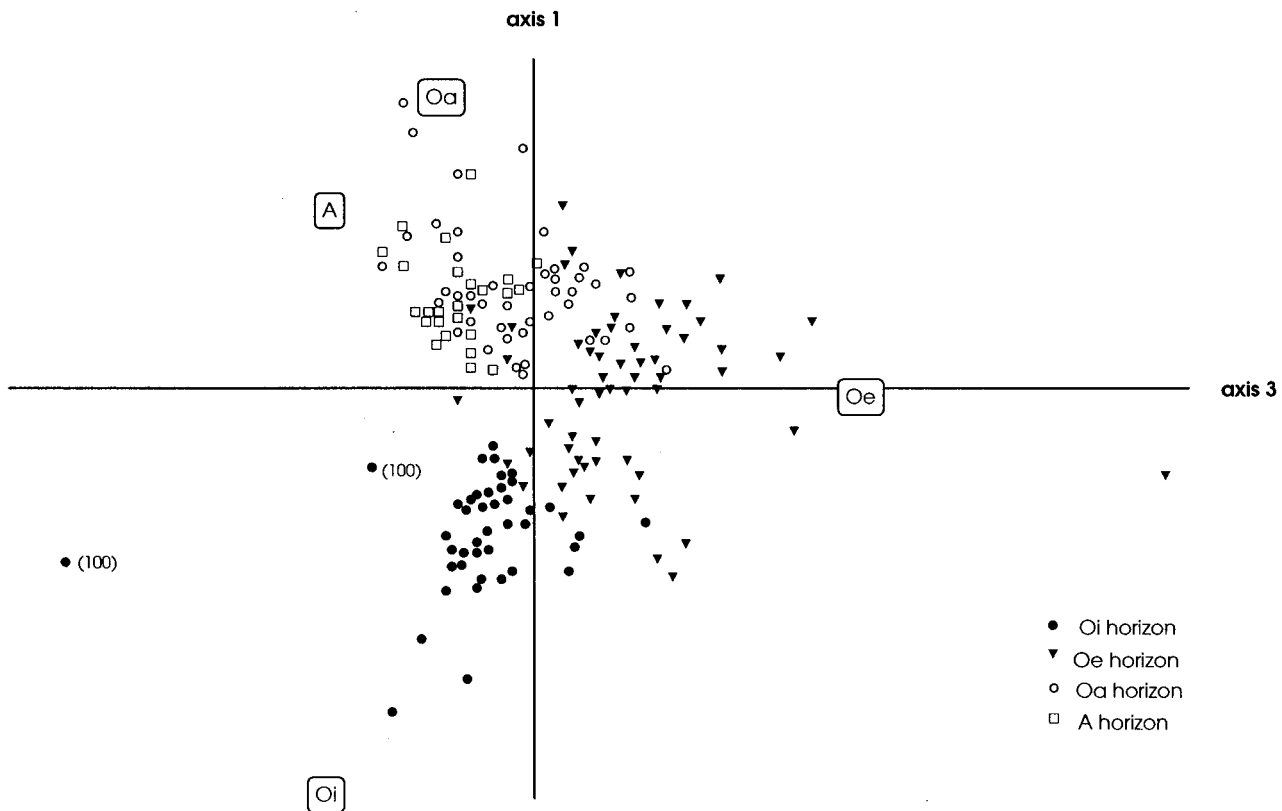


Fig. 1. Results from total correspondence analysis of organic horizons with faunal characteristics in beech forests of the Belgian Ardennes. Projection of horizons (rows) in the plane of Axes 1 and 3. Indicated names of horizons were based on field observation and were not included as main variables.

Table 2. Most typical categories in the three main groups of horizons depicted by correspondence analysis.

Oi
Entire brown leaves of beech
Entire bleached leaves of beech
Intact bud scales of beech
Intact male inflorescences of beech
Entire variegated leaves of beech
Intact twigs
Hologranic faecal material smearing beech leaves
Organo-mineral material smearing beech leaves
Oe
Sandwich material made of beech leaf fragments and hologranic enchytraeid faeces
Brown decaying male inflorescences of beech
Fragments of grass stems browsed by fauna
Pollen
Woodlice shells
Petioles and nerves of beech filled with faeces of phthiracrid oribatid mites
Bud scales of beech, entire but brown and soft
Intact unidentified fragments of seed wings
Intact seed coats of beech
Twigs filled with enchytraeid hologranic faeces
Twigs filled with oribatid hologranic faeces
Living leaf bases of <i>Luzula albida</i>
White rhizomorphs
Oa + A
Dead pale yellow creamy mycorrhizae of beech
Sclerotia of <i>Cenococcum geophilum</i>
Intact dead fine long roots of beech
Compacted hologranic enchytraeid faeces
Intact living woody roots of beech
Strongly decayed bud scales of beech
Well-decayed bark fragments
Intact stones
Decaying woody roots of beech
Weathering stones
Charcoal
Dead fine long roots of beech tunnelled by fauna
Decaying grass roots
Dead black mycorrhizae of beech
Compacted organo-mineral material

strong variation in the composition of litter. All studied sites were located on nutrient-poor geological substrates (schists, graywackes, quartzites) ranging from Cambrian to Devonian age. Altitude and related regional factors (climate, mineral richness of parent rock) were found to be the main source of variation of soil animal communities, humus forms, and site quality over the studied range (Ponge et al., 1997). Results of litter and soil chemical analyses were also reported in the aforementioned paper.

Categories of the Soil Matrix in Humus Horizons

At each site, two humus profiles were sampled for micro-morphological description of horizons. These profiles were chosen to represent the range of observed within-site variation of humus forms. Sampling was completed in June 1989. Preparation of the samples (5- by 5-cm section monoliths) was carried out according to the method of Bernier and Ponge (1994), except that only the top 1 cm of the A horizon was sampled. Horizons were separated in the field on the basis of variation visible to the naked eye, without reference to any a priori classification. Afterwards, they were classified into Oi, Oe, and Oa horizons according to the abovementioned field criteria, and numbered according to their order from the top to the bottom of a given horizon, i.e., Oi1, Oi2, Oi3, Oe1, Oe2, etc. All 172 horizons were immediately immersed in ethyl alcohol and transported to the laboratory. The composition of each horizon was analyzed by observing the soil matrix in alcohol under a dissecting microscope. No attempt was made to quantify the volume or mass of each category. Rather,

I used the following visual semi-quantitative coding of the abundance of a given category in a given horizon: absent, 0; present but scarce, 1; present and common, 2; and present and dominant, 3.

A total of 185 categories were recognized. Most of them were plant litter, in varying degrees of decomposition or comminution by fauna. Animal feces were classified according to the corresponding animal group, their degree of comminution by other animals, and their degree of connection with uneaten plant categories. Animals were counted and classified into broad groups.

Multivariate Analysis

Correspondence analysis (Greenacre, 1984) was used to give an overall picture of affinities and differences between horizons and/or categories. This method, using the chi-square distance, allows horizons and categories to be simultaneously projected on factorial axes; thus, groups of samples could be directly associated with groups of categories. As was theoretically developed by Benzécri (1973), this method has been refined for particular purposes such as community gradient analysis [detrended correspondence analysis (Hill and Gauch, 1980)] or the study of community-environment relationships [canonical correspondence analysis (Ter Braak, 1987)]. Here, my purpose was to analyze the structure of a data matrix (the composition of horizons) without any a priori hypotheses concerning their relationships with environmental factors and with more than one single factor suspected to result from the analysis. Additional (passive) variables were used to help interpretation of the factorial axes and not to quantify causal relationships. Thus, I used the approach of original correspondence analysis, that was devised to evaluate global patterns underlying complex data matrices, and not that of the aforementioned derived methods.

Matrices were analyzed so that horizons were observations (rows) and categories were active variables (columns). Animal groups, horizon names, humus form names, phytosociological types, and altitude were added as passive variables. They had no influence on the results, but they were projected on factorial axes as the active variables.

