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What controls the variability of wood-decay rates?

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ABSTRACT

Decaying wood provides essential habitats for forest biota, and its CO_2 return to the atmosphere is comparable to that from fossil-fuel combustion. Decomposition rates for wood debris (WD) from three tree species were measured by CO_2 release in a subtropical forest over two years. Wood temperature and moisture were measured along with CO_2, and each WD piece ($n = 320$) was characterized by its initial weight, density, volume, surface area, and decay class. For individual pieces of WD in each wood-species and decay-class group, predictions of release rates based on temperature and moisture together had R^2 values ranging from 0.25 to 0.57, predictions based on moisture alone had R^2 values ranging from 0.16 to 0.35, and R^2 values from 0.07 to 0.35 were seen in temperature-only predictions. Wood density and surface area were negatively related to CO_2 release rates ($R^2 = 0.10$ and 0.04 respectively, over all groups). We also used daily meteorological measurements to predict WD temperature and moisture. Average air temperatures predicted WD temperatures with R^2 values above 0.7 over 35 days, but total rainfall was a very weak predictor of WD moisture over any interval. We used temperature – decay relationships to estimate annual total CO_2 release from WD groups, and found that their average exponential decomposition rate (K) was 0.09 year^{-1}. Based on density loss, most WD in the studied forest would be in the late stage of decay, in contrast to some previous studies. Our results support previous studies on the importance of environmental factors in determining WD decomposition, but with only half of the variation explained, we are challenged to explain the rest. Aggressive interactions are common among WD decomposers, and previous work with simplified microbial communities suggests that high diversity leads to slower decomposition. Uncertain predictions for WD decomposition rates, and their global C- cycle implications, will persist until interactions of WD microbial communities are better understood.

1. Introduction

Wood debris (WD) is an important component of forest ecosystems, because it influences nutrient cycling, humus formation, carbon storage, fire frequency and water cycles. It also serves as habitat for both heterotrophic and autotrophic organisms (Brais et al., 2006; Harmon et al., 1986; Hart, 1999; Nalder and Wein, 1999; Paletto et al., 2012; Rayner and Boddy, 1988; Woodall and Liknes, 2008). However, the dynamics of WD decomposition remain poorly understood (Harmon et al., 1986; Scheller and Mladenoff, 2002; Yatskov et al., 2003).

The global WD carbon pool has been estimated as 73 petagrams (Pg, 10^{15} g; Pan et al., 2011). Decomposition of WD has been measured in many regions and median exponential decay rates (K; year^{-1}) range from 0.024 in boreal to 0.167 in tropical humid forests (e.g., Bond-Lamberty et al., 2003; Gough et al., 2007; Liu et al., 2006; Tang et al., 2008; Wang et al., 2002; Wu et al., 2010). Globally, wood decomposition represents a large return of CO_2 to the atmosphere, variously estimated as 2.1–11 Pg C year^{-1} (Harmon et al., 1993), 6 Pg C year^{-1} (Matthews, 1997), 7.7–9.5 Pg C year^{-1} (Harmon et al., 2001) and 8.6 Pg C year^{-1} (Luyssaert et al., 2007). The return of CO_2 by wood decomposition is thus similar in magnitude to that from current global fossil-fuel combustion (9.5 Pg C year^{-1} in 2011; Le Quéré et al., 2012). An improved understanding of WD decomposition is essential to assess the role of WD in C sequestration by forest ecosystems (Pregitzer and Euskirchen, 2004; Van Miegroet et al., 2007).

For these reasons, factors influencing WD decay are of interest. Tree species and functional traits are important (Weedon et al., 2009), as are environmental factors including temperature and wood-moisture content (Boddy, 1983; Bond-Lamberty et al., 2003; Jomura et al., 2008; Liu et al., 2006; Remsburg and Turner, 2006). Most detailed studies to date have used CO_2 release to estimate wood decomposition rates (e.g., Boddy et al., 1989; Bond-Lamberty et al., 2003; Chambers et al., 2000, 2001; Hérault et al., 2010; Jomura et al., 2008; Liu et al., 2006; Mackensen and Bauhus, 2003; Progar et al., 2000; Yoneda, 1980), but overall suggest that environmental factors explain 50% or less of observed variations.

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Several studies have linked fungal community structure to WD decomposition rates (e.g., Boddy et al., 1989, Boddy, 2000, 2001; Heilmann-Clausen and Boddy, 2005; Progar et al., 2000; Rayner and Boddy, 1988; Worrall et al., 1997). This is important, because lignin in wood cell walls represents a challenging substrate, and is mostly decomposed by fungal exo-enzymes (Kirk and Farrell, 1987). Early WD decay appears limited by fungal colonization; limited to fungi already present in living wood (Parfitt et al., 2010), the arrival of airborne fungal spores (Vasiliauskas et al., 2005), fauna delivering spores (Persson et al., 2011), and hyphal in-growth from nearby fungi (Boddy, 2001; Carpenter et al., 1988; Jönsson et al., 2008; Watkinson et al., 2006). Intermediate WD generally decays more rapidly, with late stages again becoming limited by the exhaustion of materials most beneficial to microbes (e.g., Harmon et al., 1986). At all stages, fungal activity may be limited by aggressive interactions among fungi (e.g., Boddy, 2000; de Boer et al., 2010; Heilmann-Clausen and Boddy, 2005). For these reasons, exponential models used for leaf decay have been seen as inappropriate for wood (Harmon et al., 1986; Zell et al., 2009). Instead, time spent in defined decay classes has been used to define WD decomposition (Aakala, 2010; Kruys et al., 2002; Ranius et al., 2003; Vanderwel et al., 2006).

