SOIL NITROGEN FLUX ACROSS A GRASSLAND

TO FOREST VEGETATION GRADIENT IN

SOUTHEASTERN OKLAHOMA, USA

By

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Abstract: The Forest Habitat Research Area located in the Pushmataha Wildlife Management Area in southeastern Oklahoma provides a unique opportunity for research into vegetation effects on soil nitrogen cycling. Long term treatments combining a range of initial harvesting practices with different prescribed fire intervals have created a gradient of ecosystems from restored tallgrass prairie and savanna systems, to undisturbed closed canopy forest. Prescribed fire intervals ranged from one to four years, resulting in marked structural changes, with higher frequency fire intervals resulting in grassland or savanna structures, and longer intervals returning to a forested structure after thirty years of continuous treatment. To compare vegetation structural influences on litter decomposition rates, fresh pine foliage was deployed in litter bags placed at 76 locations across the forest-grassland continuum. There was no statistical difference in decomposition rates over the 14 study months. The foliage lost on average 30 percent of initial mass, with no detectable differences of vegetation structure on cellulose, hemi-cellulose or lignin loss rates. *In situ* placed ion exchange resin beads over the same deployment interval as the litter study showed total inorganic nitrogen flux in the upper soil layer was higher in forested areas compared to grassland or savanna. Nitrate levels were similarly higher in the forest compared to the grassland or savanna. To assess differences in potential soil nitrogen flux, aerobic incubation of soil samples also showed total inorganic nitrogen flux was higher in forest soils and lowest in grassland soils. However there were no significant differences in nitrate levels. This study showed significant, although slight differences in nitrogen flux caused by savanna restoration treatments continuously applied for thirty years. The undisturbed forested treatments generally showed higher nitrogen flux, with low fire return frequency, savanna structured treatments showing somewhat higher flux rates than higher return, grassland structured treatments.

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1. Introduction

1.1. The Forest-Grassland Continuum

Across the world, landscapes can be found that fall on a spectrum between forests and

grasslands: the "forest-grassland continuum" (Breshears 2006). The term savanna or woodland is

the preferred nomenclature for these landscapes, which can be loosely defined as areas

dominated by grass with scattered woody trees and shrubs (Scholes and Archer 1997). This

broad definition includes systems with great variation in structure and function across ranges of

rainfall, soil types, fire regime, and intensity of herbivory (Skarpe 1992). Tropical savannas

occur on about 1600 M ha, over 12% of the earth's land surface (Scholes and Hall 1996) while

temperate savannas in North America cover more than 50 M ha (McPherson 1997).

Historically, the gradient between grassland and forest in the central area of North

America could be observed where the tallgrass prairie met the eastern deciduous and southern

pine forests. This transition zone curved southeast from the provinces of Alberta, Saskatchewan,

and Manitoba in Canada to Minnesota and Illinois, then southwest through Oklahoma and into

Texas (Anderson 1983). From west to east, grasses gradually gave way to trees as the climate

changes. Annual precipitation increases while the chance of drought decreases, creating an

environment more hospitable to woody species (Borchert 1950). There is no definite boundary

line between the grassland and forest, but rather a gradient as grass abundance decreases and

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woody plant abundance increases, resulting in a vegetation continuum (Anderson 1986). The

vegetation continuum is not a smooth transition however, it is a mosaic of grassland, savanna,

and forest. In this transition zone, the climate would support either forest or grassland. A

patchwork of vegetation types is created by the occurrence of edaphic features as well as local

changes in topography. These landscape variations create micro-climates with distinct variations

in soil water and nutrient availability, temperature, and light availability. Historically these

features also had an effect on fire severity and intensity, which has great influence on the

vegetation communities (Anderson 1983). Areas subjected to regular, high intensity fires

maintained characteristics of a grassland (Risser *et al*. 1981), while areas less prone to fire, such

as riverbanks, bluffs, and lowlands were maintained as closed-canopy forests (Gleason 1922).

Some areas burned less frequently and less intensely than the grasslands, permitting the

establishment of fire-tolerant woody species, such as oaks (*Quercus spp.*). These areas had a

scattered overstory of trees with an understory of grassland species, the North American

savanna.

Prior to European settlement, the transition zone between the prairie and the forest was

regularly burned by Native Americans (Irving 1835, Higgins 1986). Burning was conducted for

many reasons, including hunting, forage production, and warfare. There are few records of

Native Americans making any attempts to contain or put out these fires, which would burn until

a natural firebreak prevented them from continuing, or they were put out by rainfall (Stewart

1951). Changes in topography could act to increase or decrease fire intensity, or stop the fire all

together. This led to the establishment of a mosaic of grassland, savanna and forest (Anderson

1983). European settlement lead to an era of fire suppression across the continent, as well as the

introduction of agriculture on a large scale (Umbanhowar 1996). In the northern United States,

the vast majority of savannas were cleared of trees for cultivation. In the southern United States, savannas quickly grew into closed canopy forests following fire suppression (Anderson 1983).

Landscapes that fall in the middle of the forest-grassland continuum can neither be defined as forest or grassland. The uniqueness of these systems raises many questions regarding issues such as the role of disturbance, stability, productivity, and controls on nutrient cycling (Scholes and Archer 1997). An increasing amount of research is being conducted on the effects of trees on other species through alterations in light availability, soil moisture, and nutrient cycling (Jackson *et al*. 1990, Belsky 1994, Haworth and McPherson 1994, Scholes and Archer 1997, Reich *et al.* 2001).

1.2. Fire Effects on Vegetation

Both wildfires and prescribed burns can have a profound effect on the vegetation present in an area. Areas with a relatively low fire frequency (once per decade) tend to succeed to forests while areas with a high fire frequency (greater than eight per decade) tend to succeed towards grasslands (Towne and Owensby 1984, Axelrod 1985, Anderson and Brown 1986, Collins and Wallace 1990, Peterson and Reich 2001, Heisler *et al*. 2004). A decrease in fire frequency may lead to changes in structural composition, such as increased tree basal density and closure of the canopy (Bragg and Hulbert 1976, Abrams, Knapp, and Hulbert 1986, Knapp and Seastedt 1986, Collins and Gibson 1990, Knight *et al*. 1994, Scholes and Archer 1997, Hoch and Briggs 1999, Peterson and Reich 2001). This will create varying levels of light and light availability in the area which may lead to a shift in species composition (Willis *et al*. 2010).

In the tallgrass prairie of eastern Kansas, Knapp and Seastedt (1986) found that fire stimulates the productivity of grasses through the removal of aboveground biomass, leading to increased light availability and higher soil temperatures. The positive effects of frequent fire on aboveground net primary productivity (ANPP) of grasslands has been well documented (Towne and Owensby 1984, Briggs and Knapp 1995, Abrams *et al*. 1986). Frequent fire (less than four year return interval) also limits the recruitment of shrubs and trees (Heisler *et al*. 2003). If shrubs are able to become established, however, they may respond positively to fire; increasing in cover faster than in areas of unburned prairie (Briggs *et al*. 2002, Heisler *et al*. 2003, Heisler *et al*. 2004). Heisler *et al*. (2004) observed that increases in stem densities of roughleaf dogwood (*Cornus drummondii*) individuals following fire were three times greater than those not exposed to fire. Vigorous resprouting following aboveground mortality due to fire has been observed in other species, such as *Gaylussacia baccata* (Matlack 1993), *Rourea induta, Myrsine guianensis, Roupala montana* (Hoffmann 1998) and *Andira legalis* (Cirne and Scarano 2001). While fire is very effective at preventing woody species establishment, it may not be as efficient at removing trees and shrubs post-establishment (Wright *et al*. 1976, Roques *et al*. 2001, Heisler *et al*. 2003, Heisler *et al*. 2004).

In a forest, fire can have numerous effects on the overstory and understory vegetation, depending on variations in season, fire intensity, severity, and frequency (Certini 2005). Low severity fires have been shown to increase the abundance and diversity of the herbaceous layer in many different forest types (Masters *et al*. 1996, Gilliam 1988, Elliott *et al*. 1999, Hutchinson *et al*. 2005 Knapp *et al*. 2015). While Elliott *et al*. (1999) found that, post fire, woody species in the herbaceous layer tended to decrease in abundance, while non-woody species tended to increase. The increase in the abundance and richness has been attributed to many factors. Fire removes the

litter layer from the forest floor, which may be a barrier to establishment to herbaceous species (Hiers *et al*. 2007). Herbaceous plants may also benefit from increased light levels on the forest floor, due to removal of woody plants from the understory (Harrington and Edwards 1999, Peterson *et al*. 2007, Kinkead *et al*. 2013). In the forest understory, frequent fire can cause the mortality of advanced regeneration, favoring fire adapted species, such as oaks (*Quercus* spp.) (Elliot *et al*. 2004, Elliot and Vose 2005, Dey and Hartman 2005, Alexander *et al*. 2008). Mortality of advanced regeneration due to fire has been shown to be negatively correlated with stem diameter and positively correlated with frequency (Dey and Hartman 2005).

In oak-hickory forests, long-term studies (Huddle and Pallardy 1996, Peterson and Reich 2001, Knapp *et al*. 2015) have shown that annual and biennial prescribed fire can increase mortality in the overstory, though this may take decades to become apparent. The species composition of the overstory can also be influenced by prolonged periods of high fire frequency, with *Quercus* species being favored. Brockway and Lewis (1997), however, showed that the overstory of a longleaf pine wiregrass system was largely unaffected by high fire frequencies, while the understory was negatively affected and the herbaceous layer responded positively to high fire frequency. Haywood *et al.* (2001) also found similar results in a longleaf pine forest in Mississippi. In a mixed pine-oak-hickory forest in Missouri, Fan *et al*. (2011) found that after repeated annual burning, surviving shortleaf pine (*Pinus echinata*) individuals showed increases in mean height compared to other species. Variations in forested systems, such as forest type, climate, and soil moisture also have significant effects on vegetation responses to fire. Waldrop *et al.* (2007) and Phillips *et al*. (2008) compared prescribed fire effects on vegetation in a hardwood forest in the Central Hardwood region and a mixed-hardwood forest in the southern Appalachian Mountains. They found that only understory trees significantly increased in the

mixed-hardwood forest, whereas all vegetation classes (trees, shrubs, grasses, and forbs) increased in the hardwood forest. This was attributed to different moisture regimes in the two forests.

Repeated annual burning can have effects on plant production and carbon allocation. In the tallgrass prairie of Kansas, Ojima *et al*. (1994) found significantly higher nitrogen levels in dead grass roots in annually burned areas compared to unburned areas. After just two years of annual burning, Ojima *et al*. (1994) observed higher C:N ratios of live shoots and roots of grasses. This is supported by Blair *et al*. (1997), who observed lower nitrogen concentrations in roots and shoots of grasses in annually burned plots compared to unburned plots. Reich *et al*. (2001) found that oaks in a savanna retranslocate proportionally larger amounts of nitrogen from their leaves prior to senescence compared to oaks in a closed forest. Soil inorganic nitrogen was found to be lowest in frequently burned and grass-dominated treatments. Reich *et al*. (2001) also observed higher root biomass in frequently burned grass-dominated treatments, compared to tree-dominated treatments. This was attributed to low root turnover rates. Areas subjected to a high fire frequency tend to be shifted to grass-dominated systems with elevated overall C:N ratios and root biomass with lower turnover rates.

1.3. Fire Effects on Nutrient Cycling

Fire can have multiple effects on soil nutrients, regardless of vegetation type. Because of the potential of nitrogen to limit primary productivity, considerable research has been conducted on the effects of fire on nitrogen availability (Christensen 1977, Ojima *et al*. 1994, Turner *et al*. 1997, Blair 1997 Reich et al. 2001). During combustion, some organically bound nitrogen is lost

to the system due to a relatively low volatilization temperature of 200°C (White *et al*. 1973). While this is true for all ecosystems, fuel loads certainly vary along the grass-land forest continuum. Shortly after a fire, however, net nitrogen mineralization rates often increase (Christensen 1973, White 1986, Knoepp and Swank 1993, Wan *et al.* 2001). This has been attributed to increased microbial activity, altered microclimate, and changes in soil temperature and pH values (Dunn *et al.* 1985, White 1986, Klopatek 1990, DeBano 1991, Knoepp and Swank 1993, Wan *et al*. 2001). Post fire, soil inorganic nitrogen levels can be elevated in areas that have not been burned frequently, due to its release through pyrolysis of organic matter (Ojima *et al*. 1994). It has also been shown that a decrease in fire frequency can lead to faster nitrogen cycling, attributed to increases in detrital production and higher litter N concentrations (Reich *et al*. 2001).

While fire can stimulate net nitrogen mineralization in the short-term, the long-term effects of fire on nitrogen may be quite different. After a single fire, average loss of nitrogen due to volatilization has been estimated at 10-40 kg N ha^{-1} yr^{-1} (Ojima *et al*. 1994, Blair *et al*. 1998). Elwell *et al*. (1941) reported that volatilization could range up to 30 kg ha^{-1}. If nitrogen deposition levels are less than this, frequent burning will result in a net loss of nitrogen from the system. In the tallgrass prairie of Kansas, following the initial pulse of nitrogen release after fire, surface soil inorganic nitrogen (ammonium and nitrate) has been shown to be lower in areas burned annually compared to unburned areas (Ojima *et al*. 1994). This is supported by Blair (1997) and Turner *et al*. (1997) who found similar results comparing infrequently burned and annually burned tallgrass prairie. After a single fire, an increase in microbial biomass C:N ratios has been observed. In areas where annual burning has occurred, microbial biomass C:N ratios

were even higher (Ojima *et al*. 1994), indicating that fire frequency may change microbial composition over time.

