Initial white rot type dominance of wood decomposition and its functional consequences in a regenerating tropical dry forest

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ABSTRACT

Efforts to model woody debris dynamics are limited by our empirical understanding of the patterns and drivers of decomposition. This knowledge gap is significant in tropical forests, particularly in the dry tropics where research has been minimal and where forest regeneration is a management priority. Here, we coupled trait-function relationships in decomposing logs with indices of microbial and insect activity in a regenerating Costa Rican dry forest. We cut and placed logs (~18 cm dia) of eight tree species in ground contact at two sites. We assessed density loss and element dynamics in sapwood and heartwood twice annually over two years. At time 0 and year 2, we measured lignin, nitrogen, structural carbohydrates, extractives, insect galleries, and two residue 'signatures' of fungal rot type: dilute alkali solubility (DAS; higher for brown rot) and lignin:glucan loss (higher for white rot). After two years, sapwood mean density losses ranged from 11.6 to 44.4% among tree species (excluding one thoroughly-degraded species). The best predictor of sapwood density loss was initial pH, but this correlation was negative, contrasting positive correlations proposed for temperate forests. Mean heartwood density losses were consistently less than those in sapwood, and although heartwood extractives contents were as high as 16.4%, trait correlations were insignificant. Insect galleries contributed little to density loss (<3%), and DAS and lignin loss patterns indicated dominance by white rot fungi. This was often matched by dense fungal zone line patterns (spalting), outlining many small territories. Perhaps as a consequence, element patterns were spatially variable, with overall trends roughly similar to those from temperate studies (e.g., Ca gain, P, K loss). Estimated CO_2 fluxes from logs ranged from ~25 to 75% percent of annual fluxes from litter fall. This collectively implies an important role for wood decomposition in dry forest carbon cycling, and in our case, it shows an interesting pattern suggesting high decomposer spatial complexity but low functional diversity.

1. Introduction

As a forest regenerates, coarse woody debris stocks (CWD, diameter >10 cm) can take over a century to equilibrate as woody inputs gradually increase and exceed outputs from decomposition (Harmon et al., 1986, 1993). Given the slow change in the woody litter fraction over time, understanding CWD dynamics is challenging using short-term projects, and wood has historically been underrepresented in carbon inventories (Matthews, 1997; Woodall et al., 2009). Nearly 50% of wood is carbon (dry wt%; Harmon et al., 2013), and wood comprises the majority of carbon in living biomass on Earth (Woodwell et al., 1978). For these reasons, efforts to link woody inputs and traits to decomposition and CO_2 outputs have increased recently (Trofymow et al., 2002; Cornwell et al., 2009; Weedon et al., 2009; van Geffen et al., 2010; Freschet et al., 2012).

Modeling mass loss and CO_2 evolution from wood pools presents challenges distinct from other litter types such as fine roots or leaves in which decomposition has been commonly quantified in short-term field studies using litterbags. Durability of wood (secondary xylem) can vary depending on its age and stem position (Zabel and Morrell, 1992). Heartwood durability in deadwood usually exceeds that of sapwood, attributable not only to traits such

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as density, the ratio of carbon to nitrogen (C/N), and lignin/N, but also to the presence of antibiotic compounds within solvent-extractables ('extractives') produced by the tree (Harmon et al., 1986; Wang and DeGroot, 1996). Decomposition also slows with decreasing surface area/volume, a standard consideration when testing lumber (ASTM, 2007) that has confounded trait-based CWD studies in the field (van Geffen et al., 2010). Finally, the number of fungal colonizers per wood volume decreases with increasing CWD diameter (Heilmann-Clausen and Christensen, 2004), as fungi create defensive pseudosclerotial plates along the mycelial perimeter known as 'spalting' (Pearce, 1990). This opportunity to defend wood volume favors priority effects among colonizers (Boddy, 2000; Fukami et al., 2010) including the earliest infections of standing trees as endophytes (Boddy, 2001; Parfitt et al., 2010; Rodríguez et al., 2011). Because decomposers employ functionally distinct mechanisms to deconstruct wood (Eriksson et al., 1990; Riley et al., 2014), the community structure among wood colonizers can significantly alter the overall decomposition rate (Fukami et al., 2010; Dickie et al., 2012; Song et al., 2012; van der Wal et al., 2015).

