

EFFECTS OF PRESCRIBED FIRE AND FOREST  
THINNING ON WHITE-TAILED DEER FORAGE  
PRODUCTIVITY AND QUALITY IN A SOUTHERN  
OAK-PINE FOREST-SAVANNA CONTINUUM

By

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Abstract: White-tailed deer (*Odocoileus virginiana*) represent an important economic component in the management of forest lands in the USA with over 16 billion dollars of expenditures annually related to deer hunting. Climate change is expected to increase temperature and variability in rainfall, and traditional management of forests for timber production may become less viable on marginal sites on the western fringes of the eastern deciduous forest. Managing these forests for multiple objectives, including improved deer habitat, could increase the economic viability of forest management in the region. The goals of this study were to evaluate the long-term impacts of different combinations of fire return intervals and tree harvest on three major aspects of deer forage; forage productivity, timing of forage availability, and nutrient quality of forage. Aboveground net primary production (ANPP) of six functional groups (grass, panicum, forb, legume, woody, sedge) was measured in October 2019 and 2020. Percent cover of vegetation functional groups was measured monthly March through October 2019 and 2020. Foliar crude protein (CP) concentration was sampled in spring, summer, and fall of 2020 and calcium, phosphorus, potassium, in the summer of 2020. Total ANPP increased with fire frequency and tree harvest. Annual burning resulted in herbaceous dominated ANPP and longer fire return intervals resulted in roughly equal woody and herbaceous ANPP. Most functional groups peaked in coverage mid-summer, then plateaued or declined slightly in the fall. The average annual coverage results had similar trends to those for ANPP. Forb coverage peaked in April and had very little coverage in summer and fall indicating a possible source of forage early in the growing season. Crude protein concentrations were significantly greater in the forest ecosystems than in the savanna ecosystems for seven of the eleven species sampled. This increase in CP was most noticeable in the summer when deer needs for quality forage are the greatest. Foliar Ca, P, K concentrations followed a similar trend to CP concentration but were generally not significant. Increased protein and mineral concentrations in the forests indicates that a mix of savanna and forest could be ideal for balancing forage quantity and quality.

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## CHAPTER I

### INTRODUCTION

The understory is often overlooked in forest research. However, the understory is often home to the vast majority of forest plant biodiversity and provides habitat for many wildlife and livestock species. In a review comparing understory and overstory species richness, Gilliam (2007) found that on average the understory accounts for about 80% of a forest's plant species richness, and in extreme cases like longleaf pine (*Pinus palustris*) forests, can account for a ratio of 1:250 overstory to understory species. A similar situation may occur for shortleaf pine (*Pinus echinata*) woodlands as both are fire-adapted southern pines known for diverse and productive understories. Prescribed fire has an important role on the understory as it increases diversity (Platt et al. 2006) and understory net primary productivity (Masters 1991 and 1993, Reich et al. 2001). This in turn improves habitat for a wide diversity of wildlife (Wilson 1995, Masters 1998, Howze and Smith 2021), including economically important game species like white-tailed deer (*Odocoileus virginiana*), Wild Turkey (*Meleagris gallopavo*) and Northern Bobwhite (*Colinus virginianus*).

White-tailed deer hereafter (deer) represent an important economic component in the management of forest lands in the United States (Fuller 2016). With climate change expected to increase temperature and variability in rainfall, traditional management of

forests for timber production may become less viable, especially on the western fringes of the eastern deciduous forest (Will et al. 2015, Kloesel et al. 2018, Shepard et al. 2021). Managing forests for multiple objectives, including deer habitat, has the potential to increase the economic viability of forests in these regions (Grado et al. 2001). In southern pine or oak-pine forests, deer habitat is usually marginal because of limited biomass production of the understory resulting from a dense, often multi-layered tree canopy. A combination of thinning, vegetation management, and prescribed fire reduces forest overstory and has the potential to improve forests for deer habitat (Masters et al. 1993, Sparks et al. 1998).

Total expenditures in the United States for hunting were 25.6 billion dollars in 2016 with over half of that, 12.9 billion, spent on deer hunting (DOI 2017). This figure does not include non-consumptive uses like wildlife viewing. White-tailed deer are the most sought-after game species in North America by a wide margin. Nearly 11 million people hunted deer in 2011, a figure 3.5 times greater than the number of people hunting for the second most pursued species, Wild Turkey (Fuller 2016). This is a result of many factors, including the large geographic range of deer, large and widespread populations of deer, and the ability to effectively hunt deer on small tracts of land. Also, deer are highly abundant and are at or nearing nuisance densities in highly populated regions in the eastern United States (Witmer and DeCalesta 1991, Weckel and Rockwell 2013). However, movement of deer into areas with high human populations can also be an impediment to deer hunting as urban and suburban sprawl can reduce hunting opportunities through local ordinances (DeStefano and DeGraaf 2003, Williams et al. 2013).

Improving southern pine forests for deer often involves maintaining early successional habitat through timber harvesting, prescribed fire, or a combination of these treatments (Masters et al. 1993, Lashley et al. 2011, Glow et al. 2019). Untreated southern oak-pine forests have very little understory biomass and, as a result, low forage quantity and carrying capacity for herbivorous wildlife or livestock (Masters 1991, Edwards et al. 2004, Feltrin et al. 2016). In addition to total forage quantity, forage quality is also important. The most widely used measure of forage quality is crude protein (CP). Crude protein is proportional to nitrogen in a forage, and nitrogen is a critical component in forming proteins and supports all life functions. Crude protein is an important measure because it is often limiting in native forages for wildlife or livestock. Timing of forage availability and the associated quality of that forage are important for deer because antler growth and lactation increase forage and nutrient demand in summer when forage quality has declined from its early peak in the growing season.

The purpose of this study was to quantify deer forage quality and productivity across a wide range of ecosystem types, ranging from forest to grassland, that were created by various combinations of tree harvest, thinning, and prescribed fire. The goal was to understand which stand conditions maximize the potential carrying capacity for an economically important game species within oak-pine forests of the southeastern United States. The objectives were to 1) Compare the understory aboveground net primary productivity (ANPP) of eight different management regimes that created conditions ranging between grassland and closed-canopy forest. 2) Compare changes in the understory vegetation community throughout the growing season. 3) Track changes in

forage CP concentration throughout the growing season along with other key nutrients in the summer.

## **CHAPTER II**

### **REVIEW OF LITERATURE**

#### **2.1 Historical conditions and changes in oak-pine forest**

Historically, the Cross Timbers and oak-pine forests of the southeastern United States existed as a mosaic of grasslands and savannas interspersed with woodlands and forests of varying density (Nowacki et al. 2008). Within Oklahoma, soil type plays a role in this mosaic with coarser, sandy textured soils favoring forest and finer, clay soils favoring grasslands (Bell and Hulbert 1974). The other driving factor controlling vegetation cover type was fire. Research indicates a 3-year fire return interval threshold is required for maintaining grassland or savanna type environments, with less frequent fire return resulting in tree-dominated systems (Masters et al. 1993). In eastern Oklahoma, data from fire scars indicate an average fire return interval of 5 years from 1650-1830 before widespread European settlement (Stambaugh et al. 2013). Fire frequencies are believed to have increased somewhat after the arrival of European-Americans to the area before declining greatly due to fire exclusion practices (Clark et al. 2007).

Beginning in the early to mid 1900s the practice of fire exclusion largely removed the critical process in maintaining grasslands and savannas in eastern and central Oklahoma. This resulted in widespread transition from savanna and woodlands to closed-

canopy forest (Desantis et al. 2011). Additionally, encroachment of fire-intolerant woody species like eastern redcedar (*Juniperus virginiana*) is a growing problem in both grassland and forested areas of eastern and central Oklahoma (Desantis et al. 2011, Briggs et al. 2002).

This change in forest structure greatly altered the ecosystem services provided by the area. One important impact is that carrying capacity for white-tailed deer has been reduced due to limited biomass production of the understory within closed-canopy oak-pine forests (Sparks et al. 1998). Additionally, the conversion of grassland and savannas into closed-canopy forests alters the ability of the ecosystem to support many species of conservation concern or economic potential, such as Red- cockaded Woodpecker (*Leuconotopicus borealis*) and Northern Bobwhite (Wilson et al. 1995, Cram et al. 2002,). Thinning of the canopy and the use of prescribed burning have the potential to improve habitat for deer and other key species by greatly increasing understory productivity (Masters et al. 1993, Edwards et al. 2004, Lashley et al. 2011).

## **2.2 Nutritional requirements for deer**

Daily food intake for deer is highly variable and is a function of deer size and sex along with the nutrient and energy contents of the forage being consumed. The average daily dry matter intake for adult deer is around 2-2.3 kg per day (Mccall 1997, Hewitt 2011) with a maximum intake up to 4.8% body weight of dry matter per day for lactating females (NRC 2007, Lashley et al. 2015). However daily intake is often lower if adequate



digestible energy is available in the diet and nutrient demands are met (Amman et al. 1973).

Nutrient demands for deer vary greatly throughout the year and among different age and sex classes. A basic maintenance diet for an adult deer contains around 6-8% CP (French et al. 1956, Holter et al. 1979, Asleson et al. 1996). Protein demands are higher for young deer that are rapidly growing. Deer less than 1-year-old (fawns) exhibited greater rates of weight gain as CP concentration increased, up to 25% CP for male fawns and up to 14% CP for female fawns Ullrey et al. (1967). Male fawns may have had greater protein demands than female fawns as antler growth increases CP demand to nearly double that of a maintenance diet, and female fawns were not bred. A diet with 12% CP is needed to maximize antler growth (Asleson 1996). The deer with highest dietary CP needs are lactating females. A female nursing a single fawn requires a diet of 14% CP and 19% CP for two fawns (Jones et al. 2009, Lashley et al. 2011). Phosphorus and calcium are important nutrients for both antler growth and milk production, and phosphorus is often limiting in forage in southeastern forest sites (Lashley et al. 2011). Digestible energy ( $\text{kcal kg}^{-0.75}$ ) is also an important nutrient measure for deer, but is usually not limiting except in winter when deer are often consuming poorly digestible woody plants (Gray and Servello 1995).

### **2.3 Deer diet composition**

Deer are concentrate selective browsers with a digestive tract adapted to process highly digestible forages. As a result, they avoid lignified plant material when possible (Hoffman 1989, Lashley et al. 2014). As expected for a selective browser, deer select for

forages high in limiting nutrients. Lashley et al. (2015) found that deer selected for forages high in phosphorus concentrations 10 times more than expected based on availability along with significantly greater CP and calcium than in non-selected forages. Berteaux et al. (1998) found that when presented pre-mixed commercial diets that met mineral and protein needs for a maintenance diet, deer selected the more easily digestible blend. However, Vangilder et al. (1982) found a negative correlation for diet digestibility in selected browse species, indicating meeting nutrient thresholds may outweigh increased digestibility, and that focusing on any single measure of forage quality is prone to error such that evaluating forage quality is best viewed in a holistic approach.

Deer diet composition usually consists of a variety of forbs, legumes, woody browse, and hard and soft mast with significant seasonal variation (Johnson et al. 1995, Gee et al. 1994). Woody browse is the single largest component of deer browse, and is consumed throughout the entire year (Johnson et al. 1995, Gee et al. 1994). The importance of woody browse varies by forest type. In the post oak (*Quercus stellata*)-dominated Cross Timbers forest, Gee et al. (1994) found roughly equal use of forbs (44%) and woody species (41%) in deer diet composition with more forbs consumed in the spring and summer, and more woody material in fall and winter. In contrast, forbs formed only 15% of deer diets during spring and summer in oak-hickory forests in Georgia (Johnson et al. 1995). In a similar forest type, Lashley et al. (2012) found little selection for herbaceous plants by deer with a ratio of only one herbaceous plant species to seven woody species selected. The reasons for these discrepancies may be a result of a less diverse forb and legume community in the mostly closed-canopy oak-hickory sites as Shaw et al. (2010) found no significant deer use of herbaceous plants in two closed-

canopy oak hickory forests in Tennessee, but noted most herbaceous species present were grasses or other non-preferred species.

Deer rarely consume grasses due to poor digestibility and lower nutrient concentrations (Stransky and Harlow 1981). However, there is some use of tender sprouts shortly after spring green-up especially at burned sites (Lewis et al. 1982, Masters et al. 1993). Deer also consume cool season panicum (*Dichanthelium spp.*, *Panicum spp.*) grasses in the winter (Gee et al. 1994). Deer also consume many agricultural and ornamental grasses especially grains like corn (*Zea mays*), wheat (*Triticum spp.*), and oats (*Avena sativa*). At high densities, deer are an agricultural pest (Conover and Decker 1991).

Deer consume a variety of soft and hard mast with acorns being highly preferred. However, mast has limited seasonal availability and high variability among years (Greenberg 2000, Brooke et al. 2019). When hard mast is available in the fall and winter, it is a major component of deer diets in the Ouachita Mountains of Oklahoma and accounted for over 90% of fall diet composition in high productivity years (McCullough 1985, Fenwood et al. 1985). In years with a good acorn crop, deer will often select acorns over standing vegetation during the fall or winter. However, as a result of the high variability between years, over-reliance on mast production can lead to severe winter nutritional stress and deer mortality during years of low production (Rogers et al. 1990).

## **2.4 Factors influencing forage quality**

### **2.4.1 Plant maturity**

Numerous factors influence within-species foliar nutrient concentrations which form the basis in determining forage quality for wildlife and livestock. In general, forage quality declines with foliage maturity for herbaceous plants (Kilcher 1981, Cogswell and Kamstra 1976, George and Bell 2001, Mysterud et al. 2011). This is often erroneously attributed to seasonal effects, but new growth after late growing season disturbances like fires have similarly high nutrient quality values as plant material during initial green-up early in the growing season (Grelen and Epps 1967). This is largely a result of changes in plant development, namely changes in proportions of leaf and stems in herbaceous plants. As plants progress throughout their life cycle the ratio of leaf to stem declines, and leaf material typically contains two to three times the protein when compared to stem (Woodman and Evans 1935, Mowat et al. 1965).