Categories were coded and counted as indicated above. Animal groups were recorded as total counts. Horizons, humus forms, and phytosociological types were coded as 1 when a given horizon (row) belonged to a given category (column), 0 when not. Altitude was recorded in meters. All variables (active and passive) were standardized with unit variance and a mean of 20. This allowed contributions to factorial axes to be proportional to factorial coordinates and data of a different nature, such as counts, semi-quantitative coding and measurements, to be included in the same analysis (Ponge and Delhaye, 1995). In the case of altitude, high elevation and low elevation were distinguished. Standardized altitude values (high elevation) were complemented to 40 to create a new variable, varying in an opposite sense (low elevation). The new variable had similar mean (20) and standard deviation (1). Following this procedure, already used by Ponge and Delhaye (1995), the range of elevation values was described by two symmetrical points.

RESULTS

Composition of the Humus Profile

I first analyzed all 172 horizons and 185 categories. Only Axes 1 and 3 were considered for the global description of humus horizons. Axis 2 was neglected, because it isolated only one horizon (Oe1 in the second

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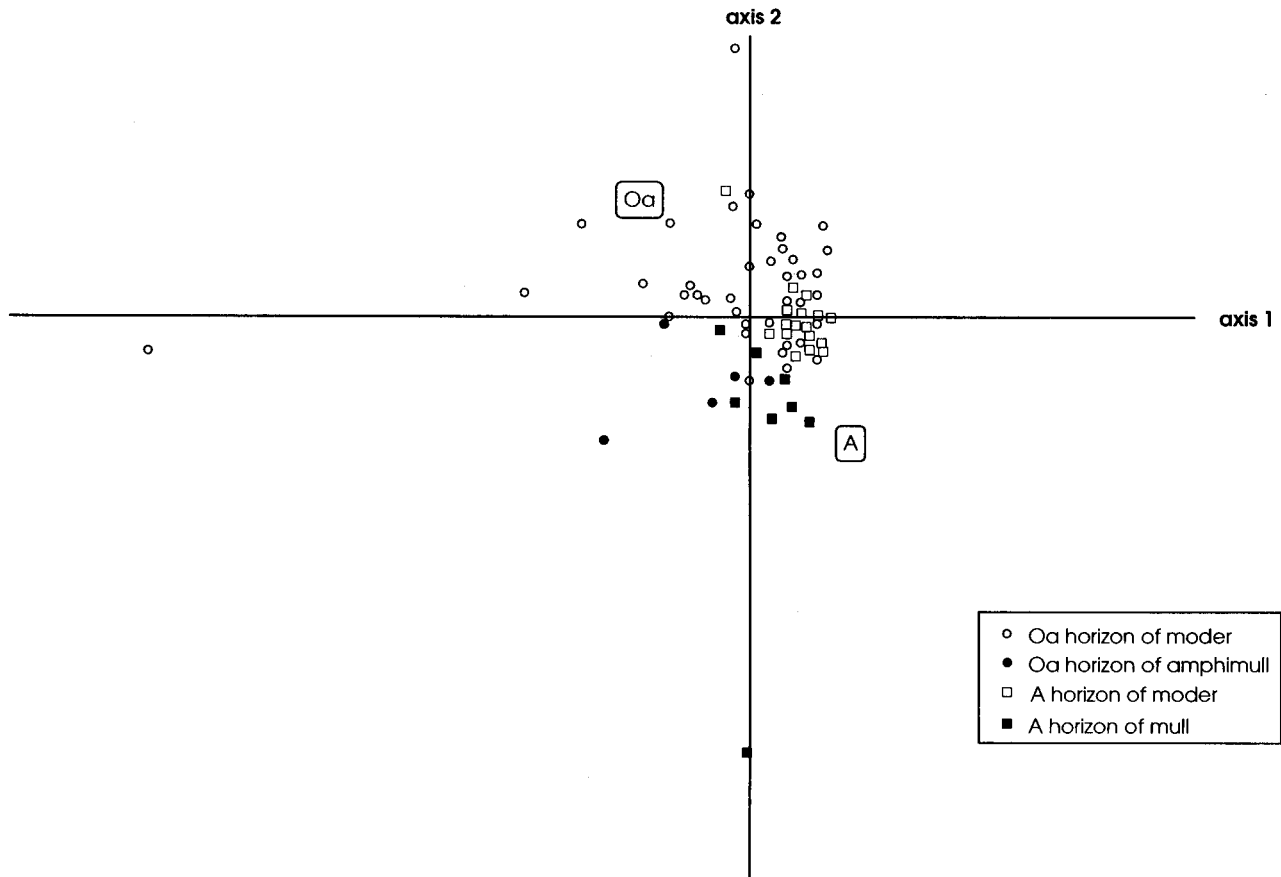


Fig. 2. Partial correspondence analysis on Oa and A horizons. Projection of horizons (rows) in the plane of Axes 1 and 2. Otherwise as for Fig. 1.

profile studied in Site 16), which was characterized by the development of the root system of hair-grass (*Deschampsia flexuosa* (L.) Trin.) at the inside of decaying plant fragments. This development was not apparent in other humus profiles because of scarcity of ground vegetation, and I preferred to discard the corresponding axis rather than to discard this horizon from the analysis.

The projection of horizons in the plane of Axes 1 and 3 (Fig. 1) indicated that they could be classified into three groups, corresponding to Oi, Oe, and Oa+A horizons, respectively. None of the horizons sampled fell exactly in each of the three branches depicted by the plane of Axes 1 and 3. This does not indicate that Oi, Oe, and Oa+A horizons were poorly differentiated on the basis of their composition. Rather, this phenomenon indicates that a few horizons had been badly classified in the field; correspondence analysis revealed that they had more points in common with another group than with their own group. Differences between Oa and A horizons were negligible when compared with differences between Oi and Oe horizons. Oa and A horizons did not exhibit distinct branches. In addition, differences

within each of the Oi, Oe, or Oa horizons were negligible compared with differences between these horizons.

The projection of categories in the plane of Axes 1 and 3 (Appendix 1) allowed us to characterize each horizon or group of horizons by its composition (Table 2). The Oi horizon was characterized by entire leaves of beech at varying stages of fungal conditioning and small recently fallen tree categories such as bud scales, male flowers, and twigs. Smears of fecal material, holorganic or organo-mineral, were observed at the surface of some beech leaves. A laminated mixing of leaf fragments and feces of litter-consuming enchytraeids, which I called "sandwich material", together with plant categories such as male flowers of beech, grass stems, twigs, at some stage of decomposition, was characteristic of the Oe horizon. The presence of beech petioles and nerves, mycelial strands and living bases of wood-rush [*Luzula forsterii* (Sm.) DC.] was also noticeable. Both Oa and A horizons were characterized by dead or senescent fine roots, living and dead woody roots, old (compacted) holorganic enchytraeid feces, and fragments of parent rock (both intact or weathered). Charcoal was also present in this group of horizons. Sclerotia of the

