

# Ecosystem consequences of selective feeding of an insect herbivore: palatability–decomposability relationship revisited

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**Abstract.** 1. The relationship between leaf palatability and litter decomposability is critical to understanding the effects of selective feeding by herbivores on decomposition processes, and several studies have reported that there is a positive relationship between them.

2. However, palatability is not always positively correlated with decomposability, because of species-specific feeding adaptation of herbivores to host plants. Moreover, the effects of selective feeding by herbivores on soil decomposition processes should be understood in terms of the inputs of leaf litter and excrement.

3. The present study examined the relationships between leaf palatability and the decomposability of litter and frass, using *Lymantria dispar* Linnaeus and 15 temperate deciduous tree species.

4. Larvae of *L. dispar* exhibited a clear feeding preference, and subsequently the excreted frass mass differed among tree species. Litter and frass decomposability also differed among tree species, and frass was more rapidly decomposed than litter. There were no positive or negative correlations between palatability and decomposability of litter and frass.

5. These results indicate that *L. dispar* larvae may accelerate the decomposition process in temperate deciduous forests through selective feeding on plants with relatively low litter decomposability and the production of frass with higher decomposability than the litter.

**Key words.** Decomposition, frass, host plant selection, *Lymantria dispar*, plant–insect interaction.

## Introduction

Insect herbivores can influence soil decomposition processes through various pathways (Wardle & Bardgett, 2004): changes in the quality and quantity of litter as a consequence of selective feeding on preferred plants and herbivore-induced plant responses (Chapman *et al.*, 2003; Schmitz, 2009) and the return of the waste products and carcass to the soil (Christenson *et al.*, 2002; Yang, 2006; Frost & Hunter, 2007). The relationship between leaf palatability and litter decomposability is one of the factors determining the direction of effects of selective feeding by herbivores on decomposition processes (Bardgett & Wardle, 2010). Several previous studies

have shown that plants with foliage more palatable to generalist herbivores produce faster decomposing litter (Grime *et al.*, 1996; Schädler *et al.*, 2003; Pálková & Leps, 2008; but see Kurokawa & Nakashizuka, 2008). Therefore, it is hypothesized that selective feeding by herbivores results in slow decomposition of leaf litter, according to such a positive relationship between palatability and decomposability (Hartley & Jones, 2004; Bardgett & Wardle, 2010), i.e. highly palatable (= highly decomposable) plants are selectively consumed by herbivores in a plant community and, as a result, poorly palatable (= poorly decomposable) plants remain, and, therefore, overall litter decomposition will be slow. The positive correlation between leaf palatability and litter decomposability results from the fact that plant defence traits against generalist herbivores, e.g. low nitrogen (N) and phosphorus, and high tannins and lignin, also reduce decomposer activity (Bardgett & Wardle, 2010).

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In most of the previous studies investigating the relationship between leaf palatability and litter decomposability, leaf palatability was determined by feeding experiments using slugs or crickets (Grime *et al.*, 1996; Schädler *et al.*, 2003; Pálková & Leps, 2008; Kurokawa *et al.*, 2010), which are suitable test organisms as generalist herbivores in determining leaf palatability. However, the leaf palatability derived from those herbivores would not always be applicable to other insect herbivores, because leaf palatability would depend on the identity of insect species as a result of species-specific feeding adaptation to host plants (Keathley & Potter, 2008). Hence, a positive correlation between leaf palatability and litter decomposability may not always be expected in all plant–insect systems (Kurokawa & Nakashizuka, 2008). To understand the effects of insect herbivores on the decomposition process through selective feeding, it is important to evaluate the leaf palatability using insect herbivores which are likely to have a significant impact on the decomposition process.

