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Humus Index: An Integrated Tool for the Assessment of Forest Floor and Topsoil Properties

Jean-François Ponge,* Richard Chevalier, and Philippe Lousot

ABSTRACT

A quantitative assessment of forest humus forms is suggested, on the basis of a scale ranging from 1 (Eumull) to 7 (Dysmoder) which is called the *humus index*. Regression analyses showed that this index was well-correlated with several morphological as well as chemical variables describing forest floors and topsoil profiles: thickness of the Oe horizon, depth of the crumbly mineral horizon, Munsell hue, pH_{KCl} and $\text{pH}_{\text{H}_2\text{O}}$, H and Al exchangeable acidity, percentage base saturation, cation-exchange capacity, exchangeable bases, C and N content and available P of the A horizon. The suggested humus index could be used as a cheap and rapid method for the bulk assessment of organic matter accumulation, soil acidity, and soil biological activity.

FOREST HUMUS FORMS have been used for the assessment of site quality, as they are strongly indicative of tree growth and regeneration conditions (Knapp and Smith, 1982; Mallik and Newton, 1988; Topoliantz and Ponge, 2000), vegetation types (Manil et al., 1963; Klincka et al., 1990; Ott et al., 1997), and soil animal communities (Van der Drift, 1962; Ponge and Delhay, 1995; Ponge et al., 1997). In a given forest stand, most variation in humus form (spatial as well as temporal) can be attributed to the interaction between stable site conditions (climate, parent rock, slope, aspect, exposure) and changing conditions such as those induced by land use (Little and Bolger, 1995; Koerner et al., 1997), silvicultural practices (Fisher, 1928; Ovington, 1954; Aber et al., 1978) and the natural development of forest vegetation (Switzer et al., 1979; Nielsen et al., 1987; Gallet et al., 1999). Despite the complexity of patterns and processes taking place in the development of humus forms (Ponge et al., 1998; Ponge, 1999a, 1999b) functional and evolutionary links between humus forms and organisms have been demonstrated at the ecosystem level (Belotti and Babel, 1993; Ulrich, 1994; Wardle et al., 1997). This may explain why some simple relationships may be expected to occur between humus forms and other ecosystem properties. In particular, the three main humus forms mull-moder-mor (Green et al., 1993; Brêthes et al., 1995; Ponge et al., 2000) can be scaled in an order of decreasing plant, microbial, and animal biodiversity; soil fertility; and stand productivity (Ponge et al., 1997; Van Delft et al., 1999; Ponge, 2000).

The present study extends a qualitative assessment

of forest humus forms, based on taxonomic studies (Green et al., 1993; Brêthes et al., 1995), to a quantitative evaluation of humus quality, through development of a humus index. This index assumes that humus forms can be scaled and this scale can be correlated with morphological or chemical data describing forest floors and topsoil profiles. In particular, it can be hypothesized that scaling humus forms according to the degree of incorporation of litter (development of Oi, Oe, and Oa horizons) and to the development of a crumbly structure in the A horizon will give us a cheap, reliable indicator of soil fertility. In their classification of humus forms Green et al. (1993) and Brêthes et al. (1995) stressed the importance of the visual assessment of animal and microbial activities for characterizing horizons and humus forms. This followed an older contribution by Kubiëna (1953). Contrary to Green et al. (1993) who focused their classification of humus forms on O (organic) horizons (the forest floor), Brêthes et al. (1995) separated mull from moder on the basis of the structure of the A (hemorganic) horizon. Their classification used the existence of biogenic structures created by earthworms in the A horizon (casts and galleries) for delineating mull from moder and mor, whatever the thickness (and subdivision) of O horizons. This allowed extension of the mull group to all humus forms with a biomacrostructured hemorganic horizon. Qualitative criteria described by Brêthes et al. (1995) for separating humus forms on the basis of both O and A horizons were used in the present study to test whether each humus form could be given a score along a scale of decreasing biological activity. Transforming qualitative data into a semi-quantitative index could allow the latter to be compared with analyses of soil fertility such as pH, C/N, CEC, C, N, and P content.

MATERIALS AND METHODS

Study Sites

The present study was undertaken as part of a research project focused on the influence of management practices on forest biodiversity in the Brie natural geographic region (northern France). Four nearby hardwood forests were selected, on the basis of (i) the presence of common oak [*Quercus petraea* (Mattuschka) Liebl.] as a dominant canopy species or as a relict of traditional (now abandoned) coppices with standards, (ii) moderately acidic soils (Udalfs) with a silt-loam texture and not waterlogged in the top 30 cm. Seventy-two sites were chosen within this forested area, encompassing a wide array of management types (Table 1).

