INFLUENCE OF LIGHT ON HERBACEOUS LAYER ABOVEGROUND PRODUCTIVITY ALONG A FOREST – SAVANNA CONTINUUM

By

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Abstract: The herbaceous layer in forest ecosystems is often ignored because of its small stature and contribution to the overall ecosystem biomass. Unlike forests, the herbaceous layer in savanna ecosystems is more noticeable, however little is known about the factors that control the productivity in this layer, especially the influence of light. The study was conducted at Pushmataha Forest Habitat Research Area in southeastern Oklahoma that have units with different overstory densities due to previous mechanical treatments and sustained differences in fire return interval. The goal of this study was to determine relationship between light availability and intercepted photosynthetically active radiation (IPAR) on herbaceous productivity along a forest-savanna continuum. IPAR by the overstory and herbaceous plants was measured multiple times during the 2013 growing season. Herbaceous aboveground net primary production (ANPP) was measured at the end of the 2013 growing season by clipping and weighing biomass components (grass, forb, legume, woody, sedge, and litter). Overstory and herbaceous IPAR showed two distinct trends over the growing season. Forested treatments had a substantial increase in the beginning of the growing season related to canopy development of the deciduous trees. In savanna treatments, the overstory trend of IPAR was more consistent over the year. Herbaceous IPAR in forested units had a trend that was more consistent, while in savanna treatments there was a substantial increase at the onset of the growing season due to the development of the dense herbaceous layer. In general, all the categories of herbaceous ANPP were positively correlated with the light availability. The total herbaceous ANPP had a positive relationship with PAR available and IPAR by the understory. However IPAR by the understory was a better predictor for herbaceous ANPP (r^2=0.65). The ability of plants to use IPAR to produce biomass in the herbaceous layer in forest and savanna ecosystems was similar regardless of overstory density and treatment. These results indicate that the pattern of IPAR by overstory and herbaceous layer are dependent of the species and the density of plants. However the ability of plants to use PAR to produce biomass was consistent across a wide range of conditions.

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CHAPTER I

INFLUENCE OF LIGHT ON HERBACEOUS LAYER ABOVEGROUND PRODUCTIVITY ALONG FOREST – SAVANNA CONTINUMM

I. INTRODUCTION

The herbaceous layer is often ignored when studying forest ecosystems due the dominance of trees. This may in part be attributed to the small contribution of the herbaceous layer to the overall forest ecosystem biomass that is often less than 1% (Ovington, 1955, Whittaker, 1966), and less than 5% to the above ground net primary production (DeAngelis et al., 1981; Muller, 2003). In terms of quantity of biomass, even though the forest floor flora doesn't present large contributions, it is important in term of carbon and nutrient cycling. Considering the energy flow and nutrient turnover, the herbaceous material is part of a small pool that decomposes faster (Muller, 2003) compared to woody plants (Wise and Schaefer, 1994) and as consequence the quickly return the nutrients to the ecosystem.

Unlike forests, the herbaceous layer in savanna ecosystems is more noticeable as the presence of woody plant cover ranges from 1 to 30% (McPherson, 1997). For instance, Lloyd et al., (2008) estimated that grasses can contribute with or more than 59%

of the total net primary production in savannas ecosystems located in different regions of the world. Although the herbaceous layer makes a large contribution to savannas ecosystems, the controls of productivity are not well understood because most of the studies have focused on the productivity of forest (McConnel and Smith, 1970; Zavitkovski, 1976) or grasslands (Gross et al., 2000; Knapp et al., 1993). In addition, most of the studies in savannas focused on the role of water and nutrients on herbaceous plants productivity with light receiving less attention.

Studies that measure productivity in forest and other ecosystems are important for climate change due the storage and sequestration of CO_2 from the atmosphere. The past of 200 years and with more significant increase in the last of 50 years, carbon dioxide in the atmosphere has increased due human's activities (Houghton, 2009) and contributes to the greenhouse effect. Related to atmospheric CO_2, terrestrial ecosystems, forests in particular, are important because they accumulate significant amounts of global aboveground carbon in vegetation and interact with atmospheric CO_2 exchange through photosynthesis and respiration (Brown et al., 1999). In the last 15 years, many models of forest productivity have been developed to evaluate the effects of carbon accumulation in trees with increased in CO_2 in the atmosphere (Landsberg and Waring, 1997; McMurtrie et al., 1992; Running and Gower, 1991; Weinstein et al., 1991). However most of these models estimate the accumulation of carbon in forest ecosystems considering only the carbon accumulation in dominant vegetation, e.g. trees, disregarding the herbaceous layer. Hence to better understand carbon accumulation and predict the productivity of the entire ecosystem the herbaceous layer should be consider in the productivity models. In addition, long-term studies are necessary to increase the knowledge regarding the effect of global change on the ecosystems. Considering that changes in the environment happen gradually and with large temporal fluctuations (Müller et al., 2010) long-term study is necessary to identify the changes or the trends (Likens, 1989) in established ecosystems.

Changes in light availability can influence herbaceous layer productivity across forest (Brezeanu et al., 1973) and savanna ecosystems (Belsky, 1994). Many studies found that the herbaceous yield can be increased due to increased light availability due to the reduction in canopy cover and tree basal area (Blair, 1971; Ehrenreich and Crosby, 1960; McConnell and Smith, 1970; Scanlan and Burrows, 1990). In addition to quantity of light available to herbaceous plants, the ability of plants to convert this light into biomass is important, especially in deciduous forest ecosystems where light availability has substantial seasonal variation. Studies have reported that plants growing under low light conditions tend to increase carbon assimilation per unit of light availability than those growing under high light levels (Bjorkman et al., 1971; Santiago and Dawson, 2014; Valladares et al., 1997). On the other hand, despite the decrease of light under the tree canopies, herbaceous productivity under isolated trees in savannas can be greater due improvement of water and nutrient status (Scholes and Archer, 1997) and because of the decrease of temperature and evapotranspiration cause by the crown shade (Belsky, 1994).

Comparisons of productivity across a forest-savanna continuum may be complicated due to fire. Savannas often are frequently burned which prevents trees from dominating. Fire can stimulate a short term increase in nitrogen availability for plants (Reich et al., 1990) as well as a long term loss of nitrogen from the ecosystem (Ojima et al., 1994). Low rates of nitrogen availability for the plants may lead low productivity due development of smaller canopies with lower foliar concentrations of nitrogen (Reich et al., 2001) consequently leading to less light interception and decreased light use efficiency (Muchow and Davis, 1988). Although the negative effect on productivity due the decrease in nutrients due to fire might be long term, fire may have a positive effect on productivity by reducing the litter and increasing the light available to grasses (Knapp, 1984) in savanna and forest ecosystems (Hiers et al., 2007).

Another challenge in comparing studies involving the herbaceous layer is due the definition of this layer (Gilliam, 2007) and the classification of biomass of the individual components (Zavitkovski, 1976). The herbaceous layer may comprise not only herbaceous species but also tree seedlings, shrubs, non-vascular plants (e.g. mosses, lichens). Most authors usually define the herbaceous stratum by the height of the vascular plants (Siccama et al., 1970).

Many resources may contribute and affect the productivity along the different ecosystems. In this study I focused on the effects of light on herbaceous aboveground productivity across forest – savanna continuum. To better understand the effects of radiation on aboveground productivity of this layer I determined (1) patterns of photosynthetically active radiation intercepted by the trees (overstory) and herbaceous plants during the growing season across the forest-savanna continuum, (2) differences of aboveground productivity for different herbaceous categories among across the forest-savanna continuum, (3) the ability of plants to use intercepted photosynthetically active radiation (IPAR) to produce dry biomass across the forest-savanna continuum. The study area located in southeastern of Oklahoma provided a good opportunity to evaluate the influence of light on herbaceous productivity because of the different overstory densities due to previous mechanical treatments and sustained differences in fire return interval.

By the fact that the units were located in the same area, I evaluated the effects of light on herbaceous productivity under the same climate and weather conditions.

II. REVIEW OF LITERATURE

2.1. Forest ecosystems

2.1.2. Importance of herbaceous layer in Forest Ecosystems

Most of the time in the forest ecosystem, the greatest species richness is found in the herbaceous layer, especially in those forest ecosystems which are fire dependent (Platt et al., 2006). In the boreal forest of Canada, the overstory species represent approximately 7% of the total number of species in the ecosystem and 93% are represented by herbaceous layer species (De Grandpré et al., 2003). Based on many studies found in literature, Gilliam (2007) reported that usually the ratio between herbaceous layer and overstory species varies between 3 and 10. The longleaf pine (*Pinus palustris*) ecosystem is one exception. This system has a ratio approximately of 250 due to the dominance of one overstory species and a very rich herbaceous layer. The ratio in conifer stands tends to be greater because of low overstory diversity. Greater numbers of species also means a greater threat for extinction. The extinction rates of herbaceous plants compared to hardwood tree species and gymnosperms are three and five times more, respectively (Levin and Wilson, 1976).

The herbaceous layer plays an important role in the forest ecosystem, especially in the establishment phase. The herbaceous plants can alter and delay tree establishment, limiting light and nutrient availability for the seedlings (Beckage et al., 2000). A study with northern red oak (*Quercus rubra* L.) and fern (*Dennstaedtia punctilobula*) showed that ferns can alter the performance of the red oak seedlings if the light becomes a limited resource. They also found higher concentrations of phosphorus, nitrogen, and potassium in fern leaves when the ferns were growing with red oak seedling than when they were growing alone (Lyon and Sharpe, 2003). Another study with *Rhododendron maximum* and red oak showed that the presence of *Rhododendron maximum* in the herbaceous layer decreased light, nutrient and water availability causing a 40% decrease in red oak seedling survival (Nilsen et al., 2001).

2.1.2. Factors controlling herbaceous productivity

2.1.2.1. Light

The variation in the angle of solar radiation and phenology of tree canopy development has a strong influence on the amount of light available for the herbaceous plants in the temperate deciduous forest (Neufeld and Young, 2003). Due to higher solar elevation in the early spring, the amount of light transmitted to the understory is greater than during the winter (Hutchison and Matt, 1976) even though the overstory is leafless during both seasons. However the amount of light available for understory during the summer is lower because the overstory canopy is fully developed (Brezeanu et al., 1973; Hutchison and Matt, 1973; Hutchison and Matt, 1977). During the fall, because of the persistence of some leaves, the amount of light transmitted to the understory is lower than compared to the early spring (Neufeld and Young, 2003). The seasonal pattern in light available for the forest floor may influence the productivity in herbaceous layer since light available and the productivity in this layer have a positive relationship (Axmanová et al., 2012; Brezeanu et al., 1973).

Some herbaceous plants have the ability to cope with the high variation in light availability at the forest floor. Uemura (1994) described six of the common phenological adaptations in plants present in the forest floor. One example are spring ephemeral plants that develop leaves in early spring when photosynthetically active radiation (PAR) is high and complete their development earlier or just after the overstory leaves start to develop. Some ephemeral species such as *Arum maculatum* (Masarovicova and Elias, 1986) and different spring blooming plants reported by Kudo et al. (2008) have the greatest net photosynthetic rate during spring. When the overstory has complete canopy closure, the spring ephemeral plants start dropping the leaves and before mid-summer almost all of species present in this group are dormant (Tessier, 2008). Contrary to the spring ephemeral plants, late summer and autumn species can persist in the understory after canopy closure. Even with the decrease in light available from spring to summer these plants can maintain high levels of photosynthesis (Ida and Kudo, 2010) and tend to have a large size due the long growing season compared with the relatively small size of spring ephemeral plants (Kawarasaki and Hori, 2001). Therefore to quantify the total productivity in herbaceous layer over a period it is necessary to consider the phenological features of the species to avoid underestimating the overall productivity in this layer.

Overall, light availability is better related to plant productivity than light quality. Stuefer and Huber (1998) found that the natural shade caused by the overstory leaves can affect the plant growth and morphological traits due changes in light quantity and quality (Stuefer and Huber, 1998). Light quality can affect the productivity by increasing the biomass partitioning to the shoot due the variation in the ratio of red/red far light (Méthy et al., 1990). However, this change in quality has more pronounced effects in morphological traits. In contrast, light availability can cause greater changes in productivity (Lieffers et al., 1999) than in morphological traits (Ballaré, 1994; Schmitt and Wuff, 1993).

