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Wood decomposition by microbes and macroinvertebrates, and soil CO_2 efflux vary in response to throughfall reduction and fertilization in a loblolly pine (*Pinus taeda* L.) plantation

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ABSTRACT

Climate and nutrient availability modify the rate of carbon loss from soil and detrital pools in forest ecosystems. In a managed loblolly pine (*Pinus taeda* L.) plantation, we examined how reduced throughfall and fertilization affected wood decomposition and soil CO_2 efflux. For ~1.5 years, soil CO_2 efflux and the mass loss of *Pinus* wood sticks were examined in relation to soil temperature and moisture and the accumulation of soil NH_4^+ and NO_3^- for a factorial combination of two treatments: a 30% throughfall reduction (TR) treatment, fertilization with nutrient additions typical for this plantation type (224 kg/ha N, 64 kg/ha P and 67 kg/ha K), and a combined treatment. Wood mass loss was estimated separately for substrates affected by only microbes and those with visual signs (e.g. tunnels) of macroinvertebrate consumption. For the 426 days of the experiment, wood sticks decomposed only by microbes lost 3–6% of their mass while those also tunneled by macroinvertebrates lost 35–45% of their mass. By the end of the study macroinvertebrates had tunneled into 54% of all sticks across treatments. Because of macroinvertebrates, fertilization increased wood decomposition overall, despite significantly lower decomposition occurring in fertilized plots for sticks only decomposed by microbes. The TR treatment decreased wood decomposition but there was an interaction with location, where inhibition occurred near trees and under throughfall excluders but not at the midpoint between two planted rows. Wood sticks placed inside a collar used to measure soil CO_2 efflux also decomposed significantly slower than all other locations. Soil CO_2 efflux was inhibited by fertilization, primarily in August when temperatures were at the annual maximum. The depressed soil CO_2 efflux from fertilization may have been the result of increased N availability, as fertilization stimulated NO_3^- production. The main effect of TR on soil CO_2 efflux or N availability was not significant, but the TR effect on soil CO_2 efflux interacted with time, reflecting generally lower efflux on different dates relative to non-TR treatments. These results suggest ecosystem C loss from soil CO_2 efflux was relatively insensitive to throughfall reduction, but wood decomposition was sensitive to both fertilization and lowered moisture availability. However for wood decomposition, the positive fertilization effect was dependent on macroinvertebrates, whose response to fertilization was the opposite to that of both microbes and soil CO_2 efflux. Predicting the fate of woody detritus in loblolly pine plantations may require models that include the response of macroinvertebrates to climate and management.

1. Introduction

Forest carbon (C) cycling is a critical component of the global C cycle (Stocker et al., 2013). The size of the pools of C found in forest soil, biomass and detrital litter are greater than that of the atmospheric pool's 750 Pg C, with biomass and detrital litter containing ~360 Pg C (Malhi et al., 2002), and forest soils containing nearly 500 Pg C (Dixon et al., 1994). In general intact forests remove more C than they lose, where ecosystem respiration is less than or equal to annual photosynthesis (Luyssaert et al., 2007). However in managed forests that undergo periodic harvesting, the forest can become a source of C when decomposer activity increases C loss from residual wood and litter, and when an increase in soil CO_2 efflux is predominately from heterotrophic respiration (Bracho

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et al., 2012; Noormets et al., 2012). Understanding the control on this ecosystem C loss is critical to estimating the effects of management on managed forest C balance.

The area of forests managed for wood production has increased worldwide over the last several decades (Fao, 2012), with the southeastern United States leading in the percentage of land area converted to intensively managed pine plantations (Wear and Greis, 2002). Managed pine forests are critical to regional C budgets, acting as C sinks between harvest cycles (Bracho et al., 2012). Management decisions in southern pine forests can affect the amount of ecosystem C accumulated under intensive management, with fertilizer increasing biomass and detrital pools of C (Vogel et al., 2011). However, increased fertilizer prices have reduced the area of plantations being fertilized (Fox et al., 2007), potentially leading to lower rates of C accumulation in tree biomass. Less predictable however, are how rates of C loss from detrital pools and soil organic matter will be affected by changing fertilization practices, as nutrient additions can have complex effects on wood and litter decomposition and soil CO_2 efflux.

Fertilization, especially nitrogen addition, can decrease (Kaufert and Behr, 1942; FOG, 1988) or increase (Downs et al., 1996; Micks et al., 2004; Allison et al., 2009; Bebber et al., 2011; Clay, 2013) wood decomposition. The negative effects of N addition on decomposition are often associated with reduced enzyme production by fungi (Sinsabaugh, 2010). Fertilization decreased soil CO_2 efflux in tropical forests (Giardina et al., 2003) and temperate forests (Olsson et al., 2005; Phillips and Fahey, 2007), and can occur because of reduced heterotrophic and autotrophic respiration. Negative effects of N addition on autotrophic root respiration have been attributed to less plant allocation of C to roots and the rhizosphere (Janssens et al., 2010). Nitrogen addition has also decreased heterotrophic respiration by reducing microbial enzyme activity (Olsson et al., 2005). Relative to microbes, less is understood about the response of macroinvertebrates to fertilization. Nitrogen addition doubled termite abundance in a West African grassland (Zida et al., 2011) and decreased macroinvertebrates in a northern temperate forest (Gan et al., 2013), however, similar studies are lacking for intensively managed pine plantations.

Decomposition and soil CO_2 efflux are both affected by abiotic environmental conditions (temperature, soil moisture) and biotic factors (types and activity of decomposer organisms) (Cornwell et al., 2009; Bradford et al., 2014). Environmental factors exert strong effects on woody debris decomposition (Kueppers and Harte, 2005; Cornwell et al., 2009). Soil warming increased wood decay rates in temperate forests (Mackensen et al., 2003; Berbeco et al., 2012), and drought decreased decomposition or decomposer activity in many ecosystems (Berg and McClaugherty, 2008; Manzoni et al., 2012). Drought has also increased wood mass loss in a dry temperate forest in the western US (Barker, 2008) and a rainforest in Puerto Rico (Torres and González, 2005). Contradictory effects of drought on woody debris decomposition are possibly explained by inhibited enzyme activity, increased aerobic condition, stimulated fungal biomass or differential response by microbes or macroinvertebrates.

Most wood decomposition experiments have focused on microbes as the primary decomposers, leaving macroinvertebrate response to climate a critical uncertainty in wood decomposition models. A large body of research in boreal and cool temperate forests suggests that microbes are responsible for more than 90% of all litter decomposition (Berg and McClaugherty, 2008), with fungi being the controlling decomposers for wood decomposition (Clausen, 1996). In contrast, researchers in tropical forests have estimated that macroinvertebrates are responsible for at least half of wood decomposition (Meyer et al., 2011), causing the release of about 1.9 Pg C yr^{-1} (Cornwell et al., 2009). Less research about macroinvertebrate decomposition has been done in temperate regions but termites in particular may be responsible for significant amounts of decomposition in North American temperate forests (Stamm, 2006; Ulyshen et al., 2014; Neupane et al., 2015). In general, macroinvertebrates may have a different response to climate than free-living microbes because some like termites can build nests to protect their colony from extreme environments, and most can avoid climate extremes through vertical migration. When microbes and macroinvertebrates have been studied together, drought has had both positive and negative effects on wood decomposition by both microbes (Kaarik, 1974; Barker, 2008; Alster et al., 2013; A'Bear et al., 2014) and macroinvertebrates as the primary decomposer (Torres and González, 2005; Jamali et al., 2011).

The objective of this study was to determine the influence of reduced moisture availability and fertilization on wood decomposition and soil CO_2 efflux in a managed loblolly pine (*Pinus taeda* L.) plantation in southeastern Oklahoma, USA. In addition, the relative decomposition response of microbes and macroinvertebrates to treatment was estimated by separating wood decomposition assays into two groups: ones where the mass loss of wood sticks occurred without macroinvertebrate tunnels, which were considered driven only by microbial decomposition, and wood sticks with evidence of macroinvertebrate feeding, primarily tunnels. This latter group was classified as being decomposed by both microbes and macroinvertebrates. We hypothesized that throughfall exclusion would decrease soil CO_2 efflux and wood decomposition and similarly, fertilization would decrease soil CO_2 efflux and decomposition.

2. Methods

2.1. Study sites

The study site was located near Broken Bow, Oklahoma (34°01′N, 94°49′W). From 1982 to 2013, the region had a mean annual temperature of 16.6 °C and a yearly summed precipitation of 130 cm (NOAA National Weather Service – http://www.ncdc.noaa.gov/cdo-web/datasets/ANNUAL/locations/ZIP:74745/detail, accessed February 2014). The average daily minimum temperature in January was −1.6 °C while the daily average maximum temperature in August was 34.2 °C. The surface (0–24 cm) soil texture was a fine sandy loam and the argillic subsoil texture was a clay loam. The soil series is Ruston, which is a Typic Paleudult. The argillic horizon had mottling and other redoximorphic visual signs beginning around 50 cm, suggesting the site was poorly drained, despite the upland position of the plots and a range in slope of 3–8%.