Sampling Design

In each of the 72 sites selected for the study, topsoil profiles were examined in the field by trenching the ground with a

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sharp knife to a 15-cm depth and along a 30-cm transect. Examination of all topsoil profiles and soil sampling was conducted during October 1999 and four estimates were done at each site. The plots were selected at a 7-m distance from a central plot in the four cardinal directions. The humus form was identified according to Brêthes et al. (1995) as mull, moder, and mor and their subdivisions. For the calculation of the humus index, humus forms present in the 72 studied sites were classified in an order of increasing accumulation of organic matter in the O horizon and decreasing burrowing activity in the A horizon as follows:

1. Eumull (crumby A horizon, Oi horizon absent, Oe horizon absent, Oa horizon absent)
2. Mesomull (crumby A horizon, Oi horizon present, Oe horizon absent, Oa horizon absent)
3. Oligomull (crumby A horizon, Oi horizon present, Oe horizon 0.5 cm thick, Oa horizon absent)
4. Dysmull (crumby A horizon, Oi horizon present, Oe horizon 1 cm or more thick, Oa horizon absent)
- 5a. Amphimull (crumby A horizon, Oi horizon present, Oe horizon present, Oa horizon present)
- 5b. Hemimoder (compact A horizon, Oi horizon present, Oe horizon present, Oa horizon absent)
6. Eumoder (compact A horizon, Oi horizon present, Oe horizon present, Oa horizon 0.5 cm or 1 cm thick)
7. Dysmoder (compact A horizon, Oi horizon present, Oe horizon present, Oa horizon more than 1 cm thick)

Mull (Eumull to Amphimull) was characterized by the presence of a crumby A horizon [bio-macro-structured sensu Brêthes et al. (1995)], made of fresh and old earthworm hemorganic faeces. Under the particular conditions of the study sites, it was often found that earthworm aggregates were visible only in the first top 1 to 2 cm, the A horizon becoming compact beneath this depth. Amphimull and Hemimoder, both exhibiting signs of weak incorporation of litter to the hemorganic horizon, were given the same humus index value of 5. In case variations in the humus form occurred over a 30-cm distance, it was decided to take into account only the most typical (dominant) one.

The thickness of Oi, Oe, and Oa horizons was measured at the place where the humus form was considered as most representative of the selected 30-cm distance. The thickness of the A (hemorganic) horizon and the thickness of the crumby horizon were measured independently to take into account cases where we found active burrowing by earthworms in a pure mineral E horizon underneath. Color patterns in the top centimeters of the A horizon were quantified using Munsell soil color charts, that is, hue, value, and chroma were measured for each topsoil profile. Soil texture of the topsoil was quantified directly on the field according to the following scale: (i) silt, (ii) silt loam, and (iii) sandy loam. The botanical composition of the litter was noted, as well as that of field and ground vegetation, adjacent to points where topsoil profiles were sampled.

The top 5 cm of the mineral soil (A or A+E horizons) were put in plastic bags then rapidly transported to the laboratory to be air-dried. The four samples taken in each site were pooled for analyses. Chemical analyses were performed at the INRA Soil Analysis Laboratory (Arras, France). Soil acidity was expressed as pH in water ($\text{pH}_{\text{H}_2\text{O}}$) and pH in 1 mol L⁻¹ KCl (pH_{KCl}). Concentrations of exchangeable cations (Al, H, Ca, K, Mg) were measured at current pH value by the cobalt hexamine trichloride method (Orsini and Rémy, 1976). Potentially available P was extracted by sulphuric acid (0.2 mol L⁻¹) and sodium hydroxide (0.1 mol L⁻¹) according to Duchaufour and Bonneau (1959). Organic C and total N content were

Table 1. Thirteen silvicultural conditions sampled for development of the humus index.

Code	Replicates	Definition
Qr0	6	seed cut with seed bearers still present
Qr5	6	seedling forest, dense thicket stage
Qr20	6	seedling forest, pole stage
Qr50	5	seedling forest, adult stage
Qt	5	old coppice-with-standards with oak standards still abundant and evenly arranged
Qs	5	old coppice-with-standards with senescent oak
Qi20a	5	old coppice-with-standards with an irregular structure made of oak trees of varying age
Qi20b	5	old coppice-with-standards with an irregular structure made of oak but deficient in pole trees
Qi0	5	old coppice-with-standards with an opened structure
B20	6	high birch/aspens coppice with few relict oak standards
T20	6	high lime coppice with few relict oak standards
C20	6	high hornbeam coppice with few relict oak standards
B5	6	low birch/aspens coppice with few relict oak standards

measured by the dry combustion method according to ISO 10694 and ISO 13878, respectively.

