Turk J Agric For
29 (2005) 429-438
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Comparison of Decomposition Rates of Beech (*Fagus orientalis* Lipsky) and Spruce (*Picea orientalis* (L.) Link) Litter in Pure and Mixed Stands of Both Species in Artvin, Turkey

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Received: 03.12.2004

Abstract: The decomposition of spruce, beech and mixed litters of spruce and beech was investigated over 3.5 years in beech, spruce and mixed (beech/spruce) stands using less than 1.5 mm mesh litter bags. Initially, carbon, nitrogen, lignin and cellulose concentrations, and C:N and lignin:N ratios were determined in beech and spruce litters. For all sampling intervals, mixed litters showed higher decay rates than individual beech and spruce litters in both pure stands and mixed stands. Spruce decomposed more rapidly than beech, and initial lignin concentration explained most of the variation in decomposition rates between beech and spruce. However, differences in decomposition rates between beech and spruce were most pronounced in the mixed stand, while they were intermediate in the beech stand and least pronounced in the spruce stand. This shows that adverse environmental conditions, mostly associated with a lower pH content of the soil under spruce stands, retard decomposition processes and individual litters appear to be more sensitive to this retardation than mixed litters. The results also indicate that abiotic and microbial factors in mixed stands could be better than those in pure stands of spruce and beech. Therefore, the establishment of mixed beech and spruce stands can counteract detrimental processes in decomposition associated with spruce monocultures.

Key Words: Decomposition, litter quality, beech, spruce, pure and mixed stands

Türkiye-Artvin Yöresindeki Saf ve Karışık Kayın (*Fagus orientalis* Lipsky) ve Ladin (*Picea orientalis* (L.) Link) Meşçerelerinde Yaprak-İbre Ayrışma Oranlarının Karşılaştırılması

Özet: Bu çalışmada, saf kayın ve ladin meşçerelerinde ve kayın-ladin karışık meşçerelerinde, kayın yapraklarının ve ladin ibrelerinin karışık ve saf olarak yerleştirildiği gözenekli naylon poşetlerde (20 X 20 cm genişliğinde ve 1.5 mm den küçük gözeneklere sahip naylon poşetler) ayrışma oranları 42 ay süresince araştırılmıştır. Çalışmanın başlangıç aşamasında, kayın yapraklarının ve ladin ibrelerinin içerdiği karbon, azot, lignin ve selüloz miktarları ile C:N ve Lignin:N oranları belirlenmiştir. Örnekleme zamanlarının hepsinde, sadece kayın yaprağı ve ladin ibresi içeren poşetlerdeki ayrışma, hem saf hemde karışık meşçereler altında, karışık örnekler içeren poşetlerden daha az olmuştur. Ladin ibreleri, kayın yapraklarından çok daha hızlı ayrışmış, bu iki türün başlangıçta içerdiği lignin miktarının bu türlerin ayrışma oranlarını etkileyen en önemli etken olduğu belirlenmiştir. Bununla beraber, ladin ve kayın arasındaki ayrışma oranları farkı, karışık meşçerelerde en fazla, kayın meşçeresinde orta derecede, ladin meşçeresinde ise en az olarak tespit edilmiştir. Bu sonuç, ladin meşçereleri altındaki olumsuz ortamların (özellikle toprakların düşük pH değerlerinin) ibre veya yaprakların tek başlarına olan ayrışmasını önemli derecede yavaşlattığını, fakat ibre ve yaprakların karışım halinde olmaları durumunda, ladin meşçereleri altındaki bu olumsuz ortamlardan daha az etkilendiğini göstermektedir. Ayrıca çalışmanın sonuçları, karışık meşçerelerdeki abiyotik şartların ve mikroorganizma faaliyetlerinin saf kayın ve ladin meşçerelerinden daha iyi olabileceğini düşündürmektedir. Bu nedenle, kayın ve ladin karışık meşçerelerin tesisinin saf ladin meşçerelerindeki ölü örtü ayrışması üzerindeki yavaşlatıcı etkileri gidermede rol oynayabileceği sonucuna varılmıştır.

