Ecol Res (2012) 27: 69–75
DOI 10.1007/s11284-011-0868-6

ORIGINAL ARTICLE

Hideki Kagata · Takayuki Ohgushi

Non-additive effects of leaf litter and insect frass mixture on decomposition processes

Received: 11 February 2011 / Accepted: 4 July 2011 / Published online: 14 July 2011

Abstract Although there is a growing body of evidence that herbivorous insects have a significant impact on decomposition and soil nutrient dynamics through frass excretion, how mixtures of leaf litter and insect frass influence such ecosystem processes remains poorly understood. We examined the effects of mixing of leaf litter and insect frass on decomposition and soil nutrient availability, using a study system consisting of a willow, *Salix gilgiana* Seemen, and a herbivorous insect, *Parasa consocia* Walker. The chemical characteristics of insect frass differed from those of leaf litter. In particular, frass had a 42-fold higher level of ammonium–nitrogen (NH_4^+–N) than litter. Incubation experiments showed that the frass was decomposed and immobilized with respect to N more rapidly than the litter. Furthermore, litter and frass mixtures showed non-additive enhancement of decomposition and reduction of NH_4^+–N, depending on the litter–frass mixing ratio. These indicate that, while insect frass generally accelerated decomposition, the effect of frass on soil nutrient availability was dependent largely on the relative amounts of litter and frass.

Keywords Aboveground–belowground interaction · Inorganic nitrogen · Insect–plant interaction · *Parasa consocia* · *Salix gilgiana*

Introduction

There is increasing appreciation that herbivorous insects have a significant impact on decomposition and soil nutrient availability in terrestrial ecosystems (Hunter 2001; Weisser and Siemann 2004; Bardgett and Wardle 2010) through changes in the quality and quantity of leaf litter due to herbivore-induced responses and selective feeding (Chapman et al. 2003; Schweitzer et al. 2005; Crutsinger et al. 2008; Kay et al. 2008; Schmitz 2009). Deposition of insect excrement to soil is also an important, direct mechanism through which herbivorous insects can influence decomposition processes and soil nutrient dynamics (Lovett and Ruesink 1995; Frost and Hunter 2004; Christenson et al. 2002). Insect frass contains higher concentration of nitrogen (N) and labile carbon (C) than does leaf litter (Lovett and Ruesink 1995; Madritch et al. 2007). Frass can enhance microbial growth (Frost and Hunter 2004), which in turn accelerates decomposition rates (Zimmer and Topp 2002), N mineralization, and N immobilization (Lovett and Ruesink 1995; Frost and Hunter 2007).

Although insect frass deposition contributes in general a minor fraction of energy and nutrients to a decomposition system, the amount of frass varies markedly with the abundance of herbivorous insects (Lovett et al. 2002; Clark et al. 2010). For example, Clark et al. (2010) showed that the amount of insect frass was negligible when the herbivory load was low, but was comparable to the amount of leaf litter when the density of herbivorous insects became high. This indicates that the ratio between leaf litter and insect frass entering the decomposition system is dependent on the density of insect herbivores. Mixing of leaf litter and insect frass is likely to occur at the soil surface in temperate forests, where leaf litter accumulates easily on the forest floor due to the relatively slow rate of litter decomposition (Barbour et al. 1998). However, it remains largely unknown how mixtures of leaf litter and insect frass, and their mixing ratio, influence the decomposition process (but see Frost and Hunter 2008; Koukol et al. 2008). Regarding leaf litter decomposition, the decomposition of mixtures of litter produced by different plant species has been well examined, and many studies have demonstrated that mixtures of litter of multiple plant species showed non-additively enhanced decomposition efficiency, compared to that predicted from the litter of single species (Gartner and Cardon

H. Kagata (✉) · T. Ohgushi
Center for Ecological Research, Kyoto University,
Hirano 2-chome, Otsu, Shiga 520-2113, Japan
E-mail: kagata@ecology.kyoto-u.ac.jp
Tel.: +81-77-5498214
Fax: +81-77-5498201

2004; Hättenschwiler et al. 2005; Gessner et al. 2010). This non-additive effect of litter mixtures shows that there are combined effects of multiple plant species on the decomposition process that cannot be explained by summing the individual species, i.e., the "diversity effect" (Gessner et al. 2010). Hence, the non-additive effect of litter mixtures indicates the importance of litter diversity as a determinant of decomposition efficiency. In addition, several studies have shown that the litter mixing effects on decomposition process differ depending on the mixing ratio of the litter (Scowcroft 1997; Salamanca et al. 1998). All these results suggest that mixtures of leaf litter and insect frass may show non-additive effects on decomposition, and that these effects may be variable depending on the mixing ratio.

