



Soil Biology & Biochemistry 37 (2005) 1695-1706



www.elsevier.com/locate/soilbio

Effects of tree species and topography on soil chemistry, litter quality, and decomposition in Northeast Turkey

T. Sariyildiz*, J.M. Anderson, M. Kucuk

Artvin Forestry Department, Kafkas University, 08000 Artvin, Turkey Received 4 November 2004; received in revised form 7 February 2005; accepted 9 February 2005

Abstract

Leaf litters from beech (Fagus orientalis Lipsky.) and oak (Quercus robur L.), and needle litters from fir (Abies nordmanniana Spach.) and pine (Pinus sylvestris L.) trees were collected from north-facing site and south-facing site and at three slope positions (top, middle and bottom) on each aspect that varied in soil chemical characteristics (soil pH, cation exchange capacity and base saturation). The litters were analysed for initial total carbon, nitrogen, acid detergent fibre, lignin and cellulose concentrations. Nitrogen, acid detergent fibre and lignin concentrations and carbon:nitrogen and lignin:nitrogen ratios varied significantly within and between species according to soil chemical characteristics on aspects and slope positions. Litter decomposition was studied in the field using the litterbag technique. The litters were placed on two aspects and at three slopes on each aspect in October 2001, and were sampled every 6-month for 2 years. The main effects of aspect, species and slope position on decomposition rates were all statistically significant. Oak leaf litter showed highest decomposition rates, followed by pine, fir and beech litter, and the litters placed on north-facing site decomposed faster than those on the south-facing site. The litters placed at the top slope position decomposed slower than at those at either the bottom or middle positions. Initial lignin concentrations explained most of the variation in decomposition rates between species, and within species for the aspects and the slope positions, but the explained variance showed differences between aspects and slope positions. This result illustrates the important point that litter quality may define the potential rates of microbial decomposition but these are significantly influenced by the biotic and abiotic environment in which decomposition takes place.

© 2005 Elsevier Ltd. All rights reserved.

Keywords: Decomposition; Slope; Aspect; Climate; Lignin; Litter; Soil fertility

1. Introduction

Decomposition of leaf litter is influenced by the physical environmental conditions under which decay takes place, by the nature and abundance of the decomposing organisms and by the chemical composition of the leaf litter, or litter quality (Heal et al., 1997; Zimmer, 2002; Sariyildiz and Anderson, 2003a,b). In general, climate (especially temperature and moisture) governs decay rates on broad regional scales, whereas initial litter quality variables (carbon:nitrogen (C:N) ratio, lignin, N, and lignin:N ratio) are of more importance in controlling decay rates at small scales, i.e. within site (Berg et al., 1993; Heal et al., 1997).

E-mail address: t_sariyildiz@yahoo.com (T. Sariyildiz).

0038-0717/\$ - see front matter © 2005 Elsevier Ltd. All rights reserved. doi:10.1016/j.soilbio.2005.02.004

However, a number of studies have shown that even at small scale topographical landforms (especially different aspects and slope positions) can create different environmental conditions which can retard or accelerate litter decomposition through negative or positive effects on the activity of organisms (Mudrick et al., 1994; Vitousek et al., 1994; Scowcroft et al., 2000).

In the northern Temperate Zone, slope aspect is an important topographic factor influencing local site microclimate, mainly because it determines the amount of solar radiation received. The amount of insolation governs air and soil temperatures, and soil water availability, which in turn affect establishment and growth of plants (Barnes et al., 1998; McNab, 1993). South-facing slopes, which receive the greatest amount of solar radiation, are typically hot, dry and subject to rapid changes in seasonal and diurnal microclimate. In contrast, north-facing slopes, which receive the least amount of insolation are cool, moist, and subject to slow changes in seasonal and daily microclimate.

^{*} Corresponding author.

Slope steepness also influences microclimate by affecting insolation and water drainage.

Another topographic factor that influences microclimate is slope position. Ridge tops or upper convex slope surfaces are exposed to intense solar radiation, experience high wind speeds, and are subject to erosion and soil movement (McNab, 1993). Therefore, they tend to be drier than is the average for the region. At the other extreme, lower slopes with concave surface tend to be sheltered from strong winds, subject to accumulation of organic matter and soil rather than to erosion and to cold-air drainage, and moister than average for the region. Mid-slopes are generally intermediate in their characteristics.

The slope position, slope aspect, and its inclination can also affect soil depth, profile development, soil chemical characteristics, and the texture and structure of the soil surface. Boerner (1984) reported that, in spite of similar parent materials, soils of north-facing sites had higher pH, soil organic matter, extractable nitrogen concentrations, and base saturation than those of south-facing sites. In a southern Appalachian watershed, Losche et al. (1970) found that soil pH and nutrient availability were highest on north-facing site, intermediate on south-facing sites, and lowest on ridge tops.

Although the effects of topographical land forms (slope aspect and position) on microclimate and soils, as well as on plant species composition, community development, and site productivity have been studied extensively (Barnes et al., 1998), very few studies have investigated their effect on litter decomposition rates.

The effects of topographical land forms (aspects and slope positions) on species composition, development, productivity, environmental conditions and soil characteristics have been well investigated (Barnes et al., 1998), whereas very few studies have investigated the effects of these different conditions on decomposition rates of a given species. For example, Mudrick et al. (1994) found that yellow poplar, red maple and chestnut oak growing on the north-facing sites decomposed faster than those growing on south-facing sites, and the same leaves placed at the middle slope position decomposed slower than those at either the upper or lower positions. They concluded that the differences in leaf litter mass loss could have resulted from differences in energy fluxes and in biotic factors between these sites. They did not consider the possibility that differences in soil chemistry and microclimate between topographical sites might result in considerable intra-specific variation in litter quality and thus decomposability.

In general, effects of topography on litter quality have received little attention. Sariyildiz and Anderson (2003a) showed for beech, oak and chestnut trees that the environmental conditions created by the tree canopy structure such as light intensity, wind, physical stress (mainly availability of water) caused considerable intraspecific variations in the litter quality and decomposition

rates of leaf litters. In another study, Sariyildiz and Anderson (2003b) showed that soil fertility significantly affected the quality and decomposition rates of beech and oak litters. For a conifer tree, Enoki et al. (1997) observed different chemical compositions of *Pinus thunbergii* Parl. needle litter along a topographical gradient of soil nutrient availability within an even-aged plantation. They suggested that the upslope decrease in nitrogen concentration of litterfall indicated an increase in nitrogen-use efficiency as a phenotypic response of *P. thunbergii* trees to low nutrient availability.

The objectives of the present study were to (1) investigate the effects of species, aspects and slope positions on soil chemistry, leaf litter quality, and rates of decomposition for four tree species, and (2) determine the effects of leaf litter quality on rates of decomposition. Beech (Fagus orientalis Lipsky.), fir (Abies nordmanniana Spach.), oak (Quercus robur L.) and pine (Pinus silvestris L.) litters and soil samples were collected from the top, middle and bottom slopes of the north- and south-facing sites (five replicate sites), so the effects of species, aspects and slope positions on soil chemical characteristics and litter quality could be evaluated. The soil samples were analysed for soil pH, cation exchange capacity (CEC) and base saturation (BS). These three factors were shown by a number of studies to be the most important soil chemical factors affecting the litter quality parameters within species (Sanger et al., 1996, 1998; Sariyildiz and Anderson, 2003a, b). Initial organic C, total N, acid detergent fibre (ADF), lignin, and cellulose concentrations were used as indices of litter quality. The litter bag technique was used to quantify rates of decomposition.