### **2.4.2 Soil Fertility**

Soil nutrient availability has a mixed impact on plant foliar nutrient concentrations. There are two hypotheses as to the effects of soil nutrients on forage quality. The first is that soils with low nutrient availability correlate to lower foliar nutrient concentrations. The second is that low soil nutrient availability reduces the production of forage, but not the quality. In a longleaf pine forest in Georgia, Lashley et al. (2015) found that poor soils did not reduce foliar CP, calcium, or phosphorus concentrations. Some research in agricultural crops like alfalfa (*Medicago sativa*)

indicates that soils low in phosphorus may increase CP concentration (Mueller and Orloff 1994). This is a result of stunted growth leading to higher leaf to stem ratio and therefore a greater CP concentration as leaves are higher in protein concentration than herbaceous stems (Mowat et al. 1965). While low soil nutrient availability appear to have minor effects on forage quality, increasing soil nutrients through application of NPK (nitrogen, phosphorus, potassium) fertilizer increase CP concentrations, but may reduce digestibility (Mitchel et al. 1994, Grant et al. 2014, Kering et al. 2011).

### **2.4.3 Prescribed Fire**

Prescribed fire is generally believed to increase forage nutrient quality and palatability, but the effects vary considerably depending on the timing and frequency of the burning. The most common way prescribed fire is utilized in southern pine forests is repeated use of dormant-season fire in 3-5-year intervals for fire hazard reduction purposes or to maintain open forest structure for wildlife purposes (Davis and Cooper 1963, Van Lear 1985, Masters et al. 1993 and 1998). This type of burning has minimal impacts to forage quality with marginal or no changes in CP or key minerals, and if any effects are present they dissipate 1-2 months post fire (Thill et al. 1987, Wood 1988, Masters 1991). Masters (1991), however, found that dormant season burning did increase phosphorus content in all sampled understory species at the end of the growing season after burning. Most studies investigating dormant-season prescribed fire found that the first fires after a long period of exclusion, usually a decade plus, increased forage quality,

but subsequent fires had diminishing effects on foliar nutrient concentrations (Hallisey and Wood 1976, Masters 1991).

Growing-season fires have the potential to greatly increase forage quality when compared to non-burned or dormant-season burned forages (Smart et al. 2016). This relates to foliage maturity being the strongest driver of forage quality, and the regrowth after a growing-season burn more closely resembles spring green up than the maturing non-burned vegetation. Grazing systems combining growing-season and dormant-season burns in relatively small patches have great potential in improving forage utilization and livestock production gains in tallgrass prairie (Fuhlendorf and Engle 2001, Allred et al. 2011). Deer did not show improved usage of recently burned patches in a region with a similar vegetation type, and authors speculated severe drought conditions reduced vegetation regrowth likely limiting the animal response (Meek et al. 2008). Patch burn herbivory has not been well studied in forested systems for native ungulates.

#### **2.4.4 Water Availability**

Water stress may actually increase foliar nutrient concentrations of understory plants by stunting growth leading to less mature plants compared to non-water stressed conditions (Guenni et al. 2002, Halim et al. 1989, Sheaffer et al. 1992). The increases in forage quality from moderate water stress are primarily a result of maturity rate differences, but also result from small changes in plant chemistry, notably a reduction in cellulose concentrations (Halim et al. 1989). While moderate water stress has a neutral or positive impact on forage quality, severe drought may accelerate plant maturation and

reduce CP concentration (Peterson et al. 1992, Lashley et al. 2012). Legumes, especially agricultural crops like alfalfa, appear to handle water stress better than do grasses and other native forage species (Halim et al. 1989, Lashley et al. 2012, Walter et al. 2012).

#### **2.4.5 Light Availability**

Plants growing underneath trees often have higher CP concentrations than plants of the same species growing in open conditions. This may result from greater nutrient availability near trees or changes in leaf structure from different light conditions (Kephart et al. 1993, Ludwig et al. 2004, Lin et al. 2001). Plants grown in low light conditions often have thinner leaves than open-grown plants do, and a higher specific leaf area (SLA; leaf area/leaf mass). Specific leaf area has a positive relationship with foliar nitrogen concentration, but a negative relationship with foliar nitrogen per leaf area (Reich and Walters 1994, Garnier et al. 1997). Since CP is calculated from concentration of nitrogen in a given mass of plant material, leaves with a higher SLA will have greater CP than low SLA leaves. While legumes grown in low light conditions also have changes in SLA, legumes may have lower CP concentrations as a result of reduced nitrogen fixation from lower rates of photosynthesis (Eskandari et al. 2009).

### **2.5 Processes affecting forest understory productivity**

#### **2.5.1 Light**

Light availability is the primary limiting resource for understory productivity in the eastern deciduous forests and in southern pine forests because it limits photosynthesis

(Pearcy et al. 1987). Light conditions near the forest floor vary throughout the year primarily as a result of canopy development, but also due to changes in solar angle (Neufeld and Young 2003). Higher solar elevations in the spring compared to winter trigger spring green up, and in forested systems with dense canopies this can be one of the more productive growth periods in the understory as trees are still leafless. This is commonly known as the spring ephemeral effect (Sunmonu et al. 2013). After overstory leaves develop, understory species are limited by light and only shade-tolerant species can grow vigorously.

While spring ephemerals should not be overlooked when determining understory productivity, the total contribution to annual understory growth is usually minor in shortleaf pine-post oak forest (Masters et al. 1993, Feltrin et al. 2016). Since the growth period for spring ephemerals is relatively short, they are usually smaller plants than species that can grow year-round or at least the entirety of the growing season in the understory (Kawarasaki and Hori 2001). Due to the small size of plants and the short period of time they are available, spring ephemerals are usually not an important forage consideration, but are consumed by deer when available (Augustine 1996, Knight et al. 2009).

### **2.5.2 Litter**

Litter accumulation can negatively affect understory productivity by inhibiting seed germination because it can form a physical barrier to plants sprouting and alters soil chemistry (Sydes and Grime 1981). Many trees, including aspen (*Populus spp.*), longleaf pine, and oaks, contain allelopathic compounds that can inhibit understory growth



(Younger et al. 1980, Hiers et al. 2007). Litter also forms a physical barrier to seeds that prevents them from reaching mineral soil and germinating. This has a greater effect on small seeded species including most herbaceous species and small seeded trees whereas trees with large seeds like oaks can tolerate deep litter layers better (Kostel-Hughes et al. 2005).

### **2.5.3 Fire**

Fire is a critical component in understory productivity in forested and savanna ecosystems as it can affect both light conditions (by reducing forest canopy cover) and litter (by combustion) which are the two most limiting factors in understory productivity. Fire consumes the litter layer and removes any physical barriers imposed by the litter layer on plant germination (Vander Yacht et al. 2019). Additionally, after fire there is often a significant nutrient release from burning forest floor litter which can further stimulate understory growth (Curtis et al. 1977). Fire can also interact with dense litter to reduce overstory density and improve light conditions. Low intensity fires, usually used for hazard reduction burning or to improve wildlife or livestock habitat, rarely kill large trees. However, leaf litter produced by trees often burns slower than herbaceous material and can kill large trees (Wade 1986).

Fire increases the amount of light that can reach the forest floor by removing understory and midstory woody species and increases herbaceous growth (Feltrin et al. 2016). This, combined with the potential for large overstory tree mortality from burning accumulated litter around the base of large trees, can overtime, shift the forest into a more open stand structure, and when combined with timber harvest, create savannas that are

dominated by herbaceous species (Masters et al. 1991 and 1993, Feltrin et al. 2016). How much fire impacts understory growth is largely dependent on the current stand characteristics and the frequency of fire (Masters et al. 1993). In forests with dense canopies and no history of fire, there is little fuel and trees are very large, so the impacts of fire are usually minor. If the time interval between fires is too long, tree saplings can grow to a point where they can no longer be top killed by fire and the effects of fire could be diminished over time (Masters et al. 1993).

## **CHAPTER III**

### **METHODOLOGY**

#### **3.1 Study area**

This study was conducted at the Pushmataha Forest Habitat Research Area (FHRA 34°31'40" N, 95°21'10" W), established in 1982 to study the effects of different treatments involving forest harvesting, thinning, and fire regimes (Masters 1991). The FHRA comprises 53 ha of the 7690 ha Pushmataha Wildlife Management Area (PWMA) established by the Oklahoma Department of Wildlife Conservation (ODWC). The FHRA is located in the Kiamichi mountains in southeastern Oklahoma. Soils in the area are an association of the Caransaw (fine, mixed, semiactive, thermic Typic Hapludults) and Stapp (Fine, mixed, active, thermic Aquic Hapludults) soil series, and are shallow and rocky with slopes ranging from 8-12% (Feltrin et al. 2016, Masters et al. 1993).

The climate is semi-humid to humid with hot summers and mild winters. The mean annual precipitation and temperature in the area from 1986 to 2016 were 1212 mm and 17.5 °C (Oklahoma Climatological Survey). Within this period there was large variation in annual precipitation, ranging from between 742 mm in 2005 to 1994 mm in 2015. The growing season averages around 210 days for the last 30 years with average first freeze coming near the end of October.

## 3.2 Treatments

In 1983, 28 (0.8 to 1.6 ha) experimental units were established in a randomized experimental design to create the FHRA (Masters 1991). Treatments were applied in 1984. The FHRA site has eight treatments with three replications of each treatment (except for HT3 which has two replicates). Six of the eight treatments were named according to the following protocol. The treatments consist of different combinations of harvesting shortleaf pine sawtimber greater than 11.4 cm at diameter at breast height (H), thinning of hardwoods to a density of approximately 9 m<sup>2</sup>/ha of basal area (BA) using single stem injection herbicide (T), and fire return interval (1–4 years as well as no fire). The other two treatments are RRB (rough reduction burn) with fire every four-years but no harvesting or thinning of trees, and CONT (Control with no thinning, harvesting, or burning). Fire return intervals (dormant-season burns) have been maintained from 1985 through the present.

The current condition of the eight treatments varies greatly as a result of the different thinning and fire regimes applied. In 1985, all the treatments receiving the H and T treatment were similar, averaging 3.9 m<sup>2</sup> ha<sup>-1</sup> basal area (BA) and 8.5% canopy cover and the non-thinned CONT and RRB averaged 26 m<sup>2</sup> ha<sup>-1</sup> BA and 77.1 % canopy cover (Adhikari et al. 2021 and in press). When measured in 2018, the RRB, CONT, HT, and HT4 treatments were classified as forests based on high basal area (over 19 m<sup>2</sup> ha<sup>-1</sup>) (Dey et al. 2017) (**Table 1**). Among the forest treatments, the HT and CONT were not burned and had greater BA and canopy closure than the burned forests, e.g., HT4 and RRB. The remaining treatments were classified as savanna in 2018 because they had

lower BA and canopy cover. Among the savanna treatments, the HT1 had the lowest canopy closure and its structure was more similar to grassland than the other savanna treatments which had BA and canopy closure near the maximum limits of savanna, e.g., BA < 7 m<sup>2</sup> ha<sup>-1</sup> or <30% canopy closure (Dey et al. 2017).

### 3.3 Vegetation Community

The PWMA sits near the transition from Cross Timbers forest to southern oak-pine forest (Duck and Fletcher 1943). While near the transition zone, the PWMA is dominated by oak-pine forest characteristics. In areas that have not been thinned and burned, a closed-canopy forest dominates, approximately 100-years-old, composed mainly of shortleaf pine, post oak, and hickory (*Carya spp.*). In this condition, there is little understory vegetation however there are sparse areas of greenbriar (*Smilax spp.*), poison ivy (*Toxicodendron radicans*), grape (*Vitis spp.*), and sedges (*Carex spp.*). In burned areas, shortleaf pine and post oak dominate the overstory. Burned area understory is mainly composed of tallgrass prairie species, mostly warm season grasses like big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), and Indiangrass (*Sorghastrum nutans*), with some cool season *Panicum* and *Dicanthelium* spp. Common native forbs and legumes include slender lespedeza (*Lespedeza virginica*), *Desmodium spp.*, showy partridge pea (*Chamecrista fasciculata*), trailing wildbean (*Strophostyles helvula*), elm-leaf goldenrod (*Solidago ulmifolia*), button snake-root (*Eryngium yuccafolium*), and stiff sunflower (*Helianthus rigidus*). In annually burned areas, the invasive sericia lespedeza (*Lespedeza cuneata*) can be found in abundance. In areas with 2-4-year fire return intervals, there are a number of shrubby plants including

resprouting oaks and hickories, winged sumac (*Rhus glabra*), American beautyberry (*Callicarpa americana*), and winged elm (*Ulmus alata*).

### **3.4 Cover methods**

#### **3.4.1 Cover field methods**

During 2019 and 2020, the understory percent cover of plant functional groups for each experimental unit in the study area was visually estimated with a standard 20x50 cm Daubenmire frame (Daubenmire 1959). To prevent outside factors, e.g., shade from other treatments, dust from gravel road, etc., from influencing results in a treatment area, no samples were taken within 19.8 m from any unit edge (Oosting 1956, Mueller-Dombois and Ellenberg 1974). Daubenmire frame sampling was conducted along two previously established randomized 100 m long transects in each unit (Masters 1991). Ten samples were taken along each transect at random intervals for a total of 20 for each unit. Data were collected monthly during the growing season (March-October) to capture seasonal changes in plant communities that make up important components of deer forage, and sampled once each year during the dormant season (November-February). Cover percentage was assumed not to change during the dormant season. The same transects were used each sampling period, but the individual frame locations were placed at different random points each month.