Anahtar Sözcükler: Ölü örtü ayrışması, yaprakların kimyasal bileşenleri, kayın, ladin, saf ve karışık meşçereler

Introduction

The decomposition of plant litter plays a significant role in the structure and function of natural ecosystems by acting as an energy source for soil organisms and as a nutrient reservoir for intra-system cycling processes (Kantarcı, 1978; Swift et al., 1979; Karaöz, 1991, 1993). Much decomposition research has focused on how litters of individual species decompose (e.g., Melillo et al., 1982; Sarıyıldız, 2000; Cox et al., 2001; Sarıyıldız and Anderson, 2003a, 2003b). These studies have led to a

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better understanding of the factors that influence litter decay. They have stated that rates of litter decomposition are influenced by a hierarchy of 3 main interacting factors: physical (climate and microenvironment surrounding the litter), chemical (the chemical composition of the litter) and biotic (the nature of the micro-organisms and soil fauna active in the litter decomposition).

The influence of climate and quality of litter on decomposition rates has been well documented for individual species (reviewed by Swift et al., 1979; Heal et al., 1997). In general, research on single-species litter dynamics on broad regional scales has shown that rates of decomposition and nutrient cycling are correlated with climatic conditions such as mean annual temperature and precipitation, whereas, at the small scale (i.e. within site), the chemical composition of the litter, especially the initial N concentrations, C:N ratio, lignin concentrations, and lignin:N ratio in the litter, is of more importance in controlling decay rates.

One factor rarely considered in such studies is the effects of one species of tree litter on the decomposition rate of litter derived from another species. Often, litter bags are exposed on different species of native litter with the implicit assumption that there is minimal interaction between the confined litter and the native litter. Only in recent years have researchers specifically examined potential interactions among leaves of different species during decomposition. 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 litter bags. Understanding these interactions is essential, since leaf litters do not segregate neatly into individual species types in ecosystems, and the composition of plant communities changes over time.

In litter mixture studies, however, only the lumped mixed litter is analysed and thus mechanistic information is lost without single-species analysis. One way to determine whether interactions among litters are occurring in mixes is to compare the decay of each species in the mix to the decay of each species when decaying alone (Prescott et al., 2000). This is not always done. Most litter mixture studies have investigated the influence of inter-specific differences in resource quality on mixing litter of different plant species using microcosms in the laboratory or litter bags in the field within the same system. However, plants can show considerable intra-specific variations in the decay rates and nutrient release in relation to differences in the forest floor types (Prescott, 1996) or soil conditions (Berg et al., 1995), but their effects on decay rates of mixed litter species have received little attention. These factors are especially important on areas where the litter mixture can be seen under both pure and mixed forests because of the effect of the slope and wind. This study was therefore set up to compare the decay rates of single beech and spruce litters to those of mixed litters of beech and spruce.

Materials and Methods

This study was carried out in Artvin province, north-east 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, average 2500 m). In this province, *Picea orientalis* (L.) Link, *Fagus orientalis* Lipsky, *Abies nordmanniana* (Stev.) Matt., *Pinus silvestris* L., *Castanea sativa* Mill. and *Quercus* spp. are generally dominant species in either pure or mixed forms. The understory is generally occupied by grasses (e.g., *Festuca drymeja*, *Trifolium repens*, *Fragaria vesca*, *Vicia* sp., *Lotus corniculatus*), ferns (e.g., *Drypteris dilatata*, *Asplenium adianthum-nigra*, *Pteridum aquilinum*) and broad leaf herbaceous plants (e.g., *Rhododendron ponticum*, *Ilex colchica*, *Rubus phyllathyphyllos*).

The climate is generally characterised by cold winters and semi-arid summers. The mean annual precipitation at lower elevations (Artvin Meteorology Station, at 597 m) is 690 mm, with the highest amounts in January (99.7 mm), and the lowest amount in August (27.1 mm) (Met. Office averages 1948-1998) (Met. Office, 2000). Average monthly temperature ranges from 32 °C in August to -2.5 °C in January. However, mean annual precipitation at higher elevations (Damar meteorology station in Borçka, at 1550 m) can reach over 1100 mm and mean temperature can drop as low as -16.1 °C (Met. Office, 2000). During winter, the ground is often covered by snow, accumulating more heavily on the upper elevations, and reaching depths of up to 2 m.

