

Changes in the composition of humus profiles near the trunk base of an oak tree [*Quercus petraea* (Mattus.) Liebl.]

Anne Deschaseaux, Jean-François Ponge*

Museum National d'Histoire Naturelle, Laboratoire d'Écologie Générale, 4 avenue du Petit-Château, 91800 Brunoy, France

*Corresponding author (fax: +33 1 60465009, e-mail: jean-francois.ponge@wanadoo.fr)

Running title: HUMUS PROFILES NEAR THE TRUNK BASE

Abstract

Humus profiles were sampled under the crown of a mature oak tree in a coppice with standards (Senart forest, 30 km south of Paris). The sampling design compared the composition of humus profiles at three distances of the trunk base (40, 140 and 240 cm) and in the four cardinal directions. An increase in the development of the OF layer (strongly decayed litter and faeces of epigeic fauna) was observed at 40 cm from the trunk base, paralleling an increase in soil titratable acidity. Since no significant change in litter composition occurred with distance to the trunk base and in the absence of stemflow reaching the ground during showers, diffusion of bark tannins from buried parts of the trunk and main lateral roots was suspected to negatively influence soil biological activity, particularly earthworm activity.

Keywords: Humus profiles / litter decomposition / soil biological activity / trunk base

Modification de la composition des profils d'humus à proximité de la base d'un tronc de chêne [*Quercus petraea* (Mattus.) Liebl.]

Des profils d'humus ont été échantillonnés sous la couronne d'un chêne adulte dans un taillis-sous-futaie (forêt de Sénart, 30 km au sud de Paris). Le plan d'échantillonnage a permis de comparer la composition des profils d'humus à trois distances de la base du tronc (40, 140 et 240 cm) et selon les quatre points cardinaux. Un accroissement du développement de l'horizon OF (litière fortement décomposée et déjections de la faune épigée) a été observé à la distance la plus courte de la base du tronc, en parallèle avec une augmentation de l'acidité titrable. Étant donné qu'aucun changement notable ne se produit dans la composition de la litière en fonction de la distance au tronc et en l'absence d'égoulement le long du tronc atteignant le sol lors des averses, la diffusion des tannins de l'écorce à partir des parties enterrées du tronc et des racines latérales principales est supposée influencer négativement l'activité biologique du sol, en particulier l'activité des vers de terre.

Mots-clés: profils d'humus / décomposition de la litière / activité biologique du sol / base du

tronc

1. INTRODUCTION

Soil acidification and litter accumulation in the vicinity of tree trunk bases have been recorded frequently since the pioneer work of Zinke [50]. Unfortunately, some controversy still exists about the possible causes of this widely observed phenomenon. Stemflow, i.e. water running down along branches and stem, has been often considered to explain acidification of the stemflow area under beech [17, 18, 19, 15, 8, 16], more especially in polluted countries [49, 48, 24, 21, 43]. Changes in litter quantity and quality under the canopy of trees have been also evoked, more especially the role of bark deposition [50, 26, 19]. Compared to Beech, Sessile Oak [*Quercus petraea* (Mattus.) Liebl.] produces little stemflow, less than 1% of incident rain near Paris [28], a little more (1.8%) in more rainy countries [13], compared to 13% under beech [24]. In a previous study in the Senart forest (30 km south of Paris), the acidification of the soil near the trunk base of sessile oak was repeatedly shown to occur in the absence of measurable stemflow [1].

Biological consequences of soil acidification near tree trunk bases can be studied by recording changes in plant, animal and microbial communities [9, 27, 14, 49, 48, 24, 15, 21, 23, 43] or biological processes [8, 22]. An alternative method is the analysis of biological traits by morphological assessment, using structural components of humus profiles (plant debris, animal faeces, roots, mineral particles) and the succession of horizons created by their accumulation as parameters describing the activity of soil organisms. A morphological method using the observation of small volumes of litter and soil has been devised, allowing qualitative [31, 32, 33, 34, 35, 36], thereafter quantitative analysis [7, 6, 3, 4] of the transformation of organic and mineral matter by fauna and microbes and the development of the root system, i.e. the development of humus profiles [37]. A multivariate method has been applied to such data, allowing a synthetic view of a population of humus profiles [38, 30].