2. Materials and methods

2.1. Study areas

This study was carried out in the Artvin province, northeast Turkey, (41°51′N, 41°06′E), a mountainous region with steep slopes (range from 30 to 65%) and high elevations (up to 3000 m). Five areas located 8 km south-west of Artvin city were chosen to collect foliar litter of beech, oak, fir and pine trees. The five areas were within a 4 km radius. The maximum elevation of the five areas ranged from 1500 to 1600 m. In each area, three slope positions were selected at the top (1300), middle (1000) and bottom (700 m) on north and south aspects (30 sites in total). Three positions were located along one long slope at each sampling area. The slope angles of the five sites on the north aspects ranged from 50 to 55%, whereas the slope angles on the south aspects ranged from 40 to 45%. Both north- and southfacing sites were commonly forested by Picea orientalis, F. orientalis, A. nordmanniana spp. nordmanniana, P. silvestris, Castanae sativa and Quercus spp. either pure or in species mixture. Common forest formation types growing on these altitudes in each area were deciduous—coniferous forest (650–1100 m) and coniferous forest (1100–1600 m). Deciduous—coniferous forest formation was dominated by *Quercus* spp., *C. sativa* Mill., *Acer cappadocium* Gleditsch., *Acer campestre* L., *Alnus glutinosa* L., *Carpinus betulus* L., *F. orientalis* Lipsky., *Piceas orientalis* Link., *P. sylvestris* L. Coniferous forest formation was dominated by *P. orientalis* Link., *P. sylvestris* L., *A. nordmanniana* Spach. The understory at the lower part of the slope was occupied by grasses, ferns and herbs, whereas the upper part of the slope was dominated by herbaceous plants especially *Rhododendron* spp. during the growing season.

Climate is generally characterized by cold winters and semi-arid summers (1948–2000 meteorological data from Artvin Meteorology Station). Mean annual precipitation in lower elevations (in 2000, Artvin meteorology station, at 597 m) was 690 mm, with the highest amounts in January (99.7 mm), and the lowest amount in August (27.1 mm). Average monthly temperature ranged from 32 °C in August to -2.5 °C in January. However, the mean annual precipitation in higher elevations reached over 1100 mm and the mean lowest temperature recorded as -6.1 °C in January 2000 (Damar meteorology station at 1550 m). In winter, the ground was covered with snow, which accumulated more heavily and melted more slowly on upper and north-facing slopes (>2 m depth) than on lower and south-facing slopes.

2.2. Sample collection and preparation

Foliar litter of beech, oak, fir and pine was sampled in September 2000 from the five areas. At all areas, the selected beech, fir and pine trees were approximately 90–100 years old and 25–30 m high, and oak trees were 70–80 years old and 15–20 m high. At each area, freshly fallen foliar litter was collected from five trees at each slope on each aspect and bulked to form a representative sample for each tree species. Material showed no signs of discoloration or of obvious mycelial development at this stage. The samples were air-dried in the laboratory and then oven-dried at 40 °C for 48 h. The oven-dried foliar litters were slightly crushed by hand, and the largest fragments of petiole in leaf samples were removed. All samples were then stored in plastic bags at 6 °C until required for chemical analyses.

Soil samples were also collected in September 2000 under the same trees from which the foliar litter samples were taken. The soil samples were collected in an area of $0.5 \times 0.5 \, \text{m}^2$ at a distance of 2 m from the base of the trunk. The soil samples were taken from the B-horizon at a depth of 20 cm. The moist field samples were sieved (<2 mm) to remove stones, roots and macrofauna and bulked to give a single representative soil sample for each slope on each aspect.

There were 4 species, 2 aspects and 3 positions for each area. The 5 areas were used as replicates. This sampling design gave us 24 litter samples and soil sample per area

and 120 litter samples total (4 species \times 2 aspects \times 3 positions \times 5 replicates=120).

2.3. Soil analysis

Soil dry mass, pH (H2O), CEC (cation exchange capacity) and percent BS (base saturation) were determined. The dry mass of soils was calculated by weight loss after drying 1 g of soil for 48 h at 80 °C. Soil pH was measured in deionized H₂O using a glass calomel electrode, after equilibration for 1 h in a solution:soil paste ratio of 10:1. Exchangeable base cations were extracted by shaking 5 g of field moist soil with ammonium acetate adjusted to soil pH. Composite cations were determined in the ammonium acetate extract using flame atomic absorption spectroscopy (AAS) (Model 211, Buck Scientific, US) with LaCl₃ as a releasing agent. Extracted soils were subsequently washed with 80% ethanol, filtered and shaken with 1 M NaCl for 1 h. The NH₄⁺ concentration in this final extract was determined by a colorimetric automatic-analyser (Multi EA 3100, AnalyticjenaAG, Germany) technique. The results obtained from both extracts were used to calculate CEC and % BS. All analyses were carried out in triplicate.

2.4. Analysis of plant materials

The stored leaf and needle litters were oven-dried at 85 °C, and then ground in a laboratory mill to a mesh fraction less than 1 mm. The ground litters were then analysed for organic carbon, total nitrogen, ADF (acid detergent fibre), lignin and cellulose. Organic C was determined by wet oxidation (Nelson and Sommers, 1982). Total N was determined by Kjeldahl digestion (Allen, 1989) followed by analysis of ammonium through the indophenol method using an auto-analyser. Acid detergent fibre (ADF), α -cellulose and lignin were determined using an ADF-sulphuric lignin method by Rowland and Roberts (1994). ADF was calculated as mass loss after heating a 0.5 g tared sample for 1 h with acidified cetryltrimethyl ammonium bromide and filtering the suspension through a tared glass sinter, and subsequent drying and reweighing. Similarly, cellulose was calculated by mass loss after acidification of the ADF with 72% H₂SO₄, and lignin content was calculated from the residual mass of filtrate after ignition at 550 °C for 2 h. Organic analyses were carried out in triplicate.

2.5. Field incubations

The five sampling areas were within a 4 km radius and thus they had similar precipitation, aspect, hydrology and climate. Therefore, the field decomposition experiment was only carried out at one area to determine rates of foliar litter decomposition. This experiment was set up to show that variations in litter quality in relation to aspects and slope positions could result in differences in

decomposition rates. However, results of this experiment do not allow legitimate extrapolation to the larger landscapes. The bags were $20\times20\,\mathrm{cm}$ with a mesh size of 1.5 mm to allow for inclusion of mesofauna but exclusion of macrofaunal decomposers. About 3 g of airdried material was placed in each bag. Samples were also taken to determine a correction factor to calculate the initial oven dry mass of the material at 85 °C.

The number of litter bags used in the experiment was 288 litter bags (4 species×2 aspects (north- and south-facing slopes)×3 positions on the slope (top, middle and bottom)×4 removal dates×3 replicates=288 bags). The litter bags with foliar litter of one of four tree species were numbered and fixed to the ground of the corresponding sites (north- vs south-facing, three slope positions, each) with metal pegs. Three litter bags of each litter species were harvested from each site after 6, 12, 18 and 24 months of decomposition to follow the continuum of litter decay over time. Percentage loss of initial mass was calculated after drying samples at 85 °C.

2.6. Data analysis

A two-way ANOVA (analyses of variance) was applied for analysing the effects of aspect and slope position on soil properties, litter qualities and mass remaining for each species using the SPSS program (Version 9.0 for Windows). Following the results of ANOVAs, Tukey's Honestly Significant Difference (HSD) test (α =0.05) was used for multiple comparisons of soil properties, litter qualities and mass remaining at each litter harvest for each species in relation to aspects and slope positions. Goodness fit for linear regression of mass losses against the litter quality variables for beech, fir, oak and pine litters from two aspects on three slope positions was determined using MS EXCEL 2000.

