Oecologia (2018) 188:1209–1226
https://doi.org/10.1007/s00442-018-4283-3

ECOSYSTEM ECOLOGY – ORIGINAL RESEARCH

Indirect effects of bark beetle-generated dead wood on biogeochemical and decomposition processes in a pine forest

Courtney M. Siegert[1] · Natalie A. Clay[2] · Juliet D. Tang[3] · Lisa G. Garrigues[1] · John J. Riggins[4]

Received: 12 January 2018 / Accepted: 21 October 2018 / Published online: 26 October 2018

Abstract

Bark beetle outbreaks are increasing in frequency and intensity, generating massive inventories of dead trees globally. During attacks, trees are pre-inoculated with ophiostomatoid fungi via bark beetles, which has been shown to increase termite presence and feeding. These events may, in turn, alter biogeochemical cycles during decomposition. We examined these relationships by experimentally inoculating dead wood with bluestain fungi in a temperate pine forest. Across ten replicate plots, eight 0.5 m-long logs were inoculated with *Ophiostoma minus* and eight with distilled water. Half of the logs from each inoculation treatment were covered from above with a mesh cage barrier to exclude aboveground beetles while permitting access by belowground decomposers. After 1 year, significant increases in mass (34%) and decreases in moisture content (− 17%) were observed across all treatments, but no consistent changes in density were evident. C concentrations were 12% greater in bark when barriers were present and 17% greater in sapwood when barriers and inoculation fungi were absent. N concentrations were 16% greater in bark for fungal-inoculated logs and 27% greater when barriers were present. C:N ratios in A horizon soils under fungal-inoculated logs were 12% greater. Furthermore, termites were present fourfold more in fungal-inoculated logs than controls and the presence of termites was associated with 6% less C in sapwood and 11% more N in both sapwood and heartwood. Together these results suggest dead wood generated via bark beetle attacks has different biogeochemical responses during initial decomposition phases, which could have implications for the C status in forests following bark beetle outbreaks.

Keywords Dead wood · Termites · Bark beetles · Decomposition · Biogeochemistry

Introduction

Nutrient dynamics in forest ecosystems govern above- and belowground processes (Wardle 2002). Sources of carbon (C) and nitrogen (N) include hydrological inputs from rain and canopy throughfall, from leaf fall, and from internal storage reservoirs released during the decomposition of dead wood. These inputs provide dynamic and long-term sources of nutrients that stimulate belowground organisms and increase mineralization in soils (Le Mellec et al. 2010; Johnson et al. 2014). Within forests, dead wood accounts for approximately 8% of total global carbon stocks (Pan et al. 2011) and serves as a long-term source of other essential nutrients like N and habitat for vertebrates and invertebrates (Laiho and Prescott 2004). Yet few studies investigate the prominent role of dead wood in nutrient cycles of forest ecosystems and even fewer in highly productive regions like the southeastern US.

Communicated by Hakan Wallander.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00442-018-4283-3) contains supplementary material, which is available to authorized users.

✉ Courtney M. Siegert
courtney.siegert@msstate.edu

[1] Department of Forestry, Forest and Wildlife Research Center, Mississippi State University, Starkville, MS, USA

[2] School of Biological Sciences, Louisiana Tech University, Ruston, LA, USA

[3] USDA Forest Service, Forest Products Laboratory, Starkville, MS, USA

[4] Department of Biochemistry, Molecular Biology, Entomology, and Plant Pathology, Mississippi State University, Starkville, MS, USA

Healthy forest ecosystems are modest C sinks in temperate latitudes (Bonan 2008), but large inputs of dead wood following disturbance events such as tornadoes, hurricanes, ice storms, and in the context of this study, insect infestations are key drivers in forest C dynamics. For example, common landscape-scale disturbances significantly increase the contribution of dead wood up to 103 Mg ha^{-1} $year^{-1}$ (Harmon et al. 1986; Kurz et al. 2008). Bark beetle activity can generate large pulses of dead wood by killing trees in aggregated areas during outbreaks or small and steady inputs of dead wood through constant, dispersed, low-level tree mortality (Coulson and Klepzig 2011). There are approximately 7000 species of bark and ambrosia beetles (Order Coleoptera: Family Curculionidae: Subfamily Scolytinae) worldwide (Bright 2014). Bark beetles in particular are important disturbance agents of global coniferous forests and can shift forest ecosystems into carbon sources (Kurz et al. 2008).

During attack of host conifers, bark beetles and associated phoretic mites vector ascomycetes in the family Ophiostomataceae (bluestain fungi) that infect the sapwood of trees and stain it a dark blue to black color, from which the common name 'bluestain' fungi is derived (Wingfield et al. 1993; Coulson and Klepzig 2011). Bluestain fungi do not directly contribute to wood decomposition, but their presence can influence the rate at which subterranean termites recruit to and subsequently decompose wood (Little et al. 2012a, b, 2013; Riggins et al. 2014; Clay et al. 2017). Bluestain fungi colonize the sapwood and can penetrate medullary rays and ray parenchyma cells and resin duct epithelium in late stages of tree infection, where they metabolize resin sugars and lipids (Robinson 1962; Ballard et al. 1984; Wingfield et al. 1993). If dead wood infected with bluestain fungi is preferred by decomposers like termites, this is likely to impact wood decomposition and nutrient cycling processes.

Decomposition is a biotic process, but little is understood about how the presence, turnover, and interactions among saproxylic organisms impact rates of decomposition. Ambient climatic conditions, such as temperature and moisture (Chambers et al. 2000), strongly influence woody decomposition rates, but substantial variability, up to 70%, remains unexplained (Bradford et al. 2014). This variation is frequently attributed post hoc to biotic effects such as termite activity, because they are the primary invertebrate wood decomposers in forests between 50°S and 50°N latitude and are known to account for as much as 2% of global C efflux from terrestrial systems (Sugimoto et al. 2000). Increased understanding of both the abiotic and biotic drivers of woody decomposition and their impacts on forest nutrient dynamics will facilitate better predictions of C fate as global climate change alters the frequency and intensity of ecosystem disturbances. Although direct measurements of C flux by termites are rare, increases in their relative density are negatively correlated with the maximum amount of standing dead wood (e.g., snags) in forest ecosystems (Maynard et al. 2015).

Nutrient fluxes in dead wood may also be constrained by rates of canopy-derived inputs. Throughfall and stemflow are important components of water cycling in forest environments (Levia and Frost 2006) that mediate nutrient and moisture inputs to soils and can directly impact heterotroph communities and their activity in deadwood (Lovett and Lindberg 1984; Progar et al. 2000; Pryor and Barthelmie 2005; André et al. 2008). However, these canopy fluxes are dynamic processes that vary throughout the year, and on a single event basis. Within stand redistribution of water can vary across small spatial scales (Siegert et al. 2016) and the redistribution of nutrients by the forest canopy has been shown to alter the spatial distribution of soil microbial communities (Moore et al. 2016). What remains unknown are the impacts of canopy hydrological processes on dead wood decomposition (Wardle 2002). Subsequently, understanding how nutrient inputs like dead wood deposition following bark beetle attacks (and the presence of beetle-vectored bluestain fungi) interacts with canopy-derived inputs to impact soils is essential to understanding the processes underlying forest dynamics.

Furthermore, the decomposition of dead wood can have significant impacts on soil properties in forests by changing soil moisture and nutrient regimes (Hicke et al. 2012). Accelerated decomposition from early recruit of termites via bluestain fungi in dead wood is one such impact that merits further investigation. Morehouse et al. (2008) observed no differences in soil C between control plots and those recently infested with bark beetle in a ponderosa pine forest, but observed increased nitrate in the organic layer and upper mineral soil and increased ammonium in deeper mineral soil in bark beetle forests. Changes in soil N availability were attributed to changes in needle chemistry, which were deposited to the forest floor in greater quantity following tree mortality, thus impacting soil N cycles. In other studies, N availability was lower under dead wood compared to forest floor litter (Busse 1994; Spears et al. 2003), resulting in decreased biomass N content (Hafner and Groffman 2005). As soil microbes utilize labile C from dead wood, soil N may be quickly immobilized (Magill and Aber 2000). Additionally, termite presence can influence soil nutrient dynamics, structure, and hydrology (Jouquet et al. 2011 and sources therein), but how the presence of bluestain fungi in wood following bark beetle attack impacts these dynamics remains unknown. Many of these interactions occur on both short and long time scales, but are not well characterized, and few studies take an integrated approach to examine these processes concurrently.

Understanding nutrient dynamics in forest ecosystems following disturbance like bark beetle attacks includes not

only quantifying nutrient sinks but also sources. Respiration from dead wood has largely been overlooked (Harmon et al. 2011) and can range from a small component (< 5%) of total ecosystem respiration (Liu et al. 2006; Gough et al. 2007; Tang et al. 2008) to a significantly higher proportion following disturbance (Zeng et al. 2009). However, because many temperate forest ecosystems are modest C sinks (Goodale et al. 2002; Pan et al. 2011), respiration from dead wood becomes comparatively more important (Valentini et al. 2000; Forrester et al. 2015). Fungal heterotroph communities can influence respiration and C efflux from deadwood (Progar et al. 2000) and termites may impact heterotroph communities. Bluestain fungi are speciose and found globally (Wingfield et al. 1993), usually in association with their insect vectors, bark and ambrosia beetles. As such, quantifying the relative nutrient fluxes from dead wood with and without initial bluestain fungi presence is essential to understand forest ecosystem contributions to the terrestrial C cycle. Rates of respiration likely change over time as succession occurs during dead wood decomposition although the temporal patterns these respiration changes are not well characterized (Progar et al. 2000; Goulden et al. 2011; Harmon et al. 2011).

Bark beetles can have large direct impacts on forest processes through changes in forest structure following tree death (Bearup et al. 2014). However, bark beetle activity may have significant indirect effects on forest ecosystem processes through the presence of fungal associates deposited in bark beetle-attacked trees (Progar et al. 2000), and their interactions with termites (Little et al. 2012b, 2013). Many of these interactions occur on both short and long time scales (Riggins et al. 2014; Clay et al. 2017), but are not well characterized for either scale, and few studies take an integrated approach to examine these processes concurrently. This study focuses on the potential indirect effects of bark beetle-attacked trees on wood decomposition and nutrient cycling via bluestain fungus presence and potential interactions with termites. Additionally, initial rapid changes in the first months and years following disturbances like insect outbreaks can have lasting impacts and are rarely quantified experimentally in the decomposition of dead wood (Carpenter et al. 1988; Schowalter et al. 1992a). As such, the objectives of this study were to identify the influence of termite association with bluestain fungus on C and N (1) in dead wood, (2) in soils below dead wood, and (3) in respiration from dead wood during the first year of decomposition in the humid and warm-temperate climate of Mississippi. Additionally, this study considers the spatial and temporal variability of canopy inputs. Biogeochemical changes that occur across shorter time scales are of particular interest as they relate to the rapid recruitment and changing abundance of invertebrate and microbial decomposer activity.

Materials and methods

Study site

The study was conducted in a humid, warm-temperate forest of Mississippi (33.2639°N, 88.8884°W) composed of loblolly pine and mixed hardwood species. The loblolly pine (*Pinus taeda* L.) overstory on this site was approximately 60 years in age and succession has resulted in a vigorous hardwood midstory of sweetgum (*Liquidambar styraciflua* L.), red maple (*Acer rubrum* L.), winged elm (*Ulmus alata* Michx.), and red oak species (*Quercus* spp.). The soil on this site is an urbo silt loam, with a depth to the water table of 12–14 in. and somewhat poor drainage with occasional flooding (Natural Resources Conservation Service 2015). Average 30-year mean temperatures in summer (JJA) and winter (DJF) are 26.5 °C and 6.9 °C, respectively (National Oceanic and Atmospheric Administration 2010). Total annual precipitation is 140.3 cm, which falls fairly evenly throughout the year, with the lowest rainfall occurring in September (8.6 cm) (NOAA 2010).