Fire frequency can also affect the rate net nitrogen mineralization. Repeated annual burning of the tallgrass prairie results in lower net nitrogen mineralization rates, compared to unburned prairie (Ojima *et al*. 1994, Turner *et al*. 1997, Blair 1997). In the oak savanna of Minnesota, Reich *et al*. (2001) observed a negative relationship between net nitrogen mineralization and fire frequency. High fire frequencies can also shift vegetation towards being more grass-dominated (Towne and Owensby 1984, Axelrod 1985, Anderson and Brown 1986, Collins and Wallace 1990, Peterson and Reich 2001, Heisler *et al*. 2004), which will cause shifts in soil organic matter quantity and quality. Grass-dominated communities have higher fine root biomass as soil organic matter compared to forests (Reich *et al*. 2001). The longevity of grass fine roots is higher than that of tree fine roots, thus an increase in fine root biomass will lead to the immobilization of organic nitrogen (Reich *et al*. 2001). Fire can also increase the C:N ratios of both plants and microbial communities increase over time (Ojima *et al* 1994). Higher biomass C:N ratios have been shown to immobilize greater amounts of N (Holland and Detling 1990). Increasing grass fine root biomass with more longevity and higher C:N ratios will lead to lower net nitrogen mineralization rates.

1.4. Soil Nutrient Availability in the Forest-Grassland Continuum

The various ecosystems along the forest-grassland continuum have different controls on soil nutrients and nutrient cycling. In grasslands, fire has a great effect on nutrient cycles (Chapin *et al*. 1986, Ojima 1987, Seastedt 1988, Eisele *et al*. 1989, Ojima *et al*. 1990, Seastedt and

Ramundo 1990). It has been suggested that repeated annual burning (20+ years) may also reduce net nitrogen mineralization rates by 10 kg N ha^{-1} yr^{-1} (Ojima 1987). Atmospheric deposition of nitrogen for the tallgrass prairie has been estimated at 10-17 kg ha^{-1} yr^{-1} (Woodmansee 1979, Seastedt 1985). This suggests that N deposition from the atmosphere is a substantial component of the nitrogen budget of the tallgrass prairie. Eisele *et al*. (1989) found that N loss from combustion in the tallgrass prairie may be partially compensated for by nitrogen fixation by cyanobacteria. They showed nitrogen fixation rates linearly decreased as a function of the natural log of the ratio of available nitrogen to available phosphorus. Through volatilization, fire decreases inorganic nitrogen levels in the soil, while increasing phosphorus levels through ash deposition, thus decreasing the available N: available P ratios. A lower available N: available P ratio can create more favorable conditions for cyanobacteria, facilitating nitrogen fixation. Nitrogen fixation may be an important input of inorganic nitrogen in the tallgrass prairie.

In a savanna system, trees have been shown to affect nutrient cycling and allocation. Jackson *et al*. (1990) found that in blue oak (*Q. douglasii*) savanna in the Sierra Nevada foothills of California, surface soils (0-10 cm) under the tree canopies had about 33% more carbon and total nitrogen (inorganic and organic), as well as higher phosphate levels compared with soils in the open grassland areas. In the soils under the canopy, inorganic nitrogen pools, ammonium in particular, tended to be greater than in the grassland. Similar results were found by Belsky *et al*. (1989) in a semi-arid savanna in Kenya. Surface soil samples collected under tree canopies had higher amounts of soil organic matter and extractable potassium, phosphorus, and calcium, though these levels decreased significantly with distance from the base of the trunk. Net nitrogen mineralization rates were higher in surface soils from underneath the tree canopies compared to those the open grassland. In an oak savanna in the Cedar Creek Natural History area in MN,

Dijkstra *et al.* (2006) found net N mineralization rates to be highest in soils from forested areas, as well as significantly higher net N mineralization in soils under savanna trees than in open grassland. They also noted that, following natural tree mortality, mineralization rates quickly slowed to rates very near those of the open grass areas.

Many theories have been proposed to explain the higher levels of nitrogen under trees compared to open areas of savannas. Belsky (1994) attributed the higher nitrogen pools to higher inputs from animal droppings or because of a higher N content in leaf litter due to increased uptake from tree roots. Kellman (1979) and Bernhard-Reversat (1982) claimed that higher levels of atmospheric N deposition under tree canopies account for the higher N availability. Herman *et al.* (2003) theorized that greater carbon inputs under tree canopies support higher microbial activity, leading to higher nutrient turnover.

While these studies have focused on differences between soils in savannas, much less research has been conducted looking at these ecosystems as a whole (Reich *et al.* 2001). Reich *et al.* (2001) aimed to assess the effects fire frequency and vegetation type had on productivity and nitrogen cycling in different ecosystem types along the forest-grassland continuum. Their results showed a strong positive relationship between aboveground net primary production (ANPP) and nitrogen cycling. These trends were also seen in areas with similar fire frequencies that differed in woody plant densities. This is an indication that vegetation effects on soil nutrition are greater than the effects of fire frequency, though fire frequency can have an effect on vegetation communities. In a longleaf pine-wiregrass savanna, Mitchell *et al.* (1999) found a negative correlation between soil net nitrogen mineralization and ANPP, the opposite of the findings of Reich et al. (2001). These contradictory results suggest another driver of ANPP. Reich *et al.* (2001) studied areas with similar amounts of annual rainfall. The study areas used by Mitchell *et*

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al. (1999), however, occurred on a gradient of water availability ranging from xeric to wet-mesic. Their results suggest that, when water is limiting, it may have more of an effect on productivity than N availability.

1.5. Nutrient Input From Litter Decomposition

Decomposition refers to the physical and chemical processes that break down organic matter into elemental chemical components. These processes play a pivotal role in the nutrient cycles of terrestrial ecosystems (Meentemeyer 1978, Aerts and De Caluwe 1997). Decomposition of plant material thus provides a large input of nutrients across the forest-grassland continuum. The processes of decomposition can be seen as having two stages. First, detritivores physically break down litter into pieces small enough to be reduced chemically. These smaller pieces of organic matter are then broken down further by micro-organisms such as bacteria and fungi. These micro-organisms mineralize the organic matter into inorganic molecules, including water, carbon dioxide, ammonium, nitrate, and phosphate (Aerts 1997).

The decomposition rate of leaf litter is determined by both biotic and abiotic factors. Tenney and Waksman (1929) proposed four factors that exerted control over decomposition rates: a sufficient supply of nitrogen for microbial activity, the decomposing microbial community, the chemical composition of the organic matter, and environmental conditions, such as moisture, temperature, aeration, and soil pH. Lavelle *et al*. (1993) proposed a hierarchical model of controls on decomposition rates with environmental conditions having the greatest effect, followed by litter chemistry, and finally soil organisms. These controls on decomposition operate at different scales of time and space, i.e., climate operates on a much larger spatial scale

compared to litter chemistry and soil organisms. Soils in a forested system will receive more shade and slightly cooler temperatures compared to soils in a grassland system, as well as higher moisture content, due to decreased evapotranspiration (Wesser and Armbruster 1991, Wilson 1993). If the differences in microclimate along the forest-grassland continuum are strong enough, differences in decomposition rates are expected to occur.

1.6. Objectives

Landscapes on the forest-grassland continuum may shift along the vegetation gradient given certain environmental conditions, including temperature, soil moisture, and fire frequency. These conditions can be altered by climate change and management practices. It is important to understand how these alterations may or may not affect soil nutrients, as they are an important variable in net primary productivity. Data from this study will be used to parameterize the CENTURY model of net primary productivity across the forest-grassland continuum in southeastern Oklahoma, USA. The objective of this study were to measure the differences in soil nitrogen cycling, specifically nitrogen inputs from decomposition, inorganic nitrogen pools, and net nitrogen mineralization rates, across the forest-grassland continuum. To reach this objective, measurements of litter mass loss and chemistry, soil nitrogen pools, and potential net nitrogen mineralization rates were assessed.

The research goals include:

1. Determine whether position on the forest-grassland continuum alters the potential decomposition rate of a unified substrate

2. Determine how position on the forest-grassland continuum affects soil inorganic nitrogen concentrations.

3. Determine how potential net nitrogen mineralization rates vary across the forest-grassland continuum, and how these are affected by the amount of woody cover.

1.7. Hypotheses

Hypotheses addressing the preceding objectives, respectively, are as follows:

1. Position on the forest-grassland continuum will not affect decomposition rates. There will be no significant differences in decomposition rates of fresh pine foliage across the forest-grassland continuum, because the differences in microclimate will not be large enough to induce an observable effect.

2. Position on the forest-grassland continuum will influence soil inorganic nitrogen pools. Soil inorganic nitrogen levels will increase as position on the continuum shifts from grassland to savanna to forest, because higher fire frequencies will lead to increased volatilization of soil nitrogen. Grass-dominated systems may have higher soil organic matter levels, most will be fine root material with relatively low turnover rates, leading to lower soil nitrogen availability.

3. Position on the forest-grassland continuum will influence net nitrogen mineralization rates. Potential soil nitrogen net mineralization rates will increase as position on the continuum shifts from grassland to forest, due to higher burning frequencies resulting in lower litter quality (higher C:N), leading to lower nitrogen mineralization rates.

2. Methods

2.1. Study Location

The study was conducted inside the Forest Habitat Research Area (FHRA) located in the Pushmataha Wildlife Management Area (PWMA), Pushmataha County, Oklahoma (34°32'N, 95°21'W). The Pushmataha WMA was established by the Oklahoma Department of Wildlife Conservation after they had acquired several tracts of land in 1946, 1949, and 1950 (Okla. Game and Fish Dep. 1950:26). It lies on the western edge of the Ouachita Mountains in rocky mountainous terrain. The FHRA was established in 1983 with the intent to examine the effects of fire intervals and timber harvest practices on plant communities (Figure 1). It is located along a ridge in the Pushmataha WMA at approximately 335 m elevation with a 5-15% slope on a southeastern aspect (Masters et al. 1993). The soils at this location belong to the Carnasaw-Pirum-Clebit association, with shale and sandstone parent material, although the study area is predominately sandstone. These are thin and drought-prone soils, having a sandy loam texture with a high proportion of surface rock (Bain and Watterson 1979). The region has a semi-humid climate characterized by hot summers and mild winters. The average frost free period is one hundred and nine days and the average annual precipitation is 1159 mm. March and December are typically the wettest months, while July and August are the hottest months with mean

temperatures of 27.7 °C and 27.2 °C, respectively, and January and February are the coldest

months with a mean temperature of 5.5 °C (Crandall 2003). The vegetation of the area is mainly

classified as a closed canopy mixed pine-hardwood forest primarily composed of *Pinus echinata*,

Quercus stellata, Carya tomentosa, and *Quercus marilandica* with the understory dominated by

Schizachrium scoparium, Aster spp., Panicum spp., Dchanthelium spp., legumes, *Toxicodendron*

radicans and *Andropogon gerardii.*

2.2. Experimental Design

A completely randomized design was used to lay out the study site in the winter of 1982

(Figure 1). A bulldozer was used to construct firebreaks around 1.2-1.6 ha contiguous,

rectangular units in 1983 (Chambers and Brown 1983). Nine treatments, replicated three times,

were randomly assigned to the units (Figure 1). In the summer of 1984, merchantable pine

timber was harvested from selected treatments while hardwoods were selectively thinned using

2,4-D in single stem injection. Prescribed burning using the strip-head method were applied to

appropriate treatments beginning in winter 1985 and then subsequently in intervals ranging from

one to every four years, depending on treatment. Nine treatments have been applied to examine

the effects of harvesting techniques coupled with fire frequency on vegetation communities.

Eight of these treatments were used in the current study. These management practices have led to

the creation of a gradient of ecosystem types. The most notable of these are grassland, oak-pine

savanna, immature oak-pine forest, and mature oak-pine forest (Table 1).

In each unit, two transects were placed running parallel to the slope. On each transect,

five permanent 4x4 m plots were placed at 19.8 m intervals (Masters *et al*. 1993). For this study,

Control, RRB, HNT1, HT1 HT2, HT3 HT4, and HT treatments, with three replications each, were used, with the exception of HT3, which only had two replications. In the Control, no treatments were applied in 1984 or 1985. The Control has maintained characteristics of an uneven aged, closed canopy forest. The RRB treatment received a rough reduction burn every four years. This treatment can be described as an uneven aged, closed canopy forest, with a less developed midstory compared to the Control. In the HNT1 treatment, merchantable pine timber was harvested while the hardwoods were not thinned. This treatment is burned annually, which has resulted in a savanna landscape dominated by grasses and dotted with large trees. In the HT1 treatment, merchantable pine timber was harvested, hardwoods were thinned, and an annual prescribed burn was applied. This has resulted in a grassland/savanna landscape with few large trees. The HT2, HT3, HT4, and HT treatments received the same initial harvesting and thinning treatments as the HT1, with prescribed burn frequencies of every 2, 3, 4, years, and no burn applied respectively. In the HT2 treatment, these management practices have created a savanna landscape dominated by grasses and dotted with woody shrubs and a few large trees. The HT3 treatment can be described as a savanna dotty with large woody shrubs, a few small trees, and a few large trees. In the HT4 treatment, there is enough time between fires for advanced tree regeneration to occur, leading to the regeneration of a closed canopy forest. There is a large amount of variation between replications of this treatment, however. In the absence of fire, the HT treatment has regenerated into a closed canopy forest dominated by trees in lower diameter classes compared to the Control and RRB treatments. In each replication of treatments, a subsample of three plots that represented a range of conditions within a replication were used, with the exception of the HT4, treatments, in which five plots were used, due to inherent differences in the structure of each replication.

2.3. Decomposition Study

Fresh foliage from a recently harvested mature loblolly pine tree was collected in March 2013 and dried at 60 °C until no mass loss was observed. After the litter was oven dried, approximately ten grams was placed into a litter bag. Litter bags were made from 1mm fiberglass mesh and were approximately 20 cm by 20 cm. Blocks of untreated loblolly pine wood (2.5 cm x 7.5 cm) were also dried at 60 °C until there was no observed mass loss and weighed. The purpose of using loblolly pine foliage and wood was to assess the environmental effects on decomposition of a given litter quality. In April 2013, six litter bags and six wood blocks were placed in each of the plots. Care was taken to make sure that at each plot litter bags and wood blocks were placed on substrate representative of the plot as a whole. At every plot, one litter bag and one wood block were collected approximately every three months. I sampled a total of 76 plots across the study. The wooden blocks were quickly destroyed by termites in some treatments, so no accurate measurements could be taken from them. Because of this, the data was removed from the study.