2.2. Study design

This research was conducted within a loblolly pine plantation that had a mixture of open-pollinated first-generation genotypes from the Western Gulf region of the loblolly pine range (Oklahoma, Arkansas, Louisiana, Texas) (Will et al., 2015). Loblolly pine seedlings were planted in rows in January of 2008 at an approximate spacing of 2 m between trees and 3 m between rows. The plantation had received site preparation and competition control prior to our study's installation. In August 2007 before planting, a broadcast application of 680 g ha^{-1} of Chopper® (27.6% imazapyr) (BASF Corporation, Florham Park, NJ, USA) plus 2.8 L ha^{-1} of glyphosate (53.8% active ingredient) was conducted. Prescribed burning was then done in October 2007. In November 2007 subsoiling was done along contours to ~50–60 cm depth with a D8 Caterpillar dozer and attached subsoiling shanks (Caterpillar Corporate, Peoria, IL, USA), with seedlings planted in the furrows. Additional woody plant and herbaceous weed control was conducted in March

2008, with the broadcast application of 420 g ha^{-1} of Arsenal® (27.6% imazapyr) (BASF Corporation, Florham Park, NJ, USA) and 175 g ha^{-1} of Oust Extra® (56.25% Sulfometuron methyl, 15.0% Metsulfuron methyl) (E.I. Du Pont De Nemours and Company, Wilmington, DE, USA).

The study design was a randomized complete block design with four blocks and four treatments. Treatment plots were set up in 2011. Each plot was approximately 0.08 ha with an outside buffer area and an internal measurement plot (around 0.04 ha). Before treatment establishment, all competing woody understory vegetation was killed with 2% glyphosate by directed spray, and the plots were maintained weed free for the duration of the experiment with follow-up directed spray. The experimental design was a factorial combination of fertilization and throughfall reduction. Fertilization (432 kg ha^{-1} urea, 140 kg ha^{-1} diammonium phosphate and 112 kg ha^{-1} potash) was conducted in April 2012 to achieve 'optimum' nutrition as reflected by the elemental rates of 224 kg N ha^{-1}, 27 kg P ha^{-1} and 56 kg K ha^{-1}. To reduce nitrogen volatilization, Agrotain Ultra (Koch Agronomic Services, LLC, Wichita, KS) was applied at a rate of 0.43 ml kg^{-1} of urea. A micronutrient mix was also added (6% sulfur, 5% boron, 2% copper, 6% manganese, and 5% zinc; Southeast Mix, Cameron Chemicals, Inc., Virginia Beach, VA) at a rate of 22.4 kg ha^{-1}. Plastic sheeted troughs were installed both in open areas between planted rows and below the tree canopy in June of 2012 to divert approximately 30% of precipitation and throughfall off the plot. This treatment is referred to as 'throughfall reduction' (TR) hereafter. Two 0.5 m wide troughs, separated by an open space 0.5 m wide, were elevated between 0.6 and 1.2 m high above the soil surface (depending on slope and position along the trough run). Both troughs were ~0.5 m from a planting row, running parallel to a row with a slight height change that allowed for the captured throughfall to be gravimetrically funneled away from the plots. Will et al. (2015) described trough construction in more detail. In each of four blocks, there was a plot with no rainfall manipulation or fertilization (control (C)), a TR, an optimum fertilization (F), and a combined F + TR plot.

2.3. Field measurements

Measurements of soil CO_2 efflux were conducted over 18 months from May 2012 to October 2013. Eight 20 cm diameter polyvinyl chloride measurement collars were permanently installed at random locations within the measurement plot, with collar edges placed to a mineral soil depth of ~3–4 cm. Soil CO_2 efflux was measured with an infra-red gas analysis system (Li-Cor 6200, Li-Cor Environmental, Lincoln, NE). Measurements were conducted approximately every 4–8 weeks. Soil temperature at 10 cm depth, and volumetric soil moisture (Hydrosense, Campbell Scientific Inc., Logan, UT) across the depth interval 0–12 cm, were measured concurrently with soil CO_2 efflux measurements.

To assess the response of decomposition to treatments and spatial variation, common wood substrates (southern pine wood sticks with the dimension of 12.7 cm × 1.8 cm × 0.6 cm) were placed in August 2012. Sticks were cut from two pieces of dimensional lumber (2.54 cm × 30.5 cm × 243.8 cm) that were pulled from the same bundle. It is highly likely these sticks derived from *P. taeda* but shortleaf pine (*Pinus echinata* Mill.) is also harvested in the region. Sticks were dried at 105 °C for two days before placement in the field and the initial dry weight for each stick was recorded. For the field placement of sticks, six trees were randomly selected in each plot and a set of two sticks were set close, middle and far from the tree. The 'close' sticks were placed at the base of a tree, while the 'far' sticks were located exactly in the middle of two tree rows or about 70 cm from the base of a tree, and the 'middle' sticks were placed ~0.5 m from the tree and directly under the trough when present. Another six sticks were put on the soil surface inside the soil CO_2 efflux collars. Half of the wood sticks were collected after 216 days and the other half collected after 426 days. On removal, sticks were cleaned, assessed for consumption by macroinvertebrates, oven dried at 105 °C for 48 h, and weighed to determine the woody mass loss.

The ammonium and nitrate concentration response to treatments were measured on exchange membranes. Three pairs of cation and anion exchange membranes (5 cm × 10 cm) (GE Osmotics, Inc., Westborough MA, US) were installed in random locations. Resins were placed from the surface to ~7.1 cm soil depth adjacent to each other and at a 45° angle from the soil surface. The membranes were installed and collected every 3–4 months from August 2012 to September 2013. To extract ammonium and nitrite, deionized H_2O was first used to rinse membranes of soil particles and then each pair of cation and anion exchange membranes were combined and were shaken for 1 h in 1*M* KCl. Ammonium and nitrate concentrations were analyzed with an Eon Microplate Spectrophotometer (Bio-Tek, Winooski VT, US).

2.4. Calculations

The woody mass loss of all (D_{all}) individual sticks before separation by tunnel presence was calculated as follows:

$$D_{all} = \frac{M_i - M_T}{M_i} \times 100\% \quad (1)$$

where M_i is the initial weight of the sticks, and M_T (T = 216 days or 426 days) is the weight of the stick collected after 216 days or 426 days. Subsequent analysis of the effects of the decomposer community were conducted two ways, using individual sticks within treatments, and averages of sticks within plots, as each approach offers different sensitivity to the change in sample size caused by varying levels of macroinvertebrate tunneling.

The decomposer (d) community effect was estimated for microbes and macroinvertebrates, where sticks were separated into two groups: the decomposition of sticks without macroinvertebrates tunnels was microbial decomposition (D_m), while the decomposition of sticks with macroinvertebrate tunnels was considered contributed by both microbes and macroinvertebrates (D_{m+m}). Similar to the all sticks estimation:

$$D_m = \frac{M_{mi} - M_{mT}}{M_{mi}} \times 100\% \quad (2)$$

$$D_{m+m} = \frac{M_{mmi} - M_{mmT}}{M_{mmi}} \times 100\% \quad (3)$$

To reduce the sensitivity of results to the varying colonization rates of macroinvertebrates, the total carbon pool mass loss of each plot (D_{plot}) and the mass loss caused by a decomposer (D, microbes or macroinvertebrates) was summed, where:

$$D_{allplot} = \frac{\sum M_i - \sum M_T}{\sum M_i} \times 100\% \quad (4)$$

$$D_{mplot} = \frac{\sum M_{mi} - \sum M_{mT}}{\sum M_{mi}} \times 100\% \quad (5)$$

$$D_{m+mplot} = \frac{\sum M_{mmi} - \sum M_{mmT}}{\sum M_{mmi}} \times 100\% \quad (6)$$

and $\sum M_i$ is the initial sum weight of sticks in each plot, and $\sum M_T$ is the sum weight of all sticks after 216 days or 426 days in each plot; $\sum M_{mi}$ is the initial sum weight of the sticks that attacked only by microbes in each plot, while $\sum M_{mT}$ is the sum weight of sticks that attacked by microbes after 216 days or 426 days in each plot;

$\sum M_{mmi}$ is the initial sum weight of the sticks that were attacked by both microbes and macroinvertebrates in each plot, while $\sum M_{mmT}$ is the sum weight of sticks that attacked by both microbes and macroinvertebrates after 216 days or 426 days in each plot.