The experiment was designed to test for the effect of inoculation with bluestain fungi on the recruitment of termites to wood killed by bark beetles and the impact on decomposition and nutrient cycling. Two treatments were employed: an inoculation treatment and an aboveground barrier treatment. The former treatment was designed to test the effect of bluestain fungi vs. a water control and the latter treatment was designed to test the effect of subterranean termites and belowground decomposers alone vs. the suite of aboveground saproxylic invertebrates (e.g., other wood boring beetles) that can impact decomposition processes through the creation of tunnels and inoculation of additional fungi (Grove 2002). The inoculation treatments are referred to as "BS" for bluestain and "H_2O" for water. The barrier treatments are referred to as "Cage" when the aboveground cage (cage is placed only over the top of the log and not into the soil) is present and as "NoCage" when it is not. We hypothesized that termites would recruit to wood inoculated with bluestain compared to water, resulting in accelerated decomposition and nutrient exchange. Furthermore, we hypothesized that logs that did not receive cages would have accelerated decomposition over long time scales as aboveground saproxylic invertebrates can facilitate decomposers through tunneling and excreta, but short term effects would be minimal. The aboveground barrier treatment will in general inform our understanding of the role termites and belowground decomposers specifically play in decomposition when aboveground invertebrates are excluded.

To test these effects, ten 30 × 30 m replicate plots were established to monitor woody decomposition in fall 2014

(Online Resource, Fig. A). Ten visually healthy loblolly pine trees were harvested from an adjacent stand. Each tree (1 per plot) was cut into 18 log segments of 0.5 m length and sealed with wax on both ends to minimize desiccation and better approximate water loss of a whole fallen tree. Log segment diameters ranged from 16.0 to 25.4 cm depending on location along tree trunk. One log segment was immediately collected for determination of initial mass, density, moisture, and nutrient content. Additionally, one un-modified log segment was deployed in each plot as an untreated control. The untreated control logs in each plot ($n = 10$) were intended to serve as long-term, non-destructive control for baseline log and soil respiration measurements. The remaining 16 logs were randomly assigned one of four treatments including (1) inoculation with the bluestain fungus, *Ophiostoma minus* (Hedgc.) Syd. & P. Syd., the primary bluestain fungi vectored by southern pine beetle, *Dendroctonus frontalis* Zimmerman in the southeastern USA (referred to as BS + NoCage), (2) control inoculation with sterile distilled water (referred to as H_2O + NoCage), (3) inoculation with bluestain fungus and covered by a brass cloth cage (mesh size: 0.26 mm × 0.47 mm) (referred to as BS + Cage), and (4) control inoculation with distilled water and covered by a brass cloth cage (referred to as H_2O + Cage). Inoculation was performed by drilling twelve 3 mm wide × 10 mm deep holes into logs to simulate colonization by southern pine beetle (e.g., Progar et al. 2000). The drill bit was flame sterilized between each use. Bluestain treated logs received a 100-µL slurry of *O. minus* and water control logs received 100 µL deionized water (DI H_2O). Inocula were prepared from cell stock of previously identified cultures of *O. minus* from prior studies (see Little et al. 2012a, b, 2013). Reference cell stock is stored in the Forest Entomology Laboratory at Mississippi State University. Liquid cultures of mycelia were prepared as described in Little et al. (2013). Fungal slurries contained 5 g hyphae macerated in 100 mL of sterilized deionized water. The brass cloth cage excluded aboveground access to the bolt by other bark beetles, thereby preventing additional fungal inoculations (Edmonds and Eglitis 1989). Deployment of 16 logs, or four complete treatment replicates per plot, enabled four collection periods. The first year collection occurred in fall 2015 (October 22–23), the results of which are presented herein.

Canopy-derived inputs

To control for climatic variables, a meteorological station was installed in a central location beneath the forest canopy to monitor temperature, vapor pressure deficit, net radiation, and wind characteristics (speed and direction). A tipping bucket rain gauge was also installed at the station and roving canopy throughfall collectors were deployed in each of the ten plots to control for throughfall variability as a result of canopy heterogeneity. Throughfall collectors were constructed with a 23.5 cm^2 collection funnel draining into a 7.5-L carboy. During actual bark beetle outbreaks, it is likely that tree mortality alters the quantity and quality of stemflow water which is deposited to forest soils in the vicinity of dying and dead tree boles (Siegert et al. 2017b). Given that the forest canopy at our site was alive and healthy and stemflow from pines is generally less than 1% of precipitation (Silva and Rodriguez 2001; Buttle et al. 2014; Fan et al. 2015) stemflow was not considered in this study. Another manual collector and an automated tipping bucket rain gauge (HOBO RG3-M, Onset, Inc.) were placed 100 m from the study site to monitor open precipitation.

Wood decomposition: mass loss, density change, and percent moisture content

Wood decomposition was measured by comparing mass, density, and moisture content of wood samples cut from logs prior to deployment and then upon harvest. Specifically, one 2 cm-thick cross section was sliced from one end of the logs before deployment and at harvest (excluding the waxed ends). The cross sections were measured for circumference and diameter and photographed on both sides to provide visual information on wood quality and to compare subsequent fungal growth and damage from wood boring arthropods. From each cross section, we cut 6 blocks approximately 2 × 2 × 2 (8 cm^3) along the radial ends of each section: 2 from bark (outer edge of the bark until 2 cm toward center of the cross section), 2 from sapwood (approximately 2–4 cm from the inner edge of the bark toward the center of the cross section), and 2 from heartwood (including the pith). Blocks were weighed to determine field wet mass (see percent moisture content below), dried at 105 °C for 48 h until they reached constant mass, then reweighed to determine oven-dry weight, which was used to determine mass change between initial deployment and 1 year later. The change in mass was based on blocks cut from a new cross section from the same log after collection and was calculated as follows:

$$\mathrm{MLD} = \frac{m_0 - m_1}{m_0} \times 100, \quad (1)$$

where MLD is the mass loss difference as a percent, m_0 is the initial oven-dry mass at time of deployment, and m_1 is the oven-dry mass at time of harvest. For ease of interpretation throughout the manuscript, MLD values were multiplied by negative one, such that positive MLD values indicate a gain in mass and negative MLD values indicate a loss in mass from year 0 to year 1. Density change was also measured and compared to mass loss for accuracy determination of decomposition data. Mass loss data assume that all samples have

exactly the same volume, which may be a source of error. As such, density measurements take into account changes in mass over time as well as minor differences in sample wood volume. Density for each sample was calculated using oven-dried mass from above divided by volume where volume of the oven-dried block was measured in radial, tangential, and longitudinal directions using a digital micrometer. The change in density was calculated as follows:

$$\mathrm{DD} = \frac{D_0 - D_1}{D_0} \times 100, \quad (2)$$

where DD is the density difference as a percent, D_0 is the density at time of deployment, and D_1 is the density at time of harvest. Eight samples from year 1 (bark, sapwood, and heartwood) lacked comparable samples from year 0 for volumetric measurements. For missing values, year 0 averages for each tissue type were used to fill data gaps, following analysis of variance (ANOVA) which showed that wood density was significantly different by wood tissue ($P < 0.001$; bark = 0.47 g cm^{-3}, sapwood = 0.53 g cm^{-3}, heartwood = 0.41 g cm^{-3}), but not by location along tree trunk (i.e., base, middle, or top, $P = 0.078$). DD values were also multiplied by negative one, where positive DD values indicate an increase in density and negative DD values indicate a decrease in density from year 0 to year 1. Moisture content of each block was calculated as follows:

$$\mathrm{MC} = \frac{\mathrm{MC_{wet}} - \mathrm{MC_{dry}}}{\mathrm{MC_{wet}}} \times 100, \quad (3)$$

where MC is the moisture content as a percent, m_{wet} is the field wet mass, and m_{dry} is the oven-dried mass. Moisture content difference (MCD) was calculated as the difference between year 0 and year 1 MC values, where positive values indicate an increase in MC and negative values indicate a decrease in MC from year 0 to year 1.

Wood chemistry

To quantify changes in wood nutrient availability, blocks cut from logs both before deployment and at year 1 harvest were analyzed for C and N content. Oven-dried block samples were ground to particle size < 0.25 mm, and stored in air-tight containers until analysis. Wood C and N nutrient content was determined using an elemental combustion analyzer (ECS 4010 CHNS-O, Costech). One week prior to year 1 collection, randomly selected logs from each of the four treatments in each of the ten study plots (Online Resource, Fig. A) were outfitted to measure respiration following the soda lime method (for detailed methods see Keith and Wong 2006). Respiration measurements were also taken on the untreated control log in each plot following the same methods. Logs were outfitted with 15.2 cm-diameter PVC collars cut to an average height of 7.0 cm, shaped to fit snuggly to bolt curve, and sealed to the top center of the bolt with silicon caulk. Petri dishes with 11 g oven-dried (110 °C for 24 h) soda lime were inserted into each collar, sealed with a PVC lid, and left in the field for 24 h. Petri dishes were retrieved, oven dried (110 °C for 24 h), and weighed to determine change in mass due to CO_2 absorption (Keith and Wong 2006).

Soil chemistry

To quantify the movement and mineralization of C into soil organic carbon (SOC) reservoirs, paired soil samples were taken directly underneath the harvested logs and at a 0.5-m distance from each harvested log in both the A (0–5 cm) and B (5–10 cm) horizons at the time of harvest. Soil samples were also taken from a control point in each plot away from any treatment logs at both soil depths. Soil samples were air dried, ground to particle size < 0.25 mm, oven-dried (105 °C for 24 h), and stored in air-tight containers until analysis. Soil C and N nutrient content was determined using an elemental combustion analyzer (ECS 4010 CHNS-O, Costech). Respiration was also measured from soils following the same methods described above. For soils, the bottom was removed from an 18.9-L bucket and inserted 5.0 cm into the soil. These buckets were placed over soils from which first year logs were harvested from each of the four treatments. A bucket was also placed near the untreated control log in each plot to serve as a control point for soil respiration. Buckets were sealed with a lid and respiration was determined as the difference in mass change of 37 g soda lime in the sealed container over 24 h (Keith and Wong 2006).

Termite presence

To determine if subterranean termites preferentially infest bluestain-inoculated dead wood, and what changes in wood and soil chemistry were related to termite presence, all invertebrates were reared out of year 1 logs after they were collected from the field. After removing a cross section for photography and chemical analyses, an eyehook was attached to one end of the log and used to suspend it within a plastic bag connected to a container of antifreeze at the bottom. Each bag was supplied with constant airflow through a small tube, which prevented mold growth within the bag and forced emergent insects down the bag and into the antifreeze. Logs were reared for 6 months. Presence and absence of termites were then recorded for each log from the antifreeze collections. Termite quantity was not assessed in this study due to limitations with collection apparatuses. In limited instances, termites escaped from rearing bags by chewing holes in the plastic. When this occurred, bags were resealed or replaced,

but escapees confounded any ability to quantify termites in each experimental unit.

Statistical analysis

A one-way analysis of variance (ANOVA) was performed to identify significant differences in throughfall volume across all ten study plots, as well as for differences between months and seasons. Permutational multivariate analysis of variance (PERMANOVA) was used to identify differences in wood chemistry, soil chemistry, soil respiration, and wood decomposition (mass and density) in response to treatment factors of bluestain/water inoculation, the presence/absence of cages as barriers, and the interacting effects between the two factors. The analysis was run with 9999 random permutations of the data and Euclidean distance measure. All data were tested for normality (Shapiro–Wilk test) and homogeneity of variance (Bartlett's test) first. Mass difference data met the assumption of equal variance ($P = 0.317$) but did not meet the assumption of normality ($P = 0.004$). Upon further inspection of residuals, one log from plot 7 was a source of the outliers. The three data points from this log (bark, sapwood, heartwood) were omitted from the analysis, after which assumptions of normality ($P = 0.937$) and equal variance ($P = 0.436$) were met. Moisture content change data also failed to meet these assumptions (normality: $P < 0.001$, equal variance: $P < 0.001$). There were six outliers with very large percent decreases in moisture content but they were not consistent across samples or treatments and, therefore, did not justify exclusion. To analyze these samples, nonparametric Kruskal–Wallis rank sum test was used. Analyses were performed in R v. 3.3.2 using the vegan package (Oksanen et al. 2005; R Development Core Team 2007).