2.1.2.2. Nutrients

Vascular plants usually show a close relationship between the nutrients available in the soil and concentrations of foliar nutrients (Barber, 1995). However it is not always possible to find this same pattern in the herbaceous layer of forests. Gilliam (1988) found that the plants in the herbaceous layer in Coastal Plain of South Carolina had a correlation between foliar nutrient concentration and the amount of nutrient available in the soil. However other studies found little variation in relationship between foliar nutrient concentration and site quality. It was suggested by Gagnon et al. (1958) that this small variation can be attributed to changing herbaceous species composition with changing site quality which makes it difficult to isolate site quality effects on foliar nitrogen concentration. Conversely (Bard, 1949) found that common herbaceous species located on three distinct soil types had only small variation in foliar nutrient concentrations. The strength of the relationship between foliar nutrients and site quality may be due to temporal changes. Gilliam and Adams (1995) proposed that foliar nutrients and site quality are strongly related in the early successional stands because in later successional stands light becomes more limiting resource, which obscures the relationship between the foliar chemistry and soil nutrient available.

Nutrient cycling in forest ecosystems can be influenced by the herbaceous layer due to greater foliar nutrient concentrations (Lapointe, 2001, Likens and Bormann, 1970) and faster decomposition (Wise and Schaefer, 1994) compared to woody vegetation which causes faster nutrient mineralization rates and faster plant growth. Usually plants grow faster on productive sites where the decomposition of their litter is more quickly assimilated and mineralized than on unproductive sites (Cornelissen et al., 1999). Many studies reported higher concentrations of nutrients in the herbaceous leaves compared to woody foliage. The study from Hubbard Brook Experimental Forest showed that the concentration of nitrogen and phosphorus in herbaceous plants was 30% greater than for woody species; magnesium was almost two times more and potassium three times more (summarized by Muller (2003)). He also summarized from the literature that decomposition of the herbaceous plants is twice as fast than for trees at different sites in temperate forests.

The decomposition of herbaceous plant litter is faster when compared with decomposition of the tree litter. Within the herbaceous layer, dicotyledonous species decompose more rapidly than grasses (Cornelissen and Thompson, 1997). The faster decomposition of herbaceous litter compared to tree litter may be attributed to litter quality of the species. Some components in the litter, such as lignin (Cornelissen, 1996) and cellulose (Melillo et al., 1989), can slow the decomposition of the litter. Dwyer and Merriam (1984) observed that the low contents of these two components in herbaceous litter can be a reasonable explanation for the fast turnover of the nutrients to the system. In addition, the rapid decomposition contributes in energy flux and nutrient transfer in the ecosystem. Generally the herbaceous stratum is not considered in the overall biomass in forest ecosystems. However this layer is very important in terms of return nutrients to the ecosystem (Muller, 2003).

2.1.2.3. Water

Most of the studies related to abiotic effects on herbaceous productivity in forests are more focused on effects of light in this layer (as described above) because it is considered the main driver of understory productivity. Therefore, the effects of water are not as well studied. However the productivity of herbaceous layer maybe affected by the availability of water in the soils especially during the summer and winter in the temperate forest (Neufeld and Young, 2003). In a study in juniper woodland, for instance, decreases in the overstory provided greater soil moisture (Bates et al., 2000) and contributed to increased herbaceous productivity.

2.1.2.4. Litter accumulation

Litter accumulation on the forest floor may affect the productivity of herbaceous plants (Sydes and Grime, 1981a), as well as the richness and density of species (Carson and Peterson, 1990). Carson and Peterson (1990) found that litter might have negative effects on biomass productivity in some species such as *Solidago canadensis*, when a large amount of litter accumulates. However the effects of litter accumulation cannot be related just to one reason. In longleaf pine forest, litter accumulation affects the vigor of herbaceous plants acting not only as a physical barrier but also by modifying the nutrient availability or allelopathy (Hiers et al., 2007). An example of allelopathy is oaks leaves that have higher amounts of tannins. Low amounts of light available to the plants caused by shade at the soil surface can occur. This can reduce productivity and perhaps cause mortality due decreases in plant vigor as consequence of the carbon stress (Willms, 1988). However sufficient amounts of light is also important for the germination where some seeds need certain amounts of light to break the dormancy (Vázquez-Yanes et al., 1990). Both (chemical and physical) changes due to litter accumulation may decrease herbaceous growth. However Sydes and Grime (1981b) suggest that the physical properties of the litter have a stronger effect on herbaceous plants than inhibition due to the release of chemical components.

2.1.2.5. Fire

Fire plays many roles in forest ecosystem. Prescribed fire can prevent wildfire by reducing fuels, can cause changes in the ecosystem, community, and population structure, and alters resource availability (Agee, 1996). Fire may also increase productivity (Mack et al., 2008), species richness, and diversity in the understory (Brockway and Lewis, 1997). A good example of fire dependent forest and one of the most studied in terms of fire effects in herbaceous layer is longleaf pine (*Pinus palustris*) forests. In this type of forest, fire is important to maintain the structure, that is characterized by the open longleaf pine overstory and a continuous herbaceous layer dominated by grasses, but with high species diversity and richness. Decreases in fire frequency and fire exclusion in this type of ecosystem causes a development of the midstory (Brockway and Lewis, 1997, Glitzenstein et al., 2003) and consequently a decrease in understory diversity mainly by the interception of light by the midstory. However the degradation of understory due the light interception by the midstory can depend the moisture contents in these ecosystem. Hiers et al. (2007) found that on xeric sites, the forest floor composed by the accumulation of litter and duff, was the main driver in decreasing herbaceous diversity in longleaf pine ecosystems. Brockway and Lewis (1997) also found the decrease in litter accumulated in the longleaf pine forest floor by the fire consumption increased herbaceous biomass, especially in grasses and forbs. In addition, the intensity of fire also can cause change on herbaceous composition and biomass. In a study in an Alaskan black spruce (*Picea mariana*) forest, severely burned plots showed more plant biomass in the forest floor after three years of fire and differences in species composition in heavily and light burned areas (Dyrness and Norum, 1983).

2.2. Savanna Ecosystems

Defined as an ecosystem with scattered trees and a continuous layer of grasses, the savanna ecosystem has two distinct layers with woody plants in the overstory and grasses in the understory. Woody plant cover ranges from 1% to around 30%

(McPherson, 1997). By the definition of Scholes and Hall (1996), tropical savanna ecosystems have a woody plant cover between 10 to 50% and if areas have less than 10% of woody cover the ecosystem is classified as grasslands. According to Werner et al. (1990) the savanna ecosystems are present on approximately 33% of the total world's land surface. In North America, temperate savannas cover more than 50 million hectares (McPherson, 1997). There are seven types of savanna distributed across of the United States (see McPherson, 1997). The major type of savannas ecosystem present in my study area is Midwestern oak savanna. In some areas, such as southeastern Oklahoma, the oak savanna includes varying amounts of shortleaf pine (*Pinus echinata*). The most abundant oak species present in the overstory in this area is post oak (*Quercus stellata*), with occurrence of blackjack oak (*Quercus marilandica*) and mockernut hickory (*Carya tomentosa*). The understory is mainly composed of species such as big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium),* different species of panicum grasses *(Panicum* spp*.)* and *sedges (Carex* spp., *Scleria* spp., *Rhynchospora* sp.) (Masters, 1991). Frequent woody understory species found in this area are farkleberry (*Vaccinium arboreum*), poison ivy (*Toxicodendron radicans*) and geenbriar (*Smilax* spp.) (Masters et al., 1993). Plants of genus of *Dichanthelium and Aster* are also present in the area (Crandall and Tyrl, 2006).

2.2.1. Ecological Importance

Despite the inconspicuous stature compared with trees in forest ecosystems, the herbaceous layer is more visible in savannas due the scattered trees and the continuous herbaceous layer. It has been reported the grasses in this ecosystem contribute 75% of the total biomass (Belsky et al., 1993; Garnier and Dajoz, 2001). Despite the high contribution to overall biomass in the ecosystem, reference to the ecological importance of this layer is scarce. In addition the herbaceous layer is a relevant component in the carbon cycle because the woody plant and grass roots are sources for long term carbon storage (McPherson, 1993). Savannas provide resources from woody plants such as fuelwood and pulpwood while the most important human use of the herbaceous layer is livestock grazing (McPherson, 1997).

2.2.2. Herbaceous composition

The interaction between the woody plants and the herbaceous layer is important in the savanna ecosystems especially because the trees affect herbaceous plants productivity, diversity, and spatial distribution. Most studies reported the effects of isolated trees on herbaceous productivity (Belsky et al., 1993, Belsky, 1994, Scholes and Archer, 1997, Weltzin and Coughenour, 1990). The trees influence on herbaceous plant species composition and productivity can be negative to positive depending of many factors related to ecophysiology or particular features of growth habit, photosynthetic pathway, demand of resources and other factors (see Scholes and Archer (1997)). Increases in tree canopy cover can cause a change in species composition especially related to distribution of C3 and C4 plants. Species with C3 pathways occur more frequency beneath the tree canopies and C4 plants in more open systems (McPherson et al., 1991, Archer, 1995). Plants with C4 photosynthesis pathway are less tolerant to shade than C3 plants, thus it is less common to find these plants in forests where the solar radiation available for the understory drops below 20% of the total incident solar radiation (Pearcy, 1990). Also in forest ecosystems as canopy cover increases, there is a decrease in species diversity. However in savanna ecosystems it is possible to find low herbaceous plant diversity beneath the canopies like in California oak savannas (Parker, 1977) as well as high species diversity beneath the pine-juniper canopy (McPherson and Wright, 1990) compared with adjacent grassland. Besides the influence of light in species distribution and composition, the effect of radiation availability on the composition of species under the trees or in open environment in savannas is more clearly observed in areas with lower rainfall (Belsky et al., 1989).

2.2.3. Factors controlling herbaceous productivity

2.2.3.1. Light

In savanna ecosystems light as a driver of herbaceous productivity has received less attention by the fact that light is not a limited resource when the entire ecosystem is considered. Most studies reported that under the tree canopy, productivity of herbaceous plants can increase due improvement of water because the decrease in temperature and evapotranspiration (Frost and McDougald, 1989) or an increase resource availability (Scholes and Archer, 1997). However the positive effect in understory productivity beneath trees canopies is more clearly observed in drier than more moisture regions (Belsky et al., 1993, McClaran and Bartolome, 1989).

2.2.3.2. Nutrients

Most of the studies in savannas have reported greater soil fertility beneath the tree canopies compared with the adjacent grasslands. A study with fertilization in Kenya savannas showed that herbaceous productivity was increased by the fertilization in the adjacent grassland. However there was no effect on herbaceous plant productivity beneath the trees' canopy (Belsky, 1994). Three main mechanisms that can promote soil fertility beneath the trees crown are described by Scholes and Archer (1997) and McPherson (1997): deposition of nutrients that are captured by the trees in deep soils and beyond the canopy thought the litter fall; nutrients from the atmospheric dust that are deposited on the trees leaves and branches and are washed off during the rainfall events and deposited beneath the canopies; attraction of animals because of the shade, promoting deposition of nutrients by the decomposition of their bodies and feces and also deposition of seeds from trees and shrubs by birds can contribute to improvement of the environment by their germination and establishment (Archer, 1995).

Jackson et al. (1990) found the turnover of nitrogen and nitrogen available for the plants were greater beneath the tree canopy than in the adjacent grasslands. The higher concentration of nitrogen is due the decomposition of the oak leaves that was greater beneath the canopies. Besides this higher nitrogen mineralization from the oak leaves, there was no difference in total productivity and nitrogen accumulation between the plants beneath the oaks canopy and the adjacent grassland. Callaway and Nadkarni (1991) verified that beneath the canopies of *Quercus douglasii* there was a significant increase in some nutrients in the soil. In this study the increase of soil nutrients beneath the canopy was attributed to the leaf litter and canopy thoughfall. Contrary to Jackson et al. (1990) study, Callaway found a significant difference in herbaceous productivity caused by the nutrient deposition. Differences in the other essential nutrients beneath the canopy are more variable than nitrogen. Phosphorus, for example, doesn't have much variation when compared in the soil under the tree canopy and the adjacent grassland (Frost and Mc Dougald, 1989; Tiedemann and Klemmedson, 1973). Organic carbon also is found in greater amounts beneath the trees canopies than in the adjacent grasslands in this environmental (Jackson et al., 1990; Frost and McDougald, 1989). Mainly the greater accumulation is because the litter fall and the amount of organic carbon that is incorporated in the woody roots biomass (McPherson, 1997).