3. Results

3.1. Soil chemistry

Results for pH, CEC and % BS of soils under four tree species growing at three different slope positions on two aspects are shown in Table 1. The single effects and interactions of aspects and slope positions on pH, CEC and %BS for each tree species are listed in Table 2. The main effects of aspects and slope positions on these soil properties were all significant for a 95% level ($\alpha = 0.05$). Soil pH showed higher values under two deciduous tree species (beech and oak) than under two coniferous tree species (fir and pine), whereas CEC and %BS showed lower values under deciduous tree species than under coniferous tree species. On each slope position, the soil of north-facing sites had higher soil pH, CEC and %BS than that of south-facing sites. On each aspect, soil pH, CEC and %BS showed an increase from the top slope position to the bottom slope position (Table 1). All three soil chemical values had a significant aspect × slope interaction for each species, indicating that these soil chemical values show different trends according to slope positions on different aspects.

3.2. Variation in litter chemistry

Mean concentrations of C, N, ADF, lignin and cellulose and C:N and lignin:N ratios in beech, oak, fir, and pine litter from the top, middle and bottom slope positions on two aspects are given in Table 3. The single effects and interactions of aspects and slope positions on litter quality variables are listed in Table 4. The main effects of species, aspects and slope positions on total nitrogen, ADF and lignin concentrations and C:N and lignin:N ratios were all significant (P<0.001). Total carbon and cellulose concentrations were, however, not significant between aspects and slope positions.

Table 1
Soil characteristics (20 cm depth) under four tree species growing on the north- and south-facing site at the three slope positions

| | | Top slope | | Middle slope | | Bottom slope | | |
|-----------------------|-------|----------------------|--------------------|----------------------|--------------------|----------------------|--------------------|--|
| | | North | South | North | South | North | South | |
| pH (H ₂ O) | Beech | 6.1 ^{Ccd} | 5.4 ^{Bca} | 6.3 ^{Cd} | 5.6 ^{Cb} | 6.6 ^{Ce} | 5.8 ^{Cc} | |
| / | Fir | 5.6 ^{Bb} | 5.1 ^{Ba} | 5.8 ^{Bc} | 5.3 ^{Bb} | 6.0^{Bd} | 5.5 ^{Bb} | |
| | Oak | 6.2^{Cc} | 5.6 ^{Ca} | 6.4^{Cd} | 5.8 ^{Cb} | 6.7 ^{Cd} | 6.1 ^{Dc} | |
| | Pine | 4.8^{Ab} | 4.5 ^{Aa} | 5.1 ^{Ac} | 4.8^{Ab} | 5.4 ^{Ad} | 5.1 ^{Ac} | |
| CEC (meg | Beech | 13.6 ^{Ac} | 11.5 ^{Aa} | 15.1 ^{Ad} | 12.7 ^{Ab} | 16.8 ^{Ae} | 15.2 ^{Ad} | |
| 100 g ⁻¹ | Fir | 19.7^{Db} | 17.3 ^{Da} | 22.8^{Bd} | 19.2 ^{Cb} | 24.6^{De} | 21.6 ^{Cc} | |
| C | Oak | 15.3 ^{Bb} | 13.2 ^{Ba} | 16.7 ^{Ac} | 15.7 ^{Bb} | 19.1 ^{Bd} | 17.6 ^{Bc} | |
| | Pine | 16.9 ^{Cb} | 14.7 ^{Ca} | 19.8 ^{Cd} | 15.6 ^{Bb} | 21.9 ^{Ce} | 18.4 ^{Bc} | |
| BS (%) | Beech | 48^{Ab} | 41^{Aa} | 50^{Ac} | 44^{Ab} | 55 ^{Ad} | 48^{Ab} | |
| . () | Fir | 62^{Cc} | 55 ^{Ca} | 65 ^{Cd} | 60^{Cb} | 68 ^{Ce} | 65 ^{Cd} | |
| | Oak | 49^{Ab} | 41 ^{Aa} | 52 ^{Ac} | 45^{Ab} | 56 ^{Ad} | 48^{Ab} | |
| | Pine | 56 ^{Bc} | 47 ^{Ba} | 59 ^{Bd} | 51 ^{Bb} | 62 ^{Bd} | 56 ^{Bc} | |

The Tukey's Honestly Significant Difference (HSD) test was used to determine significantly different means between aspects and between slope positions for each species, and between four tree species on each slope position and aspect. Means with the same letter are not significantly different by lines (the lower case letters) and columns (the upper case letters) (N=5).

Table 2 ANOVA of soil data

| | Sources | SS | df | MS | F | Eta squared | Sources | SS | df | MS | F | Eta squared |
|-----|----------------|-------|----|-------|----------|----------------|----------------|-------|----|-------|------------|----------------|
| | Beech | | | | | | Fir | | | | | |
| pН | Aspect | 3.89 | 1 | 3.89 | 268.1*** | 0.92 | Aspect | 1.54 | 1 | 1.54 | 100.5*** | 0.81 |
| | (As) | | | | | | (As) | | | | | |
| | Slope | 1.71 | 2 | 0.86 | 59.1*** | 0.83 | Slope | 1.17 | 2 | 0.59 | 38.2*** | 0.76 |
| | (SI) | | | | | | (SI) | | | | | |
| | $As \times SI$ | 0.01 | 2 | 0.00 | 15.4* | 0.38 | $As \times SI$ | 0.14 | 2 | 0.07 | 4.52* | 0.27 |
| | Error | 0.35 | 24 | 0.01 | | | Error | 0.37 | 24 | 0.02 | | |
| CEC | As | 26.9 | 1 | 26.9 | 726.6*** | 0.97 | As | 62.8 | 1 | 62.8 | 840.9*** | 0.97 |
| | SI | 53.9 | 2 | 26.9 | 728.0*** | 0.98 | SI | 105.4 | 2 | 52.7 | 706.1*** | 0.98 |
| | $As \times SI$ | 1.5 | 2 | 0.8 | 20.4*** | 0.63 | $As \times SI$ | 1.4 | 2 | 0.7 | 9.50** | 0.44 |
| | Error | 0.9 | 24 | 0.0 | | | Error | 1.8 | 24 | 0.1 | | |
| BS | As | 563.3 | 1 | 563.3 | 341.4*** | 0.93 | As | 167.1 | 1 | 167.1 | 170.1*** | 0.88 |
| | SI | 83.5 | 2 | 41.7 | 25.3*** | 0.68 | SI | 327.2 | 2 | 163.6 | 166.6*** | 0.93 |
| | $As \times SI$ | 141.1 | 2 | 70.5 | 42.7*** | 0.78 | $As \times SI$ | 15.7 | 2 | 7.8 | 7.97** | 0.40 |
| | Error | 39.6 | 24 | 1.7 | | | Error | 23.6 | 24 | 1.0 | | |
| | Oak | | | | | | Pine | | | | | |
| pН | As | 1.88 | 1 | 1.88 | 150.0*** | 0.86 | As | 0.90 | 1 | 0.90 | 45.1*** | 0.65 |
| - | SI | 1.60 | 2 | 0.80 | 64.0*** | 0.84 | SI | 3.70 | 2 | 1.85 | 92.5*** | 0.89 |
| | $As \times SI$ | 0.21 | 2 | 0.10 | 8.24** | 0.41 | $As \times SI$ | 0.16 | 2 | 0.08 | 4.02^{*} | 0.25 |
| | Error | 0.30 | 24 | 0.01 | | | Error | 0.48 | 24 | 0.02 | | |
| CEC | As | 7.1 | 1 | 7.1 | 122.9*** | 0.84 | As | 91.9 | 1 | 91.9 | 729.2*** | 0.97 |
| | SI | 60.1 | 2 | 30.1 | 519.9*** | 0.98 | SI | 114.8 | 2 | 57.4 | 455.6*** | 0.97 |
| | $As \times SI$ | 4.9 | 2 | 2.5 | 42.5*** | 0.78 | $As \times SI$ | 11.9 | 2 | 5.9 | 47.2*** | 0.80 |
| | Error | 1.4 | 24 | 0.1 | | | Error | 3.0 | 24 | 0.1 | | |
| BS | As | 496.1 | 1 | 496.1 | 327.1*** | 0.93 | As | 396.0 | 1 | 396.0 | 325.5*** | 0.93 |
| | SI | 256.9 | 2 | 128.4 | 84.7*** | 0.88 | SI | 301.3 | 2 | 150.6 | 123.8*** | 0.91 |
| | $As \times SI$ | 28.5 | 2 | 14.2 | 9.38** | 0.44 | $As \times SI$ | 10.9 | 2 | 5.4 | 4.47* | 0.27 |
| | Error | 36.4 | 24 | 1.5 | | | Error | 29.2 | 24 | 1.2 | | |

Asterisks refers the level of significance: *, P<0.05; **, P<0.01; ***, P<0.001.