In addition to the contribution of CWD to global carbon cycles, deadwood also has multiple ecological roles within forests, including serving as habitat for cavity nesting birds, as 'nurse' logs for tree seedlings, and as a resource for wood-boring arthropods (Franklin et al., 1987). At the local scale, CWD dynamics and decomposition processes vary both qualitatively and quantitatively as a function of decomposer groups and local processes (Franklin et al., 1987; Bradford et al., 2014; van der Wal et al., 2015). Wood-degrading fungi, for example, may cause white rot (extensive lignin removed with carbohydrates) while others cause brown rot (modest lignin removal) (Eriksson et al., 1990), and these rot types vary along a spectrum of lignin selectivity as decomposition proceeds (Worrall et al., 1997; Riley et al., 2014). Decomposer nutritional modes affect CO_2 evolution and organic inputs to the soil (Berg and McClaugherty, 2008), as well as carbon content, metal-binding, redox, permeability, and sorption in resulting residues (Rypáček and Rypáčková, 1975; Gilbertson, 1980; Jurgensen et al., 1997; Filley et al., 2002; Song et al., 2012; Harmon et al., 2013). Fungal mycelial networks further connect above- with below-ground pools and create an avenue for element translocation into and out of deadwood (Ostrofsky et al., 1997; Boddy, 1999; Connolly et al., 1999; Liew and Schilling, 2012). This capacity for a rotting log to be an element sink, as well as an element source, will affect its suitability as a nurse log (Harmon and Franklin, 1989) and its ability to buffer stands against element losses through leaching, etc., thus contributing to overall forest health (e.g., exchangeable Ca, Shortle and Smith, 1988; Shortle et al., 2012). These locally-relevant, site-specific effects thus have the potential to influence stand regeneration and composition, and should be considered in forest management decisions.

In either of these global or local contexts for downed wood, our knowledge has been generated largely from research in temperate rather than tropical forests, with notable paucity in tropical dry forests (Harmon et al., 1995; Torres and González, 2005; Eaton and Lawrence, 2006). This knowledge gap is unfortunate for several reasons. 1) Nearly half of the forests on Earth are in tropical regions, and 42% of these are dry forests (Brown and Lugo, 1982; Murphy and Lugo, 1986). 2) Simple climate indices developed to predict lumber durability in temperate areas (e.g., Scheffer, 1971) are less reliable for wood on the forest floor (Bradford et al., 2014) and are unproven in the dry tropics. Extended dry periods may, for example, leave a legacy within the wood microbial community that affects dynamics upon rewetting, similar to the effect of drought on soil microbial respiration (Birch, 1964). 3) Wood decomposition, long underrepresented in ecosystem simulation models (Cornwell

et al., 2009), has been identified as a key uncertainty for prioritization in modeling efforts (Keenan et al., 2013). This uncertainty is severe in the dry tropics, where agriculture has left a legacy of regenerating forests (Murphy and Lugo, 1986). 4) Many dry forests regenerating following abandonment of pasture are now beginning to accrue CWD, but it is unclear how and if this process could be managed to optimize restoration and maximize ecosystem services (Kissing and Powers, 2010).

In this study, we wanted to measure multiple functional outcomes for CWD decomposition (density loss and element accumulation) in a tropical dry forest system and then link these patterns both to wood traits and to the collective 'signatures' left behind in wood residues by dominant decomposers. To do this, we deployed logs from eight common tree species at two regenerating tropical dry forest sites lacking significant CWD stocks. We quantified wood functional traits, element concentrations, and chemical indices indicative of decomposer type, both in initial samples and after two years of decomposition. Our goal was to observe how traits such as wood tissue type (sap- vs heartwood) would affect the dominant rot type and how this community structuring would influence density loss and the accumulation of elements from soil into the wood. CWD decomposition studies are typically done opportunistically using either chronosequences of logs from trees that died at different times or in single disturbance events. Our study is one of the first in the tropics to use an experimental approach where tree species were selected for their traits and then decomposed in a common garden. This allowed us to standardize log size and climatic conditions and to track these relationships between wood traits, decomposers, and ecologically-relevant consequences within logs as well as among them.

2. Methods

2.1. Study sites

This study was conducted in the Sector Santa Rosa of the Área de Conservación Guanacaste in northwestern Costa Rica (10°51′ N, 85°37′W). Annual rainfall from 1980 to 2010 averaged 1697 mm with a 5−6 month dry season (Becknell and Powers, 2014). The predominant vegetation in Santa Rosa is secondary tropical dry forest regenerating after prior land use of grazing or cropping, and forests contain diverse mixtures of species that vary in leaf habit (e.g. evergreen, deciduous, semi-deciduous) and soil characteristics (Powers et al., 2009). Deadwood stocks tend to increase monotonically with age of regenerating forest patches after ~20 years, suggesting that CWD was not present during prior land use of grazing and/or cropping (Kissing and Powers, 2010). Our decomposition experiment was located in two sites roughly 8 km apart. One of the sites (Santa Elena) was located on nutrient poor soils that support a predominately evergreen tree canopy including the oak species *Quercus oleoides*. The other site (Santa Rosa) was situated on richer soils that support a more diverse forest (Powers et al., 2009).

2.2. Wood species

Eight common tree species were selected to represent a range of initial wood characteristics, leaf traits, life history traits, and cultural uses (e.g., timber, handicrafts, and/or living fences) (Table 1). As trees from the family Fabaceae are abundant in these forests (Powers et al., 2009) and have particularly dense wood (Powers and Tiffin, 2010), we selected four legume species: *Acosmium panamensis* (now also known as *Leptolobium panamense* (Benth.) Sch. Rodr. & A.M.G. Azevedo), *Dalbergia retusa*, *Gliricidia sepium*, and *Hymenaea courbaril*. The other species came from different families