2.2.3.3. Water

Most the studies focusing on variation of productivity in tropical and temperate savanna ecosystems have measured effects of water and nutrients as the main drivers of productivity in this system (Ford et al., 2008; Hartnett et al., 2013; Wang et al., 2010b). One of the main factors that controls primary productivity in tropical savannas is the amount of water available for the plants (Scholes and Hall, 1996). Large seasonality in rainfall and high incidence of solar radiation combined with low humidity and high temperature lead to increase in evaporation (Scholes and Hall, 1996) thus decreasing the amount of water available for plants. In grasslands in the central Unites States, Sala et al. (1988) found that 90% of the variation in productivity in this system is explained by the annual precipitation. Inconsistent with most studies that have reported water the main driver of productivity in this systems, Whitley et al. (2011) found that in mesic savannas in Australia, even with half year of dry season, productivity was not mainly affected by water availability.

2.2.3.4. Fire

Savanna ecosystems require fire for the maintenance of their physiognomy (Landers et al., 1995; Glitzenstein et al., 1995; Miller and Wigand, 1994). However fire also influences herbaceous plant productivity (Medina et al., 1978; San Jose and Medina, 1975; Singh, 1993). Mainly the herbaceous layer in savannas is dominated by grasses, which are well adapted to frequent intervals of fire (McPherson, 1997). The positive response in aboveground productivity induced by fire can be attributed to an increase in light availability and soil temperature due the fire consumption of dead stands (Knapp and Seastedt, 1986). Buis et al. (2009) investigated the effects of fire on herbaceous productivity in savannas ecosystems in two different continents. They found that herbaceous ANPP (aboveground net primary production) had a positive response to fire in sites that have deep soil in both regions. Even though fire can stimulate the total ANPP significant contributions occurs in sites with more availability of water (Medina and Silva, 1990; Oesterheld et al., 1999). Furthermore, fire can stimulate the growth in herbaceous plants with the addition of nutrients that are released during the combustion of the fuels. Nutrients as nitrogen, phosphorus and others have been reported to increase after the fire (Christensen, 1977; Kauffman et al. 1994).

III. METHODOLOGY

3.1. Study area

The study was conducted at the Pushmataha Forest Habitat Research Area (FHRA) which was established in 1982 by Oklahoma Department of Wildlife Conservation with the intention of evaluating how herbaceous and woody vegetation respond to different treatments of harvesting timber and fire regimes (Masters et al., 2006). The study area comprises 52.6-ha on the 7690 ha Pushmataha Wildlife Management Area (WMA). It is located in the Kiamichi Mountains on the western border of the Ouachita Highland Province, southeastern Oklahoma. The soil in this region was formed from shale and sandstone (Masters et al., 1993) and it is an association of soil series Carnasaw (fine, mixed, semiactive, thermic Typic Hapludults) – Stapp (Fine, mixed, active, thermic Aquic Hapludults) with slopes between 8 to 12 percent (Web Soil Survey). Across the study area, the depth of the surface horizon ranges from 0-21 cm with a texture of stony fine sandy loam and coarse fragments greater than 7.6 cm of 5 to 30% (Bain and Watterson, 1979).

The climate is semi-humid to humid with hot summers and moderate winters (Masters, 1991). For the last 10 years (2003-2013) the overall annual average of rainfall and temperature were 1040 mm and 17.5 °C (Oklahoma Climatological Survey – Clayton Station). Between the years 2003-2013, 2003 was the driest and 2009 the wettest with annual totals of 778 mm and 1500 mm, respectively. The hottest year in this period was 2012 and the coldest 2004 with temperature averages of 18.1 °C and 13.3 °C. The total annual precipitation during the two years (2012 and 2013) that this research was conducted was 1030 mm and 1308 mm, respectively. For 2012, the months that received the most precipitation were January and March and for 2013 April and May. The hottest and coldest months in 2012 were July and January with temperature average of 29.3 °C and 7.6 °C respectively. For the year of 2013 the hottest month was August (26.8 °C) and the coldest December (3.3 °C) (Oklahoma Climatological Survey).

3.2. Vegetation

The overstory vegetation in FHRA is a mix of pine and hardwood forest (Bruner, 1931). The overstory is mainly composed of shortleaf pine (*Pinus echinata*), post oak (*Quercus stellata*), and mockernut hickory (*Carya tomentosa*). Before imposing the treatments, 55% of the overstory basal area was composed by shortleaf pine (Masters et al., 1993). The understory is mainly composed of big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium),* different species of panicum grasses *(Panicum* spp.*) and sedges (Carex* spp., *Scleria* spp., *Rhynchospora* sp.) (Masters, 1991). Frequent woody understory species found in this area are farkleberry (*Vaccinium arboreum*), poison ivy (*Toxicodendron radicans*) and geenbriar (*Smilax* spp.) (Masters et al., 1993). Plants of genus of *Dichanthelium* and *Aster* are also present in the area (Crandall and Tyrl, 2006). In this present study we considered all the herbaceous species and woody species shorter than 1.4 meter to be part of the herbaceous layer.

3.3. Treatments

The FHRA received cultural treatments since summer 1984. Twenty-eight units were established in a randomized experimental design with each unit area ranging between 0.8 to 1.6 hectares (Masters et al., 2006). This study used 23 units that represent eight cultural treatments with three replications of each (except for one treatment, listed below, that had only two replications). The interval of fire treatments in the units receiving prescribed fire ranged from 1 to 4 years. From all units except the control and rough reduction burn, the pine timber was harvested and the selected hardwoods were thinned using injection of 2,4-Dichlorophenoxyacetic acid during the summer of 1984. Afterwards, the following treatments were installed:

1) CONT: Control, there were no treatments in this plot; 3 replications.
2) RRB: Rough reduction burn; winter prescribed fire with 4 year return interval; 3 replications.
3) HNT1: Harvest no thin; treatments were harvest pine timber only (no thin of hardwoods) and prescribed fire in winter with 1 year interval; 3 replications.
4) HT: Harvest pine timber, thin hardwoods; 3 replications.
5) HT1: Harvest pine timber, thin hardwoods and prescribed fire in winter with 1 year interval; 3 replications.
6) HT2: Harvest pine timber, thin hardwoods and prescribed fire in winter with 2 years interval; 3 replications.
7) HT3: Harvest pine timber, thin hardwoods and prescribed fire in winter with 3 years interval; 2 replications.

8) HT4: Harvest pine timber, thin hardwoods and prescribed fire in winter with 4 years of interval; 3 replications.

3.4. Measurement of light and aboveground net primary production (ANPP)

3.4.1. Sampling design

Ten permanent plots that were 16 m^2 (Figure 2) were established in each treatment unit for more detailed permanent measurements. They were installed at 20 m intervals on 2 randomly, north-south oriented lines perpendicular to the edge of the unit.

Herbaceous light interception and herbaceous biomass measurements were made in a plot of 0.5 x 0.5 m area (0.25 m^2) located adjacent to each permanent plot (Figure 2).

3.4.2. Hemispherical photographs

Hemispherical photographs were taken to estimate overstory intercepted photosynthetically active radiation (IPAR) and the light transmission to the herbaceous understory. They were taken monthly from March to November of 2013 in each permanent plot (10 photographs for each treatment unit). The photos were taken with a digital camera (Model E8400, Nikon, Tokyo, Japan) with a fisheyes lens. The camera was positioned in the middle of each permanent plot 1 m above the ground and with the top of the camera pointed northward. The photos were taken near dusk and dawn or when the sun was behind the clouds to avoid interference of direct sunlight. Photos were analyzed using the program WinScanopy Version 2006a (Regent Instruments Inc. Quebec, Canada). The minimum and the maximum zenith angle used for the analyses were 0 and 75°. Zenith angles larger than 75° weren't used as they often included areas outside the units. The analysis generated values for overstory canopy openness and above and under canopy photosynthetically active radiation (PAR).

3.4.3. Overstory *f*IPAR (fraction)

Overstory IPAR (IPARo) was calculated for each day of 2013 by interpolating IPAR estimates from the hemispherical photograph data between measurement dates. Interpolation for each day assumed a constant rate of change between adjacent dates (March – November). IPAR was calculated as a fraction of PAR intercepted (Equation 1), where PARo above was the amount of PAR reaching the overstory canopy and PARo under the amount of PAR transmitted to the understory.

$$fIPARo = \frac{PARo\ above - PARo\ under}{PARo\ above} \qquad (1)$$

The daily PAR intercepted by the overstory (PIO) was then calculated by multiplying the PAR reaching the overstory for each day by IPARo (equation 2). The total solar radiation incoming was obtained from Clayton weather Mesonet station which is 25 km from the study site (Oklahoma Climatological Survey). Total incoming radiation was multiplied by 0.5 to estimate incoming PAR (Weier and Cahalan, 2003).

$$PIO = IPARo * Incoming\ PAR \qquad (2)$$

3.4.4. Ceptometer

Light interception by the herbaceous layer was measured using a ceptometer (SunScan, Delta-T, UK) in the herbaceous plots adjacent to the permanent plots. In each herbaceous plot, PAR (photosynthetically active radiation) was measured twice above and twice below of herbaceous canopy. The two measurements were arranged to form an 'X' across the subplot. These measurements were averaged thus generating only one value for PAR above and below herbaceous canopy. Measurements were collected from May to September in 2013. PAR measurements were taken only under diffuse light to avoid confounding measurements with sunflecks.

3.4.5. Herbaceous *f*IPAR, total IPAR and PAR available

The daily PAR intercepted by the herbaceous layer (IPARh) was quantified using the PAR values from the ceptometer measurements. The measurements were taken each month from May to until the vegetation was clipped for biomass determination in September of 2013. For daily calculations, I interpolated values between the IPAR that was determined by the equation 3 assuming a constant rate of change between sampling dates. The IPARh (intercepted photosynthetically active radiation for herbaceous layer) calculation is showed in the following equation:

$$IPARh = \frac{PAR\ above\ herbaceous - PAR\ under\ herbaceous}{PAR\ above\ herbaceous} \qquad (3)$$

The daily PAR available at the top of the herbaceous layer (PAh) was calculated by subtracting PAR intercepted by the overstory (PIO) from incoming PAR for each day (equation 4).

$$PAh = Incoming\ PAR - PIO \qquad (4)$$

The total PAR available (TPAh) and intercepted (TPIh) by the herbaceous layer were calculated by the summing daily values during the 2013 growing season (May 15th to November 12th) – equation 5 and 6. This period of growing season was chosen because it was when the grasses in the herbaceous layer started grow (based on observation) and ended when the minimum temperature dropped below -2 °C (measured on site with a thermocouple connected to a datalogger located in the research area).

$$TPAh = \sum PAh \qquad (5)$$

$$TPIh = \sum PAh * IPARh \qquad (6)$$

3.4.6. Total herbaceous aboveground net primary production

The total herbaceous ANPP was determined using the leaf dry mass from the annual clip plots. The samples were collected by hand and separated in categories of woody material, litter and herbaceous vegetation. The last category was separated into grass, forb, panicum, sedge, and legume. Even though panicum is a graminoid, it was separated it for future studies related with wildlife food. However for the analysis in this study I included panicum with the grass category. The category of litter was composed of dead herbaceous plants material as well as bark, leaves, and branches from the overstory (<2.5 cm diameter). The woody growth was clipped below 1.4 m and only the current year growth was collected (leaves plus current year shoots). The samples were dried at 70 °C in a forced air oven until they reached a stable weight.

3.4.7. Radiation utilization

To understand the relationship between solar radiation and herbaceous ANPP in the forest-savanna continuum, the amount of dry biomass accumulated aboveground (ANPP) for the herbaceous plants was calculated at the same TPAh and TPIh for each treatment.

3.5. Statistical analysis

All data was statistically analyzed with software SAS 9.2 (SAS Institute Inc. 2008) using proc mixed to verify the trends of PAR intercepted in the treatments (7 treatments with 3 replication and 1 treatment with 2 replication) in 2013. To compare whether seasonal trends in IPAR were different among treatments, a repeated measures analysis was conducted for each pair of treatments. For those with different trends, i.e., significant time x treatment interaction, the slice option using all treatments simultaneously was used to determine which months the various treatments were significantly different from one another ($p < 0.05$).

Differences among component and total herbaceous aboveground productivity (ANPP) across the treatments were analyzed using proc mixed and was log transformed [log (value +1)] to meet the assumption of homogenous variance. Total herbaceous ANPP was the sum of forbs, grass, legume, sedge, and woody. Duncan's multiple range test was performed to compare means when the effect of treatments was statically significant ($p < 0.05$). Within proc mixed, analysis of covariance was used to determine if the relationship between total herbaceous ANPP and TPAh and TPIh differed among treatments (both slope and LSmeans were tested).