Here, we report the effects of mixtures of leaf litter and insect frass on decomposition and soil nutrient availability, using a study system consisting of a willow, *Salix gilgiana* Seemen (Salicaceae), and an insect herbivore, *Parasa consocia* Walker (Lepidoptera: Limacodidae). We compared the quality of fresh leaves, leaf litter, and insect frass, and examined the decomposition and soil N availability of each and of their mixture with different mixing ratios in a laboratory microcosm experiment.

Materials and methods

Frass and litter collection

Parasa consocia is a generalist insect herbivore that feeds not only on Salicaceae but also on Rosaseae, Fagaceae, Ebenaceae (Inoue et al. 1982). In mid-July 2009, *Parasa consocia* larvae were collected from 20 *Salix gilgiana* trees growing in a common garden at the Center for Ecological Research (35°N, 136°E), Kyoto University, in Shiga prefecture, central Japan. The willow trees were introduced to the common garden in 2003 as plant cuttings from trees growing on a floodplain along the Yasu River (10 km north of the common garden) (Utsumi et al. 2009). *Parasa consocia* has been present at high density on various willow species in the common garden for the past several years, causing nearly complete defoliation of several trees (H.K., personal observation). The collected larvae (more than 300 individuals) were reared together as about 30 individuals each in ten rearing containers ($12 \times 27 \times 9$ cm) in an environmental chamber at 25°C with a 16L8D light cycle. Mature leaves collected from *S. gilgiana* trees in the common garden were provided to the larvae and were replaced with new ones every day. After the larvae reached the final (eighth) instar, ten larvae were selected randomly to determine the quality and quantity of excreted frass. The larvae were transferred individually to 500-ml plastic cups and kept for 24 h without food to allow them to excrete the frass present in their gut. Thereafter, the larvae were provided with a few, mature *S. gilgiana* leaves after measuring their weight. The larvae were reared for 24 h in the environmental chamber, and the remaining leaves were then removed and the larvae kept for 24 h without food to allow them to excrete frass. Thereafter, larval frass was collected. The leaves of *S. gilgiana* and frass were oven-dried at 60°C for 72 h to determine their dry weight. Leaf mass consumed was determined as the difference in leaf dry mass between the start and the end of the feeding trial. Leaf dry mass at the start of the feeding trial was estimated from the mean water concentration, which was measured for another ten mature leaves collected from each of six randomly selected *S. gilgiana* trees in late July. Leaf water content was determined from the difference between fresh and dry mass, which were measured after oven-drying at 60°C for 72 h. These leaf samples were used also for chemical analyses, i.e., total C, total N, ammonium–N (NH_4^+–N), and nitrate–N (NO_3^-–N). Frass and leaf samples were stored at −30°C until chemical analyses were performed.

Frass used for the incubation experiment (see below) was collected from other larvae reared as described above. After larvae reached the final instar, they were transferred to another rearing container with a maximum of 30 individuals per container. Frass was collected every day until pupation. In total, about 300 larvae were used for frass collection. Leaf litter of *S. gilgiana* was also collected underneath the six randomly selected trees in the common garden in late October. The collected frass and leaf litter were oven-dried at 60°C for 72 h and stored at −30°C until the incubation experiment or chemical analyses.

Frass and litter incubation experiment

To examine the decomposition of larval frass and leaf litter, we conducted an incubation experiment in the environmental chamber. We performed four treatments with different mixing ratios of litter and frass, i.e., litter:frass ratio = 10:0, 8:2, 5:5, 0:10. These ratios were roughly equal to the expected inputs into soil when leaf consumption by *P. consocia* is 0, 30, 60, and 100%, respectively, which were estimated from the frass excretion efficiency of *P. consocia* (see "Results"). Insect frass and/or leaf litter (750 mg in total) was placed in a 50-ml glass vial with 750 mg soil and 2 ml distilled water, which brought the substrates to 60–70% of their water capacity. Insect frass and leaf litter were ground roughly prior to the experiment. As the soil microbe source, we added soil that was collected underneath *S. gilgiana* trees in the common garden in late August. It was air-dried for 1 month and passed through a 2-mm sieve prior to the experiment. In addition to the treatments described above, a soil-alone treatment was also set up as a control. A total of 20 replicates were established for each treatment, and 15 of these replicates were incubated in the dark at 25°C for 2 weeks. After incu-

bation, the samples were oven-dried at 60°C for 72 h. The other five replicates were used to determine the chemical characteristics at the onset of the incubation, and therefore they were oven-dried without incubation. All samples were stored at −30°C until chemical analyses (NO_3^-–N and NH_4^+–N) after the dry weight was measured.

