Decomposability of leaf and wood litter are not correlated across species: Effects of litter traits on decomposition in field and laboratory conditions

ABSTRACT

1. Changes in tree species composition have important effects on the overall rate of litter decomposition at a community level because litter decomposability varies among species and between leaf and wood litter. To understand how changes in tree species composition affect litter dynamics and carbon sequestration at the ecosystem level, it is important to clarify interspecific variations in leaf and wood litter decomposability and the traits driving the variation.
2. Using field data, field experiments, and laboratory experiments, we explored rates of leaf and wood litter decomposition and their relationships to traits of ten deciduous hardwood species in a temperate forest in Japan. Rates of leaf and wood litter decomposition at the community level were also estimated by considering species-specific litter inputs and decomposition rates.
3. Rates of leaf and wood litter decomposition were not correlated under either field or controlled laboratory conditions. This is probably because the traits that affect decomposition rate differ between leaf and wood litter. Interspecific variation in litter decomposability of leaves and wood was generally consistent between field conditions and laboratory experiments using a single fungus, suggesting that the decomposing fungi set the species-specific decomposition rates. Moreover, the leaf and wood traits that affected decomposition by their specific fungi were different. The aboveground input of wood litter was less than half that of leaf litter, but its half-life was >3 times longer, suggesting that wood and leaves make similar contributions to litter accumulation.

4. Focusing on either leaf or wood litter alone may produce misleading estimates of how species composition changes affect litter dynamics at the community level. Our results provide insight into predicting the response of carbon dynamics to future climate change.

Key words: Carbon cycling, Coarse woody debris, Leaf litter, Litter decomposing fungi, Plant traits, Permanent plot

Introduction

Plant litter dynamics are important components of ecosystem processes such as nutrient and carbon cycling in terrestrial ecosystems (Berg and McClaugherty 2008). Litter dynamics are determined by the balance between input from the biomass pool (litterfall and mortality) and output to the soil or atmosphere (litter decomposition). Changes in tree species composition have an important effect on the overall litter decomposition rate at a community level because litter decomposability differs among species due to species' traits. For example, the community-level effects of warming-related changes in plant species composition on litter decomposition may be greater than the direct effects of climate change or of trait changes within species (Aerts 2006, Aerts et al. 2012, Cornelissen et al. 2007, Ward et al. 2015). Species composition and associated changes in litter decomposition can also be altered by anthropogenic disturbances and natural factors such as succession, fire, disease, and insect pests (Ayres and Lombardero 2000, McCullough et al. 1998, Zou et al. 1995). Linking litter trait variation among species to litter decomposition is important for understanding how changes in plant species composition affect the carbon cycle (Eichenberg et al. 2015).

Structural and chemical characteristics and decomposition rates of litter differ considerably, not only among species, but also between leaves and wood (Freschet et al.

2012, Zuo et al. 2018). To predict the effects of changes in species composition on litter dynamics at a community level, it is essential to clarify whether the decomposition rates of leaf and wood litter and their driving traits are correlated across species (Freschet et al. 2012). Effects of litter traits on decomposition of leaves (Cornelissen et al. 1999, Cornwell et al. 2008, Fortunel et al. 2009; Kurokawa and Nakashizuka 2008, Rosenfield et al. 2020, Santiago 2007, Tao et al. 2019, Zukswert and Prescott 2017) and wood (Kahl et al. 2017, Mori et al. 2014, Shorohova and Kapitsa 2014, Van Geffen et al. 2010, Weedon et al. 2009, Zell et al. 2009) have mostly been investigated separately, and only a few studies have examined them simultaneously (Freschet et al. 2012, Jackson et al. 2013, Pietsch et al. 2014, Zanne et al. 2015). In addition, although most previous studies dealt only with leaf litter decomposition, wood litter (coarse woody debris) represents an important fraction of aboveground carbon accumulation (10%–20%) in the forest, comparable to that of deciduous leaves (Chao et al. 2009, Delaney et al. 1998, Pan et al. 2011). Leaf and wood traits may be linked, because all plant organs are functionally interconnected. For example, studies in neotropical forests have shown that species with higher wood density have smaller leaves, probably because both affect water transport by the vascular system (Wright et al. 2007). If leaf and wood traits related to decomposition are correlated, their decomposition rates may also be correlated. However, if leaf and wood traits are independent, or the traits that affect decomposition rate differ between leaves and wood, their decomposition rates will not be correlated.