IV. RESULTS

4.1. Overstory *f*IPAR

Overstory IPAR (*f*IPARo) differed among months and treatments. *f*IPARo of all treatments increased beginning in April and decreased towards the end of the growing season (September) (Figure 3). Forested treatments (HT, Control, RRB) and one savanna treatment (HNT1) followed the same trends defined by no interaction ($p > 0.05$) among them when compared two at a time. The overall means of HT, RRB, and Control were similar to each other and greater than HNT1. The remainder of the savanna treatments (HT1, HT2, and HT3) and forested (HT4) followed the same trends with no treatment x month interactions among them. The overall mean of the HT4 was greater than the HT1, HT2, and HT3 treatments which were similar to one another. When each month was tested separately to compare means of treatments that interacted with one another (using slice from the full analysis), the forested treatments (Control, HT, RRB) had greater *f*IPARo than the savanna treatments (HT1, HT2, HT3, HNT1) for all months. HNT1 had significantly greater *f*IPARo than HT1 in May, July, and September and greater than HT3 in September. *f*IPARo of HT4 was significantly less than the Control and HT for all months. *f*IPARo of HT4 was similar to HNT1 in May, June, July, September, and October and similar to RRB in April.

4.2. Herbaceous *f*IPAR

Herbaceous IPAR (*f*IPARh) varied with month and by treatment. *f*IPARh increased for all treatments beginning in May (Figure 4). The RRB and Control reached a peak in July while the treatments HNT1, HT1, HT2, HT3, and HT4 treatments reached a peak in August. Given these different trends, there were significant treatment x month interactions. With the exception of the comparison between HT2 and HT4, IPARh of the savanna treatments followed the same trend (no treatment x time interaction; $p > 0.05$). In general, treatment means of *f*IPARh were opposite those for the overstory because *f*IPARh was greater in the savanna treatments than in the forested treatments. *f*IPARh of HNT1, HT1, and HT3 were greater than HT4. *f*IPARh of HT2 was greater than HT4 in all months except in May. *f*IPARh of RRB and Control followed the same trend and had similar overall means. Comparing each month separately, *f*IPARh of RRB and Control were lower than HNT1, HT1, HT2, and HT3 on all dates and only statistically similar to HT4 in May.

4.3. Aboveground net primary productivity (ANPP)

Total herbaceous ANPP in savanna treatments (HNT1, HT1, HT2, HT3) was significantly greater than the Control, RRB, and HT treatments (Figure 5). Among the savanna treatments, total ANPP was statistically similar and ranged from 354.7 to 327.1 g m^{-2} y^{-1}. Among the forested treatments total ANPP of HT4 was statistically similar to savanna treatments and greater than the other forested treatments. Total ANPP of the HT and RRB treatments were similar to Control but HT had less total ANPP than did RRB.

ANPP for each category of herbaceous vegetation varied across the treatments except for the sedge that ranged from 0 to 0.05 g m^{-2} y^{-1} and did not statistically differ among the treatments (Figure 6). Overall the grasses composed the highest ANPP among the categories of herbaceous vegetation, ranging from 0.4 to 308.7 g m^{-2} y^{-1}. The highest grass ANPP occurred in treatments with one, two, and three year fire frequency (HT1, HNT1, HT2 and HT3). Grass biomass for HT4 was significantly lower than HNT1 and HT3. Control, HT and RRB had less grass biomass than the other treatments with HT lower than the RRB (Figure 7).

Woody plants had ANPP ranged from 3.6 to 83.4 g m^{-2} y^{-1} across the treatments. Woody biomass was greatest and statistically similar for HT2, HT3, HT4, Control, and HT1. Woody plant ANPP in HNT1, HT, RRB was statistically similar to HT1 and Control, but lower than the other treatments (Figure 8). Legume ANPP was significantly different among the treatments with biomass varying from 0.03 to 6.2 g m^{-2} y^{-1}. Savanna treatments (HT1, HNT1, HT2, and HT3) as well as HT4 had the highest ANPP in this category and did not differ statistically. Among the forested treatments legume ANPP of

HT4 was greatest and differed statistically from the other treatments (RRB, Control, and HT). Legume ANPP of RRB was statistically similar to HNT1, HT2, and HT3 (Figure 9). The legume ANPP of the Control and HT treatments was lower than the HNT1, HT1, and HT4 treatments. Forbs ANPP varied among the treatments with biomass ranging from 0.21 to 13.69 g m^{-2} y^{-1}. HNT1 had the highest forbs ANPP which was similar to HT1 and HT2. Forb ANPP of HT1, HT2, and HT3 were statistically similar to HT4 and RRB (Figure 10). Forb ANPP of forested treatments (Control, HT, RRB, and HT4) were statistically with biomass of the Control and HT significantly lower than the savanna treatments.

Litter accumulation had biomass ranging from 1672.4 to 105.1 g m^{-2} . Treatments that had initial tree cutting and subsequent regular fire treatment (HNT1, HT1, HT2), had lower litter biomass compared with those that didn't have fire treatments or cutting (Control, HT, and RRB) (Figure 11). Among the treatments with a regular fire regime, RRB (burned every four years) had highest litter biomass and was statistically similar to Control and HT. Litter biomass of HT2, HT3, and HT4 were statistically similar with only HT2 statistically similar to the lower litter accumulation in the HNT1 and HT1 treatments.

Among the different herbaceous categories, grasses and woody plants had the largest contributions to ANPP in this layer. Grasses contributed between 71.9% and 92.5% of the total ANPP in the herbaceous layer across the savanna treatments. The forested treatments, HT, Control, HT4, and RRB, had contributions to total ANPP from grasses of 7.4%, 17.7%, 69.3%, and 76.6% respectively. Woody plants had most contributions in ANPP among the forested treatments ranging between 14.3 to 91.2%.

Among the savanna treatments, woody plants contributed between 25.5% and 1.8% of the total. In forested treatments, forbs contributed between 5.5% and 1.1%, legumes between 3.1% and 0%, and sedge between 1.9 and 0%. In savanna treatments forbs had contributions between 4.2% and 1.3%. Sedge had contributions less than 0.04% and legumes less than 1.8% of total herbaceous biomass in savanna treatments (Figure 12).

4.4. Radiation utilization

Total herbaceous ANPP had a positive relationship with herbaceous TPAh for forested (r^2=0.32) and savanna (r^2=0.10) treatments and the slopes of the various treatments did not differ (p= 0.053). Total ANPP was negligible below TPAh of 500 MJ m^{-2} $year^{-1}$ (Figure 13). The intercepts of the relationship between TPAh and total herbaceous ANPP for forested and savanna treatments were –74.8 and –41.5, respectively. The intercept of savanna treatments didn't differ statistically of zero (p = 0.74) while the intercept of forested treatments was statistically different from zero ($p < 0.0001$). The HT, Control, and RRB treatments had very low herbaceous ANPP and as a result individual plots were mainly along the x-axis even when TPAh reached values greater of 1000 MJ m^{-2} y^{-1}.

The TPIh had a positive relationship with total herbaceous ANPP (r^2=0.65) and the slopes of the various treatments were not statistically different from one another (p = 0.35). The intercept was -19.6 and not statistically different than zero (p=0.25) (Figure 14), in contrast to the relationship between herbaceous ANPP and TPAh.

The TPAh varied among the treatments between 2111.9 to 811.3 MJ m^{-2} y^{-1} increasing 2.6 times between the lowest (HT) and highest (HT1) treatments (Table 1). Overall forested treatments had less light available to the herbaceous layer than the savanna treatments. TPAh were statistically similar among the savanna treatments. PAR available in HT4 was statistically similar to HNT1 and lower than the savanna treatments, but greater than the other forested treatments (HT, RRB, and Control). Herbaceous ANPP per unit of TPAh (expressed as LSmean; ANPP at 1486 MJ m^{-2} $year^{-1}$) ranged from 24.8 to 69.7 g m^{-2} y^{-1} and it was greater for the savanna treatments than forested treatments ($p<0.0001$). Among the savanna treatments (HNT1, HT1, HT2, and HT3) the LSmean were similar. Likewise, there were no significant differences among the forested treatments (Table 1).

TPIh ranged from 48.1 to 915.9 MJ m^{-2} $year^{-1}$, with a difference of 19.0 times between the lowest (Control) and highest (HT1). Savanna and forested treatments were significantly differed in TPIh. Among the savanna treatments, TPIh of HT1 was greater than HNT1 and statistically similar to HT2 and HT3. TPIh in HT4 treatment was lower than the savanna treatments, but greater than the RRB and Control treatments. ANPP per unit of TPIh (expressed as LSmean; ANPP at 536 MJ m^{-2} $year^{-1}$) was similar among the treatments ($p=0.82$) and ranged from 46.8 g m^{-2} y^{-1} to 59.1 g m^{-2} y^{-1} (Table 1).

The amount of PAR intercepted by the understory vegetation was relatively low, less than 44% of the total PAR available for each treatment. Herbaceous plants in forested treatments, Control, RRB, and HT4 intercepted 5.57%, 8.42%, and 28.5%, respectively, of the total PAR available for each treatment. Among the savanna treatments the amount of PAR intercepted by the herbaceous plants varies between 43.4% and 40%.

4.5. Overstory basal area

The total overstory basal area ranged from 3.2 to 35.2 m^2 ha^{-1}, with a difference of 11.0 times between the lowest (HT1) and highest (HT) (Table 2). Among forested treatments, overstory basal area of the HT treatment was significantly greater than the RRB treatment while basal area of the Control was intermediate between the two. Overstory basal area of HT4 was significantly lower than the other forested treatments, but greater than the savanna treatments. There was not statistical differences among the savanna treatments. All forested treatments were significantly than savanna treatments.

Conifer basal area among the treatments varied between 0.6 to 24.3 m^2 ha^{-1} with a variation of 42.5 times between the lowest (HNT1) and highest (HT). All the forested treatments had conifer basal area significantly greater than the savanna treatments. Conifer basal area of the HT treatment was greater than the other forested treatments (Table 2).

Hardwood basal area ranged from 2.1 to 12.5 m^2 ha^{-1}. Among the treatments the highest hardwood basal area was Control and lowest was HT1 with difference of 5.9 times between them. Hardwood basal area of HNT1 was intermediate between the other savanna treatments and the forested treatments and was significantly different only from the Control and HT treatments. Hardwood basal area of the HT4 treatment was statistically lower than the other forested treatments but statistically similar to all savanna treatments. There was no significant difference among the savanna treatments (Table 2).

When comparing hardwood and conifer basal area in each treatment, only the HNT1 and HT4 treatments had a significant difference in basal area between the groups with p = 0.014 and 0.038, respectively. The HNT1 treatment had a greater hardwood than conifer basal area. The HT4 treatment had greater conifer than hardwood basal area.

V. DISCUSSION

5.1. Overstory *f*IPAR

Both ecosystem types, forested and savanna, had an increase in overstory IPAR during the growing season due foliage growth. Forested system had a more pronounced increase in *f*IPARo, while the savanna systems were more consistent throughout the year. This is probably because of the greater tree density in the forested systems compared to the savanna treatments. However, among our treatments there was one savanna *f*IPARo trend (HNT1) that was similar to the forested *f*IPARo trend and one forest *f*IPARo trend (HT4) that was similar to savanna treatment trend.

The HT4 treatment had a trend more like the savanna due the overstory dominance by the evergreen species shortleaf pine, i.e., 75.4% of total basal area. The HT4 treatment has more pine basal area than the HT, Control, and RRB due to excellent pine regeneration following the cutting and burning for this treatment. Shortleaf pine maintains foliage all year. While the amount of foliage in late summer is roughly twice what it is in winter, the annual dynamics in IPAR are not as pronounced as for deciduous trees which drop all their leave during fall and winter. The same trend was observed in a white pine (*Pinus strobus*) plantation where Pangle et al. (2009) found a gradual increase in IPAR from 90% to 97% comparing the beginning and end of the growing season, respectively. Therefore stands with high presence of evergreen species have a more consistent level overstory *f*IPAR.

The HNT1, a savanna treatment, had a trend like the forest ecosystem probably because of the presence of scattered large post oak trees in this treatment compared to the other savanna treatments. In HNT1, 92% of the total basal area was represented by hardwoods while the percentage of the hardwood basal area in the other savannas treatment ranged between 51% and 65%. The *f*IPARo trend in forested treatments (excluding the HT4) found in my study was similar to some studies in a deciduous forest (Pangle et al., 2009; Richardson et al., 2007) with a substantial *f*IPARo increase in the beginning of the growing season (April) due the leaf expansion followed by fairly constant *f*IPARo during the remainder of the growing season.