Moreover, insect herbivores can alter the energy and/or nutrient inputs to soil through the return of the waste products, e.g. frass (Christenson *et al.*, 2002; Frost & Hunter, 2007). Insect frass contains larger amounts of N and labile carbon (C) than leaf litter (Lovett & Ruesink, 1995; Madritch *et al.*, 2007). It can stimulate microbial activity (Frost & Hunter, 2004), and in turn increase the decomposition rate (Zimmer & Topp, 2002), N mineralisation, and N immobilisation (Lovett & Ruesink, 1995; Frost & Hunter, 2007). In addition, insect frass quality is strongly influenced by host leaf quality, such as nitrogen and tannins (Madritch *et al.*, 2007; Kagata & Ohgushi, 2011) which are chemicals known to determine the decomposition efficiency of leaf litter (Enríquez *et al.*, 1993; Kraus *et al.*, 2003). While selective feeding decreases the leaf litter produced by plants with high palatability, it would also lead to an increase in frass excreted by herbivores that fed on those plants. Therefore, the effects of selective feeding of insect herbivores on soil decomposition processes should be understood with respect to the inputs of both leaf litter and frass. However, the relationships between leaf palatability, litter decomposability, and frass decomposability in herbivorous insects remain poorly understood.

Here we examined the relationship between leaf palatability and decomposability of litter and frass, using the gypsy moth, *Lymantria dispar* Linnaeus, and 15 temperate deciduous tree species. *L. dispar* is a suitable herbivorous insect for examining the relationship between palatability and decomposability in temperate deciduous forests for the following reasons: (i) *L. dispar* is an important pest for temperate deciduous trees and sometimes occurs at an extremely high density (Kamata, 2002); (ii) *L. dispar* larvae are highly polyphagous but have a clear hierarchical feeding preference regarding tree species (Liebhold *et al.*, 1995; Shields *et al.*, 2003); and (iii) defoliation by *L. dispar* larvae can have significant impacts on decomposition and soil nutrient availability in a forest ecosystem (Lovett *et al.*, 2002; Frost & Hunter, 2004). Therefore, selective feeding and subsequent frass excretion by *L. dispar* larvae would have a potentially large impact on soil processes in temperate deciduous forests. We investigated the leaf palatability to *L. dispar* larvae by feeding tests, and

conducted incubation experiments of leaf litter and larval frass in a laboratory microcosm to determine their decomposability.

## Materials and methods

### Collection of plant leaves and litter

Plant materials used for the present study were collected in and around an experimental field of the Center for Ecological Research (Forest of CER; 35 °N, 136 °E), Kyoto University in Shiga prefecture, central Japan. The secondary forest is dominated by *Quercus serrata* Murray and *Pinus densiflora* Siebold & Zucc., and includes more than 50 tree species occurring naturally or artificially. We selected 15 tree species in 11 families for the experiment (Table 1), all of which were deciduous broad-leaved trees that are common in temperate forests. For each tree species, we collected fully expanded leaves from 4 to 6 tree individuals in late May to early June 2009 for a feeding experiment and frass collection. We also collected litter of each tree species underneath 4 to 6 tree individuals in late November 2009 for a litter incubation experiment. The litter samples were air-dried for 1 month and stored at –20 °C until the incubation experiment and chemical analysis.

### Collection of *L. dispar* larvae and frass

*Lymantria dispar* is univoltine and overwinters as eggs. In central Japan, larvae hatch in April and the larval period lasts 2 months through molting five or six times (Furuno, 1964). Larvae of *L. dispar* are commonly observed on several trees in the forest of CER. Third- and fourth-instar larvae were collected from several tree species in and around the forest of CER in late April to early May 2009. The collected larvae (more than 400 individuals) were placed with leaves of *Q. serrata* in rearing containers (3000 ml each) with a maximum of 20 individuals per container. The containers were kept in an environmental chamber at 25 °C with a LD 16:8 h cycle. Leaves of *Q. serrata* were replaced with new ones every day. When the larvae reached the sixth-instar (the last instar for most larvae, but some pass through the seventh-instar until pupation, Furuno, 1964), they were used for the feeding experiment and frass collection. It is known that approximately 70% of the leaf consumption and frass excretion of immature stages occurs during the sixth-instar period in *L. dispar* (Furuno, 1964). Hence, leaf consumption and frass excretion during this stage are critical for assessing the effects of selective feeding of *L. dispar* larvae on the decomposition process.

Frass of *L. dispar* for the incubation experiment was collected from 10 to 20 larvae of each tree species. Before the frass collection, the larvae were kept for 24 h without food to allow them to excrete the frass in their guts. The larvae were placed together with leaves of each tree species in a rearing container (3000 ml each) with a maximum of six individuals per container. They were kept in an environmental chamber at 25 °C with a LD 16:8 h cycle. Leaves of each tree species were replaced daily with new ones. The larval frass was collected

every day until pupation, and was stored at  $-20^{\circ}\text{C}$  until the incubation experiment, after it was oven dried at  $60^{\circ}\text{C}$  for 1 week.

