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Coarse woody decay rates vary by physical position in tropical seasonal rainforests of SW China

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ABSTRACT

Decomposition of woody detritus is an important but often ignored process in forest ecosystems. Moisture and temperature regimes are dominant controls over woody decay, contributing to significant variability at local, regional, and global scales. Our focus was on local variability in woody decay rates depending on their physical position. Woody detritus may decay on the forest floor, aboveground, or combination of both, depending on the mortality agent. In this study, we measured decay rates of logs, large branches on the forest floor, and snags over a three-year period. We also collected monthly respiration estimates, and analyzed woody detritus N and P content throughout the study. Logs exhibited the greatest mass loss with a decay-rate constant of $k = 0.606 \pm 0.020$, followed by large branches ($k = 0.316 \pm 0.012$) and snags ($k = 0.268 \pm 0.008$). Heterotrophic respiration was greatest prior to the peak of rainy season, and was greatest for snag material during the first two years of sampling, probably a result of water saturation in ground material. Both N and P were released in all materials, but the rate of P release was much slower in snags. There were large differences of P concentration and C:P among the materials, but their value became similar after three years, indicating P limitation on microbial activities. Our results presented robust evidence for the physical-position-dependence of coarse woody detritus decomposition in the forests.

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1. Introduction

Coarse woody detritus (CWD) is a critical component of forested ecosystems where it provides a multitude of ecosystem services. These include structural habitat for multiple vertebrate and invertebrate species (Bull et al., 1997), the primary energy source for saprophyte communities (Nordén et al., 2004), and significant contributions to long-term soil development (Tinker and Knight, 2000; Triska and Cromack, 1980). Input and loss rates of woody detritus also have implications on several ecosystem processes, including nutrient cycling and carbon dynamics (Harmon et al., 1986). Despite having relatively low concentrations of nutrients, woody detritus acts as a long-term nutrient pool with a temporal lag in nutrient release relative to more labile material (Laiho et al., 2004). Woody detritus also contributes significantly to long-term carbon storage as the largest detritus pool in forests, with implications on total carbon stores and ecosystem carbon balance (Freschet et al., 2012).

Carbon fluxes from decaying wood remain one of the largest uncertainties in biogeochemical models (Chambers et al., 2000). Part of this uncertainty can be attributed to the difficulty in quantifying the cause and extent of woody detritus inputs under various environmental conditions or disturbance events (van Mantgem et al., 2011; McDowell et al., 2015). This may be especially difficult since inputs can occur in various physical positions within forests. For example, natural disturbances such as pathogens, insects, wildfires, hurricanes and drought typically produce standing dead trees (snags) with minimal ground contact and increased exposure to solar radiation and drying wind (Harmon, 1982). In contrast, windthrow, ice damage, landslides and logging produce dead stems and branches immediately in contact with the forest floor (Whigham et al., 1991). Most woody detritus research has focused on reducing this uncertainty by quantifying input rates and stocks in various forests under different management and disturbance regimes, but relatively few have estimated decay or flux rates for this

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material which is necessary for quantifying net ecosystem carbon balance with biogeochemical models (Keller et al., 2004; Rice et al., 2004; Palace et al., 2007; Yoneda et al., 1990).

Woody detritus decomposition and nutrient dynamics, as well as factors contributing to variation in these processes, also remain uncertain in many forested ecosystems. Temperature and moisture regimes are regarded as the dominant controlling factors (Harmon et al., 1986; Chambers et al., 2000; Wang et al., 2002). Warm, moist conditions indicative of rainforest environments promote rapid decay (Chapin et al., 2002), while freezing temperatures inhibit decomposer activity by slowing metabolic processes and saturation creates anaerobic environments that suppress decomposition (Progar and Schowalter, 2000). These factors likely contributed to observed variation in woody decay rates by their physical position, where standing or elevated material decayed slower than materials decomposing on the ground in temperate and boreal coniferous forests (Yatskov et al., 2003; Dunn and Bailey, 2012). This trend has also been observed in temperate deciduous forests where the half-life of snags were 11.2 years, compared to 6.3 years for logs (Onega and Eickmeier, 1991). Resource accessibility by wood-degrading fungi has also been found to further influences woody decay rates by their physical position (Boddy, 2001). The magnitude of these observed differences suggests carbon fluxes and nutrient cycling rates may be lagged when woody detritus is inputted as elevated material, contributing to the long-term immobilization of nutrients (Laiho and Prescott, 1999). Additionally, initial concentrations of N and P have been correlated with both litter and woody decay rates (Laiho et al., 2004; Parton et al. 2007). Obtaining estimates for standing and surface decay rates, as well as the influence of variation in nutrient concentrations, are needed to more accurately model these ecosystem processes and to determine whether or not elevated material embodied a different pathway of decay and nutrient cycling than surface material.