Logistic regression tested whether inoculation with bluestain fungi was associated with increased termite presence in dead wood. Presence or absence of termites in logs was used as the binary response variable. Caging from above should have no effect on termite colonization (Ulyshen et al. 2014) and was the case for our data ($P > 0.050$), so cage was omitted from the model that tested the null hypothesis of no difference in the presence of termites in logs based on inoculation (a categorical variable: inoculated vs. controls; $n = 20$ per treatment) of bluestain fungi. Logistic regression was also used to determine the relationship between termites and wood decomposition, wood chemistry, and soil chemistry. Presence or absence of termites in logs was used as the binary response variable and wood decomposition, wood and soil C, N, and C/N, and heterotroph respiration were used as predictor variables. All statistical analyses were performed at $\alpha = 0.05$ unless otherwise indicated. Analyses were performed in R v. 3.3.2 (Oksanen et al. 2005; R Development Core Team 2007).

Results

Canopy inputs: throughfall quantity

Total throughfall observed during the period of November 2014 through October 2015, the date of year 1 log collection, was 91.9 cm with a distinct dry period occurring in the 3 months preceding collection (Fig. 1). During the growing season (April–October), 48.4 cm of rainfall was observed, with 42.1 cm (86.9%) partitioned into throughfall, ranging from 22.7 to 50.3 cm (46.9–103.8%) across the plots. In contrast, 70.0 cm of rainfall was recorded during the growing season (November–March), of which 49.8 cm (71.1%) was partitioned into throughfall, ranging from 29.0 to 64.0 cm (41.4–91.4%) across the study plots. There were no significant differences observed across the ten plots in total throughfall volume ($F = 0.772$, $P = 0.642$) or in percent of rainfall partitioned into throughfall ($F = 1.430$, $P = 0.207$) annually or seasonally (volume: $F = 0.027$, $P = 0.870$; partitioning: $F = 3.187$, $P = 0.077$) although differences were

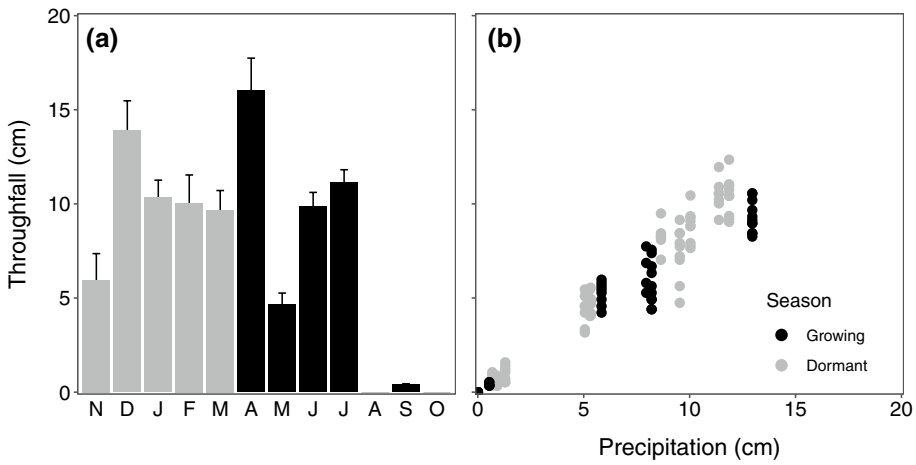

Fig. 1 **a** Monthly throughfall volumes averaged across all ten study plots with standard deviation bars and **b** relationship of throughfall as a function of rainfall magnitude for the growing and dormant seasons

observed for total throughfall volume between months (volume: $F = 3.740$, $P < 0.001$; partitioning: $F = 2.058$, $P = 0.062$). Month to month variation in throughfall flux was observed throughout the period of study, although no systematic seasonal trends were evident (Fig. 1a). All ten study plots received similar amounts of throughfall throughout the study; therefore, differences in canopy water inputs were not considered controlling factors for differences observed in decomposition rates and forest floor properties.

Wood decomposition: changes in mass, density, and percent moisture content

Bark blocks had an average initial mass of 2.47 ± 0.25 g and initial density of 0.47 ± 0.04 g cm^{-3} (mean ± standard deviation). After 1 year, bark blocks from all treatments including controls increased in mass with an average gain of 38.6 ± 21.0% ($P < 0.001$) (Fig. 2a). The 1.2% decrease in density was negligible ($P = 0.666$) (Fig. 2b). Greater mass gains were observed in logs that were pre-inoculated with fungi and/or without cage barriers (Table 1), although there were no significant differences among treatment factors (barrier: pseudo-$F = 0.133$, $P = 0.718$; inoculation: pseudo-$F = 1.430$, $P = 0.243$) or interaction between factors (inoculation × barrier: pseudo-$F = 0.937$, $P = 0.340$). Across all treatments, density of bark samples decreased on average 1.3% following 1 year of decomposition. However, density changes were not different among treatment factors (barrier: pseudo-$F = 0.189$, $P = 0.665$; inoculation: pseudo-$F = 0.001$, $P = 0.994$) or as an interaction between factors (inoculation × barrier: pseudo-$F = 0.900$, $P = 0.652$). Moisture content of bark blocks had an initial mean of 46.2 ± 4.4% and a final mean of 33.6 ± 5.5%, which represents a 26.5% decrease ($P < 0.001$). Logs without barriers had 10–15% less moisture in them in year 1 (Table 1). Differences between barrier treatments were significant (pseudo-$F = 10.572$, $P = 0.002$), while there were no differences between inoculation treatments (pseudo-$F = 0.202$, $P = 0.656$) or as an interaction between factors (pseudo-$F = 0.788$, $P = 0.368$) (Fig. 2c).

Sapwood blocks had an average initial mass of 2.87 ± 0.35 g and an initial density of 0.53 ± 0.06 g cm^{-3}. After 1 year, sapwood from all treatments

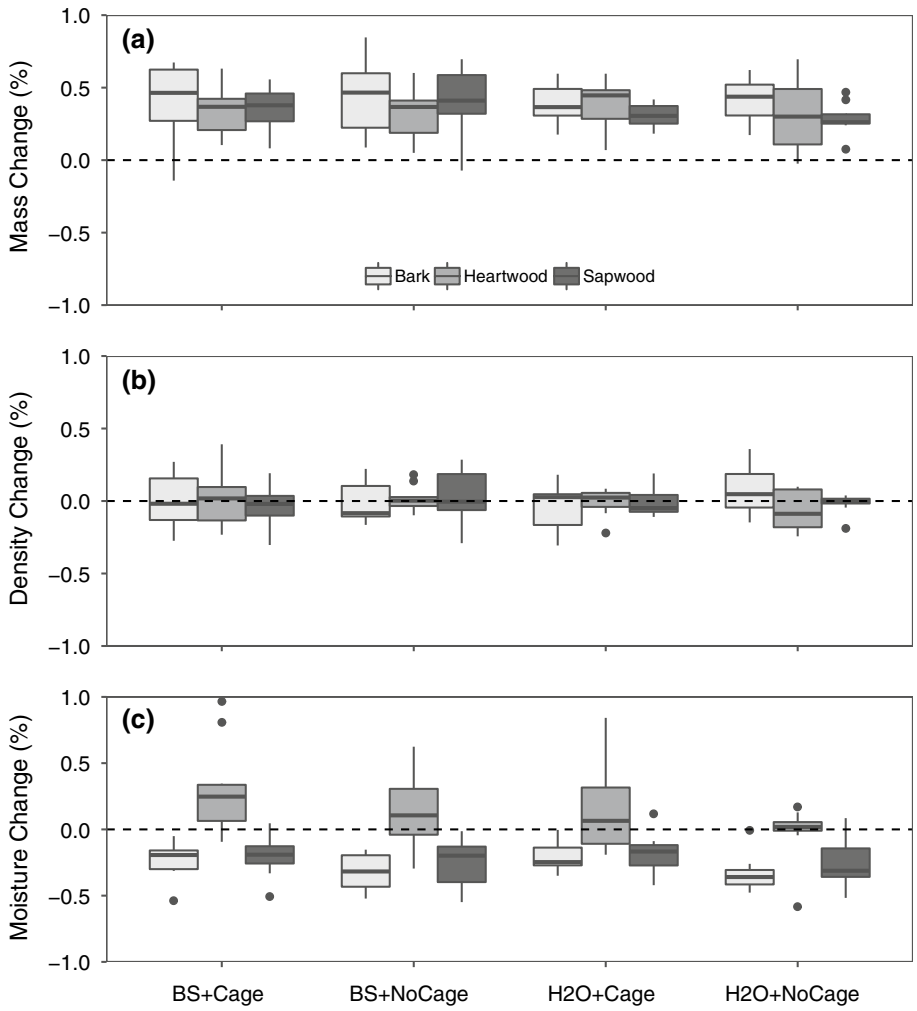

Fig. 2 **a** Mass change relative to initial mass, **b** density change relative to initial density, and **c** moisture content change relative to initial moisture content in bark, sapwood, and heartwood tissues across inoculation and barrier treatment levels after 1 year. Within the boxplots, the horizontal black line is the median, boxes indicate the first and third quartiles, whiskers represent 1.5 times the interquartile range, and circles represent outliers. *BS* bluestain

Table 1 Summary of mass, density, and moisture content in wood tissues from time of deployment (year 0), year 1, and the difference between the two sampling periods

	Mass				Density				Moisture content			
	Year 0 (g)	Year 1 (g)	Diff (%)	*P* value	Year 0 (g cm^{-3})	Year 1 (g cm^{-3})	Diff (%)	*P* value	Year 0 (%)	Year 1 (%)	Diff (%)	*P* value
All tissues	2.58	3.45	+ 33.7	< 0.001	0.47	0.46	− 1.3	0.557	40.4	33.4	− 17.4	< 0.001
Bark												
BS + Cage	**2.47**	**3.55**	**+ 43.8**	**< 0.001**	0.47	0.46	− 1.0	0.881	**45.9**	**35.0**	**− 23.4**	**< 0.001**
BS + NoCage	**2.45**	**3.45**	**+ 41.1**	**< 0.001**	0.46	0.45	− 2.0	0.675	**46.9**	**32.2**	**− 30.5**	**< 0.001**
H_2O + Cage	**2.47**	**3.20**	**+ 29.4**	**0.007**	0.47	0.45	− 4.7	0.379	**45.5**	**36.0**	**− 20.6**	**< 0.001**
H_2O + NoCage	**2.52**	**3.57**	**+ 41.5**	**< 0.001**	0.48	0.49	+ 3.0	0.616	**46.5**	**30.5**	**− 33.0**	**0.001**
Mean	**2.47**	**3.43**	**+ 38.6**	**< 0.001**	0.47	0.46	− 1.2	0.666	**46.2**	**33.6**	**− 26.5**	**< 0.001**
Sapwood												
BS + Cage	**2.91**	**3.92**	**+ 34.9**	**< 0.001**	0.55	0.52	− 4.7	0.319	**47.4**	**37.8**	**− 20.3**	**0.004**
BS + NoCage	**2.84**	**3.94**	**+ 38.8**	**0.004**	0.51	0.53	+ 4.0	0.660	**48.9**	**35.7**	**− 25.8**	**< 0.001**
H_2O + Cage	**2.82**	**3.51**	**+ 24.3**	**0.038**	0.54	0.54	+ 0.7	0.899	**48.6**	**38.1**	**− 20.8**	**0.001**
H_2O + NoCage	**2.90**	**3.73**	**+ 28.3**	**0.005**	0.53	0.52	− 2.5	0.642	**48.1**	**34.5**	**− 26.2**	**0.002**
Mean	**2.87**	**3.78**	**+ 31.8**	**< 0.001**	0.53	0.53	− 0.7	0.817	**48.3**	**36.6**	**− 23.1**	**< 0.001**
Heartwood												
BS + Cage	**2.44**	**3.24**	**+ 33.1**	**< 0.001**	0.43	0.42	− 2.5	0.778	**23.5**	**30.7**	**+ 30.1**	**0.028**
BS + NoCage	**2.45**	**3.23**	**+ 31.9**	**0.004**	0.41	0.42	+ 1.3	0.820	26.7	29.7	+ 13.3	0.375
H_2O + Cage	**2.36**	**3.07**	**+ 29.9**	**0.045**	0.44	0.41	− 5.7	0.462	24.7	28.8	+ 19.6	0.178
H_2O + NoCage	**2.32**	**2.98**	**+ 28.4**	**< 0.001**	0.41	0.40	− 5.1	0.408	33.8	30.7	− 3.3	0.178
Mean	**2.40**	**3.14**	**+ 31.0**	**< 0.001**	0.42	0.41	− 3.0	0.386	**26.7**	**29.9**	**+ 15.9**	**0.024**