Previous studies that explored leaf and wood traits and decomposition rates adopted a variety of approaches, such as field decomposition experiments (Freschet et al. 2012, Zanne et al. 2015), microcosm experiments with humus (Jackson et al. 2013), and meta-analysis (Pietsch et al. 2014); each study used only one approach. Although field experiments reflect the actual decomposition process and are useful for estimating litter accumulation in the field, the data contain a lot of noise generated by microclimatic conditions and natural disturbances.

Combining field decomposition data with decomposition experiments under controlled conditions would allow us to better understand the relationship between leaf and wood litter decomposition rates and traits, with a focus on specific factors. Here we focused on the relationship of litter traits with fungal decomposition rates, because most litter mass loss is driven by fungi that can decompose recalcitrant structures such as lignin and cellulose (van der Wal et al. 2013). Interspecific differences in decomposition rates in the field are expected to be due to differences in fungal ability to decompose litter with particular traits. However, how the relationships of fungal decomposability and litter traits differ between leaves and wood remains unclear. Therefore, selecting fungal species that contribute significantly to each of leaf and wood litter decomposition and examining relationships between traits and decomposability under controlled conditions would be ideal.

Here we explored the effects of plant traits on litter dynamics by investigating species-specific decomposition rates of leaf and wood litter of ten species of broadleaf trees common in temperate forests in Japan. Wood and leaf litter inputs of each species were estimated simultaneously in order to link species-specific decomposition rates to ecosystem-level litter dynamics. We combined field data, field experiments, and laboratory experiments using a single fungus, to answer the following questions: (i) Are litter decomposition rates correlated between leaves and wood among species? (ii) Are the traits associated with litter decomposition rates in the field and the laboratory the same for leaves and wood? (iii) How much does wood litter contribute to litter accumulation compared with leaf litter?

Materials and Methods

Study site and species

We conducted our sample collection and field experiments in a 6-ha permanent plot in the

Ogawa Forest Reserve (OFR) in Ibaraki Prefecture, central Japan (36°56′10″N, 140°35′18″E, 610–660 m a.s.l.). The mean annual temperature in this region is 12.4 °C, and the mean annual precipitation is approximately 1200 mm. This field site contains old-growth, temperate deciduous forest that is dominated by *Quercus serrata*, *Fagus japonica*, and *Fagus crenata*. All trees in the plot with a diameter at breast height (DBH) of >5 cm have been tagged since 1987 (Masaki et al. 1992). Species, location, DBH, and mortality of the tagged trees were recorded during censuses undertaken every 2 years from 1989 to 1993 and every 4 years since then (1989, 1991, 1993, 1997, 2001, 2005, 2009, 2013, 2017, and 2021) in the 6-ha plot, and annually since 2004 in a core plot (1.2 ha) within the 6-ha plot. We focused on ten tree species (*Castanea crenata*, *Fagus japonica*, *Fagus crenata*, *Quercus serrata*, *Quercus crispula*, *Carpinus laxiflora*, *Acer pictum*, *A. rufinerve*, *Swida controversa,* and *Styrax obassia*) that account for >75% of aboveground biomass in this plot.

Collection of leaf and wood litter material

We collected material for four uses: (1) leaf litter for field decomposition experiments and litter trait (initial and decomposed litter) measurements, (2) wood litter for field decomposition rate estimates and decomposed litter trait measurements, (3) wood core samples for initial trait measurements, and (4) leaf litter and wood core samples for laboratory experiments. All collections were conducted at OFR. For the field decomposition experiments and litter trait measurements, freshly senesced leaves were collected in October and November 2014 from the base of at least three individuals of each species (1–4 leaves for leaf mass per area [LMA] measurements and chemical analysis, and at least 30 g for decomposition experiments). To estimate the field decomposition rate of wood, wood litter (fallen and standing dead trees, >5 cm in diameter) was collected from November 2019 to January 2020. Wood litter was identified to individual tree from the numbered tag or by comparing the field-measured DBH, location, and species against census records when no

tags were present. For each wood litter, at least four ~1-cm^3 cubes were cut from 2–4 cm below the surface at breast height (as marked in the tree census). Samples for the initial trait measurements were collected from August to October 2021: wood cores (5 mm diameter, 50–80 mm length) were collected from three living trees of each species, one per individual, with an increment borer. Samples for the laboratory experiment were collected in the same manner from five individuals per species, two per individual. Freshly senesced leaves for the laboratory experiments were collected in October and November 2021 from the bases of at least three individuals of each species.