From collected litter bags, subsamples of the pine needles were ground to a fine powder to measure nutrient values and chemical composition. These samples were analyzed by the Soil, Water, and Forage Analytical Laboratory (SWFAL) at Oklahoma State University for ash content lignin concentration, total carbon concentration (TC) and total nitrogen concentration (TN). A sample of 0.5 g was placed in a muffle furnace at 650 °C for four and a half hours to determine ash content. An Ankom Fiber analyzer (ANKOM Technology, Macedon, NY) was

used to determine acid detergent fiber in the samples, which were subsequently dissolved in 72%

sulfuric acid to quantify lignin by weight (ANKOM 2013). A LECO TruSpec Carbon and

Nitrogen Analyzer (LECO Corporation, St. Joseph, MI) was used to quantify TN and TC of the

samples through dry combustion (Bremner 1996, Nelson and Sommers 1996).

2.4. Ion Exchange Resins

On the same subsample of plots as the decomposition study, one resin bag was deployed

5 cm below mineral soil, keeping the litter and duff layer intact. Every six to eight weeks, the

resin bags were removed and a new one was placed within 10-20 cm. Ion exchange resin bags

were constructed from nylon fabric cut into 15cm by 15cm squares filled with ten grams of

mixed bead ion exchange resins (Sigma-Aldrich Dowex Marathon MR-3 hydrogen and

hydroxide form). The fabric was secured around the resin beads with a zip tie and string. Excess

fabric was trimmed to insure maximum surface contact with the soil. The resin bags were stored

in sealed plastic bags and stored in a dark area. Prior to deployment in the field, the resin bags

were rinsed with deionized water.

After collection, resin bags were brought back to the laboratory and kept at 0 °C until

processing. First the resin bags were brushed to remove excess soil on the exterior. Five grams of

the resins were dried at 60 °C to determine moisture content. For the extraction of ammonium

and nitrate from the resins, 5 g of the resin were placed in 25 ml of 2M KCl and shaken on a

shaker table for one hour. After shaking, the extractant was filtered and kept at 0 °C prior to

analysis. The extractant was analyzed colormetrically for ammonium and nitrate on a Biotek®

Instruments Synergy H1 Hybrid (BioTek Instruments, Winooski, VT, USA).

2.5. Aerobic Incubation

In June 2014, soil samples were taken from the top 10 cm of mineral soil near each plot containing resin bags. The samples were kept on ice then stored at 0 °C prior to processing. Soils were passed through a 2 mm sieve and all fine roots were removed. Soils were then saturated with deionized water and allowed to drain to field capacity. A ten gram subsample was taken from each sample to determine moisture content, and another for chemical analysis. These samples were analyzed at SWFAL for TN and TC using a LECO TruSpec Carbon and Nitrogen Analyzer. Soil organic matter (SOM) was estimated through loss on ignition of a subsample of dried soil placed in a muffle oven at 365 °C for two hours.

Five 10 g subsamples were then taken from each sample and placed individually into 150 ml disposable plastic cups. The cups were fitted with lids with a 5 mm hole punched near the center to allow gas exchange. Cups were kept in a dark chamber at room temperature. One replicate from each sample was chosen at random approximately every ten days for inorganic nitrogen extraction, where 50 ml of KCl was added to the sample, shaken on a shaker table for one hour, filtered, and frozen prior to analysis. The extractant was analyzed colormetrically for ammonium and nitrate. Water loss on the remaining replicates was monitored gravimetrically, and they were returned to original water content every ten days.

2.6. Vegetation Measurements

In the fall of 2013, biomass measurements were taken from all permanent plots in the FHRA. Vegetation was clipped from 0.5 x 0.5 m subplots randomly placed adjacent to each permanent plot. The clippings were separated into the following categories: forbs, grasses, legumes, *Panicum* spp., sedges/rushes, and woody plant material. Only material grown in the current growing season was retained as the live vegetation components, with the rest sorted into litter. Litter and duff was also collected at each subplot down to mineral soil. Samples were brought back to the lab, dried at 60 °C , and weighed. Total biomass was calculated as the sum of all live vegetation samples. In the summer of 2011, basal area measurements were taken at each permanent plot in the FHRA. Measurements were taken from the center of each plot using a BAF 2.3 (m^2 ha^{-1}) prism. Basal area data was separated into hardwood and conifer categories.

In 2013, hemispherical photographs were taken at each permanent plot in the FHRA. These photographs were taken monthly from March to November using a digital camera (Model E8400, Nikon, Tokyo, Japan) equipped with a fisheye lens. To avoid interference from direct sunlight, photographs were taken during overcast days or during dusk and dawn. Each photograph was taken with the camera oriented northward, in the center of the plot, one meter above the ground. WinScanopy Version 2006a (Regent Instruments Inc. Quebec, Canada) was used for analyzing all photographs. A maximum zenith angle of 75° was used to insure photographs only included an area inside the given unit. The analysis generated a value for percent canopy openness for each plot in each replication.

2.7. Analysis

Analysis of foliage decomposition was performed using PROC MIXED in SAS 9.2. Replication

and plot within replication were defined as random effects. I used a common model form for

decomposition from the literature ($Y=e^{-kt}$) where Y is the proportion of mass remaining to initial

mass, t is time and k is a set of fitted parameters describing the decay rate. This model has a

natural intercept of unity at t=0. This model was fitted on the log-log transformed scale, as:

$$\ln(Y_{ij}) = (\beta_1 + TRT_j + u_k + v_{kl}) * \ln(DAYS) + e_{ijkl}$$

Where Y = proportion of mass remaining to initial mass for time i in treatment j, DAYS was

number of days since deployment, and TRT j were fitted parameters corresponding to the

treatments. Random effects for replication (u_k) and plot within replication (v_{kl}) were included to

account for the nested experimental design, with $u_k \sim N(0, \sigma^2_{rep})$, and $v_{kl} \sim N(0, \sigma^2_{plot})$. For

comparison of fit, a null (intercept only) model was fitted that retained the same random effects.

In addition, several addition covariates describing plot-level structure (e.g., basal area,

understory vegetation or litter mass) were included as modifying the slope on days. These plot-

level structural variables were first standardized to a treatment level mean and unit standard

deviation. This was done to aid interpretation by representing within treatment differences

among plots. Analysis of the soil aerobic incubation was performed using PROC MIXED in SAS

9.2 to create a linear multiplicative model. Replication and plot within replication were defined

as random effects. I used a common model form for net nitrogen mineralization from the

literature ($Y=e^{-t}$) where Y is mg N kg^{-1} soil or mg NO^3 kg^{-1} soil, t is time. This base model was fitted on the log-log transformed scale, as:

$$\ln(Y_{ijkl}) = \beta_0 + TRT_j + (\beta_1 + TRT_j) * \ln(DAYS+1) + u_k + v_{kl} + e_{ijkl}$$

Where Y was mg N kg^{-1} soil or mg NO^3 kg^{-1} soil for time i in treatment j, DAYS was number of days incubated, and TRT j were fitted parameters corresponding to the treatments modifying the intercept or slope. Random effects for replication k (u_k) and plot l within replication (v_{kl}) were included to account for the nested experimental design, with $u_k \sim N(0, \sigma^2_{rep})$, and $v_{kl} \sim N(0, \sigma^2_{plot})$.

For comparison of fit, a null (intercept only) model was fitted that retained the same random effects. In an expanded model, several additional covariates describing plot level soil characteristics (total Nitrogen, total Carbon, C:N ratio) were included to the base model as modifying the intercept and the slope on days. This was done to test the effects of SOM quality and quantity on net mineralization rate. A final model was further expanded to include covariates describing plot-level structure (e.g., basal area, understory vegetation or litter mass) as modifying the intercept or slope on days. These plot-level soil and structural variables were first standardized to a treatment level mean and unit standard deviation. This standardization was conducted to aid interpretation by representing plot to plot variation within a treatment.

Analysis of the ion exchange resins was performed using PROC MIXED in SAS 9.2 to create a nonlinear multiplicative model. Replication and plot within replication were defined as random effects. I fitted a log-log transformed model for nitrogen concentrations where the response, Y is mg N kg^{-1} soil or mg NO$_3$ kg^{-1} resin, t is collection. This base model was fitted on the log transformed scale, as:

$$\ln(Y_{ijkl}) = (\beta_0 + TRT_j) + (\beta_1 + TRT_j) * COLLECTION + u_k + v_{kl} + e_{ijkl}$$

Where Y was mg N kg^{-1} resin or mg NO$_3$ kg^{-1} resin for collection i in treatment j, COLLECTION was the collection period, and TRT j were fitted parameters corresponding to the treatments. Random effects for replication k (u_k) and plot l within replication (v_{kl}) were included to account for the nested experimental design, with $u_k \sim N(0, \sigma^2_{rep})$, and $v_{kl} \sim N(0, \sigma^2_{plot})$.

For comparison of fit, a null (intercept only) model was fitted that retained the same random effects. In an expanded model, additional covariates describing plot-level structure (e.g., basal area, understory vegetation or litter mass) as modifying the intercept or slope on days. These plot-level soil and structural variables were first standardized to a treatment level mean and unit standard deviation. This standardization was done to aid interpretation by representing plot to plot variation within a treatment.

3. Results

3.1. Foliar Decomposition

The base model included DAYS, and DAYS x TRT effects only. The DAYS x TRT effect was non-significant (p>0.1), while DAYS was highly significant (p<0.0001). As time progressed, mass remaining decreased for all treatments (Fig 2). Compared to the initial fiber analysis, percent lignin increased in all treatments over time, while the percent of nonstructural carbohydrates decreased, and percent cellulose remained relatively unchanged (Fig 3). The rate of mass loss was nearly identical for all treatments. This supports hypothesis #1, which predicted that there would be no differences in decomposition rates across treatments due to insufficient

differences in microclimate. Generally, the rate of mass loss was greatest for the respective TRT over the first two collections (Fig. 2), and declined in the last two collections.

The base model for total foliar decomposition had an AIC of -678.8, with a residual variance of 0.004054, a replication variance of 0.000423, and a nested plot variance of 0.001331 (Table 2). This base model showed no reduction in the residual variance compared to a null (intercept only) model (Table 2). Similarly, the nested plot effect (nested within replication) variance showed no change with inclusion of the TRT effects. However, the replication level variance showed a 99% reduction (Table 2).

The second, expanded model tested the significance of vegetation and litter data gathered from the permanent plots at the FHRA (Table 3). This model retained the DAYS and DAYS x TRT effects. This expanded model included basal area and canopy openness, but only basal area was shown to be significant (p=0.0269, Table 2). Variables were standardized to treatment level means and treatment standard deviations, so are interpreted as influences of within treatment structure variation (i.e., plot-plot variability within a treatment). This was done due to very large initial differences in these structural metrics between treatments. In this model, only basal area*DAYS was significant, with all other terms dropped. This model reduced replication level variance to zero, though the plot level and residual variance was largely unchanged (Table 2), suggesting that the basal area covariate accounted for microsite differences across the study, rather than treatment level effects.

The basal area x DAYS effect on decomposition was negative (p<0.0269), indicating that the curve shape of foliar decomposition over time was affected by plot level structural differences within a treatment. The main effect for DAYS was -0.36, showing a non-linear effect (i.e., decreasing decomposition rate with increasing time) which is evident from the data (Fig 2),

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and was the expected pattern. After accounting for TRT effects, plots with higher basal area than the overall experiment mean showed a somewhat more linear relationship, while those with lower basal showed a stronger non-linear trend. This seems to refute hypothesis #1, indicating that higher basal was associated with lower decomposition rates, however no treatment level differences in decomposition rates were observed. The AIC of this model was -592.4, with a residual variance of 0.004054, a replication level variance of 0.0, and a plot level variance of 0.001510 (Table 2). This model had a larger AIC than the base model, and while replication level variances dropped, plot level and residual variances increased slightly (Table 2), indicating that this model may not fit the data as well as the base model, but was included as suggestive of possible microsite (i.e., plot-level) effects.

3.2. Aerobic Incubation

3.2.1. Net Nitrogen Mineralization

The base model for net N mineralization (ammonification and nitrification) included TRT, DAYS, and DAYS x TRT effects. The TRT and DAYS x TRT effects were non-significant (p>0.1), while DAYS was highly significant (p<0.0001). As time progressed, total inorganic nitrogen increased for all treatments (Fig 4). The forested plots generally accumulated inorganic N at a faster rate than the savanna and grassland treatments. This partially confirms my hypothesis #3, which predicted that net nitrogen mineralization rates would increase as position on forest-grassland continuum shifted from grassland to forest. The p-values among all TRT pairs for the final collection date are given in Table 5. In the final collection the CON had significantly higher total N than the HT1, HNT1, HT2, and HT3 treatments. The HNT1 treatment had significantly lower total N than all other treatments. In general, CON had similar

inorganic-N concentrations as the other forested treatments (RRB, HT and HT4), which was greater than the savanna and grassland structured treatments. Generally, the rate of accumulation stayed constant for the respective TRT over the 48 days of incubation (Fig. 4), and there did not appear to be an asymptotic effect.

The base model for total inorganic-N had an AIC of 758.6, with a residual variance of 0.4075, a replication variance of 0.04281, and a nested plot variance of 0.3625 (Table 4). This base model showed a 51% reduction in the residual variance compared to a null (intercept only) model (Table 4). Similarly, the replication level variance showed a strong reduction, owing to inclusion of the TRT effects. However, the nested plot effect (nested within replication) was relatively large (Table 4). I investigated likely reasons for this next.

The second model expanded the base model to include the soil characteristics directly measured from the soil samples taken from individual plots nested within replications: TN, TC, C:N, and SOM. These were included to test for potential influences of soil OM quality on net mineralization rate. The best model using these variables included TRT, DAYS, DAYS*TRT C:N, C:N*treatment, TC TC*treatment, and TC*ln(DAYS) (Table 4). The effect of TN was captured by TC and C:N combined, and so it was dropped from the model. SOM was only significant for one treatment, HT3, which was considered an outlier effect and so was also dropped.

