Soil acidification under the crown of oak trees. I. Spatial distribution

Frédéric Beniamino, Jean-François Ponge, Pierre Arpin

► To cite this version:

Frédéric Beniamino, Jean-François Ponge, Pierre Arpin. Soil acidification under the crown of oak trees. I. Spatial distribution. *Forest Ecology and Management*, 1991, 40 (3-4), pp.221-232. 10.1016/0378-1127(91)90041-S . hal-00506969

HAL Id: hal-00506969

<https://hal.science/hal-00506969>

Submitted on 8 Oct 2010

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Soil acidification under the crown of oak trees. I. Spatial distribution

F. Beniamino; J.F. Ponge and P. Arpin

Museum National d'Histoire Naturelle, Laboratoire d'Ecologie Générale, UA 689-CNRS, 4, Avenue du Petit-Chateau, F-91800 Brunoy, France

ABSTRACT

Thirty oak trees (*Quercus robur* L. sensu lato) growing on the same site were selected on the basis of their stem diameter ($D_{bh} \geq 0.625$ m) and their effect on soil properties was assessed. Litterfall, old litter accumulation, acidity and buffering capacity of the A₁ horizon were measured at three distances from the trunk (0.4, 1.4 and 2.4 m) and in four directions (N, E, S, W). Results led to the conclusion that on average more acidification and litter accumulation occurred near the trunk base and in the north direction, but this general trend was far from being followed by every tree. The clay content of the soil was inversely related to acidification and litter accumulation. Interrelationships between soil organisms, crown leaching, bark substances and the parent rock are proposed as working hypotheses for the future of this study.

INTRODUCTION

During the last fifteen years soil acidification processes have attracted increased interest due to consequences of industrial pollution over forested areas, especially in North and Central Europe (Tamm, 1976; Abrahamsen, 1984; Wittig et al., 1985; Van Breemen, 1985; Kauppi et al., 1986; Wittig, 1986; Falkengren-Grerup, 1986, 1987; Hallbäcken and Tamm, 1986; Tyler, 1987). Acidification markedly affects the area near the trunk base of trees, as has been assessed by soil pH and vegetation data (Zinke, 1962; Lane and Witcher, 1963; Wittig and Neite, 1985; Cloutier, 1985; Riha et al., 1986a,b; Wittig, 1986) and study of the mycorrhizal types (Kumpfer and Heyser, 1986). This phenomenon has been mainly attributed to stemflow, but bark falling near the trunk has been also implicated (Zinke, 1962). The acidic nature of water running down the trunk was established by several studies on oak (Carlisle et al., 1967) and other trees (Mina, 1967). Given its richness in cations, it may

be thought that the acidity of stemflow is mostly due to the charge of water-soluble phenolic substances leached from bark and their chelating properties (Updegraff and Grant, 1975; Olsson, 1978): Mina (1967) pointed out that rough bark gives a more acidic stemflow than does smooth bark. Wittig (1986), in view of the large amount of water collected by the trunk, especially on trees where branches fork at an acute angle (Aussenac, 1968, 1970), invoked pollution by rain and mist in order to explain the observed acidification of the stemflow area (ground area influenced by stemflow). He derived this hypothesis from a comparison of the number of acid indicators (plant species) in the stemflow area through several beech forests of Central (polluted) and South (less polluted) Europe. Doubts can be raised against this contention because of the different nature of humus in warmer countries, where organic matter rarely accumulates on the top of soil. In addition, such 'acid' indicators as *Deschampsia flexuosa* are in fact resistant to phenolic substances (Kuiters and Sarink, 1987).

In a previous study (Arpin et al., 1984) a strong modification of the humus type, with contingent acidification, was observed under the crown of an old oak tree. In the present study, this effect was investigated in order to verify its generality and derive some working hypotheses concerning the causes involved.

In this paper, soil acidity and litter accumulation will be described. Complete data have been presented in a more extensive paper (Beniamino, 1989). Experimental studies will be reported in a subsequent contribution.

