

**Herbivory effects on leaf litter decomposition vary with special leaf area in  
temperate mixed deciduous forest**

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## Abstract

Insect herbivore has great impacts on biogeochemical cycling in forest ecosystem, but experimental tests on the herbivory-decomposability relationship at the inter-specific level are rare. We conducted a 400-day field decomposition experiment in a temperate mixed deciduous forest and measured mass remaining rate, decomposition constant, total loss of carbon (C) and nitrogen (N) of litter leaf with/without obvious damage by chewing insects for different tree species. We found that herbivory effect on initial litter quality (C: N ratio) varied with species, showing a markedly negative effect on *M. alba* (-5.78%) and positive effect on *Q. acutissima* (+5.35%). Herbivory damage increased decomposition constant for *M. alba* and *L. formosana* with higher special leaf area, but decreased it for *D. kaki* and *Q. acutissima* with lower special leaf area. The contrasting effects of insect herbivory on litter decomposition could be attributed to the variability of litter initial quality caused by herbivory. Our finding that herbivore damage showed inter-specific variability in both litter quality and decomposition rate suggests that herbivory induced feedbacks to nutrient cycling and ecosystem function should be estimated at the species level in multi-species mixed deciduous forest.

**Keywords:** decomposition, deciduous forest, herbivory, initial quality, nutrient release

## Introduction

In most terrestrial ecosystems, the majority of plant productivity gets into the detritus food web through plant litters (Austin and Ballaré, 2010). Litter decomposition is a fundamental process for the recycling of carbon (C) and nutrients in terrestrial ecosystems (Austin and Vivanco, 2006; Bytnerowicz *et al.*, 2007; Yuan *et al.*, 2019). Litter decomposition is usually deemed to be altered by both abiotic and biotic factors, including climate (Lee *et al.*, 2014), substrate quality (Lucisne *et al.*, 2015; Xiao *et al.*, 2019), and biotic community (Suzuki *et al.*, 2013; Palozzi and Lindo, 2018). In regional scale, it has been suggested that precipitation and temperature can influence the decomposition rate more strongly than litter quality (Berg *et al.*, 1993; Zhang *et al.*, 2008). In local scale, however, interspecific differences in leaf traits and the subsequent quality of litter have a stronger effect on litter decomposition relative to microclimate (Ward *et al.*, 2015). Tree species characteristic, such as leaf traits and initial quality, is the most important determinant of leaf litter decomposition in a specific biome (Ge *et al.*, 2017; Xiao *et al.*, 2019). Species composition and its potential shift in a natural forest ecosystem are likely to impact litter decomposition and thus the global C cycle (Xie *et al.*, 2014). Therefore, quantify the degree to which differences in species affect the litter decomposition rates is urgently needed to improve predictions of forest C cycling under the context of future climate change.

Forest ecosystems influenced by insect outbreaks accounted for 36.5 million hectares each year (Kautz *et al.*, 2017), therefore, herbivore disturbance has a strong impact on the structure and function of forest ecosystems (Frost and Hunter, 2008; Cárdenas *et al.*,

2015). Temporary population outbreaks of insect herbivores may result in complete defoliation and even mortality of woody host species. On one hand, herbivores can directly influence aboveground plant growth and productivity by consuming plant tissues and decreasing leaf area during the outbreak period. On the other hand, herbivores can also affect soil nutrient dynamics through alteration of soil microclimate, additions of frass, and changes in quantity and quality of leaf litter. Factors that change plant litter quality can have large “afterlife” effects on the decomposition. Therefore, herbivore-induced changes in leaf litter quality can modify litterfall decomposition and subsequent nutrient release. For example, herbivore attack to the leaf can result in an increase (Hutchens and Benfield, 2000; Chapman *et al.*, 2006), decrease (Findlay *et al.*, 1996), and no effect (Frost and Hunter, 2008) on decomposition rate in forest ecosystems. One possible interpretation for the inconsistent results is that insect herbivory can lead to differential changes in leaf traits among different species. In response to herbivory damage, evergreen trees tend to employ premature leaf abscission than deciduous trees, whereas deciduous trees are more likely to induce secondary compounds (Chapman *et al.*, 2006). Hence, inter-specific variability in response to herbivory may lead to differences in litter quality, decomposition rate, and nutrient release. Despite the abundance of studies on herbivore-induced changes in plant chemical properties, few studies have estimated the influences of these changes on litter decomposition and nutrient cycling, especially for different tree species.