This study was conducted at Ailao Mountain, which preserves the largest area of undisturbed subtropical forest in China, and has a substantial pool of WD (74.9 Mg ha^{-1}; Yang et al., 2008). We measured environmental factors and WD decay by CO_2 release rates to investigate variations through time. We examined decay rates of three dominant tree species, *Lithocarpus chintungensis* (LC), *Lithocarpus xylocarpus* (LX) and *Schima noronhae* (SN), six times during two years. Three decay classes were defined for each of these species, yielding nine groups. The objectives of our study were: (1) to quantify WD decay rates and their variability, (2) to identity environmental and other variables linked with WD decay, and (3) to explore decay-rate variability unrelated to those factors.

2. Materials and methods

2.1. Site description

This study was conducted in a subtropical moist forest located at Xujiaba in the Ailao Mountains National Nature Reserve, SW China. The study site was at an elevation of 2476 m, about 2 km north of the Ailao Field Station for Forest Ecosystem Studies (24°32′ N, 101°01′ E), administered by Xishuangbanna Tropical Botanical Garden of the Chinese Academy of Sciences. The site receives 1840 mm annual average precipitation. The climate is monsoonal with distinct cool/dry (November–April) and warm/wet (May–October) seasons (Zhang, 1983). Annual mean air temperature is 11.3 °C with monthly means ranging from 5.4 to 23.5 °C. The frost-free period is about 200 days. The accumulated degree-days above 10 °C are 3,420; similar to the warm temperate zone (Liu, 1993). Surface soils (0–10 cm) of the area are Alfisols with pH of 4.2 (water). The surface organic layer is of 3–7 cm deep (Liu et al., 2002). The study site is a broad-leaved evergreen forest, dominated by *Lithocarpus chintungensis*, *Rhododendron leptothrium*, *Vaccinium ducluoxii*, *Lithocarpus xylocarpus*, *Castanopsis wattii*, *Schima noronhae*, *Hartia sinensis*, and *Manglietia insignsis* (Wu et al., 1983). Strong winds and occasional heavy snowfall contribute to large WD pools (74.9 Mg ha^{-1}; Yang et al., 2008).

2.2. Sample preparation

At our site, most wood debris (WD) came from *Lithocarpus chintungensis*, (LC), *Lithocarpus xylocarpus* (LX), or *Schima noronhae* (SN), so we limited the study to those three species. In June 2010, a total of 320 WD pieces were cut to fit the field respiration chamber (20 × 30 cm), permanently labeled, weighed and measured for size and decay class as described below. They were placed on the forest floor within a 60 × 3 m belt transect following an elevation contour. The pieces of WD were originally collected from the forest within 500 m of the belt transect.

We assigned each piece to one of three decay classes; DKC1 = a knife could not penetrate, DKC2 = knife could slightly penetrate with appreciable resistance, DKC3 = knife could deeply penetrate with little resistance (Lambert et al., 1980). We selected WD pieces to achieve similar sample numbers for each species and DKC. The length and diameter at three points were measured for each piece. The diameters were averaged and volumes were calculated as cylinders. Each piece was weighed with a GLL portable electronic balance and its moisture content measured with an Extech MO210 moisture meter. Calibration of this meter is described in the supplemental material. The moisture meter readings corresponded closely with gravimetric measurements made before ($R^2 = 0.83$) and after ($R^2 = 0.79$) the study. All references to WD moisture in this study refer to unadjusted moisture-meter readings. A carbon to dry weight ratio of 0.5 was used throughout, based on earlier analyses of WD in this forest (Yang, 2007). The physical properties of the WD pieces are presented in Table 1. Temperature and moisture contents of the WD pieces at each sampling period are presented in Table 2.

2.3. WD CO_2 release-rate measurements

Individual CO_2 release rates were measured in the field in a closed, ventilated chamber (10 L) connected to an infrared gas analyzer (Licor 820, Lincoln, Nebraska, USA). After initial stabilization, linear CO_2 concentration-increase rates were logged for at least 5 min. These measurements were made six times from September 2010 to June 2012 (total > 1800 measurements). Pieces remained

Table 1

Physical properties of the sampled wood-debris pieces for different species and decay classes at Ailaoshan, Yunnan, China. Carbon content is half of the dry weight, based on wood debris having 50% carbon. SE = standard error.

Species	Decay class	Number of samples	Radius (cm)		Length (cm)		Density (g cm^{-3})		Carbon content (g)	
			Mean	SE	Mean	SE	Mean	SE	Mean	SE
Lithocarpus chintungensis	1	39	3.2	0.06	20.9	0.32	0.54	0.011	174.9	7.9
	2	53	3.1	0.06	22.2	0.40	0.46	0.009	146.7	4.9
	3	31	3.5	0.09	22.4	0.38	0.36	0.012	158.1	7.3
Lithocarpus xylocarpus	1	37	3.4	0.07	22.4	0.35	0.59	0.008	231.4	12.9
	2	35	3.1	0.09	22.2	0.37	0.46	0.012	151.4	9.1
	3	28	3.0	0.10	21.2	0.44	0.42	0.010	138.5	8.2
Schima noronhae	1	37	3.0	0.06	22.0	0.43	0.51	0.013	132.5	6.0
	2	29	2.6	0.07	21.1	0.50	0.46	0.012	110.6	8.7
	3	31	3.0	0.08	21.2	0.397	0.37	0.010	135.3	9.98

Table 2
Moisture and temperature measurements of the wood-debris pieces at Ailao Mountain, Yunnan, China. Three wood species in three decay classes (DKC) were examined. The dates of these measurements correspond to those of CO_2 release rates. Values are means, with standard deviations in parentheses. LC = *Lithocarpus chintungensis*, LX = *Lithocarpus xylocarpus*, SN = *Schima noronhae*.