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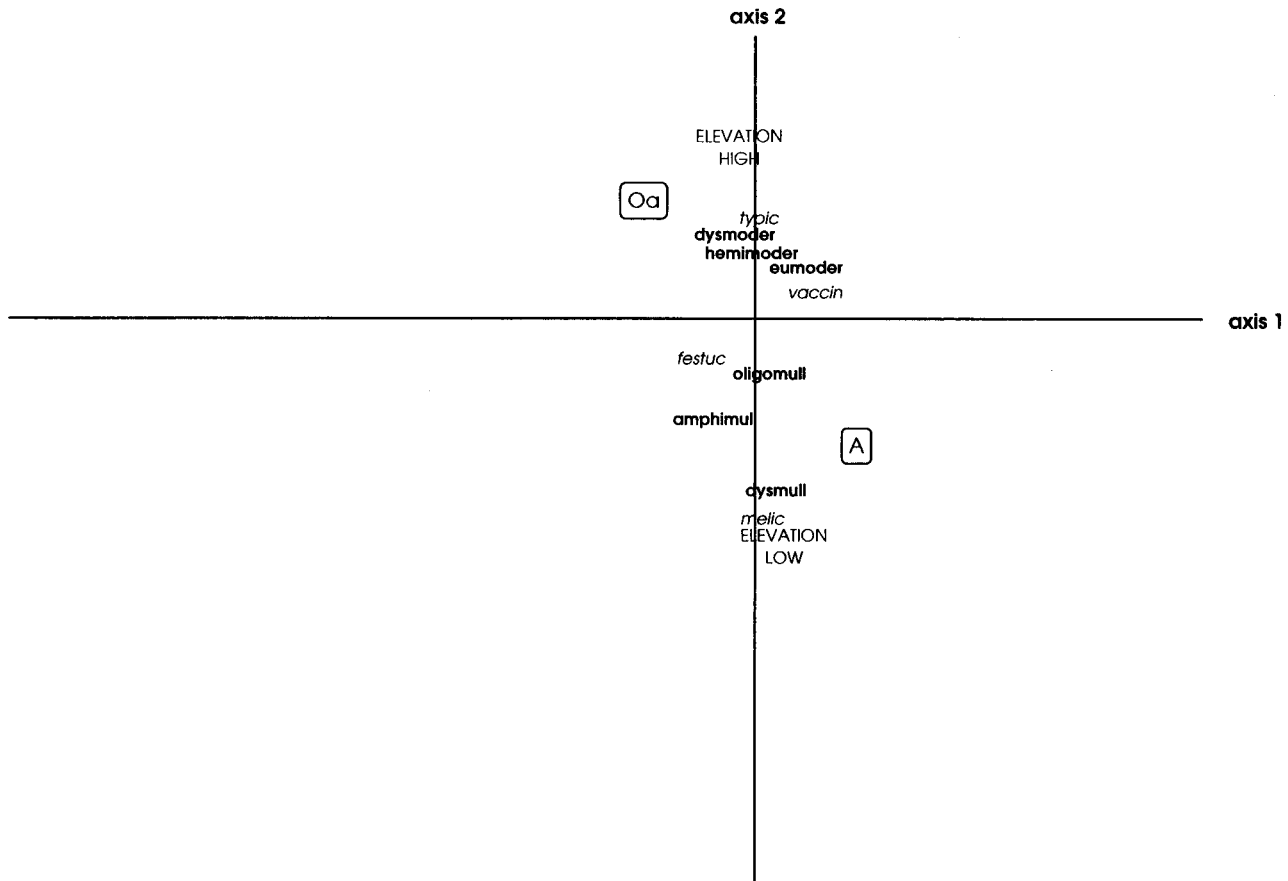


Fig. 3. Partial correspondence analysis on Oa and A horizons. Projection of passive variables in the plane of Axes 1 and 2. (*festuc* = *Luzulo-Fagetum festucetosum*; *melic* = *Melico-Fagetum festucetosum*; *typic* = *Luzulo-Fagetum typicum*; *vaccin* = *Luzulo-Fagetum vaccinietosum*).

mycorrhizal ascomycete *Cenococcum geophilum* Fr. also occurred.

Living fine roots of beech and feces of litter-consuming enchytraeids were placed in an intermediate position between the Oe horizon and the Oa+A horizons. This indicated that they were present in all of these horizons and, thus, they did not help in differentiating among horizons. Maple (*Acer pseudoplatanus* L.) and ash (*Fraxinus excelsior* L.) plant materials were different. These categories only occurred at one site (100) which was characterized by an intense earthworm activity, with abundant cast deposition within the Oi horizon (Fig. 1). The projection of corresponding samples was influenced by the presence of organo-mineral material (typical of the A horizon of mull humus) together with categories typical of the Oi horizon, which influenced in turn the position of the abovementioned ash and maple categories.

Oa and A horizons, which were considered as diagnostic horizons for the separation of mull versus moder humus forms (Delecour, 1983; Brêthes et al., 1995), were not clearly separable on the basis of composition as revealed by the use of a dissecting microscope. To reveal

possible variation in the composition of these horizons, I analyzed separately Oa and A horizons (partial analysis). The projection of horizons in the plane of Axes 1 and 2 (Fig. 2) separated Oa and A (classified by field observation), but with a high degree of overlapping. This indicated that the distinction between Oa and A horizons that had been made in the field (Oa = holorganic, A = organo-mineral) did not reflect true composition. The projection of some passive variables such as humus form, altitude and phytosociological type (Fig. 3) helped to establish a link between Axis 2 of partial analysis and ecological conditions prevailing in the studied sites. Mull humus forms were on the negative side of Axis 2; moder humus forms were placed on the positive side of Axis 2.

The composition of Oa and A horizons, as indicated by the projection of categories in the plane of Axes 1 and 2 of partial analysis (Appendix 2), depended on the humus form. The Oa horizon of moder humus forms (eumoder, hemimoder, and dysmoder) was mostly characterized by compacted holorganic feces of enchytraeids, different plant organs hard to decay, bundles of skeletonized beech leaf fragments, living woody roots

Table 3. Mean number of animals which were found during the dissection of humus horizons ($L \times l \times h = 5 \times 5 \times 1$ cm).

		Oi (n = 24)	Oe (n = 59)	Oa (n = 44)	A (n = 24)
ADB	Adult beetles	0.02	0	0.02	0
AD	Adult flies	0.01	0.02	0	0
ANT	Ants	0.01	0	0	0
BEE	Beetle larvae (miscellaneous)	0.14	0.3	0.09	0.04
BOO	Booklice	0.01	0.02	0	0
CEC	Cecidomyid fly larvae	0.27	0.32	0.22	0.17
CEN	Centipedes	0	0.06	0.09	0
CER	Ceratopogonid fly larvae	0.05	0.02	0	0
CHI	Chironomid fly larvae	0.25	0.3	0.64	0.25
CLI	Click-beetle larvae	0.06	0.03	0.19	0.04
COC	Cochineals	0.01	0.11	0	0
COP	Copepods	0.04	0.01	0	0
DIP	Diplura	0.14	0.21	0.15	0.08
DOL	Dolichopodid-empidid fly larvae	0.02	0.21	0.28	0.33
EAR	Earthworms	0.07	0.01	0.19	0
ENC	Enchytraeids	12	113	231	50
FLY	Fly larvae (miscellaneous)	0.02	0.11	0.06	0.04
MIL	Millipeds	0	0	0	0.04
MIT	Mites (miscellaneous)	10	19	10	2
ORI	Oribatid mites (miscellaneous)	10	20	14	2
PAU	Paupods	0.37	0.48	0.64	0.08
PHT	Phthiracarid oribatid mites	2	24	8	1
PLA	Platynothrus peltifer (oribatid mite)	6.9	4.9	3.5	0.5
PRO	Protura	0	0.01	0.2	0.17
PSE	Pseudoscorpions	0.06	0	0	0.04
SCI	Sciarid fly larvae	1.5	4.8	4.4	0.5
SLU	Slugs	0.07	0	0	0
SPI	Spiders	0.17	0.25	0.06	0
SPR	Springtails	14	64	52	17
SYM	Symphiles	0.1	0.17	0.34	0.13
THR	Thrips	0.02	0.02	0	0
TIP	Tipulid fly larvae	0.02	0.02	0	0
WOO	Woodlice	0.05	0.01	0	0

of beech, and dead black mycorrhizae of beech produced by *Cenococcum geophilum* Fr. . The upper part of the A horizon of mull humus forms (oligomull, amphyomull, dysmull) was mostly characterized by organo-mineral earthworm feces, milliped feces, intact stones, beech leaves skeletonized by macrofauna or mesofauna, and categories belonging to ground vegetation such as the root system of grass species or bleached leaves of wood-sorrel (*Oxalis acetosella* L.). The Oa horizon of amphyomull shared many features with the A horizon of the mull group (indicated by its position on the negative side of Axis 2). The A horizon of the moder group was placed in an intermediary position (not far from the origin, on both sides of Axis 2), thus without characteristic features distinguishing both the horizon and the humus form.

Distribution of Soil Animals

Animal groups found during the dissection of humus horizons (Table 3) were projected as passive variables in the plane of Axes 1 and 3 of total analysis (Fig. 4). Comparison with the position of horizons (Fig. 1) revealed that the Oi horizon was very poor in fauna at the time of sampling (June), no animal group being placed far from the origin in the direction of the Oi horizon (see also Table 3). The Oe horizon was characterized by mites other than *Platynothrus peltifer* (Koch) (MIT, ORI, PHT) and springtails (SPR), the latter being present at a greater depth than the former as ascertained

by the respective position of corresponding points along Axis 1. The only group that characterized the Oa+A horizons was enchytraeids (ENC). Enchytraeids mainly characterized the Oa horizon, as it appeared from the comparison of Oa and A horizons (Fig. 5, Table 3). Most fauna (here mostly mesofauna) were concentrated in the Oe and Oa horizons, the most abundant group being enchytraeids, followed at a far lower level of abundance by mites and springtails, with an increasing preference for deeper horizons at the time of sampling in the order mites < springtails < enchytraeids.