#### Feeding experiment

The relative leaf palatability of 15 deciduous tree species for *L. dispar* was determined by a non-choice feeding trial, using the sixth-instar larvae obtained from laboratory rearing as described above. Before the feeding trial, the larvae were kept for 24 h without food to allow them to excrete the frass in their guts. One larva was placed in a 250-ml plastic cup with a few leaves, about 2 g fresh weight equivalent, for each tree species in an environmental chamber at  $25^{\circ}\text{C}$  with a LD 16:8 h cycle. The larvae and leaves were weighed before the feeding trial. After 24 h, the leaves were removed and the larvae were kept for 24 h without food to allow them to excrete the frass in the gut. Thereafter, the larval frass was collected. Leaves, larvae, and frass were oven dried at  $60^{\circ}\text{C}$  for 1 week to determine the dry weight. Leaves and frass were stored at  $-20^{\circ}\text{C}$  until C and N analyses. Nine to 11 replicates were conducted for each tree species (Table 1).

Consumed leaf mass, as an index of leaf palatability, was determined as the difference in leaf dry mass between the start and the end of the feeding trial. Leaf dry mass of each tree species at the start of the feeding trial was estimated from the leaf water concentration, which was measured using additional samples ( $n = 4-6$  for each tree species). The water concentration was determined from the difference between the fresh and dry mass, which was measured after oven drying at  $60^{\circ}\text{C}$  for 1 week. In addition, larval growth mass was also determined as the difference in larval dry mass between the start and the end of the feeding trial. Similarly, larval dry mass

at the start of the feeding trial was estimated from their water concentration, which was measured using additional samples ( $n = 10$ ). Palatability was also evaluated by excreted frass mass, because there was a strong positive correlation between consumed leaf mass and excreted frass mass (see Results). We noted that the palatability of *L. dispar* larvae observed in the present study may, to some degree, be affected by a previous food experience before the feeding trials (Mattson & Scriber, 1987), i.e. all larvae were reared on leaves of *Q. serrata* until the feeding trials.

#### Incubation experiment

Decomposability of leaf litter and insect frass was examined by incubation experiments in a laboratory microcosm. Before the experiment, leaf litter and insect frass were roughly ground, and mixed well for each treatment to obtain homogeneous quality. Litter or frass (750 mg) was placed in a 50-ml glass vial with 750 mg of soil and 2 ml of distilled water, which brought the samples to 60–70% of the water capacity of the substrates. Soil was added as a soil microbe source, and soil-alone treatment was set as a control. The soil was collected underneath (<5 cm in depth) several *Q. serrata* trees in the forest of CER in late November 2009. It was air-dried for 1 month and passed through a 2-mm sieve, and was stored at  $5^{\circ}\text{C}$  until further use. Fifteen replicates were established for each leaf litter and frass, except for the frass originated from five tree species which were not examined as a result of insufficient mass of frass for the experiment (Table 1). The test samples were incubated in the dark at  $25^{\circ}\text{C}$  in an environmental chamber for 4 weeks. After incubation, the samples were oven dried at  $60^{\circ}\text{C}$  for 2 weeks to measure

**Table 1.** Tree species used in the present study.

Family	Species	Sample size or replication					
		Tree	Feeding	L inc	F inc	L CN	F CN
Magnoliaceae	<i>Magnolia obovata</i> Thunb.	5	11	15	—	5	11
Betulaceae	<i>Alnus sieboldiana</i> Matsumura	6	11	15	15	6	11
Fagaceae	<i>Castanea crenata</i> Siebold & Zucc.	5	10	15	15	5	10
	<i>Quercus acutissima</i> Carruth.	6	9	15	15	6	9
	<i>Quercus serrata</i> Murray	6	10	15	15	6	10
Ulmaceae	<i>Zelkova serrata</i> Makino	6	10	15	15	6	10
Rosaceae	<i>Prunus grayana</i> Maxim.	6	10	15	—	6	10
	<i>Prunus jamasakura</i> Nakai	6	11	15	—	6	—
Fabaceae	<i>Wisteria floribunda</i> (Willd.)	4	10	15	15	4	10
Euphorbiaceae	<i>Mallotus japonicus</i> (Thunb.)	6	10	15	15	6	10
Salicaceae	<i>Salix eriocarpa</i> Franch. & Sav.	5	10	15	15	5	10
	<i>Populus tremula</i> L.	6	9	15	15	6	9
Anacardiaceae	<i>Rhus javanica</i> L.	6	11	15	15	6	11
Clethraceae	<i>Clethra barbinervis</i> Siebold & Zucc.	6	11	15	—	6	—
Araliaceae	<i>Gamblea innovans</i> (Siebold & Zucc.)	6	11	15	—	6	—

