# EFFECTS OF CLIMATE AND FOREST MANAGEMENT ON WOOD DECOMPOSITION

A Thesis

by

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## ABSTRACT

Wood debris is an important C pool in forest ecosystems. Understanding the controls on wood decomposition is necessary for predicting the response of forest ecosystem carbon cycling to management and climate. The productivity of managed pine plantations, primarily loblolly pine (*Pinus taeda* L.), in the southeastern United States has been improved through nutrient management. Although uncertainty exists, climate change may drive a reduction of precipitation of 10%-30% by 2080 for the region and an increase in temperature. In managed forests that undergo periodic harvesting, the forest can become a source of C when decomposer activity increases C loss from residual wood. Two questions motivated this research. How does reduced precipitation, interacting with fertilization, affect wood decomposition in managed pine forests? How does wood decomposition vary for decomposer community, across climatic regions and within forest ecosystems?

To address these questions, the mass loss of southern pine wood substrates were analyzed under a factorial combination of two treatments: soil moisture (30% throughfall removal) and nutrient addition (224 kg/ha N, 64 kg/ha P and 67 kg/ha K). The experimental sites were located in loblolly pine plantation forests in Oklahoma (OK), Florida (FL), Georgia (GA), and Virginia (VA). The results showed that throughfall reduction inhibited wood decomposition, while fertilization stimulated wood decomposition overall in OK, despite a significant inhibition of wood decomposition of fertilization when soil microbes were the only decomposer affecting the substrate. However in the following years in OK, fertilization increased wood decomposition regardless of decomposer type. Across sites, temperature was the predominant predictor for wood decomposition, but macro-invertebrates were an important modifier of cross site sensitivity to temperature.

The results suggest that the response of macro-invertebrates to climate and fertilization needs to be included in ecosystem carbon models to better predict how the cycling of woody debris will respond to climate change and forest management.

Temperature, as well as macro-invertebrate effects, were both important predictors for wood decomposition in loblolly pine forests in the southeastern US.

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## NOMENCLATURE

| | |
|---|---|
| C | Carbon |
| F | Fertilization |
| TR | Throughfall Reduction |
| L | Location |
| T | Time |
| $M_i$ | Initial weight of the sticks |
| $M_T$ | Weight of the stick collected after time of T |
| $D_{agg}$ | Aggregate woody mass loss |
| $D_m$ | Microbial decomposition |
| $D_{m+m}$ | Decomposition of sticks with macro-invertebrate tunnels |
| $D_{plot}$ | Total carbon pool mass loss in each plot |
| $D_{mplot}$ | Total microbial mass loss per plot |
| $D_{m+mplot}$ | Total mass loss of sticks with macro-invertebrate tunnels per plot |
| $k_m$ | Microbial decomposition constant k |
| $k_{m+m}$ | Decomposition constant k of microbial + macro-invertebrate |
| FL | Florida |
| OK | Oklahoma |
| VA | Virginia |
| GA | Georgia |

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## CHAPTER I. INTRODUCTION AND RESEARCH QUESTIONS

Determining forest carbon stocks and fluxes is important to understanding and predicting global climate change (Stocker et al. 2013b). Forest biomass and litter contain about 360 Pg C which is about 50% of carbon in the terrestrial biosphere (Malhi 2002). Across different forest ecosystems, 10-20% of forest C is contained in coarse woody debris (Dixon et al. 1994, Brown 2002, Cornwell et al. 2009). Despite its importance to forest C cycling, woody debris is not considered as a separate C pool in some global C cycling models such as LPJ (Sitch et al. 2003) and TEM (McGuire et al. 1992). It's important to study the mechanisms of wood decomposition to better understand forest carbon cycling. The decomposition of coarse woody debris may occur through combustion by fire, but in most ecosystems it is driven by microbial decomposition (mostly by fungi) or insect consumption (mostly by termites) (Cornwell et al. 2009).

Soil microbes are the main soil decomposers in many ecosystems, but in some ecosystems termites are the primary decomposers. For example in boreal and temperate forests, microbes were responsible more than 90% of all litter decomposition (Berg and McClaugherty 2008). Termites are found in large numbers in tropical and subtropical forests, temperate forests, savannas, and deserts. For example, in the tropical forest, termites are responsible for at least half of wood decomposition, causing the release of about 1.9 Pg C $yr^{-1}$ (Cornwell et al. 2009). Less research about termite decomposition has occurred in temperate forests but it has been recently demonstrated that significant decomposition occurs in North American temperate forests from termites (Stamm 2006, Ulyshen et al. 2014). Termites are important soil insects that could decompose wood cellulose with the help of their symbiotic microbes and enzymes. With this context, the scientific understanding of forest C cycling depends in part on understanding the sensitivity of woody debris decomposition rates to biotic and abiotic environmental factors (Cornwell et al. 2009, Freschet et al. 2012).

Environmental factors exert strong effects on woody debris decomposition (Kueppers and Harte 2005). UV light causes wood decay by converting the cell-wall components into soluble forms which can then be leached or decomposed (Henry et al.

2008), but the primary drivers of decomposition in most ecosystems are temperature and moisture (Cornwell et al. 2009). Soil warming has increased wood decay rates in temperate forests (Berbeco et al. 2012). Drought decreased decomposition in many ecosystems (Berg and McClaugherty 2008, Manzoni et al. 2012a). However, drought was also found to increase wood mass loss in temperate forests in the western US (Barker 2008) and rainforests in Puerto Rico (Torres and González 2005). Soil texture can interact with soil moisture to affect SOM decomposition (Berg and McClaugherty 2008) by restricting $O_2$ and enzyme flow, in particular in clay soils having small pores (Gregorich et al. 1991). These results highlight the importance of soil moisture in affecting litter decomposition.

Drought and increased management intensity are common phenomena in southern managed pine forests. It is estimated that in the next 30-90 years, global warming would cause increased widespread droughts in many land areas including the southern US (Dai 2012) and precipitation may decline by 10-30% for the southeastern region (Christensen et al. 2007). The region has approximately 13-20 million acres of intensively managed forests and harvesting in these forests often leaves large amounts of residue (Eisenbies et al. 2009) but it unclear how climate will interact with management to affect this residue decomposition.

Increasing management intensity of pine forests has been observed in the southeastern United States (Jokela et al. 2004), with loblolly pine forests often receiving both N and P to offset nutrient limitations (Valentine and Allen 1990). Increased levels of N and P fertilizer have been applied to southern pine forests from 1990 to 2004 (Fox et al. 2007), but (Eisenbies et al. 2009) the effect of altered nutrient availability by fertilization on debris decomposition and soil C dynamic are still poorly understood (Noormets et al. 2012).

For my thesis, the main question was "How do climate and fertilization affect the decomposition of woody debris in southern US pine forests"? To address this, the following sub questions were addressed:

**1) What's the relative influence of microbes and termites on wood decomposition?**

**2) How do climate factors (precipitation reduction and temperature) affect wood decomposition?**

**3) How does nutrient availability, as modified by forest management, affect wood decomposition?**

I studied how wood mass loss was affected by microbial and termite activity, termite abundance, and climate factors in loblolly pine (*Pinus taeda* L.) forests. Two experiments were conducted, one in Oklahoma, that included estimates of wood decomposition, soil $CO_2$ efflux and nutrient availability, and a regional climatic analysis that compared decomposition in Oklahoma, Florida, Georgia, and Virginia. The experimental design at each site was a factorial combination of soil moisture (throughfall) reduction and fertilization. 'Fertilization' (432 kg $ha^{-1}$ urea, 140 kg $ha^{-1}$ DAP and 112 kg $ha^{-1}$ potash) was conducted in April 2012 to achieve 'optimum' nutrient that reflected elemental rates of 224 kg N $ha^{-1}$, 27 kg P $ha^{-1}$ and 56 kg K $ha^{-1}$. 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. No rainfall manipulation or fertilization was the control (C). My overall objective was to identify how forest management and future climate change might affect wood mass loss by microbes and termites.

# CHAPTER II. EFFECT OF CLIMATE AND FOREST MANAGEMENT ON WOOD DECOMPOSITION IN OKLAHOMA

## II.1 Introduction

### II.1.1 Importance of Loblolly Pine Forest on Carbon Budget

Forest carbon (C) cycling is a critical component of the global C cycle (Stocker et al. 2013a). 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 a loblolly pine forests, the C pools of vegetation include foliage (3.5 Mg C/ha), bark (4.0 Mg C/ha), branch (8.0 Mg C/ha), stem (28.0 Mg C/ha), fine roots (1.8 Mg C/ha), coarse roots (14 Mg C/ha), and standing dead tree (1 Mg C/ha) (Vogel et al. 2011). Fertilization has increased most of the C pools resulting in higher amount of woody debris (Vogel et al. 2011). Climate and fertilization would then affect the C loss from these pools although the overall rates are poorly understood.

### II.1.2 Drought Effects on Wood Decomposition

Low soil moisture was considered as a limiting factor for decomposition (Berg and McClaugherty 2008). Drought could decrease decomposition through the reduction of enzyme activity or the limitation of microbial activity by water stress (Manzoni et al. 2012a). Drought decreased beech wood decomposition in a temperate woodland and the reduced wood decomposition under drought could be explained by decreased enzyme activity (A'Bear et al. 2014). Alster (2013) assumed that the decreased enzyme efficiencies under drought were the result of higher enzyme immobilization and lower diffusion rates.

Drought has both increased and decreased termite activity and biomass (Torres and González 2005, Jamali et al. 2011). Torres and Gonzalez (2005) found increased wood mass loss under drought with higher termite abundance in a tropical forest. However, Jamali et al. (2011) showed that termite biomass in the wet season was greater than in the dry season resulting in 3.6-fold higher emitted flux of $CO_2$ and $CH_4$ in tropical savannas. Termites need moisture to survive and mound building may in part be

an adaptation to drought. Many uncertainties exist for the drought effects on termite abundance and their contribution to wood decomposition.

### II.1.3 Fertilization Effects on Wood Decomposition

Nitrogen (N) fertilization has increased leaf litter decomposition (Hunt et al. 1988, Hobbie and Vitousek 2000), decreased litter decomposition (Magill and Aber 1998, Carreiro et al. 2000b, Wang et al. 2004), or increased decomposition in the beginning (first 3 years) and decreased it later (4-7 years) (Bragazza et al. 2012). N fertilization was found to increase cellulose loss (Talbot and Treseder 2011) resulting in the increase of lignin concentrations and the increased lignin concentrations may have had a negative effect on litter decomposition rates (Fogel and Cromack Jr 1977, Berg et al. 1987). Carreiro et al. (2000a) showed that nitrogen addition stimulated decomposition of labile litters with low lignin content (6%, dogwood leaf litter) while suppressed the decomposition of recalcitrant litters with high lignin (26%, oak leaf litter).

There are two hypotheses about the effects of nutrient availability on litter decomposition: 'basic stoichiometric decomposition theory' (Melillo et al. 1982) and 'microbial nitrogen mining theory'(Moorhead and Sinsabaugh 2006). The basic stoichiometric decomposition theory posits that the stoichiometry of nutrients in substrates are satisfied and microbial demands drive the decomposition process and when C, N and P satisfy the microbial nutritional demands, the highest decomposition will be observed (Melillo et al. 1982, Hessen et al. 2004). N and P could affect microbial growth and respiration because a balanced composition of C and nutrients need to be maintained in microbial cells (Manzoni et al. 2012b). A C:N ratio of 25:1 is considered as critical for microbes to meet their N requirement, thus added N would maximize microbial growth and mineralization (Chapin III et al. 2011). In contrast, the microbial nitrogen mining theory suggests that an increase in the nutrient availability would decrease the decomposition rate. Some microbes were considered to use labile C to acquire N in the process of decomposing recalcitrant substrate which yields little energy (Fontaine and Barot 2005, Moorhead and Sinsabaugh 2006). Thus mining of recalcitrant

C which required high energy was suppressed with greater N availability (Craine et al. 2007). Like N, P is also a common limiting nutrient in terrestrial ecosystem (Elser et al. 2007, Vitousek et al. 2010). Compared to N addition, P addition has increased both labile and recalcitrant substrate decomposition (Craine et al. 2007). Compared to leaf or needle litter decomposition, less is known about how wood decomposition responds to fertilization.

Woody litter is different from leaf litter in several ways: 1) wood litter has higher C/N ratio or higher lignin than leaf litter and more complex polymers which are the dominant woody chemistry (Micks et al. 2004); 2) Fungi, especially Basidiomycetes, are the main decomposers of woody debris (Cornwell et al. 2009); 3) termites are also considered an important wood consumers. For example, termites contributed 20-30% of wood loss in a *Eucalyptus* temperate forest (Stamm 2006).

The effects of N addition on woody decomposition are controversial. Fog (1988) reviewed the literature and found that N addition usually had a negative effect on recalcitrant substrate with high lignin content. Kaufert and Behr (1942) tested the N addition effect on woody decomposition in the lab. They found that small amounts of N addition (urea, ammonium sulfate, and ammonium phosphate) didn't affect woody decomposition while high concentration of N fertilization reduced woody decomposition, which is consistent with the microbial nitrogen mining theory. However, many other field studies have showed positive effects of fertilization on woody decomposition in temperate forests (Downs et al. 1996, Micks et al. 2004, Bebber et al. 2011), boreal forest (Allison et al. 2009), and tropical forests (Clay 2013). The mechanisms that explain either positive or negative effects of fertilization on wood decomposition are poorly understood.