In this study, we were interested in characterizing the contribution of woody detritus to carbon fluxes and nutrient cycling in tropical seasonal rainforests of southwest China. Tropical seasonal rainforests have an obvious transition between dry and wet seasons, so we hypothesized that lower water availability during the dry season would result in variation in decay rates of woody detritus depending on their physical position. Additionally, since phosphorus (P) is considered a limiting factor for productivity in tropical forests, we also hypothesized that P or the C:P ratio would be closely correlated with the decay rates of this material. Therefore, we studied decomposition of three types of woody detritus in their original decay position to capture the contribution of these factors (position they were originally input into the system). Heterotrophic respiration rate, mass loss, and nutrient dynamics were measured for three years from 2006 to 2008 for woody material from logs and large branches on the ground, as well as standing snags. This study represents the initial investigation of decay dynamics for woody detritus in this forest type.

2. Method

2.1. Experimental site

This study was conducted at a long-term research site at the Tropical Rainforest Ecosystem Station of the Chinese Academy of Sciences in Xishuangbanna, Yunnan Province, China (21°55′39″N, 101°15′55″E). The climatic conditions of this forest are typical of monsoonal conditions. The 40-year mean annual temperature was 21.7 °C (minimum of 15.9 °C and maximum of 25.7 °C) and a mean annual precipitation was 1539 mm. On average, 87% of precipitation occurs during the rainy season from May to October. Latosol soils are dominant at this research site and have an average pH around 5.

The dominant vegetation type is that of tropical seasonal dry rainforests, which differs from lowland tropical rainforests because of a consistent annual dry season. This vegetation type contains a mixture of evergreen and deciduous trees and deciduous trees do not senesce leaves at the same time so canopy cover remains intact throughout the year. The forest canopy can be divided into three sublayers. The dominant overstory layer ranges from approximately 35–40 m in height and is typically comprised of *Pometia tomentosa*, *Terminnalia myriocarpa,* and *Garuga florobunda var. gamblai*. The mid-canopy layer ranges from 15 to 30 m and typically consists of *Barringtonia macrostachya*, *Chisocheton siamensis*, *Gironniera subaequalis,* and *Beilschmeidia brachythyrsa*. The subordinate layer ranges from 3 to 10 m and is typically comprised of *Millettia laptobotrya*, *Garcinia cowa*, *Drypetes indica*, *Myristica yunnanensis* and *Mezzettiopsis creaghii*.

2.2. Experimental design

We sampled woody material from fallen trees, fallen large branches and snags to test the effects of physical position and nutrient concentrations on decay rates. We obtained each material type with end diameters between 8 and 10 cm during a biomass survey of this tropical seasonal rainforest (Lü et al., 2010) from three 1 ha plots. The materials are a mixture of different tree species in those three plots and represented the major tree species. Only newly formed, lightly decayed materials were selected and brought back to our lab for further processing. These were identified based on physical and visual characteristics that included evidence of insect use, presence of saprotrophic fungi, attached bark and twigs, and friable sapwood or heartwood. The materials were cut into 20 cm segments, weighted freshly, and stored at room temperature before deployment. Five samples of each type of materials were oven dried at 80 °C for 48 h to obtain the water content (% Water of Wet weight). The initial dry mass of all materials was then calculated using their fresh weight and the average water content of the five oven-dried samples.

Five fresh pieces of fallen tree, large branch, and snag material were combined as a sample and deployed at our field site. Fallen tree and large branch material were put in litter bags with 1 mm mesh to exclude wood consuming insects. Snag material was tied together with nylon rope for hanging to simulate standing conditions. A total of 60 replicates were made for each type of material. We utilized a slope adjacent to a CO_2 flux tower so our estimates could be correlated with environmental measurements (i.e., soil temperature, soil moisture, air temperature) and to allow future integration of our findings into net ecosystem carbon balance research and modeling. Five transects perpendicular to the slope, 10 m apart from each other, were stratified from the bottom to top of the slope. The starting location of each transect was randomly located. Twelve litter bags containing log and large branch material were placed on the ground along each transect about 5 m apart in January 2006. Snag material was hung on a tree nearby each litter bag sample 1.5 m above ground.

Our initial estimates for all components of this research were conducted in January 2006 when the woody material was first collected. We visited the field site every three months for sampling, beginning in April 2006, for a period of three years. One bag of each material was randomly selected for sampling from each transect, for a total of five samples during each visit. Each sample was first collected to estimate respiration rate using the dynamic, closed-chamber method. A 22 L plastic bucket was used as the dynamic chamber. The bucket was sealed and two rubber tubes were connected to a Li-cor 820 infra-red CO_2 analyzer (Li-cor, USA). After the CO_2 concentration stabilized, we recorded these concentrations

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