

# Effects of Gap-Size Classes on Long-Term Litter Decomposition Rates of Beech, Oak and Chestnut Species at High Elevations in Northeast Turkey

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## ABSTRACT

Effects of gap-size classes on litter decomposition rates were investigated in a high-elevation forest for 4 years by placing leaf litter of beech (*Fagus orientalis* Lipsky.), oak (*Quercus robur* L.), and chestnut (*Castanea sativa* Mill.) in (1) a closed canopy, (2) small gaps with a diameter of less than 15 m, (3) intermediate gaps with a diameter of 15–30 m, and (4) large gaps with a diameter of more than 30 m. The leaf litter placed under the closed canopy or within the small gaps decayed more rapidly than those in the intermediate or the large gaps for all three deciduous species. Among the microclimatic and soil factors, soil temperature was most strongly positively correlated with litter decomposition rates, and among the three species, initial lignin concentration was the best predictor of

litter decomposition rates. Differences in litter decomposition rates among the four gap-size classes were generally significant, but varied among the three species. Litter with low lignin concentrations tended to be more responsive to canopy openings. Large forest gaps significantly reduced litter decomposition rates in this study by changing environmental conditions, especially by decreasing soil temperature and soil pH which reduced soil respiration rates. These changes may result in reduced nutrient cycling, carbon cycling, and organic matter turnover rates in these forest ecosystems.

**Key words:** gap-size classes; lignin; litter decomposition; litter quality; soil temperature; oriental beech and spruce.

## INTRODUCTION

Plant litter decomposition has long been recognized as an essential process for nutrient cycling and organic matter turnover within ecosystems that are important determinants of plant productivity and

ecosystem carbon (C) storage (for example, Anderson 1991; Heal and others 1997; Hättenschwiler and others 2005; Lensing and Wise 2007). Rates of plant litter decomposition and nutrient mineralization are influenced by temperature and moisture conditions (Berg and others 1993; Coûteaux and others 1995; Sariyildiz and others 2005a), the chemical and physical nature of the litter (Heal and others 1997; Sariyildiz and Anderson 2003a), the forest type (Chadwick and others 1998; Sariyildiz and Anderson 2003b; Sariyildiz and others 2005b), the nature and

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TS formulated the research question, designed the study, performed the field and laboratory experiments, analyzed data, and wrote the manuscript.

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abundance of the decomposing organisms (Frankland 1992; Cox and others 2001), and acidification (Berg 1986; Sariyildiz and others 2005a). In general, climate factors (soil or air temperature and moisture) govern decay rates on broad regional scales, whereas initial litter-quality variables [C:nitrogen (C:N) ratio, lignin, N, and lignin:N ratio] are of more importance in controlling decay rates at small scales, that is, within site (Heal and others 1997; Sariyildiz and Anderson 2005a, b; Polyakova and Billor 2007). However, a number of studies have shown that even at small scales, small disturbances such as gaps created by hurricanes, natural treefalls, strong winds, storms, insect damage, illegal cutting, or logging in forests can change environmental conditions, which can retard or accelerate litter decomposition through negative or positive effects on the activity of organisms (Zhang and Zak 1995, 1998; McCarthy 2001; Prescott 2002; Prescott and others 2003).

Caused by the death of individual or multiple trees with subsequent opening of the canopy, gaps have been studied in many forest ecosystems for the past 20 years (McCarthy 2001), but most studies have focused on how different gap-size classes created by these disturbances can alter forest ecosystem structure and functioning and thus affect processes such as seed germination, seedling establishment, regeneration, vegetation dynamics, and so on (Wise and Schaefer 1994; Meer and others 1994; Arunachalam and Arunachalam 2000). Brokaw (1985) found that gap size is critical in determining the recruitment and establishment of different tree species. One of the mechanisms by which gap size regulates regeneration dynamics is by increasing light levels, temperature, nutrient availability, and other properties of the environment sufficiently to influence the dynamics of populations of trees over differing spatial and temporal scales (Spies and Franklin 1989; Whitmore 1989; Zhang and Zak 1995; Zhang and Liang 1995). A number of studies have also focused on how these changes in gap sizes affect below-ground processes. Gap formation by natural disturbances can change light intensity and other environmental conditions (soil temperature and moisture) that influence litter mass, root mass, the nature and abundance of the decomposing organisms and thus may influence rates of litter and root decomposition. Surface soil temperatures (Fetcher and others 1985) and moisture content are generally higher in gaps than in the adjacent understory (Vitousek and Denslow 1986; Denslow and others 1998). The mass of litter and fine roots on the forest floor is lesser under canopy gaps than under a closed canopy (Ostertag 1998), although other studies (for example, Sanford 1990) report no difference in fine

