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Forage quantity and protein concentration changes across a forest-savanna gradient with management implications for white-tailed deer

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ABSTRACT

White-tailed deer (*Odocoileus virginianus*) hunting is an important economic activity associated with the management of forests and rangelands in the USA, with over $12.9 billion dollars of related annual expenditures. Reducing tree cover through thinning and prescribed fire both have the potential to increase the quantity and quality of deer forage. We evaluated the long-term impacts of eight different combinations of fire return intervals and tree harvest on forage productivity and protein content of the forage. Based on management regime, study units ranged from savanna to closed-canopy forest. Aboveground net primary production (ANPP) of six functional groups (grass, panicum, forb, legume, woody, sedge) of understory vegetation was measured in October 2019 and 2020 using destructive sampling. Samples for foliar crude protein (CP) concentration were collected in spring, summer, and fall of 2020. Total understory ANPP ranged from 2.9 to 466.3 g m^{-2} and was up to 566% greater in savanna systems maintained by frequent fire (return interval of three years or less) than in non-burned forest treatments. Annual burning resulted in ANPP dominated by herbaceous plants composed mostly of fire- tolerant grasses (e.g., *Andropogon gerardii, Schizachyrium scoparium*). Longer fire return intervals or no fire resulted in roughly equal ANPP from understory woody and herbaceous species. Crude protein concentrations were up to 45.7% greater in the woodland and forest units than in the savanna units for seven of the eleven species sampled. The greater CP in the forests was most noticeable in the summer when deer needs for quality forage are substantial. Increased protein concentrations of understory species in the forests, but greater ANPP in the savannas indicate that managing for a mix of savanna and woodland could be ideal for balancing forage quantity with increased forage protein.

1. Introduction

Managing forests for multiple objectives, including wildlife habitat, has the potential to achieve the varied goals of landowners, and increase the economic viability of forested habitats (Grado et al., 2001), especially where productivity is lower or plantation forestry is not preferred. In addition, expected increases in temperature and variability of rainfall under a changing climate may decrease viability of traditional timber management, especially in areas where precipitation is marginal (Will et al., 2015, Reidmiller et al., 2018). In particular, management for wildlife is important to the family forest owners who control greater than 30% of forestland in the US (Butler et al., 2021). A recent nationwide survey found 73% of family forest owners list wildlife as a reason for owning forestland. For these forest owners the most frequent form of recreation was hunting (70%), and active management emphasized wildlife more than timber (Butler et al., 2021).

The understory, i.e., herbaceous vegetation and short-stature woody plants < 1.5 m, is often overlooked in forest management, but may support the majority of plant biodiversity (e.g., Gilliam, 2007) and provides habitat components for wildlife. Increased understory productivity has the potential to improve habitat for many wildlife species including economically important game species like white-tailed deer (*Odocoileus virginianus*), wild turkey (*Meleagris gallopavo*), and northern bobwhite (*Colinus virginianus*) (Wilson et al., 1995, Masters et al., 1998, Howze and Smith, 2021). Understory aboveground net primary production (ANPP) increases as overstory canopy cover decreases (e.g., Feltrin et al., 2016). In particular, fire serves an important role for the understory as it helps maintain open canopy structures, removes litter to provide a suitable substrate for seed germination and growth, and has direct positive impacts on plant diversity (Platt et al., 2006) and understory ANPP (Masters et al., 1993b, Reich et al., 2001, Feltrin et al., 2016, Adhikari and Masters, 2021a).

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White-tailed deer (hereafter deer) are the most sought-after game species in North America with nearly 11 million deer hunters (Fuller, 2016) spending $12.9 billion per year in the USA (DOI, 2017). Deer and deer hunting, therefore, are an important cultural and economic resource associated with the management of forests. Management of woodlands and forests in the southeastern US for deer often involves increasing the availability of forages by producing and maintaining early successional habitat through timber harvesting, prescribed fire, or a combination of these treatments (Masters et al., 1993b, Lashley et al., 2011, Glow et al., 2019). However, in forests managed for objectives other than deer, such as timber production, or in unmanaged areas, habitat is often marginal because of limited understory biomass production resulting from a dense, often multi-layered tree canopy (Masters et al., 1993b, Sparks et al., 1998).

Deer diet usually consists of woody browse, a variety of forbs, legumes, and hard and soft mast with significant seasonal variation (Jenks, 1991, Johnson et al., 1995, Gee et al., 1994). While grass is not preferred, deer will consume tender sprouts shortly after spring green-up especially at burned sites (Stransky and Harlow, 1981, Masters et al., 1993b). In contrast, woody browse is the largest component of deer forage and is consumed throughout the year (Short et al., 1969, Johnson et al., 1995, Jenks , 1991, Gee et al., 1994). Nutrient demands for deer vary greatly throughout the year and among different age and sex classes, and while deer require numerous nutrients to survive, one of the most critical is protein. A basic maintenance diet for an adult deer contains around 6–10% crude protein (CP) (French et al., 1956, Holter et al., 1979, Asleson et al., 1996, National Research Council, 2007). Protein demands are greater at several key life stages for deer including, 14–22% for fawns (Ullrey et al., 1967), 11% for yearling deer (Holter et al., 1979), 11–12% for antler growth (Asleson et al., 1996), and 14% for lactating females (Jones et al., 2009, Lashley et al., 2011, Hewitt 2011). While CP is only one measure of forage quality for deer, it is easily interpreted, well-studied, and correlates well with the key life history processes listed above. Deer must acquire protein directly from forage as needs cannot be met by body reserves (Sadlier, 1987). Additionally, CP requirements appear more limiting to nutritional carrying capacity than digestible energy requirements in the southeastern US (Jones et al., 2008 and 2009, Lashley et al., 2011).

