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ORIGINAL PAPER

Effects of *Ips typographus* (L.) damage on litter quality and decomposition rates of Oriental Spruce [*Picea Orientalis* (L.) Link.] in Hatila Valley National Park, Turkey

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Abstract This study investigated the effects of *Ips typographus* (L.) damage on initial litter quality parameters and subsequent decomposition rates of oriental spruce tree species [*Picea orientalis* (L.) Link]. The needle litter was collected from highly damaged, moderately damaged and control stands on two aspects (north and south) and two slope position (top and bottom) on each aspect. The litter was analyzed for initial total carbon, lignin and nutrient (nitrogen, phosphorus, potassium, calcium, magnesium and manganese) concentrations. The variability in nitrogen and calcium concentrations and ratios of C:N, lignin:N and lignin:Ca was significantly affected by the insect damaged levels. While nitrogen concentrations in needle litter increased with increasing insect damage (and consequently the ratios of C:N and lignin:N decreased), calcium concentrations decreased (and consequently the ratio of lignin:Ca increased). Aspect and slope positions explained most of the variability in carbon, lignin, phosphorus, potassium, magnesium and manganese concentrations and lignin:P ratio between all studied stands. Litter decomposition was studied in the field using the litterbag technique. The litter from highly damaged stands showed highest decomposition rates followed by moderately damaged and control stands. The mass loss rates were significantly positively correlated with initial nitrogen concentration and negatively with C:N and lignin:N ratios. The effects of microclimate resulting from canopy damage on litter decomposition was also examined at the same time using standard litter with the same litter quality parameters, but they showed no significant differences among the insect damage levels indicating that alteration of the litter quality parameters produced by *I. typographus* damage played a more important role than altered microclimate in controlling needle litter decomposition rates. However, changes in microclimate factors due to topography influenced decomposition rates.

Keywords Litter decomposition · *Ips typographus* · Litter quality · *Picea orientalis* (L.) Link. · Nitrogen · Lignin · Aspect · Slope position

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Introduction

Most studies on plant litter decomposition are in agreement that decomposition rates are strongly influenced by climate variables (especially temperature and precipitation) (De Santo et al. 1993; Fioretto et al. 1998; Kurz-Besson et al. 2006) and general litter quality variables such as N and Klason lignin concentrations or C:N or lignin:N ratios (Couteaux et al. 1995; Sariyildiz and Anderson 2003a; Fierer et al. 2005). In general, climate governs decay rates on broad regional scales, whereas litter quality variables are of more importance in controlling decay rates at regional stand types, i.e., within site (Berg et al. 1993, 1995; Heal et al. 1997). However, a number of studies have shown that even at regional scale areas, small-scale disturbances such as insect outbreaks can change litter chemistry and also create different microclimate conditions resulting from canopy damage which can retard or accelerate litter decomposition through negative or positive effects on the activity of organisms (Schowalter et al. 1986; Chapman et al. 2003; Chapman 2006; Classen et al. 2005; Cobb et al. 2006), but very few studies have directly investigated the effects of insect herbivory on litter decomposition (Cobb et al. 2006; Chapman et al. 2003).

A less studied but mostly stated factor which insect herbivory may change litter decomposition rates is through alteration of the chemical properties of litter produced by infested plants (Chapman et al. 2003). However, there are contrasting results among the studies. For example, Findlay et al. (1996) found that foliar herbivory increased the concentration of recalcitrant compounds, which subsequently slowed down the rates of decomposition, whereas Chapman et al. (2003) showed that insect herbivory increased the rates of decomposition by increasing litter nitrogen levels, but no changes in the concentration of recalcitrant compounds, such as lignin. A recent study by Cobb et al. (2006), however, showed that insect herbivory reduced rates of mass loss primarily by reducing the amount of moisture in the forest floor, but did not significantly increase initial foliar N or lignin levels. In a result, they have concluded that whether the changes in environmental conditions or litter quality due to insect damage increase, decrease or no impact on litter decomposition rates are likely to vary among insect species and also among tree species (Cobb et al. 2006; Schowalter 2000; Mattson 1980; Hunter 2001).

Ips typographus (L.) is the most destructive species of the genus Ips, and probably the most serious pest on Norway spruce (*Picea abies* Karst.) in Europe and on oriental spruce [*Picea orientalis* (L.) Link] in Turkey (Wermelinger 2004). The extent of bark beetle damage is huge and a large number of public money has been invested in controlling damage of *I. typographus* and clearing windthrow and subsequent sanitation felling. Today, it has been estimated that the bark beetle *I. typographus* has infested and damaged 15,000 ha spruce forest in Hatila Valley National Park, Artvin, Turkey (Erbek et al. 2005). In the region, slope aspect and slope position are very important topographical factors influencing local site microclimate, soil chemistry and litter quality. In a recent study, Sariyildiz et al. (2005) showed for a variety of tree species that slope aspect and slope positions can significantly alter soil chemistry, macroclimate and litter quality. Consequently, these changes significantly affect the rates of litter decomposition in the region. Over the last decade, *I. typographus* attack rates on pure oriental spruce in the Hatila Valley National Park also seem to be influenced by topographical landforms (aspects and slope positions). Oriental spruce stands exposed on the south-facing sites and situated at higher slope positions seem to be more attacked by *I. typographus* than those on the north-facing sites and at lower slope positions. However, at all sites (regardless of being on the south or north-facing sites or at the higher or lower slope position), some stands adjacent to the damaged stands are not attacked or moderately damaged by *I. typographus*.