2.5. Statistical analyses

The effects of fertilization, TR, and time along with their interactions on macroinvertebrate's attack probability (percentage of tunneled wood) were assessed using logistic regression. The effect on wood mass loss of fertilization, TR, location and time on D_{all}, D_m, and D_{m+m} were assessed using linear mixed model conducted in the 'lme4' package in R (Bates, 2010). Fertilization, TR, location, and time along with their interactions were included as fixed effects, while blocks and subjects nested within block were included as random effects. Subjects were defined as unique locations of wood sticks, with the only difference being the collection date. Sticks from each location were collected once for each date, and considered a repeated measurement. Within each collection date, a three-way ANOVA with block as a random effect was used to test the treatment effects and post hoc contrasts (Tukey HSD) were used to evaluate differences among levels of locations. The effects of fertilization, TR, location, time and their interaction on D_{plot}, D_{mplot}, $D_{m+mplot}$ were analyzed using three-way ANOVA with block as a random effect. Logit transformation was used for D_{all}, D_m, D_{m+m}, D_{plot}, D_{mplot}, $D_{m+mplot}$ to meet the assumption of normality of the non-binomial proportion data (Warton and Hui, 2011).

Accumulated ammonium and nitrate were analyzed by three-way ANOVA. Fertilization, TR, and date intervals, along with their interactions were included as fixed effects, and block was included as a random effect. Lambda of −2 was valued by Box-cox power transformation in R to correct heterogeneity of ammonium and nitrate accumulation before conducting the ANOVA. Tukey HSD multiple comparisons were used to determine level difference of date effects and the interaction of fertilization and date.

The effects of fertilization and TR on seasonal measurements of soil CO_2 efflux were evaluated using linear mixed-effects model in R. Fertilization, TR, and time, along with their interactions were included as fixed effects, soil temperature and soil moisture were included as covariates, two random effects were blocks and collars nested within blocks. Log transformation was used for soil CO_2 efflux assessed by Box-cox power transformation. Significance of effects and model selection were evaluated in 'lmerTest' package (Kuznetsova et al., 2013). Multiple comparisons were used to determine the interactive effects between fertilization and dates by 'multcomp' package (Hothorn et al., 2014). Exponential relationship between soil CO_2 efflux and soil temperature, soil CO_2 efflux and soil moisture were analyzed by testing the linear regression of log transformed soil CO_2 efflux and the two variables. The effects of fertilization and TR on seasonal measurements of soil temperature and moisture were evaluated using linear mixed-effects model. Post hoc contrasts (Tukey HSD) were used to value interactive effects between fertilization and TR, fertilization and T or TR and T. All error terms are standard error of the mean. All statistical analysis were conducted in R version 3.1.1 (Team, 2010).

3. Results

3.1. Climate, soil temperature and soil moisture

The highest monthly precipitation was measured in July 2013 (21.6 cm) and the lowest monthly precipitation of 0.7 cm was measured in May 2013 (Fig. 1a). The highest air temperature (26.1 °C) was measured in August 2013 followed by an August 2012 temperature of 25.7 °C. The lowest air temperature was in January 2013 (6.4 °C).

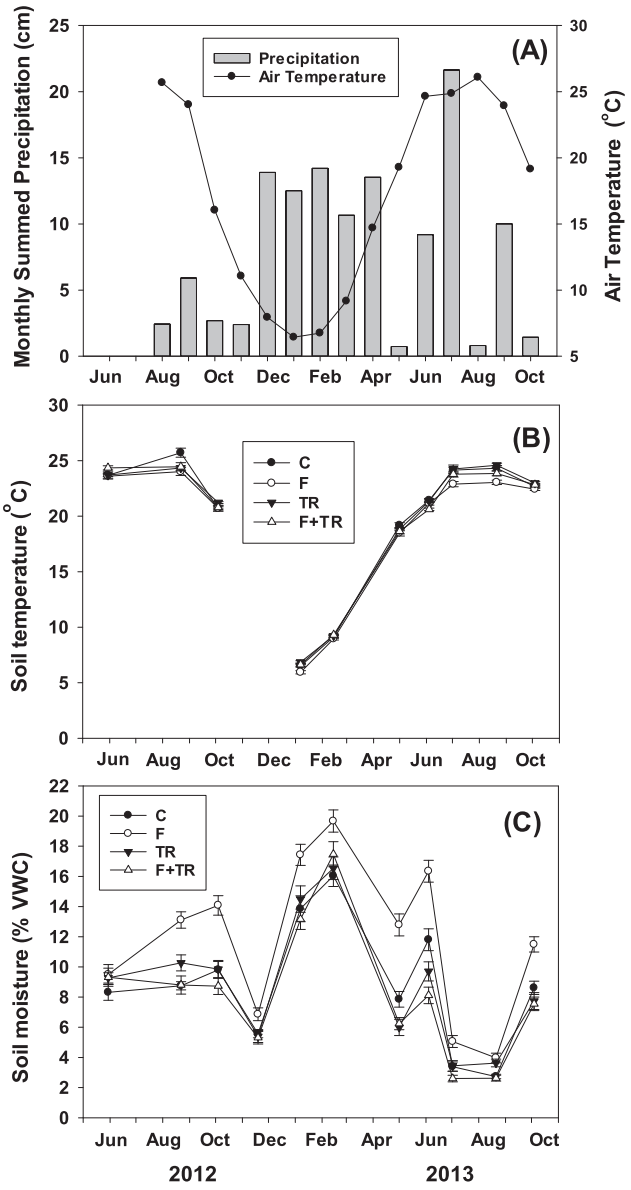

Fig. 1. Air temperature and precipitation (a), 10 cm soil temperature (b) and soil moisture (c) from May 2012 to October 2013. Air temperature and precipitation measurement began in August 2012.

Seasonal variation in soil temperature followed that of air temperature, with the lowest soil temperature (6.5 °C) measured in January 2013 (Fig. 1b). The highest soil temperature was in August 2012 (24.4 °C) followed by an August 2013 temperature of 24.0 °C. A fertilization × time interaction indicated that the fertilization treatments decreased soil temperature in January 2013 (0.40 °C, $P < 0.001$) and August 2013 (0.87 °C, $P = 0.02$) relative to the unfertilized treatments (C,TR). There was a significant interaction between TR and time such that TR and TR + F increased soil temperature in January 2013 by 0.22 °C ($P < 0.001$) relative to the control and fertilized treatment.

Volumetric soil water (0–12 cm) content varied from 0.2 to 29.4%, with the highest soil moisture found in February 2013 and the lowest in August 2013 (Fig. 1c). There was a significant F × TR interaction such that fertilization only plots had increased soil moisture ($P < 0.001$), but F + TR plots decreased soil moisture

(P = 0.003). The fertilization main effect also interacted with time, represented by soil moisture increases in February 2013 (20%, P = 0.006) and in May 2013 (38%, P < 0.001) relative to the unfertilized treatments (C, TR). Although the main effect of the TR treatment was not significant, it interacted with time, decreasing soil moisture relative to the C and F treatments in October 2012 (22%, P = 0.015), May 2013 (41% P < 0.01), June 2013 (37%, P < 0.001), July 2013 (29%, P < 0.001) and October 2013 (24%, P = 0.004).

3.2. Soil CO_2 efflux

On average, fertilization significantly decreased soil CO_2 efflux rate 20% from 2.84 μmol CO_2 m^{-2} s^{-1} to 2.28 μmol m^{-2} s^{-1} (P < 0.001, Table 1, Fig. 2). Fertilization and time had an interactive effect on soil CO_2 efflux because the separation between the fertilized and unfertilized treatments disappeared when soil temperatures were lower (P < 0.001, Table 1, Fig. 2). Multiple comparisons showed that fertilization significantly reduced soil CO_2 efflux in August 2012 by 0.83 μmol m^{-2} s^{-1} (P = 0.04) and August 2013 by 1.36 μmol m^{-2} s^{-1} (P < 0.01). TR and time also had an interactive effect on soil CO_2 efflux (P < 0.001, Table 1, Fig. 2), which reflected that in August 2013 the TR treatment was less than the control followed by a change in rank order for TR and the Control after a period of rain (Fig. 1a).

Soil CO_2 efflux showed a seasonal pattern that strongly correlated with soil temperature (r^2 = 0.559, P < 0.001, not shown) across treatments. During the hottest times in August of 2012 and 2013, fertilization decreased soil CO_2 efflux by 20% and 47%, respectively. Compared to temperature, across all treatments soil moisture explained little variance in soil CO_2 efflux (r^2 = 0.097).

3.3. Wood decomposition

3.3.1. The ratio of tunneled wood

The number of wood sticks tunneled into by macroinvertebrates significantly increased from 50 to 158 sticks from 216 days to 426 days, or on average across treatments, from 13% to 54% of the recovered sticks (Tables 2 and 3; P < 0.001). Fertilization significantly increased the ratio of tunneled wood after 426 days (Tables 2 and 3; P = 0.007), and TR significantly decreased the ratio of wood having tunnels (Tables 2 and 3; P = 0.008).

