

Influence of slope position, stand type and rhododendron (*Rhododendron ponticum*) on litter decomposition rates of Oriental beech (*Fagus orientalis* Lipsky.) and spruce [*Picea orientalis* (L.) Link]

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Abstract Oriental beech (*Fagus orientalis* Lipsky.) and Oriental spruce [*Picea orientalis* (L.) Link] are the two most common tree species in northeast Turkey. Their distribution, stand type and understorey species are known to be influenced by topographical landforms. However, little information is available as to how these changes affect litter decomposition rates of these two species. Here, we investigated the effects of slope positions (top 1,800 m, middle 1,500 m and bottom 1,200 m), stand type (pure and mixed stands) and purple-flowered rhododendron (*Rhododendron ponticum*) on litter decomposition rates of Oriental beech and spruce for 4 years using the litterbag technique in the field. Among these three factors, stand type had the strongest influence on litter decomposition ($P < 0.001$, $F = 58.8$), followed by rhododendron ($P < 0.001$, $F = 46.8$) and slope position ($P < 0.05$, $F = 11.6$). Litter decomposition was highest under mixed beech/spruce forest, followed by pure beech and spruce forest. Beech and spruce litter decomposed much faster in mixed bags (beech–spruce) than they did separately under each stand type. Purple-flowered rhododendron significantly reduced litter decomposition of Oriental beech and spruce. Beech and spruce litter decomposed much slower at top slope position than at either bottom or middle position. Differential litter decomposition of Oriental beech and spruce was mainly due to adverse conditions in spruce forest and the presence of rhododendron on the ground which was associated with lower soil pH. Higher elevations (top slope position) slowed down litter

decomposition by changing environmental conditions, most probably by decreasing temperature as also other factors are different (pH, precipitation) and no detailed investigations were made to differentiate these factors. The adverse conditions for litter decomposition in spruce forest can be effectively counteracted by admixture of beech to spruce monoculture and by using the clear-cutting method for controlling rhododendron.

Keywords Litter decomposition · Slope position · Forest floor types · *Rhododendron* · Oriental beech · Oriental spruce

Introduction

Many studies have extensively studied the effects of slope position on microclimate and soils, as well as on vegetation composition, community development and site productivity (Barnes et al. 1998; Vetaas and Gerytnes 2002). However, very few studies have investigated its effects on litter decomposition rates (Mudrick et al. 1994; Sariyildiz et al. 2005). Decomposition rate is mainly affected by climate (temperature and precipitation) and by the initial litter quality variables [carbon:nitrogen (C:N) ratio, lignin, N and lignin:N ratio; Heal et al. 1997; Sariyildiz and Anderson 2003; Lensing and Wise 2007]. On a regional scale, slope position can create different environmental conditions and increase litter heterogeneity and in turn, these changes can retard or accelerate litter decomposition rates through negative or positive effects on the activity of organisms (Mudrick et al. 1994; Vitousek et al. 1994). Slope positions can have a strong influence on stand types and understorey species composition. Under natural field conditions several plant species and shrubs usually grow closely together and,

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as a direct consequence, their litter decomposes in litter mixtures instead of in monocultures. Only in recent years have researchers specifically examined potential interactions among leaves of different species during decomposition (e.g., Hoorens et al. 2003; Dalias et al. 2003; Gartner and Cardon 2006; Smith and Bradford 2003). As suggested by Seastedt (1984), the idea is that, due to differences in litter quality between species, litter mixtures might decompose at a different rate to that which would be predicted from single-species litterbags. Therefore, many experimental studies have been carried out to investigate the contribution of litter richness and composition to decomposition rate (Vesterdal 1999; Gartner and Cardon 2004).

In Turkey, the distribution, stand types and understorey species of two most common tree species, Oriental spruce (*Picea orientalis*) and beech (*Fagus orientalis*) are also influenced by slope position. Oriental spruce forms approximately 290,000 ha of pure or mixed natural forest, while Oriental beech forms about 1,340,000 ha (General Directorate of Forestry 2008). Where the microclimate is markedly dry, Oriental spruce mostly diminishes. They mainly grow on north-facing sites with high humidity. Oriental beech and spruce begin at altitude of over 1,000 m and reach to 1,800–2,400 m in many districts (Güner 2000). At high altitudes, Oriental spruce forms pure stands over a considerable area, while at low altitude it is often accompanied by Oriental beech. At high altitude, strong wind can result in creating small and big gaps. Within these gaps, ground flora is generally occupied by rhododendrons (*Rhododendron ponticum* L.), cherry laurel (*Prunus laurocerasus* L.), hollies [*Ilex aquifolium* L., *I. aquifolium* subsp. *colchica* (Poj.)] and blackberries (*Rubus* spp.). At low altitude with mild wind speed, forest canopy cover is mostly closed. The ground flora is usually poor and consists largely of mosses, lichens and liverworts.