Temperate deciduous forests in northern mid-latitudes show high productivity (Powell *et al.*, 2006) and sequester large amounts of atmospheric CO<sub>2</sub> and contribute

substantially to the global C cycle (Pan *et al.*, 2011). In China, deciduous forests dominated by oak trees accounted for 15.2% of all forest biome in area (Liu *et al.*, 2016). Thus, oak forest plays a key role in regulating ecosystem C cycling and regional climate changes (Liu *et al.*, 2019a). Natural disturbance like insect herbivory outbreaks has been widely reported in oak forest (Mellec *et al.*, 2011), which to a large extent increases the seasonal variability and the uncertainty of ecosystem C cycling. In this study, we aimed to evaluate whether the inter-specific responses to herbivory, through changes in leaf quality, influencing the subsequent leaf litter decomposition. Addressing this aspect, we conducted a field decomposition experiment in a deciduous mixed forest in Central China. The objectives of this research were as follows: (1) assess how insect herbivory influence leaf quality of different tree species; (2) determine if the effect of herbivory damage on the decomposition rate of leaf litter varies with tree species with different special leaf area (SLA).

## **Materials and methods**

### **Study site**

The study was performed in a mixed deciduous forest on a southwest-facing hillside in Jigong Mountain (32° 06' 44" N, 114° 02' 21" E, 226 m *a.s.l.*), Central China. The area has a typical monsoon climate with a mean annual air temperature of 15.2°C, warmest monthly mean air temperature in July (33.6°C), and coldest monthly mean temperature in January (1.9°C). Mean annual rainfall of this region is approximately 1063 mm, with 60% falling from May to September (China Meteorological Data Sharing Service

System, <http://data.cma.gov.cn>). The soil is classified as a yellow-brown sandy-loam soil (Liu *et al.*, 2019b; Miao *et al.*, 2019). The vegetation at the experimental site is dominated by *Morus alba* Linn., *Liquidambar formosana* Hance, *Diospyros kaki* Thunb, and *Quercus acutissima* Carruth.

#### Plot design

In July 2016, one 50 m × 50 m plot was established in a mixed deciduous forest with homogeneous and flat topography. The background values of soil organic C and total nitrogen (N) at 0-10 cm depth were 16.6 g kg<sup>-1</sup> and 1.91 g kg<sup>-1</sup>, respectively. Canopy height averaged 18.0 m, and the mean diameter at breast height (DBH) of the living trees (DBH ≥ 5 cm) was 27.8 cm. The mean stand density was 487.4 trees ha<sup>-1</sup>. In this plot, tree species of *M. alba*, *L. formosana*, *D. kaki*, and *Q. acutissima* accounted for 5.2%, 27.3%, 16.4%, and 43.4% in total biomass, respectively. The SLA of *M. alba*, *L. formosana*, *D. kaki*, and *Q. acutissima* was 192.3 ± 7.8, 174.6 ± 10.2, 101.5 ± 6.8, and 95.7 ± 8.1 cm<sup>2</sup> g<sup>-1</sup>, respectively.

#### Litter collection

Six trees with DBH > 10 cm for each of the four species (*M. alba*, *L. formosana*, *D. kaki*, and *Q. acutissima*) were randomly selected in the plot. Three 1 m × 1 m litter traps were set out under the canopy of each selected tree with an angle of 120°. Freshly fallen leaf litter of the four species was collected 3 times each month from October to November 2016. Leaf litter was air-dried at room temperature (~25 °C) and pooled by species. Leaves of each species were sorted into two groups by the presence or absence of herbivory. Leaves with obvious damage by chewing insects were separated out as

herbivore-damaged litter (hereafter, damaged), and leaves without any damage either by insects or physical breakage were classified as undamaged litter (hereafter, undamaged). Based on our previous observation, *Lampronadata cristata* and *Ochrostigma albibasis*, feeding on live leaves, are two main leaf-chewing insects in the deciduous forest in this region. The potential differences in morphology and element induced by different insect species are not analyzed in this study. Leaf with perforation area accounted for 30-40% of the total area was selected as damaged leaf litter. Three randomly taken subsamples out of each group of different species were used for the determination of initial litter chemistry.