5.2. Herbaceous layer *f*IPAR

Similar to overstory *f*IPAR, the herbaceous layer also showed two distinct trends for IPAR. Most of the savanna treatments followed a pattern showing a substantial increase in *f*IPARh in the beginning of growing season which can be attributed to a development of warm season grasses when the aboveground begins to grow (Gautam et al., 2014). Herbaceous *f*IPAR of the savanna treatments continues to increase until the late summer when the grasses have maximum leaf area index (Madakadze et al., 1998) followed by a decrease in *f*IPARh due the leaf senescence and onset of dormancy. A forested treatment (HT4) showed a similar pattern to the savanna treatments probably because the abundance of herbaceous vegetation in the forest floor was more similar to savanna treatments than the other forested treatments. The high presence of grasses (69.3% of the total ANPP) in the HT4 treatment may contribute to the similarity between the trends.

Compared to the savanna treatments, the Control and RRB treatments had a lower and a more consistent trend of *f*IPARh over the growing season. The smaller increase in *f*IPARh that peaks sooner in these treatments is probably because the herbaceous plants in the forest floor have a leaf expansion at the same time as the overstory reaches its maximum leaf area development, limiting subsequent understory growth (Constabel and Lieffers, 1996; Fournier et al., 2004). Consequently the increase in IPAR shows a trend that is more consistent over the year. The peak of herbaceous *f*IPAR that occurred in July, and subsequent small decrease during the remainder of the growing season in the forested treatments might partly be attributed to ephemeral spring plants present in the herbaceous layer which are adapted to take advantage of light in the early spring (Lapointe, 2001) when the radiation available for the understory is higher. These plants usually complete their growth and then undergo leaf senescence and dormancy about the same time that total overstory canopy closure occurs (Vezina and Grandtner, 1965). Our sampling for herbaceous plants biomass conducted in October might underestimate spring ephemerals.

5.3. Aboveground net primary productivity

TPAh was positively associated with herbaceous productivity. This pattern is consistent with other studies in forest and woodland systems that show an inverse relationship between tree canopy cover and herbaceous productivity (Axmanová et al., 2012; McPeherson and Wright, 1990; Pieper, 1990; Sagar et al., 2012). As light is one of the main drivers of plant productivity (Liess et al., 2009; Ludwig et al., 2004; Neufeld and Young, 2003), a positive pattern in herbaceous ANPP was expected as the TPAh increases with decreasing in tree density in this system. In other words, forest ecosystems that have greater tree density compared to savanna system should have lower herbaceous productivity due the lower PAR transmittance to the understory. In general, I found that total herbaceous ANPP differed in a predictable manner compared to overstory IPAR. Even though herbaceous ANPP of the HT4, forested treatment, was statistically similar to the savanna treatments, it was intermediate between savanna and remaining forested treatments. Greater aboveground productivity in the herbaceous layer of savanna ecosystems was about 6.8 times greater than the forest ecosystems, thus the herbaceous layer has a significant contribution to the total aboveground biomass.

The differences in litter accumulation across the treatments can be mainly explained by the fire regimes. More litter accumulated in treatments where fire was excluded (Control and HT) because there is no consumption of the dead material by the fire. The RRB treatment had more litter accumulation than the HT4 treatment even though they have the same interval of fire. For the HT4 treatment, hardwoods were harvested and the pine was thinned when the experiment was initiated which provided more light for the understory and consequently a large increase plants in the forest floor and fine fuel development. In addition, the HT4 treatment currently has greater herbaceous production then the RRB treatment which increases fire intensity and litter consumption.

Comparing the results of total herbaceous ANPP and litter accumulation, the treatments with lower litter accumulation, savanna treatments, had a higher herbaceous productivity than treatments with higher litter accumulation, i.e., forested treatments. In addition to light, litter accumulation (Facelli and Pickett, 1991a; Facelli and Pickett, 1991b; Sydes and Grime, 1981a) may influence herbaceous productivity, particularly in forest ecosystems. Litter decreases the herbaceous productivity by the interception of light at the soil surface (Knapp, 1984). The fire used to maintain savanna structure increases light available for the herbaceous plants because it removes the standing dead biomass. In tallgrass prairie, Knapp (1984) reported that the amount of PAR available for the growing grass shoots after fire increased by 60% compared to grasses that weren't burned. Hulbert (1969) also reported that reduction in litter accumulation by the fire increased *Andropogon gerardii* productivity. In addition to light interception, the litter layer may interfere with understory production by inhibition of plants germination due to phytotoxins released during the leaching or decomposition of litter, changes in soil temperature and water status, and acting as a physical barrier (Facelli and Pickett, 1991b).

Overall as TPAh increased, ANPP in the different categories of herbaceous plants also increased. The grass ANPP differences across treatments can be mostly explained by growth of the dominant grasses in the system (*Andropogon girardii, Schizachyrium scoparium, and Sorghastum nutans*) which possess the C4 photosynthetic pathway. C4 plants occur in greater abundance in environments where there is plenty of radiation available, such as subtropical savannas and temperate grasslands (Knapp and Medina, 1999). Plants with C4 photosynthesis pathway are less tolerant to shade than C3 plants, thus they are largely absent in forests where the solar radiation available for the understory drops bellow of 20% of the total incident solar radiation (Pearcy, 1990). In addition, fire also may contribute to dominance of C4 grasses in the savanna treatments. In contrast to the savanna treatments, the understory of the Control and HT treatments was dominated by woody plant biomass, because woody plants have C3 photosynthesis pathway that require less energy for CO_2 assimilation. Thus woody understory plants can persist under the lower light environment in forest ecosystem. Other reason for the dominance of woody species can be due the fire exclusion that favors the establishment and increase in woody species under the forest canopy (Peterson and Reich, 2008).

Even though the percentage of the herbaceous layer composed of woody and other C3 plants was higher in the forested treatments than the savanna treatments, absolute biomass of C3 plant ANPP increased PAR availability increased across the forest-savanna continuum. For instance, forb and legume biomass, while a relatively small percentage of total understory ANPP, was greater in the savanna treatments than the forested treatments. An exception was woody ANPP in HNT1, which was lower than the other savanna treatments and similar to the forested treatments. The low ANPP in these treatments can occur because most of woody species in their seedling and sapling stages are harmed by fire (Bond and Van Wilgen, 1996). In my study, one-year fire return interval reduced woody plant growth in the understory. However a fire return interval of two years or greater appears not have a large influence on woody ANPP in the understory, probably because this interval of fire allowed the woody plants to grow enough to survive and persist even with repeated fires.

It was expected a greater sedge ANPP in forested treatments due the effects of temperature (Gorham, 1974) and competition with other plants on sedge growth. Cooler temperatures in the shaded forested plots may increase sedge growth relative to other plant types. Also, less competition from grasses in the forested treatments may have favored sedge growth. Allen and Marlow (1994) found that when competition between sedge and other plant species decreased an increase in sedge shoot occurred. However in my study sedge did not exhibit significant differences among treatments. Sedges were smallest component to total aboveground biomass (between 1.92% and 0.37%) and variable among plots of the same treatment.

In my study, forb ANPP decreased as fire return interval increased suggesting that litter accumulation, as well as light, influenced forb productivity. However contradictory to my results Turner and Knapp (1996), in a study in tallgrass prairie in Kansas, found that fire and the presence of grass negatively affected the forb biomass . In their study, fire indirectly reduced forb ANPP by increasing grass growth and competition within the herbaceous layer. In another study, McCain et al. (2010) found the same relationship between the removal of grasses and increases forbs ANPP due increases in light available. In contrast, I found that both forbs and grass biomass increased with shorter fire return intervals.

Little is known about how light influences legume growth. Factors such as soil conditions and nutrient availability have been reported to cause changes in legume distribution and biomass. Legumes are more abundant in well-drained soils than in soils poorly drained in longleaf pine systems (Hainds et al., 1999). However in this same study Hainds and colleagues suggested that the low dominance of legumes in wetter areas was attributed to soil anoxic condition and also to low levels of phosphorus. Along this forest-savanna gradient, the differences in legume ANPP could be a sum of PAR available and availability of phosphorus in the soil. In addition, fire increases light available to herbaceous plants by canopy reduction and litter consumption, as discussed before, but also can increase amount of phosphorus available (Wilbur and Christensen, 1983) due the alkalization of the soil caused by the ashes (Certini, 2005).

5.4. Influence of PAR available and IPAR on herbaceous ANPP

The analysis considering the entire forest-savanna ecosystem continuum allowed examination of the influence of light on herbaceous productivity from heavily shaded to almost open canopy. Herbaceous ANPP were positively correlated to total PAR available and PAR intercepted by the herbaceous plants. Mainly, the increase in TPAh was due to decreased in overstory canopy, i.e., trees. Although both TPAh and TPIh were related to herbaceous ANPP, my results showed that TPIh was better correlated with ANPP. Probably the lower correlation between herbaceous ANPP and TPAh was in part because a portion of PAR reaching the understory falls upon the bare soil or the litter layer in the empty spaces between plants in the discontinuous herbaceous layer, especially under forests. The empty gaps between the understory vegetation are likely due to litter accumulation on the forest floor. Litter can act as a physical barrier preventing the development of the plants (Hiers et al., 2007) or by the decreasing of amount of light available for plants or seeds under this layer. Reduction of light caused by the litter interception can be especially important for the establishment of forbs and legumes that are plants that occur mostly in open environments (Wang et al., 2010a).

Total PAR intercepted has a direct effect on herbaceous plant productivity as it represents the energy captured for photosynthesis and was a better predictor of herbaceous ANPP than was TPAh. Even though a direct measure of energy capture, the relationship between herbaceous ANPP and TPIh only explained 65% of the variation in ANPP. Other factors such as soil moisture that is usually higher in forest than in grasslands (Belsky, 1994; Li and Wilson, 1998; Peltzer, 2001), different slopes, and presence of large rocks may influence the herbaceous ANPP among treatments. The variation in slopes among the treatments may have negatively or positively influence in the productivity. Those treatments located on steeper slopes may have a negative influence due the increase in runoff and sediment discharge (Chaplot and Le Bissonnais, 2000). Conversely productivity can be favored in some areas due the deposition of sediments carried by the runoff from the other areas thus increasing the soil nutrients. Furthermore high presence of stones in some treatments can decrease the area for plant establishment.

There were large differences in TPIh and herbaceous ANPP among the treatments, but the relationship between the two variables was consistent, i.e., no slope differences or differences in LSmeans. The consistency of the relationship across treatments allows estimation of herbaceous productivity using relatively simple estimates of understory IPAR. Herbaceous plants are often not accounted for in the overall biomass of the forest ecosystems and little is known about the dynamics of herbaceous productivity. However due the increases in emissions of CO_2 in the atmosphere the carbon accumulation in this layer can be enhanced due the increased plant growth cause by high levels of CO_2 in low light conditions (Granados and Körner, 2002; Kerstiens, 2001). On the other hand, herbaceous plants in savannas ecosystems have high contributions to the overall biomass and cannot be neglected when measuring the carbon accumulation in the ecosystem. Grasses in savanna systems contribute about 59% to the total ANPP (Lloyd et al., 2008). Despite the high ANPP contribution in savannas compared to forest, the dynamic of productivity in this layer is poorly understood.

While there was not a difference, one might have expected the relationship between herbaceous ANPP and TPIh to differ due to differences in efficiency among the dominant types of vegetation found in the savanna vs forested treatments. Savannas treatments were mostly dominated by C4 grass while in forest, the dominant species were woody plants with C3 photosynthetic pathway. C4 plants have higher rates of photosynthesis under light saturated conditions than C3 plants (Gifford, 1974). In addition, the C4 plants use water more efficiently when temperature is high (Downes, 1969) which can also contribute with greater dry biomass accumulation in savannas. These differences in the efficiency of resource use might be expected to increase ANPP of herbaceous plants relative to TPIh in the savanna ecosystems. The consistency of the relationship between TPIh and herbaceous ANPP I measured might occur due to greater rates of photosynthesis of C3 plants under low light conditions compared to C4 plants because of the high energy necessary for the carbon assimilation in C4 plants (Kanai and Edwards, 1999).

This study highlights the importance of light in the process of herbaceous layer productivity. The dynamics of light intercepted in overstory and herbaceous layer are generally dependent of the species and density of plants. In forest ecosystems, the pattern of light intercepted by herbaceous plants is limited and related to the development of the overstory canopy. In savannas ecosystems, where light available to the understory is not a limiting resource, the pattern of light intercepted by the herbaceous plants was dependent of the development of the understory itself. In general, my data demonstrate that increases in herbaceous ANPP occur in this forest-savanna gradient with the increase in light availability and decreases in litter accumulation. Despite the variation in the amount of light available and intercepted in each ecosystem because of the overstory structure and density there was no variation in the efficiency to use light to produce biomass between the herbaceous plants in various ecosystems.