The same micormorphological methods have been applied to a composite sample taken under the canopy of a single oak tree, belonging to the population already studied by Beniamino *et al.* [1]. Our aim was to detect possible changes in litter composition and soil biological activity which could explain or could be ascribed to the acidification pattern described by these authors.

2. MATERIAL AND METHODS

The study site was a coppice with standards located in the South-West part of the Senart forest (30 km South of Paris). Standards were mature sessile oak individuals 100 to 200 years-old, the height of which ranged from 20 to 30m. Coppice was composed of Hornbeam (*Carpinus betulus* L.) or Lime (*Tilia cordata* Mill.) according to site conditions. Soils were luvisols according to FAO-UNESCO classification [45]. They had a loam to clay-loam texture, with silica stones of glacifluvial origin [12].

The selected tree was a sessile oak individual, which was tree number 24 in Beniamino *et al.* [1]. Under the canopy of this tree the mean particle size distribution of the <2mm fraction was 25% clay, 39% silt and 36% sand. At the time of sampling (September 1995) the ground vegetation was of Bramble (*Rubus fruticosus* L.), Ivy (*Hedera helix* L.), Solomon's Seal [*Polygonatum multiflorum* (L.) All.], Archangel [*Lamiastrum galeobdolon* (L.) Ehrend. & Polateschek], Hair-grass [*Avenella flexuosa* (L.) Trin.] and seedlings of Sessile Oak, Sycamore (*Acer pseudoplatanus* L.) and Chestnut (*Castanea sativa* Mill.). The coppice was of Lime only. Humus form was of the mull type, with a prominent earthworm activity.

Measurement of soil acidity and litter accumulation had been done two years previously by Beniamino *et al.* [1]. Humus profiles were sampled at the same places, i.e. at three distances of the trunk base (40, 140 and 240cm) and according to the four cardinal directions (N, W, S, E), thus a total of 12 plots was sampled.

At each plot a humus block 5x5x5cm was carefully excavated according to the method devised by Ponge [31]. Layers (0.5 to 2cm thick) were separated according to changes in their composition which were visible to the naked eye, and were classified into OL, OF or A horizons

[11]. They were preserved in ethanol then transported to the laboratory for further study. Fortyeight samples were thus collected. At the time of humus component analysis each layer was gently spread into a Petri dish filled with ethanol, then a 400 points grid was positioned over the studied material. This method, devised by Bernier & Ponge [5], allows measurement of the volume percentage of matrix components, visible at the x40 magnification of a dissecting microscope. The precision was given by the number of counting points, here 0.25%. Sixty-nine categories were identified (Table 1).

Data (percentage of occurrence of a given category in a given sample) were subjected to correspondence analysis, a multivariate method using the chi-square distance [20]. This method was improved according to Ponge & Delhaye [40], i.e. the different variables were standardized by equalling their mean to 20 and their standard deviation to 1. Thus coordinates along factorial axes (first eigen vectors) are proportional to their contribution to the axes. The farther a point is from the origin of an axis, the more it contributes to this axis. The different categories were the active variables. The nature of the corresponding horizon (OL, OF, A), the distance to the trunk base, the orientation and the depth at which the sample was taken were put as passive variables, i.e. they were projected on the factorial axes as if they had been involved in the analysis, without contributing to the axes. This allowed significant trends according to the influence of the distance to the tree trunk, the orientation or the depth level to be discerned by the analysis.

Further analyses were done by pooling categories and averaging percentages of occurrence of bulk categories over different depth classes. This allowed use of analysis of variance, after checking homoscedasticity of the data and gaussian distribution of the residuals, by crossing the distance to the trunk base with the orientation in a 2-way ANOVA without replication [44], followed by a Student-Newman-Keuls test procedure (SNK) in order to delineate homogeneous groups.

3. RESULTS

Axes 1 and 2 of correspondence analysis extracted 15 and 9% of total variance, respectively. Other axes displayed only ground noise or isolated single samples, thus they were not accounted for. The projection of the 69 categories and the three horizons (OL, OF, A) in the plane of the first two factorial axes (Fig. 1) revealed the existence of three groups of humus components, corresponding to the three horizons present. Table 1 indicates the horizon to which each category was assigned by correspondence analysis.