Trait measurements

Traits of leaf and wood litter samples were measured before and after decomposition. The traits of freshly fallen leaves and wood core samples are considered to represent the initial traits of leaf and wood litter just before decomposition process begins. Post-decomposition traits were measured to determine whether there is a relationship between leaf and wood decomposition rates at the component level. LMA of leaf litter was calculated from dry weight (dried at 60 °C for 3 days) and leaf area as measured from scanned images of 1–4 leaves per individual in ImageJ software (National Institutes of Health). The volume of each wood core was calculated from its diameter and length, and weight was measured after vacuum-drying. The volume of the wood litter cubes was measured by water displacement, and weight was measured after drying at 105 °C for 24 h. Leaf and wood samples for chemical analyses were vacuum-dried, powdered in a mixer mill, and used for measuring the concentration of condensed tannins, total phenolics, lignin, carbon (C), and nitrogen (N). The content of condensed tannins was determined by proanthocyanidin assay with a standard curve prepared with cyanidin chloride (Julkunen-Tiitto 1985). The total phenolic content was determined by the Folin–Ciocalteu method with a standard curve prepared with tannic acid (Waterman and Mole 1994). The lignin content was determined by an improved acetyl

bromide procedure (Iiyama and Wallis 1990), and the concentration of lignin was calculated from the fitted calibration curve as described by Fukushima and Hatfield (2001). The C and N contents were determined by elemental analyzer (Vario MAX Cube) with aspartic acid as a standard sample for calibration.

Estimation of litter decomposition rates in the field

The field decomposition rate of wood litter was evaluated by the chronosequence approach, which compares wood density and decomposition time. The time of death was assumed to be the midpoint of the census interval in which a tree died. The decomposition constant (k value) was calculated for each tree species with an exponential decay model (Olson 1963) as:

$$w/w_0 = \exp(-kt)$$

where t is the time since death, w is the density of the wood litter, and w_0 is the initial density (wood density of living tree). Decomposition constants were calculated for total litter and for each constituent (C, N, lignin, total phenolics, and condensed tannin).

The rate of leaf litter decomposition in the field was measured by the litterbag method. Collected leaves were air-dried to a constant weight, and then 3 g of each species was placed in a polyethylene bag (12 cm × 12 cm, 2-mm mesh net). In total, 150 litterbags (10 species × 3 retrieval dates × 5 sites) were prepared. The litterbags were placed at five sites (Three were set up within the 6ha-plot and the other two were in the adjacent place to the plot, all of which were on the flat forest floor under closed canopy with similar soil condition) in the OFR in December 2014 and retrieved in April 2015, November 2015, and October 2016. The retrieved litter was cleaned, dried (60 °C, 3 days), and weighed. The mass remaining at each retrieval time was corrected by comparison with the ash content of subsamples because the remaining mass sometimes contained mineral soils. The decomposition constants for leaf

litter and for each constituent were calculated using the same method as for the wood litter, from the weight of initial and decomposed litter, and decomposition time.

Laboratory decomposition experiment

Laboratory experiments were conducted to examine differences in the rates of leaf and wood decomposition among tree species under controlled conditions. As a preliminary experiment, we isolated and cultured fungi from wood and leaf litter of the target species and inoculated these fungi into wood blocks and leaf litter of *Fagus crenata* and measured decomposition rate in the laboratory. We selected *Trametes versicolor* and *Xylaria* sp. because they were frequently isolated from wood and leaf litter, respectively, and both possess high decay ability. Leaf litter disks (10-mm diameter) for laboratory experiments were cut with a cork borer, avoiding the main vein, which we then vacuum dried and weighed. Wood core samples (5 mm diameter, 50–80 mm length) collected from living trees were vacuum dried and weighed. As a preliminary experiment, we compared the effects of drying methods (in air and in vacuum) on decomposition experiments with leaf and wood samples (five replicates for each treatment) of two tree species (*A. rufinerve* and *F. crenata*), using *T. versicolor*. As no significant differences were found, all further samples were vacuum dried.

Leaf disks and wood cores that had been sterilized in an ethylene oxide gas sterilizer were placed on 2% (w/v) water agar in Petri dishes (9 cm diameter). A fungal culture plug (~5 mm diameter) was inoculated into the agar adjacent to the sample. The plates were double-sealed with Parafilm and incubated for 8 weeks at 20 °C. One hundred leaf litter disk and wood core plates (10 species, 2 fungal species, 5 replicates) were incubated. After incubation, the leaf disks and wood cores were vacuum-dried and weighed.