#### Litter decomposition

We used the litterbag method to study the decomposition process of damaged and undamaged litters for different species. Litter bags made out of nylon screen (1 mm mesh size, 20 cm × 25 cm) were filled with  $6.0 \pm 0.1$  g of air-dried leaf litter. A total of 96 litterbags (4 species × 2 groups × 4 harvest × 3 replicates) were used for the decomposition experiments. Litterbags were prepared in the laboratory and transported in individual plastic bags to the forest site in January 2017. After carefully removing loose forest floor litter, labeled litterbags were placed on the soil surface and held in place by nails. Litterbags were separated from each other by at least 40 cm and randomly distributed in the field. Three replicated litterbags for each group were retrieved in four-time steps after 90, 127, 250, and 400 days of decomposition in the field. After retrieval, the remaining litter was carefully cleaned from adhering mineral soil by gently brushing, and dried at 60°C until constant mass and weighed. Mass

remaining rate (%) was calculated as the ratio of actual dry mass of litter in the bags to the initial dry mass. The oven-dried leaf litter was milled to powder for total C and N analysis by using the dichromate oxidation method (Nelson *et al.*, 1996) and micro-Kjeldahl technique (Bremner *et al.*, 1996), respectively.

#### Statistical analysis

Annual decomposition constant ( $k$ , year<sup>-1</sup>) was calculated with a single exponential model by the equation (Olson, 1963):

$$\ln (M_t/M_o)=-kt$$

where  $M_t$  is the mass remaining at time  $t$ ;  $M_o$  is the initial mass value;  $k$  is the exponential decay coefficient;  $t$  is time in days.

Total loss of C and N (%) from leaf litter in each litterbag during decomposition process was calculated as:

$$\text{C loss (\%)} = [(M_o \times C_o) - (M_f \times C_f)] / (M_o \times C_o) \times 100$$

$$\text{N loss (\%)} = [(M_o \times N_o) - (M_f \times N_f)] / (M_o \times N_o) \times 100$$

where  $M_o$  and  $M_f$  are the initial and final dry weight, and  $C_o$  and  $C_f$  are the initial and final C concentration of litters, and  $N_o$  and  $N_f$  are the initial and final N concentration of litters.

Two-way ANOVA was conducted to assess the effects of species and herbivory on initial quality, decomposition constant, and total C and N loss across the decomposition process. In addition, we used One-way ANOVA to analyze the differences in initial quality, mass loss rate, decomposition constant, and total C and N loss between undamaged and damaged litters. Multiple comparisons of Tukey tests were performed



to examine the differences of decomposition constant, and total C and N loss among different species. To test the possible effect of initial litter quality on the decomposition process, linear regression was fitted between the decomposition constant and initial C and N content and C:N ratio. In order to assess the response sensitivity of decomposition constant to litter quality, we compared the difference of slopes illustrating the dependence of decomposition constant on litter quality between herbivory damaged and undamaged leaf litter using an analysis of covariance (ANCOVA). All statistical analyses were performed by SPSS 19.0 (SPSS Inc. Chicago, Illinois, USA) for Microsoft Windows.

## Results

### Variability of initial litter quality

Initial litter chemistries varied with both species and herbivory (Fig. 1). Initial litter C concentrations for *D. kaki* (47.3%) and *Q. acutissima* (47.8%) were significantly higher than that for *M. alba* (43.7%) and *L. formosana* (45.2%) ( $P < 0.01$ , Fig. 1a). Herbivore-damaged leaf litter, on average, had higher C concentration (46.9%) than undamaged leaf litter (45.1%) ( $P < 0.01$ , Fig. 1a), with significant differences for *M. alba* and *L. formosana* ( $P < 0.01$ , Fig. 1a). Initial N concentration of leaf litter was significantly affected by species, herbivory, and their interaction (all  $P < 0.01$ , Fig. 1b). *M. alba* had a substantially higher N content (2.05%) than the other three species ( $P < 0.01$ , Fig. 1b). Litter N content was 0.65% higher in damaged litter than undamaged litter for *M. alba* and 0.14% lower in damaged litter than undamaged litter for *Q. acutissima* (both  $P <$

0.05, Fig. 1b). Initial C:N ratio of leaf litter differed among species, and the magnitude depended on the presence and absence of herbivory. *M. alba* showed a substantially lower C:N ratio (21.8%) than the other three species ( $P < 0.01$ , Fig. 1c). The C:N ratio of the damaged litter was 5.78% lower than the undamaged litter for *M. alba*, and 5.35% higher than the undamaged litter for *Q. acutissima* (both  $P < 0.05$ , Fig. 1c).