DISCUSSION AND CONCLUSION

The existence of a transitional horizon between typical Oa and A horizons, because of a progressive enrichment in mineral particles of the Oa horizon, has been suggested by Delecour (1980, 1983). He even considered it as a characteristic feature of the humus forms belonging to the moder group, rather than the accumulation of holorganic feces in Oe and Oa horizons which is commonly used to define moder humus (Klinka et al., 1981; Green et al., 1993, Duchaufour, 1997). This feature is also used in the classification of forest humus forms by Brêthes et al. (1995) where the A horizon of moder humus forms is considered to be made of holorganic feces juxtaposed to mineral particles, without true incorporation of organic matter to mineral matter. This composition can be achieved by the vertical movements of small animals carrying mineral particles onto their

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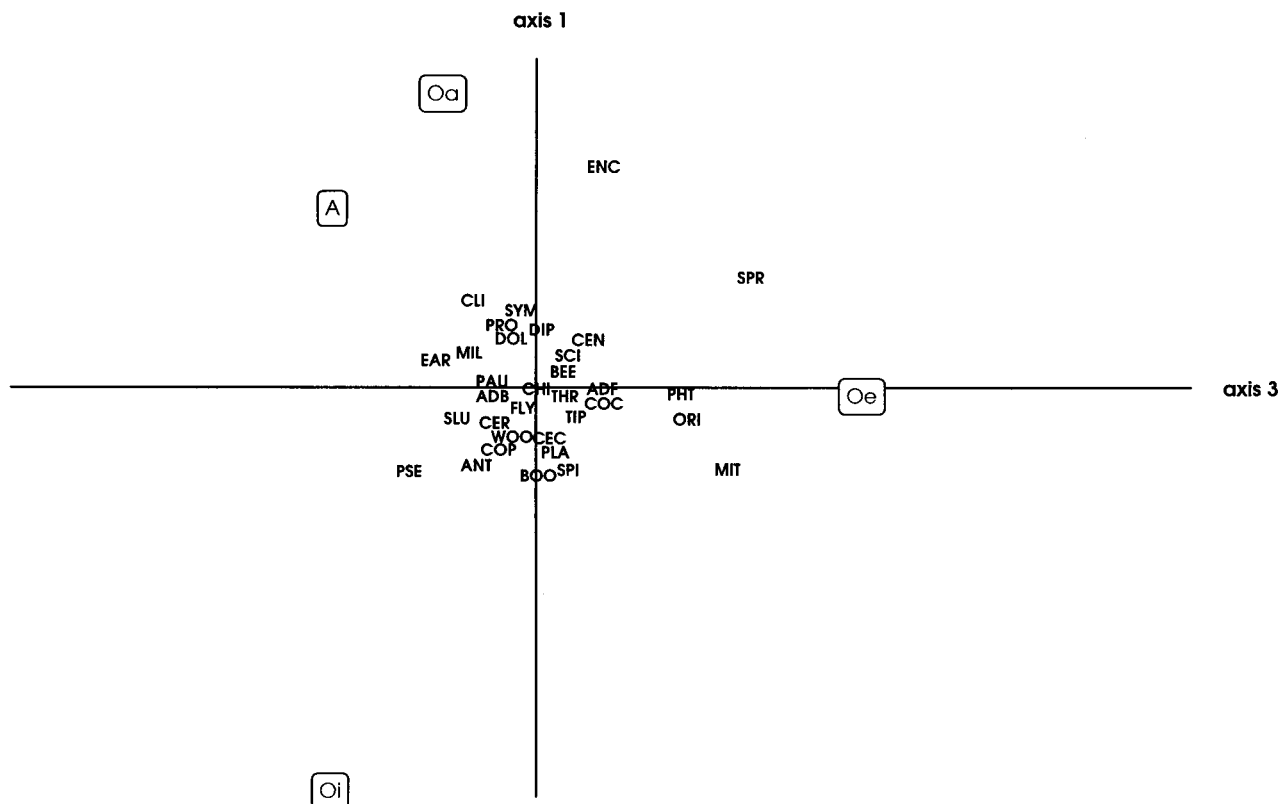


Fig. 4. Total correspondence analysis. Projection of animal groups (passive variables) in the plane of Axes 1 and 3. Coding of animal groups as in Table 3.

tegument and depositing them, together with feces, in the course of their wandering between food sources (Oe horizon) and refuges (Oa and A horizons). In moder humus forms, where no other agent mixes organic matter with mineral matter, this behavior is typical of animals with a sticky tegument such as enchytraeid worms (Ponge, 1991), whose daily vertical movements of several centimeters are well known (Springett et al., 1970). In this case, the gradual passage from the Oa to the A horizon can be interpreted as an active (biological) diffusion process, the source of organic matter being decaying litter, which is actively consumed by these animals and humified (Ponge, 1991), and the source of mineral matter being underlying mineral horizons. As has been observed in other studies (Zachariae, 1965; Ponge, 1991) enchytraeids also consume feces of other animals such as oribatid mites. As they live deeper (on average) than other litter-dwelling animals (Table 3), they progressively incorporate feces of litter-consuming animals into their own fecal material. This may explain why the Oa horizon of moder humus forms appears mainly made of compacted enchytraeid feces and unconsumed material rather than remains of the activity of all litter-feeding animals. They also ingest silt particles

(unpublished data), and carry them onto their tegument (Ponge, 1988). This pattern may lead to the observed soft transition from Oa to A horizons.

The presence of clear discontinuities between Oi and Oe horizons and between Oe and Oa+A horizon, and the absence of clear-cut subdivisions within them, may be explained by threshold levels in the vertical distribution of soil animals and other organisms. I cannot speculate from my data about the depth levels at which animals consume litter and defecate at any time of the year, and about all the factors which govern these patterns. Nevertheless, it can be inferred from existing literature that the vertical distribution of soil fauna is determined, among others, by (i) genetically fixed behavioral features (Stevenson and Dindal, 1982; Kretzschmar, 1984), (ii) ecophysiological requirements of animals (Atalla and Hobart, 1964; Haukka, 1987), and (iii) the stage of decomposition of litter (Hayes, 1963; Soma and Saitô, 1983; David, 1986). For instance, if I take into account only leaf litter as a food, the depth level at which animals will consume it can be interpreted as a compromise between the need for food of a high nutritional value such as freshly fallen litter (Soma and Saitô, 1983), the toxicity or repulsion of some compounds present in

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Horizons and humus forms in beech forests of the Belgian Ardennes