Estimation of leaf and wood litter input

193 The amount of leaf litter input was estimated by using data from the 1990, 1991, and
194 2020 litterfall surveys in the 1.2-ha core plot. Circular litter traps (0.5 m^2) were placed at
195 equal intervals in the 1.2-ha plot (263 traps in 1990 and 1991, 72 in 2020). Litter was
196 collected every 2 weeks from September to December 1990, March to December 1991, and
197 April to December 2020 and air dried. Litter collected each year (only October–November for
198 2020) were identified to species level and weighed. The peak litterfall in October–November
199 1991 accounted for 80.8% of the annual litterfall (March–December litter volume; all trees in
200 the study plots were deciduous, with little or no defoliation in winter). The October–
201 November litter volume per species correlated well with the annual litter volume per species
202 (r = 0.99). Therefore, we calculated the annual litterfall for 1990 and 2020 by multiplying the
203 October–November litterfall by the ratio of annual litterfall to the October–November 1991
204 litterfall. The litterfall per area was estimated from the area of the litter trap and the area of the
205 plot. Wood litter input was estimated from tree census data over the period 1987–2021 in the
206 6-ha plot. The above-ground mass of dead trees (including standing dead and not including
207 fallen branches from living trees) was treated as wood litter input. Wood litter mass resulting
208 from tree mortality was calculated from DBH at the last census before death, tree height
209 estimated from DBH, and species-specific wood density using the equation described by
210 Ishihara et al. (2015). Tree height of each species was estimated from DBH by using the
211 equation for the relationship between DBH and tree height of each species in the OFR
212 described by Masaki et al. (2017).

213 **Statistical analysis**

214 Initial leaf and wood litter traits were summarized into principal component analysis
215 (PCA) dimensions. The strength of the association between each trait and the PCA major axis
216 scores was evaluated with Pearson's correlation. Association of decomposition rates between
217 leaf litter and wood litter was assessed by correlation test (Pearson's coefficient). Simple

linear regression analysis was used to examine the effects of traits on decomposition rate and to identify traits that best predicted mass and density loss for each of wood and leaves.

The half-lives of leaf and wood litter for the entire community were estimated from species-specific litter decomposition rates and litter inputs; Olson's exponential decay model was used to estimate the amount of remaining litter (w_i) of species i at time t with the decomposition constant (k_i) estimated from the field data and the amount of litter input (w_{0i}) for species each year. We then calculated the time $T_{1/2}$ (the litter half-life of the ten species) at which the sum of w for all species is half of the sum of w_0 for all species. Since the target species accounted for >75% of the biomass, we considered the result as an approximate community average. All statistical analyses were conducted in R v. 3.6.0 software (www.r-project.org).

Results

Species traits

Principal component 1 (PC1) explained 43.9% and 39.8% of the total trait variation in initial leaf and wood litter (freshly senesced leaves and wood cores), respectively (Fig. 1). All initial leaf litter traits except lignin content were related to PC1, with conservative traits (such as LMA) and acquired traits (N) contributing in opposite directions along the axis. Leaf litter lignin content was associated with PC2. Among initial wood litter traits, C, wood density, and total phenolics were associated with PC1, and lignin, condensed tannin and N with PC2. We found no correlations between PC1 and PC2 (Table 1) and between individual traits (Table S1) across initial leaf and wood litter.

Rates of leaf and wood litter decomposition

The field decomposition rates and the half-life were k = 0.14–1.09 and $T_{1/2}$ = 0.6–4.9 in leaf

litter and k = 0.01–0.21 and $T_{1/2}$ = 3.2–76.7 in wood litter. The mass loss of N was similar to or slower than the overall mass loss in both leaf (Figs. S1 and S2) and wood litter (Figs. S3 and S4), and its relative contents increased with decomposition. The rate of mass losses of total phenolics and condensed tannins in leaf litter were 3.3 to 31.9 times and 4.6 to 33.0 times the rate of total mass loss respectively, whereas those in wood litter were as low as −2.3 to 4.7 times and −0.1 to 2.2 times the rate of total mass loss respectively. In the laboratory experiments, the average mass loss via *T. versicolor* decomposition was 31.8%–70.2% in leaves and 1.4%–29.0% in wood cores, and that via *Xylaria* sp. decomposition was 22.9%–62.8% in leaf litter and 0%–10.0% in wood cores.