#### Litter mass remaining

Across our 400 days of incubation, litter mass remaining showed significant differences among species. Irrespective of the herbivory effect, *Q. acutissima* showed the continuously highest values of mass remaining (94.5%-45.4%) and *M. alba* had the lowest values (55.2%-16.6%, Fig. 2) across the study period. The average mass remaining of damaged leaf litter (78.8%-32.9%) was higher than that of undamaged leaf litter (76.3%-29.3%) throughout the studied period. Herbivory effect on litter mass remaining of different species varied with incubation time. Herbivore damage increased litter mass remaining of *D. kaki* by 3.5% ( $P < 0.10$ ) and *Q. acutissima* by 12.2% ( $P < 0.05$ ) at the end of incubation, respectively (Fig. 2c, d). For *M. alba*, herbivore damage showed positive effects on litter mass remaining at 90 days incubation (Fig. 2a). *D. kaki* had significantly higher mass remaining in damaged litter than undamaged litter after 127 and 250 days incubation (Fig. 2c).

#### Decomposition constant

The decomposition rate, expressed as decomposition constant, showed substantial differences among four species, with the highest value for *M. alba*, and the lowest value

for *Q. acutissima* ( $P < 0.01$ , Fig. 3a). Furthermore, herbivory effects on the decomposition constant depended on species. Damaged leaf litter showed higher decomposition constant for *M. alba* and *L. formosana* with greater SLA, whereas *D. kaki* and *Q. acutissima* had a lower decomposition constant for damaged leaf litter compared with undamaged leaf litter (all  $P < 0.05$ , Fig. 3a).

#### Total C and N loss

Similar to the patterns of decomposition constant, total C and N loss displayed significant differences among species, with the greatest values for *M. alba* and the lowest values for *Q. acutissima* ( $P < 0.01$ , Fig. 3b, c). Herbivory damage increased total N loss by 5.0% and 12.4% for *M. alba* and *L. formosana* across our 400 days decomposition, respectively ( $P < 0.05$ , Fig. 3b). By contrast, however, total N loss of damaged litter was 7.2% and 15.5% lower than undamaged litter for *D. kaki* and *Q. acutissima*, respectively ( $P < 0.05$ , Fig. 3b). Compared with the undamaged litters, greater total C loss was found for damaged ones of *L. formosana*, whereas lower values were displayed for damaged ones of *D. kaki* and *Q. acutissima* ( $P < 0.05$ , Fig. 3c).

#### Decomposition constant vs initial litter quantity

According to the linear regression analyses, initial C content of leaf litter were negatively correlated with decomposition constant for both undamaged ( $R^2 = 0.27$ ,  $P < 0.05$ ) and damaged leaf litter ( $R^2 = 0.34$ ,  $P < 0.05$ , Fig. 4a). However, initial N content had positive effects on the decomposition constant of undamaged ( $R^2 = 0.72$ ,  $P < 0.05$ )

and damaged leaf litter ( $R^2 = 0.66$ ,  $P < 0.05$ ; Fig. 4b). In addition, significant negative effects were found between initial C:N ratio and decomposition constant for both undamaged and damaged leaf litter (Fig. 4c). Compared with the undamaged litter, herbivory damaged leaf showed lower slope of the relationship between decomposition constant and initial litter N content (ANCOVAs:  $F = 4.905$ ,  $P = 0.039$ , Fig. 4b).

## Discussion

### Herbivory effect on litter quality

It has previously been shown that insect herbivory can lead to substantial changes in leaf physico-chemical properties (Ohgushi, 2005). For example, in a semiarid woodland, insect herbivory substantially enhanced N concentration and reduced C:N ratio of pinyon pines (Chapman *et al.*, 2003). Similarly, in African savannas, outbreaks of mopane worm showed a positive effect on leaf N content of *Colosposperum mopane* (de Swardt *et al.*, 2018). In contrast, however, a decreased foliar N content following herbivory attack was found for *Quercus rubra* in North Carolina (Frost and Hunter, 2008) and for grass in riparian meadows (Sirotnak and Huntly, 2000). Therefore, the response of leaf litter quality to insect herbivory varied with tree species and ecosystem types. In agreement with previous studies, we also found that herbivory effect on leaf litter quality differed among tree species with different SLA. Increased leaf N content was found for *M. alba* (high SLA), but decreased leaf N content was found for *Q. acutissima* (relative low SLA) after herbivory attack (Fig. 1). According to the study by (Chapman *et al.*, 2003), the insect-feeding leaf generally drops prior to