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APPENDICES

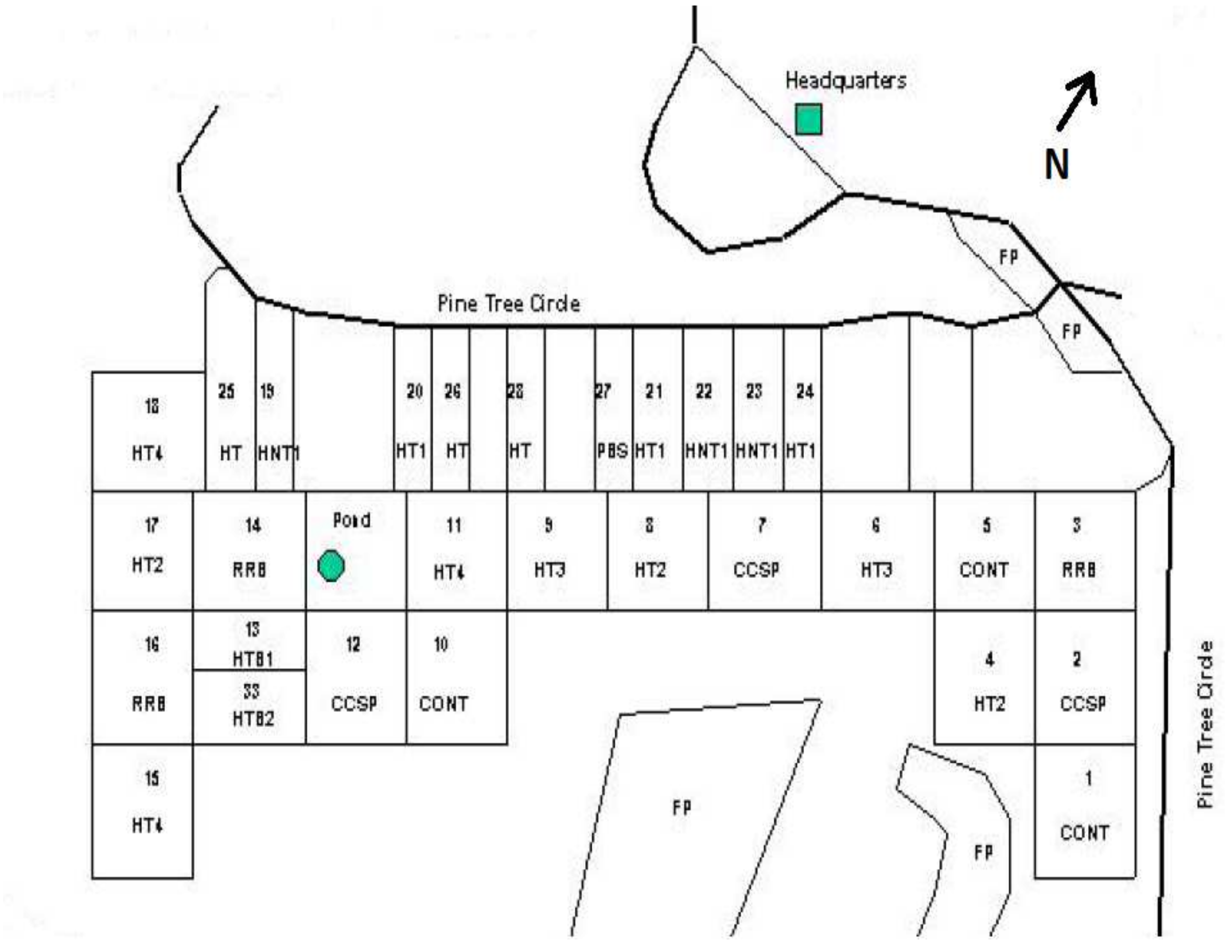

Figure 1. Unit map of Pushmataha Forest Habitat Research Area (Masters et al., 2006).

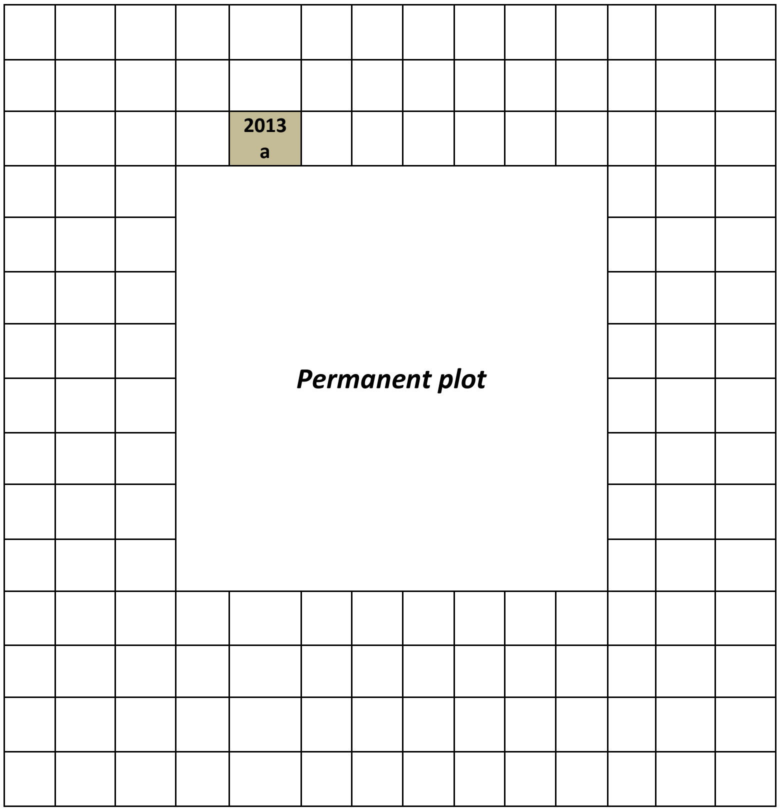

Figure 2. Overstory and herbaceous plots locations. Overstory light variables were measured in middle of the permanent plots (16 m^2). Herbaceous aboveground net primary production (ANPP) and understory light variables were measured in the plots named 2013a. Each herbaceous plot was 0.25 m^2.

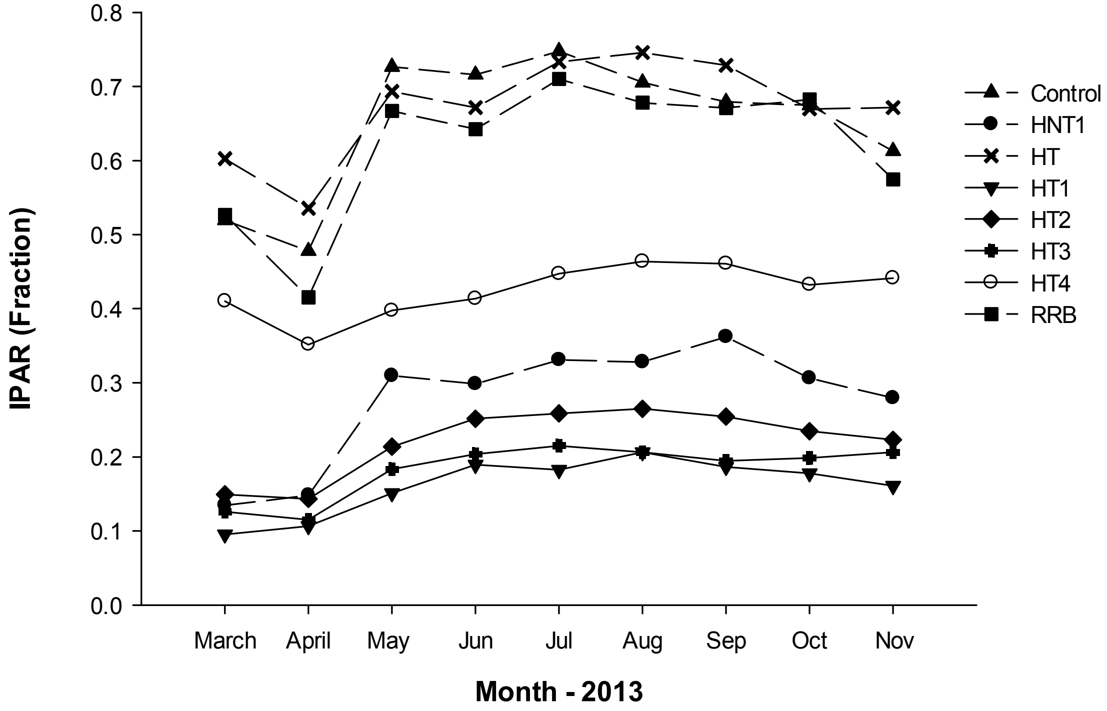

Figure 3. Temporal trends in overstory IPAR (means) among treatments in 2013. Dashed and solid lines represent the group of treatments that follow the same trend.

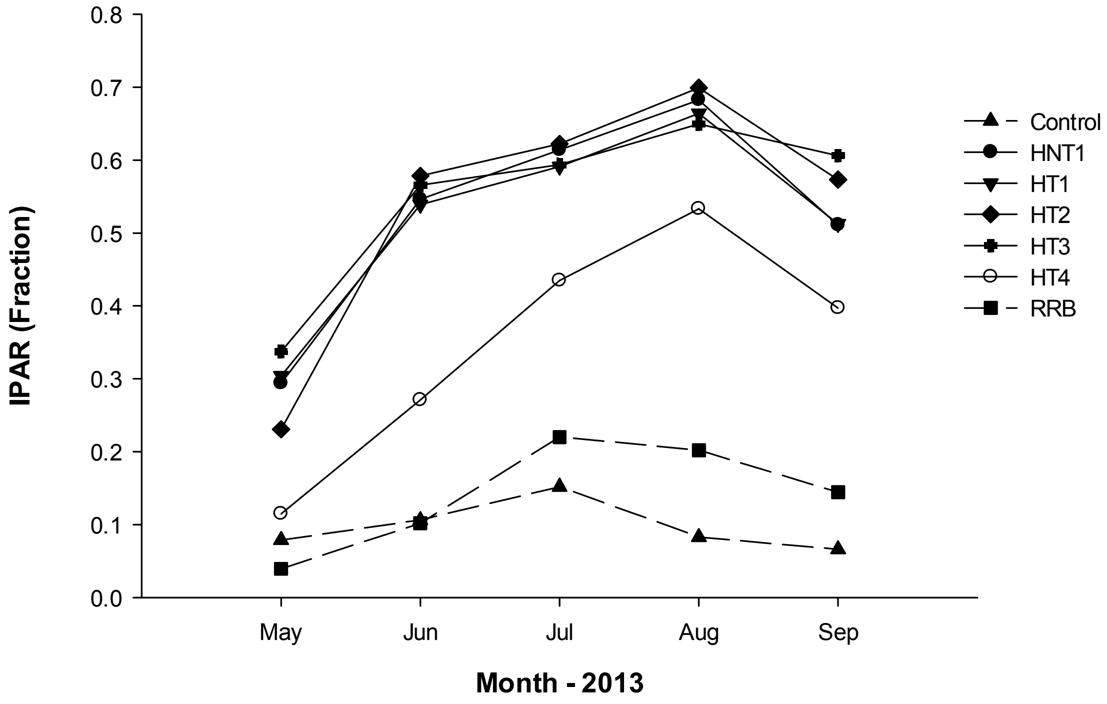

Figure 4. Temporal trends in herbaceous layer IPAR (means) among treatments in 2013. Dashed and solid lines represent the group of treatments that follow the same trend.