All positive values in Diff columns represent gains and all negative values represent losses in mass, density, and moisture content, respectively from year 0 to year 1. Significant differences ($\alpha = 0.05$) from Permutational multivariate analysis of variance between years are bolded

including controls had gained mass, with an average gain of 31.5 ± 21.1% from initial samples (~ 0.9 g) ($P < 0.001$) while there was no obvious trend in density change ($P = 0.817$). Sapwood blocks inoculated with bluestain fungi had 10–15% greater increases in mass compared to blocks inoculated with water (Table 1), but this difference was not significant (barrier: pseudo-$F = 0.416$, $P = 0.523$; inoculation: pseudo-$F = 1.690$; $P = 0.202$; barrier × inoculation: pseudo-$F = 0.324$, $P = 0.573$). For sapwood density, there was no clear trend among treatments (barrier: pseudo-$F = 0.227$, $P = 0.630$; inoculation: pseudo-$F = 0.008$; $P = 0.931$; barrier × inoculation: pseudo-$F = 1.693$, $P = 0.1939$) (Fig. 2a, b). Initial moisture content in sapwood was 48.3 ± 5.2% compared to 36.6 ± 6.3% at the end of 1 year, representing a decrease of 23% ($P < 0.001$) (Table 1). Similar to bark, moisture content in sapwood from logs without barriers decreased ~ 6% more than caged logs, although these differences were not significant (pseudo-$F = 2.286$, $P = 0.136$), nor were differences significant between inoculation treatments (pseudo-$F = 0.001$, $P = 0.984$) or as an interaction between factors (pseudo-$F = 0.000$, $P = 0.994$) (Fig. 2c).

Heartwood blocks had an average initial mass of 2.40 ± 0.41 g and a density of 0.42 ± 0.07 g cm^{-3}. After 1 year, heartwood from all treatments gained mass ($P < 0.001$), with an average mass gain per block of 32.2 ± 22.8% (~ 0.8 g). The largest mass gains occurred in heartwood blocks inoculated with fungi (Table 1). However, there was no difference among treatment factors in percent mass change after 1 year (barrier: pseudo-$F = 0.003$, $P = 0.951$; inoculation: pseudo-$F = 0.742$, $P = 0.406$) and there was no interaction between factors (barrier × inoculation: pseudo-$F = 0.002$, $P = 0.890$). Density decreased 3.0% on average across treatments ($P = 0.386$), with the largest decreases (> 5.0%) observed in blocks inoculated with water (Table 1). These modest changes in heartwood density were not significantly different among treatments (barrier: pseudo-$F = 0.035$, $P = 0.847$; inoculation: pseudo-$F = 1.341$, $P = 0.256$) or as an interaction between factors (barrier × inoculation: pseudo-$F = 0.006$, $P = 0.937$). Moisture content of heartwood had an initial mean of 26.7 ± 8.1%, which increased to 29.9 ± 8.2% after 1 year, representing an average increase of 15.9% (Fig. 2c). The largest and only significant increase, (30.1%, $P = 0.028$), was observed in heartwood from logs inoculated with fungi and with barriers present (Table 1). Heartwood moisture content increased more when barriers were present (pseudo-$F = 9.125$, $P = 0.003$) and to a marginal degree when inoculated with fungi (pseudo-$F = 3.062$, $P = 0.085$), but no significant differences in moisture content change were observed as an interaction between factors (pseudo-$F = 0.212$, $P = 0.653$.

Wood chemistry

Average bark C concentrations in logs before deployment was 490.9 µg C mg^{-1}, which increased in both levels of the barrier treatment (BS + Cage: 551.6 µg C mg^{-1}; H_2O + Cage: 573.8 µg C mg^{-1}) and in the BS + NoCage treatment (533.2 µg C mg^{-1}), but decreased in the control treatment (H_2O + NoCage: 469.0 µg C mg^{-1}) (Fig. 3a). There were no significant differences between inoculation treatments ($F = 0.984$, $P = 0.357$) but bark of caged logs had higher C concentrations than uncaged logs (562.1 µg C mg^{-1} vs. 502.8 µg C mg^{-1}, $F = 7.876$, $P = 0.003$). A significant interaction between the two main factors, barrier and inoculation, was observed ($F = 4.161$, $P = 0.038$) (Fig. 3a), indicating that the presence of barriers caused a greater increase in bark C when the log was inoculated with water compared to bluestain. In sapwood, C concentrations were initially 463.6 µg C mg^{-1}, which decreased in all treatments to 452.8 µg C mg^{-1} (H_2O + NoCage), 408.7 µg C mg^{-1} (BS + Cage), 391.9 µg C mg^{-1} (BS + NoCage), and 365.5 µg C mg^{-1} (H_2O + Cage) (Fig. 3b). There were no significant differences in sapwood C between inoculation treatments ($F = 0.368$, $P = 0.552$) or barrier treatments ($F = 1.618$, $P = 0.218$), but the interaction between the barrier and inoculation treatments was borderline significant ($F = 3.963$, $P = 0.053$). In heartwood, C concentrations decreased from the initial concentration of 509.4 to 495.4 µg C mg^{-1} (BS + NoCage), 436.0 µg C mg^{-1} (H_2O + Cage), 435.2 µg C mg^{-1} (BS + Cage), and to 431.5 µg C mg^{-1} in the control treatment, H_2O + NoCage (Fig. 3c). Despite these large decreases, there were no significant differences between inoculation treatments ($F = 0.678$, $P = 0.417$), barrier treatments ($F = 0.602$, $P = 0.445$), or as an interaction between barrier and inoculation ($F = 0.875$, $P = 0.356$).

Average bark N concentrations in logs before deployment was 1.9 µg N mg^{-1}, which increased in all treatments to 2.0 µg N mg^{-1} (H_2O + NoCage), 2.3 µg N mg^{-1} (BS + NoCage), 2.5 µg N mg^{-1} (H_2O + Cage), and 2.9 µg N mg^{-1} (BS + Cage) (Fig. 3d). There was significantly more N in logs inoculated with bluestain fungi than in water-inoculated logs (2.6 µg N mg^{-1} vs. 2.2 µg N mg^{-1}, $F = 4.280$, $P = 0.041$). Bark N in caged logs was also significantly greater than in uncaged logs (2.7 µg N mg^{-1} vs. 2.1 µg N mg^{-1}, $F = 10.233$, $P = 0.004$). However, there were no interacting effects between barrier and inoculation ($F = 0.311$, $P = 0.559$). In sapwood, N concentrations were initially 1.5 µg N mg^{-1}, which decreased in all treatments to 1.0 µg N mg^{-1} (H_2O + Cage) and 0.8 µg N mg^{-1} (H_2O + NoCage; BS + NoCage; BS + Cage) (Fig. 3e). Sapwood N was not significantly different between inoculation treatments ($F = 2.126$, $P = 0.155$), barrier treatments ($F = 1.361$, $P = 0.252$), or for the interaction between barrier and inoculation ($F = 2.681$, $P = 0.109$). In heartwood, N

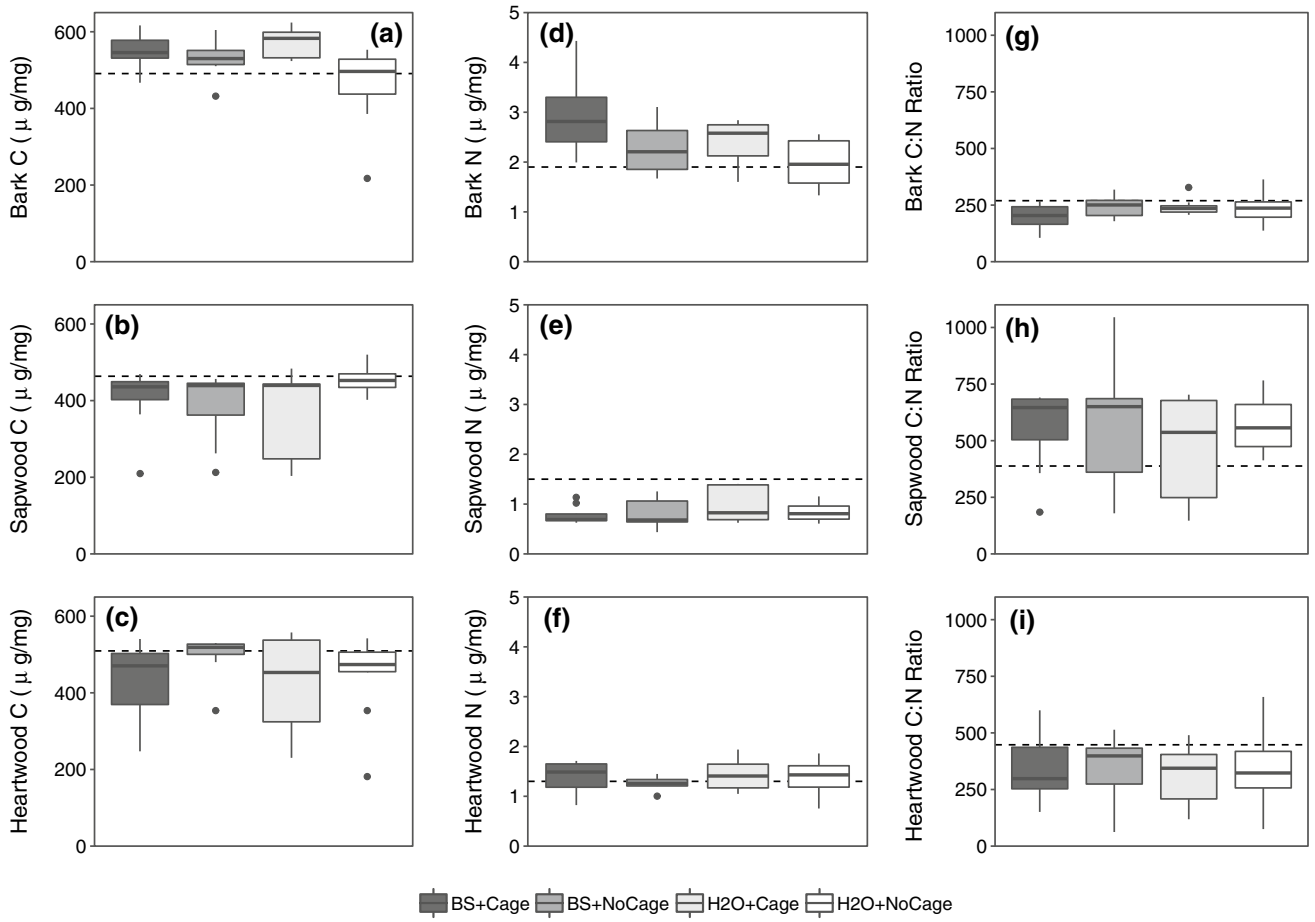

Fig. 3 Changes in tissue chemistry across inoculation and barrier treatment levels after 1 year for **a** bark C concentration, **b** sapwood C concentration, **c** heartwood C concentration, **d** bark N concentration, **e** sapwood N concentration, **f** heartwood N concentration, **g** bark C:N, **h** sapwood C:N, and **i** heartwood C:N. Within the boxplots, the horizontal black line is the median, boxes indicate values in the first and third quartiles, whiskers represent 1.5 times the interquartile range, and circles represent outliers. Initial values from logs before deployment are plotted as horizontal dashed lines. *BS* bluestain

concentrations were initially 1.3 µg N mg^{-1}, and remained unchanged in the BS + NoCage and control treatment (H_2O + NoCage), and increased slightly to 1.4 µg N mg^{-1} in the BS + Cage treatment, and to 1.5 µg N mg^{-1} in the H_2O + Cage treatment (Fig. 3f). Heartwood N was not significantly different between inoculation treatments ($F = 0.516$, $P = 0.473$), barrier treatments ($F = 1.414$, $P = 0.239$), or as an interaction between barrier and inoculation ($F = 0.002$, $P = 0.964$).