The objectives of this study were to (1) investigate whether *I. typographus* damages on oriental spruce tree species change litter quality variables and thus alter litter decomposition rates compared to the adjacent stands which were moderately damaged or not damaged by *I. typographus*, (2) study the relative effects of aspects and slope positions on the noted differences in the litter quality variables and the litter decomposition rates between highly damaged (HD), moderately damage (MD) and not damaged (control) oriental spruce stands, and (3) determine the relative direct (change in litter quality) and indirect (microclimate) impacts of *I. typographus* on litter decomposition.

Materials and methods

Study areas

This study was carried out in Hatila Valley National Park, Artvin province, northeast Turkey, (41°51′N, 41°06′E), a mountainous region with steep slopes (range from 30 to 70%) and high elevations (up to 2,300 m). Within the Hatila Valley National Park there is considerable variation in vegetation types, but over the altitude of 1,700 m up to 2,100 m forest formation type is pure oriental spruce trees, and has been under attack by *I. typographus* over the last two decades. Climate is generally characterized by cold winters and semi-arid summers (1980–2000 meteorological data from Artvin meteorology station, 597 m). In 2000, mean annual precipitation in lower elevations was 719 mm, with the highest amounts in January (110.9 mm), and the lowest amount in August (29.5 mm) (Met Office 2000). Average monthly temperature ranges from 20.5°C in June to 2.4°C in January. However, mean annual precipitation in higher elevations was over 1,200 mm, with the highest amounts in January (152 mm), and the lowest amount in August (71 mm) (Borçka-Damar meteorology station at 1,550 m). Mean annual temperature in higher elevations was 6.63°C. Average monthly temperature ranges from 18.1°C in June to −6.1°C in January. In winter, the ground was covered with snow, which accumulated more heavily on the upper elevations than lower elevations.

There is a gradient of infestation severity, with high mortality on the south-facing sites and at high altitude compared to the north and low altitude in the Hatila Valley National Park. Therefore, the study sites were chosen from the north and the south aspect and from two slope positions (top slope at about 2,100 m and bottom slope at about 1,800 m) on each aspect. The location, stand and soil characteristics of the studied sites are shown in Table 1. The studied sites in the Hatila Valley National Park are part of a long-term study investigating the effects of tree physiology, site and stand characteristics on the susceptibility of orien-

Table 1 Location, stand and soil characteristics (15-cm depth) of pure oriental spruce used as sources for soil samples and needle litter

	North						South					
	Top slope			Bottom slope			Top slope			Bottom slope		
	HD	MD	Control	HD	MD	Control	HD	MD	Cont.	HD	MD	Control
Site												
Elevation (m)	2,137	2,141	2,146	1,823	1,801	1,769	2,142	2,123	2,131	1,862	1,842	1,808
Slope angle (%)	38	48	47	45	40	38	43	43	42	62	68	65
Insect density	High	Low	Uninfested	High	Low	Uninfested	High	Low	Uninfested	High	Low	Uninfested
Picea orientalis stand												
Age (year)	81^{a}	105^{b}	136^{c}	184^{b}	135^{a}	193^{b}	111^{a}	129^{b}	133^{b}	271^{c}	160^{b}	125^{a}
Height (m)	19^{a}	20^{a}	20^{a}	23^{a}	24^{a}	24^{a}	18^{a}	25^{b}	24^{b}	21^{a}	31^{b}	30^{b}
Canopy cover (%)	57^{a}	82^{b}	90^{b}	22^{a}	63^{b}	93^{c}	50^{a}	83^{b}	90^{b}	18^{a}	70^{b}	92^{c}
Mortality (%)	90^{c}	45^{b}	3^{a}	75^{c}	40^{b}	2^{a}	95^{c}	30^{b}	1^{a}	93^{c}	45^{b}	2^{a}
Soil												
Mineral soil texture	Sand	Sand	Sand	Sandy loam	Sandy loam	Sandy loam	Sandy loam	Sandy loam	Sandy loam	Sandy loam	Sandy loam	Sandy loam
Soil organic matter (%)	1.40^{a}	5.10^{b}	4.87^{b}	4.08^{a}	6.48^{b}	6.20^{b}	1.17^{a}	2.13^{c}	1.50^{b}	4.40^{a}	6.71^{b}	7.27^{c}
Soil pH	4.16^{a}	4.08^{a}	4.75^{b}	4.22^{a}	4.05^{a}	5.26^{b}	4.72^{a}	4.61^{a}	4.61^{a}	3.89^{a}	3.62^{a}	4.16^{b}
Soil moisture (%)	6.39^{c}	5.29^{b}	4.19^{a}	4.06^{b}	3.38^{a}	3.66^{a}	6.01^{b}	6.38^{b}	5.27^{a}	3.77^{b}	2.92^{a}	4.09^{c}