During decomposition in the field, there were no significant relationships between leaf and wood litter in loss of mass/density (R = −0.12, P = 0.73, Fig. 2A), N (R = 0.52, P = 0.12), lignin (R = 0.14, P = 0.70), total phenolics (R = −0.27, P = 0.45), or condensed tannins (R = 0.21, P = 0.56). In the laboratory experiments, there was no correlation between the mass losses of leaf litter and wood cores when decomposed by either *T. versicolor* (isolated from wood litter; R = −0.34, P = 0.34, Fig. 2B) or *Xylaria* sp. (isolated from leaf litter; R = −0.28, P = 0.43, Fig. 2C). On the other hand, there was a significant correlation between leaf litter decomposition rates in the field and leaf litter mass loss via *Xylaria* sp. decomposition in the laboratory (R = 0.68, P = 0.03, Fig. S5B). There was also a significant correlation between wood litter decomposition rate in the field and wood mass loss by the wood-decomposing fungus *T. versicolor* in the laboratory (R = 0.67, P = 0.03, Fig. S5C). In contrast, there was no significant correlation between leaf litter decomposition rate in the field and leaf mass loss via *T. versicolor* in the laboratory (R = 0.18, P = 0.62, Fig. S5A), or between the wood litter decomposition rate in the field and wood mass loss via *Xylaria* sp. in the laboratory (R = 0.34, P = 0.33, Fig. S5D).

Effects of species traits on litter decomposition

Leaf and wood litter decomposability were associated with different traits (Table 2). Lignin content was negatively related to leaf litter decomposition rate, explaining 35.3% (adj. R^2, field decomposition), 36.0% (decomposition by wood litter–inhabiting *T. versicolor*), and 52.9% (decomposition by leaf litter–inhabiting *Xylaria* sp.) of the variation. Leaf litter decomposition by *Xylaria* sp. was also negatively related to condensed tannins (adj. R^2 = 0.363). Wood litter mass loss in the field was negatively related to total phenolics (adj. R^2 = 0.345), and that in the *T. versicolor* decomposition experiment was negatively related to C (adj. R^2 = 0.514) and total phenolics (adj. R^2 = 0.405).

Litter dynamics

The estimated total annual leaf litterfall of the ten species was 2.25 Mg/ha in 1990, 3.58 Mg/ha in 1991, and 2.54 Mg/ha in 2020. The estimated total annual wood litter input between 1987 and 2021 was 1.18 Mg/ha. Leaf and wood litter inputs of each species are shown in Table 3. When species-specific litter decomposition rates and litter input volumes are considered, the average half-life of leaf litter was 2.41 years in 1990, 2.17 years in 1991, and 2.42 years in 2020, and that of wood litter was 8.35 years.

Discussion

We found no correlation between the rates of leaf and wood litter decomposition of ten temperate deciduous hardwood species in either field or laboratory conditions. Initial leaf and wood litter traits of each species were not correlated, and traits associated with decomposition differed between leaf and wood litter. The amount of wood litter input was less than half that of leaf litter input, but as the time it took to halve was >3 times longer, this suggests that wood and leaf litter make similar contributions to litter accumulation. These results clearly

show the importance of considering both leaves and wood in predicting the effects of changes in tree species composition (changes in litter input composition) on litter dynamics at a community level.

Independent decomposability of leaf and wood litter

We combined laboratory experiments with field data to evaluate leaf and wood litter decomposability. Because decomposition in the field is influenced by confounding factors such as microclimate, local topography, and decomposer communities as well as by litter traits, controlled laboratory experiments are useful in examining the effects of functional traits, but few experiments have simultaneously examined wood and leaves of multiple species. Interspecific differences in rates of both wood and leaf litter decomposition were similar across our laboratory and field results. In particular, interspecific variation in rates of wood litter decomposition was consistent across field data and laboratory experiments, even though the field decomposition rates of wood litter were based on relatively long-term (~20 years) observation data. This consistency suggests that a significant portion of the interspecific variation in field decomposition rates is derived from interspecific differences in resistance to fungal decomposition.

The independence of leaf and wood decomposability reported here is consistent with the results of previous studies exploring the decomposability of multiple plant organs, including leaves and wood (Freschet et al. 2012, Jackson et al. 2013, Zanne et al. 2015), and a global meta-analysis (Pietsch et al. 2014). Leaf and wood traits are related by resource allocation strategy within the plant and trade-offs between traits (e.g., Wright et al. 2006, 2007). However, in our study system, we found no correlation between initial leaf and wood litter traits. This result is consistent with reports indicating the independence of leaf and wood trait variations in tropical trees (Baraloto et al. 2010, Vleminckx et al. 2021). The lack of

312 correlation between leaf and wood traits here may be one of the factors contributing to the
313 lack of correlation between leaf and wood litter decomposition. We also confirmed that there
314 is no relationship between leaf and wood litter decomposition rates even at the level of
315 individual components (e.g., wood lignin of species with slow-decomposing leaf lignin is not
316 necessarily slow to decompose). In addition, our results suggest that the lack of correlation
317 between leaf and wood litter decomposition is due to the fact that the traits that affect
318 decomposition differ between leaf and wood litter, as explained below.