Changing C and N in wood components had mixed impacts on overall C:N ratios. C:N was initially 269.4 in bark, 388.1 in sapwood, and 447.5 in heartwood. C:N ratios decreased in all treatments of bark (Fig. 3g), increased in all treatments of sapwood (Fig. 3h), and decreased in all treatments of heartwood (Fig. 3i). The change in bark, sapwood, and heartwood C:N ratios from initial values after 1 year was not significantly different between inoculation treatments (bark: $F = 1.190$, $P = 0.294$; sapwood: $F = 0.568$, $P = 0.456$; heartwood: $F = 0.092$, $P = 0.760$), barrier treatments (bark: $F = 2.129$, $P = 0.158$; sapwood: $F = 1.506$, $P = 0.232$; heartwood: $F = 0.010$, $P = 0.917$), or as an interaction between treatments (bark: $F = 1.516$, $P = 0.227$; sapwood: $F = 1.296$, $P = 0.267$; heartwood: $F = 0.002$, $P = 0.877$).

Soil chemistry

At the conclusion of the first year of this experiment, differences in soil C and N availability were beginning to manifest relative to soils not influenced by wood decomposition. Increased concentrations in both C and N were observed in some treatments in the A horizon and in all treatments in the B horizon, resulting in mixed results for changing C:N ratios (Fig. 4). In the A horizon, C concentrations increased from background levels of 22.3 to 22.9 µg C mg^{-1} (H_2O + Cage), 25.3 µg C mg^{-1} (BS + Cage), and 31.8 µg C mg^{-1} (BS + NoCage)

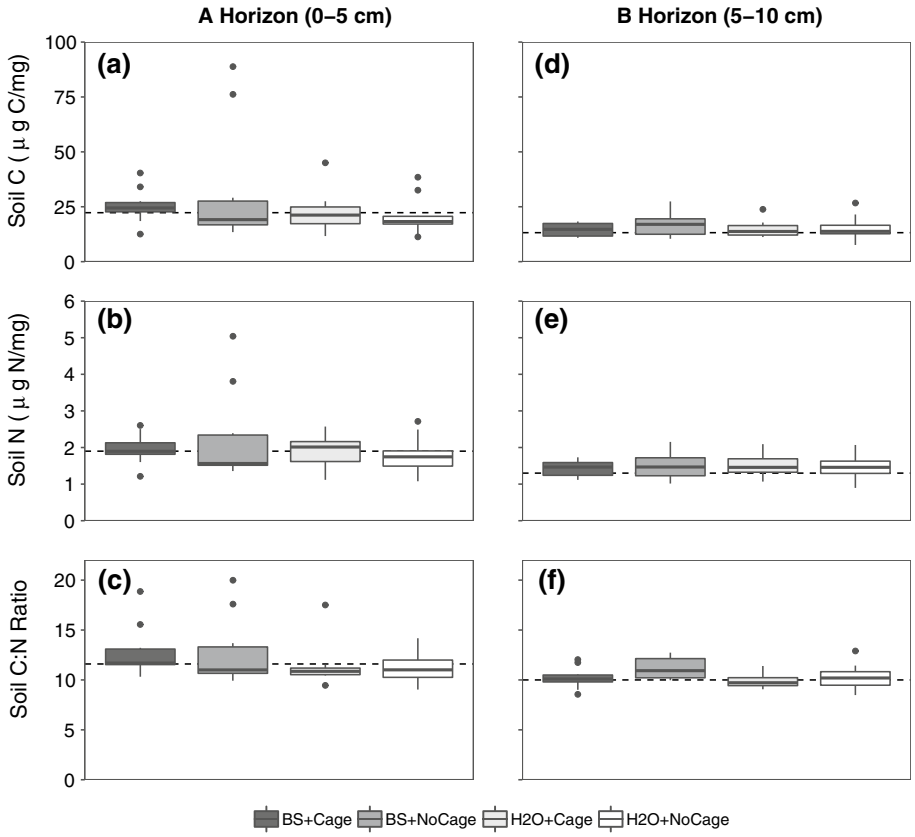

Fig. 4 Changes in soil chemistry across inoculation and barrier treatment levels beneath logs after 1 year for **a** C concentration in the A horizon, **b** N concentration in the A horizon, **c** C:N in the A horizon, **d** C concentration in the B horizon, **e** N concentration in the B horizon, and **f** C:N in the B horizon. Within the boxplots, the horizontal black line is the median, boxes indicate values in the first and third quartiles, whiskers represent 1.5 times the interquartile range, and circles represent outliers. Initial values from logs before deployment are plotted as horizontal dashed lines. BS, bluestain

and decreased to 20.0 µg C mg^{-1} under control logs (H_2O + NoCage) (Fig. 4a). However, neither inoculation treatments ($F = 2.207$, $P = 0.156$), barrier treatments ($F = 0.141$, $P = 0.715$), nor the interaction between the treatments ($F = 0.914$, $P = 0.379$) resulted in significantly different C concentrations in soils below study logs. Soil N concentrations increased in the A horizon from background levels of 1.9 to 2.0 µg N mg^{-1} (BS + Cage) and 2.2 µg N mg^{-1} (BS + NoCage), while remaining unchanged in soils under H_2O + Cage logs (1.9 µg N mg^{-1}) and decreasing slightly to 1.7 µg N mg^{-1} under logs with the control treatment, H_2O + NoCage (Fig. 4b). However, neither inoculation treatments ($F = 1.374$, $P = 0.266$), nor barrier treatments ($F = 0.042$, $P = 0.849$), or their interaction ($F = 1.057$, $P = 0.338$) resulted in significantly different N concentrations in soils below study logs. C:N ratios in the A horizon of soils under logs increased from background levels of 11.6 to 12.7 (BS + NoCage), 12.8 (BS + Cage), and decreased slightly to 11.5 (H_2O + Cage) and 11.2 (H_2O + NoCage) in the A horizon (Fig. 4c). These differences were significant at $\alpha = 0.10$ between inoculation treatments ($F = 3.320$, $P = 0.071$), suggesting that the presence of bluestain fungi increased the C:N ratio in soils directly below decomposing logs. Differences between barrier treatments ($F = 0.057$, $P = 0.814$) and as an interaction between barrier and inoculation ($F = 0.020$, $P = 0.891$) were indistinguishable.

In the B horizon, all treatments exhibited an increase in both C and N concentrations compared to soils not influenced by wood decomposition with subsequent net increases in C:N ratios, signifying a larger change in C than in N. In the B horizon, C concentrations increased from background levels of 13.2 to 14.6 µg C mg^{-1} (BS + Cage), 14.8 µg C mg^{-1} (H_2O + Cage), 15.2 µg C mg^{-1} (H_2O + NoCage), and 17.1 µg C mg^{-1} (BS + NoCage) (Fig. 4d). However, neither inoculation, barrier, northe interaction between barrier and inoculation resulted in significantly different C concentrations in the B horizon of soils below study logs (inoculation: $F = 0.318$, $P = 0.578$; barrier: $F = 0.951$, $P = 0.344$; barrier × inoculation: $F = 0.558$, $P = 0.460$). Soil N concentrations in the B horizon increased from background levels of 1.3 to 1.4 µg N mg^{-1} (BS + Cage and H_2O + NoCage) and 1.5 µg N mg^{-1} (H_2O + Cage and BS + NoCage) (Fig. 4e). However, neither inoculation, barrier, or their interaction resulted in significantly different N concentrations in the B horizon of soils below study logs (inoculation: $F = 0.000$, $P = 0.998$; barrier: $F = 0.051$, $P = 0.820$; barrier × inoculation: $F = 0.374$, $P = 0.543$). C:N in the B horizon under logs increased from background levels of 10.0 to 10.2 (BS + Cage), 10.3 (H_2O + NoCage), and 11.1 (BS + NoCage)

and decreased slightly to 9.9 in the H_2O + Cage treatment in the B horizon (Fig. 4f). These differences were significant for barrier treatments, with higher C:N for NoCage than Cage treatments ($F = 4.126$, $P = 0.049$), although no differences were observed for inoculation treatments ($F = 2.777$, $P = 0.103$). There was no interaction between barrier and inoculation ($F = 0.629$, $P = 0.431$).

Respiration

From the treatment logs, higher rates of respiration were observed from BS + Cage logs (0.84 g C m^{-2} day^{-1}), which was 38.4% higher than BS + NoCage logs, 66.6% higher than H_2O + Cage logs, and 29.8% higher than H_2O + NoCage logs, although these differences were not significant between inoculation treatments ($F = 1.205$, $P = 0.277$), barrier treatments ($F = 0.131$, $P = 0.728$), or as a interaction between barrier and inoculation ($F = 1.842$, $P = 0.184$) (Fig. 5a). No clear trend was observed in respiration as a function of inoculation treatments in soils beneath study logs ($F = 0.442$; $P = 0.507$), barrier treatments ($F = 0.014$, $P = 0.903$), or as an interaction between treatments ($F = 0.009$, $P = 0.925$) with average respiration values ranging from 1.76 to 1.89 g C m^{-2} day^{-1} (Fig. 5b). However, respiration from logs was positively related to the moisture content of the logs (multiple regression: $R^2 = 25.2\%$, $F = 3.940$, $P = 0.016$), with the best predictor being heartwood moisture content ($R = 0.011 \times MC_{heartwood} + 0.177$, $P = 0.002$, $R^2 = 22.4\%$).