Only C:N x TRT and TC x ln(DAYS) were significant in this expanded model, with all other terms dropped. This expanded model reduced plot level variance by 45% over the base model, although the residual variance was largely unchanged (Table 4). This suggested that these soil quality covariates accounted for microsite differences across the study, rather than treatment level effects.

The TC x ln(DAYS) effect was positive (p<0.0001), indicating that the curve shape of inorganic-N accumulation over time was affected by TC. The main effect for DAYS was 0.46, showing a slightly non-linear effect (decreasing effect with increasing time), although this was not evident from the data (Fig 4). After accounting for TRT effects, plots with higher soil carbon that the overall experiment mean showed a somewhat more linear relationship, while those with lower soil carbon showed a more non-linear (asymptotic) trend. This supports hypothesis #3, reflecting that higher total soil carbon was associated with higher net mineralization, likely due to higher amounts of organic substrate available for decomposition.

The effect of C:N on net mineralization rate, however, was highly significant, but unclear. The CON showed a significant and negative effect of C:N on the rate of inorganic-N accumulation, suggesting that SOM quality was having the hypothesized effect, i.e., higher C:N reflected lower SOM quality and lower net mineralization rate. However, the HT2 and HNT1 treatments showed a significant positive effect (p=0.08 and 0.04, respectively). Other treatments were not significantly different from CON. These results did not have a clear pattern. The AIC for this model was 746.1 with a residual variance of 0.3876, a replication variance of 0.09349, and a plot variance of 0.2011 (Table 4). The plot level variance decrease by 45% over the base model, further suggesting that these SOM covariates were having a substantive effect at the micro-site (i.e., plot) level.

The third and final model tested the significance of vegetation and litter data gathered from the permanent plots at the FHRA (Table 3). This model retained the TRT, DAYS and DAYS x TRT effects, and all significant soil quality variables (TC and C:N) and their interactions. This expanded model included basal area and canopy openness, where both were highly significant alone, but competed for significance when added to the model together. Basal

area was chosen because it is a more direct vegetation measurement. Also, basal area can be separated into hardwood and conifer categories. Note, these variables were standardized to treatment level means and treatment standard deviations, so are interpreted as influences of within treatment structure variation (i.e., plot-plot variability within a treatment). This was done due to very large initial differences in these structural metrics between treatments.

In this expanded model, only basal area*TRT and conifer basal area were significant from among the additional covariates tested, with all other terms dropped. This model reduced unit level variance by 81% and plot level variance by 66% over the "base + soil model", though the residual variance was largely unchanged (Table 4). This suggested that these vegetation covariates accounted for microsite differences across the study, rather than treatment level effects.

The basal area x TRT effect on net N mineralization was largely positive, supporting hypothesis #3. The CON and HNT1 treatments, however, showed negative effects. Basal area x TRT was highly significant (p<0.0001), and all other treatments were significantly different from the CON. Conifer basal area, however, had a significantly negative effect (p=0.0652) on net N mineralization. Plots in CON with the highest basal area also had the highest proportion of conifer basal area to total basal area. This may help to explain the overall negative effect of basal area on net N mineralization in the CON due to inherent differences between conifer and hardwood stem structure, where conifer wood is substantially weaker. In the HNT1 treatment, plots with the highest basal areas are located on rocky outcrops where the trees are protected from fire (personal observation). These areas have the thinnest soils found in the HNT1 treatment, so the reported negative effect of basal area on net N mineralization may be due to

sample site conditions. The AIC of this model was 719.4, with a residual variance of 0.3869, a replication level variance of 0.01765, and a plot level variance of 0.06927 (Table 4).

3.2.2. Nitrification

The base model for nitrification in the aerobic incubation included TRT, DAYS, and DAYS x TRT effects. The TRT effect was non-significant (p>0.1), while DAYS x TRT was significant (0.0610) and DAYS was highly significant (p<0.0001). As time progressed, total nitrate increased for all treatments, except the HNT1 (Fig. 4). There were generally no differences in nitrification rates across treatments. The p-values among all TRT pairs for the final collection date are given in Table 5. In general, CON had higher nitrate concentrations compared to the other treatments. However, there was a great deal of plot level variation in nitrate levels in the CON. Generally, samples from the CON with high amounts of nitrate had low ammonium levels. Conversely, samples within the CON with high ammonium levels had high nitrate levels. Also, generally, the rate of accumulation stayed constant for the respective TRT over the 48 days of incubation, i.e., there was a linear trend (Fig. 4), and there did not appear to be an asymptotic effect. The exception was the HNT1 treatment, which did not appear to accumulate any nitrate during the incubation.

The base model for nitrate had an AIC of 1407.8, with a residual variance of 3.0568, a replication variance of zero, and a nested plot variance of 3.4593 (Table 6). This base model showed a 25% reduction in the residual variance compared to a null (intercept only) model (Table 6). Similarly, the replication level variance showed a reduction to zero, owing to inclusion

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of the TRT effects. However, the nested plot effect (nested within replication) was still relatively large (Table 6). I investigated likely reasons for this next.

The second model expanded the base model to include soil characteristics directly measured from the soil samples taken from individual plots nested within replications: TN, TC, C:N, and SOM. These were included to test for potential influences of soil OM quality on net mineralization rate. The best model using these variables included TRT, DAYS, DAYS*TRT C:N, C:N*treatment, TC TC*treatment, and TC*ln(DAYS) (Table 6). The effect of TN was captured by TC and C:N combined, and so it was dropped from the model.

The C:N, C:N x TRT, TC x TRT, and TC x ln(DAYS) terms were significant in this expanded model (Table 6), with all other terms dropped. This expanded model reduced plot level variance by 84% over the base model, though replication level variation increased to levels similar to the null model, and residual variance largely remained unchanged (Table 6). This suggested that these soil quality covariates accounted for microsite differences across the study, rather than treatment level effects.

The TC x ln(DAYS) effect was positive (p=0.0523), indicating that the curve shape of nitrifcation over time was affected by TC. The main effect for DAYS was 0.91, showing a slightly non-linear effect (decreasing nitrate accumulation rate with increasing time), although this was not evident from the data (Fig 4). After accounting for TRT effects, plots with higher soil carbon than the overall experiment mean showed a somewhat more linear relationship, while those with lower soil carbon showed a more non-linear (asymptotic) trend. This supports hypothesis #3, reflecting that higher total soil carbon was associated with higher net mineralization, likely due to higher amounts of organic substrate available for decomposition.

The TC x TRT effect on nitrification rate was significant, but only for the HNT1. None of the other treatments were significantly different from zero. The HNT1 showed a significant positive effect (p=0.005), suggesting that SOM quantity was having the hypothesized effect, i.e., higher TC reflected higher SOM quantity and higher nitrification rates. This was only apparent, however, in the HNT1 treatment, which hardly accumulated any nitrate, thus this may not be a reliable result.

The effect of C:N on the nitrification rate was highly significant. The CON treatment showed a significant and negative effect of C:N on the rate of nitrification, suggesting that SOM quality was having the hypothesized effect, i.e., higher C:N reflected lower SOM quality and lower nitrification. These results support hypothesis #3, reflecting that lower SOM quality inhibits nitrification. The HT2 treatment, however, showed a significant positive effect (p=0.0071). The HT treatment was significantly lower than the CON (p=0.0006). No other treatments significantly different from CON (i.e., all were negative effects with increasing C:N). These results showed a clear pattern, with the exception of the HT2 treatment. The AIC for this model was 1388.0 with a residual variance of 3.0141, a replication variance of 0.6166, and a plot variance of 0.5482 (Table 6). The plot level variance decrease by 84% over the base model, further suggesting that these SOM covariates were having a substantive effect at the micro-site (i.e., plot) level.

The third and final model tested the significance of vegetation and litter data gathered from the permanent plots at the FHRA (Table 3). This model retained the TRT, DAYS and DAYS x TRT effects, and all significant soil quality variables (TC and C:N) and their interactions. This expanded model further included basal area and canopy openness, where both were highly significant alone, but competed for significance when added to the model together.

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Basal area was chosen because it is a more direct vegetation measurement. Also, basal area can be separated into hardwood and conifer categories. Note, these variables were standardized to treatment level means and treatment standard deviations, so are interpreted as influences of within treatment structure variation (i.e., plot-plot variability within a treatment). This was done due to very large initial differences in these structural metrics between treatments.

In this expanded model, only basal area*TRT was significant, with all other terms dropped. This model reduced replication level variance by 75% and plot level variance by 11% over the "base + soil" model, though the residual variance was largely unchanged (Table 6). This suggested that these vegetation covariates accounted for microsite differences within a treatment, rather than treatment level effects. However, the effect of basal area x TRT on nitrification was somewhat unclear. The CON and RRB treatments, showed negative effects significantly lower than zero (p=0.0268 and 0.0796, respectively), while the HT3 treatment showed an effect significantly higher than zero (p=0.0553). None of the other treatments were significantly different from zero. The AIC of this model was 1388.7, with a residual variance of 3.0172, a replication level variance of 0.1524, and a plot level variance of 0.1524 (Table 6).

3.3. Ion Exchange Resins (IER)

3.3.1. Total Inorganic Nitrogen on Resins

The base model for total inorganic nitrogen (ammonium and nitrate) on the IER included TRT, COLLECTION, and COLLECTION x TRT effects (Table 7). All effects were highly significant (p<0.0001). In general, the forested treatments (CON, RRB, HT HT4) had higher total inorganic nitrogen concentrations compared to the grassland/savanna treatments (HT3, HT2, HNT1, HT1).

This supports hypothesis #2, reflecting that as position on the forest grassland continuum shifts from grassland to forest, total soil inorganic N increases. Similar patterns in N concentration across collections periods were observed for the treatments (Table 8).

The base model, which included TRT, DAYS and DAYS x TRT for nitrate had an AIC of 914.6, with a residual variance of 0.2676, a replication variance of zero, and a nested plot variance of .05302 (Table 7). This base model showed a reduction in the replication variance to zero compared to a null (intercept only) model (Table 7). Similarly, the residual level variance showed a 88% reduction, owing to inclusion of the TRT effects. However, the nested plot effect (nested within replication) was relatively unchanged (Table 7). I investigated likely reasons for this next.

The second model expanded on the base model to test the significance of vegetation and litter data gathered from the permanent plots at the FHRA (Table 3). These were included to test for potential influences of microsite variation on net mineralization rate. The best model using these variables included TRT, DAYS, DAYS*TRT, basal area, total understory biomass x TRT, and litter x TRT. Note, these variables were standardized to treatment level means and treatment standard deviations, so are interpreted as influences of within treatment structure variation (i.e., plot-plot variability within a treatment). This was done due to very large initial differences in these structural metrics between treatments.

Basal area, total understory biomass x TRT, and litter x TRT, were significant, with all other terms dropped. This expanded model reduced plot level variance by 88% over the base model, though residual variance largely remained unchanged (Table 7). This suggested that these vegetation covariates accounted for microsite differences across the study, rather than treatment level effects. Basal area had a significant ($p=0.0294$) and positive effect on total inorganic N

concentrations across treatments and collections. This suggests that plots with higher tree biomass within a given treatment have higher soil inorganic N fluxes. This supports hypothesis #2, which predicted that inorganic soil nitrogen would increase as position on the forest-grassland continuum shifts from grassland to forest.

Total understory biomass x TRT, however, had mixed effects on effects on total inorganic N concentrations. Biomass had significantly negative effect in CON (p= 0.0439), with HT3, HT4 showing a significantly more negative effect from CON (p= 0.0679, 0.0748, respectively). However the HNT1 and HT1 treatments showed a positive relationship compared to CON (p=0.0177 and 0.0716, respectively). The other treatments were not significantly different from CON. This result might reflect strong differences in understory vegetation composition among these treatments, shifting from grass dominated in the HT1 and HNT1, and more herbaceous and shrub dominated in the others.

The effect of litter x TRT on total inorganic N concentrations was significant (p=0.0249), but with an unclear interpretation. The effect of litter was significantly less than zero in the HT1 treatment (p= 0.0388) and significantly greater zero in the HT4 treatment (p=0.0055). Litter effects were not significantly different from zero in the other treatments. The AIC of this model was 806.8, with a residual variance of 0.2685, a replication level variance of 0, and a plot level variance of 0.006125 (Table 7).

3.3.2. Nitrate on Resins

The base model for nitrate concentrations on the IER included TRT, COLLECTION, and COLLECTION x TRT effects (Table 9). All effects were highly significant (p<0.0001). In

general, the forested treatments (CON, RRB, HT HT4) had higher total nitrate concentrations compared to the grassland/savanna treatments (HT3, HT2, HNT1, HT1). This supports hypothesis #2, reflecting that as position on the forest grassland continuum shifts from grassland to forest, total soil inorganic N increases. Similar fluctuations in nitrate concentration across collections were observed in all treatments (Table 10). Nitrate concentrations ranged from accounting for less than half of the total inorganic N measured to nearly all of the total. (Table 8 and Table 10)The base model for nitrate had an AIC of 813.3, with a residual variance of 0.3288, a replication variance of 0.0, and a nested plot variance of 0.1004 (Table 9). This base model showed zero replication variance component in contrast to a null (intercept only) model (Table 9). Similarly, the residual level variance showed a 28% reduction, owing to inclusion of the TRT effects. However, the nested plot effect (nested within replication) was relatively unchanged (Table 9). I investigated likely reasons for this next.

The second model expanded on the base model to test the significance of vegetation and litter data gathered from the permanent plots at the FHRA (Table 3). These were included to test for potential influences of microsite variation on net mineralization rate. The best model using these variables included TRT, DAYS, DAYS*TRT, basal area, basal area x TRT, total understory biomass, total understory biomass x TRT, litter, and litter x TRT. Note, these variables were standardized to treatment level means and treatment standard deviations, so are interpreted as influences of within treatment structure variation (i.e., plot-plot variability within a treatment). This was done due to very large initial differences in these structural metrics between treatments.