319 **Trait control of litter decomposition**

320 Although we identified several traits that explain interspecific differences in litter
321 decomposability, traits associated with decomposition rates differed between leaves and
322 wood. For instance, lignin concentration explained differences between species in leaf litter
323 decomposition rates, whereas total phenolic content explained differences in wood
324 decomposition rates. Extensive evidence shows that the content of recalcitrant lignin inhibits
325 litter decomposition rate (Berg and McClaugherty 2008). However, in our study, lignin
326 content was not related to wood decomposition rate, although it clearly explained leaf
327 decomposition rate, maybe because interspecific differences in lignin concentration were
328 large (10%–30%) in leaves but small (24%–26%) in wood. Moreover, because the rate of
329 lignin decomposition decreases with increasing N concentration (Berg and McClaugherty
330 2008), it is possible that the inhibitory effect of lignin on litter decomposition was smaller in
331 wood, which has a lower N concentration than leaf litter.

332 The total phenolic content, a total amount of various phenolic compounds, was
333 negatively related with the decomposition rate of wood. The phenolic content of wood has
334 been shown to inhibit the growth of pathogenic fungi (Witzell and Martin 2008), and it may
335 have suppressed fungal growth, inhibiting decomposition. As only a few studies of the

relationship between wood decomposition and traits have included total phenolic content, this finding must be evaluated in more tree species. In leaves, although the total phenolic concentration was high in freshly fallen litter, it was rapidly decreased after decomposition began, unlike in wood litter (Figs S1–S4). Although various phenolic compounds are known to play a variety of roles in living leaves (e.g., defense against herbivores, colors, UV tolerance), leaf litter decomposition, and in soil processes (e.g., microbial activities, nitrification) (Chomel et al., 2016, Hättenschwiler and Vitousek, 2000), the interspecific differences in their concentration may not have had significant influence on microbial decomposition of leaf litter because of the rapid degradation or leaching at the beginning of decomposition processes for most study species. The phenolic compounds in leaf and wood may be different in their molecular weight and structure, leading to different ease of degradation or leaching, and thus may have different effects on litter decomposition after death.

The effects of traits were clearer in laboratory experiments than in field data, and the relationship between decomposition rate and traits differed between wood- and leaf-decomposing fungi. For example, decomposition by the wood-decomposing fungus was slowed by higher concentrations of C and total phenolics, but the leaf-decomposing fungus was not. Conversely, decomposition by the leaf-decomposing fungus was slowed by higher foliar condensed tannins, but the wood-decomposing fungus was not. Different fungal communities decompose wood and leaves because the substrates are very different (Bani et al. 2018), and it is likely that each type of litter is decomposed largely by substrate-specific fungi. This difference in functional characteristics between the primary fungal decomposers of leaves and wood may lead to differences in the relationship between traits and decomposition rates. Owing to the small number of fungal species examined in this study, this

hypothesis will need to be tested by examining the relationship between functional traits and litter characteristics in more species of litter-decomposing fungi.

Effects on carbon storage

Changes in the species composition of tree communities under climate change and anthropogenic disturbance are important factors in altering the carbon cycle. An empirical study of the relationship between plant species traits and litter decomposition rates in both wood and leaves is important for accurate prediction of the future carbon cycle. There is extensive research on leaf litter decomposition, and there is increasing evidence that fine root and twig litter decomposition correlates with leaf litter decomposition (Freschet et al. 2012). Nevertheless, it may be necessary to evaluate decomposition of wood, carbon storage of which is comparable to that of leaf litter, separately from leaf litter, as demonstrated here. In particular, wood litter inputs are highly variable, depending on climate, forest age, and disturbance events, but are generally reported to be around 0.8–4.9 Mg ha^{-1} y^{-1} (Baker et al. 2007, Clark et al. 2002, Liu et al. 2006). The total wood litter input (1.18 Mg ha^{-1} y^{-1} for ten species) estimated here falls within this range and is also close to values estimated at geographically and climatically similar sites (Fukasawa et al. 2014, Jomura et al. 2007, Ohtsuka et al. 2014). Although the half-lives of litter decomposition measured here differed among species by up to 7.7 times in leaves and 23.6 times in wood, we can estimate community-level litter decomposition by considering species-specific rates of litter input and decomposition. The average leaf litter input was more than twice that of wood litter, whereas the time it took to halve was estimated to be less than one-third that of wood litter. This indicates that leaf and wood litter make similar contributions to litter accumulation when both input and decomposition rates are taken into account. Since leaf and wood litter decomposition rates were independent, the effects of changes in forest species composition (changes in litter input composition) could have different effects on community-level litter