Termite presence and impact

Principal components analysis was used to compare the relationships between environmental conditions and termite presence among different treatments. At the end of 1 year, there was not a strong separation between the four treatment categories, but the relationships between the environmental variables provide insight into biogeochemical processes at the onset of decomposition (Fig. 6). After 1 year, termites were present in 25% of logs. Logs inoculated with bluestain fungi had termites present four times more than control logs ($\chi^2 = 39.1015$, $df = 1$, $n = 40$, $P = 0.003$) while barrier treatments had no effect on termite presence ($\chi^2 = 0.1103$, $df = 1$, $n = 40$, $P = 0.740$). Across all three tissue types, the presence of termites was associated with an ~ 1.3-fold increase in mass (Fig. 7a), but these results were not significant (bark: $\chi^2 = 0.506$, $P = 0.476$; sapwood: $\chi^2 = 1.422$, $P = 0.233$; heartwood: $\chi^2 = 0.703$, $P = 0.402$). The change in tissue density relative to termite presence was less consistent (Fig. 7b).Termite presence was associated with an average increase of + 4.7 mg cm^{-3} compared to an average decrease of − 8.9 mg cm^{-3} when termites were absent in bark, an average increase of + 22.2 mg cm^{-3} compared to an average decrease of − 12.3 mg cm^{-3} when termites were absent in sapwood, and an average increase of + 7.4 mg cm^{-3} compared to an average decrease of − 19.7 mg cm^{-3} when termites were absent in heartwood. Similarly though, termite presence was not a significant control of density for any of the three tissue types (bark: $\chi^2 = 0.208$, $P = 0.648$; sapwood: $\chi^2 = 1.549$, $P = 0.213$; heartwood: $\chi^2 = 01.179$, $P = 0.278$). Termites were positively associated with N concentrations in all tissue types and were negatively associated with C and subsequently C:N ratios in sapwood (Fig. 6). C concentrations in sapwood were significantly smaller in logs when termites were present (present: 389.13 µg C mg^{-1}, absent: 413.52 µg C mg^{-1}, $P = 0.030$). N concentrations were marginally smaller in sapwood (present: 0.79 µg N mg^{-1}, absent: 0.88 µg N mg^{-1}, $P = 0.087$) and marginally larger in heartwood (present: 1.48 µg N mg^{-1}, absent: 1.33 µg N mg^{-1}, $P = 0.090$) when termites were present. For soils, termite presence was strongly linked with biogeochemical processes in the A horizon, but not as strongly linked with the B Horizon (Fig. 6). Furthermore, termites were closely associated

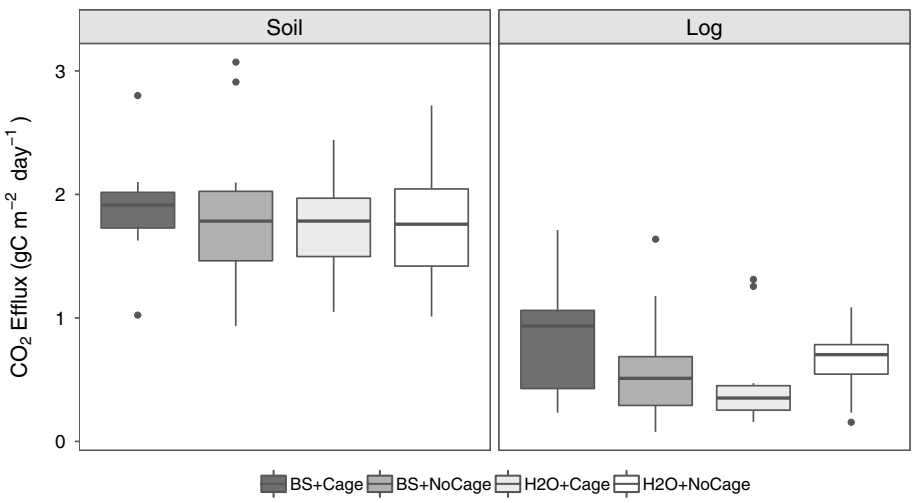

Fig. 5 Boxplots of respiration from **a** logs and **b** soils during year 1 harvest (October 2015). Within the boxplots, the horizontal black line is the median, boxes indicate the first and third quartiles, whiskers represent 1.5 times the interquartile range, and circles represent outliers. *BS* bluestain

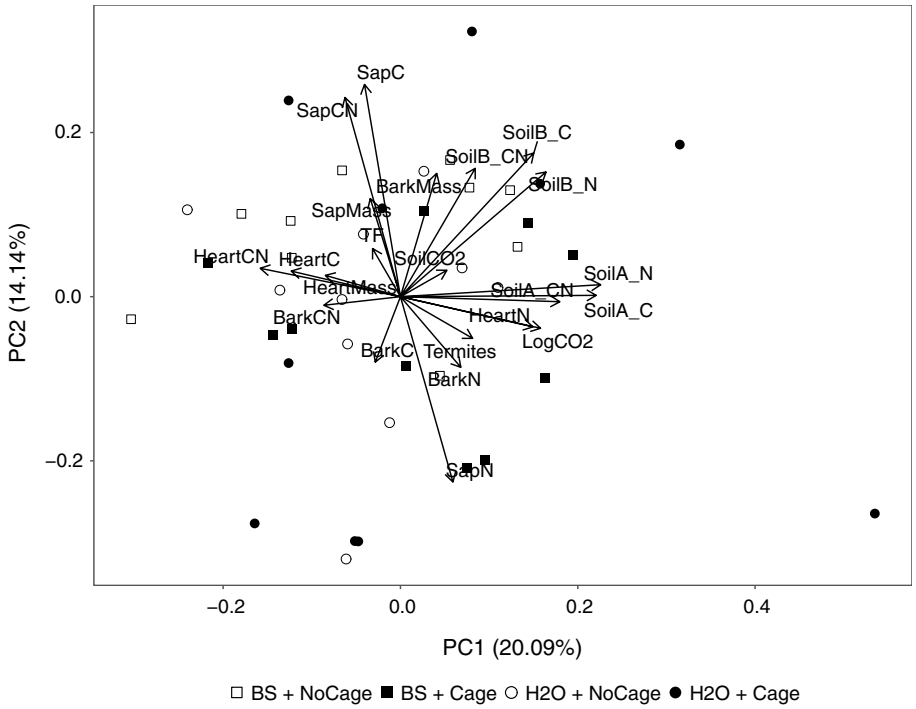

Fig. 6 Principal components 1 and 2 from PCA on environmental conditions across the four study treatments. *TF* throughfall, *BarkMass* mass change in bark, *SapMass* mass change in sapwood, *HeartMass* mass change in heartwood, BarkC = bark C concentration, *BarkN* bark N concentration, *BarkC:N* bark C:N ratio, *SapC* sapwood C concentration, *SapN* sapwood N concentration, *SapC:N* sapwood C:N ratio, *HeartC* heartwood C concentration, *HeartN* heartwood N cocentration, *HeartC:N* heartwood C:N ratio, *Termites* termite presence/absence, *SoilA_C* C concentration in A horizon, *SoilA_N* N concentration in A horizon, *SoilA_C:N* C:N ratio in A horizon, *SoilB_C* C concentration in B horizon, *SoilB_N* N concentration in B horizon, *SoilB_C:N* C:N ratio in B horizon, $LogCO_2$ log respiration, $SoilCO_2$ soil respiration

with log respiration, but not soil respiration. And last, termites were oppositely related to throughfall quantity (Fig. 6).

Discussion

Bark beetle attacks have both direct and indirect impacts on biogeochemical processes in forest ecosystems. Here, we examined indirect effects of bark beetles through their association with bluestain fungi at short temporal scales to provide evidence of short-term changes in biogeochemical properties in wood and soils at the onset of wood decomposition. This experiment quantified short-term nutrient dynamics in wood decomposition as it is impacted by bluestain fungi with or without the exclusion of aboveground saproxylic species (i.e., barrier treatments). Specifically, after 1 year, we observed changes in wood mass and moisture content, in bark and sapwood nutrient concentrations, and in soil nutrient concentrations, which we attribute to differences in treatments and resultant termite recruitment rather than external climatic drivers. Together, these results provide a snapshot of initial biogeochemical changes in decomposition processes that are often overlooked despite their role in mediating the trajectory of long-term decomposition processes (Carpenter et al. 1988; Schowalter et al. 1992a).

The processes of bark beetle disturbance itself (e.g., physical changes to forest structure through tree mortality) can alter throughfall and biogeochemical processes in forest ecosystems (Brouillard et al. 2017), but here we show that bark beetles may also indirectly alter ecosystem processes by pre-inoculating coarse woody debris with bluestain fungi. At our study site, throughfall quantity exhibited variability between sampling intervals due to storm characteristics and seasonality, which are common trends in all forest types (Levia and Frost 2006; Van Stan et al. 2012; Siegert et al. 2017a). As a result, study logs received variable inputs of water and nutrients throughout the year, with minimum water inputs in late summer and autumn (Aug–Nov) (Fig. 1). However, there were no systematically observable differences in canopy inputs between the plots, suggesting that the changes in dead wood decomposition and resulting nutrient dynamics between plots could be attributed to the treatment inoculations and barriers. Quantifying these inputs are essential for understanding inter-annual variation in nutrient dynamics and wood decomposition in forest ecosystems.

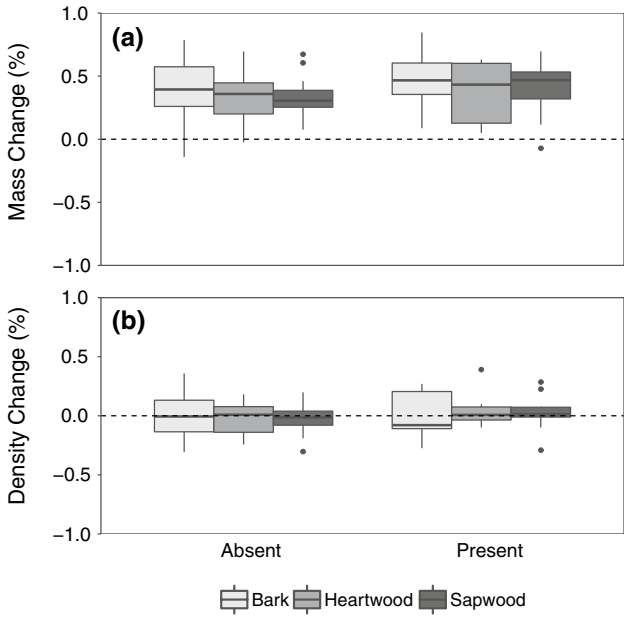

Fig. 7 Change in **a** mass and **b** density of bark, sapwood, and heartwood tissues relative to initial conditions when termites were present vs. absent after 1 year. Within the boxplots, the horizontal black line is the median, boxes indicate the first and third quartiles, whiskers represent 1.5 times the interquartile range, and circles represent outliers

These small, but significant changes to C and N in wood and soil 1 year after a simulated influx of bark beetle-generated dead wood, and the increased presence of primary wood decomposers like termites, are likely to alter rates of wood decomposition and nutrient fluxes over the long-term in forest ecosystems impacted by bark beetle disturbances.

Wood decomposition includes an initial lag phase where there is no decrease in mass (Sollins et al. 1987; Harmon 2009). As expected, we found no difference in wood decomposition among barrier or inoculation treatments. Wood from all parts of the logs gained ~ 30% mass after 1 year, but the presence of termites had no observable effect on mass change. Most studies use observational methods to determine mass loss, and those that do experimentally examine changes typically use small pieces of wood (e.g., blocks or dowels < 10 cm diameter) and few look at short-term changes in during wood decomposition (Schowalter et al. 1992a). As such, wood in many studies may have increased in mass and nutrients during initial decomposition stages due to fungal colonization and invertebrate colonization, but there is a lack of data collected at this timescale to document these trends. It is documented that termites bring soil and feces with them during colonization and can account for up to 59% of dry wood weight in logs within 5 years (Ulyshen and Wagner 2013). This is supported by the trend for 1.3-fold higher mass gain observed in logs with termites than without. Colonization by other invertebrates could similarly generate these results, suggesting that dead wood initially acts as a large C reservoir.

Significant differences in density were not found but trends showed density increases when termites were present and density decreases when termites were absent for all three wood tissue types. These results suggest that termites might be actively removing decay fungi, their direct competitor for wood. As decay fungi remove chemical nutrients from wood, they cause a slow progressive decrease in wood density and strength. Termites, in turn, are known to have evolved a multi-tiered defense system involving cellular, physiological, and behavioral mechanisms that not only inhibit fungal spore germination (Rosengaus et al. 1998) but also protect them against fungal pathogens (Chouvenc and Su 2010). There is a paucity of literature though on the effects of the termite defense system on wood colonization by decay fungi.