3.3.2. Individual wood stick decomposition

Both fertilization and TR treatments significantly affected microbial only and microbial + macroinvertebrate decomposition, but in different ways and there were no significant effects on decomposition of the wood sticks attacked by macroinvertebrates. Fertilization decreased D_m (Fig. 3b, p < 0.001) but increased the D_{all} decomposition (Fig. 3a, p = 0.047) (Table 4). Mean wood mass loss from D_{m+m} was much higher in the fertilization treatment plots (26% by March 2013 and 43% by October 2013) compared to control plots (18% by March and 39% by October), however, the effects were not significant (Fig. 3c, p = 0.686). TR reduced all stick decomposition from 15% to 12% (Fig. 3a, p < 0.001) and microbial decomposition from 3% to 2% (Fig. 3b, p < 0.001) averaged over the two collection periods.

Besides the main treatment effects, we also tested the location effects on individual wood decomposition (Table 4, Fig. 4a–c). Location of sticks (three distances to the tree and one within respi-

Table 1
Summary of linear mixed model results testingfixed effects of (fertilization (F), Throughfall Reduction (TR), time and their combination) and random effect (collar nested in each block) on soil CO_2 efflux.

Treatment	Df		Soil CO_2 efflux
	N	D	
Soil Temperature	1	1136	**<0.001**
Soil moisture	1	1171	0.341
F	1	135	**<0.001**
TR	1	137	0.976
Time	9	1066	**<0.001**
F * TR	1	137	0.148
F * Time	9	1048	**<0.001**
TR * Time	9	1050	**<0.001**
F * TR * Time	9	1047	0.054

Significant p-values (p < 0.05) are in bold.

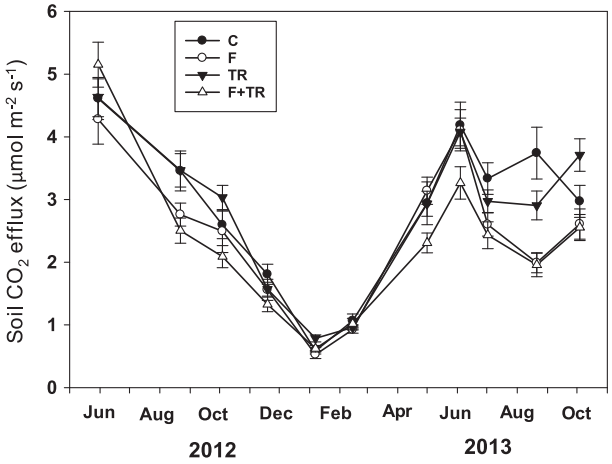

Fig. 2. Treatments effects on soil CO_2 efflux from May 2012 to October 2013.

Table 2
Summary of average number of recovered wood sticks with tunnels and the percentage of tunneled wood in each plot by treatment at different collection times for treatments (Fertilization (F), Throughfall Reduction (TR) and the combined treatment).

Time (Days)	Treatment	Number of sticks with tunnels (#)	Tunneled sticks (%)
216	C	15	16
	F	15	16
	TR	8	9
	F + TR	12	13
426	C	37	59
	F	51	67
	TR	25	32
	F + TR	45	59

Table 3
Summary of P values (>Chi) from generalized linear model (logistic regression) testing the treatment and time effects on macroinvertebrate's attack ratio (degrees of freedom equals 1 for all treatments) on wood sticks for treatments (Fertilization (F), Throughfall Reduction (TR) and the interactions).

Treatment	Tunneled sticks
Time	**<0.001**
F	**0.007**
TR	**0.008**
F × TR	0.052
F × Time	0.174
TR × Time	0.535
F × TR × Time	0.647

Significant p-values (p < 0.05) are in bold.

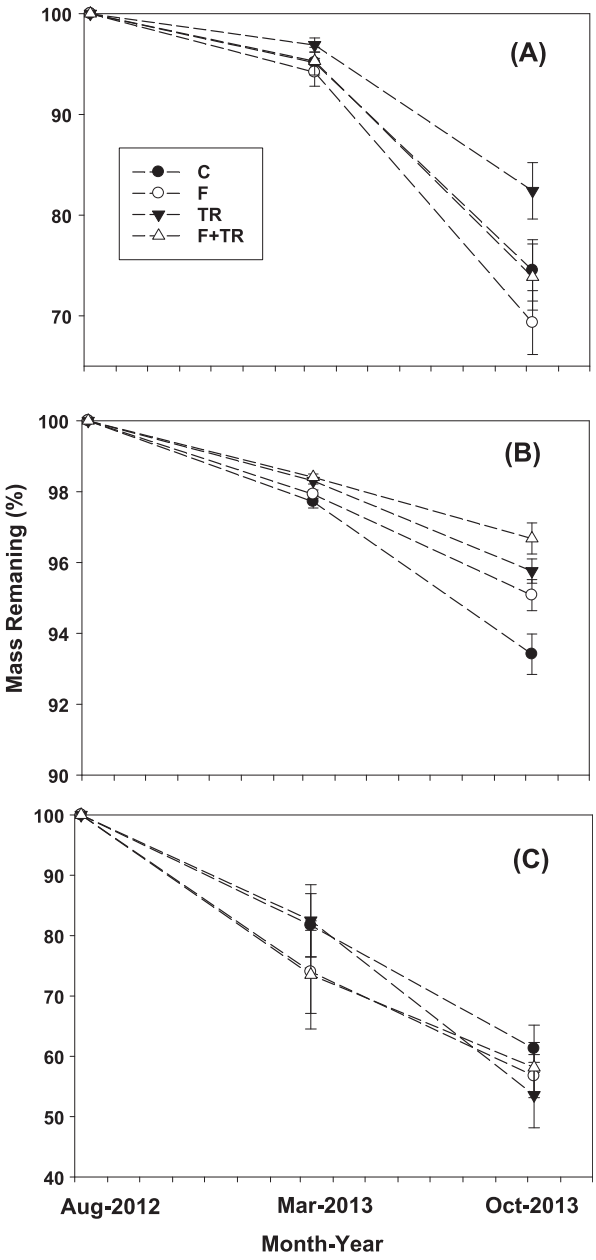

Fig. 3. Treatment effects over time on mass loss of the individual wood sticks (n = 16) for (A) all sticks (B) microbial-only decomposed sticks (without tunnels) and (C) sticks decomposed by both microbes and macroinvertebrates (with tunnels). Note change in scale of Y-axis.

ration collars) had significant effects on D_{all} ($p < 0.001$), D_m ($p < 0.001$), and D_{m+m} ($p = 0.006$) (Table 4). Post hoc analysis revealed that all three estimates indicated faster decomposition closer to the tree than the other locations, especially during the last time period. D_{all} and D_m in the respiration collars decomposed 33% and 19% less compared to wood decomposition outside the collars. Collars did not have an effect on D_{m+m}. These results suggested that tree distance had a negative effect on both microbial and macroinvertebrate decomposition while respiration collars had a negative effect on microbial decomposition both alone and in combination with macroinvertebrates. TR and location had a significant interaction effect ($P = 0.020$; Table 4). Post hoc analysis showed that all sticks inside collars decomposed less compared to the location nearest the tree ($P = 0.047$) for the control plots ($P = 0.035$) and TR plots ($P = 0.012$). While all wood decomposition in the middle location was not different from near or far both in the control plot and TR plot.

3.3.3. Plot level wood mass loss

For whole plot level wood mass loss, only the main effect of fertilization significantly decreased mass loss by microbes (Table 5). Fertilization tended to increase D_{m+m} decomposition, but not significantly ($P = 0.121$). Similar to the carbon mass loss by each wood stick, the negative effect of fertilization on plot's carbon mass loss for microbes only was overwhelmed by the macroinvertebrates' effect, resulting in a non-significant trend toward more wood mass loss under fertilization for all sticks (Fig. 5a). Time also interacted with fertilization for sticks only decomposed by microbes (Table 5), reflecting that the negative effect of fertilization was observed at the 426 day collection (Fig. 5b).

3.4. Ammonium and nitrite concentration

Neither fertilization nor drought affected ammonium accumulation (Table 6). However, ammonium accumulation decreased significantly across dates ($P < 0.001$, Table 6, Fig. 6a).

Across all time periods, ammonium accumulation from August 2012 to December 2012 was significantly higher than the other three intervals ($P < 0.001$). Fertilization had a positive effect on nitrate accumulation ($P = 0.006$, Table 6, Fig. 6b). Time also had a significant impact on nitrate accumulation ($P = 0.002$, Table 6) and a multiple comparisons test showed that less nitrate accumulated on the resin strips from March 2013 to June 2013 than what accumulated from December 2012 to March 2013 ($P = 0.006$)

4. Discussion

4.1. Wood decomposition

Our study demonstrates that microbes and macroinvertebrates may differ in how each responds to fertilization, and to a lesser degree, reduced precipitation. Fertilization negatively affected microbial decomposition but a positive response was observed for tunnel excavation by macroinvertebrates. In the TR treatments microbial decomposition was suppressed, but the decomposition rate caused by the combined microbial + macroinvertebrate community was not affected even as the number of tunnels was suppressed. This suggests that the extent of macroinvertebrate foraging was inhibited by the TR treatment, but once a stick was found, the rate of microbial + macroinvertebrate decomposition was not different from the other treatments.