The objectives of this present study were to (1) study the effect of slope position on litter decomposition rates by placing Oriental beech and spruce litter at three slope positions on the north-facing site, (2) investigate the effect of stand types (pure and mixed beech and spruce stands) on litter decomposition by placing beech, spruce and mixed beech–spruce litters under beech, spruce and mixed beech–spruce stands, (3) determine the effect of understorey species by placing beech and spruce litter with and without purple-flowered rhododendron (*Rhododendron ponticum*) on the ground and (4) evaluate the single and interactions of slope position, stand type and understorey species on litter decomposition rates of Oriental beech and spruce. To understand the driving forces of different decomposition rates according to forest floor types and soil conditions, water content in the forest floor, soil moisture content and soil pH, which have been shown by a number of authors to be factors strongly affecting decomposition processes

(e.g., Smolander et al. 1996; Chadwick et al. 1998) were determined.

Materials and methods

Study sites

This study was carried out in 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 2,500 m). Three slope positions were selected on the top (1,800 m), middle (1,500 m) and bottom (1,200 m) on the north aspect. Three positions were located along one long slope. The slope angle was 45%. At these altitudes, *Picea orientalis* (L.) Link, *Fagus orientalis* Lipsky, *Abies nordmanniana* (Stev.) Matt., *Pinus silvestris* L., *Castanea sativa* Mill. and *Quercus* spp. are generally the dominant species in either pure or mixed forms. Oriental spruce forms pure or mixed stands over a considerable area (ca 95,000 ha) in Artvin, while Oriental beech forms approximately 52,000 ha. Oriental spruce is often accompanied by Oriental beech in the area (ca 4,800 ha). The understorey is generally occupied by grasses (e.g., *Festuca drymeja*, *Trifolium repens*, *Fragaria vesca*, *Vicia* sp., *Lotus corniculatus*), ferns (e.g., *Dryopteris dilatata*, *Asplenium adianthum-nigra*, *Pteridium aquilinum*) and broad leaf herbaceous plants (e.g., *Rhododendron ponticum*, *I. colchica*, *Rubus phyllathyphyllos* sp.).

The climate is characterized by cold winters and semi-arid summers in the region. The mean annual precipitation at the elevation of 1,200 m was 1,051 mm, with the highest amounts in January (139 mm), and the lowest amount in August (57 mm; Artvin meteorology station) between 1980 and 2005. The mean annual temperature was 8.9°C. The average monthly temperature ranges from 20°C in August to –3.2°C in January. At the elevation of 1,500 m the mean annual precipitation and temperature were 1,216 mm and 6.6°C, while at the elevation of 1,800 m the mean annual precipitation and temperature were 1,381 mm and 4.4°C. The mean temperature and mean rainfall during the 4 years of the investigation did not differ from the mean annual values. In winter, the ground was covered with snow, which accumulated more heavily on the upper elevations than on the lower elevations.

The parent rock of the study area was mostly granite covered with a sandy loam, shallow soil and an organic layer of the humus form more under spruce and mor-like moder under beech (Sariyildiz 2003). The soil type of the study area is defined as Inseptisol according to the United States Department of Agriculture (USDA) soil taxonomy system, which is undeveloped soil characterized by undeveloping soil profile which shows distinct A- and C-horizons,

but mineral B-horizon is almost absent in the studied areas. The mean soil and forest floor pH among three stand types situated at the top slope (1,800 m) was ranked in the order as spruce < beech < mixed beech–spruce (Table 1). The soil and forest floor water contents were higher under beech forest than under spruce and mixed beech–spruce. At the bottom slope (1,200 m), the mean soil and forest floor pH were ranked in the order as spruce–rhododendron < beech–rhododendron < spruce < beech (Table 1). The mean forest floor water content was also lower under beech and spruce stands with rhododendron on the ground (49 and 42%, respectively) than that under beech and spruce stands without rhododendron on the ground (58 and 52%, respectively). The mean soil water content was however similar between beech and spruce stands with and without rhododendron on the ground.

Sample collection, preparation and field incubation

Freshly fallen litter of beech and spruce was sampled beneath five mature trees at the beginning of October 2002 by spreading nets on the forest floor and bulked to form representative samples for each tree species. The selected beech and spruce trees were approximately 90–100 years old and 25–30 m high. The main period of litter fall in this area was of short duration, reaching a peak in autumn. The weather was cold when the litter material was collected and the litters showed no visible 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 leaves 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 (Anderson and Ingram 1993).