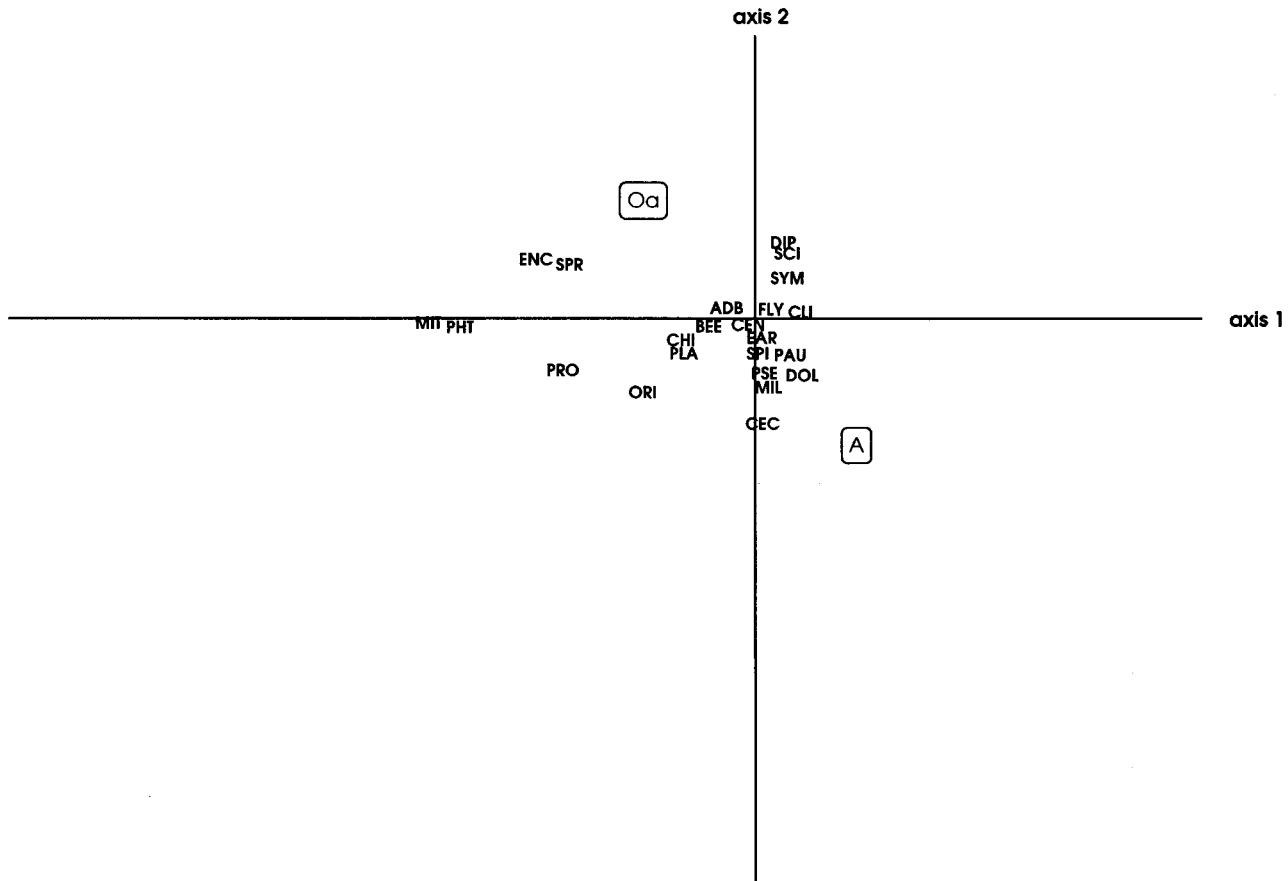


Fig. 5. Partial correspondence analysis on Oa and A horizons. Projection of animal groups (passive variables) in the plane of Axes 1 and 2. Otherwise as for Fig. 4.

undecayed litter (Satchell and Lowe, 1967), and the search for better micro-climate conditions (Joose, 1971). If we examine the diagnostic features of Oi and Oe horizons as ascertained in my analysis (Table 2), it appears that the passage from Oi to Oe horizon is characterized by the deposition of feces of small litter-consuming animals, such as oribatid mites and enchytraeids, these categories being near absent in the Oi horizon.

The passage from the Oe to the Oa+A horizon is marked by the appearance of the root system of beech (Table 2). This creates a new discontinuity along the humus profile. According to the humus form, the feeder root system of beech will develop throughout accumulated organo-mineral earthworm feces (A horizon of mull humus) or holorganic enchytraeid feces (Oa horizon of moder humus). This common feature is probably the main reason for the absence of a clear distinction between Oa and A horizons in the global analysis (Fig. 1). From existing literature, it can be concluded that the vertical distribution of root tips is strongly influenced by humus form horizons and the humus form itself (Meyer and Göttsche, 1971; Persson, 1983; Harvey et al., 1986; Ponge, 1988; Bernier and Ponge, 1994). These

results point out that the upper part of the Oa horizon together with the bottom of the Oe horizon is the main micro-site for mycorrhizal root development in moder humus forms, mull humus forms being characterized by a lower number of root tips which are widely distributed throughout the A horizon. Unfortunately, mechanisms which could explain these patterns are poorly understood, although the need for available water and nutrients has been advocated as a reason for the preferential development of feeder roots in carbon-rich substrates (Persson, 1983).

As this is now well admitted, the genesis of humus form horizons, and thus of humus forms, is placed under the influence of microflora, fauna, and plant subterranean parts, whose activity is determined by climate, parent rock, and quantity and quality of vegetation (Kubišna, 1955; Bal, 1982; Toutain, 1987; Green et al., 1993; Brêthes et al., 1995). The existence of horizons, not for the purpose of classification, but as a discernable entity, with clear emergent properties, can be understood if we take into account the accumulation through time of key categories with a high longevity. This is the case for dead leaves, enchytraeid feces, earthworm feces, or fine roots of trees. If a category present in a given horizon

Appendix 1. Categories used for the description of humus horizons. Coordinates on factorial axes 1 and 3 of total correspondence analysis.

Categories	Axis 1	Axis 3
Entire brown leaves of beech	-0.0280	-0.0142
Bundles of entire brown leaves of beech	-0.0114	-0.0058
Brown leaves of beech skeletonized by macrofauna	-0.0140	0.0020
Bundles of brown leaves of beech skeletonized by macrofauna	-0.0124	0.0011
Brown leaves of beech skeletonized by mesofauna	-0.0085	-0.0056
Bundles of brown leaves of beech skeletonized by mesofauna	-0.0065	-0.0035
Entire variegated leaves of beech	-0.0219	-0.0146
Bundles of entire variegated leaves of beech	-0.0146	-0.0078
Entire variegated leaves of beech skeletonized by macrofauna	-0.0050	-0.0013
Entire variegated leaves of beech skeletonized by mesofauna	-0.0077	0.0018
Bundles of variegated leaves of beech skeletonized by macrofauna	-0.0045	0.0030
Entire bleached leaves of beech	-0.0265	-0.0108
Bundles of entire bleached leaves of beech	-0.0143	-0.0066
Bleached leaves of beech skeletonized macrofauna	-0.0160	0.0090
Bundles of bleached leaves of beech skeletonized by macrofauna	-0.0131	0.0048
Bleached leaves of beech skeletonized by mesofauna	-0.0149	0.0028
Bundles of bleached leaves of beech skeletonized by mesofauna	-0.0106	-0.0083
Pits done by caterpillars in beech leaves	-0.0115	-0.0017
Nests done by foliage-consuming insects	-0.0085	-0.0073
Organo-mineral material smearing beech leaves	-0.0184	-0.0128
Holorganic faecal material smearing beech leaves	-0.0216	-0.0035
Intact petioles and nerves of beech	-0.0022	0.0027
Petioles and nerves of beech tunnelled by fauna	0.0001	0.0092
Petioles and nerves of beech filled with enchytraeid faeces	-0.0084	0.0045
Petioles and nerves of beech filled with faeces of <i>Adoristes ovatus</i> (oribatid mite)	-0.0045	0.0030
Petioles and nerves of beech filled with faeces of phthiracarid oribatid mites	-0.0025	0.0188
Petioles and nerves of beech filled with faeces of sciarid dipteran larvae	-0.0014	0.0091
Petioles and nerves of beech filled with grass roots	-0.0045	0.0030
Petioles and nerves of beech brown and tough	-0.0112	-0.0027
Petioles and nerves of beech bleached	-0.0018	0.0009
Sandwich material made of beech leaf fragments and holorganic enchytraeid faeces	0.0039	0.0250
Sandwich material made of beech leaf fragments and holorganic earthworm faeces	-0.0045	0.0034
Sandwich material made of beech leaf fragments and holorganic oribatid faeces	0.0033	0.0106
Sandwich material made of beech leaf fragments and organo-mineral earthworm faeces	-0.0003	0.0024
Sandwich material made of beech leaf fragments and organo-mineral enchytraeid faeces	0.0037	-0.0025
Sandwich material made of beech leaf fragments and holorganic sciarid faeces	0.0001	-0.0007
Skeletonized beech leaf fragments	0.0098	-0.0046
Bundles of skeletonized beech leaf fragments	0.0055	0.0060
Brown beech leaf fragments untouched by fauna	0.0141	-0.0019
Intact bud scales of beech	-0.0299	-0.0037
Bud scales of beech, entire but brown and soft	0.0008	0.0191
Strongly decayed bud scales of beech	0.0217	-0.0043
Intact male inflorescences of beech	-0.0232	-0.0120
Brown decaying male inflorescences of beech	-0.0057	0.0236
Pollen mass	-0.0022	0.0204
Intact seed coats of beech	0.0038	0.0175
Seed coats of beech tunnelled by phthiracarid mites	0.0006	0.0077
Seed coats of beech tunnelled by enchytraeids	0.0051	0.0037
Seed coats of beech tunnelled by sciarid larvae	-0.0009	0.0025
Seed coats of beech penetrated by roots	0.0028	0.0004
Intact fragments of beech burr	0.0098	0.0019
Soft fragments of beech burr	0.0099	0.0028
Soft fragments of beech burr tunnelled by oribatid mites	0.0025	0.0108
Soft fragments of beech burr tunnelled by enchytraeids	0.0068	0.0069
Soft fragments of beech burr tunnelled by sciarid larvae	0.0029	0.0069
Soft fragments of beech burr tunnelled by springtails	0.0012	0.0043
Soft fragments of beech burr penetrated by grass roots	0.0033	-0.0048
Beech cupules tunnelled by fauna	0.0006	-0.0024
Intact beech gallnuts	0.0051	0.0010
Intact twigs	-0.0225	-0.0033
Twigs decayed by white-rot	-0.0087	-0.0031
Twig fragments tunnelled by fauna	-0.0074	0.0106
Bark remnants of twigs	0.0079	0.0072
Twigs filled with enchytraeid holorganic faeces	0.0115	0.0205
Twigs filled with enchytraeid organo-mineral faeces	0.0102	-0.0024
Twigs filled with sciarid holorganic faeces	0.0015	0.0101
Twigs filled with oribatid holorganic faeces	0.0085	0.0138
Twigs penetrated by beech roots	0.0129	0.0009