The purpose of this study was to quantify deer forage quality and productivity across a wide range of plant communities and structures in an experimental setting. Experimental units, which ranged from forest to grassland, were created by various combinations of tree harvest, chemical thinning, and prescribed fire. The objectives were to 1) compare understory ANPP of eight treatments representing different management regimes that created conditions ranging from grassland to closed-canopy forest and 2) track changes in forage CP concentration during the growing season and among treatments. With these objectives in mind, we hypothesized that 1) understory ANPP for vegetation functional groups utilized by deer increase with more frequent fire return interval and greater thinning intensity and that 2) CP concentration declines later in the growing season as plants mature, but that treatments do not affect CP concentration. Our results further understanding of how forest structure and management affect the quality of deer habitat and help natural resource managers make informed decisions to meet landowner goals that include wildlife.

2. Materials and methods

2.1. Study area

This study was conducted at the Pushmataha Forest Habitat Research Area (FHRA; 34°31′40″ N, 95°21′10″ W), established in 1983 to study the effects of different treatments involving tree harvesting and chemical thinning combined with different prescribed fire return intervals to create and maintain early successional environments for white-tailed deer (Masters, 1991, Masters et al., 1993b). The FHRA comprises 53 ha of the 7690 ha Pushmataha Wildlife Management Area (PWMA), which is owned and managed by the Oklahoma Department of Wildlife Conservation. The FHRA is located in the Kiamichi Mountains in southeastern Oklahoma at an elevation of 320–340 m above sea level. 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 to 12% (Masters et al., 1993a, b). 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, respectively (Oklahoma Climatological Survey). The growing season averaged around 210 days for the last 30 years with the average first freeze occurring near the end of October.

The PWMA is located near the western edge of the southern oak-pine forest (Duck and Fletcher, 1943). In areas that have not been thinned and burned, a closed-canopy forest dominated, approximately 100- years-old (Adhikari et al., 2021b), composed primarily of shortleaf pine (*Pinus echinata*), post oak (*Quercus stellata*), and hickory *(Carya* spp.*)*. In this condition, there was little understory vegetation. However, there were areas of shade-tolerant plants such as greenbrier (*Smilax* spp.*),* poison ivy *(Toxicodendron radicans)*, grape (*Vitis* spp.*),* and sedges (*Carex* spp.). In burned areas, shortleaf pine and post oak also dominated the overstory, but hickory was less common. In more open areas, understory of burned units was mainly composed of tallgrass prairie species such as big bluestem (*Andropogon gerardii)*, little bluestem (*Schizachyrium scoparium)*, and Indiangrass (*Sorghastrum nutans*), with some mostly, cool-season *Panicum* and *Dichanthelium* spp. Common native forbs and legumes included slender lespedeza (*Lespedeza virginica*), *Desmodium* spp., showy partridge pea (*Chamaecrista fasciculata*), trailing wild bean (*Strophostyles helvola),* elm-leaf goldenrod (*Solidago ulmifolia*)*,* button snake-root (*Eryngium yuccifolium),* and hairy sunflower (*Helianthus hirsutus*). In annually burned areas, the invasive sericea lespedeza (*Lespedeza cuneata*) was common. In areas with 2 to 4-year fire return intervals, understory woody plants included resprouting oaks and hickories, winged sumac (*Rhus copallinum*), American beautyberry (*Callicarpa americana),* and winged elm (*Ulmus alata*).

2.2. Treatments

In 1983, 28 (0.8 to 1.6 ha) experimental units were established in a randomized design, 23 of which represent the 8 treatment types measured in this study (Masters, 1991). Treatments were applied in 1984 (Table 1). The eight treatments had three replications of each, except for HT3, which had two replicates. The treatments consisted of different combinations of harvesting (H) shortleaf pine trees greater than 11.4 cm diameter at breast height (DBH = 1.4 m), thinning (T) of hardwoods to a basal area of approximately 9 $m^2 ha^{-1}$ using single stem injection of herbicide, and fire return interval (1–4 years as well as no fire). Six of the eight treatments were named according to the application of H, T, and fire return interval. The treatment designated HNT1 had pine harvested, but did not have hardwoods thinned (no thin, NT). The other two treatments were 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. The array of treatments can broadly be classified into four structural types; grassland/ savanna (HT1), savanna (HNT1, HT2, HT3), burned forests (HT4, RRB), and non-burned forests (HT, CONT). Fires (dormant-season burns; January through April) were initiated on selected units in 1985 using strip head and flank fires. Fire treatments continued as scheduled through the duration of the study. However, in 1995 the 1- and 2-year burn interval treatments were not burned. Data for this study were collected in 2019 and 2020. In 2019 and 2020, the HT1 and HNT1

Table 1

Description of treatments, and stand structure in 2017 at the FHRA. Basal area and canopy closure are presented as means ± SE based on management unit averages. For comparative purposes post-treatment stand structure in 1985 is also presented. Treatment acronym letters are defined as follows: H = commercial harvest of pine trees, T = thinning via single stem injection of hardwoods, NT = no thinning, and 1–4 = prescribed fire intervals. RRB = rough reduction burn, as commonly practiced by federal land management agencies. Forest structure is defined after Dey et al. (2017).

Treatment	Harvest pine	Thin hardwoods	Fire return interval (years)	Basal Area $(m^2 ha^{-1})$	Canopy closure (%)	Post-treatment stand structure 1985	Structure 2017
CONT	No	No	No fire	28.5 ± 1.7	87.2 ± 2.4	Forest	Forest
RRB	No	No	4	25.6 ± 1.0	81.6 ± 5.5	Forest	Forest
HT	Yes	Yes	No fire	33.2 ± 4.4	89.0 ± 2.9	Savanna	Forest
HT4	Yes	Yes	4	19.1 ± 4.9	52.4 ± 13.8	Savanna	Woodland
HT3	Yes	Yes	3	5.9 ± 0.3	19.0 ± 6.6	Savanna	Savanna
HT2	Yes	Yes	2	7.2 ± 1.1	28.7 ± 5.0	Savanna	Savanna/ Woodland
HT1	Yes	Yes	1	3.4 ± 1.1	19.5 ± 6.3	Savanna	Grassland/Savanna
HNT1	Yes	No	1	6.5 ± 0.7	24.4 ± 8.9	Savanna	Savanna/ Woodland

(annual burn) treatments were burned. In 2019, the HT2 treatment units were burned. The HT3 units were burned in 2018 and the HT4 and RRB treatments were burned in 2017. Therefore 2020 data represent all burn treatments at their maximum extent for time since burned.