SITE DESCRIPTION

The study area has been described previously (Arpin et al., 1984, stations 3 and 4). It is a coppice with standards (full-grown trees) approximately 150 years old, growing on a gentle slope facing the river Seine (state forest of Senart, 30 km south of Paris). Standards are sessile oaks [*Quereus petraea* (Mattuschka) Liebl.] except one single pedunculate oak [*Q. robur* L.], but hybridation, indicated by thorough examination of the leaves, seems to be very frequent. Some trees are isolated but generally the crowns join each other. The coppice comprises lime (*Tilia cordata* Mill.) and hornbeam (*Carpinus betulus* L.). Their development is hampered by competition for light with oak canopies, except in some places. The soil is a loam to clay loam brown leached soil (luvi- to cambisol under the FAO classification; Duchaufour, 1983), with boulders up to the ground surface. Usually the humus is an acid mull, with a pH of the A₁ horizon ranging from 4 to 5, and we noticed an obvious mole activity, whose importance in mull formation has been stressed by Bornebusch (1930). The ground

vegetation is mainly of bramble (*Rubus* sp.), ivy (*Hedera helix* L.), dog's mercury (*Mercurialis perennis*), yellow dead-nettle (*Galeobdolon luteum* Huds.), oak seedlings and abundant spring flowering species, such as squill [*Scilla bifolia* (L.)], bluebell [*Endymion non-scriptus* (L.) Garcke] and wood-anemone (*Anemone nemorosa* L.). More detailed description of the site has been presented elsewhere (Beniamino, 1989).

METHODS

Thirty trees were randomly selected among 74 growing in the same compartment, each with ~0.625 m breast-height diameter. Four directions corresponding to the cardinal points were sampled in order to assess the possible influence of winds on litter distribution and influence of light and rains on soil properties. Since it was quite impossible to compare the soil under an oak crown to other places not influenced by trees, it was arbitrarily decided to sample at three distances from the trunk base, i.e. 0.4, 1.4 and 2.4 m. Combination of the two factors under study (direction and distance from the tree trunk base) gave $30 \times 4 \times 3 = 360$ sampling points.

Litter fall and accumulation were measured at each sampling point just after the main fall (end November 1988). A stainless steel 15 cm $\varnothing$ cylinder with chamfered edge was forced into the soil. Fresh litter (L_1 layer) and accumulated organic matter (L_2 to H layers) were separately collected, air-dried then weighed. Fresh litter was expressed as total litter, and in addition subdivided into oak, beech, lime, hornbeam, sycamore, bramble leaves and miscellaneous (wood, bark, acorns, etc.). The A_1 horizon was sampled down to 10 cm, then air-dried, sieved to 2 mm and preserved for acidity and buffering capacity measurements.

Acidity of the soil solution was measured in a 1:2 soil:water suspension (50 g soil + 100 g deionized water) after the mixture had settled for 24 h. Measurement of pH was made with a glass electrode (with a KCl electrode included as a reference) in constant agitation. Titration was made with a 1N NaOH solution up to pH 7. Immediate titration indicated the more easily available acidity. Titration after 1 and 24 h revealed more stable acidity forms. The buffering capacity was expressed as the quantity of NaOH necessary to rise the pH of one half-unit above the immediate reading. All these measurements were made on the same soil suspension.

Statistical analyses were performed using three-way analyses of variance (Sokal and Rohlf, 1969; Dagnélie, 1975). Given the strong heterogeneity between trees, they were considered as blocks. Combinations of the three distances and the four orientations were the treatments applied to each block. The mixed model used was:

$$X_{ijk} = \mu + \alpha_i + \beta_j + C_k + \varepsilon_{ijk}$$

where X was the observed value, μ was the mean, α and P were fixed treatment effects (distance and orientation), C the random block effect and ε the residual. Interaction terms have been omitted. Data were transformed whenever necessary in order to normalize the distribution of the residues (homoscedasticity of the data), thus insuring additivity of the effects. Multiple comparisons were made between means using Newman-Keuls a posterior tests. Product-moment correlation coefficients between variables were calculated with trees as pairs. Ranks were used instead of measured values, in order to include some variates that did not meet assumption of analysis of variance, particularly variates with too many null values (leaf components other than oak). Measurements that were not made at each sampling plot but pooled for each tree, such as data (%) on soil particle size, were included only in correlation studies (Spearman rank correlation coefficient: Sokal and Rohlf, 1969). This was also the case for tree height, stem diameter, and degree of crown competition. Simple correlation was used as a tool for measuring the degree of co-variation between two variables. Testing the null hypothesis was made using statistical tables (Fisher and Yates, 1963; Rohlf and Sokal, 1969) but the authors are conscious of the fact that some significant correlation coefficients might have been produced by chance when calculated on a great number of couples. The threshold of significance of the tests, both for variance analysis and correlation studies, was fixed at 1 %.

RESULTS

Variance analysis

Table 1 summarizes the results of the analyses of variance which were run on ten variables, after suitable transformations. The more conspicuous phenomena are acidification and accumulation of organic matter near the tree trunk base. The most significant trends are exhibited by old litter areal weight ($\times 1.5$ between 1.4 and 0.4 m, $\times 2.4$ between 2.4 and 0.4 m), immediate titration ($\times 1.4$ between 1.4 and 0.4 m), and titration after 24 h ($\times 1.7$ between 1.4 and 0.4 m). All these trends are significant at the 0.0001 level. Although this variation is significant only at the 0.01 level, pH is lowered by 0.17 unit (proton concentration magnified by 1.5) between 1.4 and 0.4 m. Thus all these trends are of the same order of magnitude. Total fresh litter and miscellaneous litter do not exhibit any significant trend, but this is not true of oak litter, with a slight but marked increase in fall

between 1.4 and 0.4 m ($\times 1.14$).

Interaction between the two treatment levels (distance and orientation) was never significant even at the 5% level, thus enabling the testing of these two treatment levels separately. Variation between trees was always highly significant ($P < 0.0001$), indicating that large discrepancies exist between them in their response to distance and orientation. Table 2 summarizes the variation between trees.

Correlation

It was necessary to know whether or not the trees around which organic matter was accumulating and those around which soil acidification was occurring were the same. This was not indicated by separate analyses of variance and so data were pooled for each tree (Table 2) and compared from one tree to another. In addition, gradients from 1.4 to 0.4 m for the most significant variates were calculated by subtracting values at 1.4 m from the values measured at 0.4 m (pooled for the four directions). The same calculations were performed between north and south values.

Total, miscellaneous and lime litter are correlated ($r = 0.85$ between total and miscellaneous litter, $r = 0.54$ between lime and miscellaneous litter). Lime litter and beech litter are correlated with the fine-silt content of the soil but in an opposite way ($r = -0.49$ and 0.54). In this case we may question the validity of rejecting the null hypothesis, but we cannot discard some possible influence of the substrate on the presence or development of lime and beech understory under the crown of trees. Bramble and hornbeam litters are not correlated with any other measurement.

Oak litter data, when pooled under each tree, do not exhibit any significant correlation, but the difference between 0.4 and 1.4 m is correlated to that for pH of the A1 horizon ($r = -0.50$). This means that the higher oak litter accumulates at the tree trunk base the higher is the corresponding gradient of acidification.

Soil pH and accumulated old litter are negatively correlated at the 0.001 level ($r = -0.76$). Thus, trees that accumulate organic matter in the upper horizons of the soil are the same under which the A₁ horizon is acid. Nevertheless, the same relation was not found between decrease of pH between 1.4 and 0.4 m (sample points) and increase of old litter accumulation at the same distance.

Other relationships are quantified by the product-moment correlation, but they concern the different kinds of acidity and their relation to accumulated organic matter. Both pH and old litter areal weight are correlated with immediate titration ($r = -0.58$ and 0.50 respectively) and titration after 1 h ($r = -0.59$ and 0.54). Decrease of soil pH between 1.4 and 0.4 m is negatively correlated with a similar gradient in immediate titration ($r = -0.55$), titration after 1 h ($r = -0.55$) and titration after 24 h ($r = -0.65$). Immediate titration is correlated with titration after 1 h ($r = 0.74$). Buffering capacity is correlated with pH ($r = -0.46$), immediate titration ($r = 0.90$), titration after 1 h ($r = 0.70$) and accumulation of organic matter ($r = 0.53$).