Species	DKC	Moisture						Temperature					
		2010/9/25	**2011/2/24**	**2011/5/22**	**2011/10/1**	**2012/3/3**	**2012/6/12**	**2010/9/25**	**2011/2/24**	**2011/5/22**	**2011/10/1**	**2012/3/3**	**2012/6/12**
LC	1	45.1 (10.1)	12.1 (3.5)	49.3 (9.6)	43.7 (6.2)	23.3 (10.7)	46.9 (5.8)	11.6 (1.4)	8.1 (0.5)	10.7 (0.2)	13.8 (2.2)	9.0 (2.4)	15.8 (0.9)
LC	2	54.3 (3.3)	12.9 (2.3)	54.5 (5.1)	45.6 (6.5)	28.0 (11.6)	49.3 (7.0)	11.8 (1.6)	8.2 (0.5)	10.6 (0.3)	12.9 (2.4)	7.5 (1.8)	15.9 (0.8)
LC	3	51.5 (7.1)	13.7 (2.2)	56.3 (4.3)	47.6 (6.8)	25.4 (12.6)	51.2 (7.1)	11.7 (1.5)	8.1 (0.5)	10.7 (0.2)	13.1 (2.4)	8.7 (2.5)	15.6 (0.7)
LX	1	51.1 (5.5)	14.0 (1.4)	53.0 (5.9)	45.0 (6.4)	22.2 (9.3)	48.1 (5.6)	12.2 (1.3)	8.1 (0.3)	10.6 (0.3)	13.5 (2.3)	8.5 (2.5)	15.9 (0.8)
LX	2	53.2 (4.1)	14.8 (1.5)	55.4 (4.1)	48.3 (5.1)	30.9 (13.2)	49.9 (6.0)	12.0 (1.7)	8.2 (0.4)	10.7 (0.3)	13.0 (2.3)	7.8 (2.1)	15.7 (0.9)
LX	3	54.0 (4.3)	14.5 (1.2)	55.4 (5.4)	50.1 (4.7)	24.9 (13.8)	52.8 (6.6)	10.9 (1.7)	8.2 (0.6)	10.6 (0.3)	13.4 (2.1)	8.8 (2.2)	16.0 (0.9)
SN	1	52.4 (4.3)	14.8 (2.0)	56.3 (3.8)	45.5 (6.0)	25.5 (11.4)	48.2 (6.8)	11.5 (1.7)	8.1 (0.4)	10.7 (0.3)	13.1 (2.2)	8.2 (2.2)	15.9 (0.9)
SN	2	51.9 (7.1)	14.3 (1.8)	54.7 (5.6)	47.2 (4.9)	26.7 (13.8)	52.7 (4.5)	12.2 (1.8)	8.2 (0.4)	10.6 (0.4)	13.6 (2.2)	8.3 (2.0)	15.6 (0.7)
SN	3	52.2 (4.5)	15.0 (1.5)	56.7 (3.3)	47.7 (4.5)	27.3 (12.8)	51.0 (7.1)	11.3 (1.6)	8.1 (0.4)	10.6 (0.3)	13.1 (2.3)	8.4 (2.2)	15.8 (0.8)

in the field for CO_2 measurements (within 5 m) and were handled carefully to limit fragmentation. Temperature and moisture were measured for each WD sample at each sampling time. The WD CO_2 release rates (R_{WD}, μmol C g^{-1} h^{-1}) were calculated using the following equation:

$$R_{WD} = \frac{1000 * \Delta CO_2 * P(V - V_s)}{24 * R(T_s + 273) * w_C} \quad (1)$$

where $\triangle CO_2$ represents CO_2 concentration changes (ppm/day), P is the internal pressure (kPa), V is the volume of the system (10.08 L, including the chamber volume and tubing volume), V_s is the volume of the WD piece (L), R is the gas constant (8.314 $L^*kPa^*K^{-1}$ mol^{-1}), T_s is the wood temperature (°C), and W_C is the carbon weight of each piece (g; half of its dry weight).

2.4. Interpolating WD CO_2 release-rates for non-measurement times

Temperature and moisture of WD vary at time scales shorter than our CO_2 measurements. Daily records of air temperature (AT) and rainfall (PPT) were available from a station within 2 km of the WD transect. Based on those records and WD temperature and moisture measured in the six CO_2 sampling periods, we used linear regressions to predict daily WD temperature and moisture throughout the study. For each wood species and decay class, we regressed AT averaged over different preceding periods against group-average WD temperature, and selected precedent periods with the highest R^2 values. We followed the same procedure in regressing PPT sums over different preceding periods against WD group moisture contents. Based on daily predictions of WD temperature and moisture, our goal was to develop more accurate estimates of WD CO_2 release rates through time than would result from simple interpolations of measurements during the six CO_2 sampling periods. We found that daily WD moisture could not be predicted well from precedent PPT, so we regressed WD CO_2 only against WD temperature for each wood species and DKC.

Daily predictions of WD CO_2 were accumulated over time, yielding weight loss and (assuming that WD volume does not change) density loss. As we also measured densities of decay classes for each wood species, we could estimate time spent in each decay class. For DKC3, the constant-wood-volume assumption is not accurate because of bark loss and WD fragmentation (LWJ and DAS, pers. obs.), inflating the time that WD spends in that class. On the other hand, CO_2 release rates from wood very late in DKC3 may differ from those we measured for the relatively intact DKC3 pieces here. We also compared these estimates (driven by daily air temperature) to the CO_2 release rates from each group, simply averaged over the six sampling periods.

2.5. Estimating exponential decay rates “K” and Q_{10}

Wood CO_2 loss was converted to weight loss based on 50% carbon. From the WD weights determined initially, we calculated fractional weight loss on an annual basis. Exponential decay rates K are the natural logarithms of the annual fractional weight losses. Wood CO_2 losses (and thus, K values were determined separately from averaging the six rates, and from temperature interpolations.

The rate increase of any process under a 10 °C temperature increase is referred to as Q_{10}, with a doubled rate corresponding to Q_{10} of 2. We solved the WD-group temperature models at 5 and 15 °C to obtain the Q_{10} values presented in Table S1.