The study sites were located in the Genya area, Artvin (41° 11' 06'' N, 41° 51' 57'' E). All sites were in close vicinity within a 3 km radius. The study sites were about 1500 m above sea level. The slope angle of the sites was 32% and they were located on the north aspect. Leaf, needle and mixed leaf/needle litters were sampled from pure and mixed stands of beech and spruce in autumn 2000 by spreading nets on the forest floor. In all stands, beech and spruce trees were approximately 90-100 years old and 25-30 m high. The canopy closure of the stands was normal. The percentage of beech and spruce trees in the mixed stand (per hectare) was 41% for pine and 21% for beech (Güner, 2000). Further details of the sites and the Genya area are given by Güner (2000). At each stand, freshly fallen leaf and needle litter was collected from 5 trees and bulked to form a representative sample for each tree species. The main period of litter fall in this area is 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 ^{o}C for 48 h. The oven-dried leaves and needles were slightly crushed by hand, and the largest petiole fragments in leaf samples were removed. All samples were then stored in plastic bags at 6 ^{o}C until required for chemical analyses (Anderson and Ingram, 1993).

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 also determined.

Soil samples were collected in autumn 2000 under the same trees from which leaf, needle and mixed leaf/needle litters were taken. The soil samples were collected in an area of 0.5 x 0.5 m^2 at a distance of 2 m from the base of the trunk. The parent rock of Genya was granite covered with a sandy loam, shallow soil and an organic layer of the humus form mor-like moder for the beech stands, mor for the spruce stands and mull-like moder for the mixed stands. The soil profiles showed distinct A and C horizons; the mineral B-horizon was almost absent. The soil samples were taken from the A-horizon at a depth of 15 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 stand. Forest floor material was sampled from the upper part of the organic matter on the forest floor of each stand.

Soil dry mass and pH (H_2O) were determined. Dry mass of soils was calculated by weight loss after drying 1 g of soil for 48 h at 80 ^{o}C. Soil pH was measured in deionised H_2O using a glass calomel electrode, after equilibration for 1 h in a solution:soil paste 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 ^{o}C (Anderson and Ingram, 1993).

The stored leaf and needle litters were oven-dried at 85 ^{o}C, and then ground in a laboratory mill to a mesh fraction less than 1 mm (Anderson and Ingram, 1993). The ground litters were then analysed for organic carbon, nitrogen, acid detergent fibre (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 persulphate) 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-analyser. Cellulose and lignin were determined using an ADF-sulphuric 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 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% H_2SO_4, and lignin content was calculated from the residual mass of filtrate after ignition at 550 ^{o}C for 2 h. Organic analyses were carried out in triplicate.

The litter bags method (Swift et al., 1979) was carried out in the field to determine rates of leaf, needle and mixed leaf/needle litter in pure and mixed stands of beech and spruce. The litter bags were 20 cm x 20 cm with a mesh size of less than 1.5 mm to allow for inclusion of mesofauna but exclusion of macrofaunal decomposers. The litter bags were filled with about 5 g of air-dried litters of either a single tree species or a combination of 2 tree species (ratio of 1:1). On an area basis this amount of litter is equivalent to 1-2 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 ^{o}C for 24 h.

The number of litter bags used in the experiment was 135 (3 litter types (leaf, needle and mixed leaf/needle) x 3 stands (beech, spruce and mixed stand) x 3 sampling times (12, 24 and 24 months) x 5 replicates = 135 bags). The randomized block design method was used to homogenise the sample setting in the field (Anderson and Ingram, 1993). The litter bags were numbered and fixed to the ground of the corresponding sites with metal pegs after removal of freshly fallen litter. Samples were taken after 12, 24 and 42 months of exposure in the field to follow the continuum of litter decay over time. At each sampling, 5 litter bags were harvested from each stand and percentage loss of initial mass was determined after drying samples at 85 °C for 24 h. The decomposition rate of the litter was calculated using the standard single component decay function (Olsen, 1963) $M_t = M_o e^{-kt}$ with M_t the remaining mass at t, M_o the initial weight of the litter, k the decomposition constant and t the duration of exposure of the litter bags in the field in months.