RESULTS

The distribution of Humus Index values over the whole set of samples (288) showed an even distribution from 2 to 6, and a decrease above (Dysmoder, Humus Index 7) as well as below (Eumull, Humus Index 1) these values (Fig. 1). Regression analyses were done using means of four samples per site, recognizing that (i) these samples were not randomly chosen thus were not true replicates, (ii) they were autocorrelated since the within-site variance was significantly lower than the between-site variance, as ascertained by an *F*-test (Sokal and Rohlf, 1995).

As ascertained by regression analysis (Sokal and Rohlf, 1995) the humus index was correlated with two parameters measuring the degree of litter incorporation and the development of the soil structure. The thickness of the Oe horizon increased, and the depth of the crumby mineral horizon decreased, when the humus index increased (Fig. 2). The correlation was linear and highly significant ($R^2 = 0.48$, $P < 10^{-11}$ and $R^2 = 0.43$, $P < 10^{-9}$, respectively). The Munsell hue within the YR (yellow-red) range decreased when the humus index increased ($R^2 = 0.41$, $P < 10^{-9}$). This means that the first top centimeters of the A horizon turned from yellowish to reddish as far as the humus index increased.

Several components of soil acidity (measured in the A horizon) were well-described by the humus index (Fig. 2). The pH_{KCl} as well as the $\text{pH}_{\text{H}_2\text{O}}$ decreased when the humus index increased ($R^2 = 0.40$, $P < 10^{-8}$ and $R^2 = 0.35$, $P < 10^{-7}$, respectively). Aluminium, H, and total exchange acidity increased with the humus index ($R^2 = 0.42$, $P < 10^{-9}$, $R^2 = 0.29$, $P < 10^{-6}$, and $R^2 = 0.44$, $P < 10^{-9}$, respectively). The ratio of exchangeable acidity to total cation-exchange capacity increased with the humus index ($R^2 = 0.42$, $P < 10^{-9}$). Several other components of soil fertility were also described by the humus index, although at a lower level of significance. The cation-exchange capacity ($P < 0.01$), the exchangeable Ca ($P < 10^{-6}$), the exchangeable Mg ($P < 10^{-4}$) and the exchangeable K ($P < 0.01$) decreased when the humus index increased. The C ($P < 0.05$) and the N

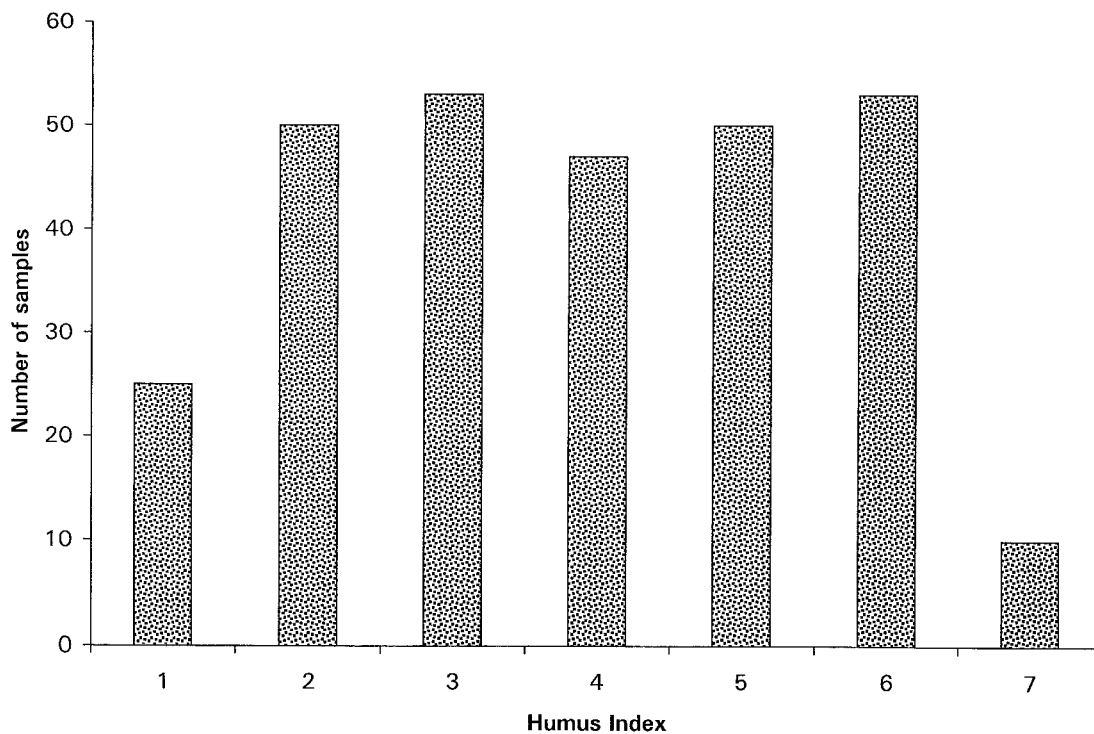


Fig. 1. Distribution of the seven humus index classes among the 288 humus profiles studied.