Chemical analyses

Before chemical analyses, all samples were ground to a fine powder. Total C and N concentrations were determined using an elemental analyzer (JM 1000CN, J-Science, Kyoto, Japan). NO_3^-–N and NH_4^+–N were extracted using 1.5 mol/l KCl and their concentrations were determined using a continuous flow analyzer (Integral Futura, Alliance Instruments, Frépillon, France).

Statistical analyses

Differences in the chemicals of fresh leaves, litter, and insect frass were tested by one-way ANOVA, and the Tukey–Kramer HSD test ($P < 0.05$) was conducted as a post hoc test. Percentage data were arcsine-square root-transformed prior to analysis. Changes in substrate mass and inorganic N mass in the incubation experiment were tested by one-way ANOVA with the Tukey–Kramer HSD test ($P < 0.05$). Additive and non-additive effects of frass and litter mixing on decomposition and nutrient dynamics were tested following Wardle et al. (1997) and Ball et al. (2008). The expected value of mass loss in the mixture (MIX_E) was calculated using the following equation:

$$MIX_E = Litter_O P + Frass_O(1 - P)$$

where $Litter_O$ and $Frass_O$ are the mean observed value of mass loss in the pure litter and pure frass incubation, respectively, and P is the fraction of the litter mass relative to the total substrate mass. Then, the log response ratio (LRR) was calculated as:

$$LRR = \ln(MIX_O/MIX_E),$$

where MIX_O is the observed value found experimentally for the litter and frass mixture treatments. LRR was calculated for each sample, and the average with 95% confidence limit (CL) was determined for each mixture treatment. When the 95% CL does not cross 0, the effect is considered non-additive, and when the average LRR is >0 or <0, the effects are considered to be synergistic or antagonistic, respectively. Expected changes in inorganic N mass were also calculated for the litter and frass mixture, and whether effects were additive or non-additive was tested in the same manner as described above. All analyses were conducted using JMP version 6 (SAS Institute Japan, Tokyo, Japan).

Results

Chemical characteristics of leaves, litter, and frass

On average, *P. consocia* larva consumed 99.9 mg leaf material and excreted 62.4 mg frass during a 24 h feeding trial. This shows that the larva excreted 62.5% of consumed leaf mass as frass.

Although the total N and C:N ratio of the frass did not differ significantly from those of the fresh leaves, they differed significantly from those of litter. The frass total N was approximately twice that of the litter and the C:N rate was half of that in litter (Table 1). The frass NH_4^+–N concentration was significantly higher than those of fresh leaves and litter, being about 66- and 42-fold higher than in fresh leaves and litter, respectively (Table 1). The frass NO_3^-–N was also higher than those of fresh leaves and litter, but the overall concentration was low (<0.05 mg/g, Table 1).

Frass and litter decomposition

Substrate mass (soil, litter, and frass) after 2 weeks incubation differed significantly among the treatments (ANOVA: $df = 4,74$, $F = 71.5$, $P < 0.0001$). While the mass decreased by only 10 mg in the soil alone treatment (control), the mass decreased by 100–180 mg in the frass and/or litter treatments (Fig. 1a). The frass treatment (i.e., litter:frass ratio = 0:10) caused a 1.8-fold greater decrease of mass than the litter treatment (i.e., litter:frass ratio = 10:0). The mass loss in the frass and litter mixture treatments did not differ significantly from that in the litter treatment.

NH_4^+–N mass decreased in all treatments during the incubation, and there was a significant difference in the NH_4^+–N mass loss among the treatments (ANOVA: $df = 4,74$, $F = 97.9$, $P < 0.0001$, Fig. 1b). The reduction in NH_4^+–N mass in the frass treatment was nine-fold greater than that in the litter treatment (Fig. 1b). Although reduced NO_3^-–N mass also differed among the treatments (ANOVA: $df = 4,74$, $F = 424.1$, $P < 0.0001$), the amount of mass change was <0.02 mg, except for the control treatment, in which NO_3^-–N mass increased 0.06 mg (Fig. 1c). The total mass of inorganic N (NH_4^+–N and NO_3^-–N) after the incubation differed among the treatments (ANOVA: $df = 4,84$, $F = 48.2$, $P < 0.0001$, Fig. 2). The inorganic N mass was significantly higher in the frass treatment than in the soil alone treatment. In contrast, it was lower in the litter treatment than in the soil alone treatment.