normal abscission, thus the increased litter quality might be caused by the incomplete nutrient resorption (Zvereva and Kozlov, 2014). Notably, all leaf litters used in this study were collected at the end of the growing season. It means that the incomplete nutrient reabsorption may persist even though the leaf does not defoliate, probably due to the insect damage on the vein. Compared to low-SLA leaves, high-SLA leaves always shows thinner thickness and finer vein, and thus more vulnerable to herbivory chewing. Therefore, lower probability of nutrient reabsorption could be expected for high-SLA leaves. Another possible explanation for the reduced leaf N content and an increased C:N ratio for *Q. acutissima* may be the increased proportion of recalcitrant content during the insect feeding process (Uriarte, 2000). More nutrients may be allotted to synthesize structural matters (cellulose/lignin) for *Q. acutissima* due to its greater leaf thickness. Previous study has shown that insect herbivory effect on litter quality varied between evergreen coniferous trees and deciduous broadleaf ones (Chapman *et al.*, 2006). Our finding corroborates that litter quality responses to herbivory vary even among different deciduous broadleaf trees probably due to the variation in leaf traits.

#### Herbivory effect on litter decomposition constant

Previous studies have shown that insect herbivores can increase litter decomposition in grassland (Wang *et al.*, 2018), tropical forest (Cárdenas and Dangles, 2012; Moreno *et al.*, 2017), and coniferous forest (Chapman *et al.*, 2006). However, insect feeding showed no effects on leaf litter decomposition in neotropical rain forest (Cárdenas *et*

288 *al.*, 2015), Malaysian tropical forest (Kurokawa and Nakashizuka, 2008), and *Quercus*  
 289 *rubra* forests (Frost and Hunter, 2008). Our findings showed that the impacts of  
 290 herbivory damage on litter decomposition rate varies with species SLA, showing  
 291 positive effects on *M. alba* and *L. formosana*, and negative effects on *D. kaki* and *Q.*  
 292 *acutissima*. The differential responses could be attributed to the changes in litter quality  
 293 induced by herbivory damage. The decomposition constant was positively dependent  
 294 on litter initial N content and negatively related to the initial C: N ratio (Fig. 4). The  
 295 increased leaf N content of damaged litter for *M. alba* and *L. formosana* can offer more  
 296 nutrient sources for microbes activity. It has been reported that higher leaf N content  
 297 generally elevated leaf palatability for the aboveground consumers (Schädler *et al.*,  
 298 2003) as well as belowground decomposers (Talbot and Treseder, 2012). Therefore, leaf  
 299 litters with high N content show greater decomposition constant. In addition to the  
 300 reduced leaf N content for *D. kaki* and *Q. acutissima*, herbivory-induced secondary  
 301 compounds such as polyphenols, alkaloids, and terpenes (Berenbaum, 1995; Chapman  
 302 *et al.*, 2006), which may also contribute to the depressed decomposition rate.  
 303 By comparing the slopes of the regression models between decomposition constant and  
 304 initial quality, we assessed the differences in response sensitivity of decomposition  
 305 constant to initial quality between herbivory damaged and undamaged leaf litters. The  
 306 dependence of decomposition constant on initial N content for the damaged leaf litter  
 307 showed a lower slope (Fig. 4b), which indicates that herbivory damage decreased the  
 308 sensitivity of decomposition rate to the changes in leaf N content.

## Implication for forest management

In this study, we investigated the short-term effects of herbivory on leaf litter decomposition, which implies that herbivory foraging shows negative influences on the decomposition of *Q. acutissima* but positive effects on *L. formosana* (Fig. 3). As two dominant tree species in this region, the potential fluctuation of proportion with forest natural succession may lead to uncertainty in forest nutrient cycling due to the different responses of decomposition rate to herbivory damage. Given the suppression of herbivory damage on the decomposition of *Q. acutissima*, two aspects should be considered for forest managers to maintain nutrient balance. First, both the intensity and frequency of insect outbreak should be properly managed in *Q. acutissima* dominated forest. Second, the seedling of *Q. acutissima* could be partly removed during forest tending to release resources for other species. Our previous study conducted in this forest demonstrated that soil CO<sub>2</sub> emission during herbivory outbreak was 36.3% higher than that without herbivory disturbance forest (Liu *et al.*, 2017). Herbivory-mediated organic matter in particulate and dissolved forms contribute considerably to the overall throughfall input of organic substances into the forest soil (Michalzik and Stadler, 2005). To maintain the health and stability of forests, the influence of natural disturbance such as insect herbivores outbreak, have to be taken into account by forest management and policies.