Fertilization has a negative effect on wood decomposition by the inhibition of enzyme activity or microbial biomass. The negative effects of N addition have been associated with reduced phenol oxidase and peroxidase activities produced by fungi (Sinsabaugh 2010). It seems that phenol oxidase activity is reduced in decomposing litter with higher lignocellulose index (>0.4) (LIC, lignin/(lignin+cellulose)) by N addition

(Sinsabaugh 2010). Reduced microbial biomass is another possible reason for the negative effects of N addition on decomposition (Söderström et al. 1983, Nohrstedt et al. 1989). Treseder (2008) discussed the possible mechanisms to explain negative effects of N addition on microbial growth: 1) osmotic potentials increased through addition of ions by fertilizer which were toxic to the microbes (Broadbent 1965); 2) N addition decreased soil pH resulting in leaching of Mg and Ca and mobilization of Al, leading to the limitation of Mo and Ca or toxic of Al to microbes (Vitousek et al. 1997); 3) N addition reduced the availability of C by inhibiting ligninase production (Waldrop and Zak 2006); 4) N addition decreased belowground NPP investment resulting in less turnover of fine roots or mycorrhizal fungi; 5) nitrogenous compounds could react with carbohydrates creating recalcitrant compounds (FOG 1988). Reduced enzyme production or activity and decreased microbial biomass contributed to the negative effect of fertilization on wood mass loss. However, many studies also found that fertilization increased wood decomposition.

Fertilization has also increased wood decomposition with positive effects on microbial biomass and termite abundance. One possible reason for increased wood decomposition under fertilization is that nutrients remained limiting and thus microbes still needed to mineralize wood to acquire the limiting nutrient, which is consistent with the basic stoichiometric decomposition theory. It is also possible that N addition alleviated C limitation of microbes through increased aboveground litter production (LeBauer and Treseder 2008). Another possible reason is that although fertilization inhibits microbial decomposition, increased arthropod consumption under fertilization contributed to the positive effect. Previous studies have focused on microbial contribution to wood decay but ignored the arthropod contributions (termites mainly) (Ulyshen and Wagner 2013). Furthermore, little is known about how nutrients affect termite's abundance and their associated decomposition. A recent study showed that NaCl fertilization increased termites by 17-fold and decomposition rate for both labile and recalcitrant substrates in an Amazonian forest (Kaspari et al. 2014). In a West African cropland, N addition increased termite's abundance from 101 termites $m^{-2}$ to 272

termites $m^{-2}$. However, in plots with recalcitrant materials (straw), N addition decreased termites abundance significantly from 1621 individuals $m^{-2}$ to 155 individuals $m^{-2}$ (Zida et al. 2011).

Phosphorus (P) is generally added with N in southern pine managed forests (Albaugh et al. 2010), but relatively less is understood about its effects on both microbial and termite decomposition. In tropical forests, P concentration correlates with litter decomposition (Cleveland and Townsend 2006). P addition was found to increase decomposition rate by 49% in a tropical forest (Kaspari et al. 2008). Different from N, P could increase decomposition of recalcitrant substrate (Craine et al. 2007). The effect of P on termite driven decomposition is poorly understood. Fertilization not only could affect the original substrate decomposition, but also could affect the litter chemical composition, which will respond differently to the treatment from the original substrate.

### II.1.4 Interactive Effects of Drought and Fertilization on Wood Decomposition

With the fact that both fertilization and drought could affect wood decomposition through microbes and termites, interactive effects are expected. A conceptual model addressing drought and nitrogen effects on litter decomposition was proposed (Allison et al. 2013). The model predicted that fertilization and drought could affect litter decomposition directly through change of microbial biomass and physiology and indirectly through change of community composition or bacteria to fungi ratio. Considering the contribution of termites on wood decomposition, a two decomposer model is a better way to predict drought and N addition effects on wood decomposition (Ulyshen and Wagner 2013).

In this model, drought and N addition could affect wood decay rate either through an effect on microbes or through an effect on termites. Drought and N addition may also affect termite's biomass or physiology directly, resulting in change of wood decomposition rate. My study tests the interaction of nutrient additions and drought effects on termite decomposition. In this model, drought tends to decrease wood decomposition through multiple mechanisms. Nutrient additions, which include N, tend to show negative effects when microbes dominate the decomposer systems. Further

negative effects may be found under both drought and N addition. The positive effect of N addition on wood decomposition is expected if termites dominate the decomposer system.

**II.2 Hypotheses**

**H1: Precipitation reduction will decrease wood decomposition.**

**Rationale:** Negative effect of precipitation reduction is associated with its negative effect on both microbial decomposition and termite's consumption of wood.

**H1a: Precipitation reduction will decrease microbial wood decomposition.**

**Rationale:** The reduced microbial decomposition was likely explained by a reduction in enzyme activity or limitation of microbial activity by water stress (Manzoni et al. 2012a). Enzyme activity was highly inhibited by low water availability (A'Bear et al. 2014). Thus, microbial decomposition likely to be inhibited under reduced precipitation.

**H1b: Precipitation reduction will decrease wood decomposition by termites.**

**Rationale:** Termites are often considered to be drought-adapted due to their occurrence and success in arid-and semi-arid ecosystems (Cornwell et al. 2009). But these termites make mounds as protection from drought (Abe et al. 2000), while those in temperate North America do not, suggesting a higher sensitivity to drought. Previous studies have found the positive drought effects on wood-feeding termite's decomposition in rain forest (Torres and González 2005) and negative drought effect on termites in tropical savannas (Jamali et al. 2011). My study is the first test of the drought effect on termite's wood consumption in the temperate forest. I assumed that the wood consumption by termites will decrease.

**H2: Fertilization will increase common woody substrate decomposition.**

**Rationale:** Although fertilization will decrease microbial decomposition of wood because of N effects, overall wood decomposition will be increased because of higher contribution of termites. The positive effect of fertilization on wood consumption by termites will dominate the decomposition rate. In a temperate forest, a study was conducted to analyze the effect of decomposer on wood mass loss. They found that wood mass loss contributed by termites was 11.5% more than wood without termite's

impact. However, fungus only removed 4% more wood mass compared to the woods without fungus (Warren II and Bradford 2012).

**H2a: Forest management (Fertilization addition) will decrease microbial decomposition of loblolly pine wood.**

**Rationale:** N fertilization tends to inhibit decomposition of litter with 'low quality' (high-lignin N ratio or lignin-cellulose ratio) (Carreiro et al. 2000b, Knorr et al. 2005, Sinsabaugh 2010). Sinsabaugh (2010) concluded that decomposition of substrate with lignocellulose index higher than 0.4 tends to be inhibited by N addition. Loblolly pine wood was found to contain 26.7–34.7% lignin, 35.7–48.0% cellulose, and 24.4–25.9% hemicellulose (Tuskan et al. 1999). Lignocellulose index of loblolly pine wood was higher than 0.4 so I hypothesis that loblolly pine wood decomposition contributed by microbes will decrease under N addition. P will increase the decomposition regardless the substrate is labile or recalcitrant (Craine, Morrow et al. 2007). However, the amount of P addition was much less compared to N addition (224 kg/ha N VS 64 kg/ha P). Here, N is assumed as the dominant controller in my research sites, resulting in the hypothesis that fertilization will inhibit microbial decomposition.

**H2b**: **Fertilization will increase the woody mass loss consumed by termites.**

**Rationale:** Knowledge of fertilization effect on termite's decomposition is limited. N addition tend to increase termite's abundance (Zida et al. 2011). Wood-feeding termites consume wood for cellulose as the energy source. Both cellulose-digesting and hemicellulose-digesting enzymes were used in the guts of termites (Brune 2014). N addition was found to increase cellulose loss and cellulase activity during litter decomposition stages, suggesting that N fertilization favored cellulose users in the decomposition system (Talbot and Treseder 2012).

### II.3 Experimental Methods

#### II.3.1 Study Design

The study site is located near Idabel, Oklahoma (34°01'N, 94°49'W). Loblolly pine seedlings were planted in rows in 2008 at an approximate spacing of 2 m between trees and 3 m between rows. The region has a mean annual temperature of 16.6 °C and

annual 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 is -1.6 $^{\circ}$C while the daily average maximum temperature in August is 34.2 $^{\circ}$C. The surface soil texture is a fine sandy loam and the subsoil texture is clay loam. The soil series is Ruston ,the soil surface texture is fine sandy loam and subsoil texture is clay loam. The soil profile is well drained, and the site has a slope of 3-8% (NCSS, Web Soil Survey http://websoilsurvey.sc.egov.usda.gov/App/WebSoilSurvey.aspx, accessed February 2014).

Treatment plots were set up in 2011 within a loblolly pine forest that had a mixture of open-pollinated genotypes from across the range of loblolly pine (Will et al. 2015). Each plot was approximately 0.08 ha and comprised of an outside buffer area and an internal measurement plot (around 0.04 ha). Before treatment establishment, all competing woody understory vegetation was killed by directed spray with glyphosate. The experimental design was a factorial combination of fertilization and throughfall reduction. 'Fertilization' (432 kg ha$^{-1}$ urea, 140 kg ha$^{-1}$ DAP and 112 kg ha$^{-1}$ potash) was conducted in April 2012 to achieve 'optimum' nutrient that reflected 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. The troughs were 0.5 and 1.5 m high above the soil surface at two sides and the rainfall was captured and funneled away from the plots gravimetrically. No rainfall manipulation or fertilization was the control (C), paired with a TR, an optimum fertilization (F), and a combined F+TR treatment within 4 blocks.

### II.3.2 Field 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 of lumber. 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 setting up in the field and initial 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' stick was 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 directly under the trough. Another six sticks were put in the soil $CO_2$ efflux collars. Half of common substrate was collected in 216 days and the other half were left and picked up in 426 days. On removal, sticks were cleaned, assessed for damage by macro-invertebrates, oven dried at 105 °C for 48 hours, 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 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 shook for 1 hour in 1*M* KCl. For ammonium, each 20 µl extracted sample was added by 90 µl salicylate solution and 90 µl bleach solution. For nitrate, the Vanadium "Cocktail" reagent solution was added to the sample solution. The Vanadium "Cocktail" reagent solution was made by 50 ml saturated vanadium chloride solution, 3.3 ml 2% sulfanilamide solution, 3.3 ml 0.2% NED solution and 400 ml DI water. Ammonium and nitrate concentrations were analyzed

with an Eon Microplate Spectrophotometer at 650 nm and 540 nm respectively (Bio-Tek, Winooski VT, US).

**II.3.3 Calculations**

Aggregate woody mass loss ($D_{agg}$) of each stick was calculated as follows:

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

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. 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 macro-invertebrate tunnels was considered contributed by both microbes and macro-invertebrates ($D_{m+m}$). Analysis was also performed on all sticks (aggregate)

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

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

Treating individual sticks as replicates makes contrasts of total wood mass by microbes vs. macroinvertebrates sensitive to changing sample size as macroinvertebrate colonize new sticks. To explore the relative contribution of macro-invertebrates, 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:

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

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

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

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 macro-

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

The decomposition turnover rate ($y^{-1}$) was estimated as the value (k):

$$k = -\frac{\log(\frac{M_T}{M_i})}{T} \quad (7)$$

where $M_T$ is the weight of the stick collected after some time period (216 or 426 days), and $M_i$ is the initial weight of the sticks before the experiment (T).

**II.3.4 Statistical Analysis**

The effects of fertilization, TR, and time along with their interaction on macro-invertebrate's attack ratio (percentage of tunneled wood) were assessed using a generalized linear model. Logistic regression was used and P values (>Chi) were analyzed. The effect of fertilization, TR, location and time on $D_{agg}$, $D_m$, and $D_{m+m}$ were assessed using a 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 determined by wood sticks with the same block, plot, tree and location, with the only difference being the collection date. Each subject was collected once on each date and considered as a repeated measurement. Within each 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 value differences among levels of locations. The effects of fertilization, throughfall reduction, time and their interaction on $D_{plot}$, $D_{mplot}$, $D_{m+mplot}$ were analyzed using three-way ANOVA with block as random effect in R. Logit transformation was used for $D_{agg}$, $D_m$, $D_{m+m}$, $D_{plot}$, $D_{mplot}$, $D_{m+mplot}$ 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 blocks were included as random effects. 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 dates effect and interaction effect of fertilization and dates.

**II.4 Results**

*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 from 13% to 54% of the recovered sticks (Table 2-1, 2-2; $P < 0.001$). Fertilization significantly increased the ratio of tunneled wood after 426 days (Table 2-1, 2-2; P=0.007), and TR significantly decreased the ratio of wood having tunnels (Table 2-1, 2-2; P=0.008).