root biomass between canopy gap and understory. Soil respiration at the center of gaps is generally lower compared to mature stands (Brumme 1995; Arunachalam and Arunachalam 2000). Elevated N mineralization rates and nitrate availability have been observed in openings of 0.25 ha (Prescott and others 1992), 0.1 ha (Prescott and others 2003), a 30-m diameter, 0.07 ha patch (Bauhus and Barthel 1995), and in a gap created by the removal of 15 trees (Parsons and others 1994). Similarly, Ritter (2005) found that nitrification, net mineralization, and soil N concentrations tended to be increased in the gaps. A number of authors also reported higher soil  $\text{NO}_3\text{-N}$  and extractable  $\text{PO}_4\text{-P}$  in gaps than in adjacent understory (for example, Matson and others 1987; Denslow and others 1998; Hope and others 2003). Bartsch (2000) stated that the most obvious changes in element cycles in gaps occurred in the ecosystem losses of nitrate, cations, and nitrous oxide. Similarly, Bauhus and Bartsch (1995) reported that disruption of the N cycle in gaps led to substantial nitrate losses. On the other hand, some authors (for example, Bauhus 1996; Arunachalam and Arunachalam 2000; Bauhus and others 2004; Ritter and Bjørnlund 2005) found no differences between the gap and the stand in forest floor and mineral soil N concentrations and soil C.

The effects of gap sizes on litter decomposition rates have also been investigated in a number of studies. One of the earliest studies by Zhang and Zak (1995) showed that plant litter decomposing under a closed canopy or within small gaps (diameter < 5 m) lost mass more rapidly than those in large gaps (> 30 m). Initial N concentrations and soil moisture content in their study were most strongly correlated with annual decay rates. They concluded that large gaps significantly reduce microbial activity and decomposition rates by changing environmental conditions. Similar results were also reported by Ritter (2005) and Prescott and others (2003), whereas the other studies (for example, Luizão and others 1998; Alvarez-Sanchez and Enriquez 1996; Denslow and others 1998; Bauhus and others 2004) found no significant relationships between gap sizes and litter decomposition rates or even higher litter decomposition rates in large gaps (Prescott 2000). A study by Hope and others (2003) using leaf litter of three tree species indicated that the effects of gap size on litter decomposition rates can vary with tree species.

The effects of gap-size classes on litter decay rates were investigated in a high-elevation field for 4 years by placing leaf litter of beech (*Fagus orientalis* Lipsky.), oak (*Quercus robur* L.), and chestnut (*Castanea sativa* Mill.) in forest gaps that comprise a

gradient for each species: (1) closed canopy, (2) small gaps with a diameter of less than 15 m, (3) intermediate gaps with a diameter of 15–30 m, and (4) large gaps with a diameter of more than 30 m. The hypotheses were that (1) gaps that are large enough to alter environmental conditions in the gaps will affect the nature of the decomposing organisms, and consequently the rates of litter decomposition, and (2) the effects of gaps on litter decomposition rates vary with tree species. Especially, low-lignin litter would be more responsive to gap sizes because they tend to be more responsive to any manipulation. To determine which factors are most clearly related to rates of litter decomposition, microclimatic and soil factors in which litter decomposition took place were also determined throughout the study period.

## MATERIALS AND METHODS

### Study Site

This study was carried out in Artvin province, northeast Turkey (41°51' N, 41°06' E), a mountainous region with steep slopes (ranging from 30 to 65%) and high elevations (up to 3,000 m). In this province, *Picea orientalis* (L.) Link, *F. orientalis* Lipsky, *Abies nordmanniana* (Stev.) Matt., *Pinus silvestris* L., *C. sativa* Mill., and *Quercus* spp. are generally dominant species in either pure or mixed stands. Study plots were chosen in pure beech, oak, and chestnut stands. They were natural forests situated on a north aspect at a high elevation (between 1,200 and 1,800 m), and thus were frequently subject to strong winds, storms, and heavy snow during winter. In addition to these factors, illegal logging by people, insect and animal damage and also some silvicultural practices by the local Forestry Commission created several different sizes of forest gaps in these natural forests (ranging from 5 to 30 m in diameter). Beech, oak, and chestnut stands from which the study plots were taken were in close vicinity within a 4-km radius. Four forest gap-size classes were chosen for each tree species: (1) closed canopy, (2) small gaps with a diameter of less than 15 m, (3) intermediate gaps with a diameter of 15–30 m, and (4) large gap with a diameter of more than 30 m. The gap-size classes were randomly distributed in each stand. The four different gap-size classes in each tree stand were approximately within a 500-m radius. Because many different factors cause the differences in gap-size classes in these forests the ages of the gaps differed from one another. After illegal logging or heavy storms or snow, the loss of each tree was generally noted by the Forestry Commission, which

made it possible to find out the age of the lost trees in any gaps. If there was no information, the ages of the logged trees were measured on the stump or (if not possible) the age was estimated using the yield tables for each species. The age of the gap was calculated by interpolating the mean age of the representative mature trees around the gap from mean age of the logged trees in the gap. The larger gaps were generally formed earlier than the small gaps, but age of the gaps was not significantly different between the gap-size classes. The large gaps were usually formed after heavy storms and thus were formed earlier (about 25 years old), whereas the small gaps were mostly created by illegal logging and were mostly about 15 years old. The studied beech and chestnut 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. The understory of forest gaps was generally occupied by grasses (for example, *Festuca drymeja*, *Trifolium repens*, *Fragaria vesca*, *Vicia* sp., *Lotus corniculatus*), ferns (for example, *Dryopteris dilatata*, *Asplenium adianthum-nigra*, *Pteridium aquilinum*), and broad-leaf herbaceous plants (for example, *Rhododendron ponticum*, *Ilex colchica*, *Rubus phyllanthophyllos* sp.). Because of the dense broad-leaf herbaceous plants (especially *R. ponticum*), regeneration of beech, oak, and chestnut species was not abundant within larger gaps.