2.3. Aboveground net primary productivity methods

Understory ANPP was measured using clip plots between 7 and 12 October 2019 and 16–20 October 2020. Aboveground vegetation was clipped from 0.25 m^2 (0.5 × 0.5 m) quadrats along two randomly located transects per unit. Ten plots from each treatment unit were sampled in 2019 and, due to covid-19 related travel restrictions reducing available labor, six plots per unit in 2020. Only current-year leaves and shoots of woody vegetation below 1.4 m in height were clipped. In addition, litter that consisted of dead herbaceous material, leaves, and branches (<2 cm diameter) was collected from each plot. Understory vegetation was separated into the following functional groups: woody, panicum grasses, other grasses, non-legume forb, sedge, and legume. The samples for each plot and functional group were kept separate and dried at 60 °C to a constant mass. All samples were collected before first frost. October was chosen as the month to sample ANPP as it represents the maximum standing forb and grass biomass in the region (Blair et al., 1977). While there was no livestock grazing in the FHRA, wildlife herbivory might have reduced understory biomass before sampling. However, herbivore exclusion studies at the site (Masters et al., 1993a) found that herbivory had little effect on understory biomass estimates, and no signs of over-browsing were noted by observers. While the deer population on the PWMA increased since the early 90′s, this corresponded with significant landscape level-forest management at the PWMA to improve deer habitat (Masters and Waymire, 2012). While the deer population did increase it has been controlled below carrying capacity by significant hunting pressure and Epizootic Hemorrhagic Disease outbreaks (EHD). The EHD outbreaks were not a function of habitat quality or population density, but from biting midge flies that transmit the disease from domestic livestock to wild deer.

2.4. Crude protein methods

Foliar crude protein (CP) concentration (total nitrogen concentration × 6.25) of selected forage plants was measured three times during the 2020 growing season, 15–18 April, 6–10 July, and 19–23 October. The following eleven deer forage species were sampled: big bluestem, *Panicum* spp, winged elm, post oak, winged sumac, greenbriar (*Smilax bona-nox*), American beautyberry, slender lespedeza, serecia lespedeza, showy partridge pea, and *Desmodium spp*. Winged elm, greenbrier, showy partridge pea, *desmodium*, American beautyberry, and slender lespedeza are preferred deer forage plants. Serecia lespedeza, big bluestem, *Panicum* spp., winged sumac and post oak are consumed, but typically not preferred. These plants however, can form important emergency food sources or see increased seasonal use. To capture the full range of vegetation structures, samples were collected from HT1, HT2, HT3, HT4, RRB, and CONT treatments. Samples were not collected from the HT treatment due to the absence of many of the species of interest or from HNT1 due to the similarity to HT1.

Plants growing at least 19.8 m inside from the edge of a unit were sampled to reduce edge effects from adjacent units (Masters et al., 1993a). Fresh current-year growth was sampled mimicking herbivory by a concentrate selecting ruminant (Lashley et al., 2014). For woody species, the terminal 2 cm of a twig and any leaves associated with that bud were collected. For herbaceous plants, the terminal 20% of healthy- looking plants were collected. Samples were collected from 10 + individuals per unit when possible. While species were selected that occurred across the spectrum of treatments, the legumes (showy partridge pea and both lespedeza species), along with winged sumac, did not occur in all replications of the CONT treatment. Also, the legumes were absent from most treatments during the early spring, so they were dropped from the analysis for that sampling period.

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 h at 85 °C and then ground to pass through a 1.0 mm screen. For CP, total nitrogen (TN) was determined using a Leco (St. Joseph, Michigan) CN628 dry combustion Carbon/Nitrogen Analyzer .

2.5. Data analysis

All data were analyzed with SAS 9.4 (SAS Institute Inc. 2013) PROC MIXED procedure. For ANPP, all quadrats within each unit were averaged to calculate a unit mean for each of the six functional groups. The unit means were then log transformed prior to analysis to eliminate heteroskedasticity. Data presented in figures and tables are shown as non-transformed data. Total ANPP was analyzed as well as each functional group separately with treatment as a fixed effect and sampling unit as a random effect. When a significant difference occurred ($p < 0.05$), means separation was performed using the "pdiff function" to determine which treatments significantly differed from one another. Data from 2019 and 2020 were analyzed separately.

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 (AR1). Each species was analyzed separately with treatment and sampling period as fixed effects, and sampling unit as a random effect. 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. Results were considered significant at $P < 0.05$. In addition, results with $0.05 < P < 0.10$ were considered marginally significant given the consistent trend in CP response among species.

3. Results

3.1. Aboveground net primary productivity

Measured one year after establishment in 1985, all treatment units that received the H and T treatments were similar, averaging 4.0 ± 0.53 $m^2 ha^{-1}$ (mean ± SE) basal area (BA) and 9.7 ± 2.42% canopy cover while the non-thinned CONT and RRB averaged 26 ± 0.67 $m^2 ha^{-1}$ BA and 72 ± 2.3% canopy cover (Masters et al., 1993b). When measured in 2017, the HT and HT4 treatments as well as the CONT and RRB treatments were classified as forests (basal areas greater than 18.4 $m^2 ha^{-1}$; Dey et al., 2017). Among the forest treatments, the non-burned HT and CONT had greater BA and canopy closure than burned units, i.e., HT4 and RRB (Table 1). The remaining treatments were classified as savanna in 2017. Among the savanna treatments, the HT1 had the lowest canopy cover and its structure was more similar to grassland (Table 1) while the other savanna treatments had BA and canopy cover near the maximum limits for savanna, e.g., BA < 7 $m^2 ha^{-1}$ or < 30% canopy closure (Dey et al., 2017).