## Conclusions

Taken together, our study shows that the herbivory effect on leaf litter quality and its

decomposition rate varies with SLA in the temperate mixed deciduous forest. Leaf litter with higher SLA showed positive responses in leaf quality and thus decomposition rate to herbivory damage, whereas insect herbivory tends to reduce leaf quality as well as decomposition constant of species with lower SLA. Furthermore, herbivory damage decreased the sensitivity of leaf decomposition rate to leaf N content. The current study highlights the need to consider the inter-specific variability in response to insect herbivory while assessing the relationships between herbivory disturbance and nutrient cycling in forest ecosystems.

#### **Conflict of interest**

The authors declared no conflict of interest.

#### **Authorship**

Y. L. and S. L. conceived the study. Y. L. and X. L. conducted the field experiment. Z. Y. and G. L. performed the statistical analyses. Y. L. wrote the first draft of the paper and all authors contributed to revisions.

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## References

Austin, A.T., Ballaré, C.L., 2010. Dual role of lignin in plant litter decomposition in  
terrestrial ecosystems. *Proc. Natl. Acad. Sci. U.S.A.* 107, 4618-4622.

Austin, A.T., Vivanco, L., 2006. Plant litter decomposition in a semi-arid ecosystem  
controlled by photodegradation. *Nature* 442, 555-558.

Berenbaum, M.R., 1995. The chemistry of defense: theory and practice. *Proceedings of  
the National Academy of Sciences* 92, 2-8.

Berg, B., Berg, M., Bottner, P., Box, E., Breymeyer, A., De Anta, R.C., Couteaux, M.,  
Escudero, A., Gallardo, A., Kratz, W., 1993. Litter mass loss rates in pine forests of  
Europe and Eastern United States: some relationships with climate and litter quality.  
*Biogeochemistry* 20, 127-159.

Bremner, J., Sparks, D., Page, A., Helmke, P., Loeppert, R., Soltanpour, P., Tabatabai,  
M., Johnston, C., Sumner, M., 1996. Nitrogen-total. In: Sparks, D. (Ed.), *Methods of  
Soil Analysis*. SSSA Book Ser, Madison, pp. 1085-1121.

Bytnerowicz, A., Omasa, K., Paoletti, Elena., 2007. Integrated effects of air pollution  
and climate change on forests: a northern hemisphere perspective. *Environ. Pollut.*  
147(3): 438-445.

Cárdenas, R.E., Dangles, O., 2012. Do canopy herbivores mechanically facilitate  
subsequent litter decomposition in soil? A pilot study from a Neotropical cloud forest.

376 Ecol. Res. 27, 975-981.

377 Cárdenas, R.E., Hättenschwiler, S., Valencia, R., Argoti, A., Dangles, O., 2015. Plant  
378 herbivory responses through changes in leaf quality have no effect on subsequent leaf-  
379 litter decomposition in a neotropical rain forest tree community. *New Phytol.* 207, 817-  
380 829.

381 Chapman, S.K., Hart, S.C., Cobb, N.S., Whitham, T.G., Koch, G.W., 2003. Insect  
382 herbivory increases litter quality and decomposition: an extension of the acceleration  
383 hypothesis. *Ecology* 84, 2867-2876.

384 Chapman, S.K., Whitham, T.G., Powell, M., 2006. Herbivory differentially alters plant  
385 litter dynamics of evergreen and deciduous trees. *Oikos* 114, 566-574.

386 de Swardt, D.B., Wigley-Coetsee, C., O'Connor, T.G., 2018. Insect outbreaks alter  
387 nutrient dynamics in a southern African savanna: patchy defoliation of  
388 *Colophospermum mopane* savanna by *Imbrasia belina* larvae. *Biotropica* 50, 789-796.

389 Findlay, S., Carreiro, M., Krischik, V., Jones, C.G., 1996. Effects of damage to living  
390 plants on leaf litter quality. *Ecological Applications* 6, 269-275.

391 Frost, C.J., Hunter, M.D., 2008. Insect herbivores and their frass affect *Quercus*  
392 *rubra* leaf quality and initial stages of subsequent litter decomposition. *Oikos* 117, 13-  
393 22.

394 Ge, J., Xie, Z., Xu, W., Zhao, C., 2017. Controls over leaf litter decomposition in a  
395 mixed evergreen and deciduous broad-leaved forest, Central China. *Plant Soil* 412, 345-  
396 355.

397 Hutchens, J., Benfield, E., 2000. Effects of forest defoliation by the gypsy moth on

398 detritus processing in southern Appalachian streams. *The American Midland Naturalist*  
399 143, 397-405.