Basal area, basal area x TRT, total understory biomass, total understory biomass x TRT, litter, and litter x TRT were significant, with all other terms dropped (with the exception of the

base model variables which were retained). This expanded model reduced plot level variance by to zero, in contrast to the base model, though residual variance largely remained unchanged (Table 9). This suggested that these vegetation covariates accounted for microsite differences across the study, rather than treatment level effects. Basal area x TRT had a significant (p=0.00071), yet unclear, effects on total nitrate concentrations across treatments. Basal area had a significantly positive effect on the in the RRB, HT, and HT4 treatments compared to the CON (p=0.0680, 0.0027, and 0.0217, respectively). The CON was not significantly different from zero, and all other treatments were in between the CON and zero. Conifer basal area x TRT was also significant (p=0.0002), and had effects opposite those of basal area x TRT. The HT and HT4 treatments showed effects significantly less than zero (p=0.0552 and 0.0433, respectively). Conversely, conifer basal area had a positive effect in the RRB compared to zero (p=0.001), while the other treatments showed no effects. The offsetting of these two variables suggests that they are explaining the effect, and when conifer basal area x TRT was dropped from the model, the only significant effects were positive, and observed in the HT and HT1 treatments (p=0.0022 and 0.0245, respectively). This suggests that areas with more tree dominance within a given treatment have largely no effect on soil nitrate concentrations, partially refuting my hypothesis #2.

Total understory biomass x TRT also had mixed effects on effects on total nitrate concentrations. Biomass had a significantly negative effect on the CON (p= 0.039) The HNT1 HT1, HT, and RRB treatments showed positive effects which were significantly higher than the CON (p<0.0001, 0.0180, 0.0029, and 0.0609, respectively). No significant effects were observed in any of the other treatments compared to CON. The effects of total understory biomass x TRT on total soil nitrate concentrations were unclear.

The effect of litter x TRT on soil nitrate concentrations was significant (p<0.0001), and also unclear. The CON estimate was slightly negative, but not significantly different from zero. The HT1 treatment was significantly lower than the CON (p= 0.0287) While the HNT1, HT4 and HT treatments were significantly higher (p= 0.0601, 0.0217 and 0.0019, respectively). No other treatments were significantly different from the CON. The AIC of this model was 806.8, with a residual variance of 0.3104, a replication level variance of 0.0, and a plot level variance of 0.0 (Table 9).

3.4. Comparison of N Flux estimation techniques

After 48 days in incubation, soils from the forested treatments (CON, RRB, HT, HT4) showed higher net N mineralization rates compared to the grassland savanna treatments (HT1, HNT1, HT2, HT3) (Fig. 4). Similar results were observed across collections of the IER (Table 8), where total N concentrations were generally higher in the forested treatments. In the aerobic incubation, the CON had the highest net N mineralization rate, (Fig. 4). Similar results were observed across collections of the IER, where the CON generally had the highest concentrations of total inorganic N (Table 8). Throughout the aerobic incubation, the HTN1 treatment accumulated the lowest amount of total inorganic N (Fig. 4.) Across collections of the IER, however, total inorganic N levels in the HNT1 were comparable to the other grassland/savanna treatments (Table 8). Both the aerobic incubation and IER measurements showed that basal area had a positive effect on soil inorganic nitrogen. Within a treatment, areas with higher basal area had higher net N mineralization rates and inorganic N concentrations. The positive impact of basal area on net N mineralization rates as well as inorganic N concentrations partially confirms

hypotheses #2 and #3, reflecting that as position on the forest-grassland continuum shifts from grassland to forest, soil inorganic N pools and net N mineralization rates will increase.

After 48 days in incubation, no significant differences in nitrification rates were observed between treatments, with the exception of the CON and the HNT1. There was a great deal of variability in nitrification rates in the CON (Fig. 4). Across collections of the IER, however, Variation of nitrate in the CON was comparable to all other treatments (Table 10). Furthermore, during the aerobic incubation, the HNT1 appeared to have a nitrification rate near zero (Fig. 4). Across collections of the IER, however, the HNT1 had nitrate levels comparable to the other grassland/savanna treatments (Table 10). Across collections of the IER, the forested treatments (CON, RRB, HT, HT4) generally had higher nitrate levels compared to the grassland/savanna treatments (HT1, HNT1, HT2, HT3) (Table 10). Basal area, did not show a clear effect on nitrification rates in the aerobic incubation. As nitrification can be thought of as a two stage process (ammonification and nitrification), a longer incubation period may produce different results for nitrate. This seems unlikely, however, since there were clear differences in ammonium production between treatments, while nitrification rates were the same across treatments (Fig. 4).

Total understory biomass and litter were not significant in the analysis of the soil aerobic incubation, but were significant when analyzing the IER. The soil aerobic incubation was performed in the laboratory, where moisture and temperature were controlled, while the IER were incubated under field conditions. The effect of litter and understory biomass on soil temperature and moisture may be the reason why these two covariates were significant in the field measurements and insignificant in the laboratory incubations. Litter and biomass showed unclear effects on both total N and nitrate concentrations on the IER.

4. Discussion

4.1. Foliage Decomposition

I predicted no significant differences in decomposition rates across this experiment because the differences in microclimate along the forest-grassland continuum will not be large enough to induce an observable effect. After 404 days in the field, no differences were observed in decomposition of loblolly pine foliage, supporting this hypothesis. Samples decomposed at the same rate (approx. 2% month^{-1}) and generally had the same chemical changes. Changes in percentages of varying fiber types was also shown to be consistent across treatments. Lavelle *et al*. (1993) proposed a hierarchical model of controls on decomposition rates with environmental conditions having the greatest effect, followed by litter chemistry, and finally soil organisms. All treatments I used experienced the same macroclimate. While there are differences in microclimate across treatments, specifically in soil temperature and moisture, these differences were apparently not large enough to produce an observable effect on pine foliage decomposition rates. The foliage was collected from the same tree, and was well composited prior to deployment in the field, so it can be reasonably assumed that the litter chemistry is the same across all samples. Soil organisms may vary in population size and community across treatments, however, the effect of these differences was not strong enough to create differences in foliage decomposition rates.

After 404 in the field, samples had lost approximately 30% of initial mass, or a mean mass loss rate of 2% month^{-1} (Fig. 2). Gholz *et al*. (2000) observed similar mass loss rates of

Pinus resinosa foliage in grasslands, temperate broadleaf forests, and temperate coniferous forests. In the same study, hardwood foliage decomposed at a much faster rate than pine foliage across all study sites. Over the first two collections, the bulk of mass lost was in the form of nonstructural carbohydrates (Fig. 2). Percent lignin in samples increased during these collection, then began to level off. Percent cellulose also increased slightly, then stayed constant through the next two collections, implying that cellulose was beginning to be decomposed as well (Fig 2.) This pattern of decomposition follows the model suggested by Coûteaux *et al*. (1995) for *Pinus sylvestris* foliage.

All treatments were located at the same study site (FHRA) and experienced the same macroclimate. However, forested and grassland treatments should exhibit differences in microclimates. Forests tend to have higher soil moisture and lower soil temperature than grasslands, which has been attributed to increased shading and reduced evapotranspiration in forests (Wesser and Armbruster 1991, Wilson 1993). When comparing aspen forest and mixed-grass prairie, Köchy and Wilson (1997) did observes a small, yet significant microclimate effect on decomposition rates. Other studies have observed small environmental effects on decomposition rates (Hunt *et al*. 1988, Elliott *et al*. 1993, Mudrick *et al*. 1994), yet no effect was apparent in my study. Only pine foliage was used in this study. Many studies have emphasized the role of litter quality (C:N ratio, L:N ratio, nutrient concentrations) on decomposition rates (Tenney and Waksman 1929, Lavelle *et al*. 1993, Coûteaux *et al*. 1995, Gholz 2000, Zhang *et al*. 2008 and others). A decomposition study at the FHRA using a different litter types with varying quality may yield different results than those presented in this study.

4.2. Net Nitrogen Mineralization and Nitrification Rates

4.2.1 Net Nitrogen Mineralization

After 48 days of aerobic incubation, forested treatments (CON, HT, RRB, HT4) had significantly higher total nitrogen compared to grassland and savanna treatments (HT1, HNT1, HT2, HT3). I predicted that net nitrogen mineralization rates would increase as position on the forest-grassland continuum shifted from grassland to forest. Across treatments, this generally was the case (Fig. 4). Forested treatments had significantly higher mineralization rates than grassland/savanna treatments. The grassland treatments (HT1, HNT1, HT2 and HT3) had low basal areas while the forested treatments (HT4, HT, RRB, and CON) had high basal areas (Table 3). The distinct differences in basal area between the two groups of treatments are mirrored by the differences in net N mineralization rates.

Fire frequency has been shown to have an effect on nitrogen mineralization (e.g. Reich 2001, Ojima 1994, Blair 1997). In this study, an increase in fire frequency from every three years to every one year did not have a noticeable effect. Moreover, tree dominance was shown to be the overriding factor in soil nitrogen dynamics. Tree dominance has been shown to be mitigated by fire frequency (Huddle and Pallardy 1996, Peterson and Reich 2001, Knapp *et al*. 2015), and this was certainly the case for the grassland/savanna treatments (HT1, HNT1, HT2 HT3) treatments. The infrequent burning of the HT4 treatment allowed sufficient time for the establishment of woody species, and after 30 years of periodic burning, the RRB has not seen a marked reduction in basal area due to tree mortality.

Within a given treatment, soils collected from plots with a higher basal had higher total

nitrogen mineralization (ammonification and nitrification) rates than soils collected from plots

with lower basal areas. This has been observed in other savanna soils studies. For example in

Minnesota, USA, Reich *et al.* (2001), showed a positive relationship between soil net nitrogen

mineralization rates and tree dominance, given similar fire frequencies. Dijkstra *et al.* (2006)

reported higher net mineralization rates in soils found under savanna trees compared to soils in

the open grassland. Following natural savanna tree mortality, net mineralization rates quickly

dropped to rates more similar to those of grassland soils. In the savannas of the Sierra Nevada

foothills of California, Jackson *et al.* (1990) found that surface soils under tree canopies had

higher inorganic nitrogen concentrations compared to those in the open grassland. In a semi-arid

savanna in Kenya, Belsky *et al.* (1989) found higher levels of soil organic matter near the base of

trees, with SOM amounts decreasing significantly with distance from the trunk. Aerobic

incubation of these soils showed higher nitrogen mineralization rates in soils under tree canopies

compared to open grassland.

During the aerobic incubation, the CON and HNT1 treatments showed a negative

relationship between basal area and total soil net N mineralization rates, however, the CON was

marginally significantly different from 0, and the HNT1 was not significantly different from the

CON. The CON is a forest with a relatively high basal area (Table 3). Conifer basal area was

shown to have a significantly negative relationship with soil net N mineralization. Plots sampled

from the CON with the highest basal areas had much higher proportions of conifer basal area

compared to plots sampled with relatively lower basal areas (Table 3). The increase in conifer

basal area could explain why the model showed total basal area as having a negative relationship

with soil net N mineralization in the CON. In the HNT1 treatment, the reason for the negative

association may be due to edaphic features in the landscape. Trees in the HNT1 tend to be located in rocky outcroppings, which offers some protection from the annual burning. Soils in these rocky areas are quite shallow and rocky, which is likely negatively affecting net N mineralization rates.

Total soil carbon (TC) can be seen as a measurement of SOM quantity. This measurement may be skewed by chemistries like black carbon and other recalcitrant carbon. However, I found that TC had a significantly positive effect on net N mineralization in the aerobic incubations. However, in the same linear model, the total SOM in this study was non-significant. Across all treatments total initial carbon had a positive effect on net N mineralization rates. TC measurements were taken from soil samples used in the incubation, then standardized across treatments, which helped to explain the microsite variability within a given treatment. The treatments with the highest average TC values, the HT2 and HT3 (Table 11), did not have the highest N mineralization rates. The occurrence of higher net N mineralization rates in treatments containing lower TC values implied that another mechanism was overriding the influence of SOM quantity.

During the aerobic incubation, TC and C:N were the most significant metrics of SOM quantity and quality. These variables may not have completely explained the differences in SOM between treatments, however. In the grassland/savanna treatments, particularly HT1 and HNT1, SOM was likely dominated by fine roots, whereas SOM from the forested plots was likely primarily derived from leaf litter. Reich *et al.* (2001) observed an increase in mean residence time (MRT) of approximately one year to four years with increasing fire frequency. While the metric used by Reich *et al*. (2001) has a number of assumptions, it has been supported by other estimates of root turnover in forests and grasslands. Nadelhoffer *et al*. (1985), Hendrick and

Pregitzer (1992) and Eissenstat and Yanai (1997) reported fine root turnover rates of one year or less in eastern North American forests, while Milchunas and Lauenroth (1992) found turnover rates near five years for roots in the shortgrass prairie of Colorado. Nadelhoffer *et al*. (1985) also found higher fine root production on nutrient rich sites but higher fine root biomass on nutrient poor sites, implying that site fertility can also influence the mean residence time of N roots. Fine root MRT of N was not measured in this study. However, inferences can be made based on the literature. Leaf litter turns over faster than fine roots, grass roots have slower turnover rates compared to trees, and increasing fire frequency slows root turnover rates while increasing soil fertility increases turnover rates. My study showed that the forested treatments have higher soil fertility, and also higher mineralization rates. TC and C:N values are similar across treatments (Table 11). These values, however, likely come from different sources of organic material; a higher proportion of fine roots in the grasslands and a higher proportion of leaf litter in the forests. Differences in organic matter inputs were likely the cause of differences in N mineralization rates across treatments. In order to understand the role of SOM, further study is needed to evaluate the differences in quality of the organic matter inputs in the FHRA.

Basal area, total soil carbon, and initial C:N ratios were shown to have significant effects on mineralization and nitrification rates in the laboratory incubation. In the lab, temperature and moisture were kept constant and equal between samples. This is likely not the case in the field. Microclimate variation, particularly in soil moisture and soil temperature, will have a considerable role in the actual soil N mineralization rates in the field. The rockiness of the soil made an accurate and representative in situ incubation nearly impossible. The results from the resin bag study, however, show patterns in soil nitrogen cycling and transformations under field conditions.