Means with the same letter are not significantly different by lines tal spruce [*Picea orientalis* (L.) Link.] trees and stands to attack by the spruce bark beetle (*I. typographus* L.) in Artvin, Turkey. At each slope position, oriental spruce stands were divided into three *I. typographus* infested levels namely as: (1) highly damaged stands (HD) with high tree mortality, (2) moderately damaged stands (MD) with low tree mortality and (3) control stands (control) with uninfested trees. Three 20 × 20 m plots were established at each infested and uninfested stand type. At each slope position, the plots for each stand type were adjacent to each other. Total plot numbers were 36 (2 aspect × 2 slope position × 3 *I. typographus* infested levels × 3 replicate plots = 36). In each stand, each tree was measured for age and height, and tree architecture was noted. After that mean stand age, height and canopy cover were calculated. Tree age was determined by counting each annual growth ring in the trunk of the tree. The growth rings (a thin core of wood) reaching from bark to dead center were extracted from the living tree using a borer. Tree heights were measured with a Blume-Leiss altimeter. Canopy cover was determined in the field by visually estimating the amount of cover in each plot. After that, this estimation was checked for its correction by using stand parameters such as the measurements of number of stems and diameter at breast height in each plot. Diameter at the breast height was measured using the diameter tape. Length of each tree branches in north, south, east and west direction was also visually noted in order to obtain tree architecture and stand profile. Mortality (%) of the stand was decided by dividing the death tree numbers to all tree numbers within each plot.

Soil samples were also collected in each plot. The soil samples were collected in an area of $0.5 \times 0.5\ m^2$ at a distance of 2 m from the base of the trunk. Three soil core 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 give a single representative soil sample for each plot on each aspect and at each slope position.

Litter sample collection, preparation and field incubation

Oriental spruce litter was sampled in September 2006 from the HD, MD and control stand types on the north- and south-facing sites and at the two slope positions on each aspect. At each stand type, freshly fallen foliar litter was collected by hand beneath ten randomly chosen mature trees and bulked to form a representative sample. Material showed no signs of discoloration or of obvious mycelial development at this stage. The samples were air-dried in the laboratory and then oven-dried at 40°C for 48 h. The oven-dried foliar litter was slightly crushed by hand. All samples were then stored in plastic bags at 6°C until required for chemical analyses.

The litter bags method (Swift et al., 1979) was carried out in the field to determine the differences in litter decomposition rates between the insect damaged levels, aspects and slope positions. The litterbags were 20 × 20 cm with a mesh size of 1.0 mm to allow for inclusion of mesofauna but not macrofauna. 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 litterbags with foliar litter were numbered and placed on the corresponding sites where the litter samples were taken (north- vs. south-facing, two slope positions, three damaged level stands, each). They were fixed to the ground with metal pegs in the middle of September 2006. In addition to these corresponding site litter (or local site litter) with different litter quality, standard litter with the same litter quality was also placed on the same sites in order to differentiate the role of the litter quality and the microclimate conditions resulting from canopy damage. Three litterbags were collected from each site after 8 months (in the middle of May 2007) and 12 months decomposition in the field (in the middle of September 2007). Percentage loss of initial mass was calculated after drying samples at 85°C. The decomposition constant 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 (year) and k is the decomposition constant ($year^{-1}$).

Analysis of soil and plant materials

The soil samples were analyzed for pH (H_2O), soil texture, moisture and soil organic matter (Table 1). Soil pH was measured in deionized H_2O using a glass calomel electrode, after equilibration for 1 h in a solution:soil paste ratio of 10:1. Soil texture (sand, silt and clay) was determined by Bouyoucos' Hydrometer method described by Gülçür (1974). Moisture content of soils was calculated by weight loss after drying ca. 10 g of soil for 24 h at 105°C. Organic matter contents of the soils were determined according to the wet digestion method described by Kalra and Maynard (1991) (modified Walkley-Black method). All analyses were carried out in triplicate.

The stored needle litter was oven-dried at 85°C for 24 h and then ground in a laboratory mill to a mesh fraction of less than 1 mm. The ground litter was then analyzed for total organic carbon, lignin and nutrient concentrations (nitrogen, phosphorus, potassium, calcium, magnesium and manganese). Organic C was determined by wet oxidation method (Nelson and Sommers 1982). Lignin was determined using an ADF-sulphuric lignin method by Rowland and Roberts (1994). Total N was determined by Kjeldahl digestion (Allen 1989) followed by analysis of ammonium through the indophenol method using an auto-analyzer. The sub-samples used for the determination of total N in litter samples were also used for the determination of mineral elements. Concentrations of Ca, Mg and Mn were determined in the Kjeldahl acid digest solution by atomic absorption spectrophotometer (AAS), K by flame emission spectrophotometer and P by continuous flow colorimetry using the molybdenum blue method (Allen 1989). All analyses were carried out in triplicate.

Data analysis

Three-way ANOVA with interactions was applied for analyzing the effects of insect damaged levels, aspects and slope positions on litter qualities and 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 mass loss rates (k) and litter quality variables. The coefficients of determinant (r^2) which indicate the goodness of fit of the data to the exponential decay model was also determined using MS EXCEL 2003 and SPSS.

Results

Stand and soil characteristics

Average tree age was higher for the control stands than for the highly damaged stands (Table 1). For example, mean age of the control stand at the top slope position on the north-facing site (136 year) was older than that of the highly damaged stand (81 years). The exception was the stands at the bottom slope position on the south aspect. There, average tree age was younger for the control stands (125 years) than for the highly damaged stands (271 years). Mean tree height between the three damaged stand types was similar at the slope positions on the north-facing site. However, on the south-facing site, mean tree height was lower for the highly damaged stands than for the moderately damaged and the control stands which showed more or less the same tree height. The high damaged stands had greater percent open sky (lower percent canopy cover) and poorer health as indicated by percent mortality compared with the control stands for each slope position (Table 1).