Among factors which may influence pH or accumulation of litter, the clay content of the soil, which is correlated with these two variates ($r = 0.65$ and -0.56 respectively), may be highlighted. This means that the trees growing on a soil containing more clay do not acidify and accumulate organic matter as much as trees growing on a soil poorer in clay. This is confirmed by a significant correlation between old litter accumulation and the coarse sand content of the soil ($r = 0.47$). Significant correlation between fine-sand content of the soil and titration after 24 h ($r = 0.56$) may be also related to the same phenomenon. Unlike oak litter, beech litter exhibits a significant correlation with accumulation of organic matter ($r = 0.54$), but this cannot be taken as a causal relationship, since beech is very sparsely distributed in the stand under study.

Height of the trees and stem diameter are never correlated with the other variates, they are just correlated between themselves ($r = 0.57$). It must be noticed that these two measurements are not informative either of the age of the trees or of their productivity, since some of the trees grew freely, but some others did not, as ascertained by crown development and height of the main branching.

Differences between north and west in soil acidity and litter accumulation were calculated and compared to the other variates. Opposition between north and west is correlated with the trunk effect (gradient between 1.4 and 0.4 m) for litter accumulation ($r = 0.49$), indicating that similar factors influence these two phenomena. A similar relation was not evidenced for pH, but it must be noticed that the contrast between the north and the west side of the tree for pH is correlated with the gradient 0.4–1.4 m for titration after 24 h ($r = -0.56$).

DISCUSSION

Despite of the fact that autumn litterfall is highly variable from one tree to another (from 580 to 807 g/m²), no relation was found between litter accumulation and litter fall ($r = 0.08$ and 0.04 respectively). The question which arises is whether or not litter is displaced by wind once on the ground. Since no influence of the direction was visible on the data, and oak litterfall is more pronounced near the trunk base (which correspond to the position of the top of the crown) this indicates that redistribution under the influence of winds was probably negligible. Relation between the increase in the part played by oak leaves in litter near the trunk base and increase of acidity in the same area may nevertheless be highlighted. Examination of the data of Ovington (1953), and our own measurements on oak leaves (L layer) soaked in water, show values around pH 5 in the leaf leachate. This is not very different from the pH of deionized or distilled water (after equilibration with air). More probably, oak leaf litter and oak foliage have effects through the organic acids they produce during crown leaching and decomposition. These are weak proton producers but very active complexing agents, especially aliphatic acids (King and Bloomfield, 1968; Bruckert, 1970).

The relation between stemflow and acidification of the soil around the trunk may be questioned in the case of oak-trees, since most of the rain running down branches does not reach the soil. Stemflow is only 0.62% of the incident rain in an oak stand of similar age and in the same geographic region, with trees branching at a more acute angle (Nizinski and Saugier, 1988). In the present study, observations during showers in winter did not indicate any arrival of water to the ground, probably due to the right-angle branching of the trees. The stem is wetted only by rainwater falling directly on the bark, the effect being well-marked when trees are bending down eastwards. Nevertheless, slow diffusion of water-soluble substances from the stump bark and the fall of pieces of bark must be considered. Given the high tannin content of bark (Updegraff and Grant, 1975; Olsson, 1978) and pH of the leachate when soaked in water (between 3 and 4 in our own experiments, against 5 in Olsson's experiments), it is probable that some area around the trunk base is affected by this source of acidity. This does not explain why the north side is more affected than the west side of the tree. We may hypothesize that perhaps some pollutants such as SO₂ whose absorption by foliage is very feeble (Lovett and Lindberg, 1984), are responsible for such a situation: pollution, which is not negligible in the Senart forest (indicated by the absence of hairy lichens), comes mainly from true north, this forest being situated 30 km south of Paris.