Table 2-1. Summary of average number of recovered wood stick assays with tunnels and the percentage of tunneled wood in each plot by treatment over time (approximately a 0.5y and 1y) for treatments (fertilization (F), throughfall reduction (TR) and the combined treatment).

| **Time (Year)** | **Treatment** | **Number of sticks with tunnels (#)** | **Tunneled sticks (%)** |
|---|---|---|---|
| **Half** | **C** | 15 | 16% |
| **Half** | **F** | 15 | 16% |
| **Half** | **TR** | 8 | 9% |
| **Half** | **F+TR** | 12 | 13% |
| **One** | **C** | 37 | 59% |
| **One** | **F** | 51 | 67% |
| **One** | **TR** | 25 | 32% |
| **One** | **F+TR** | 45 | 59% |

Table 2-2. Summary of P values (>Chi) from generalized linear model (logistic regression) testing the treatment and time (T) effects on macro-invertebrate's attack ratio (df=1 for all treatments) on wood sticks for treatments (fertilization (F), throughfall reduction (TR) and the interactions).

| Treatment | Tunneled sticks |
|---|---|
| **T** | **<0.001** |
| **F** | **0.007** |
| **TR** | **0.008** |
| **F*TR** | *0.052* |
| **F*T** | 0.174 |
| **TR*T** | 0.535 |
| **F*TR*T** | 0.647 |

*Individual wood stick decomposition*

Both fertilization and TR treatments significantly affected aggregate and microbial only decomposition, but there were no significant effects on decomposition of the wood sticks attacked by macro-invertebrates. Fertilization decreased $D_m$ (Fig. 2-1, $p<0.001$) but increased the $D_{agg}$ decomposition (Fig. 2-1, $p=0.047$) (Table 2-3). 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. 2-1, $p=0.686$). TR reduced both aggregate decomposition (Fig. 2-1, $p<0.001$) and microbial decomposition (Fig. 2-1, $p<0.001$). These results are consistent with my hypothesis that TR and fertilization will decrease microbial decomposition.

Besides the main treatment effects, I also tested the location effects on individual wood decomposition (Table 2-3, Fig 2-2). Location of sticks (three distances to the tree and one within respiration collars) had significant effects on $D_{agg}$ ($p<0.001$), $D_m$ ($p<0.001$), and $D_{m+m}$ ($p=0.006$) (Table 2-3). 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. $D_{agg}$ 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 $D_{m+m}$. The above results suggested that tree distance had a negative effect on both microbial and macro-invertebrate decomposition while respiration collars only had a negative effect on microbial decomposition.

TR and location had a significant interaction effect (P=0.020; Table 2-3). Post hoc analysis showed that aggregate wood decomposition inside collars was only less compared to the location near the tree (P=0.047) both in control plots (P=0.035) and in TR plots (P=0.012). Aggregate decomposition in the middle location was not different from near or far both in the control plot and TR plot.

*Carbon mass loss at the whole plot level*

For treatment effects, only fertilization significantly decreased carbon mass loss by microbes at the whole plot level (Table 2-4). 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 contributed by microbes only was overwhelmed by the macro-invertebrates' effect, resulting in a non-significant trend toward more wood mass loss under fertilization (Fig. 2-3). Time exerted highly significant effects on aggregate and macro-invertebrates, highlighting that the negative effect of fertilization on microbial decomposition only showed in the later period.

Figure 2-1: Treatment effects over time on mass loss of the individual wood sticks (n=16) for (a) the aggregate of all decomposers (b) microbial-only decomposed wood and (c) wood decomposed by both microbes and macro-invertebrates.

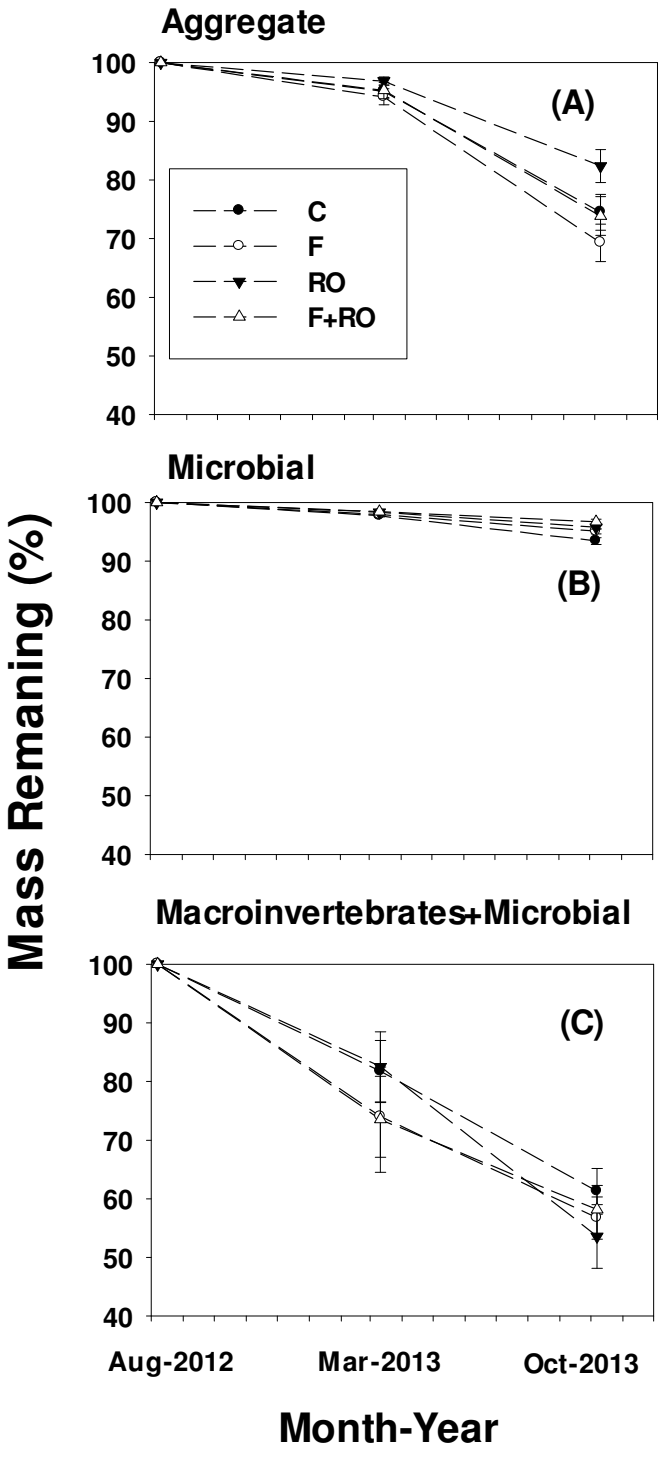

Aggregate
(A)
C
F
RO
F+RO
Microbial
(B)
Macroinvertebrates+Microbial
(C)
100
90
80
70
60
50
40
Mass Remaning (%)
Aug-2012
Mar-2013
Oct-2013
Month-Year

Table 2-3: Summary of degrees of freedom and p values from linear mixed model with repeat analysis testing for aggregate (all wood sticks), microbial and microbial plus macro-invertebrates decomposition with individual stick as a carbon pool. Treatments include Fertilization (F); throughfall reduction (TR); Location (L); and Time (T).

| Treatment[a] | df | | Aggregate | df | Microbes | df | Microbes & Macro-invertebrates |
|---|---|---|---|---|---|---|---|
| | N[b] | D[b] | | D[b] | | D[b] | |
| **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** |
| **T** | 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*T** | 1 | 323 | 0.224 | 287 | **0.012** | 171 | 0.775 |
| **TR*L** | 3 | 323 | **0.020** | 340 | 0.624 | 171 | *0.063* |
| **TR*T** | 1 | 322 | **0.047** | 287 | **0.019** | 170 | 0.874 |
| **L*T** | 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*T** | 1 | 322 | 0.349 | 287 | 0.460 | 171 | 0.611 |
| **F*L*T** | 3 | 322 | **0.049** | 280 | 0.691 | 171 | 0.705 |
| **TR*L*T** | 3 | 322 | 0.227 | 280 | 0.246 | 171 | 0.122 |
| **F*TR*L*T** | 3 | 322 | 0.642 | 280 | 0.298 | 171 | 0.960 |

[a] N is numerator; D is denominator

Figure 2-2: Location effects over time on mass loss of the individual wood sticks (n=16) for (a) the aggregate of all decomposers (b) microbial-only decomposed wood and (c) wood decomposed by both microbes and macro-invertebrates.

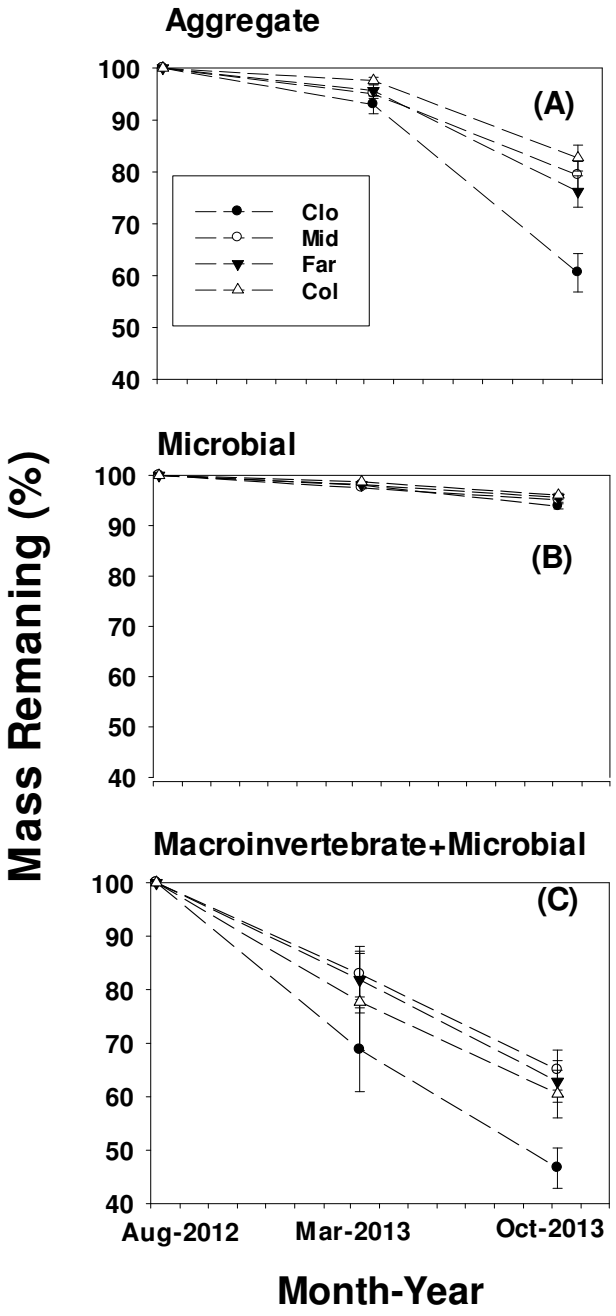


Table 2-4: Summary of p values from three-way ANOVA analysis of treatment effects testing for aggregate, microbial and microbial plus macro-invertebrates decomposition with the summed plot of wood as the response variable of tests of fertilization (F), throughfall reduction (TR), and time (T) and their combination.

| Treatment | df | Aggregate | Microbes | Microbes & Macro-invertebrates |
|---|---|---|---|---|
| **F** | 1 | 0.178 | **0.007** | 0.121 |
| **TR** | 1 | 0.106 | 0.348 | 0.294 |
| **T** | 1 | **<0.001** | 0.124 | **<0.001** |
| **F*TR** | 1 | 0.423 | 0.939 | 0.166 |
| **F*T** | 1 | 0.794 | **0.024** | 0.917 |
| **TR*T** | 1 | 0.289 | 0.420 | 0.282 |
| **F*TR*T** | 1 | 0.908 | 0.967 | 0.783 |

*Ammonium and nitrite concentration*

Neither fertilization nor drought affected ammonium accumulation (Table 2-5). However, ammonium accumulation decreased significantly across dates (P<0.001, Table2-5, Figure 2-4a). 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 2-5, Figure 2-4b). Time also had a significant effect on nitrate accumulation (P=0.002, Table 2-5) and multiple comparisons showed that nitrate accumulated on the resin strips less from March 2013 to June 2013 was than what accumulated from December 2012 to March 2013 (P=0.006). The interaction between fertilization and dates revealed that fertilization only significantly increased nitrate accumulation between December 2012 and March 2013 (P=0.001).

Figure 2-3: Treatment effects over time on mass loss of the whole plot (n=4) for (a) the aggregate of all decomposers (b) microbial-only decomposed wood and (c) wood decomposed by both microbes and macro-invertebrates.