Caged dead wood inoculated with bluestain fungi had the largest gains in N and subsequent decreases in C:N ratios relative to logs that were not inoculated, indicating an important interaction between caging and bluestain fungi. This interaction could be explained by the fact that caged logs were protected from attack by aboveground wood boring insects, which when present, can hinder subterranean termite activity and subsequently slow N accumulation. Excluding aboveground woodborers could result in greater N accumulation by limiting direct effects from resource competition and intra-guild predation, or indirectly via the incidental introduction of phoretic decomposition fungi (Swift and Boddy 1984), many of which are termite antagonists (Amburgey 1979). While C concentrations were 12% greater in bark when cages were present and that difference was greater when logs were inoculated with water (+ 15%) than bluestain (+ 10%) (Fig. 3a), N concentrations in bark were 27% greater when cages were present and 16% greater when logs were inoculated with bluestain fungus (Fig. 3b). These results suggest that bluestain inoculation accelerated the process of recruiting and obtaining N critical to the breakdown of C in coarse woody debris. Similarly, increased C in bark was most prominent when bluestain fungus was not present and when cages excluded the colonization by other decomposers, which further limited N availability. Cages were intended to exclude post-deployment colonization of logs by additional bark beetles and the bluestain fungi species they carry. In the absence of barriers, aboveground saproxylic species would also have the opportunity to colonize logs and may have contributed to the patterns observed in this study (Boddy and Watkinson 1995; Smyth et al. 2016). N concentrations generally increase in dead wood, especially during later stages of decomposition (Holub et al. 2001; Laiho and Prescott 2004) as a result of N production by decomposer communities (Ulyshen 2015). Here we found termites were associated with ~ 6% less C and ~ 10% more N in sapwood,

in agreement with other studies that have reported termites may also directly and/or indirectly influence nutrient dynamics within dead wood (Chen and Forschler 2016; Ulyshen et al. 2017).

Soils underneath bluestain-inoculated logs had different nutrient distributions after just 1 year as well. Soils below logs with bluestain inoculation had 12% higher C:N ratios in the A horizon and logs without barriers had 6% higher C:N ratio in the B horizon. Changes in C and N throughout the soil profile were consistently greatest (C: 18%, N: 5%) under logs treated with bluestain fungus compared to other treatments (Fig. 4), but the variability between treatments obscured significant differences at this early stage of decomposition. Not surprisingly, bark beetles can increase inorganic N in mineral soils in stands following bark beetle outbreaks due to increased rates of litterfall and from reduced root uptake from tree mortality (Huber et al. 2004; Morehouse et al. 2008; Brouillard et al. 2017); however, in our study, the increase in C:N ratios in soils below logs inoculated with bluestain suggests that the saproxylic fungi and invertebrates may be removing soil N for use in dead wood decomposition. These preliminary observations following 1 year, which were also observed in Norway spruce logs across a decay gradient (Mäkipää et al. 2017), provide evidence of a novel, indirect effect of bark beetles on soil nutrients following outbreaks.

Last, respiration from logs after 1 year was within the range of similar studies on this time scale and moisture content similarly accounted for a significant proportion of the wide variation in respiration among logs (Schowalter et al. 1992b; Progar et al. 2000; Chambers et al. 2001). Respiration from logs was tied to the presence of decomposers with 11% higher rates when termites were present and 26% higher rates when bluestain was present. Although differences in soil respiration beneath dead wood were not yet observed, respiration from logs was associated with changes in A horizon biogeochemical properties (Fig. 6) and is likely an early indicator of changes to come.

Conclusion

This study demonstrates how the presence of bluestain fungi in dead wood can change nutrient dynamics in the short-term that may have long-term impacts on decomposition. In particular, we demonstrate that subterranean termites, which are major decomposers in southeastern US forests (Hanula 1996) prefer dead wood from simulated bark beetle attacks, presumably because of the presence of dead wood inoculated with bluestain (*O. minus*) fungal associates. Consequently, if this recruitment is sustained and termites persist in bluestained dead wood, then this is likely to enhance decomposition rates and biogeochemical dynamics. However, the lack of quantitative measurements of termite biomass, distribution, and impact on woody decomposition has precluded their incorporation into ecosystem models (Bradford et al. 2014; Maynard et al. 2015). Additional studies across climactic and temporal gradients are needed to better quantify termite impacts on decomposition processes.

Decomposition is regulated by biogeochemical, hydrological, and invertebrate dynamics that happen over multiple time scales. This study quantified both the dynamics that occur in initial decomposition stages of dead wood in general and how the presence of one ophiostomatoid fungus differentially impacts these processes. Experiments capturing decomposition dynamics during this stage of decomposition, and particularly for wood this size (> 10 cm diameter), are rare. Given the recent increases in bark beetle outbreaks, this is likely to impact forest C cycling and biogeochemistry. Future data collection events from this project will occur at 2, 4, and 8 years post deployment and offer longer-term views of the data reported herein.

Acknowledgements This work is a contribution of the Forest and Wildlife Research Center and the Mississippi Agricultural and Forestry Experiment Station, Mississippi State University. This work was funded through the National Science Foundation (DEB # 1660346) and supported by the National Institution of Food and Agriculture, US Department of Agriculture, Mclntire Stennis capacity Grant # MISZ-069390 and Hatch project #069410. Any opinions, findings, conclusions, or recommendations expressed in this publication are those of the author(s) and do not necessarily reflect the view of the US Department of Agriculture. This project was made possible by the Mississippi State University Undergraduate Research Scholars Program, the Mississippi Agricultural and Forestry Experiment Station Small Research Initiative program, the Office of Research and Economic Development Cross-College Research Grant, the Department of Biochemistry, Molecular Biology, Entomology and Plant Pathology, the Institute for Genomics, Biocomputing and Biotechnology, and the field and laboratory assistance of Craig Bell, Sasith Karunarathna, Katy Limpert, Leana Rapp, Mercedes Siegle-Gaither, Jacob Landfield, John Formby, John Thomason, and Natalie Dearing. Special thanks to Misty Booth and the College of Forest Resources at Mississippi State University for site use in the John W. Starr Experimental Forest. Thank you to anonymous reviewers for their time and careful consideration.

Author contribution statement CMS, NAC, JDT, and JJR conceived and designed the experiments. CMS, NAC, JDT, LGG, and JJR conducted fieldwork. CMS and LGG analyzed the hydrology and soil chemistry data. NAC analyzed the decomposition and invertebrate data. CMS, NAC, JDT, LGG, and JJR wrote the manuscript.

Compliance with ethical standards

Conflict of interest J. J. Riggins is an inventor on a patent involving bluestain fungi in baiting methods for termites (US9924706B2). The author and his institution may financially benefit from this patent.

References

Amburgey T (1979) Review and checklist of the literature on interactions between wood-inhabiting fungi and subterranean termites. 1960–1978. Sociobiology 4:279–296

André F, Jonard M, Ponette Q (2008) Spatial and temporal patterns of throughfall chemistry within a temperate mixed oak–beech stand. Sci Total Environ 397:215–228. https://doi.org/10.1016/j.scitotenv.2008.02.043

Ballard RG, Walsh MA, Cole WE (1984) The penetration and growth of blue-stain fungi in the sapwood of lodgepole pine attacked by mountain pine beetle. Can J Bot 62:1724–1729. https://doi.org/10.1139/b84-233

Bearup LA, Maxwell RM, Clow DW, McCray JE (2014) Hydrological effects of forest transpiration loss in bark beetle-impacted watersheds. Nat Clim Chang 4:481–486. https://doi.org/10.1038/nclimate2198

Boddy L, Watkinson SC (1995) Wood decomposition, higher fungi, and their role in nutrient redistribution. Can J Bot 73:1377–1383. https://doi.org/10.1139/b95-400

Bonan GB (2008) Forests and climate change: forcings, feedbacks, and the climate benefits of forests. Science 320:1444–1449. https://doi.org/10.1126/science.1155121

Bradford MA, Warren RJ II, Baldrian P et al (2014) Climate fails to predict wood decomposition at regional scales. Nat Clim Chang 4:625–630

Bright D (2014) A catalog of Scolytidae and Platypodidae (Coleoptera), Supplement 3(2000–2010). NRC Research Press, Ottawa

Brouillard BM, Mikkelson KM, Bokman CM et al (2017) Extent of localized tree mortality influences soil biogeochemical response in a beetle-infested coniferous forest. Soil Biol Biochem 114:309–318. https://doi.org/10.1016/j.soilbio.2017.06.016

Busse MD (1994) Downed bole-wood decomposition in lodgepole pine forests of central Oregon. Soil Sci Soc Am J 58:221. https://doi.org/10.2136/sssaj1994.03615995005800010033x

Buttle JM, Toye HJ, Greenwood WJ, Bialkowski R (2014) Stemflow and soil water recharge during rainfall in a red pine chronosequence on the Oak Ridges Moraine, southern Ontario, Canada. J Hydrol 517:777–790. https://doi.org/10.1016/J.JHYDROL.2014.06.014

Carpenter SE, Harmon ME, Ingham ER et al (1988) Early patterns of heterotroph activity in conifer logs. In: Boddy L, Lyon A, Watling R (eds) Proceedings of the Royal Society of Edinburgh, Section B: Biological Sciences. Royal Society of Edinburgh Scotland Foundation, London, pp 33–43

Chambers JQ, Higuchi N, Schimel JP et al (2000) Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon. Oecologia 122:380–388. https://doi.org/10.1007/s004420050044

Chambers JQ, Schimel JP, Nobre AD (2001) Respiration from coarse wood litter in central Amazon forests. Biogeochemistry 52:115–131. https://doi.org/10.1023/A:1006473530673

Chen Y, Forschler BT (2016) Elemental concentrations in the frass of saproxylic insects suggest a role in micronutrient cycling. Ecosphere 7:e01300. https://doi.org/10.1002/ecs2.1300

Chouvenc T, Su N-Y (2010) Apparent synergy among defense mechanisms in subterranean termites (Rhinotermitidae) against epizootic events: limits and potential for biological control. J Econ Entomol 103:1327–1337. https://doi.org/10.1603/EC09407

Clay NA, Little N, Riggins JJ (2017) Inoculation of ophiostomatoid fungi in loblolly pine trees increases the presence of subterranean termites in fungal lesions. Arthropod Plant Interact 11:213–219. https://doi.org/10.1007/s11829-016-9473-5

Coulson RN, Klepzig K (2011) Southern Pine Beetle II. Gen Tech Rep SRS-140 Asheville, NC US Dep Agric For Serv South Res Station 512 p 140:1–512

Edmonds RL, Eglitis A (1989) The role of the Douglas-fir beetle and wood borers in the decomposition of and nutrient release from Douglas-fir logs. Can J For Res 19:853–859. https://doi.org/10.1139/x89-130

Fan J, Oestergaard KT, Guyot A et al (2015) Spatial variability of throughfall and stemflow in an exotic pine plantation of subtropical coastal Australia. Hydrol Process 29:793–804. https://doi.org/10.1002/hyp.10193

Forrester JA, Mladenoff DJ, D'Amato AW et al (2015) Temporal trends and sources of variation in carbon flux from coarse woody debris in experimental forest canopy openings. Oecologia 179:889–900. https://doi.org/10.1007/s00442-015-3393-4

Goodale CL, Apps MJ, Birdsey RA et al (2002) Forest carbon sinks in the northern hemisphere. Ecol Appl 12:891–899. https://doi.org/10.1890/1051-0761(2002)012%5b0891:FCSITN%5d2.0.CO;2

Gough CM, Vogel CS, Kazanski C et al (2007) Coarse woody debris and the carbon balance of a north temperate forest. For Ecol Manag 244:60–67. https://doi.org/10.1016/j.foreco.2007.03.039

Goulden ML, McMillan AMS, Wintston GC et al (2011) Patterns of NPP, GPP, respiration, and NEP during boreal forest succession. Glob Chang Biol 17:855–871. https://doi.org/10.1111/j.1365-2486.2010.02274.x

Grove SJ (2002) Saproxylic insect ecology and the sustainable management of forests. Annu Rev Ecol Syst 33:1–23. https://doi.org/10.1146/annurev.ecolsys.33.010802.150507

Hafner SD, Groffman PM (2005) Soil nitrogen cycling under litter and coarse woody debris in a mixed forest in New York State