The litterbags used for the experiment were 20 cm × 20 cm with a mesh size of 1 mm to allow for inclusion of mesofaunal but exclusion of macrofaunal decomposers. The litterbags were filled with about 5 g of air-dried litters of either a single tree species or a combination of two tree species (beech and spruce; ratio of 1:1). On an area basis this amount of litter is equivalent to one to two times the annual leaf or needle litter input at the study sites (personal data from research in this area). Samples were also taken to determine a correction factor to calculate the initial oven dry mass of the material at 85°C. At the end of October 2002, the litterbags numbered and fixed to the ground of the corresponding sites were: (experiment 1) Oriental beech litter and spruce litter originated from the elevation of 1,500 m, which was used as standard litter in order to leave out the effects of initial litter quality, were placed separately under pure Oriental beech and spruce stands at three different elevations (1,200, 1,500 and 1,800 m), (experiment 2) litterbags of Oriental beech, spruce and mixed beech/spruce litter were together placed both under pure beech and spruce forest and also under mixed beech/spruce forest at the elevation of 1,800 m on the north-facing site in order to understand the effect of stand type on litter decomposition and (experiment 3) Oriental beech and spruce litter were separately placed under pure beech and spruce stands with and without rhododendron on the ground at the elevation of 1,200 m on the north-facing site.

Five litterbags of each litter were harvested from each corresponding site every 6 months for 4 years in order to see the continuum of litter decomposition rates over time. Percentage loss of initial mass was determined after drying samples at 85°C for 24 h. Moisture content of the litter material was calculated by weight loss after drying the material for 24 h at 105°C (Anderson and Ingram 1993).

Table 1 Forest floor water content, soil water content and soil pH values from pure and mixed beech and spruce stands

Stand type	Altitude (m)	Parent material	Soil texture	Soil pH (H ₂ O)	Soil water content (%)	Forest floor pH (H ₂ O)	Forest floor water content (%)
Beech	1,800	Granite	Sandy loam	5.15 ^b	37.5 ^b	4.55 ^b	68.3 ^b
Spruce	1,800	Granite	Sandy loam	4.32 ^a	34.1 ^a	3.45 ^a	65.4 ^a
Mixed beech/spruce	1,800	Granite	Sandy loam	5.55 ^c	35.1 ^a	5.65 ^c	64.3 ^a
Beech							
With <i>Rhododendron</i>	1,200	Granite	Sandy loam	4.90 ^b	36.2 ^a	4.85 ^b	49.4 ^b
Without <i>Rhododendron</i>	1,200	Granite	Sandy loam	5.35 ^c	34.2 ^a	5.12 ^c	58.3 ^c
Spruce							
With <i>Rhododendron</i>	1,200	Granite	Sandy loam	4.35 ^a	34.5 ^a	4.25 ^a	42.4 ^a
Without <i>Rhododendron</i>	1,200	Granite	Sandy loam	4.92 ^b	33.4 ^a	4.84 ^b	51.5 ^b

Tukey method of multiple pairwise comparison at $\alpha = 0.05$ used to determine significantly different mean values. Mean values with the same letter are not significantly different by columns

Analysis of plant materials

The stored litter was oven-dried at 85°C and then ground in a laboratory mill to a mesh fraction of <1 mm (Anderson and Ingram 1993). The ground litter was then analyzed for organic carbon, nitrogen, acid detergent fiber (ADF), lignin and cellulose. Organic C was determined by wet oxidation (Nelson and Sommers 1982). This method is based on oxidation in an acid dichromate (or persulfate) solution with a series of traps for moisture and recovery of carbon dioxide as for dry combustion. Total N was determined by Kjeldahl digestion (Allen 1989) followed by analysis of ammonium by the indophenol method using an auto-analyzer. Cellulose and lignin were determined using an ADF-sulfuric lignin method described by Rowland and Roberts (1994). ADF was calculated as mass loss after heating a 0.5-g tared sample for 1 h with acidified cetyltrimethyl 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.

Soil and forest floor sampling and analysis

Soil and forest floor samples were collected in autumn 2002 from pure beech and spruce stands and also from mixed beech–spruce stands. In addition, soil and forest floor material was sampled from beech and spruce stands with and without rhododendron on the ground. The upper part of the forest floor material (0–4 cm) was sampled from the studied sites. The soil samples were collected in an area of 0.5 m² × 0.5 m² at a distance of 2 m from the base of the trunk. The soil samples were taken from A-horizon between the depths of 0–15 cm. Soil cores (5.7 cm in diameter and 10 cm height) were used to collect the soil samples. The moist soil field samples were sieved (<2 mm) to remove stones, roots and macrofauna and bulked to give a single representative soil sample for each stand. Forest floor material was sampled from the upper part of the organic matter on the forest floor. Analyses of soil and forest floor pH and water content were carried out throughout the study period and mean values of soil and forest floor pH and

water content were used for correlation between these values and mass losses.