In 2019, total understory ANPP was up to 566% greater in the savanna treatments (HT1, HT2, HT3, HNT1) than in the forest treatments (HT4, HT, RRB, CONT) (Fig. 1). The savanna treatments, HT1 and HT2 in particular, had the greatest ANPP with over 450 g m^{-2}. The other two savanna treatments HT3 and HNT1 had just over 300 g m^{-2} of ANPP and were similar to other savanna treatments as well as the most

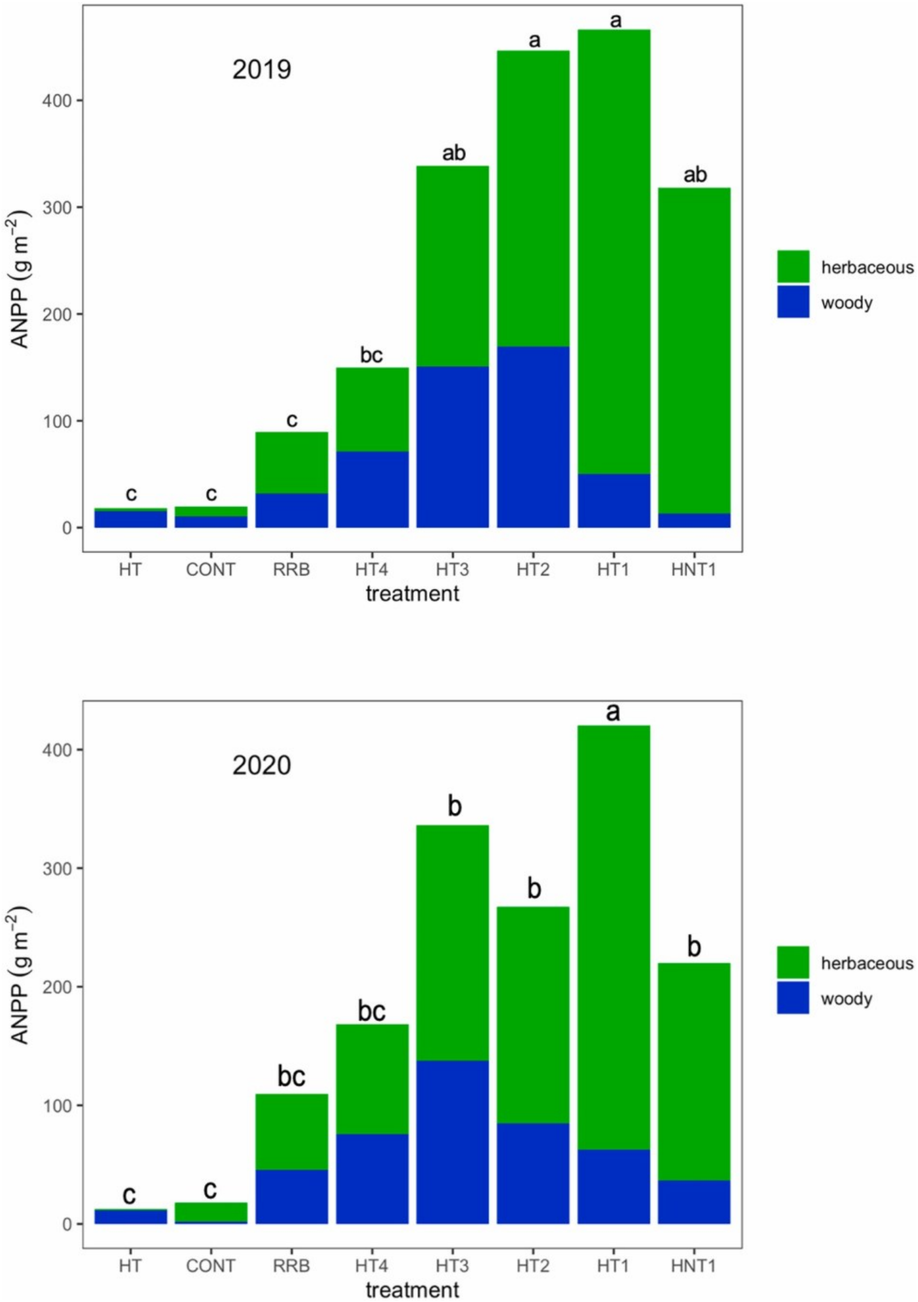

Fig. 1. Herbaceous and understory woody aboveground net primary production (ANPP) for eight treatments on the FHRA in 2019 and 2020. Within each year, letters indicate significant differences based on total ANPP (woody + herbaceous) at $p < 0.05$. See Table 1 for definition of treatments.

productive forest treatment (HT4). There was considerable variation (18.3 to 149.6 g m^{-2}) among the forest treatments with lower values for treatments that were not burned. However, the forested treatments were similar ($P \geq 0.05$) given large within-treatment variation. Results were similar in 2020, except the HT1 treatment had greater ANPP than all other treatments. Compared to 2019, ANPP of the HT2 treatment declined by 40% in 2020 (second year after burning), whereas the other treatments declined by an average of 15%. In general, treatments with annual or biannual burning were dominated by herbaceous vegetation, treatments with fire intervals of 3–4 years had more equal proportions of herbaceous and woody ANPP, and non-burned treatments were dominated by woody ANPP.