2.6. Statistical analyses

The statistical analyses used R software (Version 2.13.2, R Development Core Team, 2011). To develop models for predicting WD CO_2 release rates, ANCOVA was used to evaluate effects of wood species, DKC, moisture and WD temperature. The mixed effect model in package lme4 (Bates et al., 2011) was used to relate WD decomposition rates to water content and temperature; with species, decay class, temperature, water content, and interactions assigned as fixed effects, and WD sample measurements of temperature, water content and their combinations treated as random effects. Natural-logarithm transformation of R_{WD} was used to achieve homoscedasticity. The effects were added to the model individually, with the final model selection based on the lowest Akaike's Information Criterion (Burnham and Anderson, 2002).

3. Results

3.1. Environmental drivers of wood decomposition

Monthly average temperatures and rainfall totals are shown in Fig. 1. This site has a monsoon climate with co-varying temperature and rainfall. However, annual rainfall patterns are more variable than those of temperature, and seasonal temperatures increase earlier than rainfall does.

Although they were all located together, WD demonstrated individual variability in temperature and moisture (Table 2). The highest temperature variability was observed in October 2011 and the lowest in June 2011. Moisture variability was highest in February 2012 and lowest in February 2011. Much more rainfall preceded the October 2011 than the June 2012 sampling (Fig. 1), yet WD moisture contents were similar during those two sampling periods. The relatively high WD moisture measured in 2011 June was surprising, given the small amount of rainfall preceding that CO_2 sampling period.

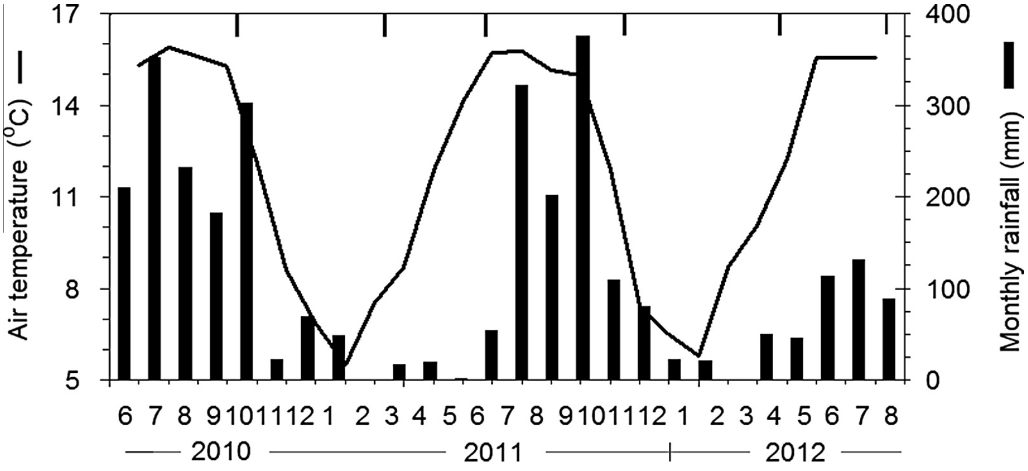

Fig. 1. Monthly average temperatures (lines) and total rainfall (bars) at Ailao Mountain, China during this study. The 6 WD CO_2 sampling times are shown by vertical dropped lines.

3.2. Seasonal patterns and average rates of wood decay

In this study, there were three wood species and three decay classes. The CO_2 release rates of these nine groups on each sampling date were summarized as box and whisker plots (Fig. 2). Strong seasonal patterns were apparent, with the lowest CO_2 release rates in dry/cool seasons and the highest rates early in warm/wet seasons. Lower rates were seen later in warm/wet seasons, despite high measured temperature and moisture in WD (Table. 2). In DKC1, the wood species with the largest seasonal variability was LC, while for DKC3, LX was the most variable. Rates for DKC3 of LX were higher than those of its earlier decay classes, while for both LC and SN, rates were highest in DKC2 (Fig. 2).

Decay rates of WD can be estimated by averaging measured CO_2 release rates, assuming that all values should be equally weighted. Daily meteorological data available for this site offered another approach. Measured moisture content or temperature of wood pieces can be related to earlier patterns of rainfall or AT. Based on relationships with measured CO_2 release rates, such daily data lead to alternate estimates for the nine WD groups. We had 116 days of daily temperature and rainfall data before the first CO_2 sampling. We compared average air temperature over the this entire period, and successively shorter antecedent periods, to measured temperatures of each group of WD at each CO_2 sampling time. For rain we compared the total amounts to the measured WD moisture of each group. We found weak relationships between previous rainfall over any period and wood moisture content (data not shown). However, previous daily AT predicted measured wood temperatures with R^2 values above 0.7 (Table 3). Even though all available previous intervals were examined, the temperature of WD of 10 cm diameter on the forest floor was best predicted by averaged daily air temperature over 34–35 days. While all of the precedent-T-driven models had high R^2, they still under- or over-predicted wood temperature by as much as 2 °C (Supplementary Fig. 4).

For WD groups, average wood-temperature values were regressed against measured CO_2 release rates (Table 4). We used these relationships to predict CO_2 release rates through time from each wood group. The models for WD groups having the lowest and highest R^2 were presented along with their measured values in Supplementary Fig. 4 as examples. Even though WD temperature was always predicted well from AT (Table 3), WD CO_2 release rates were over-predicted during the months of September and October (open circles in Fig. 3; Supplementary Fig. 4). As WD temperature and moisture remained high in the months of September and October (Table 2), environmental factors could not explain reduced decay rates at those times. Additional CO_2 release-rate measurements on a subset of the WD in 2012 September showed similar decreases (data not shown).

The R^2 values in Table 4 indicated that modeled wood temperature could explain between 38% and 78% of the CO_2 variation for WD groups. These models were relatively strong for all LX groups but not for any SN group. For LC, predictions varied among decay classes. The temperature-only model had higher R2 than the moisture-only model for LC decay class 1 and 2, for all LX decay classes, but not for any SN decay classes (Supplementary Tables 1–3). For the other WD groups, the moisture-only model made better predictions than the temperature-only model.