When conducting the Daubenmire frame sampling, ground cover was separated into the following functional groups, warm season grass, cool season grass, forb, legume, woody, sedge, litter, bare ground, and rock. Only understory woody vegetation less than

1.4m in height was sampled (Feltrin et al. 2016). After determining the functional group coverage, plants were sampled that are considered important deer forage (Gee et al. 1994), defined as species or plant complexes making up 1% or more of diet. The percent cover for these important deer forage species, or plant complexes when identification to species was impossible or unnecessary, was recorded.

### **3.4.2 Cover statistical methods**

Data were analyzed with SAS 9.4 (SAS Institute Inc. 2013) using Proc Mixed (7 treatments with 3 replications and one treatment with 2 replications). The 20 frame samples collected each month were averaged to calculate the monthly unit means for each functional group. The unit means were then arcsine transformed prior to analysis. Data presented in figures and tables are shown as non-transformed data. Data from 2019 and 2020 were analyzed separately. To compare whether monthly trends in plant functional group coverage differed among treatments, a repeated measures analysis using an autoregressive covariance structure was conducted incorporating month of sampling. Each functional group was analyzed separately. For treatments where monthly trends differed among treatments, i.e., a significant season\*treatment interaction, an analysis was conducted using the pdiff function to determine which months the treatments significantly differed from one another ( $p < 0.05$ ).

### **3.5 ANPP methods**

#### **3.5.1 ANPP field methods**

Between 7-12 October 2019 and 16-20 October 2020, understory ANPP was measured using clip plots. Aboveground vegetation was clipped by hand from 0.25 m<sup>2</sup> plots located along the same transects used for Daubenmire sampling. Ten plots from each treatment unit were sampled in 2019, and six plots per unit in 2020. Understory vegetation was separated into the following functional groups - woody, warm season grass, cool season panicum grass, forb, sedge, and legume. Only woody vegetation below 1.4 m in height was clipped and current year growth was collected (leaves and current year shoots). In addition, litter including dead herbaceous material, leaves, and branches (<2 cm diameter) was collected from each plot. The samples for each plot and functional group were kept separate and dried at 60°C and weighed. All samples were collected before the first frost. October was chosen as the month to perform ANPP sampling as it represents the maximum standing forb and grass biomass in this region (Blair et al. 1977). While there was no livestock grazing in the FHRA, wildlife herbivory might have reduced understory biomass before sampling. However, herbivory exclusion studies at the site (Masters et al. 1993) previously found that herbivory had little effect on understory biomass estimates.

#### **3.5.2 ANPP statistical methods**

Data were analyzed with SAS 9.4 (SAS Institute Inc. 2013) using Proc Mixed (7 treatments with three replications and one treatment with two replications). Ten subsamples from each unit were averaged to give a unit mean for each of the six



functional groups. The unit means were then subjected to a Proc Mixed analysis and any significant ( $p < 0.05$ ) effects were noted. Total ANPP was analyzed as well as each functional group separately. For treatments with a significant effect, means separation was performed using the pdiff function to determine which treatments significantly differed from one another ( $p < 0.05$ ). Data from 2019 and 2020 were analyzed separately.

### **3.6 Foliar nutrient methods**

#### **3.6.1 Foliar nutrient field methods**

Foliar CP concentration (total nitrogen concentration\*6.25) of selected forage plants was measured three times throughout the 2020 growing season, 15-18 April, 6-10 July, and 19-23 October. The summer (July) sampling also included analyses of other key foliar nutrients including calcium, potassium and phosphorus. The following eleven species known to be good deer forages, or plants that were major contributors to total understory productivity were sampled: warm season grass (big bluestem), Scribner's panicum (*Panicum scribnerianum*), winged elm, post oak, winged sumac, greenbriar, American beautyberry, slender lespedeza, sericia lespedeza, showy partridge pea, and *Desmodium spp.* Samples were collected from HT1, HT2, HT3, HT4, RRB, and CONT treatments.

Only plants >19.8 m from an edge were sampled. Samples were collected in a manner that mimics herbivory by a concentrate selecting ruminant, like a deer, in that only fresh current-year growth was sampled (Lashley et al. 2014). For woody species the terminal 2cm of a twig and any leaves associated with that bud were collected. For

herbaceous plants, healthy looking leaves in the terminal 20% of the plant were collected. Samples were collected from 10+ individuals per unit when possible. While species were selected that occur across the spectrum of treatments, some of the legumes, showy partridge pea and both lespedeza species, along with winged sumac did not occur in all replications of the CONT treatment. The legumes were absent from most treatments for the early spring sampling so they were dropped from the analysis for that sampling period.

### **3.6.2 Foliar nutrient lab methods**

All plant material was refrigerated after collection until they could be processed and oven dried. All forage samples were analyzed at the Soil, Water, and Forage Analytical Laboratory (SWFAL) at Oklahoma State University. Samples were first dried for 12 hours at 85 °C then weighed and ground to pass through a 1.0 mm screen. For CP, total nitrogen (TN) and carbon were determined using a Leco (St. Joseph, Michigan) CN628 dry combustion Carbon/Nitrogen Analyzer, (NFTA, 1993). CP was calculated as  $TN \times 6.25$ . Mineral contents of the forage were analyzed by a Spectro (Kleve, Germany) Arcos II ICP following acid digestion (NFTA, 1993).

### **3.6.3 Foliar nutrient statistical methods**

Data were analyzed with SAS 9.4 (SAS Institute Inc. 2013) using Proc Mixed (five treatments with 3 replications and one treatment with 2 replications). To compare

whether seasonal trends in CP concentration differed among treatments, a repeated measures analysis was conducted using season of sampling as the repeated factor with an autoregressive covariance structure. Each species was analyzed separately. For species with a significant season\*treatment interaction, means separation was conducted using the pdiff function to determine which seasons the treatments significantly differed from one another ( $p < 0.05$ ). For potassium, calcium, and phosphorus, a Proc Mixed analysis similar to the protein analysis was performed without the repeated measures component.

## CHAPTER IV

### RESULTS

#### 4.1 Aboveground net primary productivity

In 2019, total ANPP was greater in the savanna treatments (HT1, HT2, HT3, HNT1) than in the forest treatments (HT4, RRB, CONT, CONT) (**Figure 1**). Among the savanna treatments, HT1 and HT2 in particular, had the greatest ANPP with over 450 g m<sup>-2</sup>. The other two savanna treatments HT3 and HNT1 had just over 300 g m<sup>-2</sup> of ANPP and were statistically similar to both the other savanna treatments and the most productive forest treatment (HT4). There was considerable variation among the forest treatments ranging from 18.3 g m<sup>-2</sup> in the HT to 149.6 g m<sup>-2</sup> in the HT4 treatment. However, all were statistically similar given large within-treatment variation. Results were similar in 2020 with wide variation in the forest treatments and statistical similarity. Among the savanna treatments, HT1 was significantly greater than all treatments. The other savanna treatments were statistically similar to both the HT4 and RRB forest treatments but greater than the CONT and HT treatments (**Figure 2**).

Grasses and woody plants were the largest contributors to ANPP for most treatments (**Tables 2 and 3**). In 2019, grasses accounted for 73% of total ANPP in the HT1 and HNT1 treatments and ranged from 44% to 53% of total ANPP in the other

burned treatments. Legumes were a substantial component in savanna treatments especially in 2019 accounting for between 4.5% (HT3) to 12.5% (HNT1). Annual burning favored the production of herbaceous vegetation composing over 85% of ANPP in both years for the HT1 and HNT1 treatments. Longer fire intervals of 2-4 years resulted in roughly equal woody and herbaceous productivity with 35% to 47% of total ANPP being woody vegetation in 2019 and 32% to 45% in 2020 for those treatments (**Figures 1 and 2**). Non-burned treatment ANPP was primarily woody growth with 52% in the CONT treatment and 86% in the HT treatment in 2019. The only exception was the CONT treatment in 2020 which had only 12% woody ANPP while the HT treatment had 90% woody ANPP.

Grass ANPP was the largest contributor to ANPP for most treatments in both years. In 2019, grass ANPP ranged from 341.9 g m<sup>-2</sup> in the HT1 treatment to 1.5 g m<sup>-2</sup> in the HT treatment (**Table 2**). The grass ANPP for the HT1 treatment was significantly greater than the HT3 and forested treatments, the HNT1 and HT2 treatments were greater than the forested treatments, and the HT3 treatment was greater than the HT and CONT treatments. Grass ANPP was smaller for most treatments in 2020 ranging from 292.3 g m<sup>-2</sup> in the HT1 treatment to 0.1 g m<sup>-2</sup> in the HT treatment (**Table 3**). The HT1 treatment grass ANPP was significantly greater than all other treatments and the savanna treatments were greater than the RRB, HT, and CONT treatments.

Legume ANPP was generally greater in the savanna than forested treatments. In 2019, legume ANPP ranged from 54.7 g m<sup>-2</sup> in the HT1 treatment to 0.1 g m<sup>-2</sup> in the HT treatment (**Table 2**). The legume ANPP of the HT1 treatment was significantly greater than the forested treatments and the CONT and HT treatments were lower than the HT1,

HNT1, and HT2 treatments. In 2020, legume ANPP was a smaller component for all treatments except for the HT1 treatment which had 46.1 g m<sup>-2</sup>. ANPP for the HT1 treatments was significantly greater than for the other treatments (**Table 3**).

In 2019, woody ANPP ranged from 169.6 g m<sup>-2</sup> in the HT2 treatment to 10.3 g m<sup>-2</sup> in the HT treatment, and in 2020 ranged from 137.6 g m<sup>-2</sup> in the HT3 treatment to 0.7 g m<sup>-2</sup> in the HT treatment. Despite the wide range in woody ANPP, no significant differences were found due to very high within-treatment variation. In both years, forb ANPP was largest, significantly so, in the HNT1 (2019) or HT1 (2020) treatments, and was < 1.5 g m<sup>-2</sup> in all other treatments in 2019 or <4.5 g m<sup>-2</sup> in 2020. Panicum grasses were a small contributor to ANPP for both years and not significantly different among treatments. All treatments had less than 10 g m<sup>-2</sup> of panicum grass ANPP in all instances except HNT1 in 2020 (10.4 g m<sup>-2</sup>). Sedges were an extremely small component in both years. In 2019, they composed less than 5 g m<sup>-2</sup> with less than 1 g m<sup>-2</sup> in six of nine treatments (**Table 2**). Sedges in 2020 were a slightly larger ANPP contributor, up to 8.9 g m<sup>-2</sup> in the HT3 treatment, and only two treatments had less than 1 g m<sup>-2</sup>.

## **4.2 Percent cover**

### **4.2.1 Percent cover of functional groups**

The treatments created a wide range in percent cover of understory functional groups with treatment significantly affecting all functional groups in both years (**Table 4 and 5**). However, the treatment effects were not consistent for all sampling periods, i.e., a significant treatment\*month interaction, for grass and legumes in both 2019 and 2020,

panicum in 2019, and woody in 2020. These interactions occurred primarily because all treatments had almost no coverage in the dormant-season and differences among treatments were maximum during the middle of the growing-season (**Figure 3**). As treatments were largely consistent in rank during the growing season, main effects are discussed below. However, for grass, treatments burned that year (HNT1 and HT1 both years, and HT2 in 2019) maintained greater grass coverage into the fall when compared to non-burned treatments.

Average coverage of warm season grasses was greatest in the savanna treatments (HNT1, HT1, HT2, HT3) with 41.9% to 50% coverage in 2019 and 24.1% to 39.7% in 2020 (**Tables 6 and 7**). However, coverage in the HT3 treatment was lower than annual burn treatments in 2020. In 2019, warm season grass coverage in the HT4 treatment was greater than all other forest treatments, 21.5%, and the RRB treatment, 12.1% was greater than the non-burned CONT and HT treatments, 1.4% and 0.5% respectively. In 2020 grass coverage of the HT4 (13.3%) and RRB (10.7%) were similar, but greater than the HT and CONT treatments with less than 1% coverage.

Woody plant coverage had the second greatest percent coverage among functional group for most treatments ranging from 2.6% to 9.6% in 2019 (**Table 6**) and 1.5% to 13.6% in 2020 (**Table 7**). Woody plant coverage was highest in treatments with longer fire return intervals (HT3, HT4, and RRB), and declined with annual burning or in the absence of burning. The exception was that in 2020, the woody coverage for the HT2 treatment, which was in its second year since burning, was similar to the less frequently burned treatments. Woody coverage was greater for most treatments in 2020 than in 2019.

In 2019, forb coverage ranged from 3.8% in the HNT1 treatment and 0.3% in the HT treatment. Coverage was the greatest in treatments burned that year (HNT1, HT1, HT2) and RRB. Forb coverage of the HT4 treatment was lower than HNT1 treatment, but not significantly different than the other treatments in highest category. Forb coverage was the lowest in HT along with CONT and HT3 treatments (**Table 6**). In 2020, forb coverage ranged from 2.3% in the RRB treatment to 0.1% in the HT. The HT2 and HT4 treatments were statistically similar to RRB, and all other treatments were lower, with the HT and HT3 treatments significantly so, except when compared to the CONT treatment (**Table 7**).