Additive and non-additive effects of the litter and frass mixing

The litter and frass mixing had additive or non-additive effects on mass loss of the substrate and inorganic N,

Table 1 Chemical characteristics of leaf and litter of *Salix gilgiana*, and frass of *Parasa consocia*

	Leaf	Litter	Frass	*df*	*F* value	*P* value
Total N (%)	2.00 ± 0.07 a	1.09 ± 0.01 b	2.01 ± 0.05 a	2,19	106.4	< 0.0001
C:N ratio	23.61 ± 0.76 a	42.81 ± 0.20 b	23.83 ± 0.51 a	2,19	361.6	< 0.0001
NH_4^+–N (mg/g)	0.031 ± 0.001 b	0.049 ± 0.001 b	2.039 ± 0.066 a	2,19	525.9	< 0.0001
NO_3^-–N (mg/g)	0.032 ± 0.002 b	0.016 ± 0.002 c	0.048 ± 0.003 a	2,19	28.3	< 0.0001

Values presented are means ± SE. Different letters indicate significant difference ($P < 0.05$)

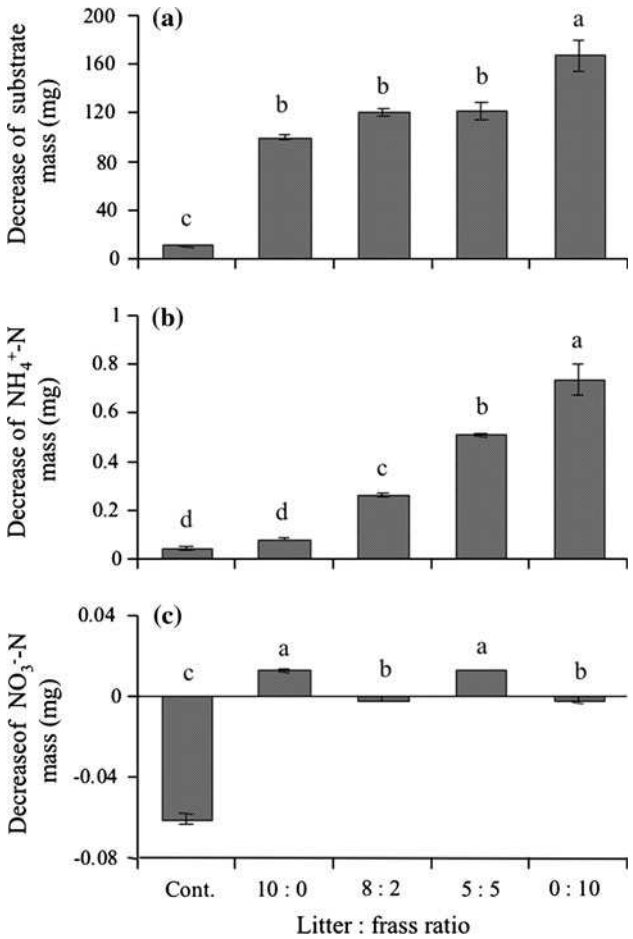

Fig. 1 Decrease of **a** substrate mass, **b** NH_4^+–N, and **c** NO_3^-–N after 2 weeks incubation in different mixing ratio of litter and frass. Soil alone treatment was also set as a control (*Cont.*). Means ± SE are presented. *Different lower case letters* indicate significant difference ($P < 0.05$)