The OL horizon consisted of entire (categories 1, 3, 5, 7, 8, 9, 10, 11, 16) and fragmented (categories 2, 4, 20) tree and shrub leaves, together with herb litter and aerial parts (categories 17, 18, 27) and tree seedlings (category 28). Petioles (category 22), seeds (categories 23, 24) and caterpillar faeces (category 48) were also components of the OL horizon. Thus a great variety of litter components were present in this horizon, some of them being already decayed by white rots and soil animals, which indicated a high level of soil biological activity in the recently fallen litter.

The OF horizon was made of still more decayed leaf litter (categories 6, 21), holorganic faeces of epigeic fauna (categories 49, 50, 51, 52, 57, 58), arthropod cuticles (category 47), recalcitrant litter such as woody litter (categories 29, 30, 32, 33, 34) and moss (category 44). It should be highlighted that ivy litter (categories 12, 13, 14, 15) and bracts (category 26) were present in this horizon rather than in the OL horizon, probably for a seasonal reason. Fine sand particles (category 69) were also present.

The A horizon was made of hemorganic animal faeces (categories 53, 54, 55, 56, 59, 60, 61, 62), hemorganic masses (categories 63, 64), gross mineral particles (categories 65, 66, 67, 68), roots (categories 35, 36, 37, 38, 39, 40, 41, 42) and strongly recalcitrant litter such as bark (category 31) and cupules (category 25). This horizon was the site of most visible fungal activity (category 43). Snail shells (category 46) were also present.

No changes in the composition of horizons according to orientation and distance to the trunk base were displayed by the analysis but the particular development of the OF horizon at 40 cm from the trunk base became clearly apparent when depth indicators were put as additional (passive) variables (Fig. 2). When following the composition of a mean profile from surface (Ocm) to deeper layers (4cm), then a distinct shift towards OF categories appeared at 2cm depth in samples taken at 40cm from the trunk base. At farther distances to the trunk base the humus profile passed directly from an OL to an A horizon. This could be due to a change either in litter composition or in soil biological activity. The first explanation could be ruled out since the composition of the OL horizon (0 to 1 cm depth) did not display marked changes with distance to the trunk base.

When visualizing changes in the composition of the humus profile in relation to depth at 40 (Fig. 3), 140 (Fig. 4) and 240cm from the trunk base (Fig. 5), some detailed trends appeared which had been synthetically summarized by correspondence analysis. The percentage of hemorganic faeces increased more sharply from O-1cm to 3-4cm depth at 140 and 240cm of the trunk base than at 40cm, where this percentage remained always less than 30%, in place of 50% or more at farther diatance. While the percentage of recalcitrant litter (bark, wood, cupules, scales) increased then decreased abruptly along the studied profile at 140 and 240cm from the trunk base, it increased from 0-1cm to 1-2cm depth then remained unchanged at 40cm distance, indicating a decrease in the capacity of soil animals to transform it into faecal pellets. The percentage of mineral material increased sharply from 2-3cm to 3-4cm depth at 140 and 240cm of the trunk, while it remained negligible even at 3-4cm depth at 40cm distance from the trunk base. Another trait was the presence of a weak but noticeable amount of moss material at 40cm distance only.

Analysis of variance of bulk categories (Table 2) revealed a significant decrease in the mean percentage of OF categories (over the whole studied profile) from 40 to 140cm distance to the trunk base. When data from a previous study [1] were analysed in the same way, a similar decrease was observed in the amount of OF horizon per unit surface, paralleled by a decrease in titratable acidity at pH 7. No significant effect of orientation was detected.