Sample size for the leaf and litter collection, and the number of replications in the feeding trial, litter and frass incubation experiments are also presented. Blanks indicate no data. F CN, sample size in C and N analyses for frass; F inc, number of replications of frass incubation; Feeding, number of replications in the feeding trial; L CN, sample size in C and N analyses for leaves and litter; L inc, number of replications of the litter incubation; Tree, number of tree individuals for which leaves and litter were collected.

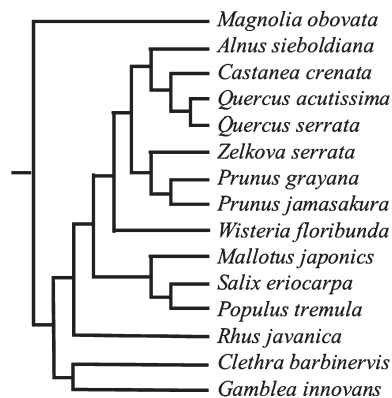
the dry weight. The decomposability of litter and frass was determined by the reduction in dry mass during the incubation.

### Carbon and nitrogen analyses

Before the analysis, all samples (fresh leaves, leaf litter, and insect frass) were ground to a fine powder. Total C and N contents were determined using an elemental analyser (JM 1000CN; J-Science Co., Ltd, Kyoto, Japan). Carbon and N contents of the frass from three tree species were not measured as a result of insufficient mass of the frass for the analyses (Table 1).

### Statistical analyses

Leaf consumption, frass excretion, and litter and frass decomposition were compared among plant species using one-way ANOVAs. Differences in the C : N ratio among leaf, litter, and frass were tested using paired *t*-tests. The difference between decomposition of litter and frass was also tested using a paired *t*-test. Relationships among the litter and frass C : N ratio, palatability, and decomposability of litter and frass were evaluated using correlation coefficients (i.e. species-level analysis in which plant phylogeny was not considered). These relationships were also analysed using phylogenetically-independent contrasts (PICs) (Garland *et al.*, 1992). A phylogenetic hypothesis for the studied plants was constructed using a recently inferred phylogenetic tree based on the Angiosperm Phylogeny Group classification (APG-III, 2009). This phylogenetic tree was resolved at the family level. Hence, we placed the genera as branches within families and species as branches within genera, where we had multiple species within a family (Fig. 1). We calculated PICs for each measured parameter, assuming that all branch lengths were equal. Because the statistical results in PICs were similar to the results in species-level analysis (see Table 2), the results were described on the basis of PICs in the Results section. All analyses were conducted using JMP version 6 (SAS Institute



**Fig. 1.** Phylogenetic hypothesis used to calculate phylogenetically independent contrasts, which is based on the Angiosperm Phylogeny Group classification (APG-III, 2009).

Japan, Tokyo, Japan), except for the PICs which were analysed using the package *ape* in R (R Development Core Team, 2010).

## Results

### Feeding experiment

Larvae of *L. dispar* showed strong preferences for certain tree species: consumed leaf mass differed significantly among tree species (ANOVA: d.f. = 14, 139,  $F = 17.39$ ,  $P < 0.0001$ , Fig. 2a). Excreted frass mass also differed significantly among tree species (ANOVA: d.f. = 14, 139,  $F = 22.48$ ,  $P < 0.0001$ , Fig. 2b). A strong positive correlation was detected between consumed leaf mass and excreted frass mass ( $r = 0.88$ ,  $P < 0.0001$ , Table 2). Larvae converted approximately 60% of consumed leaf mass to frass. Larval growth was significantly and positively correlated with consumed leaf mass ( $r = 0.89$ ,  $P < 0.0001$ ).