Moisture content of soils was calculated by weight loss after drying ca. 10 g of soil for 24 h at 105°C. Soil pH (H₂O) and forest floor material pH were measured in deionized H₂O using a glass calomel electrode, after equilibration for 1 h in a solution:soil and solution:forest floor material ratio of 10:1 (Allen 1989). Moisture content of the forest floor material was calculated by weight loss after drying 10 g of material for 48 h at 105°C (Anderson and Ingram 1993). All analyses were carried out in triplicate.

Data analysis

Three-way ANOVA was applied for analyzing the effects of slope positions, stand types and rhododendron on mass losses of beech and spruce litter using the SPSS program (Version 11.5 for Windows). Following the results of ANOVAs, Tukey's honestly significant difference test ($\alpha = 0.05$) was used for multiple comparisons to examine significant responses. Goodness fit for linear regression of mass losses against the litter quality variables and environmental factors in relation to slope positions, stand types and rhododendron was also determined by linear regression using MS EXCEL 2003 and SPSS.

Results

Litter chemistry of Oriental beech and spruce

Nitrogen concentration was higher in beech than in spruce litter (Table 2). Carbon did not differ between beech and spruce litter (47.1 and 46.4%, respectively). However, nitrogen concentration was higher in beech litter (1.26%) than in spruce litter (1.16%). Similar to nitrogen, beech litter had higher ADF, lignin and cellulose concentrations and lignin:N ratio than spruce litter (Table 2). Only C:N ratio was higher in spruce litter than in beech litter (Table 2).

Effects of slope positions, stand types and rhododendron on litter decomposition

Figure 1 shows mean mass losses of Oriental beech and spruce litter at three different slope positions on the north-facing

Table 2 Concentrations of carbon (C), nitrogen (N), acid detergent fiber (ADF), lignin and cellulose, and ratio of C:N and lignin:N in Oriental beech (*Fagus orientalis* Lipsky.) and spruce (*Picea orientalis*) litter ($n = 3$)

	Carbon (%)	Nitrogen (%)	C:N	ADF (%)	Lignin (%)	Cellulose (%)	Lignin:N
<i>Fagus orientalis</i>	47.1 ± 0.55	1.26 ± 0.21	37:1	75.5 ± 0.85	48.5 ± 0.62	27.6 ± 0.95	38:1
<i>Picea orientalis</i>	46.4 ± 0.25	1.16 ± 0.05	40:1	64.2 ± 0.35	39.9 ± 0.38	25.0 ± 0.74	34:1

Fig. 1 Mean percent mass losses of Oriental beech and spruce litter on top (1,800 m), middle (1,500 m) and bottom (1,200 m) slope position for the north-facing site. Vertical bars represent the standard error of the mean. Columns with the same letter for each year are not significantly different

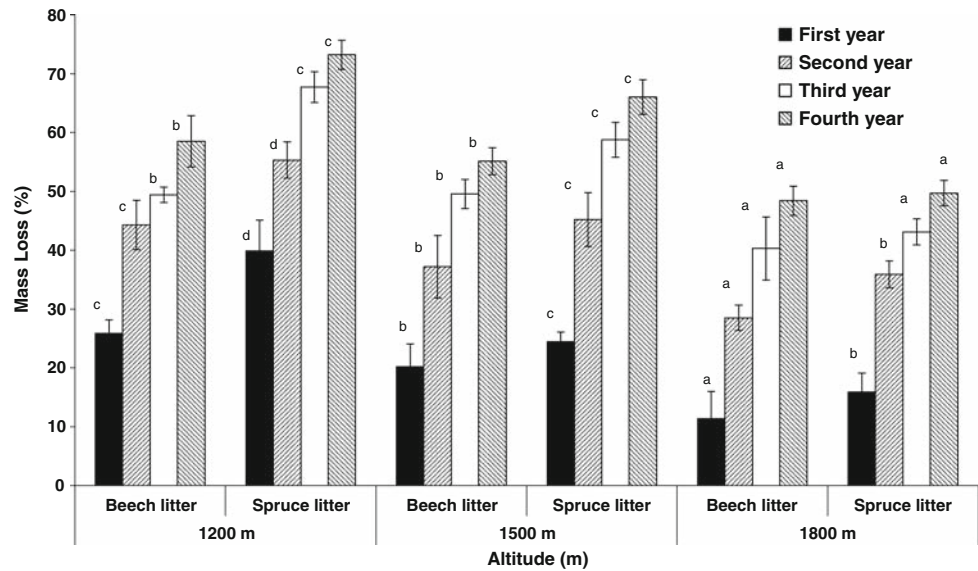


Table 3 Three-way ANOVA was carried out in order to analyze the single effects and interactions of forest types, rhododendron and altitude on litter decomposition rates of beech and spruce litter