Beech and oak litters had higher total nitrogen than fir and pine litters. Beech had the highest ADF and lignin, whereas oak had the lowest ADF and lignin. Although total carbon did not show any variations between four tree species, mean C:N ratios showed highly significant variations between four tree species because of the differences in total nitrogen. Pine and fir had higher C:N ratio than beech and oak. Oak litters also had the lowest lignin:N ratio, whereas beech showed the highest lignin:N ratio.

All species had higher total nitrogen on the north-facing sites than on the south-facing sites. Conversely, they showed lower ADF and lignin concentrations and C:N and lignin:N ratios on the north-facing sites. There was a trend of increasing total nitrogen concentration from the top slope to the bottom slope position, whereas ADF and lignin concentrations and C:N and lignin:N ratios showed a decrease from the top slope to the bottom slope position for all tree species.

Aspect×slope interaction was significant for nitrogen and ratios of C:N and lignin:N for all species, indicating that nitrogen behaves in different ways according to slope positions on different aspects. However, ADF and lignin did not have any significant aspect×slope interaction. That indicates that these litter quality constituents behave in

similar way according to slope positions on different aspects.

3.3. Decomposition among species, aspects and slope positions

Mean mass losses of four tree litters on the top, middle and bottom slope positions for the north- and south-facing sites are shown in Fig. 1. The single effects and interactions of aspects and slope positions on the mass loss for each tree species at each harvest are listed in Table 5. The main effects of aspects and slope positions on the mass were all significant (P < 0.001).

Of the four tree species, oak showed highest mass loss, followed by pine, fir and beech litters at each sampling interval. All tree litters decomposed much faster on north-than on south-facing site (Fig. 1). At 6 months, mean mass losses on the north-facing site were 15.3% for beech, 18.3% for fir, 22.4% for pine and 25.8% for oak, and on the south-facing sites were 12.8% for beech, 16.4% for fir, 20.4% for pine and 23.6% for oak. During the same period, mass losses were ranked in the slope position order bottom>middle> top for all species on each aspect. At 12 and 18 months, these trends were maintained with increasing mass losses until the final sampling of the experiment. At 24 months,

Table 3
Litter quality variables in dry matter of beech, fir, oak and pine litters from the top, middle and bottom slope position on two aspects

| | | Top slope | | Middle sope | | Bottom slope | | |
|---------------|-------|-----------------------|----------------------|-----------------------|----------------------|----------------------|-----------------------|--|
| | | North | South | North | South | North | South | |
| C (%) | Beech | 48 | 50 | 45 | 46 | 47 | 47 | |
| | Fir | 45 | 46 | 46 | 47 | 48 | 47 | |
| | Oak | 45 | 47 | 48 | 45 | 46 | 45 | |
| | Pine | 47 | 47 | 46 | 45 | 47 | 49 | |
| N (%) | Beech | 1.3 ^{Ab} | 1.2 ^{Aa} | 1.4 ^{Ac} | 1.3 ^{Ab} | 1.4 ^{Ac} | 1.3 ^{Ab} | |
| . , | Fir | 1.1 ^{Bb} | 0.9^{Ba} | 1.2^{Bc} | 1.1^{Bb} | 1.3 ^{Bd} | 1.2 ^{Bc} | |
| | Oak | 1.3 ^{Ab} | 1.2^{Aa} | 1.4 ^{Ac} | 1.3 ^{Ab} | 1.4 ^{Ac} | 1.3 ^{Ab} | |
| | Pine | 1.1^{Bb} | 1.0^{Ba} | 1.2^{Bc} | 1.1 ^{Bb} | 1.3 ^{Bd} | 1.2 ^{Bc} | |
| ADF (%) | Beech | 74^{Dcb} | 78^{Cd} | 72^{Cb} | 77^{Cd} | 68^{Ca} | 75 ^{Cc} | |
| (,-) | Fir | 65 ^{Ccd} | 69 ^{Be} | 63^{Bb} | 66 ^{Bd} | 61 ^{Ba} | 64 ^{Bbc} | |
| | Oak | 52 ^{Ac} | 58 ^{Ae} | 50 ^{Ab} | 56 ^{Ade} | 48^{Aa} | 54 ^{Acd} | |
| | Pine | 55 ^{Bb} | 60^{Ae} | 53 ^{Ab} | 58 ^{Ad} | 51 ^{Aa} | 55 ^{Ac} | |
| Lignin (%) | Beech | 44Cab | 49Cc | 43Ca | 48Cc | 41Ca | 45Cb | |
| | Fir | 35Bbc | 41Be | 34Bab | 39Bd | 32Ba | 37Bc | |
| | Oak | 28Ab | 33Ac | 26Aab | 31Ac | 25Aa | 28Ab | |
| | Pine | 33Bbc | 39Be | 30ABab | 36Bd | 28ABa | 32ABc | |
| Cellulose (%) | Beech | 30^{B} | 28^{B} | 28^{B} | 29^{C} | 27^{B} | 30^{B} | |
| ` ' | Fir | 29^{B} | 28^{B} | 29^{B} | 27^{Bc} | 28^{B} | 26^{A} | |
| | Oak | 23 ^A | 27 ^B | 23 ^A | 25 ^B | 22 ^A | 26^{A} | |
| | Pine | 21 ^A | 22^{A} | 23 ^A | 22^{A} | 23 ^A | 24^{A} | |
| C:N | Beech | 36.9:1 ^{Ab} | 41.6:1 ^{Ad} | 32.2:1 ^{Aa} | 35.4:1 ^{Ac} | 33.6:1 ^{Aa} | 36.2:1 ^{Ab} | |
| | Fir | 40.9:1 ^{Bcd} | 51.2:1 ^{Be} | 38.3:1 ^{Bab} | 42.7:1 ^{Bd} | 36.9:1 ^{Ba} | 39.2:1 ^{Bbc} | |
| | Oak | 34.6:1 ^{Ab} | 39.2:1 ^{Ac} | 34.3:1 ^{Ab} | 34.6:1 ^{Ab} | 32.9:1 ^{Aa} | 34.6:1 ^{Ab} | |
| | Pine | 42.7:1 ^{Bcb} | 47.0:1 ^{Bd} | 38.3:1 ^{Bab} | 40.9:1 ^{Bb} | 36.2:1 ^{Ba} | 40.8:1 ^{Bb} | |
| Lignin:N | Beech | 33.8:1 ^{Cb} | 48.4:1 ^{Dd} | 30.7:1 ^{Ca} | 36.9:1 ^{Cc} | 29.2:1 ^{Ca} | 34.6:1 ^{Db} | |
| | Fir | 31.8:1 ^{Bc} | 45.3:1 ^{Ce} | 28.3:1 ^{CBb} | 35.5:1 ^{Cd} | 24.6:1 ^{Ba} | 30.8:1 ^{Cc} | |
| | Oak | 21.5:1 ^{Ab} | 27.5:1 ^{Ad} | 18.6:1 ^{Aa} | 23.8:1 ^{Ac} | 17.9:1 ^{Aa} | 21.5:1 ^{Ab} | |
| | Pine | 30.1:1 ^{Bc} | 39.1:1 ^{Be} | 25.2:1 ^{Bb} | 32.7:1 ^{Bd} | 21.5:1 ^{Aa} | 26.7:1 ^{Bb} | |

The Tukey's Honestly Significant Difference (HSD) test was used to determine significantly different means between aspects and between slope positions for each species, and between four tree species on each slope position and aspect. Means with the same letter are not significantly different by lines (the lower case letters) and columns (the upper case letters) (N=5).

mean mass losses recorded on the north-facing site for beech, fir, pine and oak were still higher (38.9, 47.3, 49.9 and 55.4%, respectively) than on the south-facing site (30.8, 35.6, 38.4 and 42.5%, respectively). Final mass losses for the slope position were still remained in the slope position order as bottom>middle>top for all species.