The climate is characterized by cold winters and semi-arid summers. Mean annual precipitation at higher elevations was 1,216 mm, with the highest amount in January (152 mm), and the lowest amount in August (71 mm) (Borçka-Damar meteorology station at 1,550 m) between 1980 and 2005 (Met Office 2005). Mean annual temperature was 6.63°C. Average monthly temperature ranges from 18.1 in August to –6.2°C in January. In winter, the ground was covered with snow, which accumulated more heavily on the upper elevations than 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 mor-like moder under beech, mull-like moder under oak, and mull under chestnut (Güner 2000; Sariyildiz 2003). The soil profiles showed distinct A- and C-horizons; the mineral B-horizon was almost absent.

### Leaf Litter Collection, Preparation, and Field Incubation

Beech, oak, and chestnut leaf litter were sampled in autumn 2002 by spreading nets on the forest floor. Freshly fallen leaf litter was collected beneath five trees and bulked to form representative samples for each tree species. Materials 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 leaves were slightly crushed by hand, and the largest fragments of petioles 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. About 3 g of air-dried 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 litterbags used for the experiment was 960 [3 species (beech, oak, and chestnut) × 4 gap-size classes (closed canopy, small, intermediate, and large gaps) × 8 removal dates (every 6 months, at the end of March and September) × 5 replicates (litterbags) × 2 replicate sites for each gap-size class = 960 litterbags]. The litterbags were numbered and fixed to the ground of the corresponding gap sites (under the four different gap-size classes of beech, oak, and chestnut tree species). The litterbags were randomly distributed within each gap-size class starting from the center of the gap toward the side of the gap.

All litterbag samples from the experiment were taken after every 6 months of exposure in the field for 4 years. At each sampling, 10 litterbags were harvested from each corresponding site and percentage loss of initial mass was determined after drying samples at 85°C for 24 h. The 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). The decomposition rate ( $k$ ) was calculated from the percentage of dry mass remaining using an exponential decay model (Olson 1963):  $W_t/W_o = e^{-kt}$ , where  $W_t/W_o$  is the fraction of initial mass remaining at time  $t$ , and  $t$  is the elapsed time (years) and  $k$  is the decomposition constant ( $y^{-1}$ ). As suggested by Olson (1963), the time required for 95% mass loss was calculated as  $T_{95} = 3/k$ .

### Analysis of Plant Materials

The stored leaf litter was oven-dried at 85°C and then ground in a laboratory mill to a mesh fraction less than 1 mm (Anderson and Ingram 1993). The ground litter was then analyzed for organic C, N, 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 the 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%  $H_2SO_4$ , 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

To understand the driving forces of different decomposition rates according to the different gap-size classes, soil samples and forest floor material were also collected initially and at each litterbag sampling time from three replicate gaps for each gap-size class of beech, oak, and chestnut. The soil samples were taken from the B-horizon at a depth of 15 cm. The moist field samples were sieved (<2 mm) to remove stones, roots, and macrofauna and bulked to obtain a single representative soil sample from each species. Soil and forest floor pH, moisture, and soil texture were determined. Soil respiration rates in the field were also determined under each gap-size class using the soda-lime method (Edwards 1982; Raich and others 1990). Buckets, 20-cm tall and 27.5-cm diameter, were used as measurement chambers. One day prior to measurements, plastic rings with the same diameter were placed over the soil and carefully pushed about 1 cm into the soil. All live plants inside the plastic rings were cut to prevent aboveground plant respiration. Carbon dioxide was absorbed with 60 g of soda lime contained in 7.8-cm diameter by 5.1-cm tall cylindrical tins. In the field, the plastic rings were removed, measurement chambers were placed over the tins of soda lime, and the chambers were held tightly against the soil with rocks. After 24 h the tins were removed, and the contents oven dried at 105°C for 24 h and then weighed. Blanks were used to account for carbon dioxide absorption during handling and drying (Raich and others 1990). Soda-lime weight gain was multiplied by 1.69 to account for water loss (Grogan 1998). At the same time, air and soil temperature values were

measured. The studied sites were located at altitudes of 1,200–1,800 m on the north aspect with very steep slopes. Measurements of soil and air temperature were started in the morning at the bottom of the elevation (1,200 m) and finished at noon at the top of the elevation (1,800 m). The measurements were carried on after noon at the top and finished in the evening at the bottom. Average daily soil and air temperature in each gap class were then calculated. In each gap-size class, soil and air temperature were measured five times. The first measurement was done at the center of the gap, and then while walking from the center toward the four directions (up, down, left, and right). Average values were then calculated for each gap-size class. Soil temperature was determined at a 5-cm soil depth.