Hanula JL (1996) Relationship of wood-feeding insects and coarse woody debris. In: McMinn J (ed) Proceedings of the workshop on coarse woody debris in southern forests: effects on biodiversity. United States Department of Agriculture, Athens, pp 55–81

Harmon ME (2009) Woody detritus its contribution to carbon dynamics of old-growth forests: the temporal context. In: Wirth C, Gleixner G, Heimann M (eds) Old growth forests. Springer, Berlin, pp 159–190

Harmon ME, Franklin JF, Swanson FJ, et al (1986) Ecology of coarse woody debris in temperate ecosystems, pp 133–302

Harmon ME, Krankina ON, Sexton J (2011) Decomposition vectors: a new approach to estimating woody detritus decomposition dynamics. Can J For Res 30:76–84

Hicke JA, Allen CD, Desai AR et al (2012) Effects of biotic disturbances on forest carbon cycling in the United States and Canada. Glob Change Biol 18:7–34. https://doi.org/10.1111/j.1365-2486.2011.02543.x

Holub SM, Spears JD, Lajtha K (2001) A reanalysis of nutrient dynamics in coniferous coarse woody debris. Can J For Res 31:1894–1902. https://doi.org/10.1139/x01-125

Huber C, Baumgarten M, Göttlein A, Rotter V (2004) Nitrogen turnover and nitrate leaching after bark beetle attack in mountainous spruce stands of the Bavarian Forest National Park. Water Air Soil Pollut Focus 4:391–414. https://doi.org/10.1023/B:WAFO.0000028367.69158.8d

Johnson CE, Siccama TG, Denny EG et al (2014) In situ decomposition of northern hardwood tree boles: decay rates and nutrient dynamics in wood and bark. Can J For Res 44:1515–1524. https://doi.org/10.1139/cjfr-2014-0221

Jouquet P, Traoré S, Choosai C et al (2011) Influence of termites on ecosystem functioning. Ecosystem services provided by termites. Eur J Soil Biol 47:215–222. https://doi.org/10.1016/J.EJSOBI.2011.05.005

Keith H, Wong S (2006) Measurement of soil CO_2 efflux using soda lime absorption: both quantitative and reliable. Soil Biol Biochem 38:1121–1131. https://doi.org/10.1016/j.soilbio.2005.09.012

Kurz WA, Dymond CC, Stinson G et al (2008) Mountain pine beetle and forest carbon feedback to climate change. Nature 452:987–990. https://doi.org/10.1038/nature06777

Laiho R, Prescott CE (2004) Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: a synthesis. Can J For Res 34:763–777. https://doi.org/10.1139/x03-241

Le Mellec A, Meesenburg H, Michalzik B (2010) The importance of canopy-derived dissolved and particulate organic matter (DOM and POM)—comparing throughfall solution from broadleaved and coniferous forests. Ann For Sci 67:411. https://doi.org/10.1051/forest/2009130

Levia DF, Frost EE (2006) Variability of throughfall volume and solute inputs in wooded ecosystems. Prog Phys Geogr 30:605–632. https://doi.org/10.1177/0309133306071145

Little NS, Blount NA, Londo AJ et al (2012a) Preference of formosan subterranean termites for blue-stained southern yellow pine sapwood. J Econ Entomol 105:1640–1644. https://doi.org/10.1603/EC12081

Little NS, Riggins JJ, Schultz TP et al (2012b) Feeding preference of native subterranean termites (Isoptera: Rhinotermitidae: Reticulitermes) for wood containing bark beetle pheromones and blue-stain fungi. J Insect Behav 25:197–206. https://doi.org/10.1007/s10905-011-9293-5

Little NS, Schultz TP, Diehl SV et al (2013) Field evaluations of subterranean termite preference for sap-stain inoculated wood. J Insect Behav 26:649–659. https://doi.org/10.1007/s10905-013-9380-x

Liu WH, Bryant DM, Hutyra LR et al (2006) Woody debris contribution to the carbon budget of selectively logged and maturing mid-latitude forests. Oecologia 148:108–117. https://doi.org/10.1007/s00442-006-0356-9

Lovett GM, Lindberg SE (1984) Dry deposition and canopy exchange in a mixed oak forest as determined by analysis of throughfall. J Appl Ecol 21:1013–1027

Magill AH, Aber JD (2000) Variation in soil net mineralization rates with dissolved organic carbon additions. Soil Biol Biochem 32:597–601. https://doi.org/10.1016/S0038-0717(99)00186-8

Mäkipää R, Rajala T, Schigel D et al (2017) Interactions between soil- and dead wood-inhabiting fungal communities during the decay of Norway spruce logs. ISME J 11:1964–1974. https://doi.org/10.1038/ismej.2017.57

Maynard DS, Crowther TW, King JR et al (2015) Temperate forest termites: ecology, biogeography, and ecosystem impacts. Ecol Entomol 40:199–210. https://doi.org/10.1111/een.12185

Moore LD, Van Stan JT, Gay TE et al (2016) Alteration of soil chitinolytic bacterial and ammonia oxidizing archaeal community diversity by rainwater redistribution in an epiphyte-laden *Quercus virginiana* canopy. Soil Biol Biochem 100:33–41. https://doi.org/10.1016/j.soilbio.2016.05.016

Morehouse K, Johns T, Kaye J, Kaye M (2008) Carbon and nitrogen cycling immediately following bark beetle outbreaks in southwestern ponderosa pine forests. For Ecol Manag 255:2698–2708. https://doi.org/10.1016/j.foreco.2008.01.050

National Oceanic and Atmospheric Administration (2010) National Centers for Environmental Information 1987–2010 US Climate Normals. National Oceanic and Atmospheric Administration, Silver Spring

Natural Resources Conservation Service (2015) Web soil survey. Natural Resources Conservation Service, Washington

Oksanen J, Kindt R, Legendre P, O'Hara RB (2005) Vegan: community ecology package

Pan Y, Birdsey RA, Fang J et al (2011) A large and persistent carbon sink in the world's forests. Science 80(333):988–993

Progar RA, Schowalter TD, Freitag CM, Morrell JJ (2000) Respiration from coarse woody debris as affected by moisture and saprotroph functional diversity in Western Oregon. Oecologia 124:426–431. https://doi.org/10.1007/PL00008868

Pryor SC, Barthelmie RJ (2005) Liquid and chemical fluxes in precipitation, throughfall, and stemflow: observations from a deciduous forest and a red pine plantation in the midwestern USA. Water Resour Res 163:203–227

R Development Core Team (2007) R: a language and environment for statistical computing. R Development Core Team, Vienna

Riggins JJ, Little NS, Eckhardt LG (2014) Correlation between infection by ophiostomatoid fungi and the presence of subterranean termites in loblolly pine (*Pinus taeda* L.) roots. Agric For Entomol 16:260–264. https://doi.org/10.1111/afe.12053

Robinson RC (1962) Blue stain fungi in lodgepole pine (*Pinus contorta* Dougl. var. latifolia engelm.) infested by the mountain pine beetle (*Dendroctonus monticolae* hopk.). Can J Bot 40:609–614. https://doi.org/10.1139/b62-056

Rosengaus RB, Guldin MR, Traniello JFA (1998) Inhibitory effect of termite fecal pellets on fungal spore germination. J Chem Ecol 24:1697–1706. https://doi.org/10.1023/A:1020872729671

Schowalter T, Caldwell B, Carpenter S et al (1992a) Decomposition of fallen trees: effects of initial conditions and heterotroph colonization rates. In: Singh K (ed) Tropical ecosystems: ecology and management. Wiley Eastern, New Delhi, pp 371–381

Schowalter T, Caldwell B, Carpenter S et al (1992b) Decomposition of fallen trees: effects of initial conditions and heterotroph colonization rates. In: Singh K, Singh J (eds) Tropical ecosystems: ecology and management. Wiley Eastern Limited, New Delhi, pp 373–383

Siegert CM, Levia DF, Hudson SA et al (2016) Small-scale topographic variability influences tree species distribution and canopy throughfall partitioning in a temperate deciduous forest. For Ecol Manag 359:14. https://doi.org/10.1016/j.foreco.2015.09.028

Siegert CM, Levia DF, Leathers DJ et al (2017a) Do storm synoptic patterns affect biogeochemical fluxes from temperate deciduous forest canopies? Biogeochemistry 132:273–292. https://doi.org/10.1007/s10533-017-0300-6

Siegert CM, Renninger HJ, Karunarathna AA, et al (2017b) Biogeochemical hotspots around bark-beetle killed trees. In: Proceedings of the 19th Biennial Southern Silvicultural Research Conference. Blacksburg, VA **(in Press)**

Silva IC, Rodriguez HG (2001) Interception loss, throughfall and stemflow chemistry in pine and oak forests in northeastern Mexico. Tree Physiol 21:1009–1013. https://doi.org/10.1093/treephys/21.12-13.1009

Smyth CE, Titus B, Trofymow JA et al (2016) Patterns of carbon, nitrogen and phosphorus dynamics in decomposing wood blocks in Canadian forests. Plant Soil 409:459–477. https://doi.org/10.1007/s11104-016-2972-4

Sollins P, Cline SP, Verhoeven T et al (1987) Patterns of log decay in old-growth Douglas-fir forests. Can J For Res 17:1585–1595. https://doi.org/10.1139/x87-243

Spears JD, Holub SM, Harmon ME, Lajtha K (2003) The influence of decomposing logs on soil biology and nutrient cycling in an old-growth mixed coniferous forest in Oregon, USA. Can J For Res 33:2193–2201. https://doi.org/10.1139/x03-148

Sugimoto A, Bignell DE, MacDonald JA (2000) Global impact of termites on the carbon cycle and atmospheric trace gases. Termites: evolution, sociality, symbioses, ecology. Springer, Dordrecht, pp 409–435

Swift M, Boddy L (1984) Animal–microbial interactions in wood decomposition. In: Anderson J, Rayner A, Walton D (eds) Invertebrate–microbial interactions. Cambridge University Press, Cambridge, pp 89–131

Tang J, Bolstad PV, Desai AR et al (2008) Ecosystem respiration and its components in an old-growth forest in the Great Lakes region of the United States. Agric For Meteorol 148:171–185. https://doi.org/10.1016/j.agrformet.2007.08.008

Ulyshen MD (2015) Insect-mediated nitrogen dynamics in decomposing wood. Ecol Entomol 40:97–112. https://doi.org/10.1111/een.12176

Ulyshen MD, Wagner TL (2013) Quantifying arthropod contributions to wood decay. Methods Ecol Evol 4:345–352. https://doi.org/10.1111/2041-210x.12012

Ulyshen MD, Wagner TL, Mulrooney JE (2014) Contrasting effects of insect exclusion on wood loss in a temperate forest. Ecosphere 5:1–15. https://doi.org/10.1890/ES13-00365.1

Ulyshen MD, Shefferson R, Horn S et al (2017) Below- and aboveground effects of deadwood and termites in plantation forests. Ecosphere 8:e01910. https://doi.org/10.1002/ecs2.1910

Valentini R, Matteucci G, Dolman AJ et al (2000) Respiration as the main determinant of carbon balance in European forests. Nature 404:861–865. https://doi.org/10.1038/35009084

Van Stan JT, Levia DF, Inamdar SP et al (2012) The effects of phenoseason and storm characteristics on throughfall solute washoff and leaching dynamics from a temperate deciduous forest canopy. Sci Total Environ 430:48–58. https://doi.org/10.1016/j.scitotenv.2012.04.060

Wardle DA (2002) Communities and ecosystems: linking the aboveground and belowground components. Princeton University Press, Princeton

Wingfield M, Seifert K, Webber J (1993) Ceratocystis and Ophiostoma: taxonomy, ecology, and pathogenicity. American Phytopathological Society Press, St. Paul

Zeng H, Chambers JQ, Negrón-Juárez RI et al (2009) Impacts of tropical cyclones on US forest tree mortality and carbon flux from 1851 to 2000. Proc Natl Acad Sci USA 106:7888–7892. https://doi.org/10.1073/pnas.0808914106