Soil texture type was sand for the three stand types at the top slope position on the north aspect, whereas for the rest of the stands it was sandy loam. Mean soil organic matter was lower for the highly damaged stands compared with the moderately damaged or the control stands at each slope position (Table 1). Mean soil pH was generally higher for the control stands, whereas mean soil moisture showed lower values for the control stands compared with the highly damaged stands.

Variation in litter chemistry

Litter quality variables in dry matter of oriental spruce litter varied significantly among the three damaged levels and also between aspects and slope positions (Table 2). ANOVA results showed that the variability in nitrogen and calcium concentrations and ratios of C:N, lignin:N and lignin:Ca between all studied stands was significantly affected by the insect damaged levels. Oriental spruce litter had higher nitrogen concentration in the high damaged stands compared with the moderately damaged and the control stands. For example, litter from the highly damaged stands at the top slope position on the north-facing sites had highest nitrogen concentration (1.46%), whereas litter from the control stands had lowest (1.17%). Similar trend was also found for the other sites. Conversely, the same litter from the highly damaged stands had lowest calcium concentration, whereas the litter from the control stands had highest Ca concentration. Carbon:N and lignin:N ratios were also lower in the litter from the highly damaged stands, whereas lignin:Ca ratio was higher in the litter from the highly damaged stands (Table 2).

Total carbon, lignin, phosphorus, potassium, magnesium and manganese concentrations and lignin:P ratio in litter between all studied stands significant varied according to aspect and slope positions (Table 2). For example, litter originated from the south-facing sites and the top slope positions on each aspect had higher lignin concentration than litter collected from the north-facing sites and the bottom slope position. Mean lignin concentration in litter at the top slope position on the south-facing sites was for example about 43%, while lignin concentration was about 38% at the same slope position on the north-facing sites. However, there were no significant differences in initial lignin concentrations among the insect damaged levels. The other litter quality variables also showed similar trend to lignin concentration (Table 2).

Decomposition among the insect damaged levels on two aspects and slope positions

Mean mass losses of the litter from the control, moderately and highly damaged stands on the top and bottom slope positions for the north- and south-facing sites are shown in Fig. 1. Final decay constant rates, coefficients of determinant (r^2) which indicate the goodness of fit of the data to the model, percent mass remaining and the differences in mass losses between the three damaged levels in relation to aspects and slope positions are given in Table 3. The single

Table 2 Litter quality variables in dry matter of oriental spruce litter collected from highly damaged (HD), moderately damaged (LD) and control stands situated on north- and south-facing sites and at two slope positions (top and bottom) on each aspect

	North						South					
	Top slope			Bottom slope			Top slope			Bottom slope		
	HD	MD	Control	HD	MD	Control	HD	MD	Control	HD	MD	Control
C (%)	46.5^{a}	46.3^{a}	47.3^{b}	46.3a	46.6a	46.5a	47.5^{bc}	47.4^{bc}	47.4^{bc}	47.9^{c}	47.6^{bc}	47.3^{b}
N (%)	1.46^{e}	1.23^{c}	1.18^{a}	1.46^{e}	1.19^{ab}	1.17^{a}	1.39^{d}	1.25^{c}	1.17^{a}	1.34^{d}	1.21^{bc}	1.17^{a}
P (%)	0.075^{f}	0.065^{e}	0.050^{bc}	0.057^{d}	0.074^{f}	0.053^{cd}	0.063^{e}	0.045^{ab}	0.097^{h}	0.054^{cd}	0.047^{ab}	0.042^{a}
K (%)	0.136^{b}	0.175^{c}	0.137^{b}	0.183^{c}	0.124^{b}	0.283^{e}	0.258^{e}	0.224^{d}	0.254^{e}	0.088^{a}	0.175^{c}	0.201^{cd}
Ca (%)	1.182^{ef}	1.220^{f}	1.284^{g}	0.968^{b}	1.123^{d}	1.689^{h}	0.850^{a}	1.142^{de}	1.907^{i}	1.071^{c}	1.282g	1.305^{g}
Mg (%)	0.095^{b}	0.105^{cd}	0.093^{b}	0.105^{cd}	0.115^{de}	0.120^{e}	0.260^{f}	0.266^{f}	0.344^{g}	0.075^{a}	0.095^{bc}	0.116^{e}
Mn (%)	0.292^{g}	0.191^{f}	0.320^{h}	0.191^{f}	0.040^{a}	0.186^{f}	0.101^{b}	0.135^{d}	0.129^{d}	0.095^{b}	0.156^{e}	0.113^{c}
Lignin (%)	38.5^{b}	39.3^{b}	40.5^{b}	35.1^{a}	34.8^{a}	35.4^{a}	43.4^{d}	43.0^{d}	42.5^{d}	41.3^{c}	41.3^{c}	40.8^{b}
C:N	31.7^{a}	37.5^{d}	40.2^{g}	31.8^{a}	39.0^{ef}	39.7^{fg}	34.1^{b}	38.2^{de}	40.7^{g}	35.8^{c}	39.0^{ef}	40.6^{g}
C:P	615.9^{b}	711.4^{c}	954.0^{g}	807.3^{de}	630.9^{b}	869.1^{ef}	758.8^{cd}	1,048.9^{h}	487.0^{a}	884.3^{f}	1,019.1^{gh}	1122^{i}
Lignin:N	26.3^{b}	31.8^{d}	34.4^{ef}	24.1^{a}	29.2^{c}	30.2^{c}	31.2^{cd}	34.5^{ef}	36.4^{g}	30.9^{cd}	33.8^{e}	35.0^{f}
Lignin:P	511.1^{b}	603.6^{c}	816.7^{f}	612.2^{cd}	472.3^{ab}	662.5^{de}	693.5^{e}	950.9^{h}	436.0^{a}	762.6^{f}	884.2^{g}	966.3^{h}
Lignin:Ca	32.6^{c}	32.2^{bc}	31.5^{bc}	36.3^{d}	31.0^{b}	21.0^{a}	51.1^{f}	37.6^{de}	22.3^{a}	38.5^{e}	32.2^{bc}	31.2^{bc}