In 2019 legumes ranged from 9.4% in the HNT1 treatment to 0.1% in the HT treatment. Coverage was greatest in the savanna treatments, while it was lower in the longer burn interval treatments (HT4, RRB, and HT3) and lowest in non-burned HT and CONT treatments (**Table 6**). The HNT1 treatment had legume coverage significantly greater than the forested treatments, the HNT1, HT1, and HT2 treatments were greater than the RRB, CONT and HT treatments, and the RRB treatment was greater than the HT and CONT treatments. This trend was similar in 2020 except coverage for the HNT1 treatment was significantly greater than the other savanna treatments (**Table 7**).

Sedge coverage was very low for all treatments, less than 1% coverage for all treatments in both years, with HT4 and RRB having small but significant increases from the other treatments in 2020 especially in the fall (**Table 7, Figure 3**). In both years, panicum grasses had the greatest coverage in the RRB treatment (6.0% in 2019 and 5.6% in 2020) and the lowest in the HT treatment (0.2% in 2019 and 0.1% in 2020) (**Tables 6 and 7**). The savanna treatments all were statistically similar in 2019 but panicum



coverage was greater in the HNT1 than the other savanna treatments in 2020. There were no consistent trends with fire interval or thinning history. Percent cover for litter decreased with fire interval, ranging from less 87.7% for the HT treatment in 2020 to 11.5% in 2019 for the HT1 treatment (**Tables 6 and 7**). Not surprisingly, trends for percent bare ground and rock were generally opposite those for litter coverage.

#### **4.2.2 Monthly trends**

For all functional groups, coverage varied by month, i.e., significant effect of month. In both years, most functional groups followed the same general trend with coverage low at the beginning of the growing season, increasing and peaking midsummer, and then declining in the fall (**Figure 3; Tables 8 and 9**). Warm season grasses, legumes, and woody plants reached maximum coverage in June or July in both years. Coverage of forbs peaked during April and May both years. Cool season panicum grasses peaked in April of 2019, but peaked in the summer and plateaued throughout the fall in 2020. In 2019, panicum grasses had high coverage values in the first sampling period for treatments burned that year, but a similar trend was not found in 2020. Sedges had little coverage in both years and peaked in May 2019 and October 2020.

#### **4.3 Crude protein**

As expected, CP concentration significantly decreased during the growing season (**Table 10, Figures 4-6**). The only exception was a legume, sericia lespedeza, which had only a summer and fall sampling. In all other species, CP concentration was highest in

the spring, and lower in summer and fall. Some species also declined between summer to fall while others remained fairly constant between the two sampling periods (**Figures 4-6**). If CP decreased from summer to fall the difference was small compared to the difference between spring and summer.

Three of the eleven species, i.e., Scribner's panicum, American beautyberry, and showy partridge pea, had significantly greater CP in forest treatments than in savanna treatments (**Table 11**). CP concentration of Scribner's panicum ranged from an average of 11.4% in the CONT treatment to 8.6% in HT1 treatment with the CONT treatment significantly greater than all savanna treatments. CP concentration of American beautyberry ranged from 15.3% in the CONT and 10.5% in the HT1 and HT2 treatments. The CONT treatment was significantly greater from all other treatments with RRB (12.7%) having the second highest value. CP concentration of showy partridge pea ranged from 13.7% in the RRB to 10.6% in the HT1 and HT4 treatments. CP concentration of the RRB treatment was significantly greater than all other treatments. (**Table 11**). In addition to these three species, winged elm, post oak, big bluestem, and *Desmodium* had marginally significant treatment effects ( $0.05 < p < 0.10$ ). With the exception of post oak, which had the highest CP in the HT3 treatment, the marginally significant species also showed greater concentrations in forest treatments than one or more savanna treatments.

Two species, winged elm and American beautyberry, exhibited a significant treatment\*season interaction in CP values (**Table 10, Figure 4**) because the decrease in CP between spring and summer was greater for the savanna treatments than for the forest treatments. For winged elm, spring CP was greatest in HT1 (17.4%) and lowest in HT2

(15.2%) with all other treatments intermediate and statistically similar. In the summer, HT1 had the lowest CP (6.3%), and all three forest treatments were greater (average 11%). The other two savanna treatments ranged from 7 to 8%. In the fall, all treatments were similar, (between 7 to 8% CP). American beautyberry had a similar trend. In the spring, CP values ranged from 22.5 % in the CONT treatment to 14% in the HT4 treatment. In the summer CP was greatest in the forest treatments ranging from 15.7% in the CONT to 12.3% in HT4. Savanna treatments were all very similar with CP approximately 9%. In the fall, CP ranged from 9.3% in the HT4 to 7% in the other treatments. Slender lespedeza had a near significant interaction  $p = 0.052$  with a similar trend as winged elm and American beautyberry (**Figure 4**). Likewise, Scribner's panicum and slender lespedeza exhibited a similar trend, however, the interaction was marginally significant ( $0.05 < p < 0.10$ ).

#### **4.4 Mineral nutrient results**

##### **4.4.1 Calcium**

Only American beautyberry demonstrated a significant treatment effect for foliar calcium concentration (**Tables 12 and 13**). Concentrations were greatest in the CONT (8.28 mg g<sup>-1</sup>) and RRB (8.85 mg g<sup>-1</sup>) treatments and lowest in the HT2 (5.94 mg g<sup>-1</sup>) and HT4 (6.35 mg g<sup>-1</sup>) treatments. While no other species exhibited a significant response to treatment with respect to calcium, grasses (big bluestem and scribner's panicum) had the lowest calcium concentrations ranging from 4.06 to 6.23 and 4.35 to 7.46 mg g<sup>-1</sup>, respectively. Sumac also had low foliar calcium concentrations with a maximum of 6.79

mg g<sup>-1</sup> in the HT4 treatment. Other woody species had greater foliar calcium concentrations, especially winged elm, which had 12.42 to 13.66 mg g<sup>-1</sup> calcium for all but one treatment, HT1, which was much lower at 6.65 mg g<sup>-1</sup>. While no significant relationships were found, all legume species had the highest calcium concentrations in the HT3 or HT4 treatments.

#### 4.4.2 Phosphorus

Winged elm, *Desmodium*, and showy partridge pea had a significant response to treatment for foliar phosphorus concentration with all three having the highest concentration in the RRB treatment (**Tables 12 and 14**). Winged elm ranged from 1.27 mg g<sup>-1</sup> in the RRB treatment to 0.78 mg g<sup>-1</sup> in the HT2 treatment. Showy partridge pea had the greatest phosphorus concentration in the RRB treatment at 1.60 mg g<sup>-1</sup> and the lowest concentration in HT1 with a value of 0.77 mg g<sup>-1</sup>. *Desmodium* had the highest concentration in the RRB treatment at 1.11 and was lowest in the HT1 treatment at 0.89 mg g<sup>-1</sup>. While these were the only species with significant treatment effects, several other species including American beautyberry, winged sumac, post oak, winged elm and Scribner's panicum had the highest concentrations in the forest treatments (HT4, RRB, or CONT). There was little variation between grasses, legumes, and woody species.

#### 4.4.3 Potassium

Scribner's panicum and American beautyberry exhibited a significant response to treatment on foliar potassium concentration (**Tables 12 and 15**). Scribner's panicum concentration was greater in the Control treatment with a value of 16.82 mg g<sup>-1</sup> and lowest in the HT2 treatment at 9.03 mg g<sup>-1</sup>. For Scribner's panicum, both the RRB and Control treatments were greater than the savanna treatments. Potassium concentration for American beautyberry ranged from 17.69 mg g<sup>-1</sup> in the Control treatment to 11.48 mg g<sup>-1</sup> in the RRB treatment. Post oak and sericia lespedeza were nearly significant  $p = 0.11$  and  $0.12$ , respectively, with both having the greatest concentration in the RRB treatment. All other species except for greenbriar and slender lespedeza had the greatest concentration in the forest (HT4, RRB, or CONT treatments).

## CHAPTER V

### DISCUSSION

#### 5.1 Aboveground net primary productivity

The array of treatments can be summed into four groups, grassland/savanna (HT1), savanna (HNT1, HT2, HT3), burned forests (HT4, RRB), non-burned forests (HT, CONT). Frequent fire maintained more open canopy structure, which increased understory growth (e.g., Feltrin et al. 2016) of the herbaceous-dominated grassland and savanna treatments. In addition, fire appeared to have a direct positive effect on ANPP. In particular, ANPP was greatest in the growing season following fire, i.e., greatest in annually burned treatments and in first year after fire for the HT2 treatment. At this same site, Adhikari et al. (In Press) found herbaceous ANPP decreased with year since fire in the HT2 and HT4 treatments.

The forest treatments, which had lower ANPP than the savanna treatments, fell into two categories, burned forests (HT4, RRB) and non-burned forests (CONT, HT). The non-burned forests were characterized by extremely low ANPP, less than  $20 \text{ g m}^{-2} \text{ y}^{-1}$  for both treatments in both years with most of the ANPP composed of shade-tolerant woody plants like greenbriar, poison ivy, *Vitis* etc. One of the reasons for the very low productivity in the non-burned forests was likely very low levels of light inhibiting the

growth of C4 and other shade-intolerant plants which were the primary components of the burned treatments. Plants with C4 photosynthesis are largely absent when understory available solar radiation is below 20% of total incident solar radiation (Pearcy 1990).

Feltrin et al. (2016) found light intensities well below this for the CONT treatment. While they did not measure the HT treatment, it was even lower given higher basal area and canopy closure (Adhikari et al. 2021, and in press). The ANPP of the burned forests were intermediate between the non-burned forests and the savannas, and was statistically similar to both with the exception of RRB in 2019. The burned forests had similar ratios of woody to herbaceous ANPP as the savanna treatments. Within the herbaceous ANPP, the non-burned forests were dominated by warm season grasses but also had the largest sedge and panicum components. There was considerable difference between the understory light conditions of the burned forest treatments with the RRB treatment more similar to non-burned forests and the HT4 more similar to the savanna treatments Feltrin et al. (2016). These rates of understory light availability indicate that the HT4 treatment should have sufficient light to support C4 plants and the RRB a marginal ability. Also, it indicates that fire in the RRB treatment had benefits to the understory beyond light availability.

The impact of time since fire influenced comparing ANPP in the HT2 treatment from 2019 to 2020. The HT2 treatment was burned in 2019 but not in 2020, and in 2019 it had the second greatest total ANPP, similar to HT1. In 2020, the ANPP of the HT1 treatment was significantly greater than all other treatments, and the HT2 treatment had the second lowest ANPP of all of the savanna or grassland treatments. This greater in ANPP of the HT2 treatment in 2019 could have resulted from fire removing the litter

layer during the burn year allowing for improved germination and sprouting, or changes in light availability at the soil surface (Sydes et al. 1981, Facelli et al. 1991). Previous research found that litter can be more important than shade cast by the overstory in controlling understory ANPP (Hiers et al. 2007). Feltrin et al. (2016) found a shift upward in productivity at a given light availability in the burned treatments and speculated that the additional benefit of fire beyond reducing tree canopy cover was related to litter reduction.

Burn year affected the area covered by litter in the HT2 treatment when measured at the end of the growing season, 7.3% during 2019 and 42.6% in 2020. Hulbert (1969) found that reducing litter increased big bluestem productivity, and big bluestem was the most common grass in the savanna and grassland treatments in my study. Likewise, Knapp et al. (1984) found that standing dead herbaceous material reduced light availability near the soil surface by 59% during the first 30 days after shoot emergence of C4 grasses in a tallgrass prairie which in turn reduced aboveground production by 55%. Burning also mineralizes nutrients from the litter layer and makes them plant available, serving as a fertilization effect that can increase growth shortly after fires (Curtis et al. 1977). Given the burn rotations at the study site, this effect could only be studied in the HT2 treatment in 2019 and 2020. When analyzed using ~30 years of data, Adhikari et al (In Press) found that herbaceous, but not woody understory ANPP was greatest the year after burning in the HT2 and HT4 treatments.

Treatment thinning history was also important in controlling ANPP. In both 2019 and 2020, the HNT1 treatment had over 100 g m<sup>-2</sup> less total ANPP than the HT1 treatment despite having the same fire regime. The presence of large post oak in the non-



thinned HNT1 treatment reduced herbaceous plant growth under and adjacent to the tree canopies. The ANPP in the HT1 grassland/savanna treatment was similar to annually burned, non-fertilized tallgrass prairie sites in eastern Kansas which ranged from 380 to 570 g m<sup>-2</sup> (Turner et al. 1997). Another example of the legacy of initial thinning is that the HT4 treatment had a higher (but non-significant) total ANPP than the RRB treatment despite having the same fire regime. This likely was a result of greater canopy closure in the non-harvested treatments reducing light availability (Harrington 2011, Feltrin et al. 2016).

Without continuing management, sites will eventually reach a closed-canopy state, reducing understory productivity (Harrington 2011). Tree harvest without regular prescribed fire or additional thinning may lead to greater canopy closure than non-thinned forest due to dense reproduction and lower ANPP as seen when comparing the HT and CONT treatments. Even with a 4-year fire return interval, the HT4 treatment increased in basal area from 3.6 to 19.7 m<sup>2</sup> ha<sup>-1</sup> and canopy closure from 7.4% to 53% from 1985 to 2017 (Adhikari et al. 2021).

## **5.2 Vegetation Percent Cover**

The percent vegetation cover at the end of growing season followed similar trends to that of the clip plot data used for ANPP sampling, and likewise was related to fire frequency, time since fire, and overstory characteristics. However, the Daubenmire cover sampling examined seasonal trends in the vegetation community that are missed by the end of growing season ANPP sampling. While the Daubenmire sampling provides insight

into how the vegetation community is changing over the growing season, ANPP is a better estimator of forage productivity as animals consume plants based on mass and nutrient demands not on the foliage area.