Aspect×slope interaction was also significant in litter mass loss analyses at each harvesting time for each species. That means that mass losses show different trends according to slope positions on different aspects. For example, the litters at the bottom slope position on the south aspect decomposed proportionally less than the litters at the bottom slope position on the north aspect as compared with the litter at the top and middle slope positions on the two different aspects.

3.4. Relationship between mass loss and litter quality

Mass losses were plotted against litter quality variables in beech, oak, fir and pine litters from the north- and south-facing sites placed on the top, middle and bottom slopes (data not shown). Goodness of fit statistics for the regression of mass losses on litter quality variables are shown in

Table 6. Mass losses from all four species showed the highest correlation with initial lignin for both the north- and south-facing sites, but less variation was explained on the north-facing sites (r^2 =0.91 for top, 0.88 for middle and 0.83 for bottom slope) than on the south-facing sites (r^2 =0.95 for top, 0.92 for middle and 0.87 for bottom slope). Concentration of ADF and C:N and lignin:N ratios were also significantly correlated with mass losses. Similar to lignin, less variation was explained on the north-facing sites than on the south-facing sites (Table 6). Carbon, nitrogen and cellulose concentrations showed no significant relationships to mass losses from beech, oak, fir and pine litters.

4. Discussion

4.1. Variation in soil chemistry

Soil pH, CEC and soil base status varied significantly (P < 0.001) between species, aspects and three slope positions. Soil pH, CEC and soil base status were higher on north aspects than on south aspects, but lowest on top slope, intermediate on middle slope and highest on bottom

Table 4 ANOVA of litter quality data

| | Sources | SS | df | MS | F | Eta squared | Sources | SS | df | MS | F | Eta squared |
|-----------|------------------|--------|------------|--------|---------------------|-------------|------------------|--------|------------|----------------|--------------------|-------------|
| | Beech | | | | | | Fir | | | | | |
| N | Aspect (As) | 0.21 | 1 | 0.21 | 14.5** | 0.38 | Aspect (As) | 0.56 | 1 | 0.56 | 22.1*** | 0.48 |
| | Slope (SI) | 0.21 | 2 | 0.10 | 7.19** | 0.37 | Slope (SI) | 0.98 | 2 | 0.49 | 19.4*** | 0.62 |
| | As×SI | 0.10 | 2 | 0.05 | 3.65* | 0.23 | $As \times SI$ | 0.45 | 2 | 0.23 | 8.93** | 0.43 |
| | Error | 0.34 | 24 | 0.01 | | | Error | 0.61 | 24 | 0.03 | | |
| ADF | As | 202.8 | 1 | 202.8 | 184.4*** | 0.88 | As | 116.0 | 1 | 116.0 | 81.9*** | 0.77 |
| | SI | 127.4 | 2 | 63.7 | 57.9 ^{***} | 0.83 | SI | 145.8 | 2 | 72.9 | 51.5*** | 0.81 |
| | $As \times SI$ | 36.6 | 2 | 18.3 | n.s | 0.28 | $As \times SI$ | 0.9 | 2 | 0.4 | n.s | 0.02 |
| | Error | 26.4 | 24 | 1.1 | | | Error | 34.0 | 24 | 1.4 | | |
| Lignin | As | 172.8 | 1 | 172.8 | 150.3*** | 0.86 | As | 229.6 | 1 | 229.6 | 162.1*** | 0.87 |
| Ü | SI | 39.3 | 2 | 19.6 | 17.1*** | 0.59 | SI | 115.8 | 2 | 57.9 | 40.9*** | 0.77 |
| | $As \times SI$ | 3.8 | 2 | 1.9 | n.s | 0.12 | $As \times SI$ | 7.3 | 2 | 3.6 | n.s | 0.18 |
| | Error | 27.6 | 24 | 1.2 | | | Error | 34.0 | 24 | 1.4 | | |
| C:N | As | 357.08 | 1 | 357.08 | 6138.8*** | 0.996 | As | 313.63 | 1 | 313.63 | 736.8*** | 0.97 |
| | SI | 347.73 | 2 | 173.86 | 2989.1*** | 0.996 | SI | 408.90 | 2 | 204.45 | 480.3*** | 0.98 |
| | As×SI | 45.15 | 2 | 22.57 | 388.1*** | 0.970 | As×SI | 206.85 | 2 | 103.43 | 242.9*** | 0.95 |
| | Error | 1.40 | 24 | 0.06 | | | Error | 10.22 | 24 | 0.43 | | |
| Lignin:N | As | 762.0 | 1 | 762.0 | 292.7*** | 0.92 | As | 645.9 | 1 | 645.9 | 1275.2*** | 0.98 |
| | SI | 445.9 | 2 | 222.9 | 85.6*** | 0.88 | SI | 751.0 | 2 | 375.5 | 741.3*** | 0.98 |
| | As×SI | 141.8 | 2 | 70.9 | 27.2*** | 0.69 | As×SI | 146.0 | 2 | 73.0 | 144.2*** | 0.92 |
| | Error | 62.5 | 24 | 2.6 | | | Error | 12.2 | 24 | 0.5 | | |
| | Oak | | | | | | Pine | | | | | |
| N | As | 0.10 | 1 | 0.10 | 10.3** | 0.31 | As | 0.01 | 1 | 0.01 | 11.4** | 0.43 |
| 11 | SI | 0.10 | 2 | 0.02 | 8.03** | 0.29 | SI | 0.01 | 2 | 0.07 | 8.0** | 0.43 |
| | As×SI | 0.02 | 2 | 0.01 | 4.31* | 0.23 | As×SI | 0.04 | 2 | 0.02 | 5.21* | 0.28 |
| | Error | 0.29 | 24 | 0.01 | 7.51 | 0.23 | Error | 0.20 | 24 | 0.01 | 3.21 | 0.20 |
| ADF | As | 246.5 | 1 | 246.5 | 189.6*** | 0.89 | As | 158.7 | 1 | 158.7 | 164.2*** | 0.87 |
| ADI | SI | 125.0 | 2 | 62.5 | 48.1*** | 0.80 | SI | 140.9 | 2 | 70.4 | 72.7*** | 0.86 |
| | As×SI | 5.3 | 2 | 2.6 | n.s | 0.14 | As×SI | 0.6 | 2 | 0.3 | n.s | 0.03 |
| | Error | 31.2 | 24 | 1.3 | 11.5 | 0.14 | Error | 23.2 | 24 | 1.0 | 11.3 | 0.03 |
| Lignin | As | 168.0 | 1 | 168.0 | 99.8*** | 0.81 | As | 172.8 | 1 | 172.8 | 211.6*** | 0.90 |
| Ligiiii | SI | 86.1 | 2 | 43.0 | 25.6*** | 0.68 | SI | 97.9 | 2 | 48.9 | 59.9*** | 0.90 |
| | As×SI | 32.5 | 2 | 16.2 | n.s | 0.25 | As×SI | 2.4 | 2 | 1.2 | n.s | 0.83 |
| | Error | 40.4 | 24 | 1.7 | 11.5 | 0.23 | Error | 19.6 | 24 | 0.8 | 11.5 | 0.11 |
| C:N | As | 23.06 | 1 | 23.06 | 55.3*** | 0.70 | As | 37.63 | 1 | 37.63 | 660.2*** | 0.96 |
| C.N | SI | 63.87 | 2 | 31.94 | 76.6*** | 0.70 | SI | 61.41 | 2 | 30.71 | 538.7*** | 0.98 |
| | As×SI | 13.19 | 2 | 6.60 | 15.8*** | 0.57 | As×SI | 6.39 | 2 | 3.19 | 56.0*** | 0.98 |
| | Error | 10.00 | 24 | 0.42 | 13.0 | 0.57 | Error | 1.37 | 24 | 0.06 | 50.0 | 0.02 |
| I ionin N | | 165.7 | 1 | 165.7 | 1474.9*** | 0.98 | As | 239.7 | 1 | 239.7 | 1938.7*** | 0.99 |
| Lignin:N | As SI | 165.7 | 2 | 56.8 | 505.9*** | 0.98 | As SI | 239.7 | 2 | 239.7 104.0 | 1938.7 860.9*** | 0.99 |
| | As×SI | 3.0 | 2 | 1.5 | 13.6*** | 0.98 | As×SI | 2.2 | 2 | 1.1 | 860.9 9.16** | 0.99 |
| | As × S1 Error | 2.7 | 24 | 0.1 | 13.0 | 0.55 | As × S1 Error | 2.2 | 24 | 0.1 | 9.10 | 0.43 |
| | EHOF | 2.1 | <i>2</i> 4 | 0.1 | | | EHOF | 2.9 | Z 4 | 0.1 | | |