Means with the same letter are not significantly different by lines

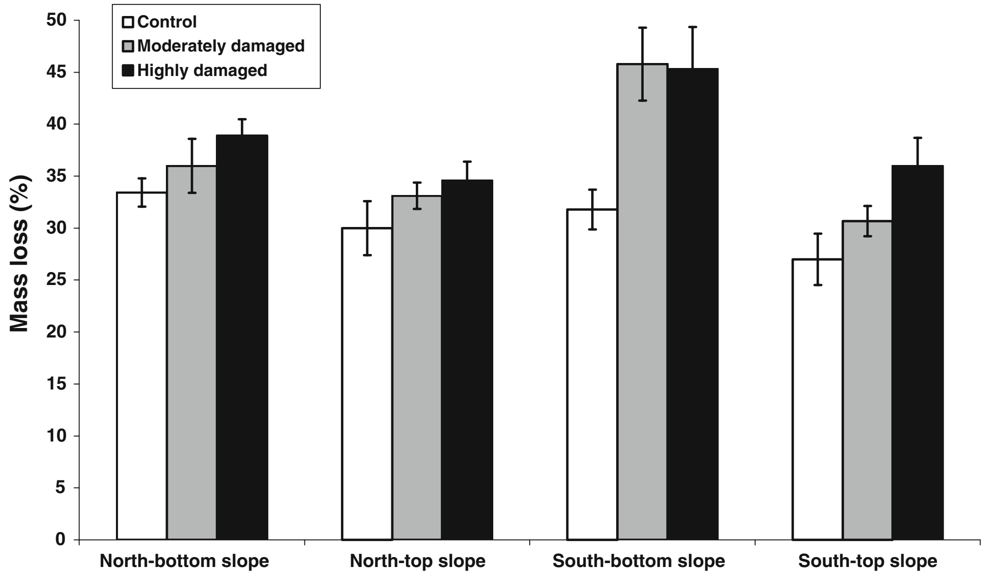

Fig. 1 Mean percent mass losses of oriental spruce litter from the highly damaged, moderately damaged and control stands on the top and bottom slope positions for the north- and south-facing sites (*vertical bars* represent the standard error of the mean)

Table 3 Annual decay rates (k) of oriental spruce litters placed on highly damaged (HD), moderately damaged (LD) and control (control) stands situated on north- and south-facing sites and at two slope positions (top and bottom) on each aspect

Aspect	Slope position	Level of damage	k mean ± se	r^2	%Mass remaining mean ± se	Differences in mass remaining (%) between highly, moderately and control stands	
North	Top	Highly	-.424 ± 0.023	0.996	65.4 ± 1.84	1.5[a]	
		Moderately	-.402 ± 0.012	0.988	66.9 ± 1.26	3.1[a]	4.6[b]
		Control	-.357 ± 0.011	0.972	70.0 ± 2.60		
	Bottom	Highly	-.493 ± 0.015	0.989	61.1 ± 1.58	2.9[a]	
		Moderately	-.447 ± 0.013	0.995	64.0 ± 2.55		5.5[b]
		Control	-.408 ± 0.005	0.988	66.6 ± 1.36	2.6[a]	
South	Top	Highly	-.448 ± 0.009	0.965	64.0 ± 2.67	6.7[b]	
		Moderately	-.367 ± 0.007	0.953	69.3 ± 2.48		9.0[c]
		Control	-.315 ± 0.017	0.958	73.0 ± 2.45	3.7[a]	
	Bottom	Highly	-.613 ± 0.007	0.962	54.7 ± 1.92	0.5[a]	
		Moderately	-.616 ± 0.016	0.998	54.2 ± 3.52		13.5[b]
		Control	-.383 ± 0.013	0.991	68.2 ± 4.02	14.0[b]	

ANOVA of mass loss data

Source	SS	df	MS	F	p
Corrected Model	1096.0	11	99.6	278.8	
Intercept	44743.5	1	44743.5	125215.1	
Damage level (DL)	442.7	2	343.3	960.4***	0.0001
Aspect (As)	20.5	1	20.5	57.3*	0.025
Slope (Sl)	343.1	1	221.1	619.3***	0.0001
DL x As	85.2	2	42.6	119.2**	0.001
DL x Sl	42.4	2	21.2	60.0*	0.031
As x Sl	103.9	1	103.9	290.8**	0.002
DL x As x Sl	58.3	2	29.2	81.6*	0.042
Error	8.58	24	0.357		
Total	45848.1	36			
Corrected Total	1104. 6	35			

Values are means ± SE

Coefficients of determinant (r^2) are presented to indicate goodness of fit of the data to the model

Asterisks refer to the level of significance; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

effects and interactions of damaged levels, aspects and slope positions on the mass losses are also listed in Table 3. The main effect of the damaged levels on the mass losses was highly significant ($F = 960$, $P < 0.001$). The second significant effect on the mass losses was slope position ($F = 619$, $P < 0.01$) and the third one was aspect ($F = 57$, $P < 0.05$).