dynamics of leaves and wood. Consequently, focusing on either leaf or wood litter alone may produce misleading estimates of how species composition changes affect litter dynamics at the community level. For example, an increase in the biomass of *F. japonica*, a dominant species at the study site, would be expected to decrease the community-averaged rate of leaf litter decomposition, but conversely increase the community-averaged rate of wood litter decomposition. As the "afterlife effects" of plant traits vary among organs, the contribution of traits to overall carbon and nutrient cycling is not simple, and the effects of multiple organs should be integrated.

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564 Table 1. Pearson's correlation coefficients and p-values between the first two PC scores (PC1 and PC2) summarizing the trait data for leaf litter

565 and wood cores) among ten tree species.

	R	p
Leaf litter PC1 vs wood core PC1	0.06	0.87
Leaf litter PC1 vs wood core PC2	−0.12	0.74
Leaf litter PC2 vs wood core PC1	0.08	0.83
Leaf litter PC2 vs wood core PC2	−0.16	0.66

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568

569 Table 2. Relationships between functional traits and decomposition constant (*k*) in each organ across species. Estimated slopes and *P*-values

570 determined by simple regression analyses are shown.

	Field decomposition				Laboratory decomposition (*Trametes versicolor*)				Laboratory decomposition (*Xylaria* sp.)			
	Leaf litter		Wood litter		Leaf litter		Wood litter		Leaf litter		Wood litter	
	Estimate	*P*-value	Estimate	*P*-value	Estimate	*P*-value	Estimate	*P*-value	Estimate	*P*-value	Estimate	*P*-value
Trait												
LMA/density	0	0.33	0.24	0.49	0	0.53	0.79	0.07	0	0.26	0.27	0.09
Nitrogen	−0.06	0.87	0.20	0.76	0.08	0.67	1.48	0.08	0.04	0.82	0.48	0.12
Carbon	−0.04	0.50	−0.07	0.20	−0.04	0.1	**−0.16**	**0.01**	−0.04	0.13	−0.04	0.17
Total phenolics	0.01	0.15	**−0.01**	**0.04**	0	0.62	**−0.02**	**0.03**	0	0.24	0	0.26
Condensed tannin	−0.04	0.31	0.05	0.64	−0.03	0.09	0.07	0.6	**−0.03**	**0.04**	0.02	0.64
Lignin	**−0.03**	**0.04**	0.01	0.54	**−0.02**	**0.04**	−0.01	0.67	**−0.02**	**0.01**	0	0.57

571 LMA: leaf matter per area.

572 Table 3. Annual litter input of leaf and stem wood litter (Mg ha^{-1}).

	Leaf litter 1990	Leaf litter 1991	Leaf litter 2020	Wood litter 1987–2021
Castanea crenata	0.147	0.148	0.054	0.078
Fagus japonica	0.521	0.419	0.567	0.385
Fagus crenata	0.436	0.636	0.299	0.129
Quercus serrata	0.677	0.729	1.001	0.290
Quercus crispula	0.085	0.086	0.098	0.093
Carpinus laxiflora	0.091	0.116	0.062	0.045
Acer pictum	0.200	0.227	0.227	0.024
Acer rufinerve	0.003	0.008	0.010	0.044
Swida controversa	0.087	0.146	0.140	0.050
Styrax obassia	0	0.059	0.083	0.038