The Tukey's Honestly Significant Difference (HDS) test was used to determine significantly different means between aspects and between slope positions for each species, and between four tree species on each slope position and aspect. Means with the same or no letter are not significantly different by lines (the lower case letters) and columns (the upper case letters) (N=5). Asterisks refer the level of significance: *, P<0.05; ***, P<0.01; ***, P<0.001.

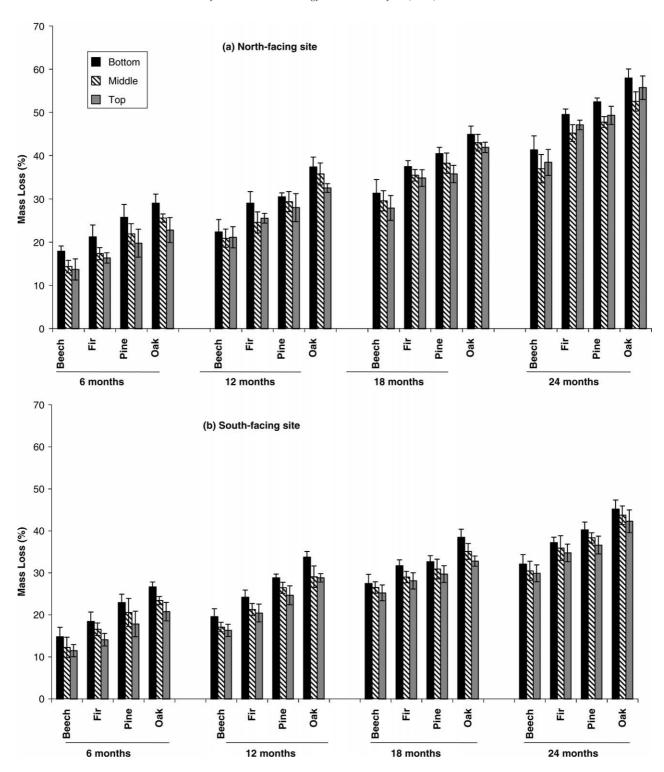


Fig. 1. Mean per cent mass losses of beech, fir, pine and oak foliar litters on the top, middle and bottom slope position for the north-facing (a) and south-facing (b) sites (vertical bars represent the standard error of the mean).

slope. These results were similar to the finding by Losche et al. (1970). Layton-Smith (1984) also found the highest soil pH values on north aspects. She pointed out that this finding coincided with the distribution of species (*Liriodendron tulipifera*) whose leaves were know to have a higher pH.

Soil pH under two deciduous tree species (beech and oak) was higher than that under coniferous tree species (pine and fir). It is well known that conifer litter is more acidic than deciduous leaf litter and acidification of the soil is more pronounced in the first case (Swift et al., 1979).

Table 5 ANOVA of mass loss (ML) data at 6, 12 and 24 months

| | Sources | SS | Df | MS | F | Eta squared | Sources | SS | Df | MS | F | Eta squared |
|-------|----------------|--------|----|-------|------------|-------------|----------------|--------|----|-------|------------|-------------|
| | Beech | | | | | | Fir | | | | | |
| ML-6 | Aspect (As) | 26.84 | 1 | 26.84 | 1530.3*** | 0.9922 | Aspect (As) | 17.62 | 1 | 17.62 | 28576.2*** | 0.9996 |
| | Slope (SI) | 47.11 | 2 | 23.55 | 1343.0*** | 0.9956 | Slope (SI) | 65.88 | 2 | 32.94 | 53416.9*** | 0.9999 |
| | As×SI | 0.92 | 2 | 0.46 | 26.2*** | 0.8135 | $As \times SI$ | 3.28 | 2 | 1.64 | 2661.3*** | 0.9978 |
| | Error | 0.21 | 24 | 0.02 | | | Error | 0.01 | 24 | 0.00 | | |
| ML-12 | As | 65.7 | 1 | 65.7 | 27456.1*** | 0.9996 | As | 88.1 | 1 | 88.1 | 4689.4*** | 0.9974 |
| | SI | 17.4 | 2 | 8.7 | 3643.0*** | 0.9984 | SI | 56.8 | 2 | 28.4 | 1511.1*** | 0.9960 |
| | $As \times SI$ | 3.0 | 2 | 1.5 | 626.7*** | 0.9905 | $As \times SI$ | 3.3 | 2 | 1.6 | 86.6*** | 0.9352 |
| | Error | 0.0 | 24 | 0.0 | | | Error | 0.2 | 24 | 0.0 | | |
| ML-24 | As | 307.2 | 1 | 307.2 | 13140.2*** | 0.9991 | As | 563.9 | 1 | 563.9 | 9938.9*** | 0.999 |
| | SI | 32.7 | 2 | 16.3 | 699.3*** | 0.9915 | SI | 38.8 | 2 | 19.4 | 341.5*** | 0.983 |
| | $As \times SI$ | 6.5 | 2 | 3.3 | 139.6*** | 0.9588 | $As \times SI$ | 7.1 | 2 | 3.5 | 62.5*** | 0.912 |
| | Error | 0.3 | 24 | 0.0 | | | Error | 0.7 | 24 | 0.1 | | |
| | | | | | | | Pine | | | | | |
| ML-6 | As | 21.19 | 1 | 21.19 | 8220.3*** | 0.9985 | As | 14.69 | 1 | 14.69 | 68.9*** | 0.8517 |
| | SI | 114.30 | 2 | 57.15 | 22166.8*** | 0.9997 | SI | 102.33 | 2 | 51.17 | 240.1*** | 0.9756 |
| | $As \times SI$ | 0.13 | 2 | 0.06 | 25.1*** | 0.8069 | $As \times SI$ | 2.40 | 2 | 1.20 | 5.64* | 0.4845 |
| | Error | 0.03 | 24 | 0.00 | | | Error | 2.56 | 24 | 0.21 | | |
| ML-12 | As | 100.7 | 1 | 100.7 | 19621.8*** | 0.9994 | As | 32.8 | 1 | 32.8 | 2065.1*** | 0.9942 |
| | SI | 75.6 | 2 | 37.8 | 7361.0*** | 0.9992 | SI | 31.6 | 2 | 15.8 | 995.1*** | 0.9940 |
| | $As \times SI$ | 8.3 | 2 | 4.1 | 804.2*** | 0.9926 | $As \times SI$ | 1.3 | 2 | 0.7 | 41.0*** | 0.8723 |
| | Error | 0.1 | 24 | 0.0 | | | Error | 0.2 | 24 | 0.0 | | |
| ML-24 | As | 592.3 | 1 | 592.3 | 7202.1*** | 0.9983 | As | 602.5 | 1 | 602.5 | 4426.0*** | 0.9973 |
| | SI | 52.1 | 2 | 26.1 | 317.1*** | 0.9814 | SI | 49.9 | 2 | 25.0 | 183.3*** | 0.9683 |
| | $As \times SI$ | 17.1 | 2 | 8.6 | 104.2*** | 0.9455 | $As \times SI$ | 14.1 | 2 | 7.0 | 51.7*** | 0.8960 |
| | Error | 1.0 | 24 | 0.1 | | | Error | 1.6 | 24 | 0.1 | | |