We cannot say definitively what macroinvertebrate was responsible for the tunneling at this site because we did not perform continuous trapping and some beetle and ant species may consume or excavate wood (Similä et al., 2003); however we primarily found termites on sticks during both collections (Zhang personal observation). The subterranean termite *Reticulitermes flavipes* (Kollar) was identified (B. Puckett, personal communication) in the tunnels of a number of wood sticks from the last sample collection, and the tunnels were generally consistent with termite feeding. Recent research in the southeastern United States has identified regional wood decomposition as being sensitive to termite activity (Ulyshen and Wagner, 2013; Bradford et al., 2014) and our results suggest that termite driven wood-decomposition may be sensitive to fertilization and throughfall reduction.

Macroinvertebrate contributions to wood decomposition have been ignored in many past studies (Frouz et al., 2015), and there is a general lack of information on how fertilization affects this decomposer community. Similar to our findings of a positive fertilization effect on macroinvertebrates, Zida et al. (2011) found that

Table 4
Summary of mixed model analysis of decomposition of all wood sticks, microbial (without tunnels) and microbial plus macroinvertebrates (with tunnels) with individual sticks as the replicate Treatments include Fertilization (F); Throughfall Reduction (TR); Location (L); and Time.

Treatment	df		All sticks	df	Microbial	Df	Microbial & macroinvertebrates
	N	D		D		D	
F	1	332	**0.047**	348	**<0.001**	170	0.686
TR	1	333	**<0.001**	348	**<0.001**	171	0.493
L	3	331	**<0.001**	340	**<0.001**	170	**0.006**
Time	1	322	**<0.001**	287	**<0.001**	171	**<0.001**
F × TR	1	337	0.313	348	0.570	171	0.981
F × L	3	331	0.956	340	0.827	170	0.906
F × Time	1	323	0.224	287	**0.012**	171	0.775
TR × L	3	323	**0.020**	340	0.624	171	0.063
TR × Time	1	322	**0.047**	287	**0.019**	170	0.874
L × Time	3	322	**0.002**	280	**<0.001**	170	0.477
F × TR × L	3	332	0.734	340	0.125	171	0.833
F × TR × Time	1	322	0.349	287	0.460	171	0.611
F × L × Time	3	322	**0.049**	280	0.691	171	0.705
TR × L × Time	3	322	0.227	280	0.246	171	0.122
F × TR × L × Time	3	322	0.642	280	0.298	171	0.960

Significant p-values ($p < 0.05$) are in bold.

in a West African cropland, N addition increased termite abundance from 101 individuals m^{-2} to 272 individuals m^{-2}. In contrast, Gan et al. (2013) found for a temperate forest that macroinvertebrate numbers were suppressed by N fertilization at rates that simulated atmospheric N deposition. In general, the literature on macroinvertebrates is heavily dominated by N fertilization studies focused on atmospheric N deposition. In our study, fertilization included other macronutrients (P, K, S) and micronutrients (Mn, Cu, B, Zn) that could also affect macroinvertebrates or microbial decomposition processes, limiting direct comparability but indicating a need for more research, particularly on nutrients other than N. Given that multi-element fertilization is common in pine plantations (Fox et al., 2007), modeling decomposition in these managed ecosystems likely requires a detailed understanding of interactions among decomposer communities and multiple elements.

Similar to our results, previous studies found negative effects of fertilization on wood decomposition where microbial decomposition dominated (Knorr et al., 2005, Hobbie, 2008). The microbial N mining theory has been used to explain these results (Moorhead and Sinsabaugh, 2006), where increased nutrient availability decreases decomposition rates because mining recalcitrant substrates for N requires high energy input from soil microbes. We observed much higher NO_3^- after fertilization likely because under relatively high N availability and low vegetation cover, plant competition for NH_4^+ is lower and microbes increase nitrification rates (Schimel and Bennett, 2004), suggesting excess N was found in the soil. Sinsabaugh (2010) concluded that decomposition of substrate with lignocellulose index higher than 0.4 tends to be inhibited by N addition, although counter-examples have been reported (c.f. Hobbie, 2008). With the lignocellulose index of loblolly pine wood generally being above 0.4 (Tuskan et al., 1999), this wood attribute and the N-mining theory may in our study explain the negative effect of fertilization on microbial wood decomposition.

The TR effect on macroinvertebrate tunnels suggested that macroinvertebrate activity and foraging behavior were differently affected by this treatment. No previous studies of wood decomposition in temperate forests exist for a throughfall manipulation treatment, but observational studies suggest varying effects of precipitation on macroinvertebrates. Torres and González (2005) found macroinvertebrates (termites as the most important wood decomposer) decayed more logs in a tropical dry forest compared to a tropical wet forest, and the tropical dry forest was associated with greater numbers of microbial functional groups and a diverse group of wood decomposers. In contrast, Jamali et al. (2011) found termite biomass and a mound's activity was higher in wet season compared to dry season in tropical savannas. They assumed that climate had no effect on forage activity per termite, but rather affected overall termite biomass. In our study, macroinvertebrate activity was reduced by decreased precipitation inputs, as evidenced by the tunneling results (Table 2), although the wood mass loss of D_{m+m} was not significant for the individual sticks (Table 4). Tunnel presence likely reflects macroinvertebrate activity, population size, and foraging behavior, all of which are poorly understood (Ulyshen, 2014). For foraging behavior alone, termites and other macroinvertebrates can be affected by vegetation cover (Jones et al., 1987), predators (Ulyshen, 2014), temperature and precipitation (Haverty and Nutting, 1976), and topography (Crist, 1998).

4.2. Soil CO_2 efflux

The main effect of TR on soil CO_2 efflux was not significant, rather the treatment only occasionally decreased soil CO_2 efflux and surface soil moisture. In contrast, Borken et al. (2006) found precipitation exclusion depressed CO_2 efflux from the forest floor in a temperate deciduous forest during co-occurring droughts, but also noted that surface mineral soil moisture was not affected by the treatment. In our study, TR treatment did significantly reduce stand growth (Will et al., 2015), but the significant interactions for soil moisture (Fig. 1c) and soil CO_2 efflux (Fig. 2) occurred on different dates. Indeed for the last measurement, the TR treatment soil CO_2 efflux was greater than the control (Fig. 2). For a number of reasons, mixed results are common for moisture effects on soil CO_2 efflux. First soil temperature generally dominates abiotic effects on soil CO_2 efflux (Boone et al., 1998) and temperature is generally negatively correlated with moisture, resulting in moisture effects being a relatively small residual of temperature effects that are increasing as moisture decreases. Second, soil moisture effects are often nonlinear and have characteristics of a threshold response (Borken et al., 2006), and soils or ecosystems may have different thresholds. Nonetheless, even directly under the TR troughs there was little evidence of consistent soil CO_2 efflux suppression because of moisture limitations. For example, all of the respiration collars were randomly placed throughout the plot and 20% (13 of 64) of them exactly fell under the water exclusion troughs. Additional analysis of soil CO_2 efflux of the collars under excluders showed no difference from the collars not under excluders ($P = 0.62$) or partially under the excluders ($P = 0.95$) (not