($P < 0.01$) content of the A horizon increased with the humus index.

We may wonder whether the humus index reflected trends or only the opposition between mull and moder. In addition, autocorrelation could be suspected for morphological variables such as thickness of the Oe horizon and depth of the crumby horizon, since they were used as visual criteria for the separation of humus forms. To verify that the scale used for calculating the humus index was not superfluous, the same variables were regressed against humus index for mull humus forms only (humus index less than 5, 50 sites). The same relationships were found between humus index and thickness of the Oe horizon ($P < 10^{-12}$, this high level of significance being nevertheless an artifact because of autocorrelation), depth of the crumby mineral horizon ($P < 0.05$), Munsell hue ($P < 0.0001$), pH_{KCl} and $\text{pH}_{\text{H}_2\text{O}}$ ($P < 0.01$), Al, proton, and total exchange acidity ($P < 0.01$), ratio of exchangeable acidity to cation-exchange capacity ($P < 0.01$), exchangeable Ca ($P < 0.05$) and N ($P < 0.01$). A similar comparison could not be made with moder humus forms (humus index more than 5) because of lack of replication.

DISCUSSION

Several studies have demonstrated that morphological features of humus profiles were connected with their physicochemical as well as biological properties. In particular, mull can be separated from moder or mor by a decreased level of acidity (Mader, 1953; Klinka et al., 1990; Ponge et al., 1997), an increased level of nutrient availability (Lemée, 1967; Klinka et al., 1990; Ponge et al., 1997), and a higher diversity of functional groups

(Phillipson, 1989; Ponge et al., 1997; Van Delft et al., 1999). For finer separations within the mull group, Michalet et al. (2000) demonstrated that dysmull (mull with a thick Oe horizon) exhibited less nutrient availability and earthworm activity than oligomull (mull with a thin Oe horizon).

The humus index offers an opportunity to test morphological properties on the basis of the continuous variation of a single parameter. In the present study, we demonstrated that the humus index was linearly correlated with some important morphological and chemical properties of topsoil profiles: thickness of the forest floor, acidity of the soil solution, exchange acidity, cation-exchange capacity, exchangeable bases, C and N content. All these features have been demonstrated to influence the composition, richness and abundance of mull-forming animal species, mainly through the intermediary of nutrient availability (Ponge et al., 1997, 1999; Wolters, 1999). Thus, correlations between physicochemical and morphological properties were expected to occur, as this has been already demonstrated by Klinka et al. (1990). Less expected was the ability of an arbitrary scale such as the humus index, to correlate with continuous variables and, thus, to furnish a synthetic view of forest floor and topsoil properties, in particular those related to soil acidity.

The reddish hue of the A horizon under moder (5YR or less in place of 10YR for mull) has been already observed in other woodlands (Ponge and Delhaye, 1995). This feature, which is very easy to measure directly on the field, could be added to the morphological characteristics of moder humus forms. It could be caused either by mobilization of Fe in the form of iron oxides