Highly damaged litter showed highest decomposition rates followed by moderately damaged and control at each slope position on each aspect (Fig. 1). At 8 months (data not shown), the differences in percent mass remaining between the highly damaged and the control stands on the north-facing sites were 5.7% at the top slope and 3.4% at the bottom slope, whereas on the south-facing sites the differences in percent mass remaining were 4.9% at the top slope and 6.6% at the bottom slope.

At 12 months, percent mass remaining were still ranked in damaged order highly damaged > moderately damaged > control (Table 3). On the north-facing sites, mean mass remaining in the highly damaged stands at the top slope (65.4%) were lower than that in the control stands (70.0%). This presented difference in the mass remaining between the highly damage and the control stands of 4.6%. At the bottom slope, the difference in the mass remaining between the highly damage and the control stands was higher (5.5%) than that at the top slope. At both the slope positions on the south-facing sites, the differences in the mass remaining between the highly damage and the control stands were much higher than those on the north-facing sites. The differences in the mass remaining were 9.0% at the top slope and 13.5% at the bottom slope.

Several interactions between the main effects of damaged levels, aspect and slope position on mass remaining were also significant ($\alpha = 0.05$). That means that the differences in the percent mass remaining between the damage levels show different trends according to slope positions on different aspects. For example, at 12 months, the differences in the percent mass remaining between the highly damage and the control stands at the top slope position on the south aspect were much higher (9.0%) than those at the top slope position on the north aspect (4.6%).

Relationship between mass loss, litter quality and microclimate

Mean mass losses of standard litter incubated in the control, moderately and highly damaged stands on the top and bottom slope positions for the north- and south-facing sites in order to determine the effects of *I. typographus*-altered microclimate resulting from canopy damage on litter decomposition rate are shown in Fig. 2. The standard litter placed within the highly damaged, moderately damaged and the control stands did not show significant differences in decay rates. However, the litter decomposition rates of the standard litter varied according to aspect and slope positions. The standard litter placed at bottom slope position on both aspects decayed faster than the same litter at top slope position. They also generally showed higher decomposition rates on the south-facing sites than on the north-facing sites.

A correlation matrix was created using data from all sites in order to determine the degree of relationship between the litter mass losses and litter quality variables (Table 4). Initial nitrogen concentration strongly positively correlated with mass losses ($r = 0.635$), while C:N and lignin:N ratios negatively correlated with mass losses ($r = -0.623$ and $r = -0.625$, respectively). Lignin:Ca ratio also correlated well with mass losses ($r = 0.578$ and $r = 0.497$, respectively). Single carbon or lignin concentrations showed, however, no significant relationships to mass losses.

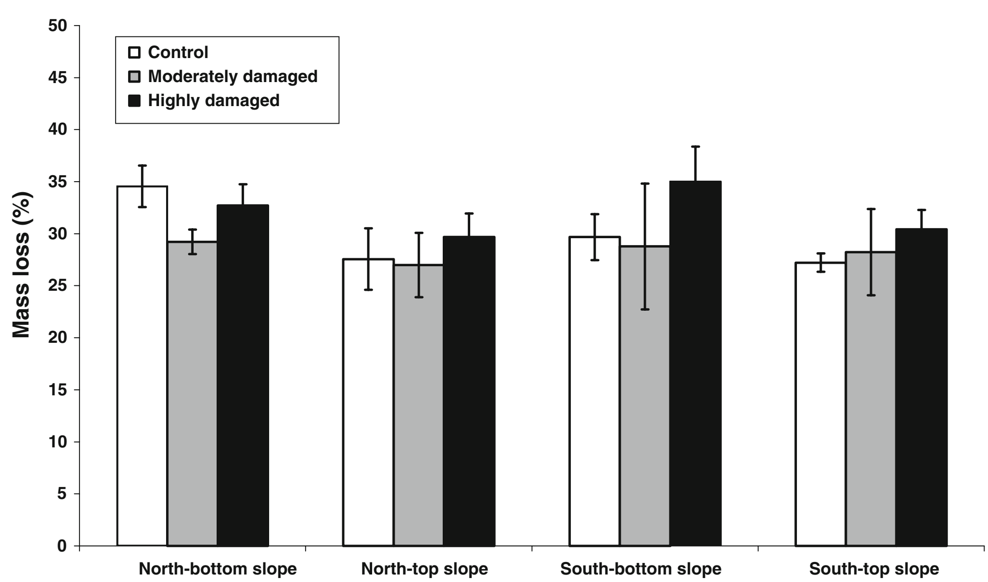

Fig. 2 Mean percent mass losses of standard oriental spruce litter in the highly damaged, moderately damaged and control stands on the top and bottom slope positions for the north- and south-facing sites (*vertical bars* represent the standard error of the mean)

Table 4 Correlation coefficients for the relationships between litter mass losses and initial litter quality variables