Forb coverage was greater in the early spring for both sampled years in most treatments. This was likely a result of spring ephemeral plants which were mostly forbs growing and completing their life cycle early in the growing season. The fact that this response was noted across most treatments, including the forested treatments, likely indicates that spring ephemeral trait is an adaptation for plants to grow under high tree cover (Sunmonu et al. 2013), i.e., complete life cycle before trees fully leaf-out. While representing a relatively small cover area of 2-6 %, spring ephemerals are some of the first plants to appear in the growing season when animals are often nutritionally stressed by low forage quantity (Augustine 1996, Knight et al. 2009). Notably, forb cover responded differently in the RRB treatment than all other treatments and was likely a result of a different species composition. Parlin's pussytoes (*Antennaria parlini*), a shade-tolerant, short-statured forb, was most abundant in the RRB treatment and does not have a spring ephemeral growth strategy.

Percent cover can be used to estimate changes in forage availability early in the growing season. Percent cover is not a perfect estimator of plant productivity as different growth forms can result in a small amount of biomass covering a large area, such as a species with large, thin compound leaves like a hickory sapling. Alternatively, a tall species with many small leaves and few branches, like slender lespedeza, may have a lot of biomass in a small cover area. Despite these challenges, percent cover can predict productivity of understory forest plants with reasonable accuracy (Röttgermann et al.

2000, Porté et al. 2009). Macdonald et al. (2012) found percent cover explained 61-93% of the variation in biomass depending on the growth form of the functional group. With these considerations it is reasonable to use percent cover as an alternative to productivity for estimation of forage productivity in the early growing season when combined with end of year productivity data.

### **5.3 Foliar crude protein and minerals**

Thinning and fire treatments influenced CP of the measured species. With the exception of post oak, all had the greatest CP in the forest treatments. The most likely explanation for this are changes in leaf structure as a result of reduced light availability in the forested treatments. Leaves of plants in low light environments are thinner with a higher specific leaf area ( $\text{cm}^2 \text{g}^{-1}$ ; SLA), and leaves with high SLA tend to have higher nitrogen concentration than low SLA leaves (Reich and Walters 1994, Garnier et al. 1997). The reasons for this are that leaves with low SLA accumulate more carbohydrates than high SLA leaves which ‘dilutes’ the nitrogen content and because leaves with high SLA have greater concentrations of photosynthetic proteins which are nitrogen rich (Reich et al. 1991, Reich and Walters 1998). Alternatively, the dense canopy and litter layers in the forest treatments restrict light availability, and may slow growth or delay germination. As a result, the plants sampled in the forest treatments may be comparatively “younger” than plants of the same species in the more open savanna treatments. Tree canopies can lower air and soil temperatures which can delay seed germination and growth (Breshears et al. 1998, Devkota et al. 2009). Finally, frequent

fire return intervals over multiple years cause loss of nitrogen from the ecosystem possibly restricting CP concentration of understory plants (Gillon and Rapp 1989, Caldwell et al. 2002). However, research in this site (Masters et al. 1993) and similar ecosystems did not find a decrease, and in some cases even a slight increase in soil nitrogen (Binkley et al. 1992, Liechty et al. 2005).

Four of the species exhibited a treatment\*season interaction for CP. In all of these cases, the interaction appeared to be a result of forest treatments, especially the RRB and CONT treatments, having greater CP concentrations in the summer than the savanna treatments while all treatments were similar in the fall. Since the species with significant interactions resulted from greater CP in forest treatments, this supports the idea that plant CP is influenced by forest conditions via changes in SLA or rate of plant maturity. In particular, the interaction provides support for the idea that maturity is the primary influencer of CP concentration. Therefore, effects from treatments are likely to be the most pronounced in the early or middle stages of plant maturity found in the spring or early summer (Kilcher 1981, George and Bell 2001, Mysterud et al. 2011). Further supporting this idea, the plants in the fall 2020 sampling, where were similar in CP among treatments, were collected at the very end of the expected growing season, approximately one week before the expected first freeze.

Crude protein concentrations followed expected seasonal trends for most species with the greatest concentrations early in the spring then declining greatly in the summer and slightly again in the fall. While all were significant except for *sericia lespedeza*, legume CP concentration did not decline from summer to fall to the same extent as woody plants and grasses. This may be a result of legume's ability to fix nitrogen

allowing the plants to maintain higher CP as the plants mature. However, in studies with agricultural legumes, CP does decline with foliage age (Balde et al. 1993, Karayilanli and Ayhan 2016). As there was no spring data for legume protein concentrations to compare early in the growing season, it is also possible that legume's CP concentration had already declined to a stable level before their first sampling in summer.

Foliar concentration of calcium, phosphorus, and potassium sampled in the summer were mostly not influenced by treatment. However, when significant treatment effects were found, nutrient concentrations were greater in the forest treatments. Similar to CP concentration, variation in light availability among treatments and its effects on SLA likely account for these effects. Hoffman et al. (2005) found that phosphorus and potassium concentrations increased with higher SLA. Volatilization after fire is less likely to be important as minerals like phosphorus and calcium have much greater volatilization temperatures than nitrogen (Gray and Dighton 2006). Since the calcium, phosphorus, and potassium followed the same trend as CP, this likely indicates that long-term loss of nitrogen from volatilization loss is not happening. Alternatively, soil nutrient availability may only have a minimal impact on forage quality (Lashley et al. 2015). This supports research that despite short-term loss of nutrients after fire (Gillon and Rapp 1989, Caldwell et al. 2002), long-term, low intensity fires may minimally effect or even increase nutrient availability (Scharenbroch et al. 2012).

## 5.4 Management implications

When managing forested ecosystems for livestock grazing or wildlife forage, increasing forage availability is usually the most important factor (Masters et al. 1993, Edwards et al. 2004). The ideal plant species composition varies among target species, but deer usually prefer forbs, legumes, and woody understory vegetation (Gee et al. 1994). When looking at the eight treatments evaluated in this study, it is apparent that the closed-canopy, non-burned forests (HT, CONT) had a much lower forage potential for deer with less than 200 kg ha<sup>-1</sup> of total ANPP. Even without tree harvest, regular prescribed burning resulted in a nearly 5 times more total ANPP (RRB treatment) and some savanna treatments had over 20 times more ANPP than the non-burned forests reaching 4660 kg ha<sup>-1</sup>.

Determining which of the six treatments that include prescribed fire provides the greatest potential for deer forage is difficult and depends on management goals. The savanna treatments had the highest total ANPP and therefore the most potential forage. However, a large percentage of that ANPP was warm season grasses that are rarely consumed by deer (Stransky and Harlow 1981). Savannas also had greater legume ANPP cover, and legumes are typically high in CP and an important summer food source for deer (Gee et al. 1994). The savanna treatments with longer fire return intervals (HT2 and HT3) also had sizeable woody browse components, but slightly less total ANPP compared to the HT1 treatment. If management goals are to combine improving deer habitat along with livestock production, particularly cattle grazing, savanna treatments are a good option as cattle and deer have little diet overlap (Thill and Martin 1986). The cattle can utilize the large quantity of warm season grasses and the deer can consume the

forbs and woody browse. While the burned forest treatments had lower total ANPP, a smaller percentage was warm season grass, and many plants had increased CP especially in the RRB treatment. Increasing the CP and in some cases P, K, and Ca concentrations can improve antler growth and support milk production for lactating females (Asleson 1996, Jones et al. 2009, Lashley et al. 2011). For these reasons, using prescribed fire in forests greatly improves deer habitat even when overstory trees are not killed.

It is likely that a management regime using two or more of these treatments would be more effective than a single treatment to improve deer forage. If both savanna ecosystems with high productivity rates and forests with lower productivity, but higher nutritive values occur in close enough proximity, deer could utilize both. Deer could consume the large amounts of available forage in the savannas even if it is slightly below the CP needed, and supplement it with the higher quality forage in the forested areas. This mixing concept is noted in both calculating carrying capacity for wildlife (Hobbs and Swift 1985) and observed in grazing systems utilizing growing season fire (Allred et al. 2011). This combination of treatments could also provide different vegetation structure for bedding and fawning cover which could also improve utilization of an area.

The study site at the FHRA didn't include any growing season fire treatments, but growing season fire can increase forage quality in the summer when deer are often limited by CP concentration (Lewis et al. 1982, Wood 1998). Patch burn heterogeneity grazing involves burning small patches of a larger pasture at different times throughout the year to maintain areas of different vegetation structure and quality to improve wildlife habitat and rangeland utilization by livestock (Hovick et al. 2015). The mosaic pattern maintains patches of young, high-quality understory growth along with patches that are

not as recently burned with greater total biomass, but lower quality forage. This technique has shown great potential for livestock (Fuhlendorf and Engle 2001, Allred et al. 2011) and a similar benefit deer management.

Cherry et al. (2018) found that after a wildfire, deer increase their home range to include both burned and non-burned areas in their post-fire range if the pre-fire range overlapped or was near the fire boundary. However, other research found that deer increase home range size and avoid freshly burned areas in the summer, and it was speculated that deer, especially females with young, were responding to reduced cover in the burned areas (Lashley et al. 2015, Cherry et al. 2017). A patch burn experiment adapted for a southern pine forest using GPS collared deer similar to the one used by Fuhlendorf and Engle (2004) in Cross Timbers forest/tallgrass prairie for cattle could provide new insight into how deer respond to summer fire. Based on the current understanding, it appears that deer likely weigh the costs of increased predation risk from the loss of cover with increased forage quality and the results likely vary based on site specific characteristics.

Total ANPP is not the amount of forage available to livestock or wildlife as some of that productivity is not useable forage and not all is consumed. Having material left is a good thing for future understory growth. In rangeland sites used for cattle production, it is often recommended to leave at least 50% of available forage behind to prevent deterioration of the rangeland (Pratt 2001). This may not be as applicable to selective browsers like deer that typically leave behind large amounts of plant material, and are often limited by the amount of quality forage not by total forage as are grazing species such as cattle and elk (Lashley et al. 2014).



When estimating the amount of available forage for highly selective species like deer, a nutritional constraints model is often used (Hobbs and Swift 1985). Models like this consider both the amount of forage and the nutritional quality of that forage, often nitrogen content but also digestible energy in some cases (Mccall et al. 1997). Collecting biomass data for each of the plant species along with the nutrient data would allow for a true nutritional carrying capacity estimation to be conducted at the FHRA. The model orders forages by nitrogen concentration, and multiplies the biomass of the first ranked forage by its nitrogen concentration then divides by the forage biomass. Forages are then added together until the final product falls below a set value called the “nutritional constraint”. The nutritional constraint is typically a key biological threshold like a maintenance diet or minimum value needed to support lactation (McCall 1997, Lashley et al. 2011).

In conclusion, understory productivity increased with increased fire frequency and with tree harvest, likely a result of increased light availability and reduced litter. Monthly percent cover measurements also support this, and reveal that most functional groups peak midsummer and plateau or decline slightly into the fall. Forbs are an exception with peak coverage in April or March and very little cover in the fall indicating a possible food source early in the growing season when there is limited forage available. Forage quality, particularly CP concentration, was greater in the forest treatments especially in the summer when animal needs for protein and minerals are often the greatest. With these factors in mind it is difficult to pinpoint a best treatment for improving deer forage. Maintaining both forest and savanna conditions in close proximity should have greater potential to meet deer forage needs throughout the growing season than large continuous

areas of either forest or savanna. Future research examining how deer utilize areas that have multiple patches of forest and savanna ecosystems, similar to the ones at the FHRA, within the size of a deer normal home range could help answer this question.

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## APPENDICES

**Table 1.** Description of treatments, and current stand conditions (2018) at the Pushmataha Forest Habitat Research Area.

| Treatment | Harvest<br>Pine | Thin<br>Hardwoods | Fire return<br>interval<br>(years) | Current BA<br>(m <sup>2</sup> ha <sup>-1</sup> ) | Canopy<br>closure<br>(%) | Current condition |
|-----------|-----------------|-------------------|------------------------------------|--|--------------------------|-------------------|
| CONT      | No              | No                | No fire                            | 28.6±1.3   | 87.2                     | Forest            |
| HT        | Yes             | Yes               | No fire                            | 33.2±2.0   |                          | Forest            |
| RRB       | No              | No                | 4                                  | 25.6±1.0   |                          | Forest            |
| HT4       | Yes             | Yes               | 4                                  | 19.7±1.9   | 52.4                     | Forest            |
| HT3       | Yes             | Yes               | 3                                  | 5.9±1.0  | 25.6                     | Savanna           |
| HT2       | Yes             | Yes               | 2                                  | 7.2±0.9  | 28.7                     | Savanna           |
| HT1       | Yes             | Yes               | 1                                  |  | 19.5                     | Grassland/Savanna |
| HNT1      | Yes             | No                | 1                                  | 9.0±2.4  | 24.4                     | Savanna/Woodland  |



**Table 2.** Aboveground net primary production (ANPP) ( $\text{g m}^{-2}$ ) for the 2019 growing season for eight treatments at the FHRA. Within a functional group, the same letter indicates no significant difference at  $p > 0.05$ . Treatment designations are defined in (Table 1).

| Treatment | grass    | panicum | forb    | woody | sedge  | legume    |
|-----------|----------|---------|---------|-------|--------|-----------|
| HNT1      | 232.5 ab | 4.5     | 27.6 a  | 13.1  | 0.2 b  | 40.4 ab   |
| HT1       | 341.9 a  | 2.0     | 15.2 ab | 50.3  | 2.2 ab | 54.7 a    |
| HT2       | 238.1 ab | 3.9     | 1.5 b   | 169.6 | 0.0 b  | 33.3 abc  |
| HT3       | 168.3 bc | 4.5     | 0.1 b   | 150.9 | 0.1 b  | 14.7 abcd |
| HT4       | 66.1 cd  | 2.5     | 0.5 b   | 71.0  | 0.9 b  | 8.6 bcd   |
| RRB       | 44.2 cd  | 1.9     | 1.0 b   | 31.8  | 4.1 a  | 6.3 bcd   |
| CONT      | 6.7 d    | 1.3     | 0.8 b   | 10.3  | 0.1 b  | 0.7 cd    |
| HT        | 1.5 d    | 1.0     | 0.0 b   | 15.7  | 0.0 b  | 0.1 d     |