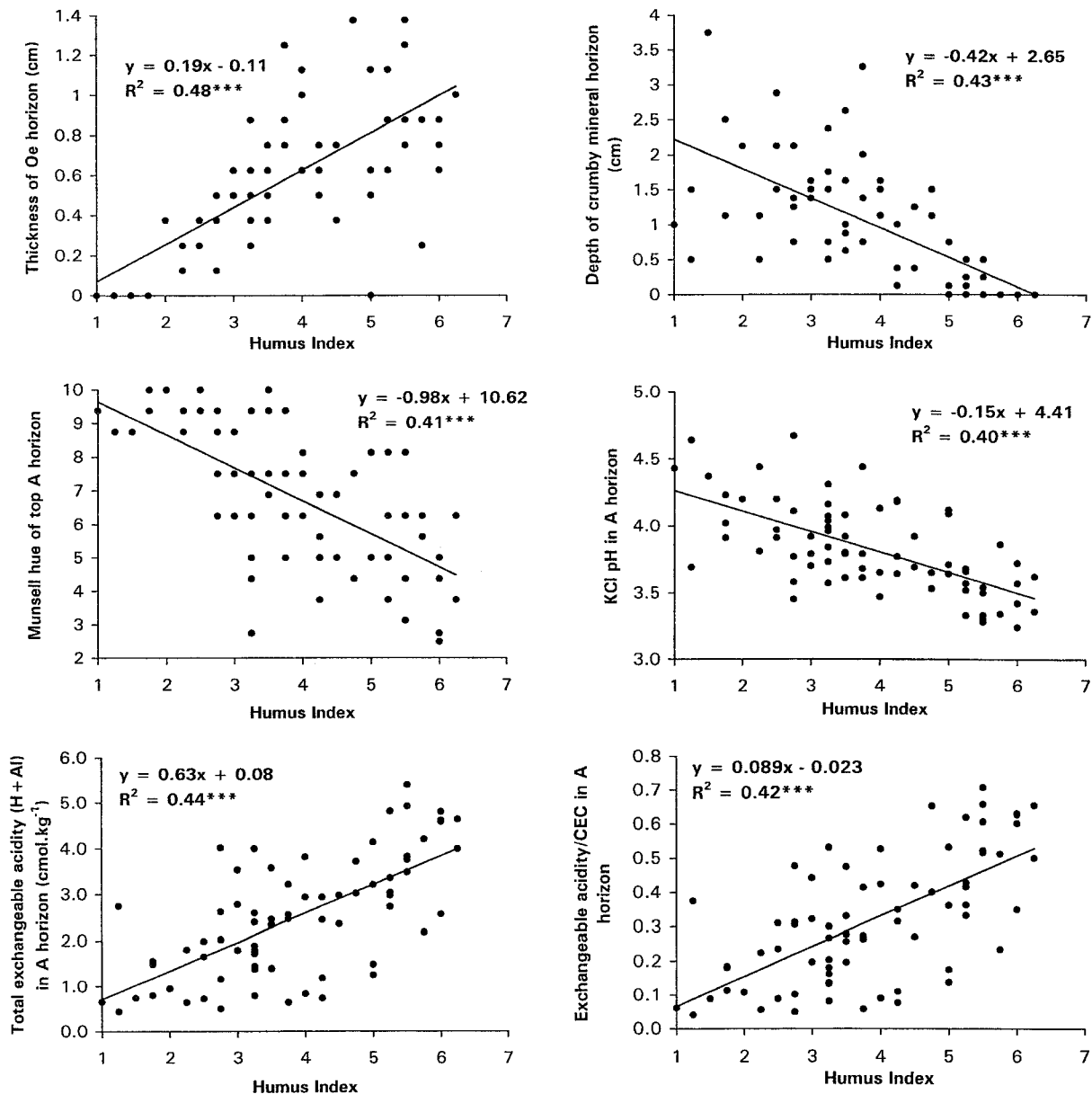


Fig. 2. Correlation of the humus index with some variables measured in the topsoil profiles (means of four replicates).

(Schwertmann, 1985) or changes in optical properties of humic compounds (Kumada, 1987) or both.

The lateral variability of forest humus forms and forest floor properties has been described by several authors (Arp and Krause, 1984; Riha et al., 1986; Torgersen et al., 1995) and, consequently, composite samples are normally used for site assessment (Carter and Lowe, 1986). In the present study, we observed a better correlation between the humus index and other topsoil properties when data from within-site replicates were pooled than when they were considered separately, despite a collapse in the degrees of freedom (data not shown). Individual measurements (the humus index comprised) provide only a truncated view of complicated processes (biological, physicochemical) taking place at a varying rate and at a varying scale (Belotti and Babel, 1993). For instance, the thickness of the Oe horizon results,

among others, from the burying activity of earthworms (Bocock et al., 1960; Van der Drift, 1963; Staaf, 1987), the decaying activity of white rots (Gourbière, 1982), foliage quantity and quality (Prusinkiewicz, 1978; Ponge et al., 1997; Peltier et al., 2001), and displacement of fallen leaves by wind (Garay and Hafidi, 1990). Year-to-year and place-to-place changes may occur in one or several of these parameters (Witkamp and Van der Drift, 1961; Ehrenfeld et al., 1997), which are not immediately reflected in the humus form thus in the humus index (Bernier and Ponge, 1994; Emmer and Sevink, 1994).