The role of the clay content of the soil, as an antagonism to the process of acidification, becomes apparent from our data, since a great part of the variation between trees may be explained by this soil component. The role of clay (and iron) as a driving agent in mull formation is well-known (Duchaufour, 1983),

but many hypotheses may account for it. Between them, we may highlight the detoxifying role of clay minerals: they precipitate phenolic and aliphatic acids (Tan, 1982), thus rendering the soil solution more suitable to mull-forming species.

ACKNOWLEDGEMENTS

We are very grateful to Dr. Gloria Nombella for her assistance. We also like to thank Prof. Amyan Macfadyen (U.K.) and Prof. Dennis Parkinson (Canada) for careful examination of the manuscript and revision of the English language.

REFERENCES

- Abrahamsen, G., 1984. Effects of acidic deposition on forest soil and vegetation. *Philos. Trans. R. Soc. Lond. B*, 305: 369–382.
- Arpin, P., Ponge, J.F., Dabin, B. and Mori, A., 1984. Utilisation des nématodes Mononchida et des Collembolés pour caractériser des phénomènes pédobiologiques. *Rev. Ecol. Biol. Sol*, 21: 243–268.
- Aussenac, G., 1968. Interception des précipitations par le couvert forestier. *Ann. Sci. For.*, 25: 135-156.
- Aussenac, G. , 1970. Action du couvert forestier sur la distribution au sol des précipitations. *Ann. Sci. For.*, 27: 383–399.
- Beniamino, F., 1989. Etude de l'acidification sous les chênes de réserve dans un T.S.F. de la forêt domaniale de Sénart. Unpublished memo., 62 pp. +outlier 42 pp.
- Bornebusch, C.H., 1930. The fauna of forest soil. *Forstl. Forsoegsvaes.*, 11: 1–158.
- Bruckert, S., 1970. Influence des composés organiques solubles sur la pédogénèse en milieu acide. I. Etudes de terrain. *Ann. Agron.*, 21: 421–452.
- Carlisle, A., Brown, A.H.F. and White, E.J., 1967. The nutrient content of tree stem flow and ground flora litter and leachates in a sessile oak (*Quercus petraea*) woodland. *J. Ecol.*, 55: 615–627.

- Cloutier, A., 1985. Microdistribution des espèces végétales au pied des troncs d'*Acer saccharum* dans une érablière du sud du Québec. *Can. J. Bot.*, 63: 274–276.
- Dagnélie, P., 1975. Théorie et méthodes statistiques. Applications agronomiques. II. Les méthodes de l'inférence statistique. Les Presses Agronomiques de Gembloux, Belgium, 463 pp.
- Duchaufour, P., 1983. Pédologie. I. Pédogénèse et Classification. (2nd edition). Masson, Paris, 491 pp.
- Falkengren-Grerup, U., 1986. Soil acidification and vegetation changes in deciduous forest in southern Sweden. *Oecologia* (Berlin), 70: 339–347.
- Falkengren-Grerup, U., 1987. Long-term changes in pH of forest soils in southern Sweden. *Environ. Pollut.*, 43: 79–90.
- Fisher, R.A. and Yates, F., 1963. Statistical Tables for Biological, Agricultural and Medical Research. Oliver and Boyd, Edinburgh, 146 pp.
- Hallbäck, L. and Tamm, C.O., 1986. Changes in soil acidity from 1927 to 1982–1984 in a forest area of South-West Sweden. *Scand. J. For. Res.*, 1: 219–232.
- Kauppi, P., Kamari, J., Posch, M., Kauppi, L. and Matzner, E., 1986. Acidification of forest soils: model development and application for analyzing impacts of acidic deposition in Europe. *Ecol. Modelling*, 33: 231–253.
- King, H.G.C. and Bloomfield, c., 1968. The effects of drying and ageing tree leaves on the ability of their aqueous extracts to dissolve ferric oxide. *J. Soil Sci.*, 19: 67–76.
- Kuiters, A.T. and Sarink, H.M., 1987. Effects of phenolic acids on growth, mineral composition and chlorophyll content of some herbaceous woodland species. *Z. Pflanzenernähr. Bodenkd.*, 150: 94–98.
- Kumpfer, W. and Heyser, W., 1986. Effects of stemflow on the mycorrhiza of beech (*Fagus sylvaticus* L.). In: V. Gianinazzi-Pearson and S. Gianinazzi (Editors), *Physiological and Genetical Aspects of Mycorrhizae*. Proc. 1st European Symposium on Mycorrhizae, 1–5 June 1985, Dijon, France. INRA, Paris, pp. 745–750.
- Lane, C.L. and Witcher, W., 1963. Comparison of pH of pine stem, bark, roots, and adjacent soil. Unpublished