**Table 3.** Aboveground net primary production (ANPP) ( $\text{g m}^{-2}$ ) for the 2020 growing season for eight treatments at the FHRA. Within a functional group, the same letter indicates no significant difference at  $p > 0.05$ . Treatment designations are defined in (Table 1).

| Treatment | grass   | panicum | forb   | woody | sedge | legume |
|-----------|---------|---------|--------|-------|-------|--------|
| HNT1      | 159.2 b | 10.4    | 5.6 b  | 36.4  | 1.3   | 7.3 b  |
| HT1       | 292.3 a | 2.0     | 16.0 a | 62.6  | 1.5   | 46.1 a |
| HT2       | 166.2 b | 2.8     | 4.1 b  | 84.9  | 2.1   | 7.2 b  |
| HT3       | 184.8 b | 0.1     | 0.1 b  | 137.6 | 8.9   | 5.0 b  |
| HT4       | 76.4 bc | 6.3     | 1.0 b  | 75.7  | 8.8   | 0.4 b  |
| RRB       | 47.8 c  | 9.1     | 0.8 b  | 45.7  | 3.1   | 3.3 b  |
| CONT      | 8.1 c   | 0.2     | 0.4 b  | 1.0   | 0.6   | 0.6 b  |
| HT        | 0.1 c   | 0.0     | 1.0 b  | 0.7   | 0.5   | 0.6 b  |

**Table 4.** Results from mixed effects model testing the effects of treatment, month of sampling, and interaction between treatment and month for the percent cover of vegetation functional groups in 2019. Effects were considered significant at  $p < 0.05$ .

| Functional group | grass   | forb    | legume  | woody   | panicum | sedge | litter  | bare    | rock  |
|------------------|---------|---------|---------|---------|---------|-------|---------|---------|-------|
| Treatment        | <0.0001 | 0.002   | 0.001   | 0.0003  | <0.0001 | 0.428 | <0.0001 | <0.0001 | 0.001 |
| Month            | <0.0001 | <0.0001 | <0.0001 | <0.0001 | 0.001   | 0.002 | <0.0001 | <0.0001 | 0.226 |
| Treatment*Month  | <0.0001 | 0.313   | 0.001   | 0.132   | <0.0001 | 0.367 | <0.0001 | 0.004   | 0.687 |

**Table 5.** Results from mixed effects model testing the effects of treatment, month of sampling, and interaction between treatment and month for the percent cover vegetation functional groups in 2020. Effects were considered significant at  $p < 0.05$ .

| Functional group | grass   | forb  | legume  | woody   | panicum | sedge  | litter  | bare    | rock    |
|------------------|---------|-------|---------|---------|---------|--------|---------|---------|---------|
| Treatment        | <0.0001 | 0.001 | <0.0001 | <0.0001 | <0.0001 | 0.0001 | <0.0001 | <0.0001 | <0.0001 |
| Month            | <0.0001 | 0.001 | <0.0001 | <0.0001 | <0.0001 | 0.001  | <0.0001 | 0.044   | 0.036   |
| Treatment*Month  | <0.0001 | 0.937 | 0.001   | 0.023   | 0.557   | 0.312  | <0.0001 | 0.019   | 0.019   |

**Table 6.** Means for percent coverage of the nine functional groups for the eight treatments sampled in 2019. Means with the same letter are not significantly different ( $p > 0.05$ ). See (**Table 1**) for definition of treatments.

| Treatment | grass  | panicum | forb   | woody  | sedge  | legume  | litter | bare   | rock   |
|-----------|--------|---------|--------|--------|--------|---------|--------|--------|--------|
| HNT1      | 44.8 a | 2.8 b   | 3.8 a  | 2.6 d  | 0.2 ab | 9.4 a   | 12.3 e | 13.4 a | 6.2 ab |
| HT1       | 50.0 a | 3.0 b   | 2.0 ab | 3.8 c  | 0.1 b  | 8.7 ab  | 11.5 e | 9.2 b  | 7.1 ab |
| HT2       | 41.9 a | 3.4 b   | 2.0 ab | 6.8 ab | 0.2 ab | 9.1 ab  | 17.3 e | 12.6 a | 7.8 a  |
| HT3       | 45.6 a | 2.2 bc  | 0.8 cd | 9.6 a  | 0.3 ab | 7.5 abc | 43.6 d | 1.3 c  | 7.1 ab |
| HT4       | 21.5 b | 2.5 b   | 1.3 bc | 9.6 a  | 0.3 a  | 6.6 bc  | 62.8 c | 0.7 c  | 2.5 bc |
| RRB       | 12.1 c | 6.0 a   | 2.0 ab | 8.5 a  | 0.1 ab | 4.1 c   | 72.2 b | 1.8 c  | 1.0 c  |
| CONT      | 1.4 d  | 0.7 cd  | 0.8 cd | 5.5 bc | 0.2 ab | 0.3 d   | 88.0 a | 1.2 c  | 0.6 c  |
| HT        | 0.5 d  | 0.2 d   | 0.3 d  | 3.7 cd | 0.2 ab | 0.1 d   | 86.5 a | 0.8 c  | 1.0 c  |

**Table 7.** Means for percent coverage of the nine functional groups for the eight treatments sampled in 2020. Means with the same letter are not significantly different ( $p > 0.05$ ). See (**Table 1**) for definition of treatments.

| Treatment | grass   | panicum | forb   | woody  | sedge  | legume | litter | bare   | rock   |
|-----------|---------|---------|--------|--------|--------|--------|--------|--------|--------|
| HNT1      | 36.0 a  | 2.2 b   | 0.8 b  | 3.3 c  | 0.1 c  | 8.9 a  | 10.7 d | 18.7 a | 15.1 a |
| HT1       | 39.7 a  | 0.9 c   | 0.8 b  | 7.0 b  | 0.1 b  | 5.6 bc | 13.5 d | 16.2 a | 13.3 a |
| HT2       | 28.9 ab | 0.9 c   | 1.2 ab | 12.6 a | 0.1 bc | 5.6 b  | 42.6 c | 0.8 b  | 6.1 b  |
| HT3       | 24.1 b  | 1.5 bc  | 0.1 c  | 13.6 a | 0.1 b  | 4.4 cd | 51.5 c | 0.0 b  | 5.3 bc |
| HT4       | 13.3 c  | 2.5 b   | 1.1 ab | 12.8 a | 0.6 a  | 3.0 de | 62.9 b | 0.5 b  | 2.2 cd |
| RRB       | 10.7 c  | 5.6 a   | 2.3 a  | 10.4 a | 0.5 a  | 2.6 e  | 64.7 b | 0.2 b  | 1.7 de |
| CONT      | 1.0 d   | 1.8 bc  | 0.5 bc | 3.4 c  | 0.2 b  | 0.1 f  | 85.1 a | 0.5 b  | 0.6 e  |
| HT        | 0.2 d   | 0.1 d   | 0.1 c  | 1.5 c  | 0.1 b  | 0.1 f  | 87.7 a | 0.0 b  | 0.5 e  |

**Table 8.** Means of percent coverage for the nine functional groups across the six months sampled in 2019. Means with the same letter are not significantly different ( $p > 0.05$ ).

| Month   | grass   | panicum | forb   | woody  | sedge | legume | litter | bare   | rock   |
|---------|---------|---------|--------|--------|-------|--------|--------|--------|--------|
| April   | 12.3 d  | 4.4 a   | 2.4 ab | 2.2 c  | 0.1 b | 0.4 e  | 59.6 a | 10.8 a | 4.7 ab |
| May     | 20.3 c  | 2.2 bcd | 2.7 a  | 5.8 b  | 0.5 a | 5.9 bc | 46.3 b | 7.3 a  | 4.7 a  |
| June    | 30.8 ab | 2.6 abc | 1.7 b  | 6.8 ab | 0.1 b | 7.6 b  | 47.7 a | 4.6 bc | 3.7 b  |
| July    | 34.3 a  | 3.3 ab  | 1.9 ab | 8.6 a  | 0.2 b | 9.6 a  | 35.6 c | 4.8 b  | 2.7 b  |
| August  | 31.1 b  | 1.7 cd  | 1.1 c  | 7.0 ab | 0.2 b | 6.0 c  | 53.8 a | 1.5 d  | 3.8 ab |
| October | 29.9 b  | 1.5 d   | 0.2 d  | 6.3 b  | 0.1 b | 4.4 d  | 44.2 b | 2.6 cd | 4.5 ab |

**Table 9.** Means of percent coverage for the nine functional groups across the seven months sampled in 2020. Means with the same letter are not significantly different ( $p > 0.05$ ).

| Month     | grass  | panicum | forb   | woody   | sedge  | legume | litter  | bare     | rock   |
|-----------|--------|---------|--------|---------|--------|--------|---------|----------|--------|
| March     | 1.1 d  | 0.4 d   | 0.4 b  | 1.0 e   | 0.1 c  | 0.2 d  | 74.6 a  | 10.1 abc | 6.6 a  |
| April     | 8.5 c  | 0.7 cd  | 1.4 a  | 3.4 d   | 0.1 c  | 0.7 d  | 64.0 b  | 9.2 a    | 5.9 a  |
| June      | 27.7 a | 1.4 bc  | 1.5 a  | 10.9 ab | 0.1 c  | 5.8 ab | 41.6 cd | 3.6 bc   | 4.2 bc |
| July      | 25.4 a | 3.1 a   | 0.7 b  | 13.1 a  | 0.2 bc | 5.9 ab | 37.4 d  | 3.1 bc   | 7.4 a  |
| August    | 27.5 a | 2.4 ab  | 0.5 b  | 9.4 b   | 0.3 bc | 6.3 a  | 43.7 c  | 2.6 c    | 5.7 ab |
| September | 26.8 a | 2.9 a   | 0.8 ab | 9.8 b   | 0.4 ab | 4.8 bc | 43.5 c  | 2.7 c    | 5.6 a  |
| October   | 16.2 b | 2.9 a   | 1.0 ab | 7.1 c   | 0.5 a  | 3.3 c  | 61.9 b  | 2.5 c    | 3.6 c  |



**Table 10.** P values for treatment, season, and treatment x season interaction on crude protein concentration for a variety of forage species collected at the Pushmataha Forest Habitat Research Area in 2020. Abbreviations are as follows: ABB – American beautyberry, BBS – big bluestem, SUM – winged sumac, POA – post oak, SER – sericia lespedeza, SLZ – slender lespedeza, GRB – greenbriar, WGE – winged elm, SCP – Scribner’s panicum, DES – *Desmodium*, SPP – showy partridge pea.

| Treatment            | WGE     | POA     | SUM     | SEZ  | GRB     | BBS     | SCP     | ABB     | SPP   | SLZ    | DES   |
|----------------------|---------|---------|---------|------|---------|---------|---------|---------|-------|--------|-------|
| Treatment            | 0.09    | 0.08    | 0.19    | 0.40 | 0.19    | 0.06    | 0.047   | 0.009   | 0.007 | 0.65   | 0.051 |
| Season               | <0.0001 | <0.0001 | <0.0001 | 0.74 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | 0.02  | 0.0003 | 0.01  |
| Treatment*<br>season | 0.006   | 0.41    | 0.19    | 0.29 | 0.46    | 0.43    | 0.45    | 0.04    | 0.096 | 0.052  | 0.26  |

**Table 11.** Average crude protein values for eleven forage species collected across six different forest management regimes at the Pushmataha Forest Habitat Research Area in 2020. Letters denote significant differences at  $p < .05$ . Treatments are defined in (Table 1). Abbreviations are as follows: ABB – American beautyberry, BBS – big bluestem, SUM – winged sumac, POA – post oak, SER – sericia lespedeza, SLZ – slender lespedeza, GRB – greenbriar, WGE – winged elm, SCP – Scribner’s panicum, DES – *Desmodium*, SPP – showy partridge pea. An ‘X’ indicates the species was not sampled due to lack of occurrence.

| treatment | WGE*    | POA*    | SUM  | GRB  | BBS*   | SCP**   | ABB**  | SPP**  | SLZ  | SEZ  | DES*    |
|-----------|---------|---------|------|------|--------|---------|--------|--------|------|------|---------|
| HT1       | 10.5 ab | 11.0 b  | 9.9  | 13.3 | 9.3 ab | 8.6 b   | 10.5 b | 10.6 b | 9.7  | 9.5  | 13.8 b  |
| HT2       | 10.2 b  | 11.9 ab | 10.9 | 13.1 | 8.3 b  | 8.6 b   | 10.5 b | 11.3 b | 9.3  | 10.6 | 13.1 b  |
| HT3       | 10.9 ab | 12.7 a  | 11.2 | 12.3 | 9.7 ab | 9.0 b   | 11.6 b | 11.3 b | 9.8  | 11.1 | 14.7 ab |
| HT4       | 11.8 a  | 11.1 b  | 11.3 | 13.6 | 8.9 ab | 9.7 ab  | 11.8 b | 10.6 b | 10.3 | 11.4 | 13.0 b  |
| RRB       | 11.6 a  | 11.5 b  | 11.6 | 12.9 | 10.4 a | 10.1 ab | 12.7 b | 13.7 a | 10.7 | 11.9 | 15.2 ab |
| CONT      | 11.6 a  | 11.5 b  | X    | 14.5 | 10.3 a | 11.4 a  | 15.3 a | X      | X    | X    | 17.2 a  |