CONCLUSION

The humus index offers a cheap and reliable method for the assessment of topsoil properties, avoiding expen-

sive and time spending chemical measurements. It could be used when a large number of samples are required, laborious analyses being then limited to a selection of representative samples, used to build a series of regression lines. Changes of the humus index in the course of time could help to follow the effects of stand development (Beniamino et al., 1991; Bernier and Ponge, 1994; Emmer and Sevink, 1994), management practices (Terlinden and André, 1988; Muys and Lust, 1993; Deleporte and Tillier, 1999), and anthropic threats such as atmospheric pollution (Falkengren-Grerup, 1986; Belotti and Babel, 1993). Application of the humus index to the assessment of other ecosystem properties (such as stand productivity), will need further research effort. Although the present study was focused on forest floor and topsoil properties, it should be noted that the number of plant species growing in the vicinity of our sampling plots, as well as the total number of plant species (over the four sampling plots) increased significantly with the humus index ($P < 0.05$). In a study on 13 beech (*Fagus sylvatica* L.) stands of varying site quality Ponge et al. (1997) and Ponge (2000) demonstrated that the humus form was reflected in the composition and functional diversity of soil animal communities, which points to a possible use of the humus index for the assessment of biodiversity. The hypothesis that the humus index could also describe the biodiversity of terrestrial ecosystems will be tested within the BIOASSESS European Community program over a wide range of countries and land use types. In the present study, this index was based on the key for the identification of temperate forest humus forms by Brêthes et al. (1995), which describes five humus forms within the mull group, only three within the moder group and only one within the mor group. In colder countries it could be extended easily to the variety of moder and mor humus forms described by Green et al. (1993) for British Columbia, using the criteria defined by Ponge et al. (2000) for the separation of mor from dysmoder humus forms.

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REFERENCES

- Aber, J.D., D.B. Botkin, and J.M. Melillo. 1978. Predicting the effects of different harvesting regimes on forest floor dynamics in northern hardwoods. *Can. J. For. Res.* 8:306–315.
- Arp, P.A., and H.H. Krause. 1984. The forest floor: Lateral variability as revealed by systematic sampling. *Can. J. Soil Sci.* 64:423–437.
- Belotti, E., and U. Babel. 1993. Variability in space and time and redundancy as stabilizing principles of forest humus profiles. *Eur. J. Soil Biol.* 29:17–27.
- Beniamino, F., J.F. Ponge, and P. Arpin. 1991. Soil acidification under the crown of oak trees. I. Spatial distribution. *For. Ecol. Manage.* 40:221–232.
- Bernier, N., and J.F. Ponge. 1994. Humus form dynamics during the sylvogenetic cycle in a mountain spruce forest. *Soil Biol. Biochem.* 26:183–220.
- Bocock, K.L., O. Gilbert, C.K. Capstick, D.C. Twinn, J.S. Waid, and M.J. Woodman. 1960. Changes in leaf litter when placed on the surface of soils with contrasting humus types. I. Losses in dry weight of oak and ash leaf litter. *J. Soil Sci.* 11:1–9.
- Brêthes, A., J.J. Brun, B. Jabiol, J.F. Ponge, and F. Toutain. 1995. Classification of forest humus forms: A french proposal. *Ann. Sci. For.* 52:535–546.
- Carter, R.E., and L.E. Lowe. 1986. Lateral variability of forest floor properties under second-growth Douglas-fir stands and the usefulness of composite sampling techniques. *Can. J. For. Res.* 16:1128–1132.