Mass loss at 18 is not given since it shows similar results as ML at 12 months. Asterisks refer the level of significance: *, P < 0.05; ***, P < 0.01; ***, P < 0.001.

Table 6
Goodness fit for linear regression of mass losses against the litter quality variables for beech, fir, oak and pine litters from two aspects on three slope positions

| Litter quality parameters | r^2 | | | | | | | | | | |
|---------------------------|-------|------|--------|-------|------|--------|---|--|--|--|--|
| | North | | | South | _ | | | | | | |
| | Тор | Mid | Bottom | Тор | Mid | Bottom | | | | | |
| Carbon | 0.17 | 0.24 | 0.18 | 0.21 | 0.23 | 0.19 | + | | | | |
| Nitrogen | 0.60 | 0.45 | 0.36 | 0.55 | 0.48 | 0.39 | + | | | | |
| ADF | 0.83 | 0.79 | 0.75 | 0.91 | 0.87 | 0.82 | _ | | | | |
| Lignin | 0.91 | 0.88 | 0.83 | 0.95 | 0.92 | 0.87 | _ | | | | |
| Cellulose | 0.51 | 0.46 | 0.49 | 0.48 | 0.32 | 0.54 | _ | | | | |
| C:N | 0.71 | 0.67 | 0.63 | 0.75 | 0.71 | 0.68 | _ | | | | |
| Lignin:N | 0.86 | 0.83 | 0.80 | 0.93 | 0.90 | 0.85 | _ | | | | |

Correlation coefficients for the regression were significant (P < 0.01).

Although the results in this study do not provide conclusive evidence, these data give substance to the theory that litter pH affects soil pH.

Soil analyses (data not shown) revealed that concentrations of cations (especially, potassium and manganese) at 20 cm depth were greater on north aspects, where oak and pine predominated than on south aspects, where beech and fir predominated. Concentrations of iron and hydrogen were greater on south than north aspects. Higher soil cations at the topsoil found on the north aspects could be attributed to higher decomposition rates as shown in this study. The higher litter decomposition means more rapid nutrient cycling on the north aspects which could affect the greater quantities of certain elements in the topsoil at these locations and this, in turn, could be responsible for higher mineral elements input to the soils.

Differences in soil chemistry between aspects and slope positions could be also attributed to the topographic position of the sites and other landform factors since they are closely related to microclimate and to physical properties of the soil that govern soil-water and aeration relationships (Barnes et al., 1998). The differences in litter decomposition, combined with the differences in microclimate and physical properties of the soils between aspects and slope positions could be responsible for the differences in soil chemistry found in this study. However, data from more detailed studies are needed to investigate the effects of temperature, moisture, litter quality, species mixtures, forest canopy closure, decomposer communities, etc. on soil properties between aspects and slope positions, but the present study was not intended to investigate all these mechanisms.

4.2. Variation in litter quality

Litter quality parameters, especially lignin and the combined concentrations of lignin and cellulose (ADF), and lignin:N and C:N ratios in beech, oak, fir and pine litters varied significantly within and between species in relation to aspects and three slope positions. These intra-specific variations in litter quality could be attributed to differences in soil characteristics between these sites. On the basis of pH, CEC, base saturation, the north-facing sites and the bottom

slope positions had high nutrient status, whereas the southfacing sites and the top slope positions had more acidic soils and low nutrient status (Table 1). Under the more acidic soils and low nutrient status, all four species showed higher lignin and ADF concentrations (Table 3). These results are consistent with the results found in previous studies (e.g. Johansson, 1995; Sanger et al., 1996, 1998; Sariyildiz and Anderson, 2003b). Sanger et al. (1996, 1998) revealed that differences in total lignin and cellulose as well as in lignin quality (phenylpropanoid composition and degree of polymerization) and TFA-extractable carbohydrates (mainly sugar constituents of hemicellulose) vary in relation to base status of different soils under P. sylvestris. Similarly, Sariyildiz and Anderson (2003b) showed significant intra-specific variation in the chemical composition of oak and beech leaf litter from different soil types that varied in base saturation. Stafford and Ibrahim (1992) reported that these trends may be the indicative of nutrient stress which can elicit lignification in plant tissues growing under low nutrient status.

These intra-specific variations in the litter quality could be also explained by differences in the environmental conditions such as light intensity, wind, physical stress (mainly availability of water) between these sites. A number of studies have showed that under these extreme conditions, most forest trees have the faculty of developing different anatomical structures in their leaves; such as a smaller surface per unit weight, more palisade tissues, less intercellular space and spongy parencyma, more supportive and conductive tissues (Roth, 1984, 1990; Rollet, 1990). In a recent study by Sariyildiz and Anderson (2003a), similar differences were observed within species due to the differences in the tree canopy structure, which resulted in significant variations in the chemical composition of the litters of the same. The results in the present study support these findings since south-facing slopes receive more sunlight and are hotter and drier than north-facing slopes, and ridge tops or upper convex slope surfaces are exposed to intense solar radiation and experience high wind speeds. Therefore, it is reasonable to assume that the differences in soil chemical characteristics, coupled with the differences environmental conditions, could account for the variation in the litter quality of beech, fir, oak and pine trees between these sites.

4.3. Variation in decomposition rates

Litter decomposition rates over 2 years were highest for oak followed by pine, fir and beech, but also showed intra-specific differences according to aspects and slope positions. Pooled data for the litters of four tree species and origin (from two aspects and three slope positions at each aspect) showed significant relationships between initial litter quality variables and decomposition rates (Table 6). Initial lignin concentrations explained most of the variation in decomposition rates between species, and within species for the aspects and the slope positions. The explained variance was higher for the south-facing site and the top slope position than the north-facing site and the bottom slope position, suggesting that lignin was exerting a greater control over litter decomposition on the sites with lower nutrient status. This effect could be attributed to site differences in microbial metabolic functions (Bauhus et al., 1998), interactions between litter quality and soil fertility (Prescott, 1996), and litter quality effects on fungal activities (Cox et al., 2001) but our study was not intended to investigate these mechanisms.

Other studies have shown that the influence of initial N and microbial degradation of the holocellulose fraction in the early phase of decomposition is strongly dependent upon lignin concentrations in the litter (e.g. McClaugherty and Berg, 1987; Rutigliano et al., 1996) because of their intimate physical association and covalent bonding in the cell wall (Monties, 1994). Hence it is predictable that as the total lignin concentration increases from 28% in oak, 33% in pine, 35% in fir to 49% in beech it dominated decomposition rates irrespective of other constituents.