	Mass loss	Carbon	Lignin	N	P	K	Ca	Mg	Mn	C:N	C:P	Lignin:N	Lignin:Ca	Lignin:P
Mass loss	–													
Carbon	0.103	–												
Lignin	–0.189	0.742**	–											
N	0.635**	–0.088	–0.029	–										
P	0.001	–0.330*	–0.239	0.192	–									
K	–0.076	0.108	0.384*	–0.223	–0.216	–								
Ca	–0.578**	–0.047	–0.017	–0.797**	–0.098	0.347*	–							
Mg	–0.481**	–0.020	0.340*	–0.362*	0.126	0.577**	0.182	–						
Mn	–0.172	–0.485**	–0.305	0.157	–0.034	0.068	0.261	–0.342*	–					
C:N	–0.623**	0.246	0.149	–0.970**	–0.301	0.241	0.789**	0.307	–0.140	–				
C:P	0.013	0.360*	0.252	–0.186	–0.998**	0.212	0.091	–0.137	0.020	0.300	–			
Lignin:N	–0.625**	0.496**	0.674**	–0.661**	–0.352*	0.324	0.574**	0.341*	–0.115	0.756**	0.353*	–		
Lignin:Ca	0.497**	0.304	0.407*	0.809**	–0.103	–0.150	–0.848**	–0.211	–0.130	–0.737**	0.114	–0.249	–	
Lignin:P	0.012	0.459**	0.425**	–0.095	–0.963**	0.196	0.007	–0.130	–0.023	0.226	0.967**	0.413*	0.263	–

** Correlation is significant at the 0.01 level (2-tailed)

* Correlation is significant at the 0.05 level (2-tailed)

Discussion

This study has shown that *I. typographus* damage on oriental spruce can significantly influence decomposition rates of oriental spruce litter through alteration of the initial litter quality variables (especially nitrogen). In turn, these changes in litter quality affect litter decomposition rates of oriental spruce. *I. typographus* damages significantly increased nitrogen concentration, but decreased calcium concentration and ratios of C:N, lignin:N and lignin:Ca. There were no significant changes in total carbon, lignin or other nutrients such as phosphorus, potassium or magnesium. These results are consistent with the finding of other studies indicating that insect damage can increase nitrogen level in litter but no changes in lignin concentration (e.g., Pontious et al. 2002; Chapman et al. 2003; Stadler et al. 2005). Pontious et al. (2002) studied 60 eastern hemlock stands with varying levels of hemlock woolly adelgid (HWA) canopy damage, and found that nitrogen level in infested foliage slightly increased compared to nitrogen level in uninfested foliage, but no differences in percent lignin between the infested foliage and uninfested foliage. Stadler et al. (2005) reported small but significantly higher foliar nitrogen levels in infested hemlock trees than in uninfested ones. Similar results were also found by Chapman et al. (2003) for scale and moth infested pinyon pine trees (*Pinus edulis*) with increased N concentration and decreased C:N and lignin:N ratios in infested trees, but no changes in lignin concentrations between infested and uninfested tree litter.

Most studies on insect damage have concluded that the probable basis for the observed changes in litter quality is incomplete resorption prior to early abscission (Chapman et al. 2003). Premature abscission of leaf tissue can prohibit completion of senescence thereby reducing nutrient resorption and resulting in increased N concentration (Enoki et al. 1997; Chapman et al. 2003; Chapman 2006). Karban and Baldwin (1997) found that 37% of evergreen species examined induced premature abscission in response to herbivory and seldom induced foliar secondary compounds. More recently, a review by Nykanen and Koricheva (2004) supported these findings by examining damage-induced changes in woody plants. They found that evergreen plants tended to increase nutrient content following herbivory, while there were few differences in phenolic concentrations in evergreen plants.

On the other hand, other studies on tree species/soil fertility have stated that in natural forests, tree species are associated with different soil fertility (Wessman et al. 1988; Sariyildiz and Anderson 2005). These tree/soil relationships are reflected in nutrient concentrations and biochemical constituents of leaves and litter that influence herbivory, litter quality, decomposition processes and hence the development of soil properties that feed back to plant production through nutrient availability (Zak et al. 1993; Aerts and Chapin 2000). Sariyildiz et al. 2005 previously showed that trees growing on soils of low inherent fertility had lower foliar nutrient concentrations, higher reabsorption of N an P before leaf abscission and lower nutrient concentration in litter. In this present study, soil nutrient characteristics of all sites were also widely analyzed in order to relate the changes in litter quality to soil properties (data not shown). Although there was a strong relationship between nutrient availability and the incidence of insect damages, there were no clear trends relating soil nutrient concentration to initial nutrient concentrations in litter among insect damaged levels. Therefore, the observed changes in litter quality could be attributed to incomplete resorption prior to early abscission.