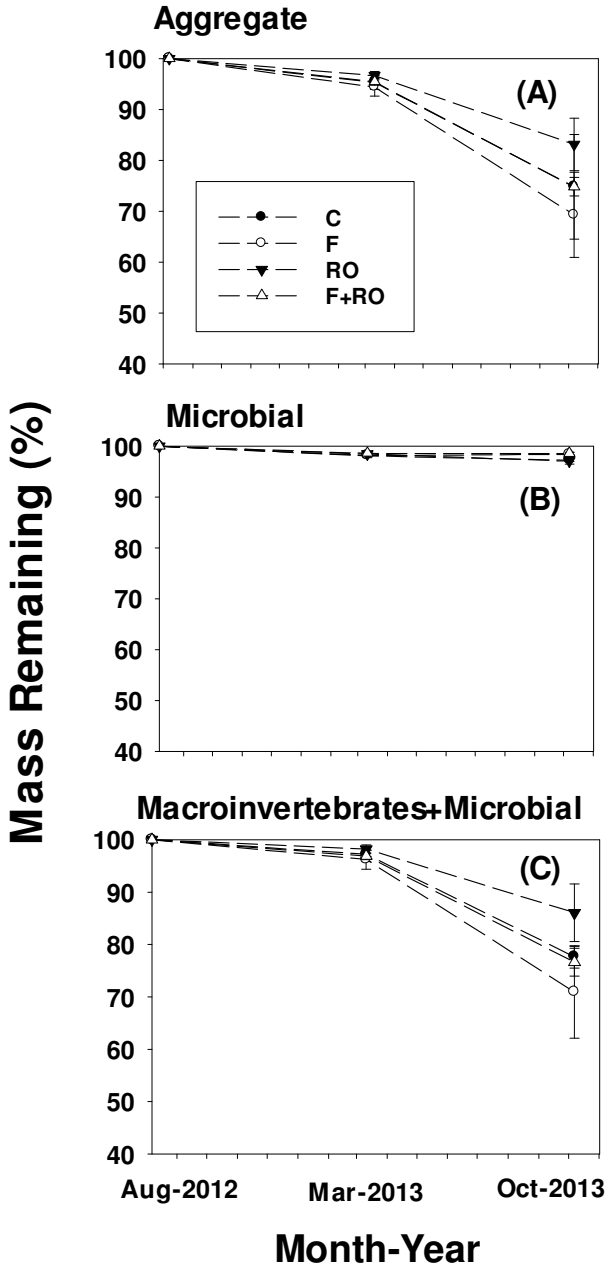
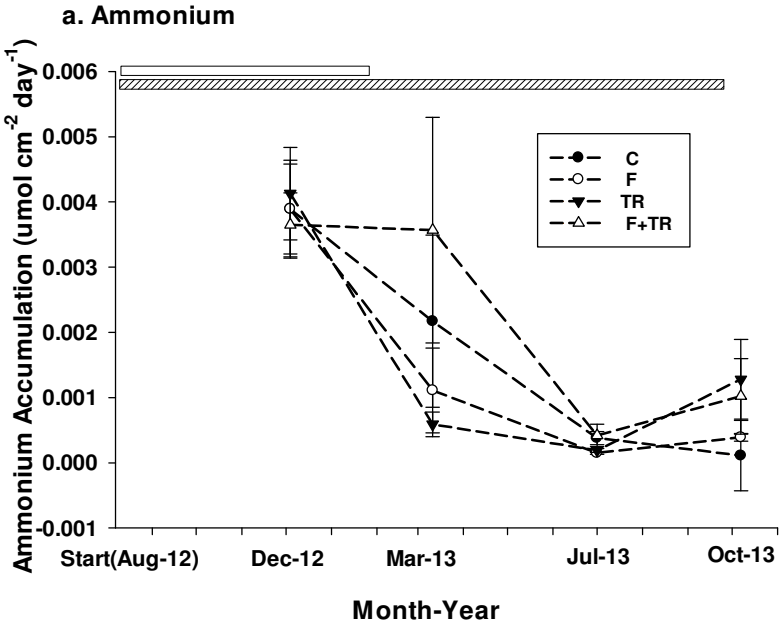
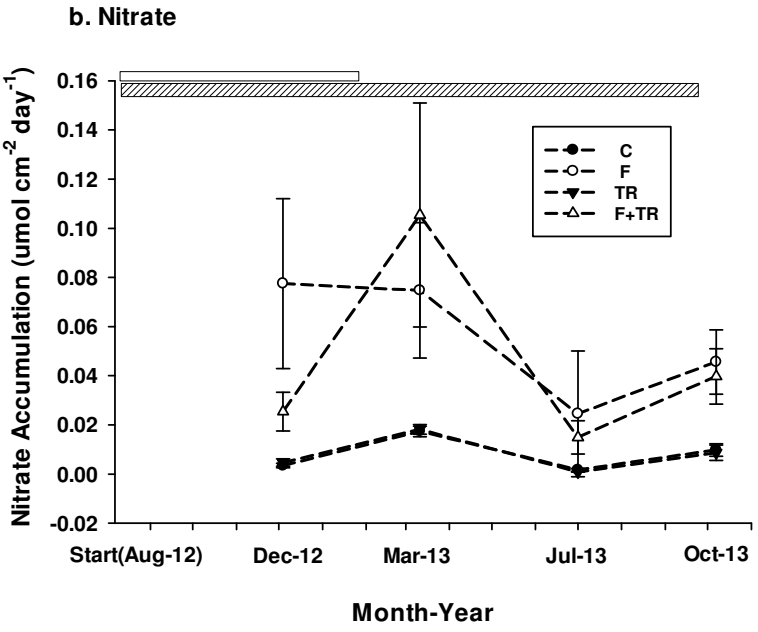


Table 2-5: Summary of p values from two-way ANOVA analysis of ammonium and nitrate accumulation (degree of freedom is 1 for all treatments) of tests of fertilization (F), throughfall reduction (TR), and time (T) and their combination.

| Treatment | Ammonium | Nitrate |
|---|---|---|
| **F** | 0.492 | **0.006** |
| **TR** | 0.378 | 0.706 |
| **T** | **<0.001** | **0.002** |
| **F*TR** | 0.392 | 0.713 |
| **F*T** | 0.706 | **0.002** |
| **TR*T** | 0.648 | 0.948 |
| **F*TR*T** | 0.644 | 0.948 |

Figure 2-4: Treatment effects on ammonium and nitrite accumulation on resin strips between August 2012 and September 2013, approximate intervals were three months. Bars at top of graph indicate when wood substrates overlapped with resins with the initial wood stick installation occurring in August 2012.




## II.5 Discussion

Wood decomposition rate is a function of temperature, moisture, and the decomposer community. Expressing the wood decomposition percentages as turnover rates (k), I found my k values ranged from 0.005 – 0.6477 $y^{-1}$, with many values being much higher than those found in a global meta-analysis of wood decomposition rates

(0.025-0.300) (Weedon et al. 2009). One possible reason is that the meta-analysis study calculated the average k value for each study site, which may obscure local scale variance (Bradford et al. 2014b). In my study the average k value was 0.201, which was higher than most studies conducted in the northern coniferous forests (Laiho and Prescott 2004) and for a loblolly pine forest (k=0.072) (Termites were not present in this study) (Barber and Van Lear 1984). Decomposition at my sites was heavily affected by invertebrates, likely termites, highlighting that the local decomposer community may accentuate differences between global and local k (Weedon et al. 2009).

*The effect of TR (throufall reduction) on wood decomposition*

The TR treatment decreased microbial decomposition of wood (the mass loss of wood without tunnels), which was consistent with my hypothesis. The reduced microbial decomposition was likely explained by a reduction in enzyme activity or limitation of microbial activity by water stress (Manzoni et al. 2012a). The decreased enzyme efficiencies under drought are often the result of higher enzyme immobilization and lower diffusion rates. Notably, the negative effect of TR was restricted to sticks affected by heterotrophic microbes only instead of sticks decomposed by microbes+macro-invertebrates. I cannot say definitively what macro-invertebrate community was responsible for wood decay because I did not perform continuous trapping and some beetle and ant species may consume wood (Similä et al. 2003); however termites are considered the most important macro-invertebrates among detrital wood consumers in many ecosystems (Stamm 2006, Cornwell et al. 2009) and I primarily found termites on my sticks during both collections (Zhang personal observation). I identified the subterranean termite *Reticulitermes flavipes* (Kollar) in the tunnels of a number of wood sticks from one sample period, and the tunnels were generally consistent with termite feeding.

To my knowledge, no manipulative research has been conducted that has determined the combined fertilization and reduced precipitation effect on termite wood consumption in these ecosystems. Torres and González (2005) found macro-invertebrates (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 high numbers of microbial functional group and species diversity 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 affected overall termite biomass. In this study, termite or macro-invertebrate activity was reduced by the TR treatment as evidenced by the tunneling results, although the wood mass loss of $D_{m+m}$ (Decomposition of woods with both microbes and macro-invertebrates) was not significant for individual sticks, the trend was consistent with tunnel presence. The insignificant result was possibly explained by the highly heterogeneous nature of termite distribution which was has been shown to be affected by multiple factors including vegetation cover (Jones et al. 1987), seasonal air temperature and precipitation (Haverty and Nutting 1976), and topography (Crist 1998).

*The effect of fertilization on wood decomposition*

Positive effects of fertilization on wood decomposition have also been found in temperate forests (Downs et al. 1996, Micks et al. 2004, Bebber et al. 2011), boreal forests (Allison et al. 2009), and tropical forests (Clay 2013). It is consistent with my result that fertilization increased total decomposition for sticks treated as a carbon pool after 426 days. However, previous studies also found negative effects of fertilization on wood decomposition. Fog (1988) reviewed the literature and found that N addition usually had a negative effect on the decomposition of recalcitrant substrates with high lignin content. Kaufert and Behr (1942) tested the N addition effect on woody decomposition in the lab. They found that small amounts of N addition (urea, ammonium sulfate, and ammonium phosphate) did not affect wood decomposition while high concentration of N fertilization reduced wood decomposition. These latter results were consistent with the microbial nitrogen mining theory (Moorhead and Sinsabaugh 2006), which suggests that increasing nutrient availability would decrease decomposition rates because mining recalcitrant substrates for N requires high energy input from soil microbe. I observed much higher $NO_3^-$ than $NH_4^+$ after fertilization, and

similar results have been observed with higher $NO_3^-$ than $NH_4^+$ in fertilized agriculture systems (Chen and Stark 2000), likely because under relatively high N availability and low vegetation cover, plant competition for $NH_4^+$ is lower and microbes increase nitrification and $NO_3^-$ becomes the dominant N form (Schimel and Bennett 2004). However, the negative effect of fertilization on microbial decomposition was overwhelmed by the positive effect of fertilization on microbial + macro-invertebrates decomposition (although not significant for mass loss), resulting in a significant increase of aggregate wood decomposition under the fertilization treatment.

Arthropod (macro-invertebrates) contributions to wood decomposition have often been ignored in past studies, although in some regions their consumption of wood is often higher than microbes (Ulyshen and Wagner 2013). My finding that fertilization significantly increased the number (or percentage) of wood with macroinvertebrate tunnels from 37 (59%) to 51 (67%) after 426 days suggested that fertilization either directly or indirectly stimulated the activity or abundance of macro-invertebrates. Similarly in a West African cropland, N addition increased termite's abundance from 101 individual $m^{-2}$ to 272 individual $m^{-2}$ (Zida et al. 2011). In this study, a positive fertilization effect was only found on decomposition of wood in the later period instead of the first period, which may suggest that a positive effect of fertilization on termite activity was more associated with higher seasonal temperatures or time was needed for the termites to respond to the treatment.

*The effect of location on wood decomposition*

The wood sticks nearest the tree decomposed faster than those farthest from the tree, 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 detritivores and microbes. For example, the rhizosphere or priming effect may be greater where microbial activity and enzymatic activity around roots stimulate decomposition (Kuzyakov et al. 2007). 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 also affected by the forest canopy (Forrester et al. 2012), with open areas being warmer and occasionally wetter compared to under canopy areas; characteristics that are then correlated with increased decomposition and respiration rate (Prescott 2002, Forrester et al. 2012). However, the spatial variability of wood decomposition may change as the stand matures because in response to stand development, canopy openings and gaps between roots will likely decrease along with the growth of trees or the dynamics of C allocation to roots and the mycorrhizal fungi associated with loblolly pines (Pritchard et al. 2014).

A surprising result was that the decomposition of wood placed directly under the TR exclusion treatments did not differ from the other locations. This suggests that the significant effect of the TR treatment was expressed at the plot level and not solely the result of the excluder's microscale effects on moisture availability. The excluders apparently warmed the soil surface (soil temperature data collected by Oklahoma University and not shown), which may have stimulated decomposer activity even as moisture may have caused some limitation to enzyme activity.

Where microbes were the only decomposers, wood decomposition inside the soil $CO_2$ efflux collars was lower than the decomposition of wood outside the collars. It is unclear why this might occur but suggests that the microbial community was altered by the presence of the soil collar barrier. Negative effects of collar depth on soil $CO_2$ efflux have been reported (Wang et al. 2005, Heinemeyer et al. 2011), and here other researchers found more negative soil $CO_2$ efflux was associated with increased collar-insertion depth and contributed to the reduced soil $CO_2$ efflux because of fine root severing. One possibility is that the collars disrupted the root-microbial connection that appears critical to the priming of recalcitrant organic matter(Kuzyakov 2010), or that rhizomorph mycelia were less likely to colonize wood inside collars.

*Interaction effects between treatments and time*

In my study, no interaction effect has been found between fertilization and TR either on wood decomposition, suggesting that these two treatments can be treated as

additive in ecosystem process models. A conceptual model that addressed the drought and nitrogen effects on litter decomposition was proposed by Allison et al. (2013). The model predicted that fertilization and drought could affect litter decomposition directly through change of microbial biomass and physiology and indirectly through change of community composition or the bacteria to fungi ratio. My results suggested that negative effect of fertilization and TR respectively on decomposition with microbes alone resulted in a low microbial wood decomposition value in the plot with both treatments; however, the negative effect was overwhelmed by the positive effect of fertilization on the activity of the macro-invertebrates, which were identified as the most important decomposer in this study. After aggregating treatment effects and two decomposer's effects, the aggregate wood mass loss in the plots with both treatments was almost the same as the control plot.