paper presented to the South Carolina Academy of Science, 27 April 1963.

Lovett, G.M. and Lindberg, S.E., 1984. Dry deposition and canopy exchange in a mixed oak forest as determined by analysis of throughfall. *J. Appl. Ecol.*, 21: 1013–1027.

Mina, V.N., 1967. Influence of stemflow on soil. *Sov. Soil Sci.*, 7: 1321–1329.

Nizinski, J. and Saugier, B., 1988. Mesures et modélisation de l'interception nette dans une futaie de chênes. *Acta Oecol., Oecol. Plant.*, 9: 311–329.

Olsson, M.T., 1978. Properties and decomposition of bark. Swedish University of Agricultural Sciences, Uppsala, Dep. For. Soils, Rep. For. Ecol. For. Soils, 34: 13 pp.

Ovington, J.O., 1953. Studies of the development of woodland conditions under different trees. I. Soil pH. *J. Ecol.*, 41: 13–34.

Riha, S.J., James, B.R., Senesac, G.P. and Pallant, E., 1986a. Spatial variability of soil pH and organic matter in forest plantations. *Soil Sci. Soc. Am. J.*, 50: 1347–1352.

Riha, S.J., Senesac, G. and Pallant, E., 1986b. Effects of forest vegetation on spatial variability of surface mineral soil pH, soluble aluminium and carbon. *Water Air Soil Pollut.*, 31: 929–940.

Rohlf, F.J. and Sokal, R.R., 1969. Statistical Tables. W.H. Freeman, San Francisco, 253 pp.

Sokal, R.R. and Rohlf, F.J., 1969. Biometry. The Principles and Practice of Statistics in Biological Research. W.H. Freeman, San Francisco, 776 pp.

Tamm, C.O., 1976. Acid precipitation: biological effects in soil and on forest vegetation. *Ambio*, 5: 235–238.

Tan, K.H., 1982. Principles of Soil Chemistry. Marcel Dekker, New York, 267 pp.

Tyler, G., 1987. Probable effects of soil acidification and nitrogen deposition on the floristic composition of oak (*Quercus robur* L.) forest. *Flora*, 179: 165–170.

Updegraff, D.M. and Grant, W.D., 1975. Microbial utilization of *Pinus radiata* bark. *Appl. Microbiol.*, 30: 722–726.

- Van Breemen, N., 1985. Acidification and decline of Central European forests. *Nature*, 315: 16.
- Wittig, R., 1986. Acidification phenomena in beech (*Fagus sylvatica*) forests of Europe. *Water Air Soil Pollut.*, 31: 317–323.
- Wittig, R. and Neite, H., 1985. Acid indicators around the trunk base of *Fagus sylvatica* in limestone and loess beechwoods: distribution pattern and phytosociological problems. *Vegetatio*, 64: 113–119.
- Wittig, R., Ballach, H.J. and Brandt, C.J., 1985. Increase of number of acid indicators in the herb layer of the millet grass-beech forest of the Westphalian Bight. *Angew. Bot.*, 59: 219–232.
- Zinke, P.J., 1962. The pattern of influence of individual forest trees on soil properties. *Ecology*, 43: 130–133.