Soil moisture content on fresh soil samples was calculated by weight loss after drying approximately 10 g of soil for 24 h at 105°C (Allen 1989). Soil pH (H<sub>2</sub>O) and forest floor material pH were measured in deionized H<sub>2</sub>O using a glass calomel electrode, after equilibration for 1 h in solution:soil and solution:forest floor material with a ratio of 10:1 (Allen 1989). Soil texture (sand, silt, and clay) was determined using the hydrometer method of Bouyoucos (1936). All analyses were carried out in triplicate.

## Data Analysis

A two-way analysis of variance (ANOVA) was applied for analyzing the effects of litter types and gap-size classes on mass losses using the SPSS

program (Version 11.5 for Windows). Following the results of ANOVAs, Tukey's Honestly Significant Difference (HSD) test ( $\alpha = 0.05$ ) was used for multiple comparisons to examine significant responses. After that, simple Pearson correlation coefficients were calculated between decay constant rates ( $k$ ) and litter quality variables, soil, and environmental factors using a similar statistical program (SPSS). The coefficients of determinant ( $R^2$ ) which indicate the goodness of fit of the data to the exponential decay model were also determined using MS EXCEL 2003.

## RESULTS

### Soil Analysis

Mean soil and forest floor pH, moisture, soil texture, soil respiration, soil and air temperature values from the four gap-size classes for each tree species are given in Table 1. Soil and forest floor pH, soil respiration, soil and air temperature varied significantly among gap-size classes (Table 2). Mean soil and forest floor pH decreased with increasing gap sizes for each tree species. Mean soil moisture was higher under larger gaps than under small gaps or closed canopy, but this was not statistically significant. Similar to soil and forest floor pH, soil respiration, soil and air temperature also decreased with increasing gap sizes. Mean soil texture (sand, silt, and clay content), however, did not significantly differ between the gap size classes (Table 1).

**Table 1.** Mean Soil Properties and Climatic Factors Determined from the Four Gap-size Classes for Beech, Oak, and Chestnut Tree Species

Species	Gap-size classes	Soil pH (H <sub>2</sub> O)	Forest floor pH (H <sub>2</sub> O)	Soil moisture (%)	Sand (%)	Silt (%)	Clay (%)	Soil respiration (g Cm <sup>-2</sup> d <sup>-1</sup> )	Soil temp. (°C)	Air temp. (°C)
<i>F. orientalis</i>	Closed canopy	5.55c	5.38c	31.5a	69.5b	16.8a	13.7a	1.54d	13.5b	19.2b
	<15 m	5.12bc	4.98b	32.6a	70.5b	18.4a	11.1a	1.37c	12.3b	18.1b
	15–30 m	4.87b	4.65b	32.1a	68.2b	17.3a	14.5a	1.24b	11.4a	16.3a
	>30 m	4.18a	4.25a	33.5a	65.9a	19.7a	14.4a	1.12a	10.3a	15.6a
<i>Q. robur</i>	Closed canopy	5.82c	5.65c	30.3a	70.2a	17.5a	12.3b	1.86d	17.3c	21.3c
	<15 m	5.62c	5.15b	31.2a	71.7a	18.8a	9.50a	1.74c	16.1b	20.1bc
	15–30 m	5.25b	5.05b	32.5a	70.3a	16.0a	13.7b	1.56b	15.4ab	18.6ab
	>30 m	4.51a	4.85a	31.4a	72.4a	16.9a	10.7a	1.23a	14.2a	17.3a
<i>C. sativa</i>	Closed canopy	5.78c	5.58c	33.3a	67.5a	16.4a	16.1b	1.79c	17.3b	20.6c
	<15 m	5.52b	5.25b	34.6a	69.7a	15.6a	14.7b	1.67b	16.6b	19.2bc
	15–30 m	5.38b	5.10b	33.2a	73.2b	14.2a	12.6a	1.36a	14.9a	18.4b
	>30 m	4.81a	4.75a	32.1a	72.8b	15.5a	11.7a	1.29a	14.3a	16.6a

Means with the same letter for each species are not significantly different by columns ( $n = 3$ ).

**Table 2.** Pearson Correlation Coefficients for the Relationships Between Gap Size and Environmental Factors

	Gap size	Soil pH	Forest floor pH	Soil moisture	Sand	Silt	Clay	Soil respiration	Soil temperature	Air temperature
Gap size	–									
Soil pH	–0.882**	–								
Forest floor pH	–0.868**	0.937**	–							
Soil moisture	0.356	–0.561	–0.665*	–						
Sand	0.203	0.135	0.160	–0.376	–					
Silt	–0.028	–0.303	–0.330	0.655*	–0.515	–				
Clay	–0.209	0.088	0.082	–0.094	–0.729**	–0.211	–			
Soil respiration	–0.832**	0.920**	0.897**	–0.522	0.000	–0.102	0.081	–		
Soil temperature	–0.634*	0.792**	0.836**	–0.787**	0.330	–0.446	–0.020	0.864**	–	
Air temperature	–0.858**	0.934**	0.954**	–0.552	0.111	–0.135	–0.018	0.962**	0.855**	–

\*Correlation is significant at the 0.05 level (two-tailed).