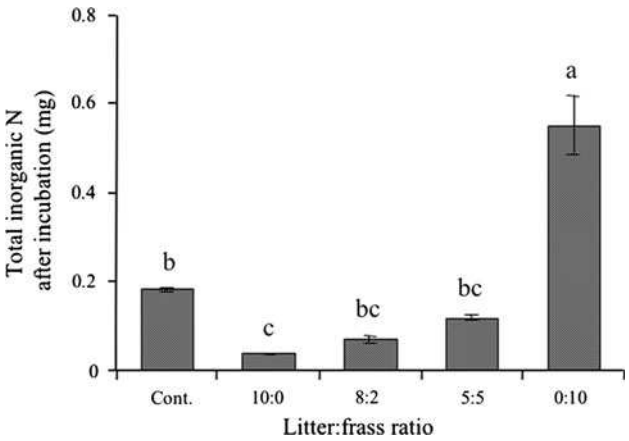

Fig. 2 Total inorganic N mass of the substrates (litter and frass) after 2 weeks incubation in different mixing ratio of litter and frass. Soil alone treatment was also set as a control (*Cont.*). Means ± SE are presented. *Different lower case letters* indicate significant difference ($P < 0.05$)

depending on the mixing ratio. The LRR (i.e., difference between observed and expected values) of mass loss differed significantly from 0 in the mixture with a litter:frass ratio = 8:2, indicating a non-additive, synergistic effect. This corresponded to a 7% greater mass reduction than expected (Fig. 3a). On the other hand, the mixture with litter:frass ratio = 5:5 showed an additive effect on mass loss (Fig. 3a).

Mixing litter and frass had non-additive, synergistic effects on the loss of NH_4^+–N at both the 8:2 and 5:5 litter:frass mixing ratios (Fig. 3b), at which NH_4^+–N was decreased 24% and 26% relative to the expected loss, respectively. The litter and frass mixing also had non-additive effects on the loss of NO_3^-–N: the 8:2 mixture treatment showed an antagonistic effect but the 5:5 mixture treatment showed a synergistic effect on the loss of NO_3^-–N (Fig. 3c).

Discussion

Litter and frass decomposition

The chemical characteristics of frass excreted by *P. consocia* larvae differed from those of the leaf litter of the host plant (Table 1). These differences between insect frass and leaf litter would result in different outcomes of their decomposition after they were deposited to soil (Lovett et al. 2002; Madritch et al. 2007). Actually, our incubation experiment showed that the frass was decomposed more rapidly than the leaf litter. Zimmer and Topp (2002) also reported that frass of geometrid moth larvae fed on the leaves of beech trees was decomposed more rapidly than beech leaf litter. In general, insect frass has a higher concentration of N and labile C relative to leaf litter, which is considered to be one of the reasons for the rapid decomposition of frass (Lovett and Ruesink 1995; Madritch et al. 2007; but see Koukol et al. 2008).

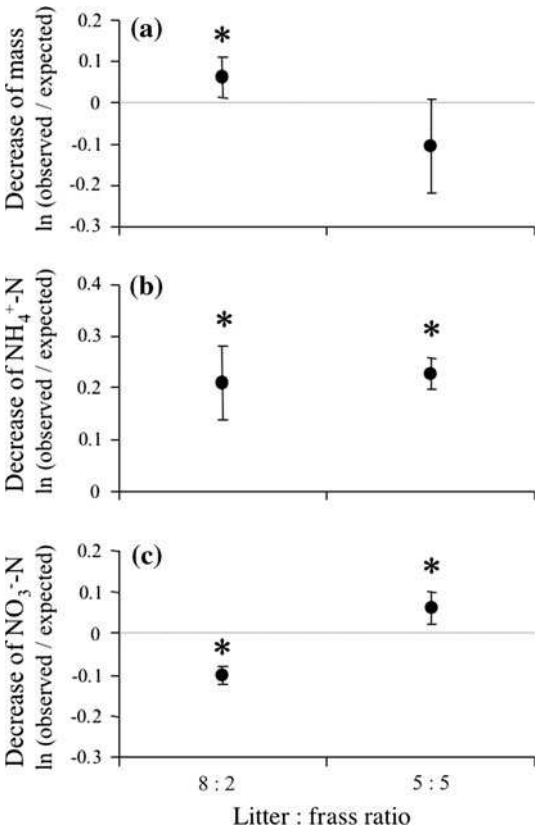

Fig. 3 Litter–frass mixing effects on **a** mass loss, **b** NH_4^+–N mass loss, and **c** NO_3^-–N mass loss. Mean values of log response ratio ± 95% confidence limits (CL) are presented. *Asterisk* Significantly non-additive effect, since 95% CL did not cross 0. See "Materials and methods" for details