TABLE 1

Analysis of variance

Measurement	Distance	40 cm	140cm	240 cm	Orientation	North	East	South	West
Total fresh litter (g/m ²)	n.s.	608	593	564	n.s.	550	624	593	578
Oak fresh litter (g/m ²)	*	371 _a	326 _b	318 _b	n.s.	340	331	342	340
Fresh litter miscellaneous (g/m ²)	n.s.	169	185	169	n.s.	144	214	169	169
Old litter (g/m ²)	***	3116 _a	2024 _b	1288 _c	*	2450 _a	2010 _{ab}	2296 _a	1596 _b
pH H ₂ O	*	4.41 _a	4.58 _b	4.49 _b	*	4.41 _a	4.45 _{ab}	4.58 _b	4.58 _b
Buffering capacity (meq/ 100 g air-dried soil)	n.s.	0.23	0.21	0.20	n.s.	0.23	0.20	0.21	0.23
Immediate titration (meq/ 100 g air-dried soil)	***	1.64 _a	1.26 _b	1.19 _b	n.s.	1.48	1.40	1.33	1.33
Titration 1 h (meq/ 100 g air-dried soil)	n.s.	0.79	0.79	0.79	n.s.	0.89	0.79	0.74	0.84
Titration 24 h (meq/ 1 00 g air-dried soil)	***	1.00 _a	0.65 _b	0.74 _b	n.s.	0.89	0.70	0.74	0.84

Titration 1 h=NaOH IN added 1 h after immediate titration to adjust pH to 7.

Titration 24 h=NaOH IN added 24 h after to adjust pH to 7.

n.s. = not significant at the 0.01 level.

*, **, *** = significant at the 0.01, 0.001, 0.0001 level.

When heterogeneity among treatments is significant, mean values belonging to the same group (Newman-Keuls test) are followed by a common letter.

TABLE 2

Pooled data for each of the 30 trees under study (each tree is indicated by a number in top of each column)

Measurement	13	27	26	21	14	17	18	15	30	20	1	7	6	3	8
Total fresh litter (g/m ²)	578	460	496	656	448	707	564	564	672	564	608	624	725	780	448
Oak fresh litter (g/m ²)	391	321	310	388	310	400	368	279	453	400	368	252	276	374	266
Lime fresh litter (g/m ²)	5	2	3	26	7	11	1	17	7	18	18	24	41	16	15
Bramble fresh litter (g/m ²)	5	4	1	3	19	4	15	21	0	10	17	31	6	9	2
Hornbeam fresh litter (g/m ²)	0	8	17	3	0	6	1	0	53	1	0	1	1	1	2
Beech fresh litter (g/m ²)	3	1	3	17	6	4	8	2	0	1	0	0	0	0	1
Maple fresh litter (g/m ²)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fresh litter miscellaneous (g/m ²)	149	107	127	190	103	227	140	196	159	107	131	262	309	317	135
Old litter (g/m ²)	7733	5853	4462	4323	4224	3559	3469	2999	2773	2450	2189	1983	1950	1943	1910
pH H ₂ O	3.76	4.12	4.37	4.33	4.24	4.45	4.08	4.16	4.41	4.58	4.20	4.37	4.20	4.67	4.54
Buffering capacity (meq/100 g air-dried soil)	0.15	0.39	0.28	0.33	0.23	0.23	0.27	0.18	0.21	0.14	0.33	0.47	0.27	0.20	0.42
Immediate titration (meq/100 g air-dried soil)	1.25	2.01	1.91	1.64	1.40	1.33	2.12	1.12	1.48	0.89	1.64	2.46	2.01	1.26	2.12
Titration 1 h (meq/100 g air-dried soil)	0.50	1.40	0.79	1.12	1.33	0.70	1.12	1.33	1.00	0.50	0.64	1.56	1.56	0.74	2.23
Titration 24 h (meq/100 g air-dried soil)	0.79	2.58	1.33	0.74	0.84	0.74	0.65	0.74	0.79	0.57	1.64	0.79	0.65	1.48	0.74
Tree height (m)	23.0	25.0	24.0	22.0	22.0	22.5	22.0	22.0	25.0	21.0	22.0	23.0	22.5	22.5	23.0
Stem diameter (cm)	71	120	79	68	68	64	69	67	82	66	71	65	64	73	82
Clay (%)	11.4	13.8	31.3	14.4	14.8	18.5	17.6	22.2	16.4	30.2	19.2	21.6	22.1	21.2	21.0
Fine silt (%)	25.6	23.2	22.1	20.9	30.7	27.1	26.4	25.4	24.4	27.5	14.6	23.1	22.7	21.5	24.3
Coarse silt (%)	18.0	14.5	1.9	15.4	12.4	18.9	18.9	16.7	17.3	2.3	3.1	18.0	14.2	10.8	16.9
Fine sand (%)	15.4	21.9	20.3	17.7	15.3	14.0	12.5	13.9	15.9	14.5	21.7	13.2	15.7	17.9	13.6
Coarse sand (%)	29.6	26.6	24.4	31.7	26.8	21.5	24.6	21.8	26.1	25.6	41.5	24.1	25.3	28.7	24.1