One-way ANOVA (Rees, 1995) was applied for analysing the effects of stands on soil pH, forest floor water content, soil water content and litter quality for each species using the SPSS program (Version 9.0 for Windows). Following the results of ANOVAs, Tukey's honestly significant difference (HSD) test ($\alpha = 0.05$) was used for significance. Differences in mass losses between stands and tree species were also tested for significance using ANOVA. Relationships between litter quality, soil pH and mass losses were determined by linear regression using SPSS.

Results and Discussion

The initial chemical composition of beech (*Fagus sylvatica* L.) and spruce (*Picea abies* (L.) Karst) and their influences on their decomposition rates have been investigated by a number of authors (e.g., Vesterdal, 1999; Albers et al., 2003). In these studies, beech and spruce litters showed little differences in nutrients and carbon compounds such as lignin. In parallel with the similar chemical composition, they found little differences in decomposition rates between beech and spruce over 4 years of field exposure. In the present study, we used different beech and spruce species (*Fagus orientalis* Lipsky. and *Picea orientalis* (L.) Link), and to our knowledge it was the first time these 2 species were investigated for their initial chemical composition and decay rates.

Initial concentrations of C, N, lignin, cellulose and hemicellulose and ratios of C:N and lignin:N in beech and spruce litters from pure and mixed stands are shown in Table 1. There were no significant differences in litter quality variables for beech and spruce between pure and mixed stand. Therefore, only differences in litter quality variables between beech and spruce litters from the pure stand are explained here. Beech litter showed a significantly ($P < 0.01$) higher N concentration (1.26%) than spruce litter (1.16%). Mean carbon concentration was very similar between the 2 species, but, because of the differences in N concentration, beech litter had a lower C:N ratio than spruce litter ($P < 0.05$). Lignin concentration in beech litter (48.5%) was significantly ($P < 0.001$) higher than that in spruce litter (39.9%). The lignin:N ratio in beech litter (38.5) was also significantly ($P < 0.001$) higher than spruce litter (34.4). Cellulose concentration showed a less significant ($P < 0.05$) variation between the 2 species.

Decay constants for beech, spruce and mixed litters in beech, spruce and mixed forests are shown in Table 2. The results showed faster decay rates for beech and spruce litters confined in the litter bags with the mesh size of less than 1.5 mm. Anderson (1973) calculated an average monthly decay constant over a 13-month period of -0.0047 for intact beech leaves confined in bags in an English wood (mesh size 175 µm). Albers et al. (2003) measured annual decomposition rates of -0.0257 for spruce and -0.0187 for beech litters. Gosz et al. (1973) obtained comparable monthly rates over 11 months of -0.0245 for beech leaves, and Melillo et al. (1982) measured an annual decomposition rate of -0.08 for beech. These estimates reflect considerable variation from one study to another despite the concentration on single species. The litters in the present study were subjected to the effects of freezing and to sudden and intensive spring leaching caused by snow melt. In addition, there was greater accessibility of invertebrates to the bagged litters. These conditions might be responsible for the higher decay rates of beech and spruce litters compared to the findings from other studies.

The decay rates for individual or mixed species measured in the first year were more than 3-4 times those measured in the second year and at the end of the study (Table 2). This pattern of decomposition, i.e. rapid weight loss followed by slower losses, is explained by

Table 1. Resource quality characteristics of beech (*Fagus orientalis*) and spruce (*Picea orientalis*). Tukey's method of multiple pairwise comparison at $\alpha = 0.05$ was used to determine significantly different means. Means with the same letter are not significantly different by columns. Asterisks refer to the level of significance; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