\*\*Correlation is significant at the 0.01 level (two-tailed).

## Litter Chemistry

Mean concentrations of total C, N, ADF, lignin and cellulose, and ratios of C:N and lignin:N in the freshly collected beech, oak, and chestnut litter are given in Table 3. Total C concentration was 45.6% for beech, 48.2% for oak, and 51.3% for chestnut. N concentration was similar between the three tree species (about 1.45%). Beech had the highest ADF (72.5%) and lignin (43.5%) concentration, whereas oak had the lowest ADF (50.2%) and chestnut had the lowest lignin (21.1). The cellulose concentration was 31.7% for chestnut, 28.8% for beech, and 23.2% for oak. The C:N ratio was 31:1 for beech, 33:1 for oak, and 35:1 for chestnut. In contrast, the lignin:N ratio decreased from beech (30:1) to oak (18:1) and chestnut (15:1).

## Decomposition in the Four Gap-Size Classes

Figure 1 shows litter decay rates ( $k$ ) of beech, oak, and chestnut tree species in the four different gap-size classes sampled for 4 years. Final decay constant rates, coefficients of determinant ( $R^2$ ) which

indicate the goodness of fit of the data to the model, percent mass remaining at the end of the experiment and the time required for 95% mass loss for the tree litter are given in Table 4. The single effects and interactions of the gap-size classes and litter types on mass losses are listed in Table 5.

Chestnut had the highest litter decomposition rate at each sampling interval, followed by oak and beech litter. All litter types decomposed faster under the closed canopy or within the small gaps than in the intermediate or large gaps (Figure 1, Table 4). Differences in mass losses were significant within the four gap-size classes and between tree species for all sampling intervals, but more pronounced and significant differences were noted between the closed canopy and the larger gaps ( $P < 0.001$ ). Beech, oak, and chestnut litter lost most of their initial masses during the first 3 years when 42, 64, and 70% (average of all gap sizes) of their original dry masses, respectively, were lost. During the same period, mass losses in the gap-size classes for all species were ranked in the order: closed canopy > small gaps > intermediate gaps > large gaps. Mass losses under closed canopy

**Table 3.** Litter Quality Characteristics (Estimates of the Means) of Beech (*F. orientalis* Lipsky.), Oak (*Q. robur* L.), and Chestnut (*C. sativa* Mill.)

	C (%)	N (%)	ADF (%)	Lignin (%)	Cellulose (%)	C:N ratio	Lignin:N ratio
<i>F. orientalis</i>	45.6 ± 0.55	1.43 ± 0.35	72.5 ± 0.25	43.5 ± 0.52	28.8 ± 0.15	31:1	30:1
<i>Q. robur</i>	48.2 ± 0.48	1.48 ± 0.62	50.2 ± 0.15	26.7 ± 0.23	23.2 ± 0.22	33:1	18:1
<i>C. sativa</i>	51.3 ± 0.43	1.45 ± 0.24	53.4 ± 0.75	21.1 ± 0.32	31.7 ± 0.41	35:1	15:1

Values are means ± 1 SE.

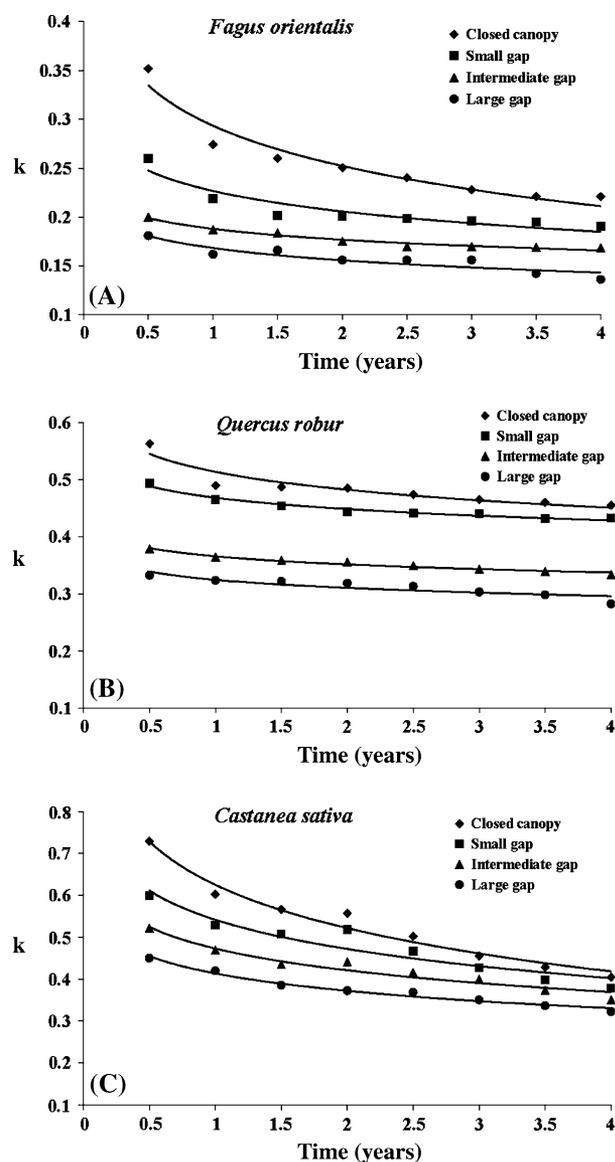


Figure 1. Decay constant rates ( $k$ ) of beech (A), oak (B), and chestnut (C) litter decomposed in the four gap sizes: closed canopy, small gaps (<15 m), intermediate gaps (15–30 m), and large gaps (>30 m).