In addition, the present study clearly showed the non-additive effect in decomposition of mixed leaf litter and insect frass, and this effect was dependent on the mixing ratio of litter and frass (Fig. 3a). Many studies have examined the effects of mixing litter from different plant species on decomposition processes, and they often showed non-additive and synergistic effects on decomposition rates (Kominoski et al. 2007; Ball et al. 2008). In their review, Gartner and Cardon (2004) pointed out that the decomposition efficiency of the litter mixture generally exceeds expectations by 20% or less. Some physical and chemical mechanisms have been proposed to explain the non-additive effects on the decomposition of litter mixtures. For example, (1) litter mixtures create diverse microhabitats and niches supporting a diverse and abundant decomposer community; and (2) nutrient transfer from one litter to the other leads to a complementary effect on nutrient status for decomposers, both of which enhance the decomposition of litter mixtures (Gartner and Cardon 2004; Hättenschwiler et al. 2005). Moreover, several studies have emphasized that the litter mixing ratio is important for determining whether the mixing effect is additive or non-additive (Scowcroft 1997; Salamanca et al. 1998). Similarly, our results showed that the mixing effects on litter and frass on their decomposition differed depending on their mixing ratio, although the reasons for the different effects remain unclear. The physical and chemical condition of the litter and frass mixture should be largely dependent on their mixing ratio, and would strongly affect the activity of microbial decomposers. The characterization of traits that explain the non-additive effects of litter and frass mixture on their decomposition will be needed in future studies.

Soil nutrient availability

Soil nutrient availability during decomposition also differed between the insect frass and leaf litter treatments, while NH_4^+–N decreased after the 2 weeks' incubation in all treatments (Fig. 2b). Unlike a litter bag experiment, which is a standard method to examine litter decomposition (e.g., Miyamoto and Hiura 2008), our incubation experiment was conducted in a closed system. Therefore, it is likely that the NH_4^+–N reduction detected in the present study would be due to changes in N forms. A change to NO_3^-–N from NH_4^+–N, i.e., nitrification, would be one possible explanation for the reduction in NH_4^+–N (Lovett and Ruesink 1995), because increased NO_3^-–N was almost completely responsible for the decreased NH_4^+–N in the soil alone treatment (see Fig. 1b,c). However, the reduction of NH_4^+–N observed in the other treatments could not have been due to nitrification alone, because NO_3^-–N did not increase in response to the NH_4^+–N reduction in those treatments. Alternatively, the NH_4^+–N reduction in those treatments was likely due to the change of NH_4^+–N to organic N by soil microbial activity; NH_4^+–N would be consumed by soil microbes and fixed as organic N in microbial tissue, i.e., immobilization (Lovett and Ruesink 1995; Lovett et al. 2002). Another possible explanation for the NH_4^+–N reduction is ammonia volatilization (Lovett and Ruesink 1995). Because NH_4^+–N concentration was analyzed using dry samples, ammonia may have partly volatilized in the present study. In addition, mixing of leaf litter and insect frass led to the non-additive decrease of NH_4^+–N in both the 8:2 and 5:5 litter and frass mixing treatments. Because leaf litter originally contained a very low level of NH_4^+–N (see Table 1), the non-additive decrease in NH_4^+–N in the mixture treatments would result from a decrease of NH_4^+–N originally presented in insect frass. It is known that soil microbes consume more inorganic N in conditions of abundant available C (Månsson et al. 2009). Therefore, leaf litter and insect frass mixing may increase microbial N immobilization by providing available C that originated from the leaf litter.

Nitrate–N concentration was also affected by the mixing of litter and frass, and the outcomes were variable depending on the mixing ratio. However, NO_3^-–N concentration in the leaf litter and insect frass was relatively low compared to that of NH_4^+–N, and the concentration remained low during the incubation.

Hence, NO_3^-–N would contribute little to the total inorganic N, and NH_4^+–N would be the major factor explaining the total inorganic N availability during insect frass decomposition.