Source	Sum of squares	df	Mean square	F value	Partial η^2
Corrected model	2,628.4	8	328.6	22.7	0.834
Intercept	120066.5	1	120066.5	8286.4	0.996
Forest types (FT)	852.2	1	852.2	58.8***	0.620
Rhododendron (Rho.)	678.4	1	678.4	46.8***	0.565
Altitude (Alt.)	336.6	2	168.3	11.6*	0.392
Alt. \times FT	145.6	2	72.8	5.16	0.218
Alt. \times Rho.	0	0	0	0	0
FT \times Rho.	24.7	1	24.7	1.70	0.045
Alt. \times FT \times Rho.	0	0	0	0	0
Error	521.6	36	14.5		
Total	142549.1	45			

Asterisks refer the level of significance: * $P < 0.05$, *** $P < 0.001$

aspect. The single effects and interactions of slope positions, stand types and rhododendron on litter decomposition are listed in Table 3. There were significant differences ($P < 0.01$) in mass losses between tree species and between slope positions (Fig. 1). Beech and spruce litter showed highest mass losses at bottom slope position, followed by middle and top slope position for each sampling interval (Fig. 1). Final year (fourth year) mass losses of beech litter were 59% at the bottom, 55% at the middle and 48% at the top, while spruce litter lost 73% at the bottom, 66% at the middle and 50% at the top. At each slope position, spruce litter decomposed much higher than beech litter.

Beech and spruce litter decomposed much faster in the mixed bags (beech–spruce) than they did separately under each stand type and at each sampling interval (Fig. 2). All litter types (single or mixed) showed highest mass losses under mixed beech and spruce forest, followed by pure beech and spruce forest. The differences in mass losses between stand types and between litter types were significant ($P < 0.01$) at each sampling interval (Fig. 2). At the

end of the study period, single beech and spruce, and mixed beech–spruce litter lost 53, 55 and 60% under mixed beech–spruce forest respectively, 48, 52 and 58% under beech forest, 44, 50 and 55% under spruce forest, respectively. Differences in soil pH between stand types mostly explained the differences in litter decomposition, i.e., litter decomposition rates of beech, spruce and mixed beech–spruce increased with increasing soil pH. Correlation coefficient (r^2) between soil pH and litter decomposition was 0.99 for mixed Oriental beech and spruce litter, 0.98 for Oriental beech litter and 0.96 for Oriental spruce litter.

Rhododendron reduced litter decomposition of Oriental beech and spruce (Fig. 3). The reduction in mass losses due to rhododendron was statistically significant ($P < 0.01$; Fig. 3). Without rhododendron, final year mass losses (fourth year) were 56% for beech and 73% for spruce litter, while beech and spruce litter with rhododendron lost only 43 and 63%, respectively. Soil pH was also strongly positively correlated with litter decomposition rates of Oriental beech and spruce ($r^2 = 0.94$ and 0.92).

Fig. 2 Mean percent mass losses of single Oriental beech and spruce litter and their litter mixture under pure beech and spruce and mixed beech–spruce forest at the elevation of 1,800 m on the north-facing site. Columns with the same letter for each year are not significantly different