4.2.2 Nitrification

After 48 days in aerobic incubation, nitrate levels were not significantly different across treatments, with the exception of the CON and HNT1 (Fig 4). The high variability in nitrate production between plots in the CON may help to explain why it appears different from the treatments. Post incubation, samples from the CON treatments that contained large amounts of ammonium contained small amounts of nitrate. Conversely, CON samples containing large amounts of nitrate contained low amounts of ammonium. Ammonium was either accumulating in a sample, or was being nitrified into nitrate. This only occurred in the CON soil samples, with no discernable reason. During the incubation, samples from HNT1 treatments produced virtually no nitrate, causing the treatment to show up as being significantly lower than the other treatments.

Within a given treatment, I found that soil characteristics had significant effects on nitrification rates. Total carbon was found to have a positive effect in the HNT1 treatment. The HNT1 treatment, however, accumulated nearly no nitrate over the 48 day incubation period (Fig. 4), making this result seem unreliable. C:N was shown to have a negative effect on half of the treatments (HNT1, HT3, HT, CON). It has been shown that no effect of C:N on mineralization was observed in the HT1, HT4, or RRB treatments. Higher biomass C:N ratios have been shown to immobilize greater amounts of N (Holland and Detling 1990), however a significantly positive effect of C:N on nitrification was observed in the HT2 treatments. The variation in C:N

ratios of the HT2 treatments were quite small relative to the other treatments (table 11), indicating that there is little difference in C:N ratios across samples in the HT2.

Basal area showed largely no effect on nitrification rates within treatments. Basal area did have a negative effect in the CON and RRB treatments, and a positive effect in the HT3 treatment. However, no other treatments showed effects significantly different from zero. The negative effect of basal area on nitrification in the CON and RRB treatments seems to refute hypothesis #3, which predicted net N mineralization rates would increase as position on the forest-grassland continuum shifted from grassland to forest. Net N mineralization, however, was significantly different between forested and grassland treatments, even though nitrification was not. Nitrification rates were not significantly different between most treatments, implying that basal area may not be the most important factor influencing nitrification. My measurements of nitrification were also performed in the laboratory, with controlled temperature and moisture. Measurements taken in the field provide different results, though the rockiness of the soil at the FHRA makes this somewhat unfeasible.

4.3. Inorganic Nitrogen Pools

4.3.1. Total Inorganic Nitrogen

I predicted that inorganic nitrogen flux would increase as position on the forest-grassland continuum shifted from grassland to forest. Across most collections of the ion exchange resins, the CON, RRB, and HT treatments generally had the highest total inorganic nitrogen levels. One exception was collection six (Table 8), where there were few significant differences between treatments. This was the shortest collection period (32 days); resins were incubated in the field

from mid-February to mid-March 2014. During this time, both temperature and precipitation

began to increase, stimulating microbial activity. Increased microbial activity combined with

decreased duration in the field may explain why this collection showed few differences between

treatments. In general, however, more inorganic nitrogen was found on resins incubated in

forested treatments compared to grassland/savanna treatments. This supported hypothesis #2,

which stated that inorganic nitrogen concentrations would rise as position on the forest-grassland

continuum shifted from grassland to forest.

Furthermore, basal area had a positive effect on total inorganic nitrogen levels within

every treatment. This also supported hypothesis #2, reflecting that inorganic nitrogen pools

increase with increasing woody dominance. Understory vegetation biomass had varying effects

on inorganic N pools across treatments. Biomass had a positive association with inorganic

nitrogen levels in the HNT1, HT1 and, HT treatments, and a negative association in the CON,

HT2, HT3, and HT4 treatments. The HNT1 and HT1 treatments had relatively high biomass

measurements, as well relatively high variation compared to the other treatments (Table 3).

Biomass measured in the HNT1 and HT1 treatments was mostly grass. These treatments are

located along a rocky ridge in the FHRA, where soils are thin and shallow (personal

observation). It is likely that plots measured in these treatments had higher biomass because of

higher soil fertility, including inorganic nitrogen concentrations. This may be true for the HT

treatment as well, where very little understory biomass was observe (Table 3). Total vegetation

biomass had a negative association with the control, HT2, HT3, and HT4 treatments. This

association was marginally significant, though it may be important. The HT2, HT3, and HT4

treatments had high variations in biomass measurements (Table 3). In these treatments, areas

with higher biomass may have higher levels of rainfall interception, leading to lower soil

moisture. Lower soil moisture may inhibit microbial activity, but will also inhibit ion collection

by the resins. Areas with higher aboveground biomass likely have higher belowground biomass.

Roots actively take in water and nutrients from the soil. The ion exchange resins, however,

passively collect the ions in the soil through direct contact. Areas with higher vegetation biomass

likely have higher root uptake of moisture and nutrients, leaving less behind for the resins.

Litter also had mixed within-treatment effects total inorganic nitrogen measured by the

IER. A positive effect on total inorganic nitrogen levels was observed in the HT4 treatment,

while a negative effect was observed in the HT1 treatment. The HT1 treatment had the lowest

litter measurements of any treatment, with the lowest variation (Table 3). The edaphic features

of this treatment may have affected my measurements. Litter in the HT1 likely accumulated in

rocky outcroppings where it was somewhat protected from annual burning. Soils in these areas

are shallow, thin, and rocky. These soils are likely less fertile than nearby soils with less rocks.

Furthermore, an IER bag placed in a soil like this would have less soil nearby to accumulate ions

from, making them a less effective measurement tool. The HT4 treatment is quite unique, with a

lot of within-treatment variation (Table 3). Areas in the HT4 treatment with large amounts of

litter were likely near large trees. Many studies have shown the positive effects of savanna trees

on soil N pools and net mineralization (Kellman 1979, Bernhard-Reversat 1982, Belsky *et al*.

1989, Jackson *et al*. 1990, Belsky 1994, Herman *et al*. 2003, Dijkstra *et al*. 2006, and others). It

is likely that the observed effect of litter on inorganic N pools in the HT4 treatment was caused

by the proximity of large trees to the sample point. This would support hypothesis #2, which

predicted that soil inorganic nitrogen pools would increase as position on the forest-grassland

continuum shifted from grassland to forest. The HT4 and HT1 treatments have substantially less

litter than the CON, RRB, and HT treatments (Table 3). The CON, RRB, and HT treatments may

have had such a high level of litter that within-treatment differences were not large enough to produce a noticeable effect.

4.3.2 Nitrate Concentrations

It was predicted that inorganic nitrogen pools would increase as position on the forest-grassland continuum shifted from grassland to forest. Across most collections of the ion exchange resins, the CON, RRB, and HT treatments generally had the highest nitrate levels. One exception was collection six (Table 10), where there were few significant differences between treatments. This was the shortest collection period (32 days); resins were incubated in the field from mid-February to mid-March 2014. During this time, both temperature and precipitation began to increase, stimulating microbial activity. Increased microbial activity combined with decreased duration in the field may explain why this collection showed few differences between treatments. In general, however, more nitrate was found on resins incubated in forested treatments compared to grassland/savanna treatments. This supported hypothesis #2, which stated that inorganic nitrogen concentrations would rise as position on the forest-grassland continuum shifted from grassland to forest.

Within treatments, total understory biomass had unclear effects on soil nitrate pools. Biomass had a negative effect on nitrate in the CON, no effect in the HT2, HT3, and HT4, and a positive effect in the HNT1, HT1, HT, and RRB treatments. Litter also had unclear within-treatment effects on soil nitrate. Litter was shown to have a negative effect in the HT1, no effect in the HT2, HT3, RRB, and CON, and a positive effect in the HNT1, HT4, and HT treatments.

There was no discernable grouping of treatments or noticeable pattern of effects for these two variables, though they were both significant in the model.

Within treatments, basal area had largely no effect on nitrate concentrations. Both basal area and conifer basal area were significant in the models, but tended to offset each other when used together. For example, basal area showed positive effects on nitrate concentration in the HT and HT4 treatments, while conifer basal area had negative effects in these treatments. The exception was the RRB treatment, where both basal area and conifer basal area had positive effects. When conifer basal area was dropped from the model, the only effect of basal area on nitrate concentrations was positive, and in the HT1 and HT treatments. The considerable lack of trees in the HT1 treatment (Table 3) suggests that the effect of basal area on anything in the treatment is inconsequential. The HT treatment, had the highest basal area of all treatments, with considerable within-treatment variation (Table 3). A positive effect of basal area on nitrate concentrations would support my hypothesis #2, reflecting that increased woody dominance would increase inorganic N concentrations. This was only observed in the HT treatment, however, with no effect observed in any other treatment, partially refuting the second hypothesis.

4.4. Comparison of Net N Mineralization and Inorganic N pools

The soil aerobic incubation showed clear differences in net N mineralization rates between forested treatments (CON, HT, RRB, HT4) and grassland/savanna treatments (HT1, HNT1, HT2, and HT3). Similar results were observed across deployments of IER bags in the field. Generally, inorganic N concentrations were highest in the forested treatments and lowest in the grassland/savanna treatments (Table 8). Within a given treatment, areas with higher basal

area had higher net N mineralization rates as well as higher inorganic N concentrations. Conifer basal area, however, was shown to have a negative effect on soil N mineralization rates in the aerobic incubation, as well as in nitrogen pools measured in the field. This effect has been well studied along successional chronosequences around the world. Merilä *et al.* (2002) observed a decline in soil N mineralization in a succession transect running from alder to birch to spruce forests. In sub-tropical forests of eastern China, where conifers dominate mid-level successional forests, Yan *et al.* (2009) observed a "U" shaped pattern in N mineralization rates; early successional lands dominated by shrubs had higher levels of mineralization, mid-level, conifer-dominated forests had low levels of mineralization, and late successional, broadleaved evergreen forests had high mineralization rates. In Alaska, Van Cleve *et al*. (1993) also observed the negative effect of conifers on N mineralization. All of these studies attributed this phenomenon to a decreased organic matter quality. Measurements of organic matter quality at the FHRA may provide useful information for comparing soil nitrogen dynamics across treatments.

Total understory vegetation and litter did not have significant effects on net N mineralization or nitrification, but did have significant effects on inorganic N concentrations. These differences may be due to the sampling methods used. Mineralization rates were measured under controlled conditions (specifically temperature and moisture) in the laboratory, while soil N pools were measured in the field. Understory vegetation and litter likely have effects on soil temperature and moisture under field conditions which were inconsequential under laboratory conditions. Also, the aerobic incubation lasted for 48 days, while soil inorganic nitrogen concentrations were measured over two growing seasons. Measurements of soil inorganic nitrogen had a large sample size and were taken over a longer time period. Variation in environmental conditions, a larger sample size, and a longer sampling period could help to

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explain why litter and understory biomass had effects on standing nitrogen pools and not mineralization rates.

During the 48 days of aerobic incubation, no significant differences in nitrification rates were observed, aside from in the CON and HNT1 treatments. The CON showed a large amount of variability in nitrification rates, and the HNT1 had virtually zero nitrate production throughout the time period. Across collections of the IER, however, nitrate levels were generally higher in the forested treatments compared to the grassland/savanna treatments. These results appear to be contradictory, however may be an artifact of the sampling method. The aerobic incubation was performed on soil samples placed in near optimal conditions. Similar nitrification rates across treatments suggest that under near optimal conditions, nitrification rates will be equal. Conversely, the IER bags were incubated in the field and thus under varying environmental conditions, suggesting that variability between treatments affects soil nitrification rates.

4.4. Summary and Implications for Future Research

After over 400 days in the field, decomposition rates of pine foliage did not differ across treatments. This supports hypothesis #1, reflecting that microclimate differences between treatments were not strong enough to influence decomposition rates. Across collections of IER, total inorganic nitrogen and nitrate were generally higher in the forested treatments (CON, HT, RRB, and HT4) compared to the grassland/savanna (HT1, HNT1, HT2, HT3) treatments. Basal area also had a highly significant, positive effect on total inorganic nitrogen within a given treatment. These results support hypothesis #2 which predicted that as position on the forest-grassland continuum shifted from grassland to forest, inorganic nitrogen pools would increase.

Furthermore, after 48 days in aerobic incubation, soils from forested treatments accumulated more total inorganic nitrogen than soils from grassland/savanna treatments. This supported hypothesis #3, which predicted that net N mineralization rates would increase as position on the forest-grassland continuum shifted from grassland to forest.

This study has implications for future research at the FHRA. A decomposition study using a reciprocal method, i.e. grass biomass from the grassland/savanna treatments, and woody foliage from the forested treatments, may produce different results from those reported in this study. Furthermore, a reciprocal method using foliage or litter from trees in the HT1 and HNT1 treatments and trees in the CON and RRB could provide information on the effects of habitat on litter quality, and the effects of litter quality on decomposition rates. A measure of biomass C:N across treatments may reveal the influence of fire on the vegetative community, as well as provide useful information on differences in SOM. Also, a measurement of lignin:N ratios in SOM across treatments may prove to be a better metric of SOM quality, and provide insight into its effect on N mineralization. Another aerobic incubation with a larger sample size, for a longer time period, may shed further light on soil processes. The HT3 and HT treatments, in particular, had a low sample size (n=4 plots), and there was a great deal of within-treatment variation for all treatments (Fig. 4). This could be due, in part, because of the selection of plots within each unit. Plots were selected to represent the variation within that unit as a whole, so it follows that there would be a level of variation associated with my measurements. At the end of the incubation, there was still an increase in total N and nitrate, for most treatments. Extending the incubation until there is no net increase in N may show different results than the ones observed. Differences in nitrate may become apparent at this point.

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Table 1. Characteristics of Forest Habitat Research Area treatments, including treatment description, burn interval, year or last burn, and number (n) of replications.