4. DISCUSSION

The single oak tree which was studied here (N° 24) can be considered as representative of the population analysed by Beniamino et al. [1]. In particular it expressed well the trend of acidification near the trunk base which had been demonstrated on the whole population (30 individuals). Despite the absence of marked changes in the composition of litter a decrease in the transformation of recalcitrant litter was observed in the vicinity of the trunk. This can be interpreted as a decrease in decomposer activity, most notably in earthworm activity. These animals are known to be one the main agents of litter disappearance [46] and building of mull humus forms [4], due to their capacity to ingest and mix a large amount of organic and mineral matter [25]. As a consequence of this decrease in the recycling of litter an accumulation of organic matter appears at the base of the tree, in the form of an increase in the thickness of the OF horizon. This can be interpreted as an imbalance between the input of litter and the capacity of earthworms to process it, which could be caused by i) an increase in litter production, ii) a decrease in earthworm activity, iii) both processes occurring together. Since an increase in litter production can be discarded on the basis of previous investigations on the same site [1], then only a possible decrease in earthworm activity remains.

Several reasons support the idea of a repellent effect of the tree trunk base towards earthworms. Bark, which is present at the surface of trunk bases and large roots, has a high tannin content [10, 47]. Even though most bark tannins are insoluble, some of them may diffuse into the soil solution, as shown by dipping bark pieces in deionized water [1], the subsequent solution being repellent to earthworms [42]. The acidification of the soil caused by the chelation of alkaline metals by bark tannins [19, 29] may also repel earthworms [41]. In the absence or scarcity of stemflow the increase in titratable acidity in the vicinity of the tree trunk can nevertheless be both a cause and a consequence of the observed accumulation of humified organic matter, both processes reinforcing themselves in a positive feed-back loop [39]. The acidifying influence of moss, which was only present in the vicinity of the trunk base, cannot be discarded either [2], even though only a small amount of moss material was present in the humus profile, without accumulation (Fig. 3).

REFERENCES

- Beniamino F., Ponge J.F., Arpin P., Soil acidification under the crown of oak trees. I.
 Spatial distribution. For. Ecol. Manag. 40 (1991) 221-232.
- [2] Berg B., Decomposition of moss litter in a mature Scots pine forest, Pedobiologia 26 (1984) 301-308.
- [3] Bernier N., Altitudinal changes in humus form dynamics in a spruce forest at the montane level, Plant Soil 178 (1996) 1-28.
- [4] Bernier N., Earthworm feeding activity and development of the humus profile, Biol.Fertil. Soils 26 (1998) 215-223.
- [5] Bernier N., Ponge J.F., Dynamique et stabilité des humus au cours du cycle sylvogénétique d'une pessière d'altitude, CR Acad. Sci. Paris, Sér. III, Sc. Vie 316 (1993) 647-651.
- [6] Bernier N., Ponge J.F., Humus form dynamics during the sylvogenetic cycle in a mountain spruce forest, Soil Biol. Biochem. 26 (1994) 183-220.
- [7] Bernier N., Ponge J.F., André J., Comparative study of soil organic layers in two bilberry-spruce forest stands (*Vaccinio-Piceetea*). Relation to forest dynamics, Geoderma 59 (1993) 89-108.

- [8] Boerner R.J., Koslowsky S.D., Microsite variations in soil chemistry and nitrogen mineralization in a beech-maple forest, Soil Biol. Biochem. 21 (1989) 795-801.
- [9] Bollen W.B., Chen C.S., Lu K.C., Tarrant R.F., Effect of stemflow precipitation on chemical and microbiological soil properties beneath a single alder tree, in: Trappe J.M., Franklin J.F., Tarrant R.F., Hansen G.M. (Eds.), Biology of alder, USDA Forest Service, Portland, Oregon, 1968, pp. 149-156.
- Bollen W.B., Lu K.C., Douglas-fir bark tannin decomposition in two forest soils, USDA Forest Service, Portland, Oregon, 1969.
- [11] Brêthe A., Brun J.J., Jabiol B., Ponge J.F., Toutain F., Classification of forest humus forms: a French proposal, Ann. Sci. For. 52 (1995) 535-546.
- [12] Cailleux A., Michel J.P., Sur la sédimentologie des alluvions plio-quaternaires d'Yerres et de Sénart au S.E. de Paris, Rev. Géogr. Phys. Géol. Dyn. 9 (1967) 415-424.
- [13] Carlisle A., Brown A.H.F., White E.J., The nutrient content of tree stem flow and ground flora litter and leachates in a sessile oak (*Quercus petraea*) woodland, J. Ecol. 55 (1967) 615-627.
- [14] Cloutier A., Microdistribution des espèces végétales au pied des troncs d'Acer saccharum dans une érablière du sud du Québec, Can. J. Bot. 63 (1985) 274-276.
- [15] Falkengren-Grerup U., Effect of stemflow on beech forest soils and vegetation in southern Sweden, J. Appl. Ecol. 26 (1989) 341-352.
- [16] Falkengren-Grerup U., Björk L., Reversibility of stemflow-induced soil acidification in Swedish beech forest, Environ. Pollut. 74 (1991) 31-37.