Among the herbaceous components, grass was the largest contributor to ANPP for most treatments in both years. In 2019, grass ANPP ranged from 1.5 g m^{-2} in the HT treatment to 341.9 g m^{-2} in the HT1 treatment (Table 2). ANPP of grass for the HT1 treatment was significantly greater than the HT3 and forested treatments (i.e., HT, CONT, RRB, and HT4), 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 for 2020 ranged from 292.3 g m^{-2} in the HT1 treatment to 0.1 g m^{-2} in the HT treatment (Table 2). Trends and significance among treatments were generally similar in 2020 with the exception that grass ANPP of HT1 treatment was greater than all other treatments. In 2019, legume ANPP ranged from 54.7 g m^{-2} in the HT1 treatment to 0.1 g m^{-2} in the HT treatment (Table 2). In 2019, legume ANPP of the savanna treatments were similar, but the HT1 treatment was greater than the forested treatments, the HNT1 was greater than the CONT and HT treatments, and the HT2 treatment was greater than the HT treatment. In 2020, legume ANPP was a smaller component for all treatments except for the HT1 treatment, which had 46.1 g m^{-2} and was significantly greater than the other treatments (Table 2).

In 2019, woody ANPP ranged from 169.6 g m^{-2} in the HT2 treatment to 10.3 g m^2 in the HT treatment, and in 2020 ranged from 137.6 g m^{-2} in the HT3 treatment to 0.7 g m^{-2} in the HT treatment. Despite the wide range in woody ANPP, no significant differences were found due to high within-treatment variation. In both years, forb ANPP was significantly greater in the annually burned HNT1 (2019) and HT1 (2020), than the other treatments, where it was<1.5 g m^{-2} in 2019 and 4.5 g m^{-2} in 2020 respectively. Panicum grasses and sedges were a small contributor to ANPP for both years and not significantly different among treatments, except for sedges in 2019 (Table 2).

Table 2
Understory aboveground net primary production (ANPP) (g m^{-2}) for the 2019 and 2020 growing seasons for eight treatments at the FHRA. Within a given year and functional group, means with the same letter were not significantly different ($p > 0.05$). See Table 1 for definition of treatments.

treatment	grass	panicum	forb	woody	sedge	legume
2019 HNT1	232.5 ab	4.5	27.6 a	13.1	0.2b	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	1.5b	169.6	0.0b	33.3 abc
HT3	168.3 bc	4.5	0.1b	150.9	0.1b	14.7 abcd
HT4	66.1 cd	2.5	0.5b	71.0	0.9b	8.6 bcd
RRB	44.2 cd	1.9	1.0b	31.8	4.1 a	6.3 bcd
CONT	6.7 d	1.3	0.8b	10.3	0.1b	0.7 cd
HT	1.5 d	1.0	0.0b	15.7	0.0b	0.1 d
2020 HNT1	159.2b	10.4	5.6b	36.4	1.3	7.3b
HT1	292.3 a	2.0	16.0 a	62.6	1.5	46.1 a
HT2	166.2b	2.8	4.1b	84.9	2.1	7.2b
HT3	184.8b	0.1	0.1b	137.6	8.9	5.0b
HT4	76.4 bc	6.3	1.0b	75.7	8.8	0.4b
RRB	47.8c	9.1	0.8b	45.7	3.1	3.3b
CONT	8.1c	0.2	0.4b	1.0	0.6	0.6b
HT	0.1c	0.0	1.0b	0.7	0.5	0.6b

3.2. Crude protein

Crude protein concentration significantly decreased throughout the growing season, and the magnitude of treatment effects was relatively small in comparison to seasonal differences (Table 3**,** Figs. 2 and 3). For all species measured in spring, summer, and fall, CP concentration was greatest 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 (Figs. 2 and 3). If CP decreased from summer to fall, the difference was smaller compared to the difference between spring and summer.

Three of the eleven species, i.e., panicum, American beautyberry, and showy partridge pea, had significantly greater CP in forest treatments than in savanna treatments (Table 3). Crude Protein concentration of 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 (Table 4). Crude Protein 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 than all other treatments with RRB (12.7%) having the second greatest value. Crude Protein concentration of showy partridge pea ranged from 13.7% in the RRB to 10.6% in the HT1 and HT4 treatments with the RRB treatment significantly greater than all other treatments (Table 4). In addition to these three species, winged elm, post oak, big bluestem, and *Desmodium* spp. had marginally significant treatment effects ($0.05 < P < 0.10$). With the exception of post oak, which had the greatest CP in the HT3 treatment, the marginally significant species also had greater concentrations in forest treatments than one or more savanna treatments (Table 4). Two species, winged elm and American beautyberry, exhibited a significant treatment*season interaction in CP concentration (Table 3, Fig. 3) because the decrease in CP between spring and summer was greater for the savanna treatments than for the forest treatments. Likewise, showy partridge pea and slender lespedeza exhibited a similar trend. However, the interaction was only marginally significant ($0.05 < p < 0.10$).

4. Discussion

The array of treatments resulted in four structural types; grassland/ savanna (HT1), savanna (HNT1, HT2, HT3), burned forests (HT4, RRB), and non-burned forests (HT, CONT). As expected, frequent fire maintained more open canopy structure, which increased understory growth of the herbaceous-dominated savanna treatments (Edwards et al., 2004, Lashley et al., 2011, Adhikari and Masters, 2021a). In addition, fire appeared to have a direct positive effect on understory ANPP which was greatest in the growing season following a fire, i.e (greatest in annually burned treatments and in the first year after fire for the HT2 treatment). Also, as expected, CP decreased during the growing season. However, CP concentration of some forage species were less in the savanna treatments when compared to the forested treatments. Combined, these effects represent a possible tradeoff when managing forests for deer in this region.

The non-burned forest treatments (CONT, HT) were characterized by extremely low understory ANPP, less than 20 g $m^{-2}y^{-1}$, with most of the ANPP composed of relatively shade-tolerant woody plants like greenbrier, poison ivy, and *Vitis* spp. Low productivity in the non-burned forests were likely due to low levels of light and the mulching effect of litter, which inhibited the growth of grasses and shade-intolerant plants (Facelli and Pickett, 1991, Hiers et al., 2007), which were the primary components of the understory for the burned treatments. Plants with C4 photosynthetic pathways are largely absent when solar radiation available to the understory is below 20% of total incident solar radiation (Pearcy, 1990). Feltrin et al. (2016) found that understory light intensities were approximately 30% of incoming solar radiation for the CONT, HT, and RBB treatments, but 60% for the HT4 treatment. Despite the different overstory and light conditions, both HT4 and RRB had

Table 3

P values for treatment, season, and treatment × season interaction on crude protein concentration for eleven forage species collected at the FHRA in 2020. Abbreviations are as follows: ABB – American beautyberry, BBS – big bluestem, DES – *Desmodium*, GRB – greenbriar, POK – post oak, PAN – panicum, SEZ – sericea lespedeza, SLZ – slender lespedeza, SHP – showy partridge pea, SUM – winged sumac, WGE – winged elm. See Table 1 for definition of treatments.