Impacts of insect herbivores on terrestrial ecosystem process

It is thought that insect frass deposition represents a minor fraction of the energy and/or nutrient inputs to the decomposition process in terrestrial ecosystems because of the low herbivory load (Cyr and Pace 1993; Cebrian and Lartigue 2004). However, several insect herbivores sometimes show outbreaks and reach extremely high densities, at which host plants are completely defoliated (e.g., Donaldson and Lindroth 2008). In these situations, the amount of insect frass would rise to a critical level as energy and/or nutrient inputs into the decomposition system (Hunter 2001; Lovett et al. 2002; Clark et al. 2010). Actually, the present study showed that total inorganic N after 2 weeks incubation was higher in the frass treatment (litter:frass ratio = 0:10) than in the litter treatment (litter:frass ratio = 10:0). This indicates that input of a large amount of frass to the soil, at a nearly complete defoliation level, may be excessive beyond the level of NH_4^+–N required by soil microbes, and it trophicates the soil before the N mineralization phase of the decomposition process. However, this may depend on the relative amount of soil and substrate (Lovett and Ruesink 1995). We arbitrarily determined the soil and substrate ratio = 1:1, but in nature the ratio depends on the amount of litter and frass and the depth of soil. On the other hand, total inorganic N in the litter and frass mixing treatments after incubation did not differ from the litter treatment. This is probably because N immobilization of NH_4^+–N in the frass was non-additively enhanced by mixing of litter and frass. Our litter and frass mixing treatments were established as 8:2 and 5:5 litter:frass mixing ratios, which corresponded to approximately 30% and 60% herbivory levels, respectively. These herbivory levels were higher than the average found in terrestrial ecosystems, i.e., $<$10–15% (Cyr and Pace 1993; Cebrian and Lartigue 2004). Therefore, frass inorganic N may make little contribution to soil inorganic N availability under conditions of mixing of leaf litter and insect frass, even when the insect herbivory level was relatively high, i.e., at least 60% herbivory level. Thus, the effect of insect frass on soil nutrient availability was not related linearly to herbivory levels (i.e., amount of frass), and there would be a threshold of amount of frass to affect soil nutrient availability.

In summary, the present study clearly illustrated that (1) insect frass contained higher levels of NH_4^+–N than did host leaf litter, (2) insect frass was decomposed more rapidly than leaf litter, and (3) litter and frass mixing non-additively enhanced decomposition and reduction of NH_4^+–N. These results indicate that insect frass generally accelerated the decomposition process, but the effects on soil N availability were dependent largely on the relative amount of litter and frass. Note that our results were derived from short-term and small-scale experiments that may not be applicable directly to real field conditions. For instance, the effects of insect frass on the decomposition process would vary with the length of decomposition period (Lovett et al. 2002), and decomposition processes are influenced greatly by the biological, chemical, and physical properties of the soil (Aerts 1997; Gessner et al. 2010). Further studies to examine the decomposition of leaf litter and insect frass mixtures under various conditions, e.g., different lengths of decomposition period and using different types of soil, will contribute to our understanding of the ecosystem level significance of insect herbivores through frass excretion.

Acknowledgments We thank S. Kita for help with measuring nitrate and ammonium concentrations, and E. Nakajima for English proofreading of our manuscript. This study was supported by a Grant-in-Aid for Scientific Research (B-20370010), and Kyoto University Global COE Program (A06).

References

Aerts R (1997) Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. Oikos 79:439–449

Ball BA, Hunter MD, Kominoski JS, Swan CM, Bradford MA (2008) Consequences of non-random species loss for decomposition dynamics: experimental evidence for additive and non-additive effects. J Ecol 96:303–313

Barbour MG, Burk JH, Pitts WD, Gilliam FS, Schwartz MW (1998) Terrestrial plant ecology. Cummings, Menlo Park

Bardgett RD, Wardle DA (2010) Aboveground-belowground linkages. Oxford University Press, New York

Cebrian J, Lartigue J (2004) Patterns of herbivory and decomposition in aquatic and terrestrial ecosystems. Ecol Monogr 74:237–259

Chapman SK, Hart SC, Cobb NS, Whitham TG, Koch GW (2003) Insect herbivory increases litter quality and decomposition: an extension of the acceleration hypothesis. Ecology 84:2867–2876

Christenson LM, Lovett GM, Mitchell MJ, Groffman PM (2002) The fate of nitrogen in gypsy moth frass deposited to an oak forest floor. Oecologia 131:444–452

Clark KL, Skowronski N, Hom J (2010) Invasive insects impact forest carbon dynamics. Global Change Biol 16:88–101

Crutsinger GM, Habenicht MN, Classen AT, Schweitzer JA, Sanders NJ (2008) Galling by *Rhopalomyia solidaginis* alters *Solidago altissima* architecture and litter nutrient dynamics in an old-field ecosystem. Plant Soil 303:95–103

Cyr H, Pace ML (1993) Magnitude and patterns of herbivory in aquatic and terrestrial ecosystems. Nature 361:148–150

Donaldson JR, Lindroth RL (2008) Effects of variable phytochemistry and budbreak phenology on defoliation of aspen during a forest tent caterpillar outbreak. Agric For Entomol 10:399–410