3.3. Decay rates and decay-class transitions

We developed a simple model for decay-class transitions, based on WD density loss entirely driven by CO_2 release. It thus ignored fragmentation and loss of soluble material from wood. For all groups, CO_2 release modeled from temperature was faster than averages of the six measurement periods, and therefore decay times were shorter (by 1/3 overall; Table 5). Wood density decreased little during DKC1 and DKC2 in this study, so times spent in those DKC would apparently be short (0.6–4.8 years). For all groups, the longest times would be spent in DKC3 (8–20 years). The total decay times for WD (11–21 years) in this climate (11.3 °C average temperature) corresponded to exponential decay rates from 0.07 to 0.14 $year^{-1}$, which bracketed the median of 83 published reports of WD decay rate (K) in subtropical forests (0.12 $year^{-1}$; Schaefer and M.E. Harmon, unpublished data).

3.4. Decay of individual WD pieces

Measured CO_2 release rates from individual WD pieces varied over more than three orders of magnitude (0.002–5.99 μmol CO_2 h^{-1} per g of WD carbon). By ANCOVA, these rates were significantly related to WD species, DKC, moisture, temperature, density, and interactions between species and DKC, moisture and T, moisture and density, and species, DKC and moisture (Table 6). We also compared WD volumes and surface areas to CO_2 release rates, and found much weaker relationships (data not shown).

As WD T and moisture are generally regarded as the strongest factors controlling decay (see Section 1), we examined them individually and then together. The variation explained by temperature alone was 0.353 or less (Supplementary Table 1). The Q_{10} of WD decomposition had previously been estimated as 2.4 (Chambers et al., 2000) and 2.5 (Mackensen et al., 2003). Most

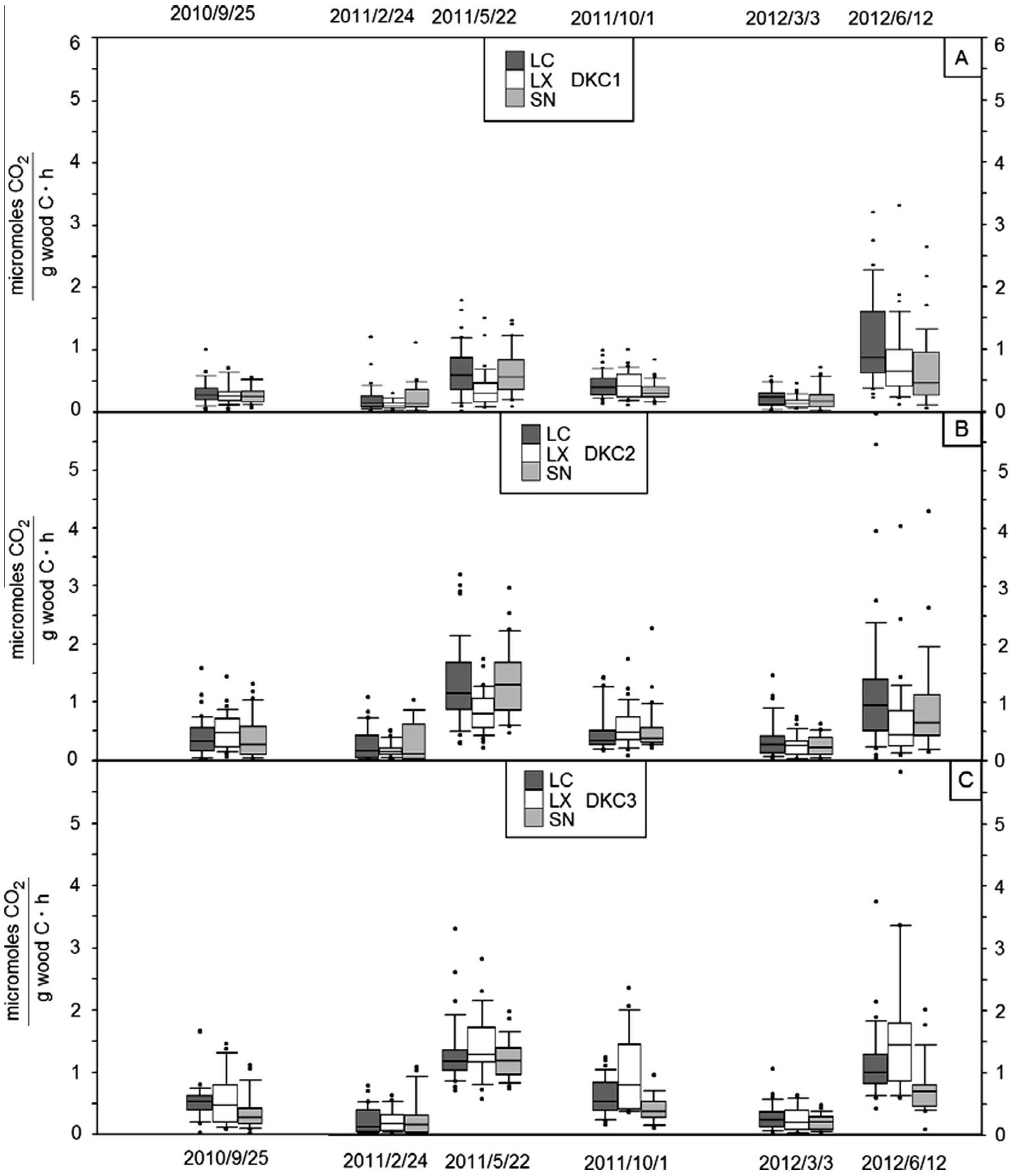

Fig. 2. Carbon dioxide release rates for (A) Decay class 1 (DKC1), (B) DKC2 and (C) DKC3 wood during this Ailao Mountain study. Median values are lines within the boxes, box limits are 25 and 75 percentiles, whiskers are 10 and 90 percentiles, and more extreme values are shown as points. Different shadings are used for *Lithocarpus chintungensis* (LC), *Lithocarpus xylocarpus* (LX), and *Schima noronhae* (SN) wood. The CO_2 sampling days are indicated.

of our derived Q_{10} values were surprisingly high (from 2.0 to 8.2; Table S1). However, we stress that our R^2 values were low, and that temperature and moisture co-vary in this forest. This co-variation confounded temperature and moisture effects and artificially inflated Q_{10}. In this study, SN appeared slightly less sensitive to temperature than LC or LX.