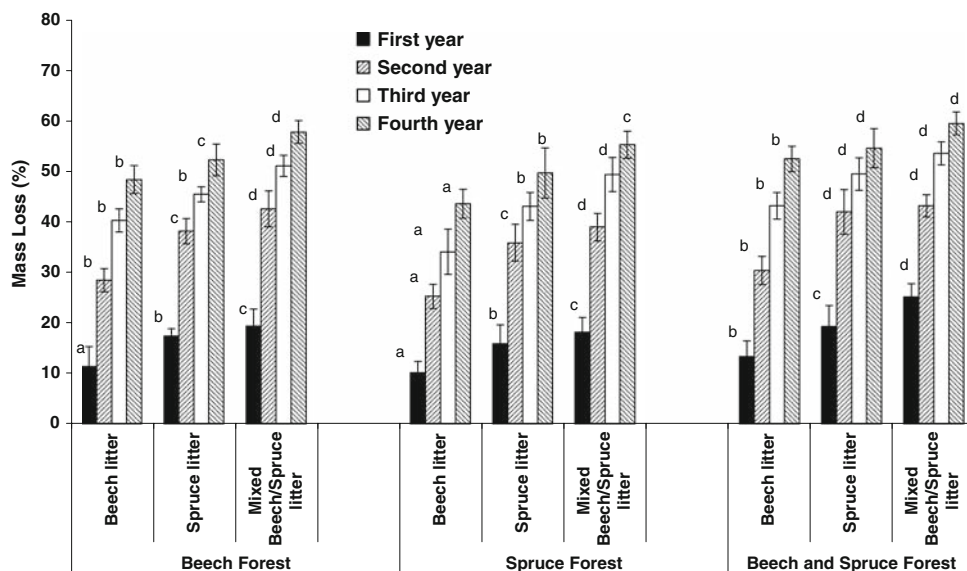
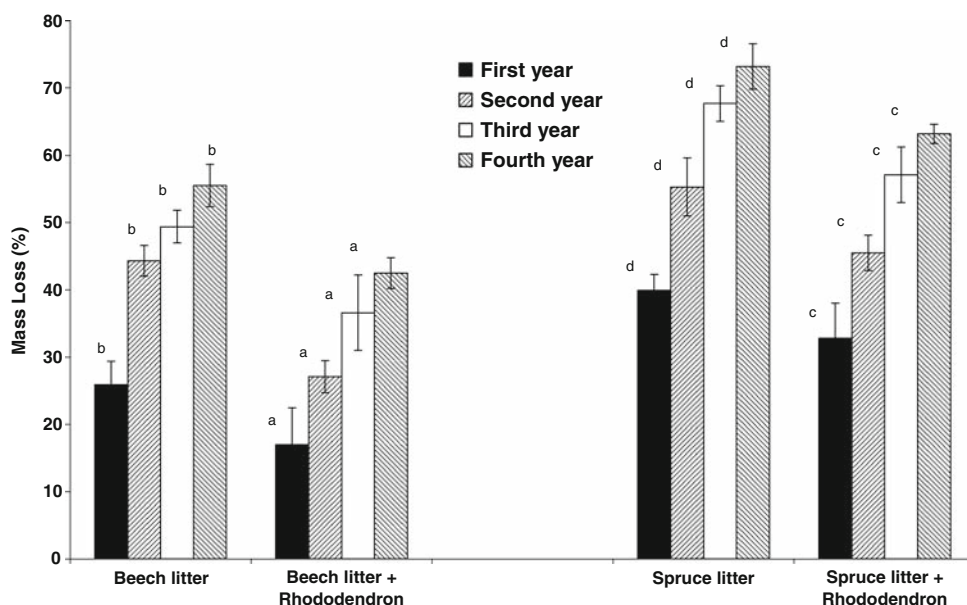


Fig. 3 Mean percent mass losses of Oriental beech and spruce litter decomposed with and without rhododendron on the ground at the elevation of 1,200 m on the north-facing site. Columns with the same letter for each year are not significantly different



When all data from slope positions, stand types and rhododendron were combined to analyze the single effects and interactions of altitudes, forest types and rhododendron on the mass losses (Table 3), it was found that litter mass losses were highly significantly influenced by stand types ($P < 0.001$, $F = 58.8$) and by rhododendron ($P < 0.001$, $F = 46.8$). Changes in elevation also influenced mass losses of beech and spruce, but this was statistically less significant ($P < 0.001$, $F = 11.6$) than stand types and rhododendron. Interactions of elevation gradients, stand types and rhododendron were not significant on the mass losses. That means that two tree species responded similarly to the differences in elevation gradients, stand types and rhododendron.

Discussion

Effects of stand type on litter decomposition rates

Among the three factors (stand type, understorey species and slope position), stand type, i.e., pure or mixed stand of Oriental beech and spruce had the strongest influence on litter decomposition rates. Differential litter decomposition of Oriental beech and spruce was mainly due to adverse conditions in spruce stand, but compared to pure Oriental spruce and beech stand, mixed beech/spruce stand enhanced litter decomposition. Higher litter decomposition rates under mixed-species stands than under pure stands were also reported by other studies. For example, Klemmedson

(1987) showed that litter decomposition rates in Ponderosa pine (*Pinus ponderosa*) forests were accelerated with increasing co-occurrence of Gambel oak (*Quercus gambelii*). He explained that these effects may be related to improved soil fertility and/or changes in forest floor microclimate induced by the presence of the oak. Carlyle and Malcolm (1986) also reported the influence of larch litter on decomposition and nutrient release processes in the mixed-species stands with Sitka spruce (*Picea sitchensis*). They further noted enhanced growth of Sitka spruce in stands that included larch (*Larix eurolepis*), which they related to greater concentrations of N and Ca and greater net N mineralization rates in the forest floor of the mixed-species stands. In this present study, soil and forest floor pH and moisture contents were determined in order to understand the driving forces of the different litter decomposition between three stand types. Among the factors, soil pH was strongly positively correlated with litter decomposition. It is well known that conifer litter is more acidic than deciduous leaf litter and acidification of soil is more pronounced in the first case (Swift et al. 1979). Indeed, it was found by Anderson and Domsch (1978) that the prevailing soil pH had a significant influence on total microbial biomass build-up with decrease in the C_{mic} -to- C_{org} ratio with progressing acidification in deciduous and coniferous forest soils. Mineralization process (Persson et al. 1989) and particularly lignin degradation (Melillo et al. 1989) are dependent on carbon availability which is also shown to decrease under low pH (Persson et al. 1989). A consequence of this decrease in lignin degradation and mineralization process, litter decomposition would be greater on sites with high soil pH and active soil microbial biomass. This seemed to be the case in this present study since litter decomposition was accelerated under mixed beech and spruce forest (less acidic condition), while it was reduced under spruce stand (more acidic conditions). Under beech stand (intermediate acid conditions), litter decomposition was intermediate.