There was no significant correlation between the leaf C : N ratio and the consumed leaf mass or between the leaf C : N ratio and the excreted frass mass (Table 2). The frass C : N ratio did not differ from the leaf C : N ratio (paired *t*-test, d.f. = 11,  $t = 2.00$ ,  $P = 0.07$ , Fig. 3a), and it was strongly, positively correlated with the leaf C : N ratio ( $r = 0.91$ ,  $P = 0.0002$ , Table 2).

### Incubation experiment

Litter decomposability, expressed by dry weight loss during litter incubation, significantly differed among tree species (ANOVA: d.f. = 12, 210,  $F = 254.92$ ,  $P < 0.0001$ , Fig. 2c). While the soil-alone treatment lost only 10.1 mg of substrate mass, litter treatments lost 40.7–179.1 mg of mass during the 4-week incubation. Frass decomposability also differed significantly among tree species (ANOVA: d.f. = 9, 1394,  $F = 876.9$ ,  $P < 0.0001$ , Fig. 2d), with a loss of substrate mass ranging from 111.6 to 311.6 mg during the incubation. A significant correlation between litter and frass decomposability was not detected ( $r = 0.55$ ,  $P = 0.09$ ; Table 2).

The frass C : N ratio was significantly lower than the litter C : N ratio (paired *t*-test: d.f. = 11,  $t = -4.55$ ,  $P = 0.0008$ , Fig. 3a). Frass decomposability was significantly greater than litter decomposability (paired *t*-test: d.f. = 9,  $t = 4.84$ ,  $P < 0.0009$ , Fig. 3b). The reduction of mass in the frass incubation was approximately double compared with that in the litter incubation. Litter and frass decomposability were not correlated with the litter or frass C : N ratio, respectively (Table 2).

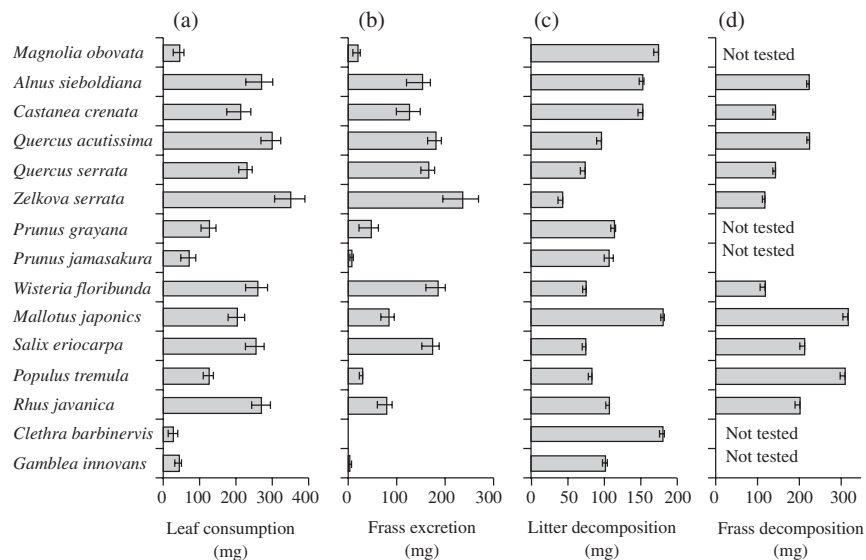
### Relationships between palatability and decomposability

Palatability, expressed by consumed leaf mass, was not correlated significantly with litter or frass decomposability, although correlation coefficients showed negative values for each relationship (Table 2, Fig. 4a,c). When the excreted frass mass was also regarded as an index of palatability because

**Table 2.** Correlation coefficients in species-level analyses (above the diagonal) and in phylogenetically independent contrasts (below the diagonal and shown by bold) between measured parameters, i.e. leaf C : N ratio, litter C : N ratio, frass C : N ratio, leaf consumption, frass excretion, litter decomposition, and frass decomposition.