400 Karban, R., Baldwin, I.T., 2007. *Induced responses to herbivory*. University of Chicago  
401 Press.

402 Kautz, M., Meddens, A.J., Hall, R.J., Arneeth, A., 2017. Biotic disturbances in Northern  
403 Hemisphere forests—a synthesis of recent data, uncertainties and implications for forest  
404 monitoring and modelling. *Global ecology and biogeography* 26, 533-552.

405 Kurokawa, H., Nakashizuka, T., 2008. Leaf herbivory and decomposability in a  
406 Malaysian tropical rain forest. *Ecology* 89, 2645-2656.

407 Lee, H., Fitzgerald, J., Hewins, D.B., McCulley, R.L., Archer, S.R., Rahn, T., Throop,  
408 H.L., 2014. Soil moisture and soil-litter mixing effects on surface litter decomposition:  
409 A controlled environment assessment. *Soil. Biol. Biochem.* 72, 123-132.

410 Liu, Y., Liu, S., Wan, S., Wang, J., Luan, J., Wang, H., 2016. Differential responses of  
411 soil respiration to soil warming and experimental throughfall reduction in a transitional  
412 oak forest in central China. *Agric. For. Meteorol.* 226–227, 186-198.

413 Liu, Y., Shang, Q., Wang, L., Liu, S., 2019a. Effects of understory shrub biomass on  
414 variation of soil respiration in a temperate-subtropical transitional oak forest. *Forests*  
415 10, 88.

416 Liu, Y., Zhang, K., Shang, Q., Ma, Y., Guan, Y., Ju, Y., 2017. Effect of a defoliator  
417 plague on soil respiration in a typical deciduous broadleaf forest on Jigong Mountain.  
418 *Act. Ecolog. Scinica*. 37, 7286-7292.

419 Liu, Y., Zhao, C., Shang, Q., Su, L., Wang, L., 2019b. Responses of soil respiration to

420 spring drought and precipitation pulse in a temperate oak forest. *Agric. For. Meteorol.*  
 421 268, 289-298.

422 Lucisine, P., Lecerf, A., Danger, M., Felten, V., Aran, D., Auclerc, A., Gross, E.M., Huot,  
 423 H., Morel, J.L., Muller, S., Nahmani, J., Maunoury-Danger, F., 2015. Litter chemistry  
 424 prevails over litter consumers in mediating effects of past steel industry activities on  
 425 leaf litter decomposition. *Sci. Total Envir.* 537, 213-224.

426 Mao, R., Zhang, X., Song, C., Wang, X., Finnegan, P.M., 2018. Plant functional group  
 427 controls litter decomposition rate and its temperature sensitivity: An incubation  
 428 experiment on litters from a boreal peatland in northeast China. *Sci Total Environ* 626,  
 429 678-683.

430 Mellec, A.L., Gerold, G., Michalzik, B., 2011. Insect herbivory, organic matter  
 431 deposition and effects on belowground organic matter fluxes in a central European oak  
 432 forest. *Plant & Soil* 342, 393-403.

433 Miao, R., Ma, J., Liu, Y., Liu, Y., Yang, Z., Guo, M., 2019. Variability of aboveground  
 434 litter inputs alters soil carbon and nitrogen in a coniferous–broadleaf mixed forest of  
 435 central china. *Forests* 10, 188.

436 Michalzik, B., Stadler, B., 2005. Importance of canopy herbivores to dissolved and  
 437 particulate organic matter fluxes to the forest floor. *Geoderma* 127, 227-236.

438 Moreno, M.L., Rossetti, M.R., Perez-Harguindeguy, N., Valladares, G.R., 2017. Edge  
 439 and herbivory effects on leaf litter decomposability in a subtropical dry forest. *Ecol.*  
 440 *Res.* 32, 341-346.

441 Nelson, D.W., Sommers, L.E., Sparks, D., Page, A., Helmke, P., Loeppert, R.,

442 Soltanpour, P., Tabatabai, M., Johnston, C., Sumner, M., 1996. Total carbon, organic  
 443 carbon, and organic matter. In: Sparks, D. (Ed.), *Methods of Soil Analysis*. Soil Sci Soc  
 444 Am Inc., Madison, pp. 961-1010.

445 Nykänen, H., Koricheva, J., 2004. Damage-induced changes in woody plants and their  
 446 effects on insect herbivore performance: a meta-analysis. *Oikos* 104, 247-268.