			Carbon (%)	Nitrogen (%)	C : N	Lignin (%)	Cellulose (%)	Lignin : N
		F values	6.18	25.6**	9.80*	405.1***	15.5*	75.8***
	Beech	Mean	47.1[b]	1.26[b]	37.4 : 1[a]	48.5[b]	27.6[b]	38.5 : 1[b]
		Std. Err.	0.53	0.34	1.07	0.63	0.91	0.72
		Max.	49.0	1.36	39.4	49.2	29.4	40.3
		Min.	45.3	1.15	36.3	46.4	25.9	36.2
Pure stand		Range	3.70	0.21	3.10	2.80	3.50	4.10
		Std. Dev.	0.86	0.05	1.86	0.90	1.75	1.25
		Coeff. Var.	0.74	0.02	3.45	0.81	3.06	1.58
	Spruce	Mean	46.4[a]	1.16[a]	40.0 : 1[b]	39.9[a]	25.0[a]	34.4 : 1[a]
		Std. Err.	0.05	0.15	0.92	0.44	0.72	1.43
		Max.	47.3	1.20	41.7	41.3	25.9	36.9
		Min.	45.2	1.12	38.6	38.3	24.1	31.9
		Range	2.11	0.08	3.07	3.00	1.81	4.96
		Std. Dev.	1.08	0.04	1.59	1.58	0.90	2.48
		Coeff. Var.	1.17	0.02	2.54	2.30	0.83	6.15
	Beech	Mean	47.8[b]	1.31[b]	36.5 : 1[a]	47.4[b]	28.3[b]	36.2 : 1[b]
		Std. Err.	0.46	0.02	0.50	0.10	0.50	0.71
		Max.	48.9	1.36	38.2	47.8	29.3	39.6
		Min.	45.8	1.20	34.9	47.1	25.9	35.1
Mixed stand		Range	3.10	0.16	3.30	0.70	3.40	4.50
		Std. Dev.	1.12	0.02	1.23	0.25	1.22	1.75
		Coeff. Var.	1.25	0.03	1.51	0.06	1.48	3.05
	Spruce	Mean	46.2[a]	1.18[a]	38.9 : 1[b]	39.6[a]	26.6[a]	32.8 :1[a]
		Std. Err.	0.28	0.02	0.48	1.50	0.51	0.71
		Max.	47.8	1.24	39.4	47.1	29.0	35.1
		Min.	44.5	1.16	35.7	37.5	25.6	30.5
		Range	1.80	0.14	3.40	9.60	3.40	4.60
		Std. Dev.	0.67	0.05	1.17	3.68	1.25	1.73
		Coeff. Var.	0.46	0.02	1.38	13.6	1.56	3.01

Table 2. Decay constant, k (n = 5), for single- and mixed-species litter bags calculated from single negative exponential model in the first and second years and at the end of the study, and measured percent mass lost at the end of the study (42 months). Values are means ± SE. Coefficients of determination (r^2) are presented to indicate goodness of fit of the data to the model. Means are significantly different between litter types, and between tree stand types ($P < 0.01$).

	Litter type	First year	Second year	Final	r^2	% mass loss
		k	k	k		
Beech stand	Beech	-0.0345 ± 0.005	-0.0412 ± 0.002	-0.0464 ± 0.007	0.992	42.9 ± 1.6
	Spruce	-0.0410 ± 0.003	-0.0476 ± 0.005	-0.0493 ± 0.003	0.960	48.5 ± 1.3
	Mixed	-0.0442 ± 0.002	-0.0511 ± 0.003	-0.0539 ± 0.004	0.954	54.0 ± 1.5
Spruce stand	Beech	-0.0328 ± 0.006	-0.0392 ± 0.002	-0.0440 ± 0.005	0.989	38.9 ± 2.1
	Spruce	-0.0376 ± 0.005	-0.0441 ± 0.005	-0.0462 ± 0.002	0.966	41.7 ± 1.8
	Mixed	-0.0418 ± 0.004	-0.0474 ± 0.006	-0.0506 ± 0.004	0.972	46.3 ± 2.2
Mixed stand	Beech	-0.0357 ± 0.001	-0.0421 ± 0.002	-0.0487 ± 0.009	0.993	46.4 ± 1.2
	Spruce	-0.0436 ± 0.005	-0.0503 ± 0.003	-0.0525 ± 0.007	0.948	53.7 ± 2.1
	Mixed	-0.0450 ± 0.006	-0.0520 ± 0.006	-0.0562 ± 0.005	0.951	60.9 ± 1.4

rapid initial losses of soluble and easily decomposable substances (hemicellulose and cellulose) and the relative enrichment of recalcitrant substances (lignin and lignified cellulose) in the later stages (e.g., Minderman, 1968; Swift et al., 1979).