	Leaf CN	Litter CN	Frass CN	Consumption	Excretion	Litter dec	Frass dec
Leaf CN	—	0.23	0.90 <sup>***</sup>	-0.16	-0.21	-0.37	0.26
Litter CN	<b>0.17</b>	—	-0.03	-0.29	-0.40	-0.21	0.37
Frass CN	<b>0.91<sup>**</sup></b>	<b>-0.08</b>	—	0.13	-0.01	-0.34	0.38
Consumption	<b>-0.13</b>	<b>-0.16</b>	<b>0.06</b>	—	0.93 <sup>***</sup>	-0.48 <sup>(*)</sup>	-0.59 <sup>(*)</sup>
Excretion	<b>-0.18</b>	<b>-0.33</b>	<b>0.01</b>	<b>0.88<sup>***</sup></b>	—	-0.52 <sup>*</sup>	-0.74 <sup>*</sup>
Litter dec	<b>-0.39</b>	<b>-0.30</b>	<b>-0.36</b>	<b>-0.40</b>	<b>-0.46<sup>(*)</sup></b>	—	0.46
Frass dec	<b>0.01</b>	<b>-0.48</b>	<b>-0.03</b>	<b>-0.35</b>	<b>-0.63<sup>*</sup></b>	<b>0.55<sup>(*)</sup></b>	—

They were explained on the basis of the analyses in phylogenetically independent contrasts in the text. <sup>\*\*\*</sup> $P < 0.0001$ , <sup>\*\*</sup> $P < 0.001$ , <sup>\*</sup> $P < 0.05$ , <sup>(\*)</sup> $P < 0.1$ .

**Fig. 2.** (a) Consumed leaf mass, (b) frass mass excreted by *Lymantria dispar* larvae in the feeding experiment, (c) decrease in litter mass, and (d) decrease in frass mass in the incubation experiment. Means with SE are presented.

there was a strong positive correlation between consumed leaf mass and excreted frass mass (Table 2), the excreted frass mass was significantly, negatively correlated with frass decomposability (Table 2 and Fig. 4d). On the other hand, it was not correlated significantly with litter decomposability, although the correlation coefficient was negative (Table 2 and Fig. 4c).

## Discussion

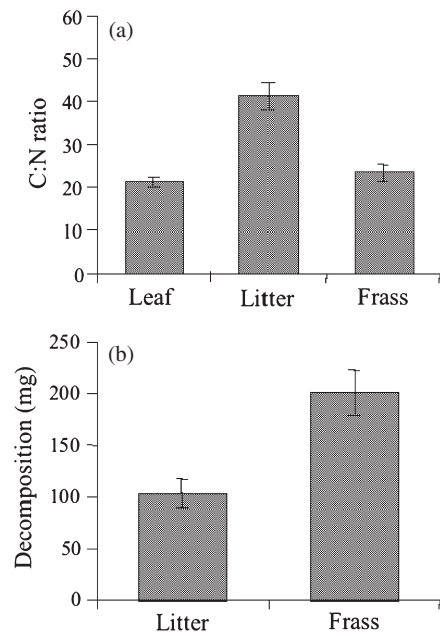
### Palatability to *L. dispar*

*Lymantria dispar* larvae are generalist herbivores, which can feed on over 500 plant species, and exhibit a clear hierarchical feeding preference (Liebhold *et al.*, 1995; Shields *et al.*, 2003). Several previous studies have examined factors involved in determining the host plant selection of *L. dispar* larvae, and demonstrated that the larvae preferred plant species that have no or low levels of alkaloids in leaves (Barbosa & Krischik,

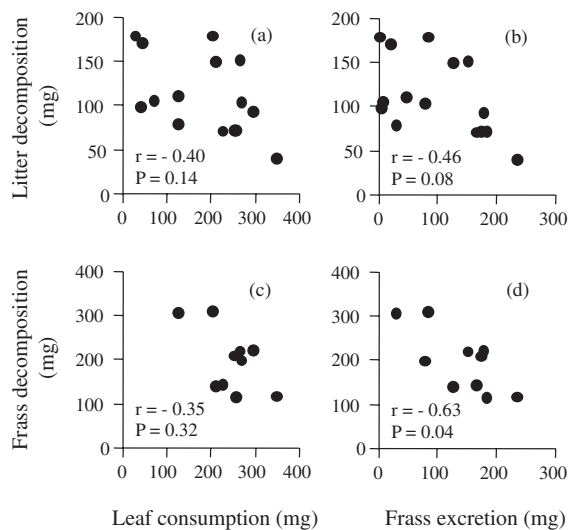
1987; Shields *et al.*, 2003), but the larval preference was not affected by foliar tannins (Barbosa & Krischik, 1987; Shields *et al.*, 2003), lignin (Brodeur-Campbell *et al.*, 2006), or other C-based secondary metabolites (Barbosa & Krischik, 1987).