were 48.3% for beech, 72.6% for oak, and 74.4% for chestnut, whereas mass losses in the large gaps were 36.3% for beech, 56.0% for oak, and 65.0% for chestnut. Thus the differences between the closed canopy and the large gap were 12.0, 16.6, and 9.4% for beech, oak, and chestnut, respectively. Mean mass losses at the end (fourth year) were 50.7% for beech, 77.1% for oak, and 76.4% for chestnut. Final-year mass losses for the gap-size classes remained in the order: closed canopy > small gaps > intermediate gaps > large gaps for all species. The differences in final litter mass losses between the closed canopy and the

large gaps were 16.6% for beech, 17.4% for oak, and 7.8% for chestnut.

A two-way ANOVA showed that the main effects of the gap-size classes, litter types, and the gap-size classes  $\times$  litter type interaction on litter mass loss were all significant at the 95% level ( $\alpha = 0.05$ ) (Table 5). Calculated times required for 95% loss for beech litter were 13.5 years under closed canopy, 15.7 years under small gaps, 17.9 years under intermediate gaps, and 22.1 years under large gaps (Table 4). The gap-size classes  $\times$  litter types interactions were also significant in litter mass loss analyses. This means that mass losses showed different trends according to the litter types under the same gap-size classes. For example, chestnut litter showed less difference in mass loss (7.8%) between the closed canopy and the large gap compared to beech (16.6%) and oak (17.4%) litter.

To estimate the degree of relationship among the litter quality variables, environmental factors, and mass losses, a correlation matrix was created using the litter decomposition data from all gap-size classes for all tree species (Table 6). Of the litter quality variables, mass loss was strongly negatively correlated with lignin concentration ( $r = -0.90$ ), lignin:N ( $r = -0.89$ ), and ADF ( $r = -0.88$ ) ( $P < 0.01$ ). Among the environmental factors, mass loss was positively correlated with soil temperature ( $r = 0.97$ ) and soil respiration rates ( $r = 0.77$ ) ( $P < 0.01$ ). This indicates that among the litter quality variables and environmental factors measured, the initial lignin concentration and soil temperature were having the greatest effect on litter mass losses either between tree species or within the gap-size classes.

## DISCUSSION

Most studies have emphasized that plant litter decomposition rates are influenced by a hierarchy of three main interacting factors: physical (climate and microenvironment surrounding the litter), chemical (the chemical composition of the litter), and biotic (the nature of microorganisms and soil fauna active in the litter decomposition) (Heal and others 1997). Forest gaps caused by the death of individual or multiple trees with different size classes can influence these factors and thus have a large influence on plant litter decomposition (Prescott 2002; Prescott and others 2003; McCarthy 2001; Ostertag and others 2003). A number of studies found that litter decomposition was lower in larger gaps than in smaller gaps or under a closed canopy (Zhang and Zak 1995; Ritter 2005), whereas others found no significant changes in litter decomposition between different gap sizes

**Table 4.** Annual Decay Rates ( $k$ ) of Beech, Oak, and Chestnut Litter under the Four Different Gap Sizes and Percent Mass Remaining at the End of the Study

Litter type	Gap-size classes	$k$ mean $\pm$ SE	$R^2$	% Mass remaining mean $\pm$ SE	$T_{95}$ (year)
<i>F. orientalis</i>	Closed canopy	$-0.221 \pm 0.012$	0.934	$41.4 \pm 0.97$	13.5
	<15 m	$-0.191 \pm 0.022$	0.868	$46.7 \pm 0.85$	15.7
	15–30 m	$-0.168 \pm 0.014$	0.965	$51.0 \pm 1.46$	17.9
	>30 m	$-0.136 \pm 0.011$	0.847	$58.0 \pm 2.70$	22.1
<i>Q. robur</i>	Closed canopy	$-0.456 \pm 0.011$	0.847	$15.0 \pm 2.05$	6.3
	<15 m	$-0.433 \pm 0.005$	0.764	$17.7 \pm 0.77$	6.9
	15–30 m	$-0.334 \pm 0.004$	0.968	$26.4 \pm 2.02$	9.0
	>30 m	$-0.282 \pm 0.010$	0.785	$32.4 \pm 1.11$	10.6
<i>C. sativa</i>	Closed canopy	$-0.405 \pm 0.012$	0.967	$19.8 \pm 0.59$	7.4
	<15 m	$-0.378 \pm 0.016$	0.867	$22.4 \pm 1.64$	7.9
	15–30 m	$-0.350 \pm 0.009$	0.903	$24.6 \pm 0.92$	8.6
	>30 m	$-0.322 \pm 0.014$	0.928	$27.6 \pm 1.13$	9.3

Values are means  $\pm$  1 SE.