Treatment	Description	Burn Interval	Year Last Burned	N
Control	Control, no thin, no burn	none		3
HT	Harvest pine, thin hardwoods, no burn	none		3
RRB	Rough Reduction, late winter prescribed burn	4 years	2013	3
HT4	Harvest pine, thin hardwoods, late winter prescribed burn	4 years	2013	3
HT3	Harvest pine, thin hardwoods, late winter prescribed burn	3 years	2012	2
HT2	Harvest pine, thin hardwoods, late winter prescribed burn	2 years	2013	3
HNT1	Harvest pine, thin hardwoods, late winter prescribed burn	1year	2014	3
HT1	Harvest pine, thin hardwoods, late winter prescribed burn	1 year	2014	3

Table 2. Models of foliage decomposition rates. The initial null model (intercept only) was fitted as a comparison. Next, the base model, which included Days and Days*Treatment was ran. The third and final model included plot level vegetation characteristics to assess the effects of microsite variability on decomposition rates.

Model	Random Effects			Fixed Effects P-Values		
	σ^2_u	σ^2_p	σ^2_e	Days	Days*TRT	Basal Area*Days
Null	0.1604	0.001610	0.004034			
Base	0.000423	0.001331	0.004054	<0.0001	0.1114	
Base + Vegetation	0	0.001510	0.004073	<0.0001	0.0122	0.0269

Note: σ^2_u = replication variance, σ^2_p = nested plot variance, and σ^2_e = residual variance.

Table 3. Vegetation characteristics across treatments, including basal area, conifer basal area, grass biomass, canopy openness, total understory biomass, and litter. Total understory biomass includes all understory biomass collected below 1.3 meters in height during vegetation clipping in 2013. Grass represents all grasses collected during vegetation clipping in 2013. Litter represents all litter, including O_a and O_i horizons collected during vegetation clipping in 2013. Values were averaged across treatments. For an overview of treatments, refer to Table 1.

Treatment	Basal Area	Conifer Basal Area	Openness	Biomass	Grass	Litter
	$m^2\ ha^{-1} \pm se$	$m^2\ ha^{-1} \pm se$	Percent $\pm se$	$kg\ m^2 \pm se$	$kg\ m^2 \pm se$	$kg\ m^2 \pm se$
Control	24.6±3.6	14.1±5.5	25.2±0.3	0.03±0.03	0.001±0.001	1.71±0.26
HT	38.8±6.8	32.1±7.3	18.4±0.5	0.05±0.04	0.05±0.05	1.66±0.05
RRB	27.6±3.4	17.8±2.3	29.5±0.8	0.03±0.01	0.02±0.01	1.13±0.22
HT4	17.4±4.5	12.8±4.3	44.7±8.4	0.24±0.12	0.08±0.01	0.37±0.08
HT3	6.0±1.1	4.9±1.7	74.7±9.2	0.37±0.09	0.30±0.07	0.61±0.22
HT2	10.1±1.1	4.9±0.2	76.5±10.9	0.30±0.09	0.30±0.09	0.13±0.03
HNT1	10.7±2.8	1.5±0.7	65.1±4.8	0.23±0.008	0.22±0.01	0.15±0.04
HT1	3.1±1.4	1.2±0.6	76.5±10.9	0.38±0.04	0.32±0.05	0.08±0.02

Note: se= standard error

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Table 4. Models of net nitrogen mineralization in a soil aerobic incubation. Soils were collected from all treatments, brought to the lab, and incubated for 48 days. The initial null model (intercept only) was fitted as a comparison. Next, the base model, which included Treatment, Days and Days*Treatment was ran. The third model included sample soil characteristics. The fourth and final model included plot level vegetation characteristics to assess the effects of microsite variability on net nitrogen mineralization rates.

Model	Random Effects			Fixed Effects P Values							
	σ^2_u	σ^2_p	σ^2_e	TRT	Days	TRT*Days	C:N*TRT	TC*Days	Basal Area	Basal Area*TRT	Conifer Basal Area
Null	0.2818	0.362	0.8284								
Base	0.0428	0.3625	0.4075	0.1443	<0.0001	0.7157					
Base + Soil	0.09349	0.2011	0.3876	0.0779	<0.0001	0.6697	0.0597	0.0003			
Base + Soil + Vegetation	0.01765	0.06927	0.3869	0.0006	<0.0001	0.6413	<0.0001	0.0003	0.0006	<0.0001	0.0652

Note: σ^2_u = replication variance, σ^2_p = nested plot variance, and σ^2_e = residual variance.

Table 5. Significance tests between treatment means showing p-values of net inorganic nitrogen (above the diagonal) and nitrate (below the diagonal) accumulation in soil aerobic incubation after 48 days. Note only the last collection (day 48) is shown. Significant values are in bold. For an overview of treatments, refer to Table 1.

Treatment	Control	HT	RRB	HT4	HT3	HT2	HNT1	HT1
Control		0.3472	0.2955	0.5658	**0.0528**	**0.0865**	**<0.0001**	**0.0564**
HT	**0.0068**		0.9236	0.6283	0.2782	0.4676	**0.0003**	0.3571
RRB	0.1762	0.1808		0.5502	0.3145	0.5266	**0.0003**	0.4071
HT4	0.1849	**0.0744**	0.8064		0.1075	0.1842	**<0.0001**	0.1228
HT3	0.1483	0.3369	0.8107	0.6313		0.6384	**0.0181**	0.7680
HT2	0.2158	0.1209	0.6893	0.9483	0.6944		**0.0018**	0.8387
HNT1	**0.0051**	0.8219	0.1339	**0.0539**	0.2602	**0.0885**		**0.0031**
HT1	0.8854	**0.0100**	0.2241	0.2438	0.1854	0.2735	**0.0075**	

Table 6. Models of nitrification rates in a soil aerobic incubation. Soils were collected from all treatments, brought to the lab, and incubated for 48 days. The initial null model (intercept only) was fitted as a comparison. Next, the base model, which included Treatment, Days and Days*Treatment was ran. The third model included sample soil characteristics. The fourth and final model included plot level vegetation characteristics to assess the effects of microsite variability on nitrification rates.

Model	Random Effects			Fixed Effects P values							
	σ^2_u	σ^2_p	σ^2_e	TRT	Days	TRT*Days	C:N	C:N* TRT	TC* TRT	TC* Days	Basal Area* TRT
Null	0.5913	3.7879	4.0546								
Base	0.0000	3.4593	3.0568	0.5615	<0.0001	0.0610					
Base + Soil	0.6166	0.5482	3.0141	0.1543	<0.0001	0.0562	0.0101	<0.0001	0.0828	0.0523	
Base + Soil + Vegetation	0.1524	0.4888	3.0172	0.1269	<0.0001	0.0555	0.0052	<0.0001	0.2569	0.0509	0.0572

Note: σ^2_u = replication variance, σ^2_p = nested plot variance, and σ^2_e = residual variance C:N = carbon:nitrogen ratio, and TC = total carbon.

Table 7. Models of total inorganic nitrogen concentrations in ion exchange resins. IER bags were buried in each treatment and incubated at approximately six week intervals over two growing seasons. The initial null model (intercept only) was fitted as a comparison. Next, the base model, which included Treatment, Days and Days*Treatment was ran. The third and final model included plot level vegetation characteristics to assess the effects of microsite variability on soil inorganic N concentrations.

Model	Random Effects			Fixed Effects P Values					
	σ^2_u	σ^2_p	σ^2_e	TRT	Collection	Collection*Days	Basal Area	Biomass*TRT	Litter*TRT
Null	0.04244	0.06145	0.4307						
Base	0.00000	0.05302	0.2676	<0.0001	<0.0001	<0.0001			
Base + Vegetation	0.00000	0.006125	0.2685	<0.0001	<0.0001	<0.0001	0.0294	0.0600	0.0249

Note: σ^2_u = replication variance, σ^2_p = nested plot variance, and σ^2_e = residual variance

Table 8. Least squared means of total inorganic nitrogen across treatments and collections on ion exchange resin bags. Resins were buried in each treatment and incubated at approximately six week intervals over two growing seasons. Values are based on the means across replications in each treatment.

Treatment	collection 1 collected 6.05.13 mg N kg(resin)$^{-1}$ ±se	collection 2 collected 7.22.13 mg N kg(resin)$^{-1}$ ±se	collection 3 collected 8.31.13 mg N kg(resin)$^{-1}$ ±se	collection 4 collected 10.25.13 mg N kg(resin)$^{-1}$ ±se	collection 5 collected 2.13.14 mg N kg(resin)$^{-1}$ ±se	collection 6 collected 3.17.14 mg N kg(resin)$^{-1}$ ±se	collection 7 collected 6.18.14 mg N kg(resin)$^{-1}$ ±se	collection 8 collected 9.10.14 mg N kg(resin)$^{-1}$ ±se
Control	2.2107 ± 0.20	2.5459 ± 0.20	2.4751 ± 0.23	2.4793 ± 0.20	2.1565 ± 0.20	1.3086 ± 0.23	2.6188 ± 0.23	2.2302 ± 0.21
HT	2.2851 ± 0.32	2.4751 ± 0.32	1.715 ± 0.25	0.9693 ± 0.39	2.0541 ± 0.23	1.0517 ± 0.23	2.6293 ± 0.25	1.6681 ± 0.25
RRB	2.5382 ± 0.23	1.8925 ± 0.23	1.2549 ± 0.25	1.9447 ± 0.23	1.4916 ± 0.23	0.8759 ± 0.23	2.4401 ± 0.23	2.6169 ± 0.32
HT4	1.7426 ± 0.16	1.9536 ± 0.16	1.8619 ± 0.16	2.016 ± 0.17	1.4065 ± 0.16	1.0312 ± 0.16	1.7305 ± 0.17	1.2001 ± 0.17
HT3	1.8103 ± 0.28	1.5041 ± 0.28	2.114 ± 0.28	2.0759 ± 0.28	1.3959 ± 0.28	0.797 ± 0.28	1.856 ± 0.28	1.9391 ± 0.32
HT2	1.3704 ± 0.21	1.7305 ± 0.21	1.6978 ± 0.21	1.5021 ± 0.21	1.312 ± 0.21	0.8509 ± 0.21	1.1236 ± 0.25	1.3842 ± 0.23
HNT1	1.3666 ± 0.21	1.819 ± 0.21	1.8661 ± 0.21	1.742 ± 0.21	1.4065 ± 0.21	1.0726 ± 0.21	1.2817 ± 0.32	1.2308 ± 0.25
HT1	1.634 ± 0.21	1.7502 ± 0.21	1.5734 ± 0.21	1.6233 ± 0.23	1.6895 ± 0.21	1.4919 ± 0.21	1.4138 ± 0.23	1.0264 ± 0.25

Notes: se= standard error. Resins were initially deployed on 4.13.13. Resins were then deployed at the time of the previous collection, with the exception of collection 7, where resins were deployed on 4.04.14, after the annual prescribed burning.

Table 9. Models of nitrate concentrations in ion exchange resins. Resins were buried in each treatment and incubated at approximately six week intervals over two growing seasons. The initial null model (intercept only) was fitted as a comparison. Next, the base model, which included Treatment, Days and Days*Treatment was ran. The third and final model included plot level vegetation characteristics to assess the effects of microsite variability on soil nitrate concentrations.

Model	Random Effects			Fixed effects P values									
	σ^2_u	σ^2_p	σ^2_e	TRT	Days	Trt*Days	Basal Area	Basal Area*TRT	Conifer Basal Area*TRT	Biomass	Biomass*TRT	Litter	Litter*TRT
Null	0.107	0.1186	0.4563										
Base	0.000	0.1004	0.3288	P<0.0001	P<0.0001	P=0.0002							
Base+Vegetation	0.000	0.0000	0.3104	P<0.0001	P<0.0001	P<0.0001	P=0.0093	P=0.0071	P=0.0002	P=0.0265	P<0.0001	P=0.0548	P<0.0001

Note: σ^2_u = replication variance, σ^2_p = nested plot variance, and σ^2_e = residual variance

Table 10. Least squared means of total nitrate across treatments and collections on ion exchange resin bags. The resin bags were buried in each treatment at the FHRA and incubated at approximately six week intervals over two growing seasons. Values are based on the means of replications in each treatment.

Treatment	collection 1 collected 6.05.13 mg N kg(resin)$^{-1}$ ±se	collection 2 collected 7.22.13 mg N kg(resin)$^{-1}$ ±se	collection 3 collected 8.31.13 mg N kg(resin)$^{-1}$ ±se	collection 4 collected 10.25.13 mg N kg(resin)$^{-1}$ ±se	collection 5 collected 2.13.14 mg N kg(resin)$^{-1}$ ±se	collection 6 collected 3.17.14 mg N kg(resin)$^{-1}$ ±se	collection 7 collected 6.18.14 mg N kg(resin)$^{-1}$ ±se	collection 8 collected 9.10.14 mg N kg(resin)$^{-1}$ ±se
Control	1.4111 ± 0.23	1.6626 ± 0.23	1.7188 ± 0.26	1.9289 ± 0.23	1.8555 ± 0.23	0.7517 ± 0.26	2.0089 ± 0.26	1.8618 ± 0.25
HT	1.5774 ± 0.37	1.7241 ± 0.37	0.9318 ± 0.29	0.2244 ± 0.44	1.4882 ± 0.27	0.5594 ± 0.27	2.0053 ± 0.29	1.0872 ± 0.29
RRB	1.6666 ± 0.27	0.9503 ± 0.37	0.6623 ± 0.29	1.5363 ± 0.27	1.2743 ± 0.27	0.4462 ± 0.27	1.6726 ± 0.27	2.3478 ± 0.36
HT4	0.7118 ± 0.19	0.9044 ± 0.19	0.9878 ± 0.19	1.0478 ± 0.20	0.9340 ± 0.19	0.5131 ± 0.19	0.8824 ± 0.20	0.5193 ± 0.20
HT3	0.5596 ± 0.33	0.3535 ± 0.33	1.3479 ± 0.33	1.5908 ± 0.33	0.9170 ± 0.32	0.2269 ± 0.33	0.8802 ± 0.33	1.2938 ± 0.37
HT2	0.1049 ± 0.25	0.1324 ± 0.25	0.8875 ± 0.25	0.5659 ± 0.25	0.5820 ± 0.25	0.4389 ± 0.25	0.3994 ± 0.29	0.4289 ± 0.26
HNT1	0.4684 ± 0.25	0.7762 ± 0.25	1.0745 ± 0.25	0.9673 ± 0.25	0.7180 ± 0.25	0.5656 ± 0.25	0.4822 ± 0.36	0.2838 ± 0.29
HT1	0.8208 ± 0.25	0.7501 ± 0.25	0.7810 ± 0.25	0.6977 ± 0.26	0.8630 ± 0.25	0.6868 ± 0.25	0.6873 ± 0.27	0.3365 ± 0.29

Notes: se= standard error. Resins were initially deployed on 4.13.13. Resins were then deployed at the time of the previous collection, with the exception of collection 7, where resins were deployed on 4.04.14, after the annual prescribed burning.