The influence of the chemical quality of litters on decomposition rates has been well documented for single species (Sarıyıldız and Anderson 2005a, 2005b) and a more detailed review can be found elsewhere (Swift et al., 1979; Heart et al., 1997). In brief, it appears that when lignin concentration increases above 20% it can dominate litter decomposition rates irrespective of other constituents. If lignin concentrations are below this level most of the litter mass consists of structural polysaccharides, which are readily degraded by micro-organisms, and the decomposition rates can be predicted from the initial C:N ratios or simply N concentrations (Heal et al., 1997). Litter quality also directly affects the abundance, composition, and activity of the decomposer community. Thus, the interactions between litter quality and the decomposer community are important controllers of organic matter decomposition and nutrient release.

In the present study, when mass losses were plotted against litter quality variables in beech and spruce litter (Table 3), it was found that initial lignin concentration explained most of the variation in decomposition rates between beech and spruce. This was not surprising since the beech and spruce litter studied in this experiment contained lignin concentrations greater than 20%. The explained variances for the litter quality variables were, however, the highest for the mixed stand, followed by the beech and spruce stands, suggesting that the litter quality variables were exerting greater control over litter decomposition on the mixed forest floor material compared to the beech and spruce forest floor materials. This effect could be attributed to site differences in microbial metabolic functions (Bauhus et al., 1998), interactions between litter quality and soil fertility (Chapman et al., 1988; Prescott, 1996), and litter quality effects on fungal activities (Cox et al., 2001), but the study was not intended to investigate these mechanisms.

Table 3. Goodness of fit for linear regression of mass losses at the end of the study (42 months) against the litter quality variables for beech and spruce litters from the 3 tree stands. Correlation coefficients for the regression were significant ($P < 0.01$, $N = 15$).

	Beech stand	Spruce stand	Mixed stand
Litter quality variables	r^2	r^2	r^2
N	0.70	0.61	0.72
C	0.52	0.47	0.59
Lignin	0.87	0.76	0.95
Cellulose	0.66	0.54	0.82
C : N	0.54	0.43	0.53
Lignin : N	0.84	0.79	0.91

The decay rates of mixed beech and spruce litters were significantly different from decay rates of individual beech and spruce litters. Litter decay rates over the 3.5 years were high for the mixed litters, intermediate for spruce litters and low for beech litters (overall means of k of 0.0539, 0.0493 and 0.0463 for mixed litter, spruce and beech litter, respectively). However, the difference was least pronounced in spruce forest (k of 0.0506, 0.0462 and 0.0440 for mixed litters, spruce and beech litter, respectively), intermediate in beech forest (k of 0.0539, 0.0493 and 0.0464, respectively), and most pronounced in mixed forest (k of 0.0562, 0.0525 and 0.0487, respectively).

In order to understand the driving forces of these different decomposition rates, we measured soil moisture content, the water content in the forest floor and soil pH (Table 4). The soil moisture content and the water content in the forest floor did not show any significant variations between the 3 stands. This was not surprising considering that all 3 stands were in close vicinity and precipitation in this area was high. However, soil pH showed significant variation between the 3 stands. Mean soil pH was 3.62 for the spruce stand, 4.92 for the beech stand and 5.76 for the mixed stand.