Continued.

has a low longevity, i.e., if it is rapidly transformed into another category or if it disappears from the soil matrix through mineralization or leaching, then it cannot directly participate in the building of this horizon. Rather, it may (i) participate in the building of underlying horizons (for instance colloidal organic compounds precipi-

tating in B horizons), (ii) be taken up by organisms, or (iii) diffuse in the atmosphere or in the water flow. This is the case, among others, of oribatid feces which rapidly disappear from the moder profile when consumed by enchytraeids (Ponge, 1991). This is also the case for enchytraeid feces when ingested in turn by earthworms

Appendix 1. Continued.

Categories	Axis 1	Axis 3
Intact wood fragments	-0.0048	-0.0029
Decayed wood fragments	0.0016	-0.0093
Wood fragments tunnelled by fauna	0.0096	0.0036
Wood fragments penetrated by grass roots	-0.0045	0.0030
Wood fragments penetrated by beech fine roots	0.0025	-0.0063
Intact bark fragments	0.0072	-0.0060
Well-decayed bark fragments	0.0179	-0.0147
Bark fragments tunnelled by enchytraeids	-0.0018	0.0094
Bark fragments tunnelled by phthiracarid mites	0.0001	0.0075
Bark fragments tunnelled by sciarid larvae	-0.0022	0.0046
Bark fragments penetrated by grass roots	-0.0045	0.0030
Intact living fine long roots of beech	0.0231	0.0184
Living fine long roots of beech browsed by fauna	0.0123	-0.0061
Intact dead fine long roots of beech	0.0238	-0.0178
Dead fine long roots of beech tunnelled by fauna	0.0145	-0.0119
Dead fine long roots of beech penetrated by grass roots	0.0031	-0.0069
Dead fine long roots of beech, voided	0.0046	-0.0075
Living woody roots of beech	0.0237	-0.0031
Living woody roots of beech browsed by fauna	0.0069	-0.0058
Decaying woody roots of beech	0.0160	-0.0133
Living pale yellow creamy mycorrhizae of beech	0.0221	0.0136
Pale yellow creamy mycorrhizae of beech browsed by fauna	0.0181	0.0003
Dead pale yellow mycorrhizae of beech	0.0260	-0.0139
Living orange brown mycorrhizae of beech with woolly mycelium	0.0106	0.0078
Orange brown mycorrhizae of beech with woolly mycelium browsed by fauna	0.0016	0.0018
Dead orange brown mycorrhizae of beech with woolly mycelium	0.0128	-0.0068
Living black mycorrhizae of beech (produced by <i>Cenococcum geophilum</i>)	0.0181	0.0104
Living black mycorrhizae of beech browsed by fauna	0.0019	0.0043
Dead black mycorrhizae of beech	0.0141	-0.0087
Living yellow mycorrhizae of beech with woolly mycelium	0.0028	0.0074
Living shoots of <i>Polytrichum formosum</i>	-0.0067	0.0087
Fragments of stems of <i>Polytrichum formosum</i> , red and tough	0.0032	0.0044
Fragments of stems of <i>Polytrichum formosum</i> , voided	0.0051	0.0095
Dead stem bases of <i>Polytrichum formosum</i>	0.0024	-0.0001
Decaying stem bases of <i>Polytrichum formosum</i>	0.0047	-0.0024
Living shoots of <i>Scleropodium purum</i>	-0.0073	0.0111
Dead shoots of <i>Scleropodium purum</i>	0.0042	0.0043
Living shoots of <i>Leucobryum glaucum</i>	-0.0064	-0.0054
Dead shoots of <i>Leucobryum glaucum</i>	0.0003	-0.0012
Dead moss, undetermined	-0.0057	-0.0035
Intact leaves of <i>Luzula forsteri</i>	-0.0060	-0.0057
Bleached leaves of <i>Luzula forsteri</i>	-0.0034	-0.0070
Living leaf bases of <i>Luzula forsteri</i>	0.0000	0.0136
Decaying leaf bases of <i>Luzula forsteri</i>	0.0047	-0.0024
Intact leaves of <i>Deschampsia flexuosa</i>	-0.0074	-0.0030
Decaying leaves of <i>Deschampsia flexuosa</i>	-0.0135	0.0017
Living leaf bases of <i>Deschampsia flexuosa</i>	-0.0037	-0.0003
Decaying leaf bases of <i>Deschampsia flexuosa</i>	0.0120	-0.0012
Intact inflorescences of <i>Deschampsia flexuosa</i>	-0.0058	-0.0045
Decaying inflorescences of <i>Deschampsia flexuosa</i>	-0.0098	-0.0003
Living grass roots	0.0090	-0.0022
Decaying grass roots	0.0144	-0.0083
Intact grass stems	0.0008	-0.0136
Fragments of grass stems browsed by fauna	-0.0022	0.0204
Fragments of decaying grass roots	-0.0062	-0.0026
Intact leaves of <i>Vaccinium myrtillus</i>	-0.0075	-0.0063
Skeletonized leaves of <i>Vaccinium myrtillus</i>	-0.0101	-0.0034
Roots of <i>Vaccinium myrtillus</i>	0.0053	0.0013
Living rhizomes of <i>Vaccinium myrtillus</i>	0.0016	0.0018
Decaying rhizomes of <i>Vaccinium myrtillus</i>	0.0072	-0.0001
Bleached leaves of <i>oxalis acetosella</i>	0.0013	-0.0039
Brown entire leaves of <i>Acer pseudoplatanus</i>	-0.0051	-0.0198
Brown leaves of <i>Acer pseudoplatanus</i> skeletonized by macrofauna	-0.0051	-0.0198
Bleached leaves of <i>Acer pseudoplatanus</i>	-0.0053	-0.0192
Bleached leaves of <i>Acer pseudoplatanus</i> skeletonized by macrofauna	-0.0051	-0.0198
Leaves of <i>Acer pseudoplatanus</i> skeletonized by mesofauna	-0.0018	-0.0002

Continued.

living in mull humus (Bal, 1982). The passage from one horizon to another should thus be considered as a check in a continuous process (the slow maturation of individual categories in the absence of disturbances), and a start for another continuous process of maturation. The fact that at a given depth level the bulk of categories

of a given type are transformed into categories of another type (because of to the activity of vertically distributed organisms) will create discontinuities visible to the naked eye and thus will help us to distinguish horizons and humus forms on the field. In the absence of these discontinuities (as between Oa and A horizons of moder

Appendix 1. Continued.