5. Conclusion

In conclusion, this study has shown significant intraspecific variation in the chemical composition of beech, oak, fir and pine litters from two aspects and three slope positions that vary in soil chemical characteristics and environmental conditions (e.g. light intensity, wind, availability of water). All four tree species responded similarly to soil and environmental conditions and it was found that variation in the chemical compositions, especially lignin concentration largely explained the litter mass losses within and between species. Differences in the decomposition rates of litter on aspects and slope positions illustrate the important point that litter quality may define the potential rates of microbial decomposition but these are significantly influenced by the biotic and abiotic environment in which decomposition takes place. This complex interaction of biotic factors such as litter decomposition and abiotic factors such as energy flux related to aspect and slope position within an ecosystem could, therefore, affect the soil

chemistry, litter quality, nutrient cycling, and in turn forest species dynamics, ecosystem development and productivity.

Acknowledgements

We are grateful for the helpful comments from two reviewers in the revision of this paper.

References

- Allen, S.E., 1989. Chemical Analysis of Ecological Materials. Blackwell Scientific Publications, Oxford.
- Barnes, B.V., Zak, D.R., Denton, S.R., Spurr, S.H., 1998. Forest ecology, fourth ed. Wiley, New York.
- Bauhus, J., Pare, D., Cote, L., 1998. Effects of tree species, stand age and soil type on soil microbial biomass and its activity in a southern boreal forest. Soil Biology & Biochemistry 30, 1077–1098.
- Berg, B., Berg, M., Bottner, P., Box, E., Breymeyer, A., Calvo de Anta, R., Coûteaux, M.M., Gallardo, A., Escudero, A., Kartz, W., Madeira, M., Mälkönen, E., McClaugherty, C., Meentemeyer, V., Muńoz, F., Piussi, P., Remacle, J., Virzo de Santo, A., 1993. Litter mass loss rates in pine forests of Europe and Eastern United States: some relationships with climate and litter quality. Biogeochemistry 20, 127–159.
- Boerner, R.E., 1984. Nutrient fluxes in litterfall and decomposition in four forests along a gradient of soil fertility in southern Ohio. Canadian Journal of Forest Research 14, 794–802.
- Cox, P., Wilkinson, S.P., Anderson, J.M., 2001. Effects of fungal inocula on the decomposition of lignin and structural polysaccharides in *Pinus* sylvestris litter. Biology and Fertility of Soils 33, 246–251.
- Enoki, T., Kawaguchi, H., Iwatsubo, G., 1997. Nutrient-uptake and -use efficiency of *Pinus thunbergii* Parl. along a topographical gradient of soil nutrient availability. Ecological Research 12, 191–199.
- Heal, O.W., Anderson, J.M., Swift, M.J., 1997. Plant litter quality and decomposition: an historical overview. In: Cadisch, G., Giller, K.E. (Eds.), Driven by Nature: Plant Litter Quality and Decomposition. CAB International Wallingford, UK, pp. 3–45.
- Johansson, M.B., 1995. The chemical composition of needle and leaf litter from Scots pine, Norway spruce and white birch in Scandinavian forests. Forestry 68, 49–62.
- Layton-Smith, D.A., 1984. Forest floor dynamics and soil pH on different aspects in the Little Laurel Drainage. Research paper for course taught at West Virginia University. Forestry 170, special topics in Forestry, fall semester.
- Losche, E.K., McCracken, R.J., Davey, C.B., 1970. Soils of steeply sloping landscapes in southern Appalachian mountains. Soil Science Society of America 34, 473–478.
- McClaugherty, C., Berg, B., 1987. Cellulose, lignin and nitrogen concentrations as rate regulating factors in late stages of forest litter decomposition. Pedobiologia 30, 101–112.
- McNab, W.H., 1993. A topographic index to quantify the effect of mesoscale landform on site productivity. Canadian Journal of Forest Research 23, 1100–1107.
- Monties, B., 1994. Chemical assessment of lignin biodegradation some qualitative and quantitative aspects. Federation of European microbiological societies (FEMS). Microbiological Reviews 13, 277–284.
- Mudrick, D.A., Hoosein, M., Hicks, R.R., Townsend, E.C., 1994. Decomposition of leaf litter in an Appalachian forest: effects of leaf species, aspect, slope position and time. Forest Ecology and Management 68, 231–250.
- Nelson, D.W., Sommers, L.E., 1982. Total carbon, organic carbon and organic matter. In: Page, A.L., Miller, R.H., Keeney, D.R. (Eds.), Methods of Soil Analysis. American Society of Agronomy, Madison, WI, pp. 539–579.

- Prescott, C.E., 1996. Influence of forest floor type on rates of litter decomposition in microcosms. Soil Biology & Biochemistry 28, 1319–1325.
- Rollet, B., 1990. Leaf morphology. In: Rollet, B., Hogermann, Ch., Roth, I. (Eds.), Stratification of Tropical Forests as Seen in Leaf Structure, Part 2. Kluwer, Dordrecht.
- Roth, I., 1984. Stratification of Tropical Forest as Seen in Leaf Structure. W. Junk, Boston, MA p. 522.
- Roth, I., 1990. Encyclopedia of Plant Anatomy, Part 1, Leaf Structure of a Venezuelan Cloud Forest in Relation to Microclimate, vol. 14. Gebruder Borntraeger, Berlin p. 224.
- Rowland, A.P., Roberts, J.D., 1994. Lignin and cellulose fractionation in decomposition studies using acid-detergent fibre methods. Communications in Soil Science, Plant Analysis 25, 269–277.
- Rutigliano, F.A., Berg, B., Alfani, A., Fioretto, A., 1996. Lignin decomposition in decaying leaves of *Fagus sylvatica* L. and needles of *Abies alba* Mil. Soil Biology & Biochemistry 28, 101–106.
- Sanger, L.J., Cox, P., Splatt, P., Whelan, M.J., Anderson, J.M., 1996.
 Variability in the quality of *Pinus sylvestris* needles and litter from sites with different soil characteristics: lignin and phenylpropanoid signature.
 Soil Biology & Biochemistry 28, 829–835.
- Sanger, L.J., Cox, P., Splatt, P., Whelan, M.J., Anderson, J.M., 1998. Variability in the quality and potential decomposability of *Pinus*

- sylvestris litter from sites with different soil characteristics: acid detergent fibre (ADF) and carbohydrate signature. Soil Biology & Biochemistry 30, 445–461.
- Sariyildiz, T., Anderson, J.M., 2003a. Decomposition of sun and shade leaves from three deciduous tree species, as affected by their chemical composition. Biology and Fertility of Soils 37, 137–146.
- Sariyildiz, T., Anderson, J.M., 2003b. Interactions between litter quality, decomposition and soil fertility: a laboratory study. Soil Biology & Biochemistry 35, 391–399.
- Scowcroft, P.G., Turner, D.R., Vitousek, P.M., 2000. Decomposition of Metrosideros polymorpha leaf litter along elevational gradients in Hawaii. Global Change Biology 6, 73–85.
- Stafford, H.A., Ibrahim, R.K., 1992. Recent Advances in Phytochemistry— Phenolic Metabolism in Plants. Plenum Press, New York.
- Swift, M.J., Heal, O.W., Anderson, J.M., 1979. Decomposition in Terrestrial Ecosystems. Blackwell Scientific Publications, Oxford.
- Vitousek, P.M., Turner, D.R., Parton, W.J., Sandford, R.L., 1994. Litter decomposition on the Mauna Loa environmental matrix, Hawaii: patterns, mechanisms and models. Ecology 75, 418–429.
- Zimmer, M., 2002. Is decomposition of woodland leaf litter influenced by its species richness? Soil Biology & Biochemistry 34, 277–284.