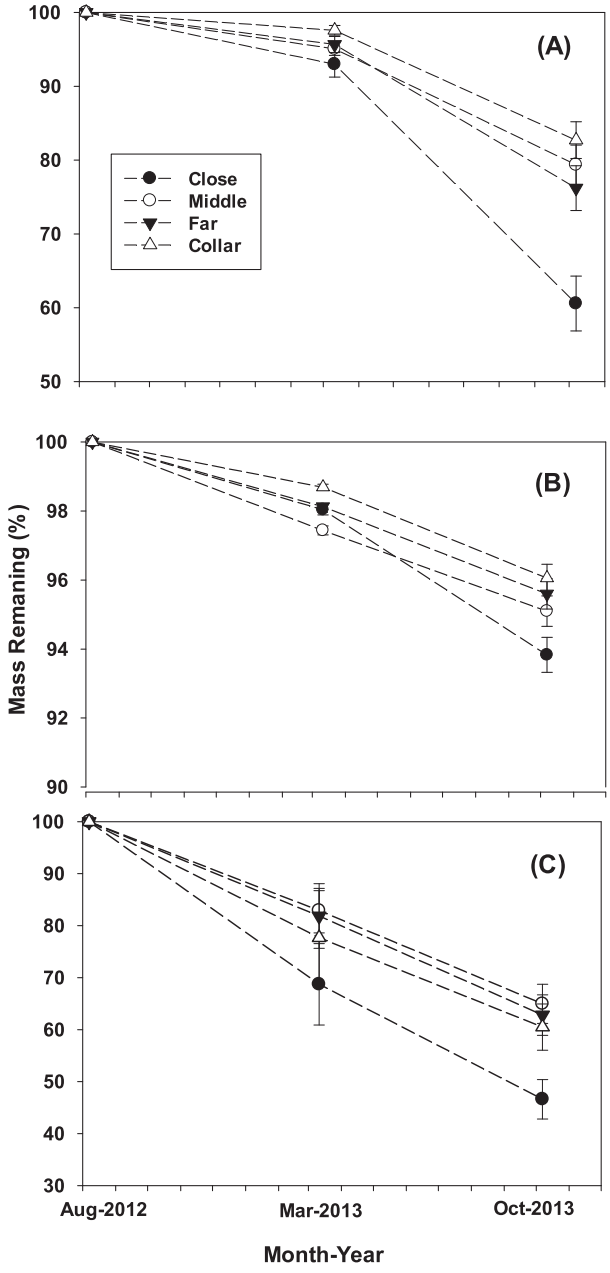

Fig. 4. Distance from tree (close, mid, far) and soil CO_2 efflux collar effects over time on wood mass loss (n = 16) for (A) the decomposition of all sticks (B) microbial-only decomposed sticks (without tunnels) and (C) sticks decomposed by both microbes and macroinvertebrates (with tunnels). Note change in scale of Y-axis.

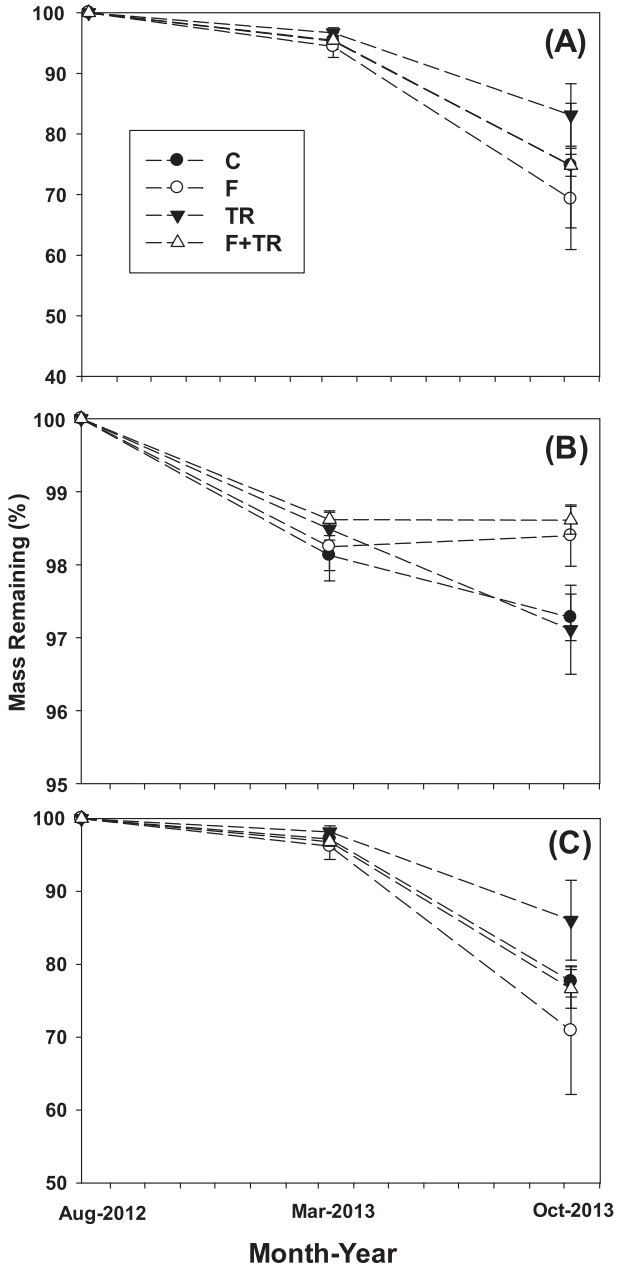

Fig. 5. Treatment effects over time on wood mass loss of the whole plot (n = 4) for (A) the decomposition of all sticks (B) microbial-only decomposed sticks (without tunnels) and (C) sticks decomposed by both microbes and macroinvertebrates (with tunnels). Note change in scale of Y-axis.

Table 5
Summary of three-way ANOVA for treatment effects testing for all sticks, microbial (without tunnels) and microbial plus macroinvertebrates (with tunnels) decomposition with the summed plot of wood as the response variable of tests of fertilization (F), throughfall (TR), and time and their combination. Degrees of freedom numerator equals 7 for all treatments.

Treatment	All sticks	Microbial	Microbial & macroinvertebrates
F	0.178	**0.007**	0.121
TR	0.106	0.348	0.294
Time	**<0.001**	0.124	**<0.001**
F × TR	0.423	0.939	0.166
F × Time	0.794	**0.024**	0.917
TR × Time	0.289	0.420	0.282
F × TR × Time	0.908	0.967	0.783

Significant p-values ($p < 0.05$) are in bold.

Table 6
Summary of p values from two-way ANOVA analysis of ammonium and nitrate accumulation (degree of freedom is 1 for all treatments) for tests of fertilization (F), Throughfall Reduction (TR), and time and their combination.

Treatment	Ammonium	Nitrate
F	0.492	**0.006**
TR	0.378	0.706
Time	**<0.001**	**0.002**
F × TR	0.392	0.713
F × Time	0.706	**0.002**
TR × Time	0.648	0.948
F × TR × Time	0.644	0.948

Significant p-values ($p < 0.05$) are in bold.

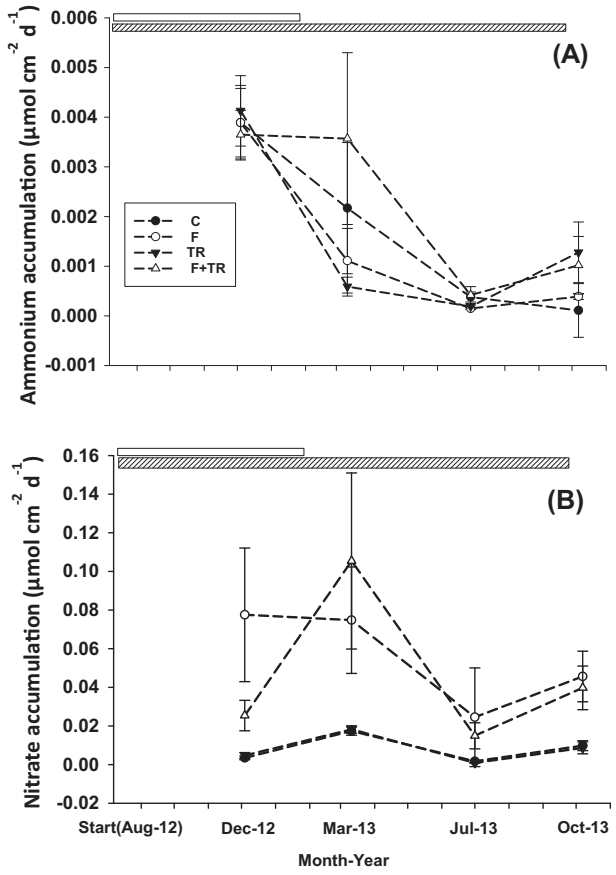

Fig. 6. Treatment effects onammonium (A) and nitrite (B) accumulation on resin strips between August 2012 and September 2013. Bars at the top of graph indicate when wood decomposition collections (216 day and 426 day) and resins experiments overlapped, with the wood decomposition installation occurring in August 2012.

shown). Thus, we may conclude that there was neither a direct nor indirect TR shelter effect on soil CO_2 efflux.

The result that fertilization inhibited soil CO_2 efflux was consistent with our hypothesis and agrees with other studies conducted in temperate forests (Olsson et al., 2005; Phillips and Fahey, 2007) and tropical forests (Giardina et al., 2003). Fertilization has decreased root respiration and soil CO_2 efflux in loblolly pine plantations but not heterotrophic respiration (Maier and Kress, 2000). In contrast, our results for the pine wood sticks suggests that microbial respiration was inhibited, which would agree with Gough and Seiler (2004) who found fertilization suppressed microbial respiration, and other studies where enzyme activity was inhibited by N fertilization (Franklin et al., 2003; Olsson et al., 2005). Fertilization also decreased soil temperatures (Fig. 1a), and as a result both heterotrophic and autotrophic respiration could have been less because of the cooler soil temperatures (Boone et al., 1998). These results seem to suggest C loss from soil and detrital pools will be reduced from a fertilized plantation, but the potential for changes in root allocation and effects of macroinvertebrates on decomposition are large enough that fertilization effects on litter and soil C requires further study.