Treatment	ABB	BBS	DES	GRB	POK	PAN	SEZ	SLZ	SHP	SUM	WGE
Treatment	0.009	0.06	0.051	0.19	0.08	0.047	0.40	0.65	0.007	0.19	0.09
Season	<0.0001	<0.0001	0.01	<0.0001	<0.0001	<0.0001	0.74	0.0003	0.02	<0.0001	<0.0001
Treatment*season	0.04	0.43	0.26	0.46	0.41	0.45	0.29	0.052	0.096	0.19	0.006

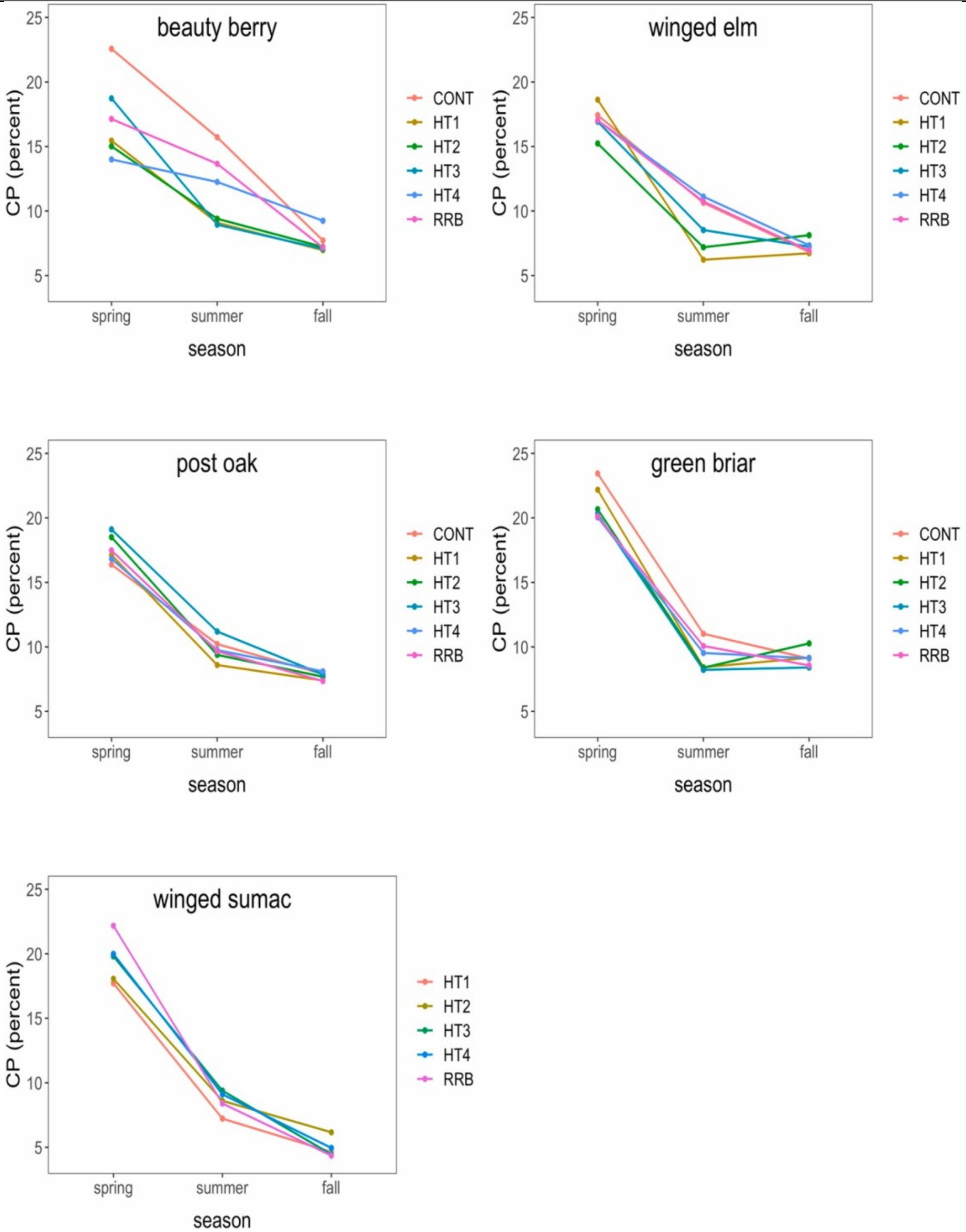

Fig. 2. Crude protein (CP) concentration for woody species throughout the 2020 growing season at the FHRA. See Table 1 for definition of treatments.