Albers et al. (2004) showed for pure and mixed stands of European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*) that microorganism in beech stand decomposed litter materials considerably more rapidly than in spruce stand with mixed beech/spruce stand being intermediate. In contrast to their study, this present study indicated for Oriental beech and spruce that the environmental conditions in mixed stands created better conditions than those in pure Oriental beech and spruce. However, in both study, the worst environmental conditions for litter decomposition was spruce stands. Albers et al. (2004) stated that adverse environmental conditions such as high polyphenol contents in the litter layer of spruce stands strongly retarded decomposition processes. Polyphenols are known to control N dynamics and facilitate the formation of thick organic layers in which N is retained (Harborne 1997; Northup et al.

1998). In fact, the high content of polyphenols in spruce needle litter likely evolved to reduce decomposition processes and the accumulation of litter in spruce stands presumably increases the competitive strength of spruce against beech in their native habitat due to reducing successful recruitment of beech in high organic soils (Hättenschwiler and Vitousek 2000; Albers et al. 2004).

Litter decomposition of mixed Oriental beech and spruce was always significantly higher than individual Oriental beech and spruce litter irrespective of stand type. Similar findings were also reported by a number of authors indicating that litter mixtures decompose faster than single litter decaying alone (e.g., Hector et al. 2000; Prescott et al. 2000; Gartner and Cardon 2006; Albers et al. 2004). An increase in litter mixture could have been attributed to changes in physical structure of litter in mixtures which could have influenced litter decomposition both directly (physically) and indirectly (through the decomposer community and its activities). Mixing litter from different species with differing litter quality and leaf structure could have most probably altered the chemical environment and physically changed the total litter surface in which litter decomposition took place (McArthur et al. 1994; Hector et al. 2000; Gartner and Cardon 2006). These changes could have also affected decomposer abundance and activity (Hansen and Coleman 1998; Cox et al. 2001). Hansen and Coleman (1998) showed that mixture of yellow birch, red oak and sugar maple provided more microhabitats (defined by physical parameters) to a greater number of microarthropod species compared to single-species litter. They found abundant community of endophagous oribatid mites in mixtures containing oak leaves which increased moisture holding capacity in the litter mixture (Hansen 1999), which itself could enhance decomposition. These complex interactions of biotic factors such as micro- and macrofauna, and abiotic factors such as microhabitats and physical litter structure could be responsible for higher decomposition in litter mixture, but the present study was not intended to investigate all these mechanisms.

Oriental beech litter decomposed much slower rate than spruce litter. This could be mainly attributed to the differences in initial chemical quality between Oriental beech and spruce litter. In many studies, structural and elemental components of plant residues have been recognized as an important predictor of their potential decomposition rates (Swift et al. 1979; Sariyildiz 2003; Sariyildiz and Anderson 2003; Sariyildiz et al. 2005). However, no single litter quality variable has consistently proven to be the best predictor of decay rates over the broad range of plant residue studies. In decomposing litter the chemical component may be degraded in a certain sequence reflecting a succession of microorganisms with different saprotrophic abilities (McClougherty and Berg 1987). This means that the heterogeneous group of

microorganisms that invades the litter initially decomposes the water solubles in the non-matrixed part of the cellulose and hemicelluloses (as energy sources), and finally, the complex of interwoven holocellulose and lignin is attacked by cellulolytic and lignolytic fungi. However, in the present study, the results indicated that the relative proportions of these fractions in cell wall may affect the response of the substrate degraded by microorganisms. For Oriental beech, the cell wall contained higher concentrations of lignins compared to Oriental spruce. The low lignin concentration means that its retarding influence was much lower than for the high lignin concentrations which strongly retarded cellulose or hemicellulose from being degraded by microorganisms (Sariyildiz et al. 2005).