When mass losses were plotted against soil pH from beech, spruce and mixed stands, it was found that the decomposition rates of mixed litters, beech and spruce litters varied significantly in relation to soil pH in the 3 tree stands (Figure 1). Pure or mixed beech-spruce litters showed an increase with increasing soil pH (Figure 1). This increase with soil pH was more pronounced in mixed litter ($R^2 = 0.9668$) than in pure spruce ($R^2 = 0.9485$) and beech ($R^2 = 0.9059$) litter (Figure 1). 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). Indeed, it was found

Table 4. Forest floor water content, soil water content and soil pH values from pure and mixed beech and spruce stands. Tukey's method of multiple pairwise comparison at $\alpha = 0.05$ was used to determine significantly different means. Means with the same letter are not significantly different by columns.

		First year	Second year	Final
Beech stand	Forest floor water content (%)	$65.4^b \pm 1.4$	$64.6^b \pm 1.5$	$68.3^b \pm 1.18$
	Soil water content (%)	$35.5^b \pm 1.3$	$34.7^b \pm 0.91$	$38.2^b \pm 1.8$
	Soil pH	$4.88^b \pm 0.11$	$4.93^b \pm 0.11$	$4.95^b \pm 0.12$
Spruce stand	Forest floor water content (%)	$58.3^a \pm 2.5$	$60.6^a \pm 2.3$	$65.4^a \pm 3.4$
	Soil water content (%)	$30.4^a \pm 2.4$	$28.5^a \pm 3.2$	$33.1^a \pm 4.2$
	Soil pH	$3.62^a \pm 0.16$	$3.71^a \pm 0.34$	$3.52^a \pm 0.21$
Mixed stand	Forest floor water content (%)	$62.3^b \pm 2.9$	$63.5^b \pm 1.1$	$64.3^a \pm 2.9$
	Soil water content (%)	$33.7^b \pm 1.8$	$35.4^b \pm 1.2$	$36.1^b \pm 3.1$
	Soil pH	$5.85^c \pm 0.21$	$5.68^c \pm 0.12$	$5.75^c \pm 0.24$

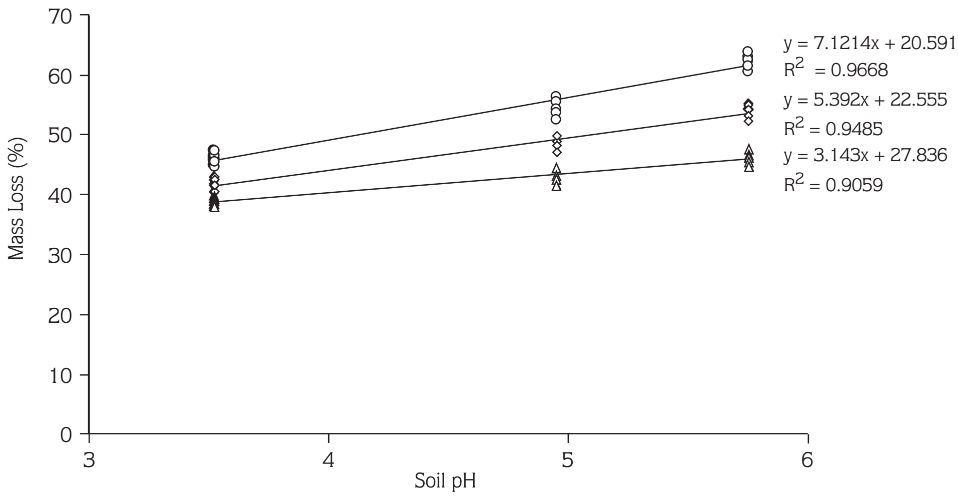

Figure 1. Percentage mass loss of mixed (R^2 = 0.9668), spruce (R^2 = 0.9485) and beech (R^2 = 0.9059) on different soil pH values from spruce, beech and mixed stands.

by Anderson and Domsch (1993) that the prevailing soil pH had a significant influence on total microbial biomass build-up with a decrease in the C_{mic}-to-C_{org} ratio with progressing acidification in deciduous and coniferous forest soils. The mineralisation 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 the mineralisation process would be a general correlation between soil pH and litter decomposition and decomposition would be greater on high soil pH sites with active soil microbial biomass. The result in the present study also supports these findings since under spruce stand (more acidic conditions) the 3 litter types show lower decay rates than under mixed beech and spruce stands (less acidic conditions) with an intermediate rate in the beech stand (intermediate acid conditions).