Frost CJ, Hunter MD (2004) Insect canopy herbivory and frass deposition affect soil nutrient dynamics and export in oak mesocosms. Ecology 85:3335–3347

Frost CJ, Hunter MD (2007) Recycling of nitrogen in herbivore feces: plant recovery, herbivore assimilation, soil retention, and leaching losses. Oecologia 151:42–53

Frost CJ, Hunter MD (2008) Insect herbivores and their frass affect *Quercus rubra* leaf quality and initial stages of subsequent litter decomposition. Oikos 117:13–22

Gartner TB, Cardon ZG (2004) Decomposition dynamics in mixed-species leaf litter. Oikos 104:230–246
Gessner MO, Swan CM, Dang CK, Mckie BG, Bardgett RD, Wall DH, Hättenschwiler S (2010) Diversity meets decomposition. Trends Ecol Evol 25:372–380
Hättenschwiler S, Tiunov AV, Scheu S (2005) Biodiversity and litter decomposition in terrestrial ecosystems. Annu Rev Ecol Evol Syst 36:191–218
Hunter MD (2001) Insect population dynamics meets ecosystem ecology: effects of herbivory on soil nutrient dynamics. Agric For Entomol 3:77–84
Inoue H, Sugi S, Kuroko H, Moriuchi S, Kawanabe A, Owada M (1982) Moths of Japan. Kodansha, Tokyo
Kay AD, Mankowski J, Hobbie SH (2008) Long-term burning interacts with herbivory to slow decomposition. Ecology 89:1188–1194
Kominoski JS, Pringle CM, Ball BA, Bradford MA, Coleman DC, Hall DB, Hunter MD (2007) Nonadditive effects of leaf litter species diversity on breakdown dynamics in a detritus-based stream. Ecology 88:1167–1176
Koukol O, Benová B, Vosmanská M, Frantík T, Vosátka M, Kovárová M (2008) Decomposition of spruce litter needles of different quality by *Setulipes androsaceus* and *Thysanophora penicillioides*. Plant Soil 311:151–159
Lovett GM, Ruesink AE (1995) Carbon and nitrogen mineralization from decomposing gypsy moth frass. Oecologia 104:133–138
Lovett GM, Christenson LM, Groffman PM, Jones CG, Hart JE, Mitchell MJ (2002) Insect defoliation and nitrogen cycling in forests. Bioscience 52:335–341
Madritch MD, Donaldson JR, Lindroth RL (2007) Canopy herbivory can mediate the influence of plant genotype on soil processes through frass deposition. Soil Biol Biochem 39:1192–1201
Månsson K, Bengtson P, Falkengren-Grerup U, Bengtsson G (2009) Plant-microbial competition for nitrogen uncoupled from soil C:N ratios. Oikos 118:1908–1916
Miyamoto T, Hiura T (2008) Decomposition and nitrogen release from the foliage litter of fir (*Abies sachalinensis*) and oak (*Quercus crispula*) under different forest canopies in Hokkaido, Japan. Ecol Res 23:673–680
Salamanca EF, Kaneko N, Katagiri S (1998) Effects of leaf litter mixtures on the decomposition of *Quercus serrata* and *Pinus densiflora* using field and laboratory microcosm methods. Ecol Eng 10:53–73
Schmitz OJ (2009) Effects of predator functional diversity on grassland ecosystem function. Ecology 90:2239–2345
Schweitzer JA, Bailey JK, Hart SC, Wimp GM, Chapman SK, Whitham TG (2005) The interaction of plant genotype and herbivory decelerate leaf litter decomposition and alter nutrient dynamics. Oikos 110:133–145
Scowcroft PG (1997) Mass and nutrient dynamics of decaying litter from *Passiflora mollissima* and selected native species in a Hawaiian montane rain forest. J Trop Ecol 13:407–426
Utsumi S, Nakamura M, Ohgushi T (2009) Community consequences of herbivore-induced bottom-up trophic cascades: the importance of resource heterogeneity. J Anim Ecol 78:953–963
Wardle DA, Bonner KI, Nicholson KS (1997) Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. Oikos 79:247–258
Weisser WW, Siemann E (2004) The various effects of insects on ecosystem functioning. In: Weisser WW, Siemann E (eds) Insects and ecosystem function. Springer, Berlin, pp 3–24
Zimmer M, Topp W (2002) The role of coprophagy in nutrient release from feces of phytophagous insects. Soil Biol Biochem 34:1093–1099