4.3. Spatial variation of wood decomposition

The wood sticks nearest the tree decomposed faster than those farthest from the rows of planted trees, regardless of the decomposer type. There are likely both biotic and abiotic reasons for why there was higher decomposition around the tree. Plantations concentrate net primary productivity in rows, which may then concentrate the activity of macroinvertebrates and microbes, potentially leading to 'priming' effects, or microbial and enzymatic activity that further stimulates decomposition (Kuzyakov et al., 2007). Moreover early site preparation and planting often turns the soil near the planted row and concentrates detritus; processes that could also stimulate or concentrate saprotrophs. It is also possible that the environmental conditions (soil temperature and moisture) near trees were beneficial, generally, to decomposer communities. Environmental factors including soil moisture and soil temperature are affected by the forest canopy (Forrester et al., 2012), with open areas being warmer than under canopy areas (Prescott, 2002; Forrester et al., 2012) and surface moisture varying with time since last rainfall, interception and radiation balance.

4.4. Method Implications

We placed wood substrates inside the soil CO_2 efflux collars because around the time this study started, other researchers in the southeastern United States' were noting a significant role of macroinvertebrates in wood decomposition (M. Jurgensen, personal communication) and we predicted the efflux collars might affect foraging behavior. However, only the wood affected by microbes and the all sticks exhibited slower decomposition inside compared to outside the soil CO_2 efflux collars. This result suggests that the microbial community's composition or activity was altered by the presence of the soil collar barrier. We are aware of no other studies that have tested the effect of soil collars on wood decomposition, and the obvious implication is that soil CO_2 efflux may be underestimated. However the efflux of CO_2 from coarse woody debris decomposition at the soil surface would be much less than that of roots (Gough and Seiler, 2004) and heterotrophic respiration from soil organic matter (Vogel et al., 2015), and we have no evidence that the decomposition of other litter fractions or soil organic matter was affected by the collars.

Our results suggest that decomposition assessment methods that exclude macroinvertebrates (e.g. mesh bags) would not accurately estimate potential wood decomposition in these ecosystems. Macroinvertebrate exclusion has altered the decomposition in many previous studies focused on litter (Frouz et al., 2015). Determining the interrelationships among organisms will require careful study designs, as complex interactions can occur among multiple macroinvertebrate types and microbial communities. For example, termite and fungal decomposition of wood were both reported to be inhibited by the presence of ants (Warren II and Bradford, 2012). Anecdotally, we observed greater numbers of fire ants (*Solenopsis* spp.) in the plots within one block, which may be the reason for this block's lower amount of wood decomposition by macroinvertebrates and lower overall decomposition. In these pine plantations, study designs likely need to allow the interaction of all wood consumers and their predators to predict wood decomposition's response to climate change or forest management.

5. Conclusions

The decomposition of wood and the cycling of C through soil are critical to the C balance of plantations. Management practices and climate will likely interact and alter these processes by modifying the function of decomposer groups. The results from this research suggest that fertilization slows wood decomposition by microbes while increasing wood foraging by macroinvertebrates. Soil CO_2 efflux was suppressed by fertilization. In turn, throughfall reduction reduced the foraging of macroinvertebrates on wood and sup-

pressed microbial decomposition, while CO_2 efflux showed little consistent response to this treatment. Models predicting climate and management effects on the cycling of woody debris may be needed that account for these divergent community responses and the unique characteristics of pine plantations, where diverse fertilization mixtures and the spatial distribution of productivity and detritus may affect decomposition processes and soil CO_2 efflux in ways that make these processes deviate from global or regional trends.

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References

A'Bear, A.D., Jones, T.H., Kandeler, E., Boddy, L., 2014. Interactive effects of temperature and soil moisture on fungal-mediated wood decomposition and extracellular enzyme activity. Soil Biol. Biochem. 70, 151–158.
Allison, S.D., LeBauer, D.S., Ofrecio, M.R., Reyes, R., Ta, A.-M., Tran, T.M., 2009. Low levels of nitrogen addition stimulate decomposition by boreal forest fungi. Soil Biol. Biochem. 41, 293–302.
Alster, C.J., German, D.P., Lu, Y., Allison, S.D., 2013. Microbial enzymatic responses to drought and to nitrogen addition in a southern California grassland. Soil Biol. Biochem. 64, 68–79.
Barker, J., 2008. Decomposition of Douglas-fir coarse woody debris in response to differing moisture content and initial heterotrophic colonization. For. Ecol. Manage. 255, 598–604.
Bates, D.M., 2010. lme4: Mixed-effects modeling with R. URL http://lme4. r-forge. r-project. org/book.
Bebber, D.P., Watkinson, S.C., Boddy, L., Darrah, P.R., 2011. Simulated nitrogen deposition affects wood decomposition by cord-forming fungi. Oecologia 167, 1177–1184.
Berbeco, M.R., Melillo, J.M., Orians, C.M., 2012. Soil warming accelerates decomposition of fine woody debris. Plant Soil 356, 405–417.
Berg, B., McClaugherty, C., 2008. Plant Litter: Decomposition, Humus Formation, Carbon Sequestration. Springer, New York.
Boone, R.D., Nadelhoffer, K.J., Canary, J.D., Kaye, J.P., 1998. Roots exert a strong influence on the temperature sensitivity of soil respiration. Nature 396, 570–572.
Borken, W., Savage, K., Davidson, E.A., Trumbore, S.E., 2006. Effects of experimental drought on soil respiration and radiocarbon efflux from a temperate forest soil. Glob. Change Biol. 12 (2), 177–193.
Bracho, R., Starr, G., Gholz, H.L., Martin, T.A., Cropper, W.P., Loescher, H.W., 2012. Controls on carbon dynamics by ecosystem structure and climate for southeastern US slash pine plantations. Ecol. Monogr. 82, 101–128.
Bradford, M.A., Warren Ii, R.J., Baldrian, P., Crowther, T.W., Maynard, D.S., Oldfield, E. E., Wieder, W.R., Wood, S.A., King, J.R., 2014. Climate fails to predict wood decomposition at regional scales. Nature Clim. Change 4, 625–630.
Clausen, C.A., 1996. Bacterial associations with decaying wood: a review. Int. Biodeterior. Biodegradation 37, 101–107.
Clay, N., 2013. Urine increases woody decomposition in an inland, but not coastal, tropical forest despite depressing the detrital communities of both. In: New Frontiers in Tropical Biology: The Next 50 Years (A Joint Meeting of ATBC and OTS). Atbc.
Cornwell, W.K., Cornelissen, J.H.C., Allison, S.D., Bauhus, J., Eggleton, P., Preston, C. M., Scarff, F., Weedon, J.T., Wirth, C., Zanne, A.E., 2009. Plant traits and wood fates across the globe: rotted, burned, or consumed? Glob. Change Biol. 15, 2431–2449.
Crist, T.O., 1998. The spatial distribution of termites in shortgrass steppe: a geostatistical approach. Oecologia 114, 410–416.
Dixon, R.K., Solomon, A., Brown, S., Houghton, R., Trexier, M., Wisniewski, J., 1994. Carbon pools and flux of global forest ecosystems. Science 263, 185–190.
Downs, M.R., Nadelhoffer, K.J., Melillo, J.M., Aber, J.D., 1996. Immobilization of a 15N-labeled nitrate addition by decomposing forest litter. Oecologia 105, 141–150.
Fao, J., 2012. Global forest land-use change 1990–2005. FAO forestry paper 169.
Fog, K., 1988. The effect of added nitrogen on the rate of decomposition of organic matter. Biol. Rev. 63, 433–462.
Forrester, J.A., Mladenoff, D.J., Gower, S.T., Stoffel, J.L., 2012. Interactions of temperature and moisture with respiration from coarse woody debris in experimental forest canopy gaps. For. Ecol. Manage. 265, 124–132.
Fox, T.R., Allen, H.L., Albaugh, T.J., Rubilar, R., Carlson, C.A., 2007. Tree nutrition and forest fertilization of pine plantations in the southern United States. Southern J. Appl. Forestry 31, 5–11.
Franklin, O., Högberg, P., Ekblad, A., Ågren, G.I., 2003. Pine forest floor carbon accumulation in response to N and PK additions: bomb 14C modelling and respiration studies. Ecosystems 6, 644–658.
Frouz, J., Roubíčková, A., Heděnec, P., Tajovský, K., 2015. Do soil fauna really hasten litter decomposition? A meta-analysis of enclosure studies. Eur. J. Soil Biol. 68, 18–24.
Gan, H., Zak, D.R., Hunter, M.D., 2013. Chronic nitrogen deposition alters the structure and function of detrital food webs in a northern hardwood ecosystem. Ecol. Appl. 23, 1311–1321.
Giardina, C.P., Ryan, M.G., Binkley, D., Fownes, J.H., 2003. Primary production and carbon allocation in relation to nutrient supply in a tropical experimental forest. Glob. Change Biol. 9, 1438–1450.
Gough, C.M., Seiler, J.R., 2004. Belowground carbon dynamics in loblolly pine (*Pinus taeda*) immediately following diammonium phosphate fertilization. Tree Physiol. 24, 845–851.
Haverty, M.I., Nutting, W.L., 1976. Environmental factors affecting the geographical distribution of two ecologically equivalent termite species in Arizona. Am. Midl. Nat., 20–27
Hobbie, S.E., 2008. Nitrogen effects on decomposition: a five-year experiment in eight temperate sites. Ecology 89 (9), 2633–2644.
Hothorn, T., Bretz, F., Westfall, P., Heiberger, R.M., Schuetzenmeister, A., 2014. Multcomp: simultaneous inference in general parametric models. R package version:1.3-2.
Jamali, H., Livesley, S.J., Dawes, T.Z., Hutley, L.B., Arndt, S.K., 2011. Termite mound emissions of CH_4 and CO_2 are primarily determined by seasonal changes in termite biomass and behaviour. Oecologia 167, 525–534.
Janssens, I., Dieleman, W., Luyssaert, S., Subke, J.-A., Reichstein, M., Ceulemans, R., Ciais, P., Dolman, A.J., Grace, J., Matteucci, G., 2010. Reduction of forest soil respiration in response to nitrogen deposition. Nat. Geosci. 3, 315–322.
Jones, S.C., Trosset, M.W., Nutting, W.L., 1987. Biotic and abiotic influences on foraging of Heterotermes aureus (Snyder)(Isoptera: Rhinotermitidae). Environ. Entomol. 16, 791–795.
Kaarik, A.A., 1974. Decomposition of wood. Biology of Plant Litter Decomposition, vol. 1, pp. 129–174.
Kaufert, F., Behr, E., 1942. Susceptibility of wood to decay. Ind. Eng. Chem. 34, 1510–1515.
Knorr, M., Frey, S.D., Curtis, P.S., 2005. Nitrogen additions and litter decomposition: A meta-analysis. Ecology 86, 3252–3257.
Kueppers, L.M., Harte, J., 2005. Subalpine forest carbon cycling: short-and long-term influence of climate and species. Ecol. Appl. 15, 1984–1999.
Kuznetsova, A., Brockhoff, P., Christensen, R., 2013. lmerTest: Tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package). R package version:2.0-0.
Kuzyakov, Y., Hill, P., Jones, D., 2007. Root exudate components change litter decomposition in a simulated rhizosphere depending on temperature. Plant Soil 290, 293–305.
Luyssaert, S., Inglima, I., Jung, M., Richardson, A., Reichstein, M., Papale, D., Piao, S., Schulze, E.D., Wingate, L., Matteucci, G., 2007. CO_2 balance of boreal, temperate, and tropical forests derived from a global database. Glob. Change Biol. 13, 2509–2537.
Mackensen, J., Bauhus, J., Webber, E., 2003. Decomposition rates of coarse woody debris—a review with particular emphasis on Australian tree species. Aust. J. Bot. 51, 27–37.
Maier, C.A., Kress, L.W., 2000. Soil CO_2 evolution and root respiration in 11 year-old loblolly pine (*Pinus taeda*) plantations as affected by moisture and nutrient availability. Can. J. For. Res. 30 (3), 347–359.
Malhi, Y., Meir, P., Brown, S., 2002. Forests, carbon and global climate. Philos. Trans. Roy. Soc. Lond. : Math., Phys. Eng. Sci. 360, 1567–1591.
Manzoni, S., Schimel, J.P., Porporato, A., 2012. Responses of soil microbial communities to water stress: results from a meta-analysis. Ecology 93, 930–938.
Meyer, W.M., Ostertag, R., Cowie, R.H., 2011. Macroinvertebrates accelerate litter decomposition and nutrient release in a Hawaiian rainforest. Soil Biol. Biochem. 43, 206–211.
Micks, P., Downs, M.R., Magill, A.H., Nadelhoffer, K.J., Aber, J.D., 2004. Decomposing litter as a sink for N-15-enriched additions to an oak forest and a red pine plantation. For. Ecol. Manage. 196, 71–87.
Moorhead, D.L., Sinsabaugh, R.L., 2006. A theoretical model of litter decay and microbial interaction. Ecol. Monogr. 76, 151–174.
Neupane, A., Maynard, D.S., Bradford, M.A., 2015. Consistent effects of eastern subterranean termites (Reticulitermes flavipes) on properties of a temperate forest soil. Soil Biol. Biochem. 91, 84–91.
Noormets, A., McNulty, S.G., Domec, J.C., Gavazzi, M., Sun, G., King, J.S., 2012. The role of harvest residue in rotation cycle carbon balance in loblolly pine plantations. Respiration partitioning approach. Glob. Change Biol. 18, 3186–3201.
Olsson, P., Linder, S., Giesler, R., Högberg, P., 2005. Fertilization of boreal forest reduces both autotrophic and heterotrophic soil respiration. Glob. Change Biol. 11, 1745–1753.