- [17] Gersper P.L., Holowaychuk N., Effects of stemflow water on a Miami soil under a beech tree. I. Morphological and physical properties, Soil Sci. Soc. Am. Proc. 34 (1970) 779-786.
- [18] Gersper P.L., Holowaychuk N., Effects of stemflow water on a Miami soil under a beech tree. II. Chemical properties, Soil Sci. Soc. Am. Proc. 34 (1970) 786-794.
- [19] Gersper P.L., Holowaychuk N., Some effects of stem flow from forest canopy trees on chemical properties of soils, Ecology 52 (1971) 691-702.
- [20] Greenacre M.J., Theory and applications of correspondence analysis, Academic Press, London, UK, 1984.
- [21] Kopeszki H., Veränderungen der Mesofauna eines Buchenwaldes bei Säurebelastung, Pedobiologia 36 (1992) 295-305.
- [22] Kopeszki H., Versuch einer aktiven Bioindikation mit den bodenlebenden Collembolen-Arten Folsomia candida (Willem) und Heteromurus nitidus (Templeton) in einem Buchenwald-Ökosystem, Zool. Anz., 228 (1992) 82-90.
- [23] Kopeszki H., Auswirkungen von Säure- und Stickstoff-Deposition auf die Mesofauna, insbesondere Collembolen. Forstw. Centralbl. 112 (1993) 88-92.
- [24] Kumpfer W., Heyser W., Effects of stemflow on the mycorrhiza of beech (*Fagus sylvatica* L.), in: Gianinazzi-Pearson V., Gianinazzi S. (Eds.), Physiological and genetical aspects of mycorrhizae, INRA, Paris, France, 1986, pp. 745-750.
- [25] Lavelle P., Pashanasi B., Charpentier F., Gilot C., Rossi J.P., Derouard L., André J.,Ponge J.F., Bernier, N., Large-scale effects of earthworms on soil organic matter and

nutrient dynamics, in: Edwards C.A. (Ed.), Earthworm ecology, Saint Lucie Press, Boca Raton, Florida, 1998, pp. 103-122.

- [26] Mina V.N., Influence of stemflow on soil, Soviet Soil Science (1967) 1321-1329.
- [27] Neite H., Wittig R., Korrelation chemischer Bodenfaktoren mit der floristischen Zusammensetzung der Krautschicht im Stammfussbereich von Buchen, Acta Oecol. Oecol. Plant. 6 (1985) 375-385.
- [28] Nizinski J., Saugier B., Mesures et modélisation de l'interception nette dans une futaie de chênes, Acta Oecol. Oecol. Plant. 9 (1988) 311-329.
- [29] Olsson M.T., Properties and decomposition of bark, Swedish University of Agricultural Sciences, Uppsala, Sweden, 1978.
- [30] Peltier A., Ponge J.F., Jordana R. & Ariño A., Humus forms in Mediterranean scrublands with aleppo pine, Soil. Sci. Soc. Am. J. (2000) *(in press)*.
- [31] Ponge J.F., Étude écologique d'un humus forestier par l'observation d'un petit volume, premiers résultats. I. La couche L1 d'un moder sous pin sylvestre, Rev. Écol. Biol. Sol 21 (1984) 161-187.
- [32] Ponge J.F., Étude écologique d'un humus forestier par l'observation d'un petit volume.
 II. La couche L2 d'un moder sous *Pinus sylvestris*, Pedobiologia 28 (1985) 73-114.
- [33] Ponge J.F., Étude écologique d'un humus forestier par l'observation d'un petit volume.III. La couche F1 d'un moder sous *Pinus sylvestris*, Pedobiologia 31 (1988) 1-64.
- [34] Ponge J.F., Ecological study of a forest humus by observing a small volume. I.Penetration of pine litter by mycorrhizal fungi, Eur. J. For. Pathol. 20 (1990) 290-303.