<sup>1</sup> Species marked with \* are significant at  $p < 0.1$

<sup>2</sup> Species marked with \*\* are significant at  $p < 0.05$

**Table 12.** P values for treatment effects on foliar calcium, phosphorus, and potassium concentration for a variety of forage species collected at the Pushmataha Forest Habitat Research Area in the summer of 2020. Abbreviations are as follows: ABB – American beautyberry, BBS – big bluestem, SUM – winged sumac, POA – post oak, SER – sericia lespedeza, SLZ – slender lespedeza, GRB – greenbriar, WGE – winged elm, SCP – Scribner’s panicum, DES – *Desmodium*, SPP – showy partridge pea.

| nutrient | WGE  | POA  | SUM  | GRB  | BBS  | SCP  | ABB   | SPP   | SLZ  | SEZ  | DEZ  |
|----------|------|------|------|------|------|------|-------|-------|------|------|------|
| Ca       | 0.44 | 0.86 | 0.23 | 0.72 | 0.65 | 0.52 | 0.03  | 0.84  | 0.69 | 0.87 | 0.26 |
| P        | 0.02 | 0.22 | 0.68 | 0.28 | 0.19 | 0.11 | 0.29  | 0.036 | 0.96 | 0.85 | 0.06 |
| K        | 0.27 | 0.11 | 0.63 | 0.96 | 0.30 | 0.02 | 0.054 | 0.67  | 0.61 | 0.12 | 0.43 |

**Table 13.** Calcium concentration (mg g<sup>-1</sup>) for eleven forage species collected in the summer of 2020 within six treatments at the Pushmataha Forest Habitat Research Area. Abbreviations are as follows: ABB – American beautyberry, BBS – big bluestem, SUM – winged sumac, POA – post oak, SER – sericia lespedeza, SLZ – slender lespedeza, GRB – greenbriar, WGE – winged elm, SCP – Scribner’s panicum, DES – *Desmodium*, SPP – showy partridge pea. An ‘X’ indicates the species was not sampled due to lack of occurrence.

| Treatment | ABB**    | BBS  | SUM  | POA  | SER  | SLZ  | GRB  | WGE   | SCP  | DES   | SPP   |
|-----------|----------|------|------|------|------|------|------|-------|------|-------|-------|
| HT1       | 7.43 abc | 4.94 | 4.81 | 6.67 | 8.04 | 7.74 | 7.30 | 6.65  | 5.47 | 4.73  | 6.84  |
| HT2       | 5.94 c   | 5.98 | 5.01 | 7.30 | 7.40 | 8.15 | 8.51 | 12.49 | 7.46 | 6.13  | 6.93  |
| HT3       | 6.28 bc  | 5.39 | 6.79 | 7.69 | 8.05 | 7.45 | 9.89 | 12.42 | 5.45 | 10.05 | 7.90  |
| HT4       | 6.35 c   | 6.23 | 6.08 | 8.50 | 6.75 | 9.20 | 8.92 | 13.66 | 5.27 | 7.39  | 10.04 |
| RRB       | 8.85 a   | 5.52 | 6.74 | 8.90 | 7.65 | 8.81 | 9.24 | 12.41 | 4.48 | 7.68  | 8.23  |
| CONT      | 8.28 ab  | 4.06 | 3.76 | 7.37 | X    | X    | 7.96 | 13.44 | 4.35 | 4.38  | X     |

<sup>1</sup> Species marked with \* are significant at p < 0.1

<sup>2</sup> Species marked with \*\* are significant at p < 0.05

**Table 14.** Phosphorus concentration ( $\text{mg g}^{-1}$ ) for eleven forage species collected in the summer of 2020 within treatments at the Pushmataha Forest Habitat Research Area. Abbreviations are as follows: ABB – American beautyberry, BBS – big bluestem, SUM – winged sumac, POA – post oak, SER – sericia lespedeza, SLZ – slender lespedeza, GRB – greenbriar, WGE – winged elm, SCP – Scribner’s panicum, DES – *Desmodium*, SPP – showy partridge pea. An ‘X’ indicates the species was not sampled due to lack of occurrence.

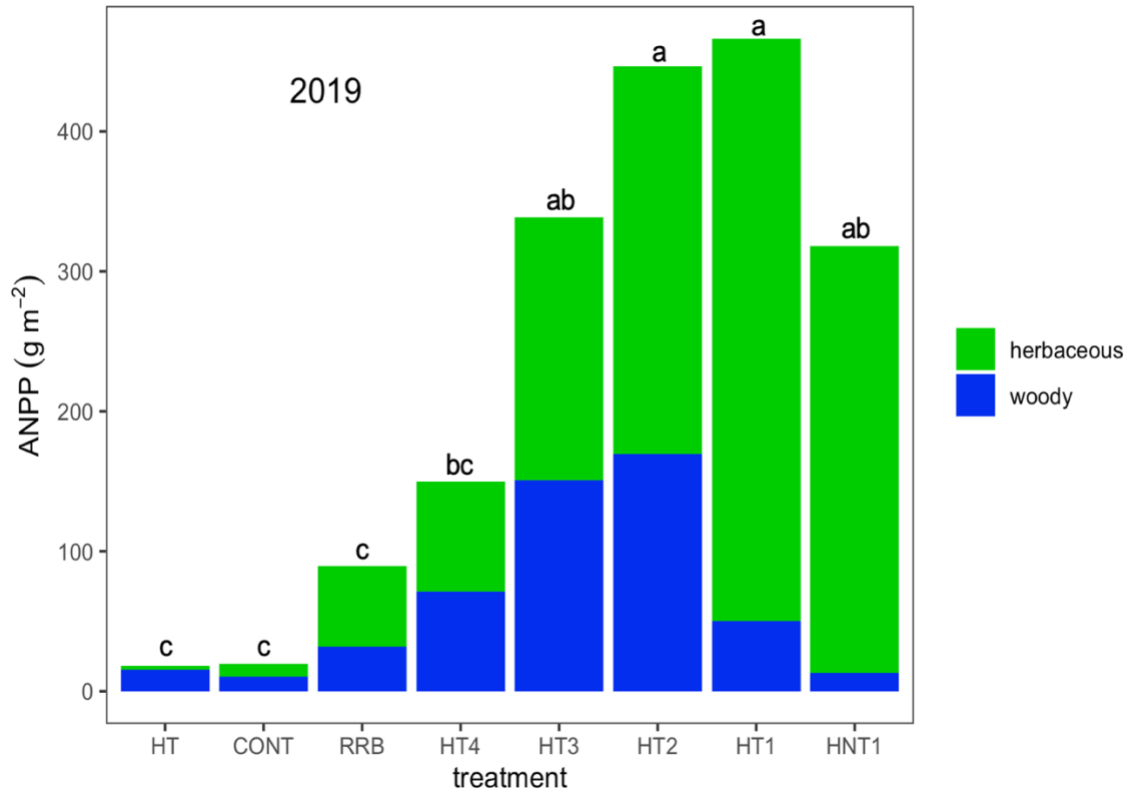
| Treatment | ABB  | BBS  | SUM  | POA  | SEZ  | SLZ  | GRB  | WGE**   | SCP  | DES*    | SPP**   |
|-----------|------|------|------|------|------|------|------|---------|------|---------|---------|
| HT1       | 1.37 | 0.69 | 0.76 | 0.82 | 0.96 | 0.95 | 1.06 | 0.79 bc | 0.68 | 0.89 b  | 0.77 c  |
| HT2       | 1.21 | 1.04 | 0.90 | 0.82 | 1.00 | 0.91 | 0.89 | 0.78 c  | 0.75 | 0.97 ab | 1.10 bc |
| HT3       | 1.11 | 1.07 | 0.97 | 0.86 | 1.11 | 1.04 | 1.29 | 1.12 ab | 0.95 | 1.05 ab | 1.38 ab |
| HT4       | 1.49 | 1.01 | 0.94 | 0.93 | 1.03 | 1.01 | 1.00 | 1.08 ab | 1.03 | 0.92 ab | 1.01 bc |
| RRB       | 1.22 | 0.89 | 1.14 | 1.23 | 1.10 | 1.03 | 0.90 | 1.27 a  | 0.83 | 1.11 a  | 1.60 a  |
| CONT      | 1.63 | 1.06 | 0.76 | 0.82 | X    | X    | 1.07 | 1.05 ab | 1.01 | 1.08 a  | X       |

<sup>1</sup> Species marked with \* are significant at  $p < 0.1$

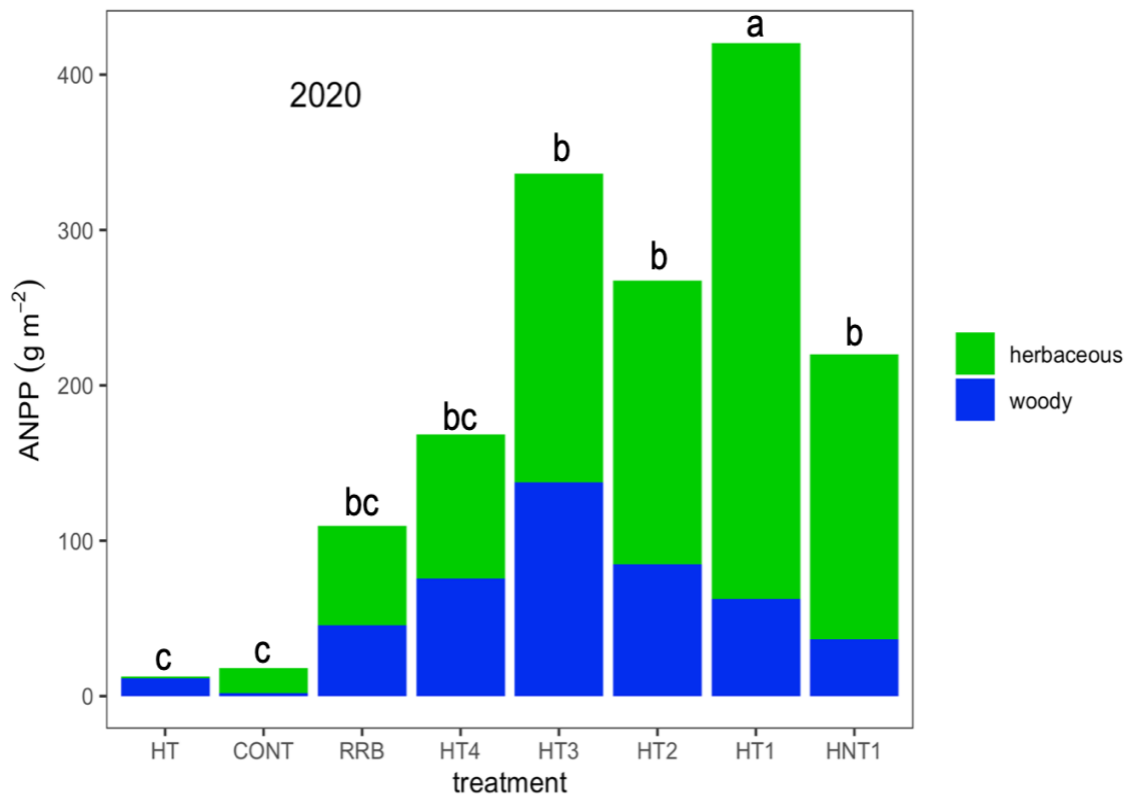
<sup>2</sup> Species marked with \*\* are significant at  $p < 0.05$

**Table 15.** Potassium concentration (mg g<sup>-1</sup>) for eleven forage species collected in the summer of 2020 within treatments at the Pushmataha Forest Habitat Research Area. Abbreviations are as follows: ABB – American beautyberry, BBS – big bluestem, SUM – winged sumac, POA – post oak, SER – sericia lespedeza, SLZ – slender lespedeza, GRB – greenbriar, WGE – winged elm, SCP – Scribner’s panicum, DES – *Desmodium*, SPP – showy partridge pea. An ‘X’ indicates the species was not sampled due to lack of occurrence.

| Treatment | ABB*     | BBS   | SUM   | POA   | SEZ   | SLZ   | GRB   | WGE   | SCP**    | DES   | SPP   |
|-----------|----------|-------|-------|-------|-------|-------|-------|-------|----------|-------|-------|
| HT1       | 15.94 ab | 8.17  | 7.85  | 7.52  | 9.39  | 8.15  | 13.57 | 10.64 | 10.86 b  | 9.18  | 11.33 |
| HT2       | 14.31 ab | 9.95  | 8.73  | 6.39  | 11.04 | 12.36 | 14.91 | 7.93  | 9.03 b   | 11.23 | 13.88 |
| HT3       | 12.39 b  | 11.73 | 8.24  | 5.77  | 10.66 | 12.71 | 15.21 | 8.71  | 11.10 b  | 9.93  | 13.14 |
| HT4       | 17.27 a  | 12.17 | 9.72  | 7.46  | 10.23 | 9.98  | 15.00 | 9.24  | 12.98 ab | 10.97 | 10.69 |
| RRB       | 11.48 b  | 11.14 | 13.13 | 10.42 | 14.25 | 9.80  | 13.48 | 10.66 | 15.72 a  | 12.55 | 15.33 |
| CONT      | 17.69 a  | 12.70 | 9.43  | 7.78  | X     | X     | 15.00 | 9.36  | 16.82 a  | 10.50 | X     |