447 Ohgushi, T., 2005. Indirect interaction webs: herbivore-induced effects through trait  
 448 change in plants. *Annu. Rev. Ecol. Evol. Syst.* 36, 81-105.

449 Olson, J.S., 1963. Energy storage and the balance of producers and decomposers in  
 450 ecological systems. *Ecology* 44, 322-331.

451 Palozzi, J.E., Lindo, Z., 2018. Are leaf litter and microbes team players? Interpreting  
 452 home-field advantage decomposition dynamics. *Soil. Biol. Biochem.* 124, 189-198.

453 Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L.,  
 454 Shvidenko, A., Lewis, S.L., Canadell, J.G., 2011. A large and persistent carbon sink in  
 455 the world's forests. *Science* 333, 988-993.

456 Powell, T.L., Bracho, R., Li, J., Dore, S., Hinkle, C.R., Drake, B.G., 2006.  
 457 Environmental controls over net ecosystem carbon exchange of scrub oak in central  
 458 Florida. *Agric. For. Meteorol.* 141, 19-34.

459 Schädler, M., Jung, G., Auge, H., Brandl, R., 2003. Palatability, decomposition and  
 460 insect herbivory: patterns in a successional old-field plant community. *Oikos* 103, 121-  
 461 132.

462 Sirotnak, J.M., Huntly, N.J., 2000. Direct and indirect effects of herbivores on nitrogen  
 463 dynamics: voles in riparian areas. *Ecology* 81, 78-87.

464 Sun, T., Hobbie, S.E., Berg, B., Zhang, H., Wang, Q., Wang, Z., Hattenschwiler, S.,  
 465 2018. Contrasting dynamics and trait controls in first-order root compared with leaf  
 466 litter decomposition. *Proc Natl Acad Sci U S A* 115, 10392-10397.  
 467 Suzuki, Y., Grayston, S.J., Prescott, C.E., 2013. Effects of leaf litter consumption by  
 468 millipedes (*Harpaphe haydeniana*) on subsequent decomposition depends on litter type.  
 469 *Soil. Biol. Biochem.* 57, 116-123.  
 470 Talbot, J.M., Treseder, K.K., 2012. Interactions among lignin, cellulose, and nitrogen  
 471 drive litter chemistry–decay relationships. *Ecology* 93, 345-354.  
 472 Uriarte, M., 2000. Interactions between goldenrod (*Solidago altissima* L.) and its insect  
 473 herbivore (*Trirhabda virgata*) over the course of succession. *Oecologia* 122, 521-528.  
 474 Wang, Z., Yuan, X., Wang, D., Zhang, Y., Zhong, Z., Guo, Q., Feng, C., 2018. Large  
 475 herbivores influence plant litter decomposition by altering soil properties and plant  
 476 quality in a meadow steppe. *Sci. Rep.* 8, 9089.  
 477 Ward, S.E., Orwin, K.H., Ostle, N.J., Briones, M.J.I., Thomson, B.C., Griffiths, R.I.,  
 478 Oakley, S., Quirk, H., Bardgett, R.D., 2015. Vegetation exerts a greater control on litter  
 479 decomposition than climate warming in peatlands. *Ecology* 96, 113-123.  
 480 Xiao, W., Chen, H.Y.H., Kumar, P., Chen, C., Guan, Q., 2019. Multiple interactions  
 481 between tree composition and diversity and microbial diversity underly litter  
 482 decomposition. *Geoderma* 341, 161-171.  
 483 Xie, J., Chen, J., Sun, G., Chu, H., Noormets, A., Ouyang, Z., John, R., Wan, S., Guan,  
 484 W., 2014. Long-term variability and environmental control of the carbon cycle in an  
 485 oak-dominated temperate forest. *For. Eco. Manag.* 313, 319-328.

486 Yuan, X., Niu, D., Wang, Y., Boydston, A., Guo, D., Li, X., Wen, H., Qin, Y., Fu, H.,  
487 2019. Litter decomposition in fenced and grazed grasslands: A test of the home-field  
488 advantage hypothesis. *Geoderma* 354, 113876.

489 Zhang, D., Hui, D., Luo, Y., Zhou, G., 2008. Rates of litter decomposition in terrestrial  
490 ecosystems: global patterns and controlling factors. *J. Plant Ecol.* 1, 85-93.

491 Zvereva, E.L., Kozlov, M.V., 2014. Effects of herbivory on leaf life span in woody  
492 plants: a meta-analysis. *J. Ecol.* 102, 873-881.