13

- [35] Ponge J.F., Food resources and diets of soil animals in a small area of Scots pine litter, Geoderma 49 (1991) 33-62.
- [36] Ponge J.F., Succession of fungi and fauna during decomposition of needles in a small area of Scots pine litter, Plant Soil 138 (1991) 99-113.
- [37] Ponge J.F., Heterogeneity in soil animal communities and the development of humus forms, in: Rastin N., Bauhus J. (Eds.), Going underground. Ecological studies in forest soils, Research Signpost, Trivandrum, India, 1999, pp. 33-44.
- [38] Ponge J.F., Horizons and humus forms in beech forests of the Belgian Ardennes, Soil Sci. Soc. Am. J. 63 (1999) 1888-1901.
- [39] Ponge J.F., Interaction between soil fauna and their environment, in: Rastin N., Bauhus J. (Eds.), Going underground. Ecological studies in forest soils, Research Signpost, Trivandrum, India, 1999, pp. 45-76.
- [40] Ponge J.F., Delhaye L., The heterogeneity of humus profiles and earthworm communities in a virgin beech forest, Biol. Fertil. Soils 20 (1995) 24-32.
- [41] Satchell J.E., Potential of the Silpho Moor experimental birch plots as a habitat for *Lumbricus terrestris*, Soil Biol. Biochem. 12 (1980) 317-323.
- [42] Satchell J.E., Lowe D.G., Selection of leaf litter by *Lumbricus terrestris*, in: Graff O., Satchell J.E. (Eds.), Progress in soil biology, North-Holland Publishing Company, Amsterdam, The Netherlands, 1967, pp. 102-119.

- [43] Scheu S., Poser G., The soil macrofauna (Diplopoda, Isopoda, Lumbricidae and Chilopoda) near tree trunks in a beechwood on limestone: indications for stemflow induced changes in community structure, Appl. Soil Ecol. 3 (1996) 115-125.
- [44] Sokal R.R., Rohlf F.J., Biometry. The principles and practice of statistics in biological research, 3rd ed., Freeman, New York, New York, 1995.
- [45] Sumner M.E., Handbook of soil science, CRC Press, Boca Raton, Florida, 2000.
- [46] Toutain F., Activité biologique des sols, modalités et lithodépendance, Biol. Fertil. Soils 3 (1987) 31-38.
- [47] Updegraff D.M., Grant W.D., Microbial utilization of *Pinus radiata* bark, Appl. Microbiol. 30 (1975) 722-726.
- [48] Wittig R., Acidification phenomena in beech (*Fagus sylvatica*) forests of Europe, WaterAir Soil Pollut. 31 (1986) 317-323.
- [49] Wittig R., Neite H., Acid indicators around the trunk base of *Fagus sylvatica* in limestone and loess beechwoods: distribution pattern and phytosociological problems, Vegetatio 64 (1985) 113-119.
- [50] Zinke P.J., The pattern of influence of individual forest trees on soil properties, Ecology 43 (1962) 130-133.

Legends of figures

- Fig. 1. Correspondence analysis crossing 69 categories (humus components) and 48 samples. Projection of the active variables (categories, coded as in Table 1) and three aditional variables (horizon names).
- **Fig. 2.** Correspondence analysis crossing 69 categories (humus components) and 48 samples. Projection of aditional variables (horizon names as in Fig. 1 and depth indicators).
- Fig. 3. Changes in the distribution of humus components (bulk categories) according to depth at 40 cm from the tree trunk base.
- Fig. 4. Changes in the distribution of humus components (bulk categories) according to depth at 140 cm from the tree trunk base.
- Fig. 5. Changes in the distribution of humus components (bulk categories) according to depth at 240 cm from the tree trunk base.