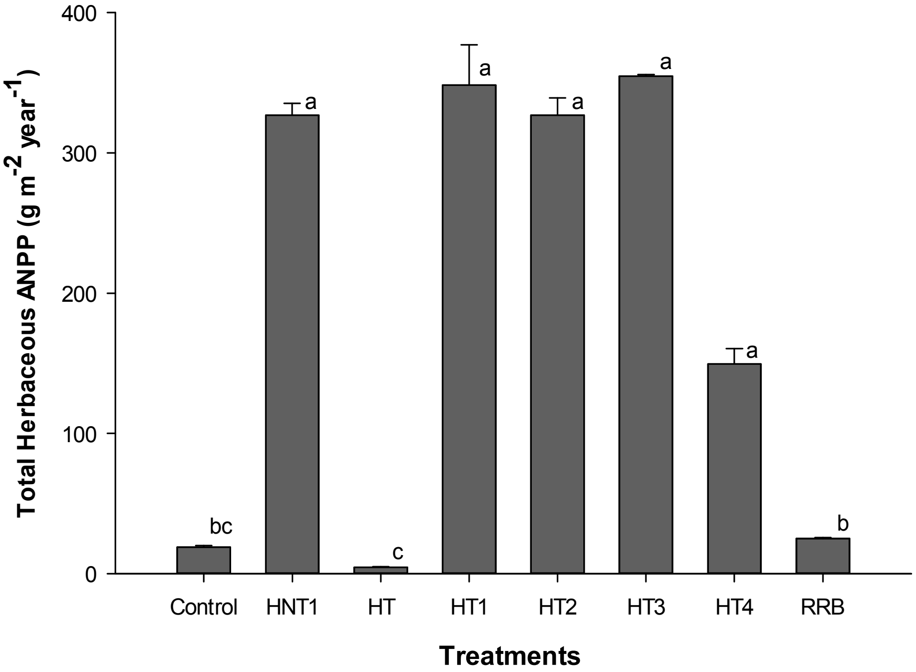

Figure 6. Total herbaceous aboveground net primary production (ANPP) and statistical differences among the treatments. Bars represent total herbaceous ANPP means ± SE. Significant differences between treatments ($p < 0.05$) are represented by different letter (based on Duncan's MRT conducted on log transformed data).

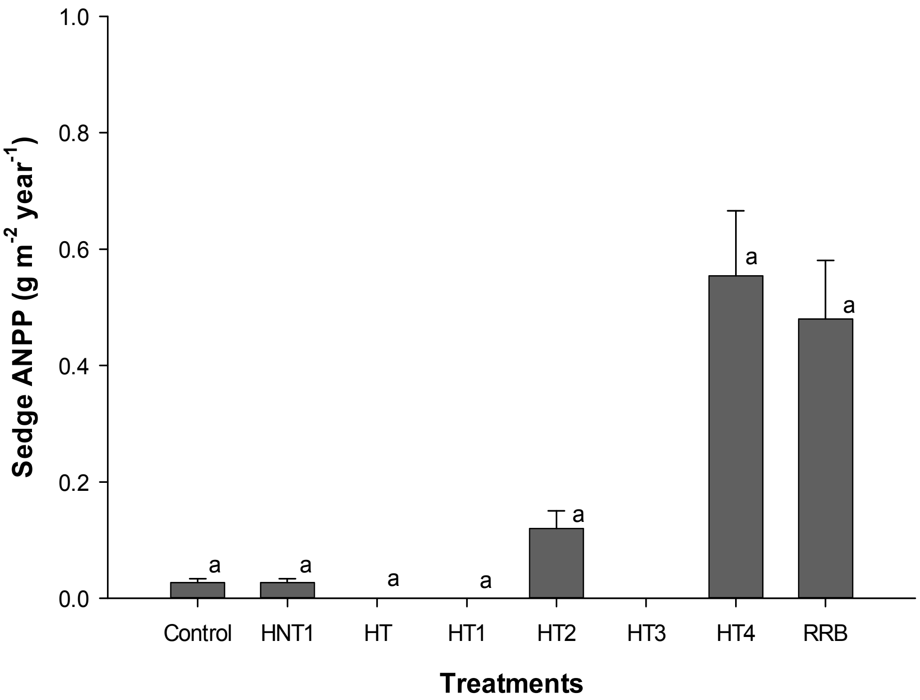

Figure 6. Sedge aboveground net primary production (ANPP) and statistical differences among the treatments. Bars represent sedge ANPP means ± SE. Significant differences between treatments ($p < 0.05$) are represented by different letter (based on Duncan's MRT conducted on log transformed data).

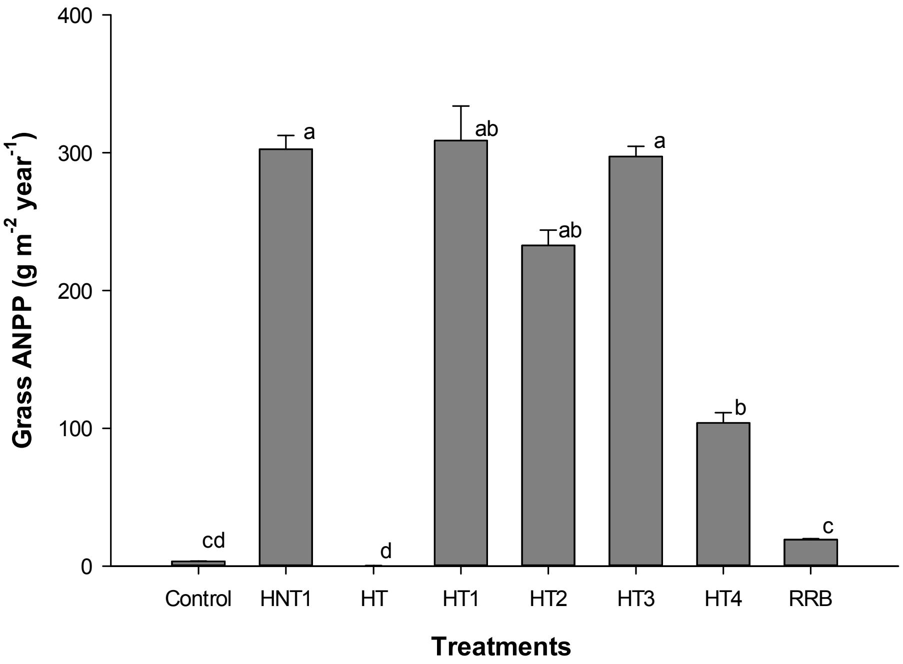

Figure 7. Grass aboveground net primary production (ANPP) and statistical differences among the treatments. Bars represent grass ANPP means ± SE. Significant differences between treatments ($p < 0.05$) are represented by different letter (based on Duncan's MRT conducted on log transformed data).

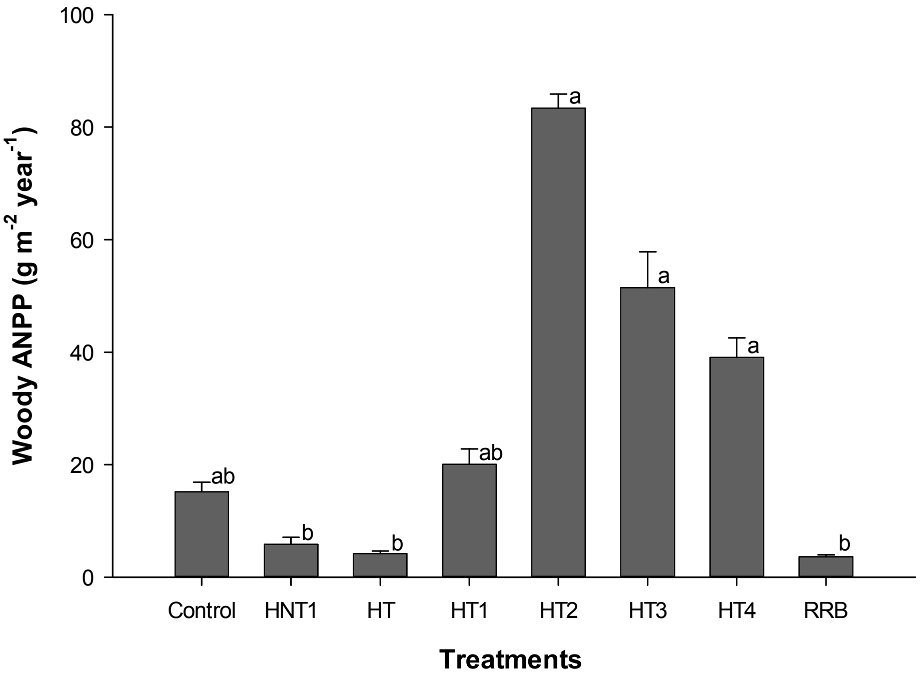

Figure 8. Woody aboveground net primary production (ANPP) and statistical differences among the treatments. Bars represent woody ANPP means ± SE. Significant differences between treatments ($p < 0.05$) are represented by different letter (based on Duncan's MRT conducted on log transformed data).

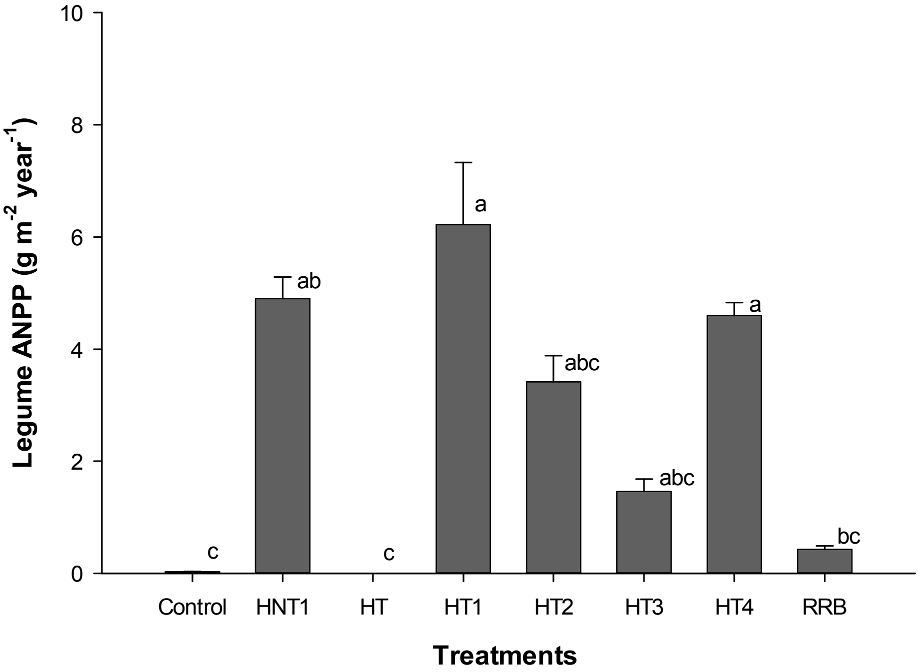

Figure 9. Legume aboveground net primary production (ANPP) and statistical differences among the treatments. Bars represent legume ANPP means ± SE. Significant differences between treatments ($p < 0.05$) are represented by different letter (based on Duncan's MRT conducted on log transformed data).

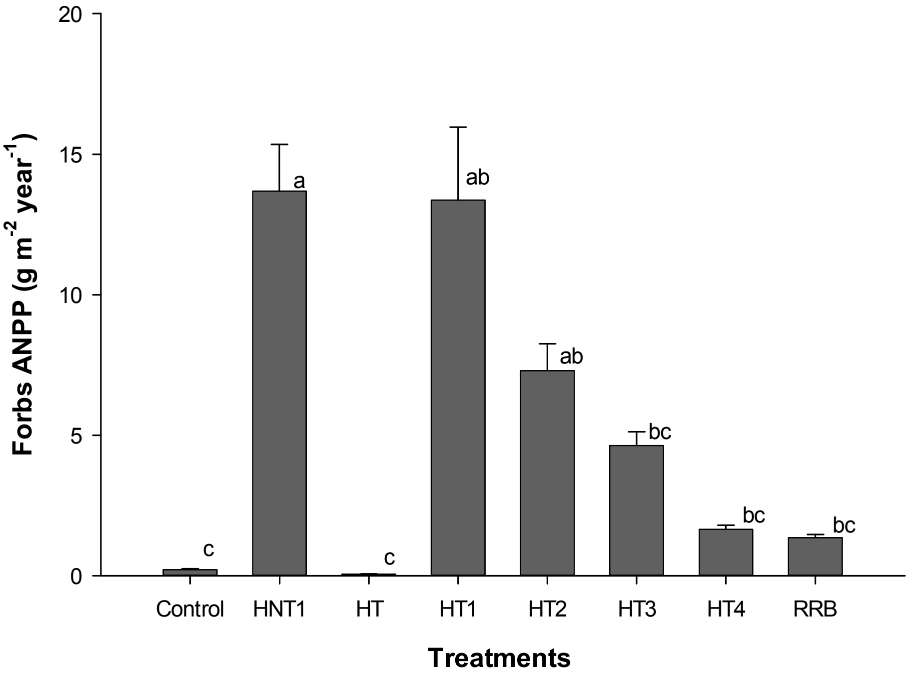

Figure 10. Forbs aboveground net primary production (ANPP) and statistical differences among the treatments. Bars represent forbs ANPP means ± SE. Significant differences between treatments ($p < 0.05$) are represented by different letter (based on Duncan's MRT conducted on log transformed data).