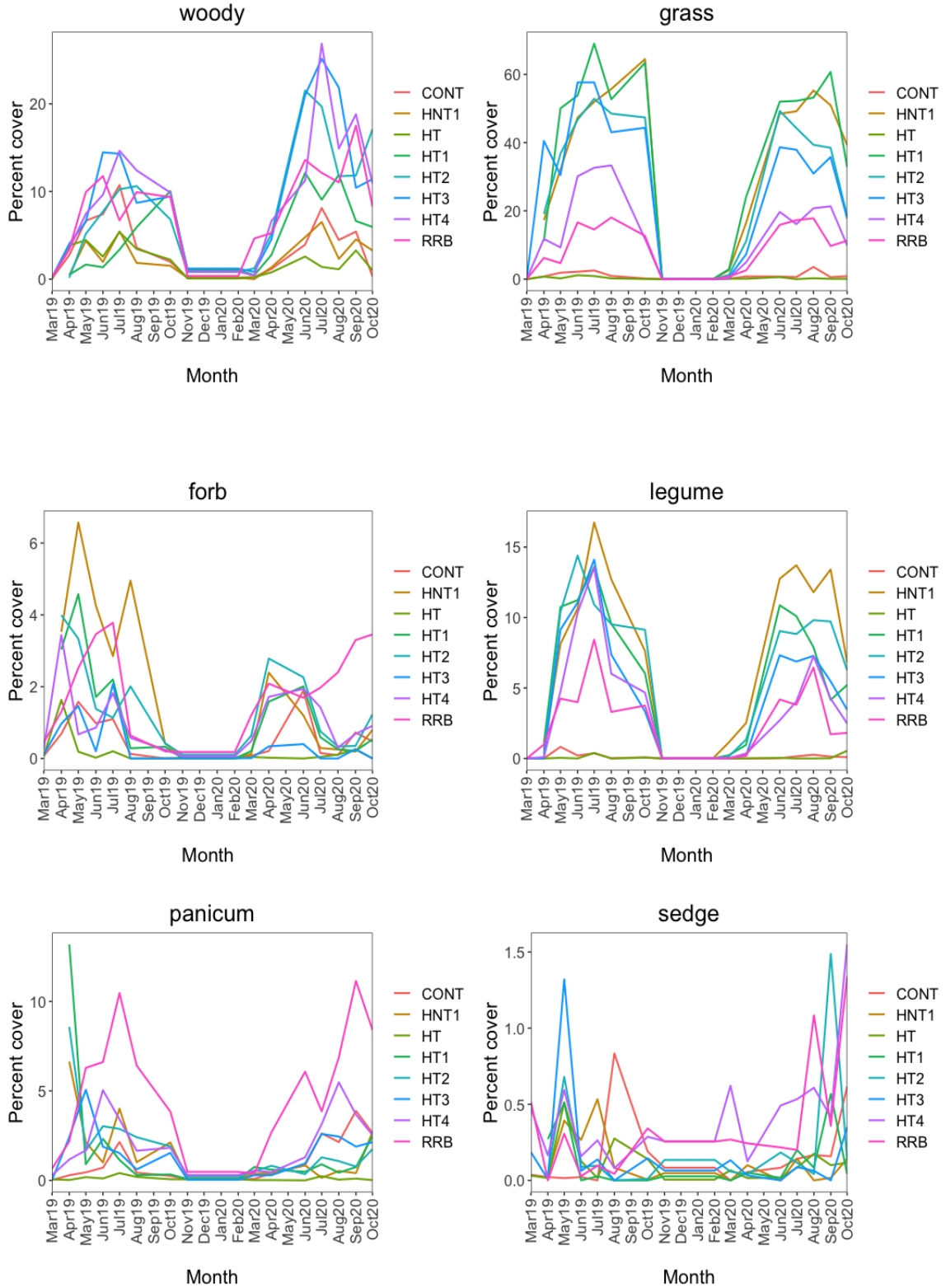


**Figure 1.** Total herbaceous and woody aboveground net primary production (ANPP) for eight treatments at the FHRA in 2019. Letters indicate significant differences based on total ANPP (woody + herbaceous) at  $p < 0.05$ . Treatment designations are defined in (Table 1).

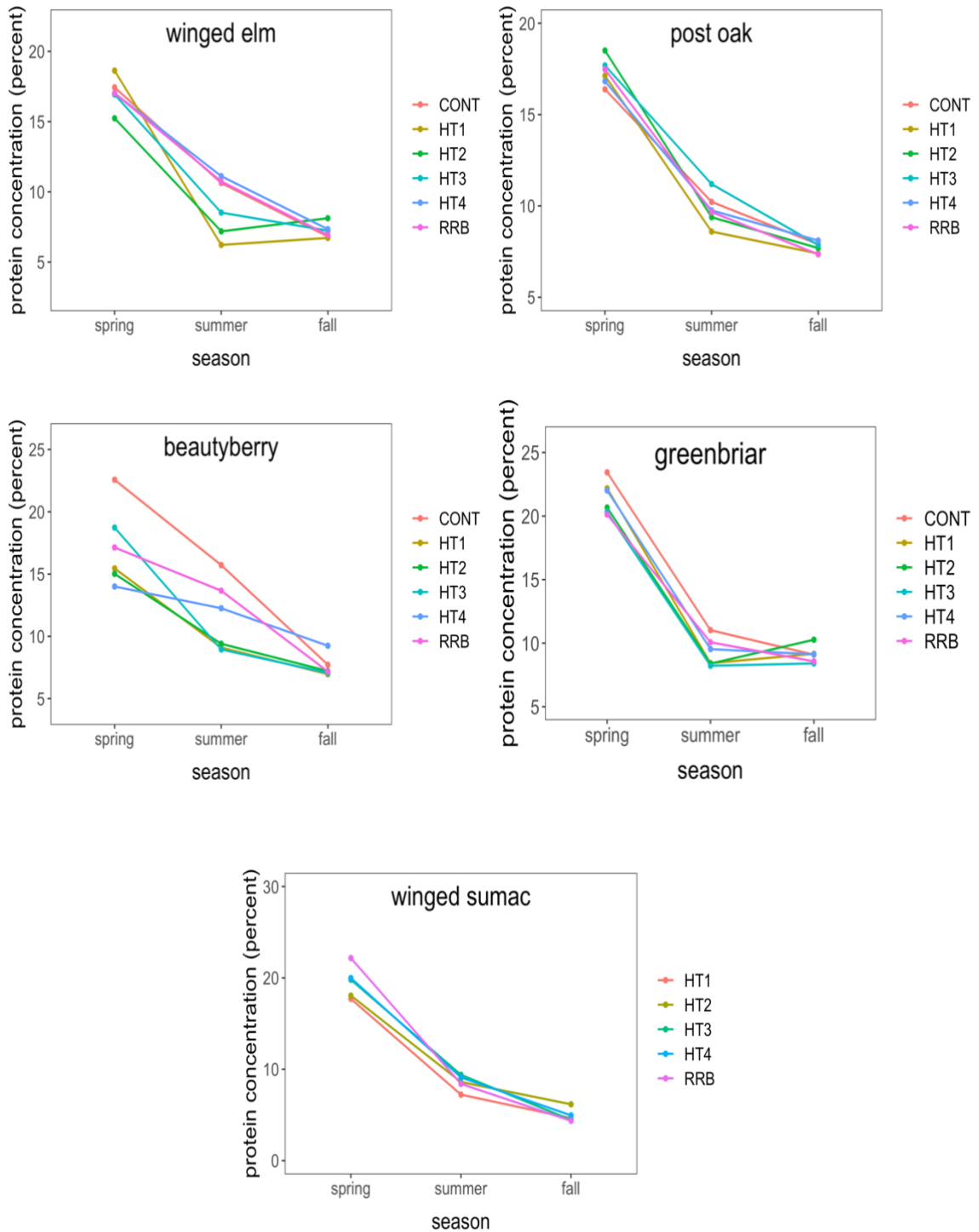


**Figure 2.** Total herbaceous and Woody aboveground net primary production (ANPP) for eight treatments at the FHRA in 2020. Letters indicate significant differences based on total ANPP (woody + herbaceous) at  $p < 0.05$ . Treatment designations are defined in **(Table 1)**.

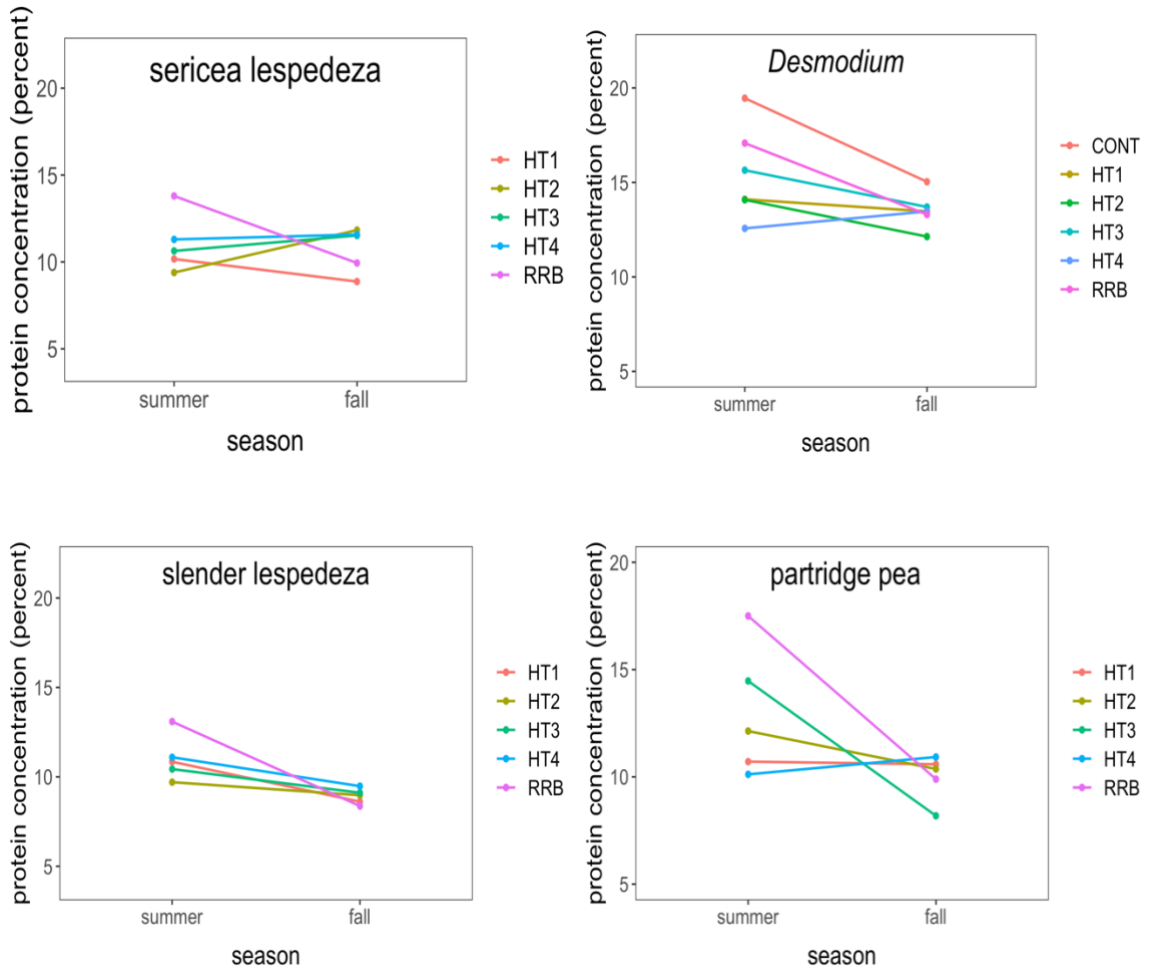




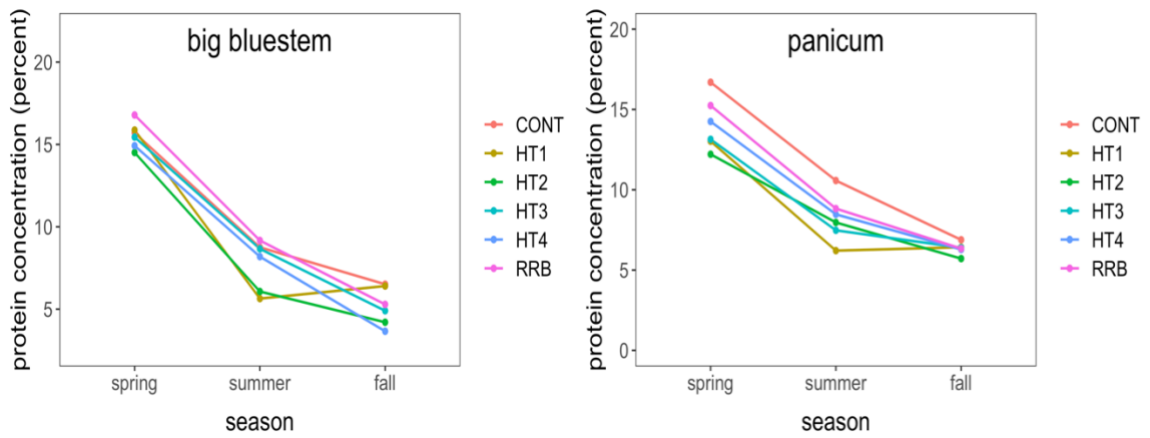
**Figure 3.** Changes in functional group coverage (%) during the 2019 and 2020 growing seasons for the eight sampled treatments. See (Table 1) for definitions of treatments.



**Figure 4.** Crude protein concentration for woody species throughout the 2020 growing season. For a description of treatment see (Table 1).



**Figure 5.** Crude protein concentration for legumes throughout the 2020 growing season. For a description of treatment see (**Table 1**).



**Figure 6.** Crude protein concentration for grass species throughout the 2020 growing season. For a description of treatment see (**Table 1**)

## VITA

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**Candidate for the Degree of**

**Master of Science**

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