The moisture-only models showed a maximum R^2 of 0.353 as well, but in a WD group that did not have the strongest temperature model (compare Supplementary Tables 1 and 2). Other WD groups having strong temperature relationships also showed relationships for moisture. Species LC, DKC2 and DKC3 deviated most strongly from this pattern. We also examined CO_2 release rates regressed against temperature and moisture together; those R^2 values ranged from 0.25 to 0.57 (Supplementary Table 3).

4. Discussion

4.1. Environmental factors

Decay of WD is an important transfer of CO_2 from forests to the atmosphere. In this study we investigated CO_2 release rates from WD of LC, LX and SN, and their responses to environmental factors in a subtropical forest. Temperature and moisture are known to strongly influence decay rates of WD (e.g., Bond-Lamberty et al.,

Table 3
Predicted WD-group temperatures from earlier measured air temperatures at Ailaoshan, Yunnan, China. LC = *Lithocarpus chintungensis*, LX = *Lithocarpus xylocarpus*, SN = *Schima noronhae*. DKC 1, 2, 3 refers to the three decay classes. The best fits to air temperature averaged for different precedent periods are shown, with the lowest and highest R^2 values **in bold.**

Group	Precedent days	Slope	Intercept	R^2
LC DKC1	35	0.66	3.29	0.79
LC DKC2	34	0.80	1.55	0.81
LC DKC3	35	0.65	3.22	0.83
LX DKC1	35	0.71	2.63	0.84
LX DKC2	34	0.72	2.26	0.84
LX DKC3	**35**	**0.64**	**3.33**	**0.72**
SN DKC1	34	0.70	2.58	0.79
SN DKC2	**34**	**0.71**	**2.53**	**0.86**
SN DKC3	35	0.66	3.00	0.78

Table 4
Regressions of (LN) measured group CO_2 release rates against measured temperatures of the wood groups at Ailaoshan, Yunnan, China, with lowest and highest R^2 values **in bold**. LC = *Lithocarpus chintungensis*, LX = *Lithocarpus xylocarpus*, SN = *Schima noronhae*. DKC 1, 2, 3 refers to the three decay classes. The natural log transformation was used because temperature responses were not linear. The model form is LN (CO_2) = slope * T (°C) + intercept, CO_2 units μmoles per g WD carbon per day.

Group	Slope	Intercept	R^2
LC DKC1	0.20	−0.02	0.59
LC DKC2	**0.13**	**1.1**	**0.38**
LC DKC3	0.20	0.29	0.71
LX DKC1	0.25	−0.89	0.76
LX DKC2	0.19	0.2	0.73
LX DKC3	**0.25**	**−0.12**	**0.78**
SN DKC1	0.15	0.43	0.48
SN DKC2	0.16	0.71	0.44
SN DKC3	0.14	0.75	0.49

2003; Liu et al., 2006). In this study, increasing CO_2 release rates *versus* temperature (Fig. S1), and moisture (Fig. S2) showed substantial variability; both of these patterns were consistent with results of previous studies (Bond-Lamberty et al., 2003; Chambers et al., 2000, 2001; Hérault et al., 2010; Jomura et al., 2008; Liu et al., 2006; Mackensen and Bauhus, 2003; Progar et al., 2000). Despite successful calibrations, some uncertainty remains in WD moisture as measured here. While we did not observe strong differences in WD moisture contents (Table 2), the possibility remains that fungal communities can influence that among pieces (Boddy et al., 1989). While the WD pieces were handled carefully, some degree of fragmentation may be unavoidable, especially for the more fragile, late-decay WD. Those would have reduced our measured CO_2 release rates to the extent that it came from lost, fragmented portions.

Observed climate patterns at Ailao Mountain (Fig. 1) were qualitatively compared to WD CO_2 release rates (Fig. 2). Although conditions were both warm and wet during the first and fourth samplings, CO_2 release rates then were relatively low. Lowest CO_2 release rates always occurred during the cool/dry season. High rates were seen in the sixth and third samplings, despite the fact that there had been little rain before the latter. Low CO_2 releases late in the warm/wet season at Ailao Mountain reduced the predictive power of our temperature- and moisture-based models. There were also interactions between wood species and DKC and these environmental factors.

4.2. Measured and modeled WD decay

For all groups, WD T was best represented by AT averaged over 34 or 35 days. Larger WD could be affected by previous AT over longer periods because of its greater heat capacity and soil contact area. Wood-moisture predictions based on antecedent rainfall totals were poor, perhaps because these WD were in direct contact with soil. Moisture content of soil responds to throughfall-water redistribution, soil hydraulic processes and root-water uptake at small spatial scales, and all such factors were absent from our model. Although responses of CO_2 release rates to WD moisture were strong, our ability to predict WD moisture from rainfall was not. This may have implications for predictions of WD decay in response to climate change. Due to the exponential response of WD decay to temperature, even small temperature increases would increase WD CO_2 release rates in aggregate. We also note that at higher temperatures, the range of variation also increases (Fig. S1). Even at higher temperature, there would continue to be WD pieces decaying slowly, and ecological implications of that remain unknown.