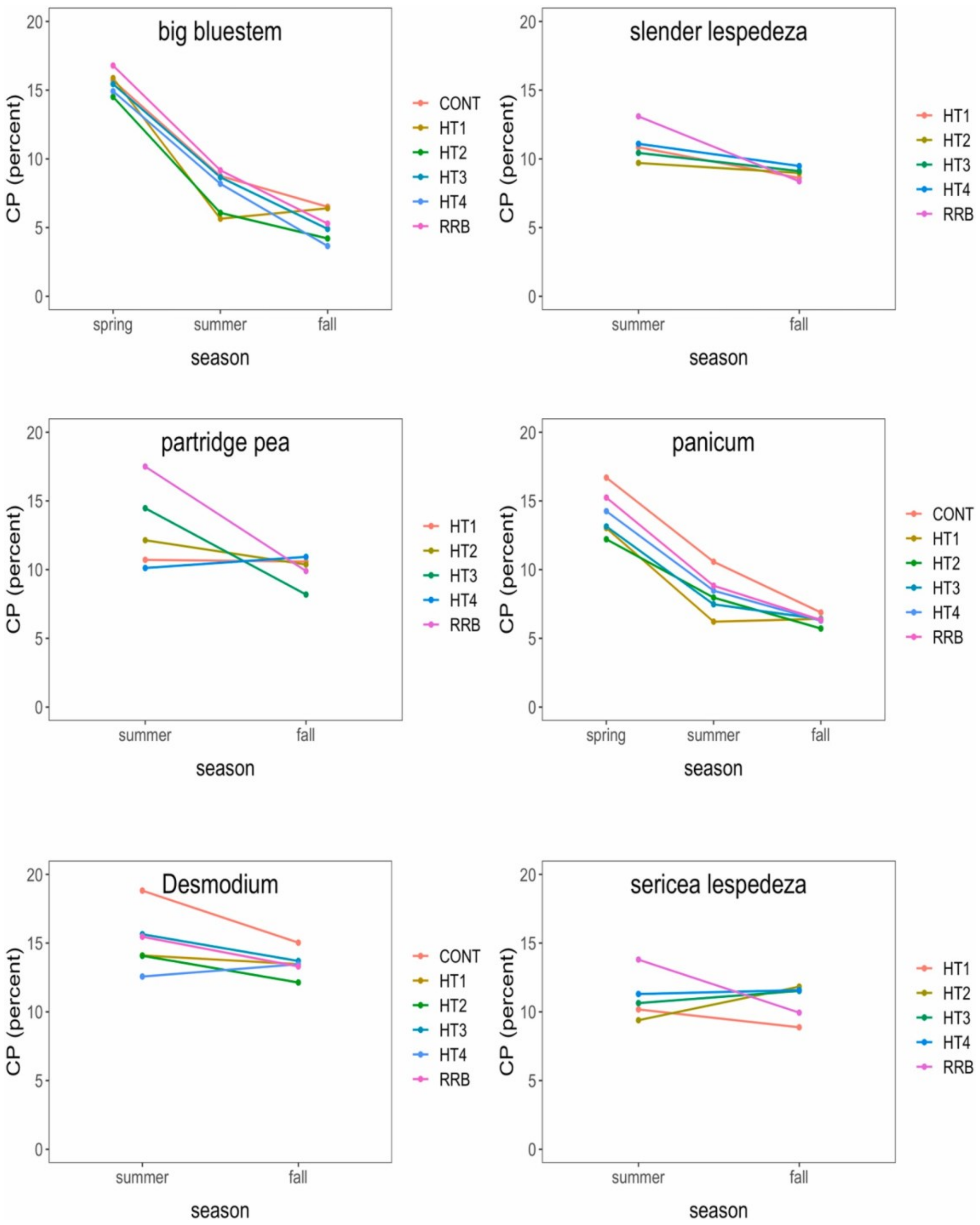

Fig. 3. Crude protein (CP) concentration for herbaceous plants throughout the 2020 growing season at the FHRA. Big bluestem and panicum are grasses and sericea lespedeza, *Desmodium* spp. slender lespedeza and partridge pea are legumes. See Table 1 for definition of treatments.

much greater ANPP and proportion of herbaceous than the non-burned forests indicating greater potential forage for deer or other wildlife species. While we only present biomass data from the end of the growing season, monthly measurements of percent cover found similar rankings among functional groups throughout the year with the exception of a small component of spring ephemeral forbs which represented 2–6% of cover during spring (Supplementary Fig. 1).

In addition to overstory cover, litter from leaves and dead herbaceous plants also reduce understory ANPP (Hiers et al., 2007). Fire removes the litter layer allowing for improved germination and sprouting of understory vegetation, and increases light availability at the soil surface (Sydes and Grime, 1981, Facelli and Pickett, 1991). Removal of the litter layer likely contributed to greater ANPP in the HT2 treatment in 2019 (first growing season after fire; 7% litter cover) compared to 2020 (second growing season after fire; 43% litter cover). Further supporting the effects of litter reducing herbaceous ANPP, Hulbert (1969) and Knapp (1984) found that reducing grass litter increased C4 grass productivity in tallgrass prairie. Other research indicates that moderate amounts of litter can increase herbaceous productivity, but declines as litter increases further (Hilger and Lamb, 2017). Another potential explanation for increased productivity after burning is that fire also mineralizes nutrients from the litter layer and makes them available for plant uptake (Curtis et al., 1977). However, on a longer timescale, removal of the litter layer through fire may reduce plant available C and N with frequent (annual or biannual) burn intervals (Carter and Foster, 2004, Wagle and Gowda, 2018). Given the burn intervals at the study site, the effect of time since burning could only be studied in the HT2 treatment in 2019 and 2020. However, when analyzed using ~ 30 years of data, Adhikari and Masters (2021a) found that herbaceous understory ANPP was generally greatest during the growing season after burning.

Table 4

Average crude protein values for eleven forage species collected across six different forest management regimes at the FHRA in 2020. Within a species, means with the same letter were not significantly different. Abbreviations are as follows: ABB – American beautyberry, BBS – big bluestem, DES – *Desmodium*, GRB – greenbriar, POK – post oak, PAN – Scribner's panicum, SEZ – sericea lespedeza, SLZ – slender lespedeza, SPP – showy partridge pea, SUM – winged sumac, WGE – winged elm. An 'N.A' indicates the species was not sampled due to lack of occurrence. See Table 1 for definition of treatments.