Table I. List of the categories found during morphologicalinvestigations of humus profiles coded by numbers.Typical horizons were indicated according to results of thecorrespondence analysis

1	0	Brown entire oak leaves
2	OL	Brown fragmented oak leaves
3	OL.	Bleached entire oak leaves
4	OL	Bleached fragmented oak leaves
5	OL	Strongly bleached entire oak leaves
6	OF	Strongly bleached fragmented oak leaves
7	OL	Brown entire lime leaves
8	OL	Bleached lime leaves
9	OL	Strongly bleached lime leaves
10	0	Brown bramble leaves
11	0	Pale brown bramble leaves
12	OF	Brown entire iw leaves
13	OF	Brown fragmented iw leaves
14	OF	Bleached entire inv leaves
15	OF	Bleached fragmented iw leaves
16	0	Brown entire chestnut leaves
17	0	Archangel leaves
18	0	Hair-grass leaves
19		Indetermined berbaceous bleached leaves
20	$\overline{\mathbf{n}}$	Fine-nerved skeletonized leaves
21		Main-nerved skeletonized leaves
22	0	Patiolas
22	0	Entire lime fruits
2J 2/		Intract miscellaneous sends and cupulos
24 2E		Decaying miscellaneous seeus allu cupules
20		Bud scales and miscellaneous breats
20 27		Solomon's soal loof mobio
21		ouomons sear real racriis
2ŏ 20		chesthul seedling
29		Twigs
30	0F	I WIG Dark
31	A	Bark
32		Brown-rotten wood
33		vvnite-rotten wood
34	0F	Fauna-tunnelled wood
35	A	Herb roots
36	A	Living fine long roots of tree
37	A	Dead fine long roots of tree
38	A	Living large roots of tree
39	A	Dead large roots of tree
40	A	Living mycorrnizae
41	A	Dead mycorrnizae
42	A	Cenococcum mycorrnizae
43	A	Mycelial strands and mats
44	OF	Mosses
45	0F	Miscellaneous plant fragments
46	A	
47	OF	Arthropod bodies
48	OL	
49		
50	OF	
51	OF	vv oodlice taeces
52	OF	Holorganic earthworm faeces
53	A	Organic-rich hemorganic earthworm faeces
54	A	Hemorganic earthworm faeces
55	A	Organic-poor hemorganic earthworm faeces
56	A	Holomineral earthworm faeces
57	OF	Woody faeces
58	OF	Holorganic faecal material
59	A	Organic-rich hemorganic faecal material
60	A	Hemorganic faecal material
61	А	Organic-poor hemorganic faecal material
62	А	Holomineral faecal material
63	Α	Hemorganic mass
64	А	Organic-poor hemorganic mass
65	А	Mineral mass
66	А	Mineral particles > 6 mm
67	А	Mineral particles 3 to 6 mm
68	А	Mineral particles 1 to 3 mm
69	OF	Mineral particles 0.1 to 1 mm

 Table II. Mean values of morphological and chemical parameters according to the distance to the tree trunk base and orientation. Significant differences among means are indicated by letters. Means are followed by standard errors. * From Beniamino et al. [1].

	North	West	South	East	40 cm	140 cm	240 cm
OL categories %	42.68±10.45	27.54±7.59	44.16±6.22	42.81±6.12	37.74±8.20	37.98±5.45	42.18±4.96
OF categories %	9.51±1.43	15.8±3.0	14.91±4.16	22.82±3.85	24.01±3.06a	10.29±2.84b	12.98±2.01ab
A categories %	47.82±11.21	56.66±9.30	40.93±9.15	34.38±8.34	38.26±10.63	51.74±5.52	44.84±6.27
OL g.m ⁻² *	318±64	422±116	724±268	884±238	601±200	617±151	542±102
OF g.m ⁻² *	3205±467	1745±203	1662±471	863±415	3917±361a	1011±328b	678±297b
pH water*	4.28±0.26	5.05±0.21	4.85±0.11	4.55±0.14	4.24±0.13	4.85±0.16	4.96±0.17
Titratable acidity (mM.100g ⁻¹)*	1.85±0.21	2.51±0.17	1.99±0.38	2.98±0.46	3.79±0.33a	1.67±0.10b	1.53±0.17b



Fig. 1



Fig. 2