Aspect and slope position also significantly affected litter quality variables of oriental spruce. In general, litter from south-facing site and top slope positions had lower nutrients, but higher lignin and ratios of lignin:N, C:N, lignin:P. These differences in litter quality variables could be attributed to differences in the environmental conditions such as light intensity, wind, physical stress (mainly availability of water) and soil nutrients between aspects and slope positions. South-facing slopes receive more sunlight and are hotter and drier than north-facing slopes, and ridge tops or upper convex slope surfaces are exposed to intense solar radiation and experience high wind speeds. It is well known that leaves which expand under low light levels (shade leaves) differ morphologically and anatomically from those which develop at high light levels (sun leaves) (Rollet 1990). Sariyildiz and Anderson (2003b) reported that shade leaves contained higher nitrogen and cellulose concentrations than sun leaves, whereas sun leaves had higher lignin concentrations than shade leaves. Similar changes were also reported for coniferous tree needles (Barnes et al. 1998). Our findings also support these findings since oriental spruce litter from the south-facing sites and the top slope positions on each aspect had higher lignin concentration than litter collected from the north-facing sites and the bottom slope position. In contrast to relationship between initial litter quality and soil nutrients among insect damaged levels differences in litter nutrients well correlated with soil nutrients characteristics of aspects and slope positions. It is reasonable to assume that differences in soil chemical characteristics and microclimate conditions between aspects and slope positions could account for the observed variation in the litter quality of oriental spruce litter found between the studies sites. On the other hand, effects of these factors on litter quality varied with the type of litter quality parameters. For example, it was noted that initial nitrogen concentration in litter from control stands did not vary according to aspects and slope positions (about 1.17%) (Table 2). However, nitrogen concentration showed similar increase in litter from the highly damaged stands (about 1.40%). This result indicates that increased nitrogen concentration in litter from the highly damaged stands was related to insect damage rather than aspects or slope position.

Variation in decomposition rates

Oriental spruce litter from highly damaged stands decayed more rapidly than litter from moderately damaged or control stands regardless of aspect and slope positions (Fig. 1; Table 3). Decomposition rates among insect damaged levels significantly correlated with initial litter quality parameters, especially nitrogen or ratios of C:N and lignin:N (Table 4). Similar result was reported by Chapman et al. (2003) for pinyon pine which was attacked by scale insect and the stem-boring moth. The attacked pinyon pine litter had high N concentrations and decomposed faster than not attacked pinyon pine trees. Nitrogen concentration or combinations of C:N and lignin:N rations has been shown in many studies as a determining factor for the overall speed of decomposition (e.g., Aber et al. 1990; Berg and Meentemeyer 2002). Nitrogen concentration in microbial tissues is generally an order of magnitude higher than in the litter so that N concentration is commonly limiting to the activity of decomposer organisms. High N concentrations enhance the decomposition of water-soluble compounds and non-lignified cellulose by enabling the development of microbial biomass since the labile fractions of litter provide a readily available source of energy for the decomposers. Hence, the availability of these labile fractions to the microorganisms in the initial phase of litter decomposition can have an important influence on subsequent processes (Swift et al. 1979; Cox et al. 2001). We also used standard litter with the same litter quality in order to differentiate the effects of variations in litter quality parameters and microclimate conditions on litter decomposition rate. Litter decomposition rates of standard litter did not differ significantly between the highly damaged, moderately damage and control stands (Fig. 2), indicating that alteration of litter quality variables by *I. typographus* damages played more important role than changed microclimate conditions resulting from canopy damage in controlling litter decomposition rates. However, we noted that differences in litter mass losses among insect damaged levels varied with aspects and slope positions. Higher differences in litter mass loss rates among insect damaged levels were observed on south-facing sites than on the north-facing sites (Table 3). This effect could be attributed to site differences in microbial metabolic functions (Bauhus et al. 1998), interactions between litter quality and soil fertility (Prescott 1996), and litter quality effects on fungal activities (Neely et al. 1991; Cox et al. 2001), but this present study was not intended to investigate all these mechanisms.

Although there were no strong relationships between microenvironmetal conditions and litter decomposition rates among the insect damaged levels, we noted that altered microenvironmetal conditions due to aspects and slope positions significantly influenced litter decomposition rates (Fig. 2). Litter decomposition was generally higher on the south-facing sites than on the north-facing sites and litter placed at bottom slope position on both the aspects decayed faster than those at top slope position. Higher litter decomposition on bottom slope and on south-facing sites could be attributed to higher temperature on these sites. South-facing sites receive the greatest amount of solar radiation and much warmer than the north-facing sites. Similarly, bottom slope positions are much warmer than the top slope positions (Sariyildiz et al. 2005). Many studies have shown that rates of litter decomposition increase with increasing temperature (Aerts 1997; Liski et al. 2003). 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 4- 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 the site and substrates quality. Therefore, in this present study, it could be possible that higher temperature on the bottom slope position and on the south-facing sites could account for higher litter decomposition rates.

Conclusion

This study has shown that *I. typographus* damage on oriental spruce can accelerate litter decomposition rates by increasing N concentration and decreasing C:N and lignin:N ratios. However, *I. typographus* damages have no significant effects on plant secondary compounds as analyzed lignin concentration here. The observed changes in litter quality did not respond to changes in soil nutrient availability in this present study. Therefore, we have concluded that incomplete resorption prior to early abscission in response to insect damage could be responsible for the changes in nitrogen concentration as stated by other studies. Among insect damaged levels, nitrogen concentration was most strongly positively correlated with litter decomposition rates. Aspects and slope positions also have a strong influence on litter decomposition rates. Litter placed at bottom slope position and on the south-facing sites decomposes higher than the same litter at the top slope position and on the north-facing sites. Aspects and slope positions can affect differences in litter decomposition rates among insect damaged levels. Higher differences in litter decomposition rates among insect damaged levels were observed on south-facing sites than on the north-facing sites. The differences in litter decomposition rates according to aspects and slope positions illustrate the important point that litter quality may define the potential rates of microbial decomposition but these are significantly influenced by the biotic and abiotic environment in which decomposition takes place. These differences could be attributed to site differences in microenvironmental factors such as soil temperature, water and nutrient availability, ground cover species composition, microbial metabolic functions and different litter quality effects on litter decomposers, and thus these mechanisms should be investigated in future studies.

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