Table 11. Characteristics of soils by treatment. Measurements were taken on soils samples used in aerobic incubation and averaged across treatments. For an overview of treatments, refer to Table 1.

Treatment	TN	TC	C:N
	Percent ±se	Percent ±se	Percent ±se
Control	0.20±0.06	3.60±0.99	17.82±0.72
HT	0.16±0.03	3.12±0.75	19.85±0.86
RRB	0.17±0.05	3.69±1.24	21.37±0.52
HT4	0.19±0.01	3.58±0.12	18.43±0.15
HT3	0.21±0.03	4.01±0.31	19.24±0.93
HT2	0.22±0.05	4.23±0.91	19.39±0.07
HNT1	0.13±0.03	2.41±0.58	18.02±0.91
HT1	0.16±0.01	2.76±0.23	16.70±0.40

Note: se= standard error TN = total nitrogen, TC = total carbon, and C:N = carbon:nitrogen ratio.
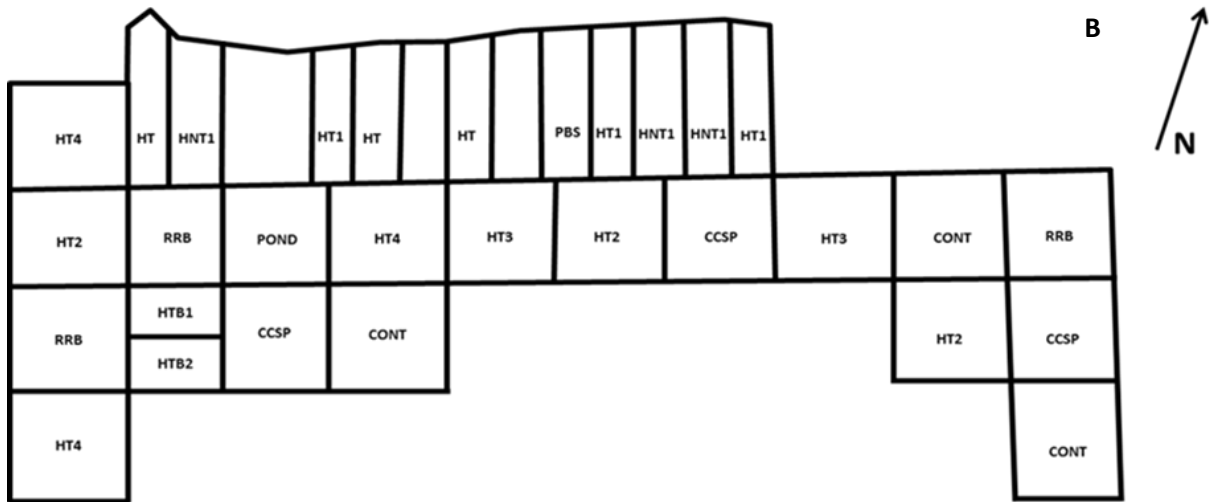
Figure 1. (A) Current (2015) aerial photograph of the Forest Habitat Research Area at Pushmataha Wildlife Management Area. Selected treatments were harvested in summer 1984 and burning regimes began in winter 1985. (B) Map showing designation of treatments to selected units.
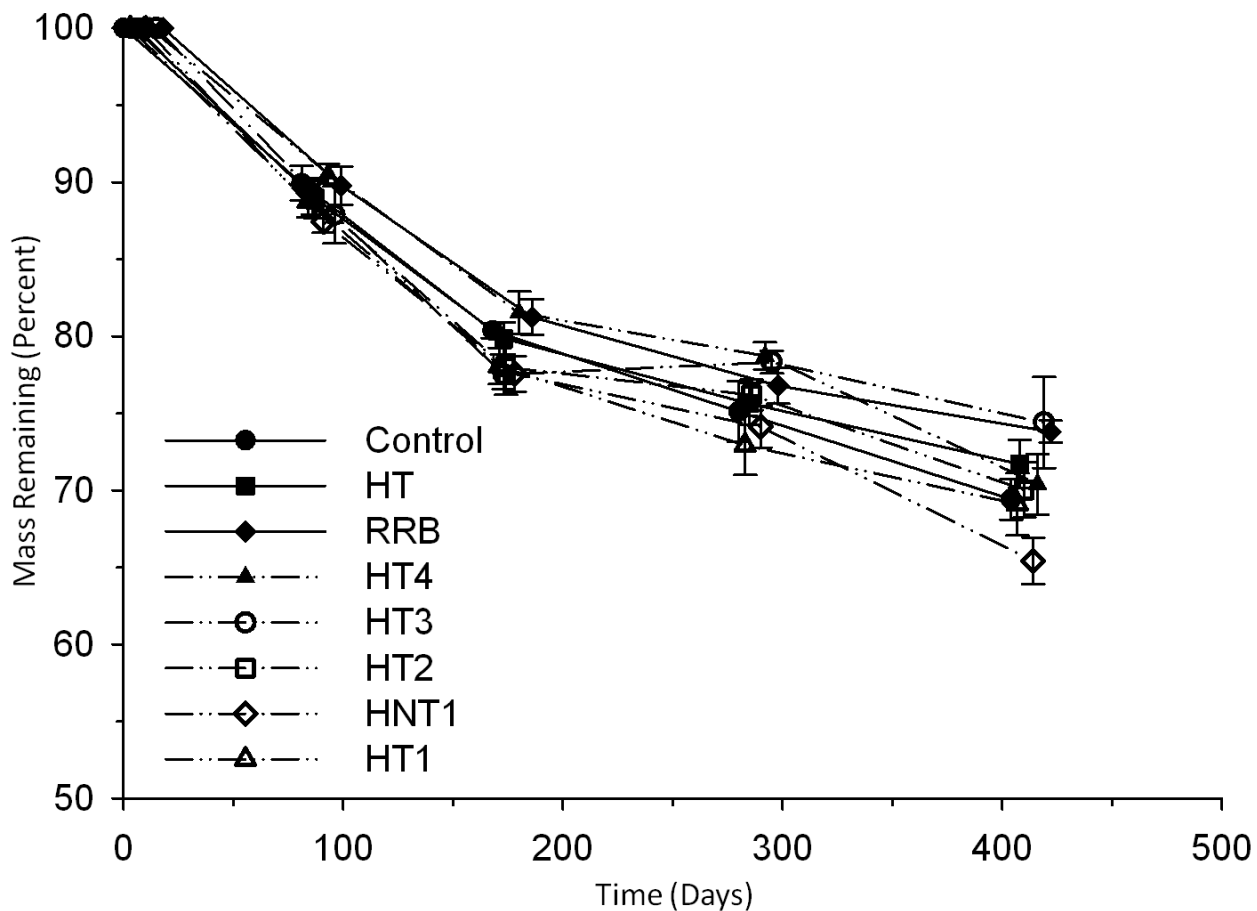
Figure 2. Pattern of pine foliage decomposition, showing percent mass remaining over time across treatments. Points have been jittered and standard errors bars added.
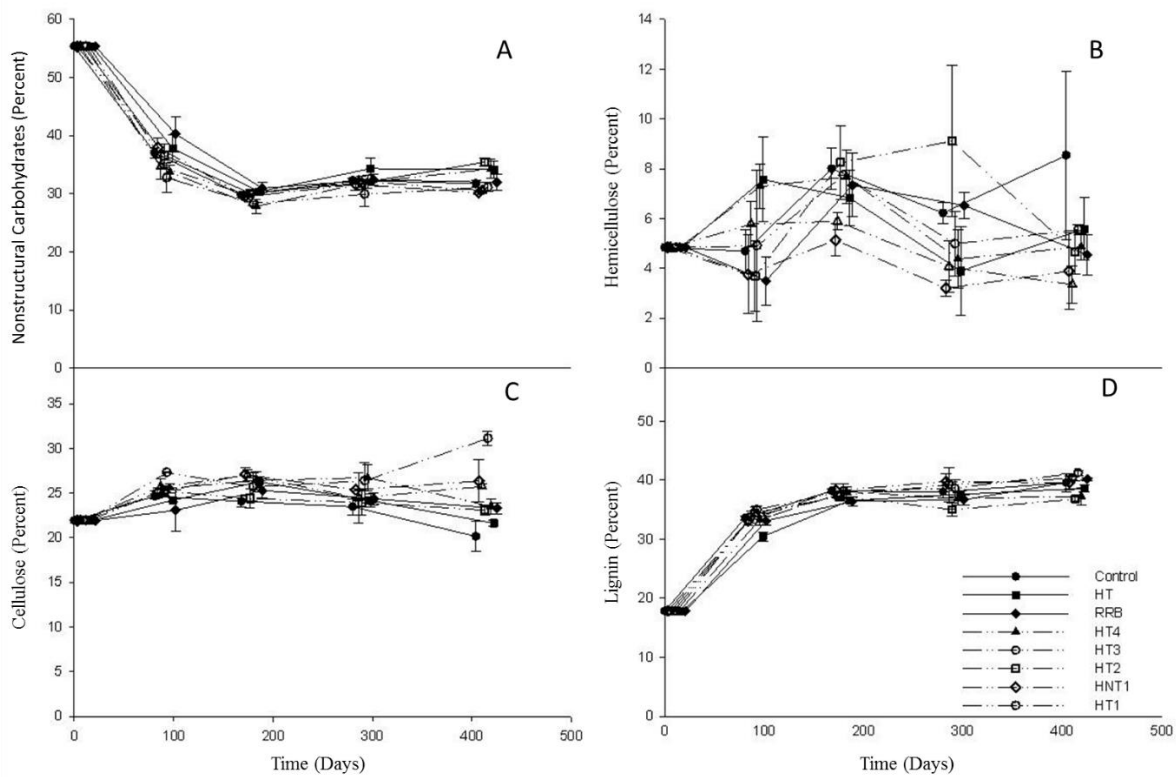
Figure 3. Changes in mean percent of (A) nonstructural carbohydrates, (B) hemicellulose, (C) cellulose, and (D) lignin of litterbag foliage across treatments over time. Points have been jittered and standard error bars shown.
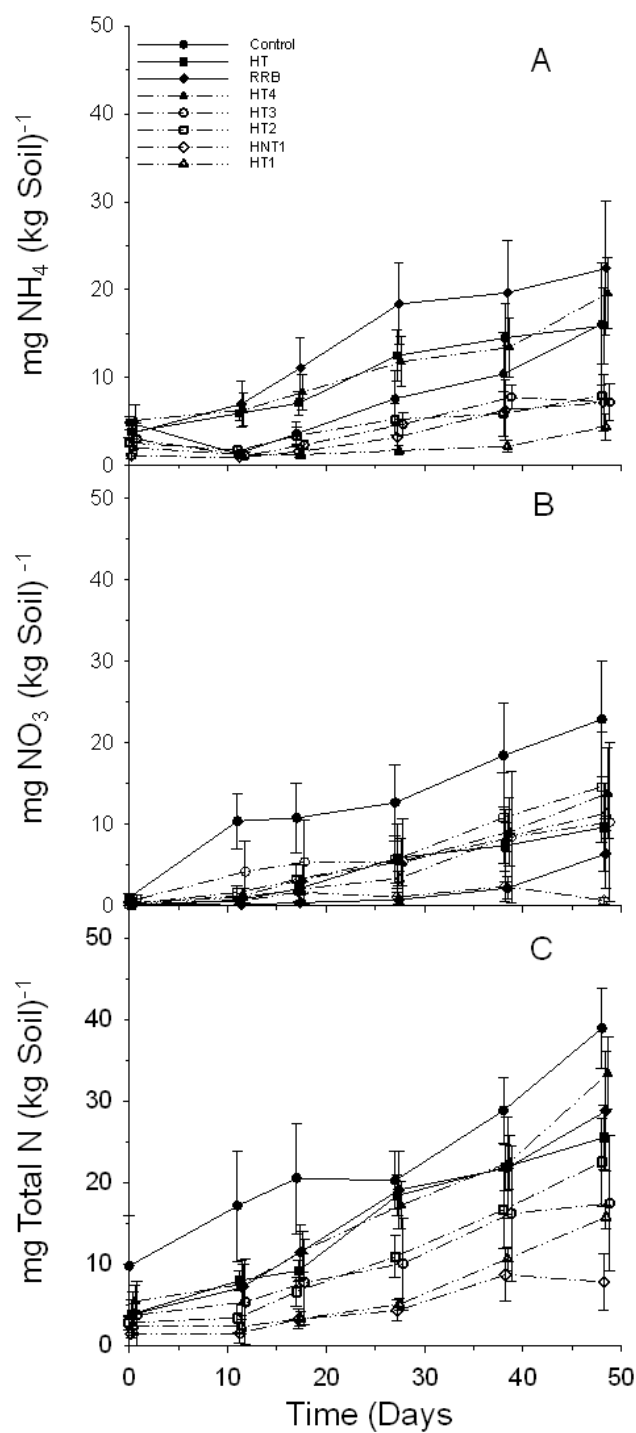
Figure 4. Accumulation in soil aerobic incubation of (A) ammonium, (B) nitrate, and (C) total N over time (Days). Soils were collected from the FHRA in June 2014 and incubated for 48 days. Soils were kept at field capacity in a dark chamber at room temperature. Points have been jittered and standard error bars attached to all treatments.

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