Tannins are common as anti-herbivore defensive substrates in a diverse group of woody plants (Feeny, 1970; Barbosa & Krischik, 1987). However, there is increasing evidence that tannins are not always a feeding deterrent against insect herbivores (Ayres *et al.*, 1997; Forkner *et al.*, 2004; Keathley & Potter, 2008). In particular, they have little or no effect on host selection of generalist insect herbivores, such as *L. dispar* and *Popillia japonica* Newman (Barbosa & Krischik, 1987; Keathley & Potter, 2008). In contrast, alkaloids have a strong feeding deterrence for the host plant selection of *L. dispar* larvae (e.g. Barbosa & Krischik, 1987). It is known that alkaloids are rare or absent in Betulaceae, Fagaceae, and Salicaceae, and are present in Magnoliaceae, Araliaceae, and *Prunus* (Rosaceae) (Barbosa & Krischik, 1987). In fact, the present results showed that the former plants were relatively





**Fig. 3.** (a) C : N ratio in fresh leaves, litter, and frass, and (b) the decomposition of litter and frass. The decomposition is shown as a decrease in substrate mass (mg). Means with SE are presented.



**Fig. 4.** Relationship between palatability and decomposability as indicated by the relationships between: (a) leaf consumption and litter decomposition, (b) frass excretion and litter decomposition, (c) leaf consumption and frass decomposition, and (d) frass excretion and frass decomposition. Statistical values were based on the analyses using phylogenetically independent contrasts (see also Table 2).

preferred, whereas the latter plants were rejected by *L. dispar* larvae. Although it is not clear whether other plant species used in the present study contain alkaloids, the leaf palatability to *L. dispar* larvae shown in the present study is most probably determined by foliar alkaloids, rather than by C-based secondary metabolites, such as tannins and lignin.

### Decomposability of litter and frass

It is well known that the decomposability of litter is largely dependent on the quality of the litter, i.e. the concentrations of N, phosphorus, tannins, and lignin, and their relative ratios across various plant species (Gallardo & Merino, 1993; Aerts, 1997; Kraus *et al.*, 2003; Osono & Takeda, 2005; Kurokawa & Nakashizuka, 2008). In particular, tannins and lignin are important chemicals which suppress the litter decomposition rate (Kraus *et al.*, 2003). Several previous studies demonstrated that litter with higher levels of tannins and/or lignin was decomposed more slowly for temperate deciduous trees (Gallardo & Merino, 1993; Osono & Takeda, 2005). In contrast, the effects of N-based secondary metabolites, such as alkaloids, on litter decomposition have not been well explored. Siegrist *et al.* (2010) showed that alkaloids were not detected in the litter of a grass, *Schedonorus arundinaceus*, in spite of high levels of alkaloids in leaves, and that alkaloids had little effect on the decomposition process in a litter bag experiment with the addition of alkaloid. Therefore, it is most likely that tannins and/or lignin, but not alkaloids, were the important determinants of the decomposability shown in the present study.

Our results also showed that frass decomposability differed among tree species, and there was no strong correlation between litter and frass decomposability. Although litter and frass traits, such as C : N ratio and tannins, tend to be positively correlated with fresh leaf traits (Madritch *et al.*, 2007; Kurokawa & Nakashizuka, 2008), we did not find a significant relationship between litter and the frass C : N ratio. Hence, the chemical characteristics of the litter and frass may be determined in independent manners, resulting in the lack of a strong relationship between litter and frass decomposability. On the other hand, our results showed that frass was more rapidly decomposed than leaf litter. In general, insect frass contains larger amounts of N and labile C than does leaf litter (Lovett & Ruesink, 1995; Madritch *et al.*, 2007), which causes acceleration of the decomposition rate of frass (Zimmer & Topp, 2002). Although the frass C : N ratio was lower than the litter C : N ratio, frass and litter decomposability was not explained by the C : N ratio (see Table 2). Specific compounds, such as condensed tannins, rather than C : N ratio, may be important in determining frass and litter decomposability (Hättenschwiler & Jørgensen, 2010).