These results can also be attributed to differences in physical and chemical properties and biological processes in tree litters. Mixing beech and spruce litters with different resource quality and leaf structures seemed to change the chemical environment and physically alter the total litter surface where decomposition occurred. These factors were not investigated in the present study, but the findings in the literature could help to explain this phenomenon. The effect of one litter on another litter's decomposition has been reported by several authors, who have shown that mixtures of litter exhibit positive interactions in increasing litter decay rates and respiration rates over those measured from the pure species (e.g., Klemmedson, 1987; Blair et al., 1990; Hector et al., 2000; Gartner and Cardon, 2004). Enhanced nutrient release from litter mixtures was shown by a number of authors (e.g., Chapman et al., 1988; Briones and Ineson, 1996; Hector et al., 2000). Their proposed hypothesis was that translocation of nutrients between litters of different quality may result in a more rapid and efficient utilisation of litter substrate by decomposers, and that these effects are mediated by the response of the litter invertebrates and microfauna to increased resource heterogeneity. These alterations could also affect decomposer abundance and activity (Hansen, 1999; Wardle, 2002).

Hansen and Coleman (1998) illustrated how physical changes in leaf mixtures could alter the decomposer community and associated decay rates in a study that examined mixed litters of yellow birch, red oak and sugar maple. The mixture of these 3 species supported a greater number of microhabitats (defined by physical parameters), which were correlated with a greater number of microarthropod species than were in the single-species litters. Increased mass loss was also well correlated with the increase in microhabitats, particularly in mixtures containing oak leaves, which supported a more diverse and abundant community of endophagous oribatid mites; the activity of these mites also increased moisture holding capacity in the litter (Hansen, 1999), which itself could enhance decomposition. Klemmedson (1987) suggested that the accelerated decomposition rates and nutrient release in Ponderosa pine needles through a physical interaction with oak litter may be related to changes in the forest floor microclimate induced by the presence of oak litter. Chapman et al. (1988) demonstrated that litter mixtures increased faunal diversity and noted an interaction effect of litter mixtures on forest floor invertebrates and total heterotrophic respiration. They found greater numbers of collembola, earthworms, enchytraeids, and nematodes on the forest floor of mixed stands than would be expected based on abundance in single-species stands.

Overall we can state that chemical, biological or physical changes in beech and spruce mixtures accelerate the decomposition rates both directly (physically) and indirectly (through the decomposer community and its activities). Whether nutrient transfers within the decomposing litter are mediated by physical or biological means, nutrients released from rapidly decaying, higher quality litters seem to stimulate decay in adjacent, more recalcitrant litter.

Conclusion

This study showed that micro-organisms in a mixed stand decompose litter materials considerably more rapidly than in a spruce stand, with a beech stand being intermediate. The differential litter decomposition is mainly due to adverse conditions for litter decay in the spruce stand, which is probably associated with a lower pH content of the soil under the spruce stand. The establishment of a mixed stand can counteract detrimental processes associated with spruce monocultures. Our results indicate that abiotic and microbial factors in a mixed stand could be better than those in pure stands of spruce and beech. Spruce litter decomposed significantly faster than beech litter, irrespective of time of exposure and forest floor type. Initial lignin concentrations explained most of the variation in decomposition rates between beech and spruce. Mixed litters decomposed more rapidly than beech litter, with spruce litter being intermediate. This result generally supports the conclusions of previous studies, namely that interactions of litters from different species in ecosystems do affect decomposition rates of individual litter types in mixes, the consequent nutrient availability to plants, and the decomposer community structure and activity. The results also 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. In order to understand the main impacts of litter quality variables, biotic and abiotic factors on litter decomposition rates according to the tree stand types, more detailed studies of these factors in forest floors under different tree species, and their influence on litter decomposition are recommended.

Acknowledgements

We wish to express our sincere gratitude to Dr. J.M. Anderson for his kindness in reading and correcting the manuscript. We are grateful to Peter Splatt, a technician at Exeter University, for his help with the sample analyses. We are also grateful for the helpful comments from the reviewers during the revision of the paper.

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