- Deleporte, S., and P. Tillier. 1999. Long-term effects of mineral amendments on soil fauna and humus in an acid beech forest floor. *For. Ecol. Manage.* 118:245–252.
- Duchauffour, P., and M. Bonneau. 1959. Une nouvelle méthode de dosage du phosphore assimilable dans les sols forestiers. (In French.) *Bull. AFES* 41:193–198.
- Ehrenfeld, J.G., X. Han, W.F.J. Parsons, and W. Zhu. 1997. On the nature of environmental gradients: Temporal and spatial variability of soils and vegetation in the New Jersey Pinelands. *J. Ecol.* 85:785–798.
- Emmer, I.M., and J. Sevink. 1994. Temporal and vertical changes in the humus form profile during a primary succession of *Pinus sylvestris*. *Plant Soil* 167:281–295.
- Falkengren-Grerup, U. 1986. Soil acidification and vegetation changes in deciduous forest in southern Sweden. *Oecologia* 70:339–347.
- Fisher, R.T. 1928. Soil changes and silviculture on the Harvard Forest. *Ecology* 9:6–11.
- Gallet, C., M.C. Nilsson, and O. Zackrisson. 1999. Phenolic metabolites of ecological significance in *Empetrum hermaphroditum* leaves and associated humus. *Plant Soil* 210:1–9.
- Garay, I., and N. Hafidi. 1990. Study of a mixed forest litter of hornbeam (*Carpinus betulus* L.) and oak (*Quercus sessiliflora* Smith). III. Organization of the edaphic macroarthropod community as a function of litter quantity. *Acta Oecol.* 11:43–60.
- Gourbière, F. 1982. Pourriture blanche de la litière d'*Abies alba* Mill. II. Évolution de la litière sous l'action des basidiomycètes du genre *Collybia*. (In French.) *Rev. Ecol. Biol. Sol* 19:163–175.
- Green, R.N., R.L. Trowbridge, and K. Klinka. 1993. Towards a taxonomic classification of humus forms. *For. Sci. Monogr.* 29:1–49.
- Klinka, K., Q. Wang, and R.E. Carter. 1990. Relationships among humus forms, forest floor nutrient properties, and understory vegetation. *For. Sci.* 36:564–581.
- Knapp, A.K., and W.K. Smith. 1982. Factors influencing understory seedling establishment of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) in southeast Wyoming. *Can. J. Bot.* 60:2753–2761.
- Koerner, W., J.L. Dupouey, E. Dambrine, and M. Benoit. 1997. Influence of past land use on the vegetation and soils of present day forest in the Vosges mountains, France. *J. Ecol.* 85:351–358.
- Kubišna, W.L. 1953. The soils of Europe. Thomas Murby, London.
- Kumada, K. 1987. Chemistry of soil organic matter. Japan Scientific Societies Press, Tokyo, and Elsevier, Amsterdam, the Netherlands.
- Lemée, G. 1967. Investigations sur la minéralisation de l'azote et son évolution annuelle dans des humus forestiers *in situ*. (In French.) *Oecol. Plant.* 2:285–324.
- Little, D., and T. Bolger. 1995. The effects of contrasting land uses on soil properties and animal communities in brown earth soils. *Proc. Roy. Irish Acad. Ser. B* 95:183–193.
- Mader, D.L. 1953. Physical and chemical characteristics of the major types of forest humus found in the United States and Canada. *Soil Sci. Soc. Am. Proc.* 17:155–158.
- Mallik, A.U., and P.F. Newton. 1988. Inhibition of black spruce seedling growth by forest-floor substrates of Central Newfoundland. *For. Ecol. Manage.* 23:273–283.
- Manil, G., F. Delecour, G. Forget, and A. El Attar. 1963. L'humus, facteur de station dans les hêtraies acidophiles de Belgique. (In French.) *Bull. Inst. Agron. Stat. Rech. Gembloux* 31:1–114.
- Michalet, R., C. Gandoy, G. Cadel, G. Girard, J.L. Grossi, D. Joud, and G. Pache. 2000. Modes de fonctionnement d'humus des forêts sempervirentes des Alpes internes françaises. (In French.) *C.R. Acad. Sci. Paris Sci. Vie* 323:1–12.
- Muys, B., and N. Lust. 1993. Ecological changes following afforestation with different tree species on a sandy loam soil in Flanders, Belgium. p. 179–189. *In* C. Watkins (ed.) *Ecological effects of*