Effects of *Rhododendron* on litter decomposition rates

Purple-flowered rhododendron significantly reduced litter decomposition of Oriental beech and spruce. Many evergreen shrubs that grow in cold, mesic climates, including rhododendron, typically contain high concentrations of organic acids in their leaves and wood (Read 1984; Latham et al. 1996; Eşen 2000). This in turn increases forest floor and soil acidity as found in this present study. As explained above, increased acidity due to rhododendron could have reduced total microbial biomass, mineralization process and lignin degradation which are major factors controlling litter decomposition rates (Pritchett and Fisher 1987). Lower litter decomposition with rhododendron could have been also attributed to low light levels, litter depth, litter quality and allelopathy characteristics of rhododendron (Eşen et al. 2006). The forest floor characteristics differ substantially between rhododendron and non-rhododendron stands. The canopy cover of rhododendron is dense and thus it limits light penetration to the ground. The foliage of rhododendron is sclerophyllous; rhododendron litter decomposes slowly and develops a thick litter layer. This thick litter layer dries out quickly and induces moisture stress (Monk et al. 1985; Eşen 2000). Rhododendron produces allelopathic compounds, which could have also affected the abundance, composition and activity of the decomposer community. All these adverse conditions with the presence of rhododendron could have been responsible for the reduced litter decomposition and they should be investigated in future studies in order to better understand the main effects of rhododendron on litter decomposition.

Effects of slope position on litter decomposition rates

We previously investigated the role of the microclimate, soil characteristics and litter quality variables on the litter mass loss rates of Oriental beech, fir, oak and pine tree species growing within a small region at which the topographical

landforms (aspects and slope positions) can significantly alter its microclimate and soil characteristics (Sariyildiz et al. 2005). We found that differences in soil characteristics due to topographical landforms (especially soil pH, cation exchange capacity and base saturation) significantly influenced the litter quality variable of tree species. Observed variations in decomposition rates of Oriental beech, oak, fir and pine litter exposed to north and south aspect and at three slope positions (700, 1,000 and 1,300 m) on each aspect showed the importance of initial litter quality and site quality effects on decomposition processes. Linear regression of the litter mass losses showed that the dominant rate-regulating factor for the litter mass loss rates was initial lignin concentration of the litter. This present study, however, has indicated the importance of microclimate effect on litter decomposition rates of tree species with the same litter quality variables. Oriental beech and spruce litter at bottom slope position decomposed faster than at middle and top slope positions. Temperature mostly explained the differences in litter decomposition among the three slope positions. Temperature was positively correlated with litter decomposition ($r^2 = 0.609$ for Oriental beech and $r^2 = 0.743$ for Oriental spruce). This result means that litter decomposition of Oriental beech and spruce increased with increasing temperature. A number of other studies have also examined rates of litter decomposition across temperature gradients (e.g., Aerts 1997; Liski et al. 2003; Berg and Meentemeyer 2002). They also observed increased rates of litter decomposition with increasing temperature. A field study of litter decomposition along elevational gradients in the Hawaiian Island by Vitousek et al. (1994) indicated that rate of litter decomposition increased fourfold to 11-fold for a 10°C increase in air temperature, but they also stated that this increase in litter decomposition rate with increasing air temperature strongly depended on substrate quality. In this present study, difference in temperature between top and bottom slope position was 4.5°C. The differences in final litter mass losses between top and bottom slope positions were 23% for Oriental spruce and only 10% for Oriental beech. These different responses to temperature could be related to differences in initial litter quality variables, especially lignin concentrations. Initial lignin concentration was 39.9% in Oriental spruce litter and 48.5% in Oriental beech litter. Thus the low-lignin litter (Oriental spruce) was more responsive to temperature as also found by Vitousek et al. (1994).

In conclusion, this study has shown that microorganisms in mixed Oriental beech and spruce stands, in stands without rhododendron and in stands at bottom slope position decompose litter materials more rapidly than in Oriental spruce stands with Oriental beech stands being intermediate, in stands with the presence of rhododendron and in stands at top slope position with middle slope position

being intermediate. When all three factors (stand type, rhododendron and slope position) were statistically considered together, stand type had the strongest influence on litter decomposition rates of Oriental beech and spruce species. Lower litter decomposition rate was mainly due to adverse conditions in Oriental spruce stands and in stands with the presence of the rhododendron which is associated with lower soil pH in the present study. Higher polyphenol content in organic layers of spruce stands and high concentrations of organic acid in rhododendron leaves and wood, dense canopy cover which can limit light penetration to the ground could be also responsible for the reduced litter decomposition rates. Spruce needles generally decomposed faster than beech leaves irrespective of site of exposure and stand type. However, under the same site and stand type, mixed litter of Oriental beech and spruce had the highest decomposition rates compared to single Oriental beech and spruce litter. This illustrates the importance of litter quality effect on litter decomposition processes. This could be due to changes in physical structure of litter in mixtures which influence litter decomposition both directly (physically) and indirectly (through the decomposer community and its activities). The adverse conditions for litter decomposition in Oriental spruce stands and in the stands with the presence of rhododendron can be effectively counteracted by admixture of beech to spruce monoculture and by using the clear-cutting method for controlling rhododendron.

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