All the treatments including TR, fertilization and location were found to significantly interact with time and wood decomposition. The negative effect of TR on aggregate and microbial wood decomposition only existed in the later collection period (March, 2013 to October, 2013), which may have been caused by the higher temperatures during that later time interacting with moisture to inhibit microbial activity. It is consistent with the previous studies which found that increased temperature has increased wood decay rates in temperate forests (Mackensen et al. 2003, Berbeco et al. 2012). Comparing the wood mass loss in control plots and fertilization plots, I found that there was no difference in the first period but higher mass loss in the control plot (4.3%) relative to the fertilized plot (2.8%), suggesting that higher temperature may interact with nutrient availability to inhibit microbial activity. Interaction between location and time also suggested that microbial decomposition near the tree base was higher in the later stage. The possible explanation was because later time period fell in the summer with higher average temperatures, there was an increased positive benefit of tree shading or greater litter layers on the activity of microbes.

The results from this research suggest that the response of microbes and macro-invertebrates may diverge in response to fertilization and reduced moisture availability,

resulting in complex predictions for the fate of woody-debris in managed southern pine forests. Future drought may inhibit microbial decomposition and decrease macro-invertebrate's decomposition, which would benefit carbon sequestration as woody-debris in the managed southern pine forest. However, fertilization management has the potential to stimulate woody mass loss through positive effect on macro-invertebrates. These results suggest that response of macro-invertebrates to climate and fertilization needs to be included in ecosystem carbon models to better predict how the cycling of woody debris will respond to climate change and forest management.

# CHAPTER III EFFECT OF CLIMATE AND FOREST MANAGEMENT ON WOOD DECOMPOSITION ACROSS THE CLIMATIC RANGE OF LOBLOLLY PINE

## III.1 Introduction

Decomposition is affected by both abiotic environmental conditions (temperature, soil moisture) and biotic factors (types of decomposer organisms) (Cornwell et al. 2009, Bradford et al. 2014b). Environmental factors exert strong effects on woody debris decomposition (Kueppers and Harte 2005, Cornwell et al. 2009). Soil warming has increased wood decay rates in temperate forests (Mackensen et al. 2003, Berbeco et al. 2012). Berbeco (2012) found that warming increased decomposition of fine woody debris at Harvard Forest in central Massachusetts regardless of tree species and size. Drought has decreased decomposition or decomposer activity in many ecosystems (Berg and McClaugherty 2008, Manzoni et al. 2012a), but has increased wood mass loss in dry temperate forests in the western US (Barker 2008) and a rainforest in Puerto Rico (Torres and González 2005).

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 has suggested 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 termites are responsible for at least half of wood decomposition, causing the release of about 1.9 Pg C $yr^{-1}$ (Cornwell et al. 2009). Less research about termite decomposition has been done in temperate regions but it has been recently demonstrated that termites are responsible for significant amounts of decomposition in North American temperate forests (Stamm 2006, Ulyshen et al. 2014, Neupane et al. 2015). Termites may have a different response to climate than free-living microbes because termites can build nests to protect their colony from extreme environments and can avoid climate extremes through movement.

The local environment conditions, such as temperature and moisture, have strong effect on wood decomposition while temperature explaining more correlation in decomposition than moisture (Bradford et al. 2014a). Kueppers & Harte (2005) suggested that warmer plots had less wood debris because of higher decay rates. However, most previous studies attributed higher decomposition rates under higher temperature to more microbial activity or enzyme activity (Melillo et al. 1982, Sinsabaugh et al. 1991, Eriksson et al. 2012). It has been well known that the metabolic rate of microbes increases exponentially with the temperature following van't Hoff-Arrhenius relationship: $e^{-E/(kT)}$ (Boltzmann 1872). However, these studies ignored subterranean termites, another important wood decomposer. Subterranean termites have been found in all states in the US except Alaska (Suiter et al. 2002). Subterranean termites usually occur in warmer regions, suggesting that sites with higher temperature may have more termite activity and therefore higher rates of wood decomposition.

The objective of this chapter was to determine the influences of reduced moisture availability and fertilization on wood decomposition and termites' foraging activity across a temperature gradient in managed loblolly pine (*Pinus taeda* L.) forests in the southeastern United States. Four experiments located in climatically different areas of loblolly pine's extent (OK, FL, VA, and GA) were used to test the following hypotheses on how the interaction between climate, fertilization and reduced throughfall+precipitation affected wood decomposition.

**III.2 Hypotheses**

**H1: Increased temperature will increase microbial wood decomposition.**

**Rationale:** Among the sites, gradient of temperature is an important factor for the prediction model of wood decomposition. Microbial wood decomposition will occur more rapidly at higher temperatures. Increased temperature has increased wood decay rates in temperate forests (Mackensen et al. 2003, Berbeco et al. 2012). Higher temperature usually increases microbial decomposition by acceleratingmicrobial activity and/or enzyme activity (Melillo et al. 1982, Sinsabaugh et al. 1991, Eriksson et al. 2012).

**H2: Increased temperature will increase termite's foraging activity and wood consumption by termites.**

**Rational:** Termites are considered as one of the main decomposers of litter in tropical and savannas ecosystems. The fact that relatively low termite biomass was found in other ecosystems suggests that temperature is an important factor for termite's activity. Cornelius and Osbrink (2011) found that there was a significant correlation between soil temperature and wood decomposition, and decreased temperature would result in termites abandoning a nest. This result suggests that increased temperature within or among research sites will increase foraging activity by termites. Increased soil moisture among research sites will also increase wood decomposition. However, the correlation between soil moisture and decomposition is weaker than temperature (Bradford, Warren Ii et al. 2014).

### III.3 Experimental Methods

#### III.3.1 Study Design

The study sites are located in Oklahoma, Florida, Virginia, and Georgia to capture the range of climatic variability that occurs throughout most of the biogeographic distribution of loblolly pine. All plantations were operationally established between 2003 and 2008 at densities ranging from 1200 to 1800 trees $ha^{-1}$, or approximately 2 x 3 m spacing. Across the four sites, hourly temperature, relative humidity, and precipitation during the experiment were monitored above the canopy (Campbell Scientific, Logan UT). When climate data were missing, gap-filling was performed using the nearest NOAA weather station. Summarized climate data are found in Table 3-1.

Table 3-1: Location and climate information for the four sites (From August 15, 2013 to August 15, 2014).

| Site | Latitude | Longitude | Annual Prec. (cm) | Annual Temp. (°C) |
|---|---|---|---|---|
| Virginia | 37°27'37"N | 78°39'50"W | 112 | 13.0 |
| Georgia | 33°37'35"N | 82°47'54"W | 122 | 16.1 |
| Florida | 30°12'22"N | 83°52'12"W | 145 | 19.1 |
| Oklahoma | 34°01'47"N | 94°49'23"W | 130 | 15.0 |

Treatment plots were set up at all 4 sites in 2011 within a loblolly pine forest that had a mixture of open-pollinated genotypes from across the range of loblolly pine. Each plot was approximately 0.08 ha and was comprised of an outside buffer area and an internal measurement plot (around 0.04 ha). Before treatment establishment, all competing understory vegetation was removed by hand or sprayed with glyphosate. The experimental design is a factorial combination of precipitation and throughfall reduction (TR) and fertilization. 'Fertilization' (432 kg $ha^{-1}$ urea, 140 kg $ha^{-1}$ DAP and 112 kg $ha^{-1}$ potash) was conducted in April 2012 to achieve 'optimum' nutrient availability with subsequent 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 $ha^{-1}$. In June of 2012, plastic sheeted troughs were installed between planted rows and, depending on tree size or row spacing, below the tree canopy to create the TR treatment. The surface area of these treatments diverted 30% of precipitation and throughfall off the plot. The troughs were 0.5 and 1.5 m high above the soil surface at two sides and the rainfall was captured and

funneled away from the plots gravimetrically. The experimental design was a factorial combination of fertilization and throughfall reduction.

### III.3.2 Study Measurements

To assess the response of decomposition to treatments and spatial variation, common wood substrates (southern pine wood sticks with the dimension of 6.3 cm × 0.9 cm × 0.3 cm) were placed in all 4 sites in August 2013. Sticks were cut from 4 pieces of dimensional lumber (2.54 cm × 30.5 cm × 243.8 cm) that were pulled from the same bundle of lumber purchased in Home Depot in college station. It is highly likely these sticks were derived from *P. taeda* but shortleaf pine (*Pinus echinata* Mill.) is also harvested in the region. For the field placement of sticks, four trees were randomly selected in each plot and the sticks were set close, middle and far from the tree. The far sticks were located exactly in the middle of two tree rows and did not fall under troughs, but the middle sticks were under troughs in the TR treatment. One third (~192 per site) of the substrate was collected at 0.5 years (y), another one third were picked up in 1 year and the remaining one-third picked up after 1.5 y . On removal, sticks collected from Florida, Virginia, and Georgia were shipped to the Forest Sciences Lab, Texas A&M University (College Station, TX) where all sticks were cleaned, assessed for damage by macro-invertebrates, oven dried at 105 $^{\circ}$C for 2 days, and weighed to determine the woody mass loss.

### III.3.3 Statistical Analyses

For all sites, a linear mixed model was used to analyze the wood decomposition after one year, in which fertilization, TR, location, and time along with their interactions were still included as fixed effects, blocks and subjects nested within block were included as random effects, while annual air temperature was included as a covariate. Exponential relationships between the decomposition constant k and temperature were estimated (as described in the previous chapter) for different associations of decomposing organisms.

Within each site, the effects of fertilization, TR, and time along with their interaction on macro-invertebrate's attack ratio (percentage of tunneled wood) were

assessed using generalized linear model. Logistic regression was used and P values (>Chi) were analyzed. The effect of fertilization, TR, location and time on $D_{agg}$, $D_m$, and $D_{m+m}$ (Defined in nomenclature) 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 determined by wood sticks with the same block, plot, tree and location, with the only difference being the collection date. Each subject was collected once on each date and considered as a repeated measurement. Within each date, post hoc contrasts (Tukey HSD) were used to value differences among levels of treatments.

**III.4 Results**

*The ratio of tunneled wood for OK and FL*

Wood tunneling by macroinvertebrates primarily occurred in OK and FL (Fig.3-2, Table 3-2), with VA and GA having too few tunnels to analyze at the 0.5 y and 1.0 y collections and relatively low numbers of tunnels at the end (30% in VA and 37% in GA).. Time corresponded to a significant ($P<0.001$) increase in the ratio of tunneled wood. The ratio of tunneled wood significantly ($P<0.001$) increased from the 0.5 y (34%) relative to the 1 y ratio (77%) and the 1.5 y ratio (84%) (Table 3-3). Site also had a significant effect on the ratio of tunneled wood ($P<0.001$), where the FL ratio (71%) was higher than OK's ratio (58%) (Table 3-3). Neither the main effect of fertilization ($P=0.08$) nor TR ($P=0.06$) were significant effects on the ratio of tunneled wood. However, there was significant interaction between fertilization and site (Table 3-3, $P<0.001$). Fertilization increased the ratio of tunneled wood from 52% to 64% ($P=0.035$) in OK but had no effect in FL ($P=0.98$). The FL ratio was only higher than the OK's ratio in the control plot ($P<0.001$) but there was no difference in the fertilization plot ($P=0.267$). Similarly, the TR treatment also had a significant interaction with site ($P<0.001$), where the treatment TR decreased the ratio of tunneled wood in OK ($P<0.001$, 67% to 49%) but there was no effect in FL ($P=0.181$). The ratio of tunnel wood in FL (75%) was only higher than OK's ratio (49%) in the TR plot ($P<0.001$)

instead of control plot. There was a significant interaction between site and time ($P<0.001$), where tunneled wood ratio for FL was only higher than OK's ratio after 0.5 y ($P<0.001$) and not for the 1 y and 1.5 y (Table 3-2, 3; Fig. 3-2).

*Wood stick decomposition*

Summary of wood mass loss over annul average temperature across 4 sites was shown in Figure 3-1. Wood mass loss was highest in FL, followed by OK. More treatment effects were shown in FL and OK compared to GA and VA. Adding annual temperature as a covariate in the linear mixed model for wood decomposition resulted in annual temperature ($P<0.001$) and location ($P<0.001$) having significant effects on wood decomposition. Treatments (F and TR) had no effects on wood decomposition across sites; however, treatment effects were significant within the site of FL and OK.

Figure 3-1: Summary of wood mass loss over annul average temperature across 4 sites (FL, OK, GA, and VA) from Aug-2013 to Aug-2014.