Categories	Axis 1	Axis 3
Winged seed of <i>Acer pseudoplatanus</i> with intact wing	0.0001	-0.0007
Winged seed of <i>Acer pseudoplatanus</i> with skeletonized wing	-0.0062	0.0030
Wingless seed of <i>Acer pseudoplatanus</i>	-0.0012	0.0051
Winged seed of <i>Fraxinus excelsior</i> with intact wing	-0.0053	-0.0192
Brown entire leaves of <i>Quercus petraea</i>	-0.0076	-0.0067
Leaves of <i>Quercus petraea</i> skeletonized by mesofauna	-0.0049	-0.0013
Intact unidentified fragments of seed wings	-0.0050	0.0176
Skeletonized unidentified fragments of seed wings	-0.0027	0.0036
Brown entire needles of <i>Picea abies</i>	-0.0010	-0.0002
Bleached entire needles of <i>Picea abies</i>	-0.0108	-0.0034
Needles of <i>Picea abies</i> browsed by fauna	-0.0002	0.0086
Seed wings of <i>Picea abies</i>	-0.0053	-0.0032
Brown rhizomorphs	-0.0047	0.0075
White rhizomorphs	-0.0023	0.0130
Yellow rhizomorphs	0.0028	0.0074
Dead rhizomorphs of <i>Armillaria</i>	0.0100	-0.0074
Dead rhizomorphs of <i>Armillaria</i> tunnelled by fauna	0.0100	-0.0074
Sclerotia of <i>Cenococcum geophilum</i>	0.0245	-0.0136
Lichens	-0.0090	-0.0053
Intact caterpillar faeces	-0.0137	0.0099
Caterpillar faeces tunnelled by phthiracarid mites	0.0056	0.0078
Intact slug faeces	-0.0142	-0.0045
Slug faeces tunnelled by enchytraeids	-0.0089	-0.0049
Slug faeces tunnelled by sciarid larvae	-0.0089	-0.0049
Intact holorganic earthworm faeces	-0.0124	0.0118
Holorganic earthworm faeces tunnelled by enchytraeids	0.0007	0.0057
Unidentified holorganic faeces	-0.0056	-0.0037
Intact organo-mineral earthworm faeces	-0.0025	0.0036
Compacted organo-mineral earthworm faeces	0.0088	-0.0016
Organo-mineral earthworm faeces tunnelled by enchytraeids	0.0042	0.0034
Holorganic woodlice faeces	-0.0120	0.0033
Holorganic milliped faeces	0.0048	0.0049
Holorganic milliped faeces tunnelled by enchytraeids	0.0036	0.0010
Holorganic milliped faeces tunnelled by phthiracarid mites	0.0036	0.0010
Holorganic crane-fly faeces	0.0004	0.0048
Intact holorganic sciarid faeces	-0.0044	-0.0007
Compacted holorganic sciarid faeces	0.0074	-0.0069
Intact holorganic enchytraeid faeces	0.0141	0.0081
Compacted holorganic enchytraeid faeces	0.0219	-0.0120
Organo-mineral enchytraeid faeces	0.0078	-0.0044
Compacted organo-mineral enchytraeid faeces	0.0070	-0.0117
Compacted organo-dominant organo-mineral material	0.0066	-0.0064
Compacted organo-mineral material	0.0114	-0.0120
Compacted mineral-dominant organo-mineral material	0.0040	-0.0085
Unidentified mineral assemblages	-0.0016	-0.0011
Charcoal	0.0132	-0.0153
Snail shells	-0.0028	0.0098
Woodlice shells	-0.0022	0.0204
Intact stones	0.0161	-0.0103
Weathering stones	0.0147	-0.0128
Weathering stones impregnated with organic matter	0.0048	-0.0096

humus forms), this distinction may be more difficult and field observation may lead to false conclusions, as has been always suggested by Bernier et al. (1993). In this case the identification of horizon components under a dissecting microscope and the use of counting methods (Bernier et al., 1993; Bernier and Ponge, 1994) may help a better characterization of these horizons.

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Appendix 2. Categories used for the description of humus horizons. Coordinates on factorial axes 1 and 2 of partial correspondence analysis (OH and A).

Categories	Axis 1	Axis 2
Brown leaves of beech skeletonized by macrofauna	-0.0002	-0.0319
Bleached leaves of beech skeletonized by macrofauna	-0.0002	-0.0319
Bleached leaves of beech skeletonized by mesofauna	-0.0002	-0.0319
intact petioles and nerves of beech	-0.0130	-0.0013
Petioles and nerves of beech tunnelled by fauna	-0.0100	0.0135
Petioles and nerves of beech filled with enchytraeid faeces	-0.0051	0.0069
Petioles and nerves of beech filled with faeces of phthiracarid oribatid mites	-0.0094	-0.0090
Sandwich material made of beech leaf fragments and holorganic enchytraeid faeces	-0.0343	0.0089
Sandwich material made of beech leaf fragments and holorganic earthworm faeces	-0.0054	-0.0001
Sandwich material made of beech leaf fragments and holorganic oribatid faeces	-0.0383	-0.0025
Sandwich material made of beech leaf fragments and organo-mineral earthworm faeces	-0.0031	-0.0038
Sandwich material made of beech leaf fragments and organo-mineral enchytraeid faeces	-0.0002	-0.0008
Skeletonized beech leaf fragments	0.0047	0.0114
Bundles of skeletonized beech leaf fragments	0.0002	0.0201
Brown beech leaf fragments untouched by fauna	0.0051	-0.0081
Intact bud scales of beech	-0.0214	-0.0201
Bud scales of beech, entire but brown and soft	-0.0292	-0.0056
Strongly decayed bud scales of beech	0.0016	0.0205
Brown decaying male inflorescences of beech	-0.0246	0.0038
Intact seed coats of beech	-0.0105	0.0065
Seed coats of beech tunnelled by phthiracarid mites	0.0020	0.0054
Seed coats of beech tunnelled by enchytraeids	-0.0015	0.0051
Intact fragments of beech burr	-0.0152	-0.0048
Soft fragments of beech burr	0.0041	0.0022
Soft fragments of beech burr tunnelled by oribatid mites	-0.0106	0.0136
Soft fragments of beech burr tunnelled by enchytraeids	0.0012	0.0197
Beech cupules tunnelled by fauna	0.0051	0.0050
Twigs decayed by white-rot	0.0000	-0.0066
Twig fragments tunnelled by fauna	-0.0013	0.0229
Bark remnants of twigs	0.0008	-0.0122
Twigs filled with enchytraeid holorganic faeces	-0.0119	0.0159
Twigs filled with enchytraeid organo-mineral faeces	-0.0289	-0.0002
Twigs filled with sciarid holorganic faeces	0.0002	0.0068
Twigs filled with oribatid holorganic faeces	-0.0287	0.0078
Twigs penetrated by beech roots	-0.0294	0.0045
Decayed wood fragments	0.0010	-0.0055
Wood fragments tunnelled by fauna	-0.0168	-0.0104
Wood fragments penetrated by beech fine roots	0.0024	-0.0066
Intact bark fragments	-0.0140	0.0038
Well-decayed bark fragments	0.0091	0.0086
Bark fragments tunnelled by enchytraeids	-0.0090	0.0079
Bark fragments tunnelled by phthiracarid mites	-0.0022	-0.0101
Intact living fine long roots of beech	-0.0212	-0.0033
Living fine long roots of beech browsed by fauna	-0.0021	0.0103
Intact dead fine long roots of beech	0.0061	-0.0014
Dead fine long roots of beech tunnelled by fauna	0.0045	0.0073
Dead fine long roots of beech penetrated by grass roots	0.0049	-0.0025
Dead fine long roots of beech, voided	0.0047	-0.0033
Living woody roots of beech	0.0028	0.0182
Living woody roots of beech browsed by fauna	0.0040	0.0103
Decaying woody roots of beech	0.0113	0.0113
Living pale yellow creamy mycorrhizae of beech	-0.0172	-0.0035
Pale yellow creamy mycorrhizae of beech browsed by fauna	-0.0016	0.0125
Dead pale yellow creamy mycorrhizae of beech	0.0040	0.0047
Living orange brown mycorrhizae of beech with woolly mycelium	-0.0052	0.0069
Dead orange brown mycorrhizae of beech with woolly mycelium	0.0058	0.0065
Living black mycorrhizae of beech (produced by <i>Cenococcum geophilum</i>)	-0.0079	0.0027
Dead black mycorrhizae of beech	0.0057	0.0152
Living shoots of <i>Polytrichum formosum</i>	-0.0054	-0.0088
Fragments of stems of <i>Polytrichum formosum</i> , voided	0.0010	-0.0105
Dead stem bases of <i>Polytrichum formosum</i>	0.0037	-0.0076
Dead shoots of <i>Leucobryum glaucum</i>	-0.0012	-0.0043
Bleached leaves of <i>Luzula forsteri</i>	-0.0012	-0.0063
Living leaf bases of <i>Luzula forsteri</i>	0.0045	-0.0002

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Appendix 2. Continued.