Predictions of WD CO_2 release rates from measured temperature varied widely among groups (Table 4). Predictions for LX, were consistently strong for the 3 decay classes, for SN all were weaker, and those for LC were variable. All WD pieces were in the same surface-soil transect under very similar environmental conditions. We estimated annual C loss as CO_2 from each WD group with these models, and also by averaging the six measurements through time.

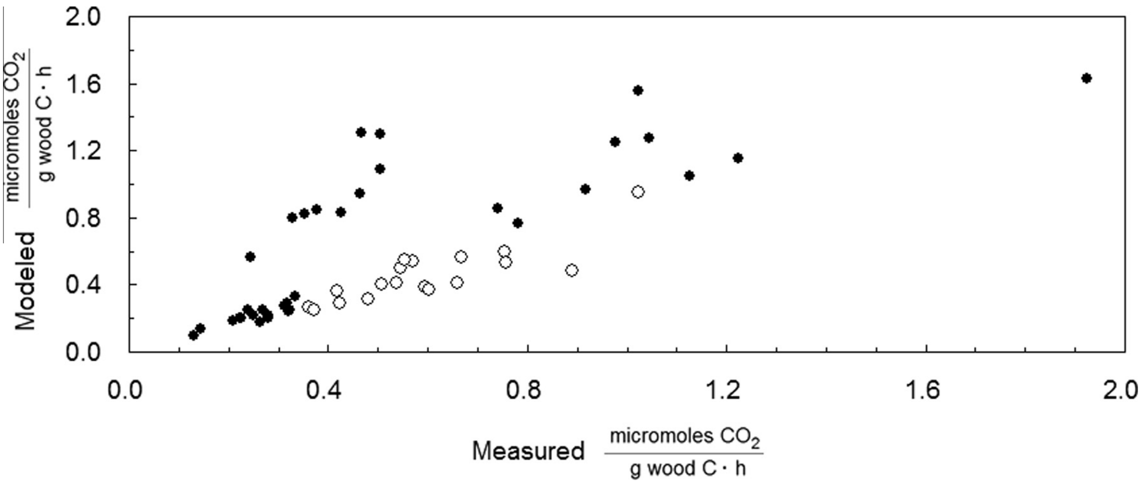

Fig. 3. Modeled CO_2 release rates compared to corresponding measured values for wood-debris groups (three wood species each with three decay classes) at Ailao Mountain, China. Models are based on previous daily air temperatures and average CO_2 release rates of the wood-debris group (see text). Open circles are September/October measurements, and filled circles represent all other measurements.

Table 5
Annual C loss as CO_2 from 9 species and DKC groups caused a loss of wood density. This loss was expressed as time spent in each decay class (DKC), and the time required for total decay. The wood species are *Lithocarpus chintungensis* (LC), *Lithocarpus xylocarpus* (LX), and *Schima noronhae* (SN). Annual C loss is (A) daily air T–> daily wood T–> daily CO_2 loss, summed per year, and (B) average CO_2 loss for each group during the 6 CO_2 measurement periods. Parts A and B also include K, the exponential decay constant, calculated as $K = -\text{LN}(1\text{-fraction of C lost per year})$.

	LC1	LC2	LC3	LX1	LX2	LX3	SN1	SN2	SN3
Wood properties									
Avg. piece C (g)	175	147	158	231	151	138	133	111	135
Avg. piece density (g L^{-1})	0.538	0.453	0.377	0.580	0.461	0.445	0.465	0.447	0.435
A. Based on T model									
C loss (g $year^{-1}$)	13.3	13.4	15.8	14.8	13.6	18.2	8.3	10.1	9.4
Decay rate (K $year^{-1}$)	0.079	0.097	0.105	0.066	0.094	0.140	0.064	0.095	0.073
Fraction C lost ($year^{-1}$)	0.076	0.092	0.100	0.064	0.090	0.131	0.062	0.091	0.070
Frac. loss for 1–>2 and 2–>3	0.158	0.169		0.205	0.036		0.038	0.028	
Years in DKC	2.1	1.8	10.0	3.2	0.4	7.6	0.6	0.3	14.4
Total years to decay			**13.9**			**11.2**			**15.3**
B. Based on average meas. rates									
C loss (g $year^{-1}$)	9.7	11.1	10.3	9.9	9.0	11.4	6.1	7.8	6.7
Decay rate (K $year^{-1}$)	0.057	0.080	0.068	0.044	0.062	0.090	0.048	0.077	0.052
Fraction C lost ($year^{-1}$)	0.056	0.076	0.065	0.043	0.059	0.082	0.046	0.070	0.050
Frac. loss for 1–>2 and 2–>3	0.158	0.169		0.205	0.036		0.038	0.028	
Years in DKC	2.8	2.2	15.3	4.8	0.6	12.2	0.8	0.4	20.1
Total years to decay			**20.3**			**17.6**			**21.3**

Table 6
Ailao Mountain WD decay ANCOVA based on CO_2 release rates with wood species and decay classes as factors and with WD temperature, moisture, and density as covariates. The CO_2 release rates were LN-transformed. Significance levels: $^{***}P < 0.001$; $^{**}P < 0.01$, $^{*}P < 0.05$.

	DF	SS	F	P
Species	2	9.56	6.47	0.0016^{**}
DKC	2	47.76	32.32	$<0.001^{***}$
Moisture	1	867.01	1173.23	$<0.001^{***}$
Temperature	1	83.08	112.42	$<0.001^{***}$
Density	1	3.49	4.73	0.0299^{*}
Species*DKC	4	10.95	3.71	0.0052^{**}
Species*Moisture	2	2.83	1.92	0.1472
DKC*Moisture	2	0.71	0.4806	0.6185
Species*Temperature	2	3.20	2.17	0.1149
Moisture*Temperature	1	5.89	7.98	0.0048^{**}
Moisture*Density	1	3.66	4.95	0.0262^{*}
Species*DKC*Moisture	4	21.60	7.31	$<0.001^{***}$
Residuals	1806	1334.62		

The modeled C losses were about 1/3 higher than the average losses. Our WD samples retained their general structure and some bark into DKC3, although some DKC3 samples were quite fragile.