Phillips, R.P., Fahey, T.J., 2007. Fertilization effects on fineroot biomass, rhizosphere microbes and respiratory fluxes in hardwood forest soils. New Phytol. 176, 655–664.
Prescott, C.E., 2002. The influence of the forest canopy on nutrient cycling. Tree Physiol. 22, 1193–1200.
Schimel, J.P., Bennett, J., 2004. Nitrogen mineralization: challenges of a changing paradigm. Ecology 85, 591–602.
Similä, M., Kouki, J., Martikainen, P., 2003. Saproxylic beetles in managed and seminatural Scots pine forests: quality of dead wood matters. For. Ecol. Manage. 174, 365–381.
Sinsabaugh, R.L., 2010. Phenol oxidase, peroxidase and organic matter dynamics of soil. Soil Biol. Biochem. 42, 391–404.
Stamm, L., 2006. Measuring and Modelling Coarse Woody Debris in Tall Wet Eucalypt Forest in Southern Tasmania. University of Tasmania, Hobart, p. 191.
Stocker, B.D., Roth, R., Joos, F., Spahni, R., Steinacher, M., Zaehle, S., Bouwman, L., Prentice, I.C., 2013. Multiple greenhouse-gas feedbacks from the land biosphere under future climate change scenarios. Nat. Clim. Change 3, 666–672.
Team, R.D.C., 2010. The R project for statistical computing.
Torres, J.A., González, G., 2005. Wood decomposition of *Cyrilla racemiflora* (Cyrillaceae) in Puerto Rican dry and wet forests: a 13-year case study. Biotropica 37, 452–456.
Tuskan, G., West, D., Bradshaw, H.D., Neale, D., Sewell, M., Wheeler, N., Megraw, B., Jech, K., Wiselogel, A., Evans, R., 1999. Two high-throughput techniques for determining wood properties as part of a molecular genetics analysis of hybrid poplar and loblolly pine. Appl. Biochem. Biotechnol. 77, 55–65.
Ulyshen, M.D., 2014. Wood decomposition as influenced by invertebrates. Biol. Rev. 91, 70–85.
Ulyshen, M.D., Wagner, T.L., 2013. Quantifying arthropod contributions to wood decay. Meth. Ecol. Evol. 4, 345–352.
Ulyshen, M.D., Wagner, T.L., Mulrooney, J.E., 2014. Contrasting effects of insect exclusion on wood loss in a temperate forest. Ecosphere 5:art47.
Vogel, J.G., He, D., Jokela, E.J., Hockaday, W., Schuur, E.A., 2015. The effect of fertilization levels and genetic deployment on the isotopic signature, constituents, and chemistry of soil organic carbon in managed loblolly pine (*Pinus taeda* L.) forests. For. Ecol. Manage. 355, 91–100.
Vogel, J.G., Suau, L.J., Martin, T.A., Jokela, E.J., 2011. Long-term effects of weed control and fertilization on the carbon and nitrogen pools of a slash and loblolly pine forest in north-central Florida. Can. J. For. Res. 41, 552–567.
Warren II, R., Bradford, M., 2012. Ant colonization and coarse woody debris decomposition in temperate forests. Insectes Soc. 59, 215–221.
Warton, D.I., Hui, F.K., 2011. The arcsine is asinine: the analysis of proportions in ecology. Ecology 92, 3–10.
Wear, D.N., Greis, J.G., 2002. Southern forest resource assessment: summary of findings. J. Forest. 100, 6–14.
Will, R.E., Fox, T., Akers, M., Domec, J.-C., González-Benecke, C., Jokela, E.J., Kane, M., Laviner, M.A., Lokuta, G., Markewitz, D., et al., 2015. A range-wide experiment to investigate nutrient and soil moisture interactions in loblolly pine plantations. Forests 6, 2014–2028.
Zida, Z., Ouédraogo, E., Mando, A., Stroosnijder, L., 2011. Termite and earthworm abundance and taxonomic richness under long-term conservation soil management in Saria, Burkina Faso, West Africa. Appl. Soil Ecol. 51, 122–129.