### Relationships between palatability and decomposability

Several studies have shown that the palatability of leaves to generalist herbivores is positively correlated with litter decomposability (Grime *et al.*, 1996; Schädler *et al.*, 2003; Pálková & Leps, 2008), which suggests that the factors determining leaf palatability might also determine litter decomposability (Bardgett & Wardle, 2010). However, we found no positive correlations between palatability and decomposability in the system of gypsy moth and temperate deciduous trees. Similarly, Kurokawa and Nakashizuka (2008) found that while litter decomposability was largely determined by condensed tannins and the lignin : N ratio, leaf palatability was not determined by such simple factors, resulting in the lack of a relationship

between leaf palatability and litter decomposability in a tropical rain forest. The lack of a positive relationship between palatability and decomposability in the present study was probably also as a result of some difference between the key factors determining palatability and decomposability: leaf palatability to *L. dispar* larvae is likely to be determined by alkaloids, whereas litter and frass decomposability are likely to be determined by tannins and lignin.

Moreover, our results showed a negative correlation between excreted frass mass and frass decomposability. The correlation coefficient was also negative between leaf palatability and litter decomposability, although it was not statistically significant at  $P = 0.05$ . These negative relationships indicate that the factors determining palatability and decomposability may be negatively associated in our experimental system. As mentioned above, the palatability in the present study was probably determined by alkaloids, whereas decomposability was probably determined by C-based secondary metabolites such as tannins and lignin. Several researchers have hypothesized that there is a negative association between C-based and N-based anti-herbivore defences in plants (Bryant *et al.*, 1983; Coley *et al.*, 1985). Actually, Stevens *et al.* (1995) showed that alkaloids were negatively correlated with tannin content in Crassulaceae plants. On the other hand, there is increasing evidence that no clear trade-offs are found between the alkaloid defence and other C-based defences (Steward & Keeler, 1988; Koricheva, 2002). Further understanding of the associations among multiple anti-herbivore defences in plants would contribute to clarifying the mechanisms responsible for the palatability–decomposability relationships.

#### *Ecosystem consequences of herbivore selective feeding*

A positive association between leaf palatability and litter decomposability implies slower litter decomposition as a result of selective feeding of generalist herbivores, because plants that produce more decomposable litter are preferentially consumed (Hartley & Jones, 2004; Bardgett & Wardle, 2010). However, the present study found no evidence of such a positive relationship, and even showed a negative relationship between palatability and decomposability. We also found that frass of *L. dispar* was decomposed faster than leaf litter. These findings indicate that *L. dispar* larvae may accelerate the decomposition process in temperate deciduous forests through selective feeding on plants with relatively low litter decomposability and producing frass with higher decomposability than the litter. In addition, selective feeding by insect herbivores could also accelerate litter decomposition via induction of plant regrowth, i.e. selective feeding on plants that tolerate defoliation by mounting a regrowth response, which would produce litter with high decomposability (Hunter, 2001). The effects of such herbivore-induced plant responses on litter decomposability were not examined in the present study. However, the plant responses to insect herbivory would be an important factor in determining the relationship between palatability and decomposability through changes in the litter decomposition process (Findlay *et al.*, 1996; Uselman *et al.*, 2011).

Although the relationship between palatability and decomposability is critical for understanding the effects of selective feeding by herbivores on the decomposition process, this relationship is still a controversial issue because it may depend on the plant-herbivore systems, mechanistic pathways by which herbivores influence decomposition processes, and temporal/spatial scale (Hunter, 2001). Our results were derived from short-term and small-scale laboratory experiments, which may have influenced the observed palatability and/or decomposability. Nevertheless, the present study points to the lack of an association (whether positive or negative) between these two factors for *L. dispar*, in sharp contrast to previous studies indicating a positive relationship in slugs and crickets (Grime *et al.*, 1996; Schädler *et al.*, 2003; Pálková & Leps, 2008). Further studies examining which types of herbivores show positive, negative or neutral relationships between palatability and decomposability will be needed to clarify how herbivores influence decomposition processes.

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