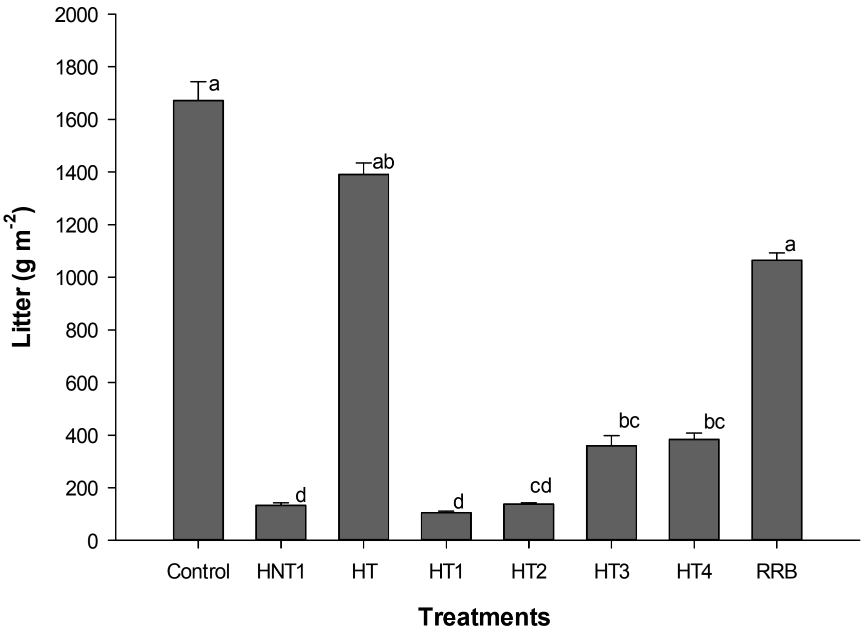

Figure 11. Total litter accumulation and statistical differences among the treatments. Bars represent total litter accumulation means ± SE. Significant differences between treatments ($p < 0.05$) are represented by different letter (based on Duncan's MRT conducted on log transformed data).

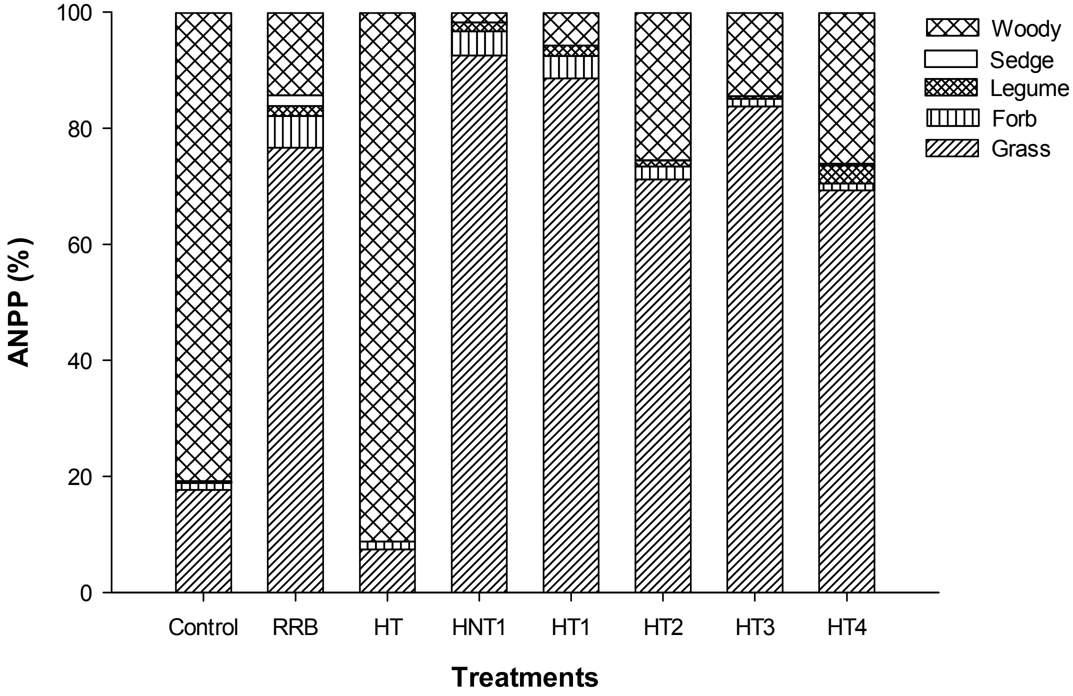

Figure 12. Grass, forb, legume, sedge, and woody contributions expressed in percentage of the total herbaceous aboveground net primary production in each treatment.

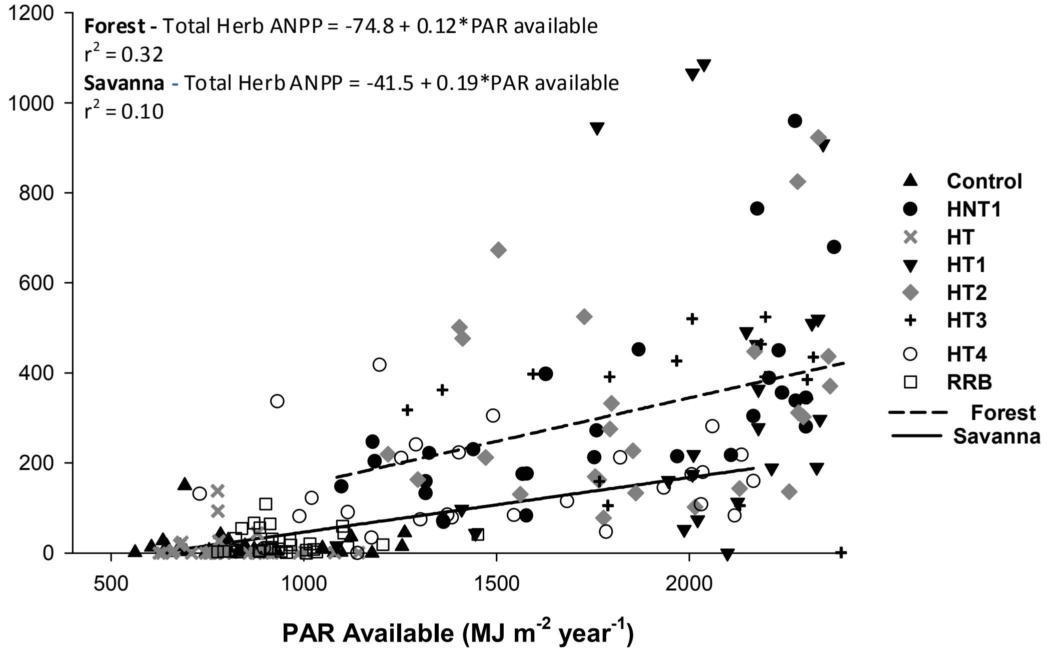

Figure 13. Total Herbaceous aboveground net primary production (ANPP) in relation to total PAR available for the herbaceous layer. Each point represents the total herbaceous ANPP in each herbaceous plot in each treatment in 2013.

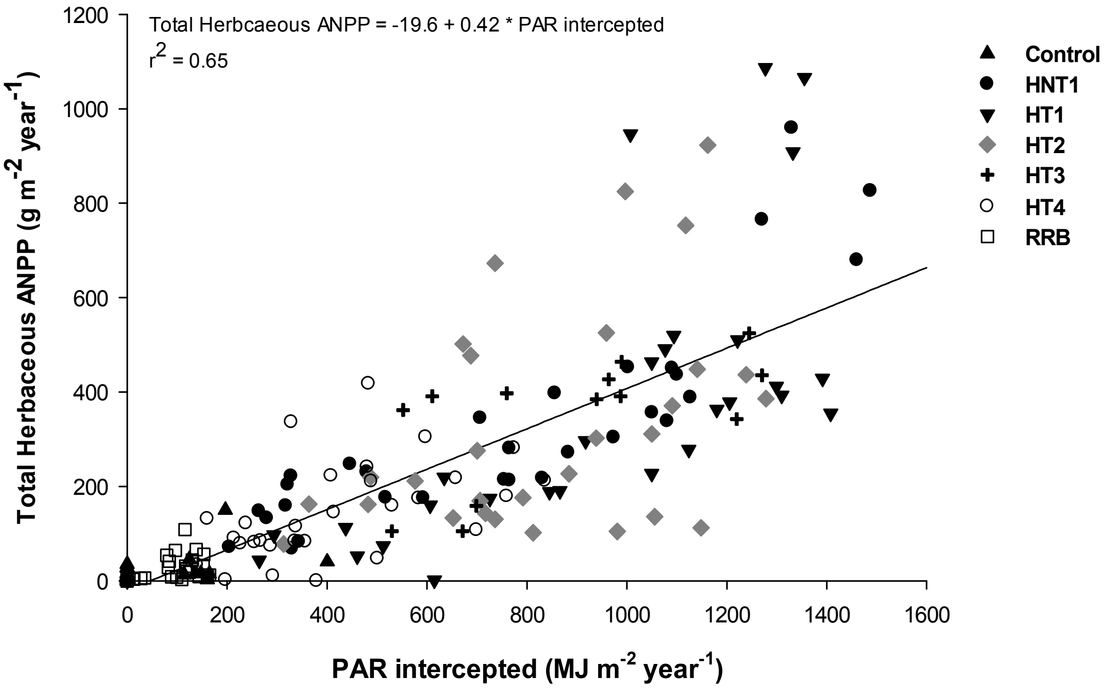

Figure 14. Total Herbaceous aboveground net primary production (ANPP) in relation to total herbaceous IPAR. Each point is represents the total herbaceous ANPP in each herbaceous plot in each treatment in 2013.

Table 1. Means of total PAR available and total IPAR by the herbaceous layer. Least Square Means of total herbaceous ANPP at a common total PAR available and a common total IPAR for 2013.

Treatments	Total PAR available for herb. layer (MJ m^{-2} $year^{-1}$)	Total Herb. Layer IPAR (MJ m^{-2} $year^{-1}$)	Herb. ANPP (g m^{-2} y^{-1})at a Total PAR available of 1486 MJ m^{-2} y^{-1} (LSmean)	Herb. ANPP (g m^{-2} y^{-1}) at a IPAR of 536 MJ m^{-2} y^{-1}(LSmean)
CONTROL	863.5 *a*	48.1 *a*	26.8 *a*	59.1
RRB	962.7 *a*	81.1 *a*	24.8 *a*	57.5
HT	811.3 *a*	-	27.0 *a*	-
HNT1	1824.8 *bc*	765.2 *c*	69.7 *b*	55.8
HT1	2111.9 *c*	915.9 *c*	64.9 *b*	48.9
HT2	1964.5 *c*	843.9 *c*	64.8 *b*	46.8
HT3	2069.6 *cd*	839.1 *c*	67.9 *b*	48.4
HT4	1476.7 *b*	421.3 *b*	37.0 *a*	49.7

Note. Different letters indicate the significant difference among treatments (*p* value < 0.05). Total PAR input was 2546 MJ m^{-2} $year^{-1}$ for each treatment. Total PAR available and IPAR are the sum of each parameter during the growing season (May 1st to November 30th) of 2013. HT does not has values for total PAR intercepted and total herbaceous at a PAR intercepted of 536 MJ m^{-2} y^{-1}.

Table 2. Means and standard error of conifer, hardwood, and total overstory basal area in 2011. Significant differences between treatments are represented by different letter (based on Least Square Mean with significant difference when *p* value < 0.05)

Treatment	Conifer	Hardwood	Total
Control	16.7 ± 2.8 a*b*	12.5 ± 0.9 *a*	29.3 ± 3.7 *ab*
RRB	15.3 ± 1.4 a*b*	10.4 ± 1.5 *ab*	25.7 ± 2.6 *b*
HT	24.3 ± 6.7 *a*	10.9 ± 3.6 *a*	35.2 ± 2.8 *a*
HNT1	0.6 ± 0.2 *d*	6.9 ± 1.1 *bc*	7.5 ± 1.2 *d*
HT1	1.1 ± 0.5 *d*	2.1 ± 0.5 *c*	3.2 ± 0.9 *d*
HT2	3.5 ± 0.7 *cd*	3.7 ± 0.4 *c*	7.2 ± 0.9 *d*
HT3	2.6 ± 0.9 *d*	3.0 ± 0.6 *c*	5.6 ± 0.3 *d*
HT4	12.9 ± 4.6 c*b*	4.8 ± 0.3 *c*	17.1 ± 4.6 *c*

Note. The means of basal area are expressed in m^2 ha^{-1}. Total overstory comprises all the trees present in the treatments.

VITA

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