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

[a] Species marked with * are significant at $p < 0.1$ [b] Species marked with ** are significant at $p < 0.05$

Seven of the eleven species sampled had the greater CP in the forested than savanna treatments ($P < 0.10$) and several other species exhibited similar nonsignificant trends. Plants adapt to low light intensity in shaded conditions by changing leaf structure. Leaves in low light environments are thinner with a higher specific leaf area ($cm^2 g^{-1}$; SLA), and leaves with high SLA tend to have higher nitrogen concentration per biomass than leaves with low SLA (Reich and Walters, 1994, Garnier et al., 1997). Leaves with low SLA accumulate more carbohydrates which 'dilute' the nitrogen content while leaves with high SLA have greater concentrations of photosynthetic nitrogen rich proteins (Reich et al., 1991, Reich and Walters, 1994).

Our study only addressed CP concentration which is only one metric of nutritional quality, and in some cases can be offset by digestibility and tannin concentrations. For example, tannin concentrations reduced protein availability by an average of 38% for moose (*Alces alces*)forages in a boreal forest setting (Spalinger et al., 2010). However, in a setting more similar to our study, tannins reduced available crude protein by less than 1% for spring and summer for a diet consisting of eight preferred deer forage species (Jones et al., 2010). At this site, Masters (1991) found reduced digestibility of several forages in forested areas when sampled in the fall. However, earlier in the growing season, when treatment effects on CP concentration are greater, digestibility concerns are less likely as reduced digestibility is a function of plant maturity (Ball et al., 2002).

Denser overstory canopy and thicker litter layers in the forest treatments restricted light availability and likely reduced air and soil temperatures, which may have delayed understory germination and slowed growth (Breshears et al., 1998, Devkota et al., 2009). Thus, plants sampled in the forest treatments, despite sampling concurrently, may be comparatively "younger" than plants of the same species in the more open savanna treatments possibly contributing to the greater CP concentrations found in forested treatments. While, all plants appeared to be at similar phenological stages among treatments, small differences in plant maturity within a phenological stage may have been present. Another potential reason for lowered CP in savanna treatments is that shorter fire return intervals in the savanna treatments also may cause loss of nitrogen from the soil, possibly restricting the CP concentration of understory plants (Gillon and Rapp, 1989, Caldwell et al., 2002). However, research at this site (Masters et al., 1993a) and similar ecosystems did not find a decrease, and in some cases even a minor increase, in soil nitrogen after prescribed fire (Binkley et al., 1992, Liechty et al., 2005). Additionally, increased soil nutrient availability had no effect on forage quality but reduced the quantity of preferred deer forages in North Carolina, USA (Lashley et al.2015).

Four of the species exhibited a treatment × season interaction involving CP. In all cases, the interaction appeared to be a result of forest treatments, especially the RRB and CONT having greater CP concentrations in the summer than the savanna treatments while all treatments were similar in the fall. Therefore, effects from treatments are likely to be the most pronounced in the early or middle stages of plant maturity during the spring or early summer (Kilcher, 1981, George and Bell, 2001, Mysterud et al., 2011). This coincides with periods of increased protein demand for deer, such as antler growth or lactation. Unlike the other species, the CP concentration of sericia lespedeza did not decline from summer to fall. This may be a result of legume's ability to fix nitrogen allowing the plants to maintain higher CP as the plants mature. Previous research, however, suggest that legume CP declines with foliage age (Balde et al., 1993, Karayilanli and Ayhan, 2016), and the other three legumes in this study also declined. It is possible that sericia lespedeza's CP concentration had already declined to a stable level before the first sampling in summer, as our study lacked legume data from the spring which limited our ability to study CP change in legumes.

5. Conclusions

Prescribed fire was necessary to increase understory ANPP in forested treatments and to maintain savanna conditions. Without the continued application of prescribed fire, the overstory canopy increases and understory productivity will diminish to the point of near non- existence as seen in the HT treatment. The savanna treatments had more potential forage because of their greater total ANPP. However, a large percentage of that ANPP was fire-tolerant, warm-season grasses that are rarely consumed by deer. The savanna treatments also did have greater ANPP of forbs and legumes, which have greater CP and are an important summer forage for deer. The savanna treatments with relatively longer fire return intervals (HT2 and HT3) also had sizeable woody browse components. Forested treatments without prescribed fire had extremely low ANPP and would not provide suitable deer foraging habitat even with the increases in protein that we measured. From a forage perspective it appears treatments with intermediate levels of prescribed fire 2–4 years provide the most value to deer.

It is likely that a landscape-level management regime using two or more of these treatments to improve deer forage quality and quantity would be more effective than a single treatment. When savanna ecosystems and forests occur in close enough proximity, deer could utilize both. Savanna treatments with longer (2–3 year) fire interval have greater amounts of potential forage for periods when deer are limited by forage quantity such as winter and early spring. Forested areas have value for deer by providing forages with greater CP particularly in the summer when deer need high-quality forages for antler growth and lactation. This combination of savanna and burned forest treatments in a landscape mosaic could also provide different vegetation structures that benefit deer in other ways besides forage such as providing bedding and fawning cover and enhance the use of the entire area. As family forest owners, Non-GovernmentalOrganizations, and government agencies focus on multiple objectives that include improvement of wildlife habitat, the maintenance or periodic establishment of patches of early successional habitat is essential to increase forage quantity. This can be done through harvesting and prescribed fire which has the additional benefits related to reduction of the litter layer. Our results reinforce the idea that heterogeneity benefits wildlife objectives by providing a variety of different forage and browse species, qualities, and timing of availabilities.

CRediT authorship contribution statement

Caleb M. McKinney: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing. **Ronald E. Masters:** Conceptualization, Resources, Writing – review & editing, Supervision. **Arjun Adhikari:** Conceptualization, Investigation, Writing – review & editing. **Bijesh Mishra:** Conceptualization, Investigation, Writing – review & editing. **Omkar Joshi:** Conceptualization, Funding acquisition, Writing – review & editing. **Chris B. Zou:** Conceptualization, Funding acquisition, Writing – review & editing. **Rodney E. Will:** Conceptualization, Funding acquisition, Project administration, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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