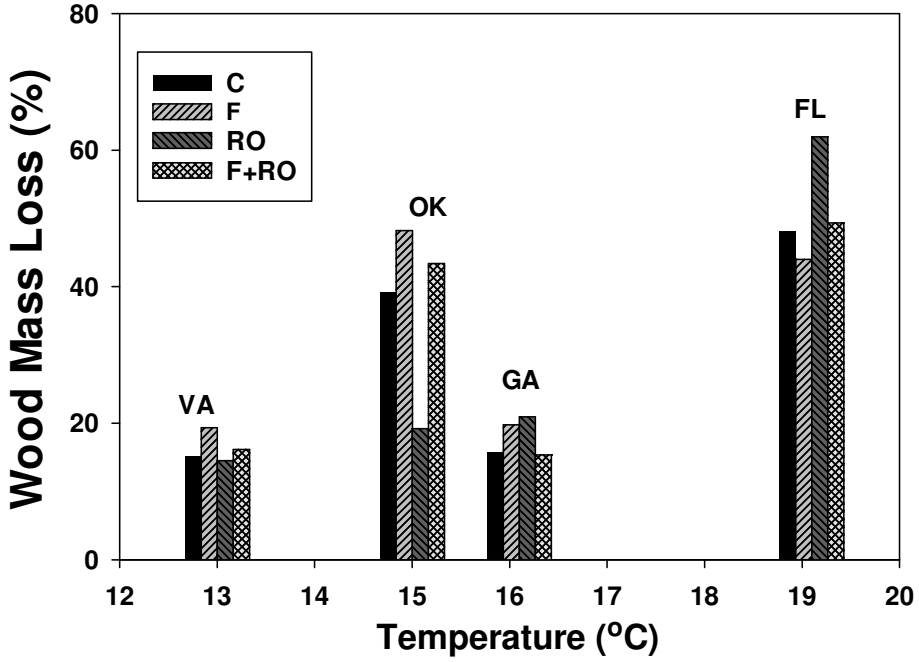
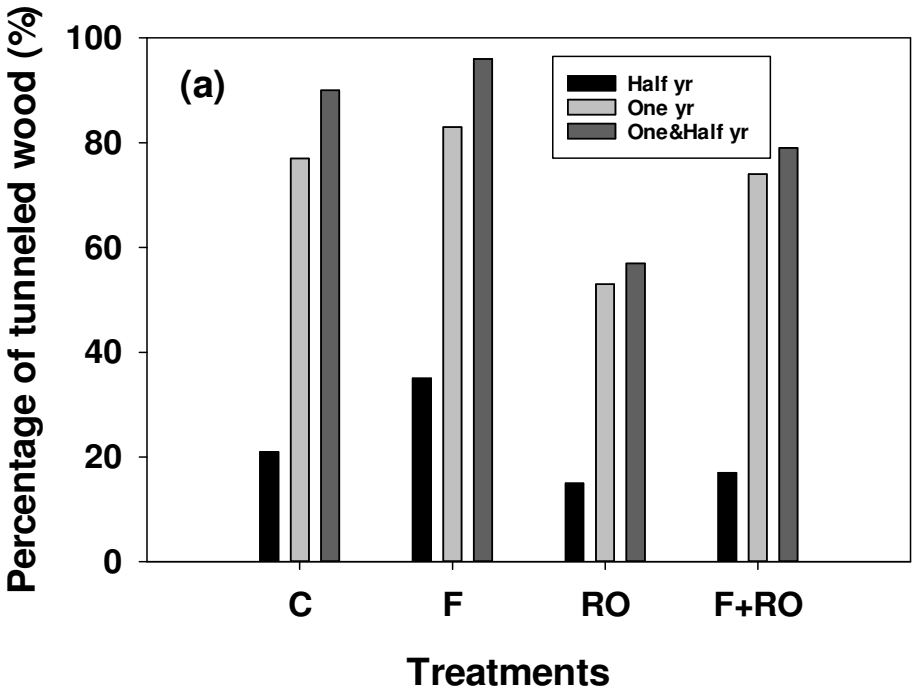


Figure 3-2: Treatment effects on percentage of tunneled wood in OK (a) and FL (b).



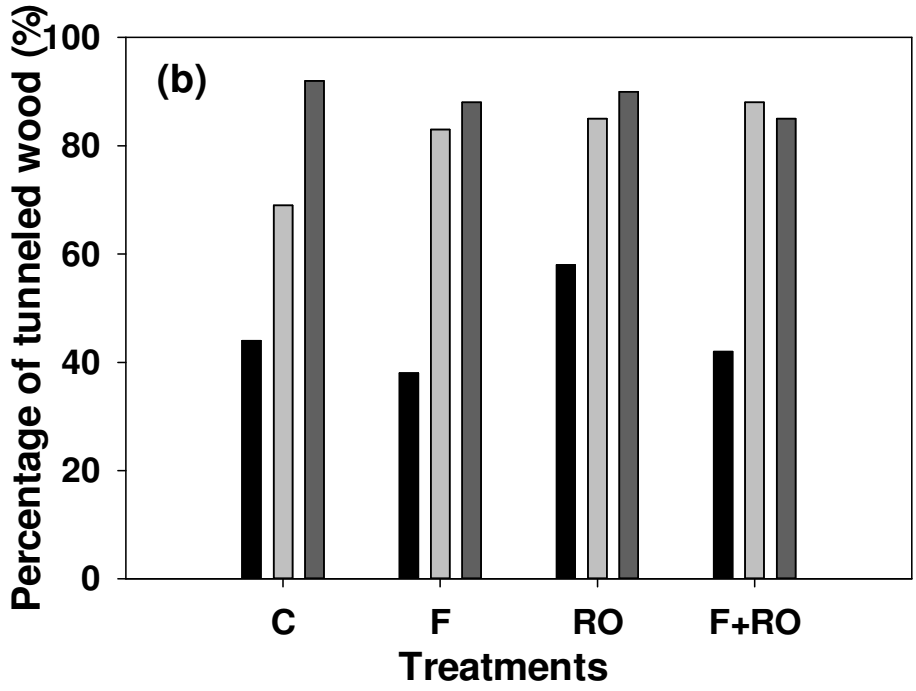



Table 3-2: Summary of average number of recovered wood stick assays with tunnels and the percentage of tunneled wood in each plot by treatment over time.

| Site | Time (Year) | Treatment | Number of wood with tunnels (#) | Tunneled wood (%) |
|---|---|---|---|---|
| **OK** | **0.5** | **C** | 10 | 21% |
| | **0.5** | **F** | 17 | 35% |
| | **0.5** | **TR** | 7 | 15% |
| | **0.5** | **F+TR** | 8 | 17% |
| | **1** | **C** | 37 | 77% |
| | **1** | **F** | 40 | 83% |
| | **1** | **TR** | 24 | 53% |
| | **1** | **F+TR** | 35 | 74% |
| | **1.5** | **C** | 43 | 90% |
| | **1.5** | **F** | 43 | 96% |
| | **1.5** | **TR** | 24 | 57% |
| | **1.5** | **F+TR** | 33 | 79% |
| **FL** | **0.5** | **C** | 21 | 44% |
| | **0.5** | **F** | 18 | 38% |
| | **0.5** | **TR** | 28 | 58% |
| | **0.5** | **F+TR** | 20 | 42% |
| | **1** | **C** | 33 | 69% |
| | **1** | **F** | 40 | 83% |
| | **1** | **TR** | 41 | 85% |
| | **1** | **F+TR** | 42 | 88% |
| | **1.5** | **C** | 44 | 92% |
| | **1.5** | **F** | 42 | 88% |
| | **1.5** | **TR** | 36 | 90% |
| | **1.5** | **F+TR** | 41 | 85% |

Table 3-3: Summary of P values (>Chi) from generalized linear model (logistic regression) testing the treatment and time effects on macro-invertebrate's attack ratio (df=1 for all treatments) on wood sticks.

| Treatment | Ratio of tunneling wood |
|---|---|
| **Time** | **<0.001** |
| **Site** | **<0.001** |
| **F** | *0.08* |
| **TR** | *0.06* |
| **F*TR** | 0.44 |
| **Site*F** | **0.014** |
| **Site*TR** | **<0.001** |
| **Time*Site** | **0.039** |
| **F*Time** | 0.155 |
| **TR*Time** | 0.205 |
| **F*TR*Time** | 0.808 |
| **Site*F*D** | 0.235 |
| **Site*Time*F** | 0.437 |
| **Site*Time*D** | 0.466 |
| **Site*Time*F*D** | 0.578 |

In FL, individual treatments had significant effects on wood decomposition but no interaction effects were found (Table 3-4). Fertilization increased microbial decomposition (P<0.001, Fig. 3-3b) while it decreased the decomposition of the wood sticks attacked by microbes+macroinvertebrates (P<0.001, Fig.3-3c). It had no effect on aggregate wood decomposition (Fig.3-3a). Fertilization increased microbial decomposition from 8% to 11% but decreased the decomposition of the wood sticks attacked by macro-invertebrates from 65% mass loss to 57% mass loss. Throughfall reduction had a significant effect on both aggregate (P=0.007) and microbial

decomposition (P<0.001), increasing aggregate decomposition from 43% to 49% and microbial decomposition from 9% to 11% (Fig. 3-3). The TR treatment also increased the decomposition of the wood sticks attacked by macro-invertebrates from 59% to 63% but this result was not significant (P=0.085) (Table 3-4, Fig. 3-3).

Besides the main treatment effects, location and time were significant effects on wood decomposition in FL (Table 3-4, Fig 3-4). Location of sticks (three distances to the tree and one within respiration collars) had significant effects on $D_{agg}$ ($p<0.001$) and $D_m$ ($p=0.005$) but not on $D_{m+m}$ ($p=0.086$) (Table 3-4). Post hoc analysis revealed that both estimates indicated faster decomposition closer to the tree than the other locations (Fig. 3-4). The above results suggested that tree distance had a negative effect on both aggregate and microbial decomposition. Sticks decomposed faster along time for all $D_{agg}$ ($p<0.001$), $D_m$ ($p<0.001$), and $D_{m+m}$ ($p<0.001$) (Table 3-4). Microbial decomposition increased from 6% at 0.5 y to 21% 1.5 y year while decomposition of the wood sticks attacked by macro-invertebrates increased from 41% after a 0.5 to 72% after 1.5 y.

In OK, significant treatment effects were found for wood decomposition and treatment interactions with each other and time and location (Table 3-5). Fertilization increased aggregate decomposition from 27% to 42% (P<0.001, Fig. 3-3a), and increased mass loss from microbial decomposition from 3.8% to 3.9% (P=0.002, Fig. 3-3b), and increased decomposition of the wood sticks attacked by macro-invertebrates from 48% to 64% (P<0.001, Fig. 3-3c). TR decreased aggregate decomposition from 40% to 29% (P=0.001, Fig.3-3a) and microbial decomposition from 4% to 3% (P<0.001, Fig.3-3b), but had no effect on decomposition of the wood sticks decomposed by macro-invertebrates (Table 3-5, Fig. 3-3c).

Besides the main treatment effects, location and time both had significant interaction effects on $D_{agg}$, $D_m$ and $D_{m+m}$ in OK (Table 3-5, Fig.3-4). Post hoc analysis showed that the three estimators close to the tree were all higher than other two locations. The three estimators also got higher with time. $D_{agg}$ increased from 7% to 60% from 0.5 year to 1.5 year (Fig. 3-4a), $D_m$ increased from 2% to 10% (Fig. 3-4b) and $D_{m+m}$ increased from 26% to 72% (Fig.3-4c).

Table 3-4: FL's summary of degrees of freedom and p values from Linear mixed model with repeat analysis testing for aggregate (all wood sticks), microbial and microbial plus Macro-invertebrates decomposition with individual stick as a carbon pool. Treatments include Fertilization (F); Throughfall reduction (TR); Location (L); and Time (T).

| Treatment[a] | df | | Aggregate | df | Microbes | df | Microbes & Macro-invertebrates |
|---|---|---|---|---|---|---|---|
| | N[b] | D[b] | | D[b] | | D[b] | |
| **F** | 1 | 158 | 0.121 | 156 | **<0.001** | 95 | **0.006** |
| **TR** | 1 | 164 | **0.007** | 155 | **<0.001** | 93 | *0.085* |
| **L** | 2 | 513 | **<0.001** | 155 | **0.005** | 360 | *0.086* |
| **T** | 2 | 513 | **<0.001** | 156 | **<0.001** | 369 | **<0.001** |
| **F*TR** | 1 | 94 | 0.374 | 142 | 0.565 | 58 | 0.409 |
| **F*L** | 2 | 500 | 0.998 | 136 | 0.563 | 355 | 0.311 |
| **F*T** | 2 | 508 | 0.470 | 139 | 0.991 | 362 | 0.389 |
| **TR*L** | 2 | 494 | 0.711 | 147 | 0.905 | 343 | 0.888 |
| **TR*T** | 2 | 511 | 0.309 | 148 | 0.353 | 364 | 0.253 |
| **L*T** | 4 | 502 | 0.422 | 151 | *0.059* | 362 | 0.389 |
| **F*TR*L** | 2 | 492 | 0.448 | 134 | 0.761 | 342 | 0.594 |
| **F*TR*T** | 2 | 506 | *0.081* | 138 | 0.277 | 363 | *0.097* |
| **F*L*T** | 4 | 496 | 0.222 | 130 | 0.784 | 340 | 0.416 |
| **TR*L*T** | 4 | 488 | 0.568 | 143 | *0.064* | 333 | 0.640 |
| **F*TR*L*T** | 4 | 484 | 0.402 | 129 | 0.491 | 329 | 0.409 |

[a] N is numerator; D is denominator

Figure 3-3: Treatment effects over time on mass loss of the individual wood sticks for (a) the aggregate of all decomposers (b) microbial-only decomposed wood and (c) wood decomposed by both microbes and macro-invertebrates across 4 sites of OK, FL, GA and VA.