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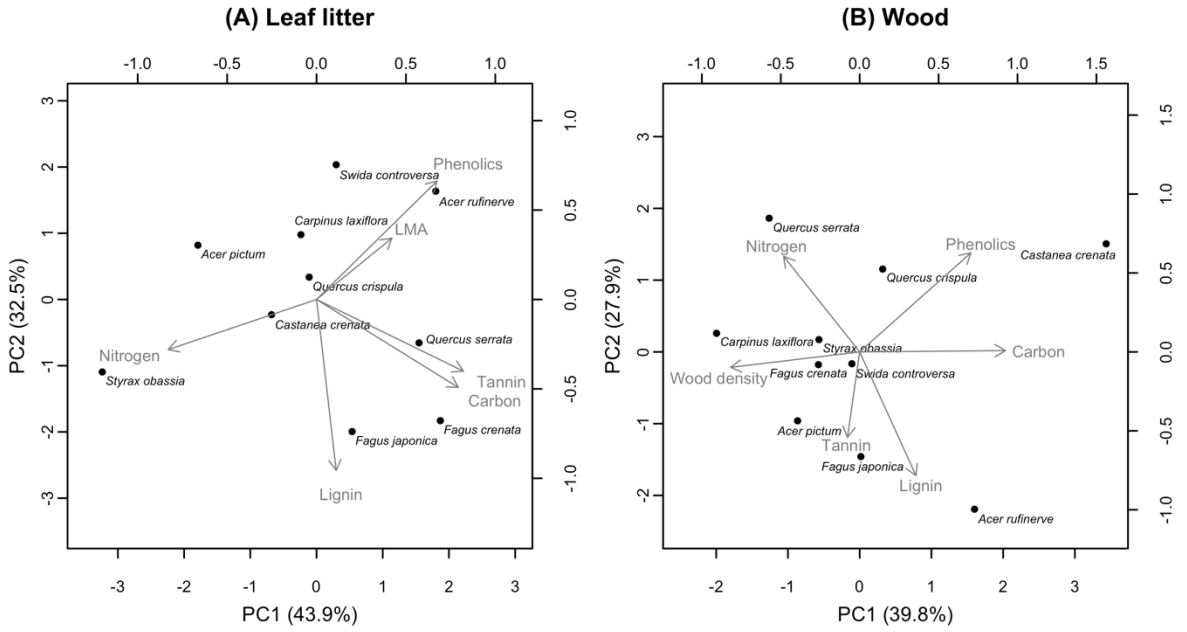
574

575 **Figure captions**

576 Figure 1. Results of the principal component analyses summarizing initial (A) leaf litter and
577 (B) wood litter traits of the ten tree species. Points and arrows represent PC scores and
578 loadings.

579 Figure 2. Decomposability of leaf and wood litter in field and laboratory conditions.
580



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582 Fig. 1

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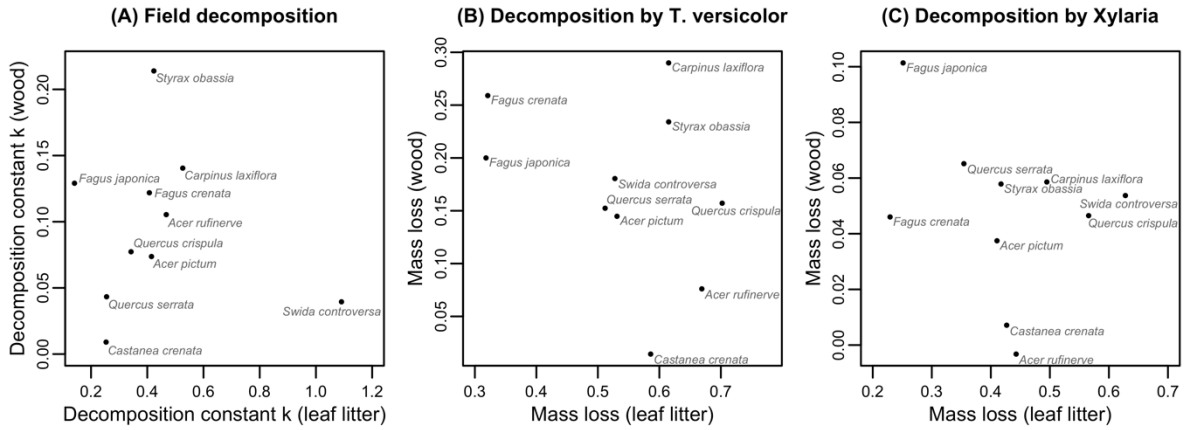
(A) Field decomposition
Decomposition constant k (wood)
Decomposition constant k (leaf litter)
Styrax obassia
Fagus japonica
Carpinus laxiflora
Fagus crenata
Acer rufinerve
Quercus crispula
Acer pictum
Quercus serrata
Swida controversa
Castanea crenata
(B) Decomposition by T. versicolor
Mass loss (wood)
Mass loss (leaf litter)
Carpinus laxiflora
Fagus crenata
Styrax obassia
Fagus japonica
Swida controversa
Quercus serrata
Quercus crispula
Acer pictum
Acer rufinerve
Castanea crenata
(C) Decomposition by Xylaria
Mass loss (wood)
Mass loss (leaf litter)
Fagus japonica
Quercus serrata
Carpinus laxiflora
Styrax obassia
Swida controversa
Quercus crispula
Fagus crenata
Acer pictum
Castanea crenata
Acer rufinerve

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585 Fig. 2