**Table 5.** Effect of Gap Sizes, Litter Types, and Their Interaction on Litter Mass Loss during Decomposition

Source	Sum of squares	df	Mean square	$F$	Partial Eta squared
Corrected model	10,926.8 <sup>1</sup>	11	993.3	626.3	0.993
Intercept	278,465.0	1	278,465.0	175,581.8	1.000
Species	9,061.5	2	4,530.8	2,856.8***	0.992
Gap-size classes	1,668.7	3	556.2	350.7***	0.956
Species $\times$ gap-size classes	196.6	6	32.8	20.7***	0.721
Error	76.1	48	1.6		
Total	289,468.0	60			
Corrected total	11,003.0	59			

<sup>1</sup> $R^2 = 0.993$  (Adjusted  $R^2 = 0.991$ ).

Asterisk refers the level of significance: \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

(Thompson and others 1998; Denslow and others 1998) or higher litter decay rates under larger gaps (Prescott 2000). In this study, these relationships were investigated for 4 years using three forest tree species (beech, oak, and chestnut) growing naturally in a high-elevation site. The results provide new information on the intra- and inter-specific relationships between gap-size classes and litter decomposition rates. The litter decomposition rates of all three species differed among the four gap-size classes, but the largest differences in litter decomposition rates were noted between the closed canopy and the larger gap size (>30 m). The litterbags placed in the large gaps decomposed more slowly than the same litterbags under the closed canopies. This finding is consistent with other studies in which decomposition rates in larger gaps were slower (Blair and Crossley 1988; Zhang and Zak 1995; Ritter 2005). The differences in decay

constant rates ( $k$ ) among the four gap-size classes were variable and generally significant, but differed among the three species. Beech had significantly different decay constant rates among the four gap-size classes throughout the study period (Figure 1A). For oak, the closed canopy and small gaps (<15 m) had significantly lower decay constant rates than the intermediate (15–30 m) and larger gaps (>30 m) during all sampling intervals. Chestnut litter had initially highly significant differences in decay constant rates among the four gap-size classes, but the differences were not apparent at year 4 (Figure 1C). These different responses could be related to differences in initial litter quality variables, especially lignin concentrations. Initial lignin concentration ranged from 21 in chestnut litter to 27% in oak litter to 44% in beech litter. Thus the low-lignin litter (chestnut litter) was more responsive to canopy openings as also

**Table 6.** Pearson Correlation Coefficients for the Relationships Between Litter Mass Losses and Initial Litter Quality and Climatic Factor Parameters

	Mass loss	C	ADF	Lignin	Lignin:N	Soil pH	Forest floor pH	Soil moisture	Soil temp.	Air temp.	Soil respiration
Mass loss	-										
C	0.751**	-									
ADF	-0.876**	-0.760**	-								
Lignin	-0.902**	-0.946**	0.930**	-							
Lignin:N	-0.887**	-0.927**	0.948**	0.999**	-						
Soil pH	0.716**	0.357**	-0.375**	-0.390**	-0.391**	-					
Forest floor pH	0.736**	0.369**	-0.440**	-0.429**	-0.434**	0.937**	-				
Soil moisture	0.745**	-0.837**	0.632**	0.789**	0.773**	-0.561**	-0.665**	-			
Soil temperature	0.968**	0.710**	-0.834**	-0.819**	-0.828**	0.792**	0.836**	-0.787**	-		
Air temperature	0.770**	0.319*	-0.494**	-0.428**	-0.441**	0.934**	0.954**	-0.552**	0.855**	-	
Soil respiration	0.773**	0.344**	-0.501**	-0.446**	-0.457**	0.920**	0.897**	-0.522**	0.964**	0.862**	-

\*Correlation is significant at the 0.05 level (two-tailed).

\*\*Correlation is significant at the 0.01 level (two-tailed).

found by Prescott (2002). Different responses to canopy openings among litter of different tree species were also shown by Hope and others (2003) for aspen, Douglas-fir, and pine leaf litter. In their study, aspen litter had the lowest lignin concentration ( $96 \text{ g kg}^{-1}$ ), followed by Douglas-fir litter ( $128 \text{ g kg}^{-1}$ ), and lodgepole pine litter ( $188 \text{ g kg}^{-1}$ ). They found that aspen litter showed a weak trend of increasing rate of decomposition over 5 years with increasing opening size. Prescott and others (2000) also found that aspen leaf litter was the only substrate that decayed faster in clear-cuts than in adjacent forests.