Categories	Axis 1	Axis 2
Decaying leaf bases of <i>Luzula forsteri</i>	0.0037	-0.0076
Decaying leaves of <i>Deschampsia flexuosa</i>	-0.0268	0.0051
Living leaf bases of <i>Deschampsia flexuosa</i>	0.0045	-0.0002
Decaying leaf bases of <i>Deschampsia flexuosa</i>	0.0066	0.0079
Living grass roots	0.0065	-0.0133
Decaying grass roots	0.0085	-0.0002
Intact grass stems	0.0026	-0.0070
Roots of <i>Vaccinium myrtillus</i>	-0.0053	0.0095
Decaying rhizomes of <i>Vaccinium myrtillus</i>	-0.0014	0.0092
Bleached leaves of <i>oxalis acetosella</i>	-0.0002	-0.0319
Brown entire needles of <i>Picea abies</i>	-0.0145	0.0016
Brown rhizomorphs	0.0010	-0.0071
White rhizomorphs	-0.0140	0.0071
Dead rhizomorphs of <i>Armillaria</i>	-0.0012	0.0015
Dead rhizomorphs of <i>Armillaria</i> tunnelled by fauna	-0.0012	0.0015
Sclerotia of <i>Cenococcum geophilum</i>	0.0012	0.0035
Intact caterpillar faeces	-0.0006	0.0123
Intact holorganic earthworm faeces	0.0018	-0.0039
Holorganic earthworm faeces tunnelled by enchytraeids	-0.0383	-0.0025
Intact organo-mineral earthworm faeces	0.0031	-0.0265
Compacted organo-mineral earthworm faeces	-0.0040	-0.0140
Organo-mineral earthworm faeces tunnelled by enchytraeids	0.0009	-0.0076
Holorganic milliped faeces	-0.0017	-0.0222
Holorganic milliped faeces tunnelled by enchytraeids	-0.0383	-0.0025
Holorganic milliped faeces tunnelled by phthiracarid mites	-0.0383	-0.0025
Holorganic crane-fly faeces	-0.0020	-0.0009
Compacted holorganic sciarid faeces	0.0059	0.0109
Intact holorganic enchytraeid faeces	-0.0083	0.0060
Compacted holorganic enchytraeid faeces	0.0109	0.0235
Organo-mineral enchytraeid faeces	-0.0068	0.0034
Compacted organo-mineral enchytraeid faeces	0.0103	-0.0041
Compacted organo-dominant organo-mineral material	0.0034	-0.0035
Compacted organo-mineral material	0.0070	-0.0078
Compacted mineral-dominant organo-mineral material	0.0048	-0.0048
Unidentified mineral assemblages	0.0051	0.0050
Charcoal	0.0063	-0.0200
Intact stones	0.0036	-0.0269
Weathering stones	0.0092	-0.0065
Weathering stones impregnated with organic matter	0.0077	-0.0002

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Phosphorus Pools in Tree and Intercanopy Microsites of a Juniper-Grass Ecosystem

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ABSTRACT

Gradients of soil-nutrient distribution between trees and intercanopy areas are common in many semiarid woodland ecosystems. To test if microsites under and between canopies influenced P pool distribution in a semiarid woodland dominated by one-seed juniper [*Juniperus monosperma* (Engelm.) Sarg.] and galleta grass [*Hilaria jamesii* (Torr.) Benth.], we compared inorganic, organic, and microbial P pools under trees and intercanopy areas of two Aridisols. Soils collected (5–15 cm depth) under eight tree canopies and in eight intercanopy areas from a Calciorthid and a Camborthid were subjected to a sequential P fractionation scheme. Soils and microsites were significant independent factors determining total soil P, which ranged from 814 $\mu\text{g P g}^{-1}$ soil (SE = 25) to 1123 $\mu\text{g P g}^{-1}$ soil (SE = 21). Resin P was significantly influenced by the interaction of soils with microsite. Organic hydroxide P was the largest organic P fraction and exceeded or equaled the amount of resin P. It differed significantly between the Calciorthid at 10.1 $\mu\text{g P g}^{-1}$ soil (SE = 1.0) and the Camborthid at 22.1 $\mu\text{g P g}^{-1}$ soil (SE = 1.6). Microsite and soil did not significantly affect microbial P, which ranged from 12.9 $\mu\text{g P g}^{-1}$ soil (SE = 2.1) to 17.0 $\mu\text{g P g}^{-1}$ soil (SE = 0.7). Nutrients and microbial activity are usually concentrated under canopies in semiarid and arid ecosystems. This research shows that P pools distribution in the studied ecosystem did not follow this general pattern, and that soils may be more important in determining P pool distribution than microsites.

PINYON-JUNIPER woodlands are a major vegetation type, occupying $\approx 325,000$ km² of the western USA (West, 1984). Despite their large extent, they are poorly characterized with regard to ecosystem function and nutrient-cycling processes. Different physical, chemical, and biological properties of tree and intercanopy microsites suggest that microsites function as distinct ecological units within the overall woodland ecosystem (Barth, 1980; Fresquez, 1990; Breshears et al., 1997). Distinct gradients of soil-nutrient distribution between trees and intercanopy areas are common in semiarid woodland ecosystems and are recognized as an important structural and functional feature in nutrient-cycling dynamics (Schlesinger et al., 1990; Schlesinger and Pilmanis, 1998). Pinyon-juniper woodlands appear to share these horizontal gradients (Barth, 1980; Padien and Lajtha, 1992); however, little information is available on the distribution and dynamics of belowground elements in soils and microsites.

Phosphorus is of particular interest in pinyon-juniper

ecosystem-nutrient dynamics because low levels of available soil P (Barth, 1980; Bunderson et al., 1985; Schlesinger et al., 1989) and a high proportion of mycorrhizal plant species (Klopatek and Klopatek, 1987) indicate that P may be a limiting element in these woodlands. It has been suggested that P could be more limiting to plant growth than N in pinyon-juniper ecosystems (Bunderson et al., 1985).

Phosphorus supply and cycling rate act as a fundamental control on C, N, and S dynamics, and P availability limits overall productivity in many natural ecosystems (Vitousek and Howarth, 1991; Chapin et al., 1994). Plants take up inorganic P (P_i) from the soil solution. Solution P makes up only a minimal fraction of total soil P. It is rapidly replenished by P from labile inorganic P minerals and by biochemical mineralization of labile organic P (P_o). Labile P_i and P_o are in exchange with slowly reacting inorganic P minerals, occluded P, and stable organic P (Chauhan et al., 1981; Smeck, 1985; Steward and Tiessen, 1987). The amount of P available to plants is determined by the pool size of labile P_i , the transformation rates between labile and slowly reacting P_i , and the amount and cycling rate of mineralizable P_o (Tiessen, 1991).

We hypothesized that labile, microbial, and total P would be higher under trees than in intercanopy areas because soil nutrients and microbial activity are usually more concentrated under canopies of shrubs and trees in semiarid and arid ecosystems (Barth, 1980; Schlesinger et al., 1996; Schlesinger and Pilmanis, 1998). We used the Hedley et al. (1982) fractionation to measure soil P pools in juniper and intercanopy microsites in two Aridisols in a juniper-grass ecosystem of the Colorado Plateau. The specific objectives were to test if these microsites and soils influenced the distribution of belowground P pools, and to determine the size of labile and moderately labile P_i and P_o , and microbial P pools in this ecosystem, which is slightly more arid than pinyon-juniper woodlands.

MATERIALS AND METHODS

Sites

We collected soils from two 0.45-ha sites in a one-seed juniper/galleta-dominated woodland of the Colorado Plateau in northern Arizona (35°33' N, 111°28' W). The sites were located about 45 km northeast of Flagstaff at Wupatki National Monument at an elevation of 1650 m. The climate at Wupatki National Monument is semiarid with 46% of the total annual precipitation occurring during thunderstorms in

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