- afforestation. Studies in the history and ecology of afforestation in Europe. CAB International, Wallingford.
- Nielsen, K.E., K. Dalsgaard, and P. Nørnberg. 1987. Effects on soils of an oak invasion of a *Calluna* heath, Denmark. I. Morphology and chemistry. *Geoderma* 41:79–95.
- Orsini, L., and J.C. Rémy. 1976. Utilisation du chlorure de cobaltihexamine pour la détermination simultanée de la capacité d'échange et des bases échangeables. (In French.) *Sci. Sol* 4:269–275.
- Ott, E., M. Frehner, H.U. Frey, and P. Lüscher. 1997. Gebirgsnadelwälder. (In German.) Verlag Paul Haupt, Bern.
- Ovington, J.D. 1954. Studies of the development of woodland conditions under different trees. II. The forest floor. *J. Ecol.* 42:71–80.
- Peltier, A., J.F. Ponge, R. Jordana, and A. Ariño. 2001. Humus forms in Mediterranean scrublands with Aleppo pine. *Soil Sci. Soc. Am. J.* 65:884–896.
- Phillipson, J. 1989. Biological processes in forest ecosystems (Enigmas of European beech). *Verh. Ges. Ökol.* 17:21–32.
- Ponge, J.F. 1999a. Horizons and humus forms in beech forests of the Belgian Ardennes. *Soil Sci. Soc. Am. J.* 63:1888–1901.
- Ponge, J.F. 1999b. Heterogeneity in soil animal communities and the development of humus forms. p. 33–44. In N. Rastin and J. Bauhus (ed.) *Going underground. Ecological studies in forest soils.* Research Signpost, Trivandrum, India.
- Ponge, J.F. 2000. Biodiversité et biomasse de la faune du sol sous climat tempéré. (In French.) *C.R. Acad. Agr. Fr.* 86:129–135.
- Ponge, J.F., J. André, O. Zackrisson, N. Bernier, M.C. Nilsson, and C. Gallet. 1998. The forest regeneration puzzle. Biological mechanisms in humus layer and forest vegetation dynamics. *BioScience* 48:523–530.
- Ponge, J.F., P. Arpin, F. Sondag, and F. Delecour. 1997. Soil fauna and site assessment in beech stands of the Belgian Ardennes. *Can. J. For. Res.* 27:2053–2064.
- Ponge, J.F., F. Charnet, and J.M. Allouard. 2000. Comment distinguer dysmoder et mor? L'exemple de la forêt domaniale de Perche-Trappe (Orne). (In French.) *Rev. For. Fr.* 52:23–37.
- Ponge, J.F., and L. Delhaye. 1995. The heterogeneity of humus profiles and earthworm communities in a virgin beech forest. *Biol. Fertil. Soils* 20:24–32.
- Ponge, J.F., N. Patzel, L. Delhaye, E. Devigne, C. Levieux, P. Béros, and R. Wittebroodt. 1999. Interactions between earthworms, litter and trees in an old-growth beech forest. *Biol. Fertil. Soils* 29:360–370.
- Prusinkiewicz, Z. 1978. Application of a mathematical model of organic matter accumulation and decomposition for comparative studies of various forest floor types. *Ekol. Pol.* 26:347–357.
- Riha, S.J., B.R. James, G.P. Senesac, and E. Pallant. 1986. Spatial variability of soil pH and organic matter in forest plantations. *Soil Sci. Soc. Am. J.* 50:1347–1352.
- Schwertmann, U. 1985. The effect of pedogenic environments on iron oxide minerals. *Adv. Soil Sci.* 1:171–200.
- Sokal, R.R., and F.J. Rohlf. 1995. *Biometry. The principles and practice of statistics in biological research.* W.H. Freeman and Company, New York.
- Staaf, H. 1987. Foliage litter turnover and earthworm populations in three beech forests of contrasting soil and vegetation types. *Oecologia* 72:58–64.
- Switzer, G.L., M.G. Shelton, and L.E. Nelson. 1979. Successional development of the forest floor and soil surface on upland sites of the East Gulf Coastal Plain. *Ecology* 60:1162–1171.
- Terlinden, M., and P. André. 1988. Effets de l'intensité d'éclaircie sur les horizons organiques et hémiorganiques du sol en futaie équienne de *Picea abies*. (In French.) *Pedobiologia* 32:301–309.
- Topoliantz, S., and J.F. Ponge. 2000. Influence of site conditions on the survival of *Fagus sylvatica* seedlings in an old-growth beech forest. *J. Veg. Sci.* 11:369–374.
- Torgersen, C.E., J.A. Jones, A.R. Moldenke, and M.P. LeMaster. 1995. The spatial heterogeneity of soil invertebrates and edaphic properties in an old-growth forest stand in western Oregon. p. 225–236. In H.P. Collins et al. (ed.) *The significance and regulation of soil biodiversity.* Kluwer Academic Publishers, Dordrecht, the Netherlands.
- Ulrich, B. 1994. Process hierarchy in forest ecosystems: an integrative ecosystem theory. p. 353–397. In A. Hutterman and D. Godbold (ed.) *Effects of acid rain on forest processes.* Wiley-Liss, New York.
- Van Delft, S.P.J., J.C.Y. Marinissen, and W.A.M. Didden. 1999. Humus profile degradation as influenced by decreasing earthworm activity. *Pedobiologia* 43:561–567.
- Van der Drift, J. 1962. The soil animals in an oak-wood with different types of humus formation. p. 343–347. In P.W. Murphy (ed.) *Progress in soil zoology.* Butterworths, London.
- Van der Drift, J. 1963. The disappearance of litter in mull and mor in connection with weather conditions and the activity of the macrofauna. p. 125–133. In J. Doeksen and J. Van der Drift (ed.) *Soil organisms.* North Holland Publishing Co., Amsterdam, the Netherlands.
- Wardle, D.A., O. Zackrisson, G. Hörnberg, and C. Gallet. 1997. The influence of island area on ecosystem properties. *Science* 277:1296–1299.
- Witkamp, M., and J. Van der Drift. 1961. Breakdown of forest litter in relation to environmental factors. *Plant Soil* 15:295–311.
- Wolters, V. 1999. *Allium ursinum* litter triggering decomposition on a beech forest floor. The effect of earthworms. *Pedobiologia* 43:528–536.