We suggest that WD decay-class transitions here are primarily driven by density loss. With carbon representing a constant fraction of weight, time spent in each decay class was controlled by accumulated CO_2–C release. Little WD density was lost in DKC1 and DKC2, so we suggest that those decay-class transitions were relatively rapid; from 0.3 to 4.8 years. Our estimates of time spent in DKC3 ranged from 7.6 to 20 years, but that would be reduced by late-stage WD fragmentation. Our CO_2 measurements showed that some of our WD groups decayed slowly compared to WD in other subtropical forests. However, temperature at our site was comparatively low, because of high elevation, which appeared to be more important than the relatively small sizes of WD we studied.

If WD persists longest in DKC3, it follows that the largest WD pools would be in this decay class. We are not aware of previous studies suggesting this, even though it could be readily tested, and is important for forest biota depending on WD. Earlier modeling studies suggested that WD in intermediate decay classes dominate forest pools (e.g., Aakala, 2010; Kruys et al., 2002; Russell et al., 2013; Vanderwel et al., 2006; Woodall et al., 2012). Those seven modeling studies divided WD into more than three decay classes, so our observations are not strictly comparable.

4.3. Variability in WD decomposition rates

From more than 1800 measurements of CO_2 release from 320 WD samples, we found support for earlier studies suggesting that half or less of the variation could be explained by environmental factors (Boddy et al., 1989; Bond-Lamberty et al., 2003; Chambers et al., 2000, 2001; Hérault et al., 2010; Jomura et al., 2007, 2008; Liu et al., 2006; Mackensen and Bauhus, 2003; Progar et al., 2000; Wang et al., 2002; Wu et al., 2010; Yoneda, 1980; Zell et al., 2009).

For individual WD pieces, several factors (wood species, decay class, moisture and temperature) were statistically significant predictors of CO_2 release rates (Table 6). Temperature and moisture positively co-varied at our site (Fig. 1), so the variance explained by T and moisture together (R^2 from 0.246 to 0.567, Supplementary Table 3) was not much improved over models based on temperature (R^2 from 0.072 to 0.353, Supplementary Table 1) or moisture (R^2 from 0.164 to 0.353, Supplementary Table 2) alone. Predictive values of temperature and moisture together might be higher in summer-dry forest climates. In this study, relationships between WD CO_2 release rates and temperature were exponential (Supplementary Table 1), and they were linear with respect to WD moisture (Supplementary Table 2). For both, individual WD pieces had substantial variation unexplained by environmental factors. That variation had three distinct components. First, individual WD pieces of the same species and decay classes showed 4-to-18-fold differences in average CO_2 release rates under the same field conditions (Table 5; Supplementary Fig. 3). Community interactions among fungal decomposers may transcend environmental factors. Aggressive interactions among WD microbes are common (e.g., Boddy, 2000; de Boer et al., 2010; Folman et al., 2008; Foster and Bell, 2012; Heilmann-Clausen and Boddy, 2005; Moita et al., 2005; Susi et al., 2011; Verma et al., 2007). Laboratory incubations indicate that the initial heterotrophic community, composed of common and early successional fungal species may influence respiration rates (Progar et al., 2000). Artificial fungal communities constructed in WD suggest that species richness is negatively related to CO_2 release rates (Fukami et al., 2010; Peay et al., 2013; Toljander et al., 2006), but see variable results from Lindner et al. (2011). Studies of fungal sporocarps on natural WD also suggest that higher diversity is linked to slower decay (Schmit, 2005). It would be interesting to apply techniques of modern microbial genetics to studies of WD decay with natural fungal communities.

Some WD decay studies place pieces in close proximity (e.g., Cornelissen et al., 2012). That approach could alter outcomes of fungal-community interactions because of hyphal in-growth from nearby fungi (Watkinson et al., 2006). Random wood-falls cause WD in forests to be widely dispersed, and their natural fungal communities may be more diverse than those developing in plots where WD pieces are artificially closely arrayed. We suggest that adjacent WD pieces may develop similar fungal communities because of hyphal ingrowth, and that such communities may respond more consistently to environmental-factor variations.

The second aspect of variability was related to WD decay late in the warm/wet season. Seasonal slowing in both years (Supplementary Fig. 5) was apparently unrelated to environmental factors. We hypothesize that fungal growth early in the warm/wet season led to more aggressive interactions later. Seasonal allocations of resources of wood-decomposing fungi towards decomposition enzymes or chemical aggression also remain to be explored.

The third aspect of variability derived from the fact that some WD pieces were consistent within their wood species and DKC group (whether slow, intermediate or fast), while others were much more variable through time. To assess this we used logarithmic response ratios (Supplementary Fig. 3). High piece-wise variability through time is distinct from the other two patterns described above. This further challenges our ability to predict WD decay rates at various spatial scales.

5. Conclusions

Throughout ecology, studies of variability are rare compared to those on mean effects (Benedetti-Cecchi, 2003). This is also the case in WD-decay studies, where regression relationships between apparent causal factors and decay rates are the typical focus. However, variability in WD decay has different aspects. This limits our ability to predict responses to climatic changes such as temperature, and presumably to other environmental factors following land-use changes. In forests, different ecological functions of WD (biogeochemical, habitat, nurse logs, etc.) occur throughout the decay process, but they may vary qualitatively and quantitatively among decay classes. Pieces of WD decaying at different rates spend different lengths of times in early, middle, and late decay classes, and ecological consequences of such patterns have yet to be addressed. Finally, in all forests, we are challenged to explore whether fungal-decomposer community interactions can explain the high variability of WD decay.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2013.09.013.

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