**(a).**

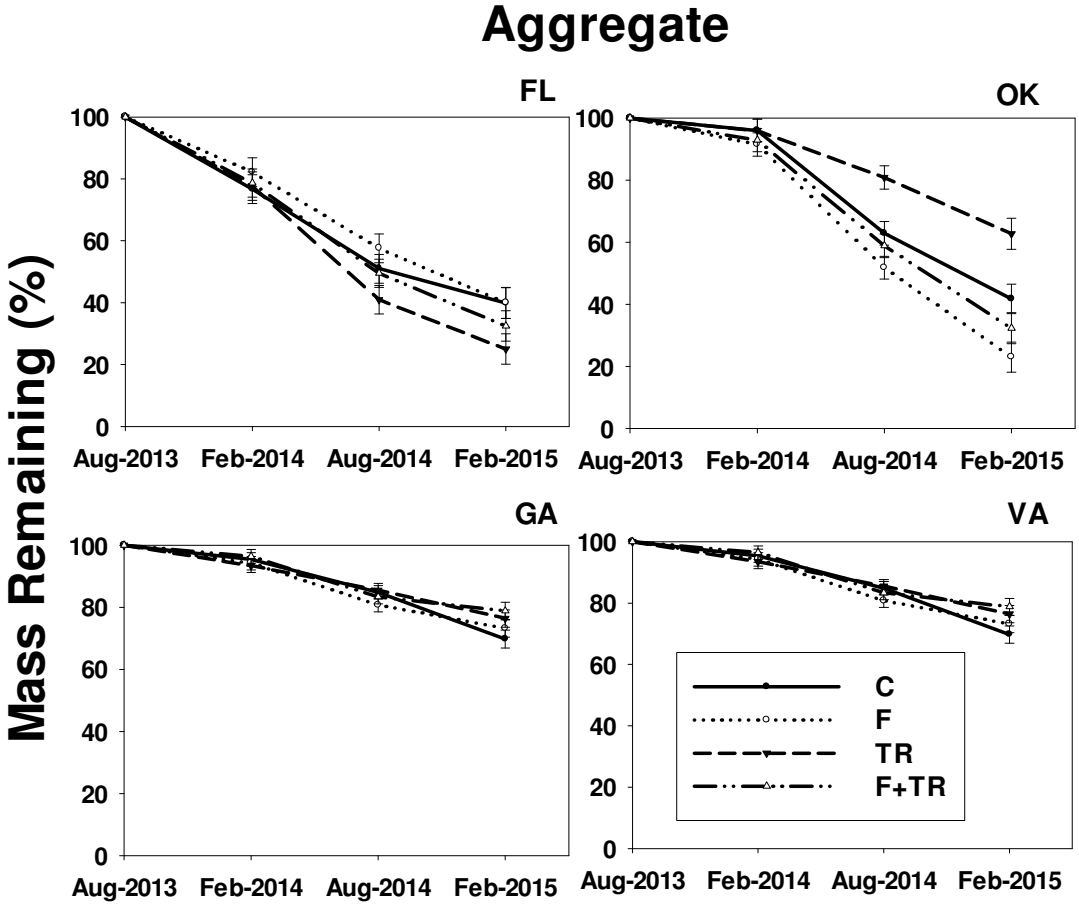
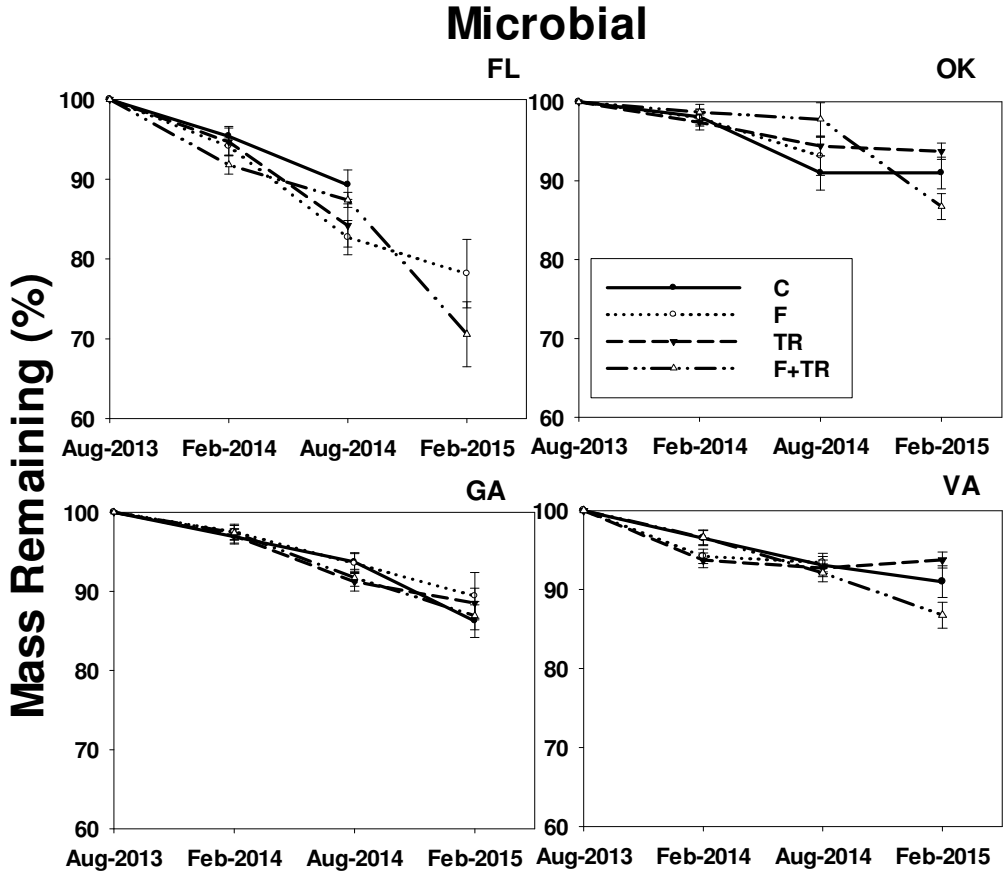


Figure 3-3 Continued:

**(b).**




**(c).**

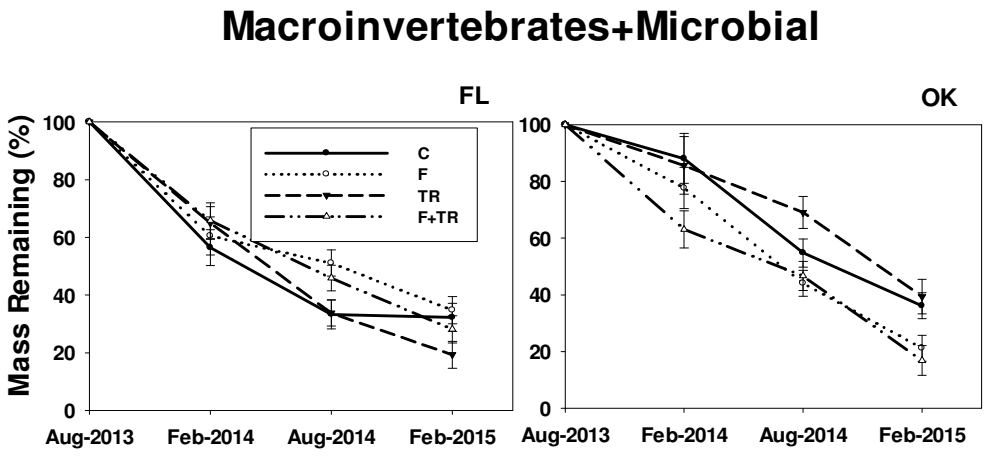


Table 3-5: Summary of degrees of freedom and p values from linear mixed model with repeat analysis testing for aggregate (all wood sticks), microbial and microbial plus Macro-invertebrates decomposition with individual stick as a carbon pool for the OK site. Treatments include Fertilization (F); Throughfall Reduction (TR); Location (L); and Time (T).

| Treatment[a] | df | | Aggregate | df | Microbes | df | Microbes & Macro-invertebrates |
|---|---|---|---|---|---|---|---|
| | N[b] | D[b] | | D[b] | | D[b] | |
| **F** | 1 | 57 | **<0.001** | 129 | **0.002** | 87 | **<0.001** |
| **TR** | 1 | 57 | **0.001** | 118 | **<0.001** | 92 | 0.648 |
| **L** | 2 | 462 | **<0.001** | 184 | **<0.001** | 269 | **0.020** |
| **T** | 2 | 468 | **<0.001** | 199 | **<0.001** | 265 | **<0.001** |
| **F*TR** | 1 | 57 | 0.672 | 129 | **<0.001** | 94 | 0.446 |
| **F*L** | 2 | 462 | **0.020** | 180 | *0.054* | 261 | 0.787 |
| **F*T** | 2 | 468 | **<0.001** | 198 | **<0.001** | 267 | 0.241 |
| **TR*L** | 2 | 462 | 0.133 | 181 | 0.165 | 271 | 0.885 |
| **TR*T** | 2 | 468 | 0.266 | 198 | **<0.001** | 265 | 0.389 |
| **L*T** | 4 | 462 | 0.142 | 180 | **0.001** | 257 | 0.680 |
| **F*TR*L** | 2 | 462 | 0.838 | 168 | 0.529 | 252 | 0.505 |
| **F*TR*T** | 2 | 468 | *0.060* | 196 | **0.033** | 267 | 0.894 |
| **F*L*T** | 4 | 462 | 0.413 | 177 | **0.024** | 253 | 0.683 |
| **TR*L*T** | 4 | 462 | 0.602 | 181 | **0.013** | 258 | 0.874 |
| **F*TR*L*T** | 4 | 462 | **0.006** | 176 | *0.057* | 248 | **0.003** |

[a] N is numerator; D is denominator

Figure 3-4: Location effects over time on mass loss of the individual wood sticks for (a) the aggregate of all decomposers (b) microbial-only decomposed wood and (c) wood decomposed by both microbes and macro-invertebrates across 4 sites of OK, FL, GA and VA.