Soil properties such as moisture and temperature regimes and pH affect litter decomposition rates by influencing the activity of decomposers (Swift and others 1979). Most studies of gap sizes have shown that small-scale disturbances increase temperature and moisture levels in forest soils (Hope and others 2003), resulting in changes to microbial communities and increased microbial activity (Gray and others 2002; Ritter and others 2005). In this study, the moisture contents of mineral soil or the forest floor material among the four gap-size classes were not significantly different. As shown by Zhang and Zak (1995) and others (for example, Ritter and others 2005), litter decomposition rates were not correlated well with soil moisture. In contrast to the findings of the other studies, mean soil and air temperature decreased with increasing gap-size classes in each forest type. The decrease in soil and air temperature with increasing gap size in this study could be attributed to the high elevation. The studied sites were situated at elevations of 1,200–1,800 m. The litter decomposition rates among the gap-size classes were strongly positively correlated with soil temperature ( $r = 0.968$ ). Many studies have shown that rates of litter decomposition increase with increasing temperature (Aerts 1997; Liski and others 2003). A field study of litter decomposition along elevational gradients in the Hawaiian Islands by Vitousek and others (1994) indicated that the rate of litter decomposition increased 4–11-fold for a  $10^\circ\text{C}$  increase in air temperature, but they also stated that this increase in litter decomposition rate with increasing air temperature strongly depended on the site and substrate quality. There was a good correlation ( $r = 0.964$ ) between mean soil respiration rates and soil temperature regimes in this study, that is, the higher the soil temperature the higher the soil respiration rates. An increase with increasing soil temperature was also reported by other researchers (for example, Kowalenko and others 1978; Raich and Tüfekçioğlu 2000). The large gaps had the lowest soil respiration rates, whereas the closed

canopies had the highest soil respiration rates. This may be attributed to root respiration in large gaps. Respiration by roots and their associated microbial components represents a significant part of soil respiration in most ecosystems (Tüfekçioğlu and Küçük 2004). Live roots directly contribute to soil respiration, and dead roots and root exudates provide C as an energy source and nutrients for microbial biomass. The root mass was not investigated in this study, but as shown in the other studies, the fine root mass in the forest floor is generally less in canopy gaps than in a closed canopy (Ostertag 1998). Soil and forest floor pH also decreased with increasing gap size. Mean mineral soil and forest floor pH also showed a good positive correlation with soil respiration rates. Lower soil pH within the larger gaps could have been the result of the dominant shrub species in the studied sites, especially purple-flowered *Rhododendron* (*R. ponticum* L.) whose leaves are known to have a high pH, or potential loss of plant nutrients through leaching and greater exposure to direct insolation in the larger canopy openings. *Rhododendron* ssp. are known to synthesize organic acids that are allelopathic to other plants and animals (Cross 1981; Read 1984; Esen 2000). Lowered soil pH as a result of exudation of these organic acids into the soil could reduce activity of the decomposers, resulting in debris accumulation on the forest floor over time in the larger gaps.

Anderson and Domsch (1978) found that the prevailing soil pH had a significant influence on total microbial biomass build-up with decrease in the  $C_{\text{mic}}$  to  $C_{\text{org}}$  ratio with progressing acidification in deciduous and coniferous forest soils. The mineralization process (Persson and others 1989) and particularly lignin degradation (Melillo and others 1989) are dependent on C availability, which may also decrease under low pH (Persson and others 1989). A consequence of this decrease in lignin degradation and the mineralization process would be a general correlation between soil pH and litter decomposition; decomposition would be greater on high soil pH sites with active soil microbial biomass. Liming of acidic forest soils is known to accelerate decomposition and mineralization processes (Deleporte and Tillier 1999). Bauhus and others (2004) showed that lime application, a routine measure in many European forests to ameliorate soil acidity, leads to accelerate litter decomposition in European beech. They attributed the faster decay rates to the increased activity of soil fauna and the disappearance of the H-layer after the lime application. In this study under natural conditions the three litter types had slower decay rates in the large gaps (more acidic

conditions) than under the closed canopy or in the small size gaps (less acidic conditions).

There were also significant differences in litter decomposition rates among the three species. These differences could be attributed to the differences in their initial litter quality variables. Among the litter quality variables measured for beech, oak, and chestnut, initial lignin concentrations were most strongly negatively correlated with the decay rate. Many studies have characterized the initial chemical composition of litter from temperate plant species as a means of predicting their inherent patterns of decomposition (Swift and others 1979; Heal and others 1997). In general terms, if the lignin concentrations are below about 20% most of the litter mass comprises 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 (McClaugherty and Berg 1987). Because of their intimate physical association and covalent bonding in the cell wall (Monties 1994), higher concentrations of lignin increasingly dominate the processes of litter decomposition and mass losses can be related to initial concentrations of lignin (Fogel and Cromack 1977; Sariyildiz 2003; Sariyildiz and Anderson 2005), or lignin:N ratios (Aerts 1997). In this study all the three litter types had lignin concentrations greater than 20% (21% in chestnut litter to 44% in beech litter) so it could be predicted that initial lignin concentration would dominate litter decomposition rates irrespective of other constituents.

In conclusion, this study has shown that canopy gaps in high-elevation beech, oak, and chestnut forests significantly alter litter decomposition rates of the three species. Large gaps significantly reduced soil respiration rates and decomposition rates by changing microclimatic and environmental conditions, especially by decreasing soil temperature and soil pH. The differences in litter decomposition rates of the three species among the four gap-size classes varied among the three species. These different responses were related to differences in initial litter quality variables, especially lignin concentrations. Low-lignin litter was more responsive to canopy openings. More extensive studies investigating the responses of tree species with different litter quality variables (especially lignin) from different regions to gap sizes are needed to substantiate this trend.

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