Measurement	16	5	9	29	4	24	22	11	2	12	23	10	25	19	28
Total fresh litter (g/m ²)	656	725	725	861	578	509	593	403	689	363	578	578	425	820	522
Oak fresh litter (g/m ²)	437	307	406	297	238	269	391	240	326	242	377	403	334	513	307
Lime fresh litter (g/m ²)	23	22	18	38	16	25	7	17	19	16	20	12	8	11	7
Bramble fresh litter (g/m ²)	2	8	1	2	34	0	0	11	6	15	1	3	1	7	0
Hornbeam fresh litter (g/m ²)	5	1	5	18	3	1	1	8	0	14	2	7	4	16	1
Beech fresh litter (g/m ²)	2	0	0	0	0	0	5	0	0	0	2	0	1	0	0
Maple fresh litter (g/m ²)	2	2	0	0	1	0	0	0	0	0	0	0	0	0	14
Fresh litter miscellaneous (g/m ²)	164	353	262	448	262	164	169	114	300	70	149	127	64	227	140
Old litter (g/m ²)	1787	1731	1687	1501	1415	1331	1182	1182	1121	1121	951	914	654	554	482
pH H ₂ O	4.41	4.67	4.49	4.16	4.88	4.75	4.54	4.58	4.41	4.45	4.75	4.67	5.24	5.52	5.20
Buffering capacity (meq/100 g air-dried soil)	0.17	0.25	0.21	0.25	0.13	0.21	0.25	0.12	0.13	0.14	0.18	0.15	0.20	0.14	0.17
Immediate titration (meq/100 g air-dried soil)	1.26	1.82	1.40	2.01	0.74	1.33	1.91	0.79	1.00	1.12	1.40	1.00	0.89	0.65	0.89
Titration 1 h (meq/100 g air-dried soil)	1.19	1.26	0.43	0.95	0.65	0.57	0.74	0.24	0.79	0.57	0.61	0.61	0.43	0.34	0.43
Titration 24 h (meq/100 g air-dried soil)	0.61	0.61	0.34	1.12	1.64	0.74	0.74	0.24	1.48	0.46	1.00	0.46	0.43	0.26	0.95
Tree height (m)	26.5	23.0	28.5	25.0	22.0	24.0	20.0	24.5	22.0	23.0	21.5	25.0	22.0	21.0	31.0
Stem diameter (cm)	97	90	91	65	67	67	65	66	69	64	63	75	63	67	74
Clay (%)	24.5	24.4	26.8	19.2	25.8	24.7	24.8	20.9	18.0	24.5	34.8	25.9	37.5	23.0	23.3
Fine silt (%)	22.6	14.4	22.5	19.4	13.6	20.9	26.4	23.2	19.4	19.4	22.4	20.7	23.1	24.3	23.9
Coarse silt (%)	18.6	12.9	12.2	19.0	15.0	18.2	13.6	16.3	13.8	19.0	5.3	18.5	2.2	17.4	17.1
Fine sand (%)	14.0	16.3	13.8	17.7	16.4	12.8	15.8	13.7	15.1	15.4	16.3	14.0	15.2	15.3	15.1
Coarse sand (%)	20.3	32.1	24.7	24.8	29.1	23.4	19.4	25.9	33.7	21.7	21.3	20.9	22.0	20.0	20.7