**(a).**

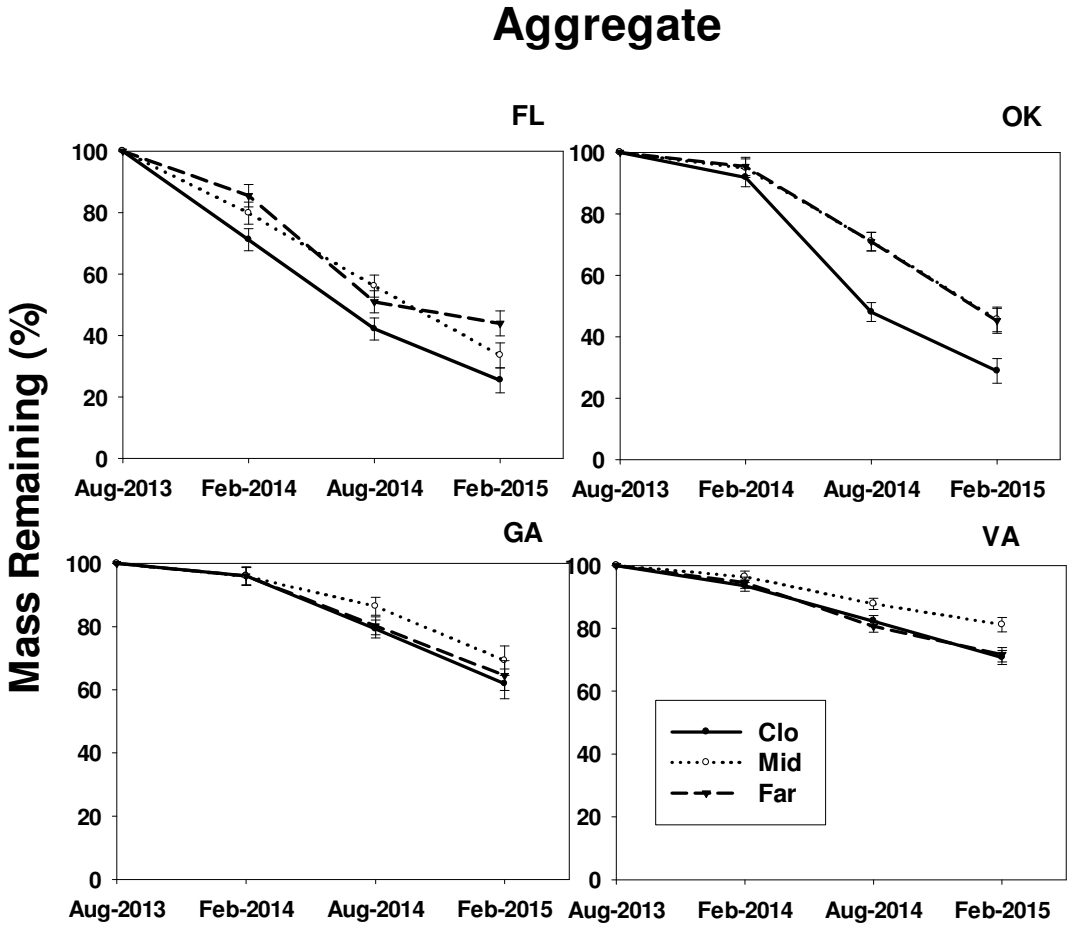
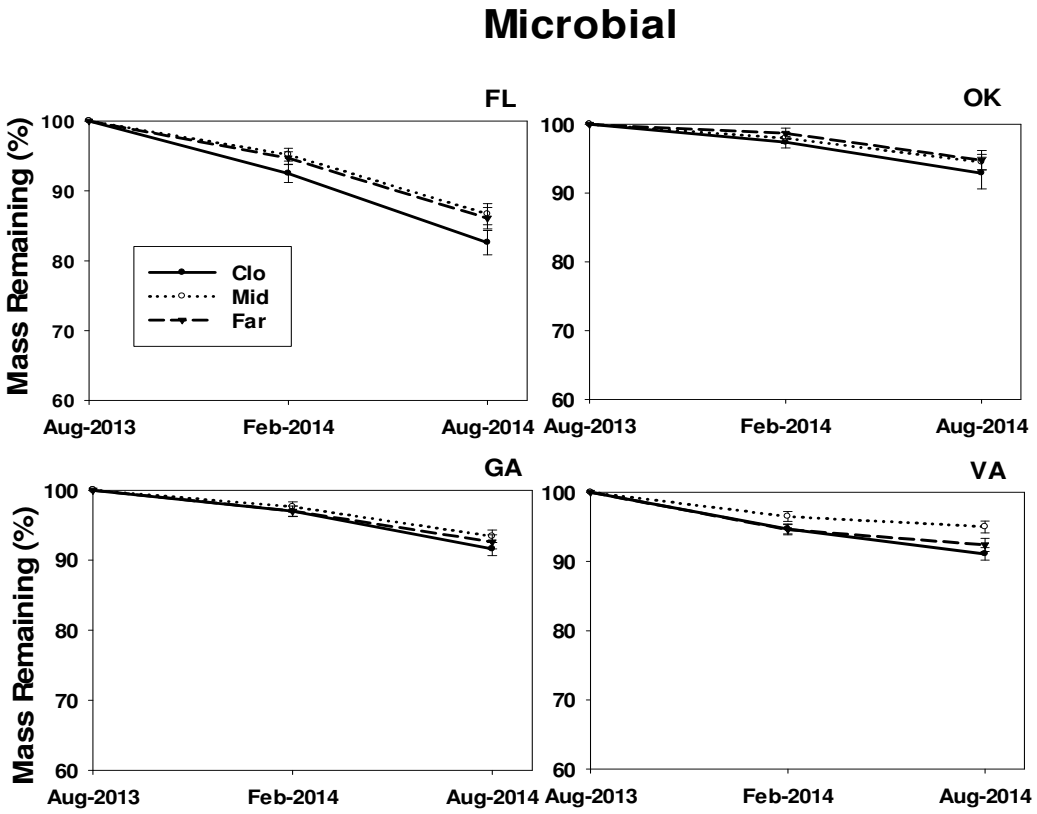
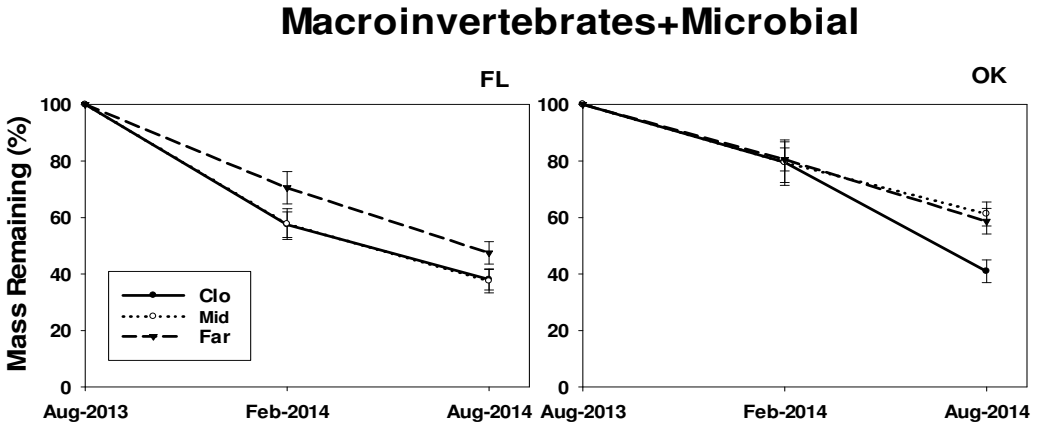


Figure 3-4 Continued:

**(b).**




**(c).**

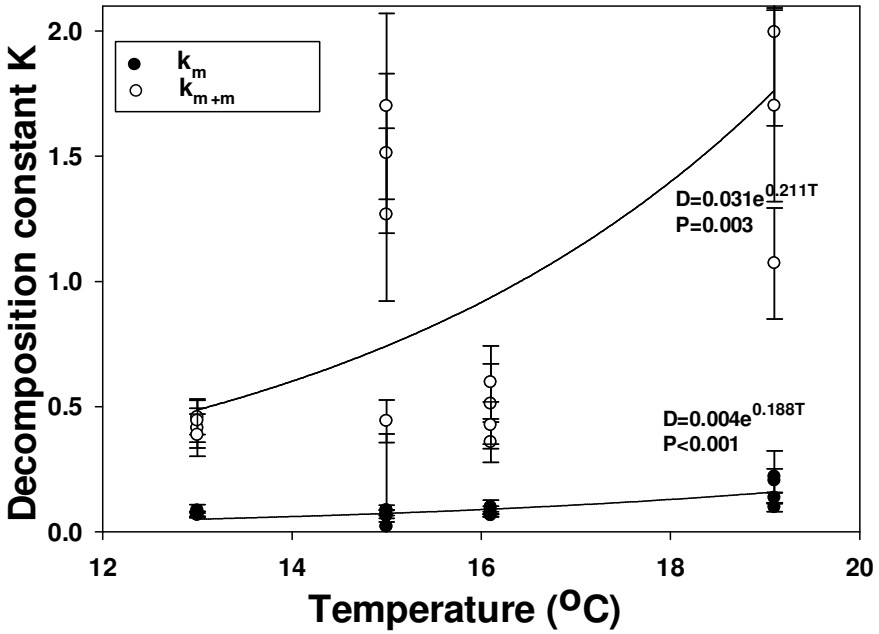


Interaction effects between treatments for microbial and aggregate decomposition were found for OK (Table 3-5). There was significant interaction between F and TR where TR only decreased microbial decomposition in the fertilized plot (P=0.017) and fertilization only decreased microbial decomposition in TR plot (2.5% vs 4.0%, P=0.012). The positive effect of F on microbial decomposition was attributed to increased decomposition in the without TR, although it was not significant (6% vs 3.5%, P=0.668). Fertilization's effect on microbial decomposition also changed with time (P<0.001). Post hoc analysis for the Fertilization only treatments revealed increased microbial decomposition after 1.5 y (P=0.032) with no effect at either the 0.5 y or 1 y collections. TR decreased microbial decomposition after 1 y (P=0.05) and 1.5 y (P=0.017). F and location showed that fertilization only increased aggregate decomposition close to the tree (P=0.002) but had no effect on other locations. Fertilization also only increased aggregate decomposition after 1.5 y (P<0.001) instead of the earlier collection periods (0.5 y and 1.0 y).

*Decomposition constant k*

Significant exponential relationships were found between annual average temperature for the period of the study and both $D_m$ and $D_{m+m}$ decomposition expressed as the turnover constant (k). The temperature response of the relationship of sticks attacked by macro-invertebrates had a greater intercept than microbial-only decomposed sticks but the exponents were similar for the two relationships (Fig. 3-5).

Figure 3-5: Summary of decomposition constant k for microbial ($k_m$) and microbial+macroinvertebrates ($k_{m+m}$) over annual average temperature across 4 sites (FL, OK, GA, and VA) from Aug-2013 to Aug-2014.




**III.5 Discussion**

*Climate Effect across Sites*

Climate is traditionally thought to be the predominant control on litter decomposition (Meentemeyer 1978, Currie et al. 2010), but a recent paper showed that climate failed to predict the wood decomposition at the local scale (Bradford et al. 2014b). In this chapter, my main question is how climate factors affect wood decomposition across the 4 sites. My finding was consistent with the previous studies that temperature is the predominant control on wood decomposition, both for microbes and macro-invertebrates. The exponential relationship between the decomposition constant k of a stick attacked by macro-invertebrates had a greater intercept compared to microbial consumption, suggesting that the decomposer type was also an important factor in predicting wood decomposition at the local scale, especially in the sites with both decomposers present (FL and OK in my study). My results also suggested that temperature was a good predictor for microbial decomposition but relatively worse for wood decomposition attacked by macro-invertebrates. This was especially accurate for

OK site, which had an annual temperature that was lower than GA, but its average wood decomposition constant k was much higher than the warmer GA because of the contribution of macro-invertebrates.

*Throughfall reduction effect*

Throughfall reduction had the opposite effect on microbial decomposition in OK and FL. TR decreased microbial decomposition in OK, which was likely explained by a reduction in enzyme activity by water stress (Manzoni et al. 2012a). However, TR increased microbial decomposition in FL which was consistent with the previous studies finding that drought increased wood mass loss in temperate forests in the western US (Barker 2008) and rainforest in Puerto Rico (Torres and González 2005). Barker (2008) attributed the increased decomposition of Douglas-fir coarse woody debris to stimulated brown-rot decomposition under drought environment. One possible reason for higher decomposition under drought is that drought will provide a better aerobic condition which is necessary to oxidase enzyme activity. This is supported by the studies of Fenner et al. (2005) that drought increased phenolic degrading bacterial biomass, phenol oxidase activity and β-glucosidase activities in a peatland. The opposite effect may be explained by higher precipitation in FL that drought increased aerobic condition which is possible a limiting for oxidase enzyme activity.

Throughfall reduction's effects on macro-invertebrates were more complex. Although TR reduced the ratio of tunneled wood in OK, its effect on decomposition of wood attacked by macro-invertebrates were not significant. The reduced ratio suggested termite or macro-invertebrate activity was reduced by the TR treatment. TR had no effect on the ratio of tunneled wood in FL, but its positive effect on decomposition of wood attacked by macro-invertebrates was significant. FL's results were consistent with the results of Torres and González (2005) who found that macro-invertebrates (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 high numbers of microbial functional group and species diversity of wood decomposers.

Microbes and termites can have synergistic effects during wood decomposition, and these may explain the contrasting results between OK and FL.

*Fertilization Effect*

Fertilization increased microbial decomposition both in FL and OK. This is consistent with many other field studies which showed positive effects of fertilization on woody decomposition in temperate forest (Downs et al. 1996, Micks et al. 2004, Bebber et al. 2011), boreal forest (Allison et al. 2009), and tropical forests (Clay 2013). The 'basic stoichiometric decomposition theory' (Melillo et al. 1982) may explain these results that added N would maxim microbial growth and mineralization if other nutrient are limiting (Chapin III et al. 2011). Another possible reason is that fertilization alleviated C limitation of microbes through increased aboveground litter production (LeBauer and Treseder 2008). Moreover, fertilization increased leaf area index at both sites (Will et al. 2015), which may have moderated swings in moisture under the forest floor layer.

Fertilization's effects on macro-invertebrates were not consistent in the two sites. The results that fertilization only increased the ratio of tunneled wood in OK instead of FL suggested that fertilization only stimulated foraging activity of macro-invertebrates (termites mostly) in OK. Also, fertilization increased decomposition of the wood sticks attacked by macro-invertebrates in OK. In contrast, fertilization decreased decomposition of the wood sticks attacked by macro-invertebrates in FL. My findings suggested that fertilization stimulated or inhibited the activity or abundance of macro-invertebrates in different sites. However, it unclear what mechansism could be associated with fertilization effects on macro-invertebrates' activity or decompositon. Sodium is considered as the most limiting nutrient for invertebrates (Pennisi 2014). A recent study showed that NaCl fertilization increased termites by 17-fold and decomposition rate in an Amazonian forest (Kaspari et al. 2014). More studies are needed to understand the mechansims of fertilization effects on macro-invertebrates and the interaction between N addition and sodium level in different sites.

*Contrary treatment effects on microbial decomposition in OK*

The studies of chapter II and part of chapter III have been both conducted in OK, respectively from August 2012 to October 2013 and from August 2013 to February 2015. However, some treatment effects were not consistent for these two time series. For example, fertilization decreased microbial decomposition in the first period but increased microbial decomposition in the latter one. The possible explanations for these opposite results were: 1) fertilization was only added before the first study once, so its effect has been faded for the second study; 2) with growth of canopy, it was possible that more litter input indirectly stimulated microbial decomposition in the latter period. The fact that there was interaction between TR and location in chapter II but the interaction was not significant anymore in the chapter III maybe be explained the growth of canopy which reduced the variation in throughfall within the forest and reduced variation in surface moisture.

# CHAPTER IV. CONCLUSIONS

The results from this research suggest that the response of microbes and macro-invertebrates may diverge in response to fertilization and reduced moisture availability, resulting in complex predictions for the fate of woody-debris in managed southern pine forests. Future drought may inhibit microbial decomposition and decrease macro-invertebrate's decomposition, which would benefit carbon sequestration as woody-debris in the managed southern pine forest. However, fertilization management has the potential to stimulate woody mass loss through positive effect on macro-invertebrates but drought and fertilization effects were not consistent effect across sites. These results suggest that response of macro-invertebrates to climate and fertilization needs to be included in ecosystem carbon models to better predict how the cycling of woody debris will respond to climate change and forest management in each site. Also, it is important to better understand the interaction between macro-invertebrates (termites) and temperature.

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