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Forage Quantity and Protein Concentration Changes Across a Forest-Savanna Gradient with Management Implications for White-Tailed Deer

--Manuscript Draft--

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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 three major aspects of deer forage – forage productivity, timing of forage availability, 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. Percent cover of vegetation functional groups was measured monthly from March through October 2019 and 2020. 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. Coverage of most functional groups reached a maximum in mid-summer, then plateaued or declined slightly in the fall. The exception was forb coverage which peaked in April and had very little coverage in summer and fall, indicating a potentially important source of forage early in the growing season. 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.
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Caleb McKinney
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16 January 2023

Dear Editor-in-Chief,

We wish to submit an original research article entitled “Forage Quantity and Protein Concentration Changes Across a Forest-Savanna Gradient with Management Implications for White-Tailed Deer” for consideration to be published in the journal, Forest Ecology and Management. We confirm that this work is original and has not been published elsewhere, nor is it currently under consideration for publication elsewhere.

In this paper, we show that forest management to reduce canopy cover, i.e., thinning and burning, increase forage quantity for white-tailed deer, but often reduce crude protein concentration. This is significant because white-tailed deer are the charismatic game species in the eastern USA with a significant amount of management effort devoted to maximizing hunting opportunities accounting for billions of dollars in economic impact. We believe that this manuscript is appropriate for publication in Forest Ecology and Management because it demonstrates results that are directly applicable to informing management decisions regarding forests for a culturally and economically important wildlife species. White-tailed deer are a well-studied species and there has been other research published that addresses similar topics, but none have studied this topic in a long running (over 35 years), replicated experimental setting with this many treatment types.

We have no conflicts of interest to disclose.

Please address all correspondence concerning this manuscript to me at caleb.mckinney@students.tamuk.edu.

Thank you for your consideration of this manuscript.

Sincerely,

Caleb McKinney

FORECO-D-23-00110

We appreciate the reviewer comments and address them in the revised manuscript. Our responses each comment are outlined in italics below. We feel the revised manuscript is improved for both content and clarity.

Reviewer 1

General comments

The authors have provided useful information for the management of mixed pine-hardwood stands in the Mid-South USA that can enable land managers to achieve multiple resource goals including development and maintenance of wildlife habitat. The manuscript is well written and is based on a strong underlying experimental framework. Most of my concerns pertain to clarity of writing and explanation of methods and in the Discussion section, alignment with some statements with stated results. With respect to the Results section, presentation in a way that better synthesizes the specific results would greatly improve readability and help readers understand main findings of this work. Additionally, the conclusions bring up many interesting suggestions that should first be addressed in the discussion section. Some specific comments are provided below.

Thank you for the positive comments. We feel the changes outlined below in response to both reviewers addresses these issues. We added hypotheses, reduced the Results, and rewrote parts of the Discussion.

Specific comments

Line 58: see comment re: lines 503-504, below.

Our response is outlined below in response to comment re: lines 503-504.

Line 91: 12.9 billion " dollars" per year (or $12.9 billion)

Added $ now reads ($12.9 Billion)

Line 101: delete "composition"

Deleted "composition" from sentence.

Line 117: replace "ecosystem types" with "plant community types" or language to that effect

Changed "ecosystem types" to "plant community and structures", structure is important to note because in many cases plant community, at least from a species assemblage *point of view, didn't appear to change greatly unless comparing opposite ends of the treatment spectrum. However, structure, e.g., post oak could be maintained at a shrub height from resprouts following fire or as an overstory species.*

Lines 121-122: 2nd objective – please rephrase here and throughout to focus on functional group cover – what you actually did. Not really "community" as stated. Too, the suggested change is more precise and is often used subsequently in the MS by the authors.

Changed as suggested here and throughout manuscript

Line 123: change, "throughout" to "during" (only collected 3x, in some cases 2x) and "between" to "among"

Changed wording as suggested

Line 151: delete "sparse"

Deleted "sparse"

Line 156: add comma after "mostly" and hyphen between "cool" and "season".

Added suggested punctuation to sentence.

Line 167: authors state that there were 28 exptl units but below (lines 168-170), only indicate there were 23 (8 x 3 = 24 -1 = 23). Please clarify.

Thanks for catching. We changed in manuscript to reflect only 23 experimental units used in this study. The study site has additional experimental that we did not use for this study.

Line 169: move reference to Table 1 up to the end of the sentence at line 168 (after "1984"). Also, consider moving the description of treatments as four structural types at line 424-426 could be useful here somewhere in this paragraph. HNT1, RRB and CONT are well defined here but not others.

Moved reference to (Table 1) to suggested location, and moved a slightly modified version of the description of treatments from line 424-426 into the paragraph.

Line 174: …named according " to" the application…

Added missing word "to" sentence.

Lines 200-202: 1993 citation is fine, but seems like in the intervening 26 years, deer popns could have increased, not sure about elk or hogs in the area. Please address how/if any of these are potential factors.

Added several sentences and references as too changes in deer population on the WMA surrounding the research area and the lack of evidence of over-browsing during sampling.

Line 211 and 338-339: Given that cover of all 6 functional groups declined to near zero during the dormant season, please justify why this period was included in analyses. Does not appear to help explain much given the objectives and seems to complicate models. Too, including it may obscure patterns during the growing season – forcing the variability from d-s into overall model? In addition, wouldn't including dormant season bias cover estimates low by including a mean at or near zero?

Based on this comment and those by Reviewer 2, we removed most of the results related to cover. The cover section adds a lot of length and complexity to the manuscript when many of the points made are redundant with the biomass data. The greatest benefit of the cover estimates was estimating spring ephemerals. However, given the very small contribution this was unlikely to bias biomass results in any way. We've moved information relating to cover to supplementary materials.

Lines 218-219: Why the very uneven bins for cover? At the low end, this makes sense, but why not divide the upper bins into more uniform sizes? Please provide a brief explanation/justification for the choice.

See comment above, about removal of this section. For the bins, we used those typically used with Daubenmire sampling.

Lines 231-232: Please briefly justify why only these treatment levels while 8 used for first two objectives.

See added sentence at the end of this paragraph. The costs of collecting and processing samples are considerable given the number of species and replicates. We feel that we adequately sampled across the wide range of functional groups and vegetation structures.

Line 242: replace "for the" with "during" and delete "sampling" and place comma after "spring"

Changed wording and added comma as suggested.

Line 252: please state what effects were entered into the model as fixed and which were random. Also, provide a brief statement about why the selected transformations were used (log and arcsine).

We revised this section to both remove description of cover type analyses and to provide information on transformation and fixed vs random effects.

Line 295, 298, 317: the word "statistically" is not necessary – please delete.

Deleted "statistically" on suggested lines.

Line 292: delete "structured"

Deleted "structured"

Line 303-304: change to 3-4 years - not sure I'd call HT2 "equal" between herb and woody, especially in 2020. 62% greater in 2019, 214% in 2020...

Good points, changed to 3-4 years as suggested, the line above now reads, 'treatments with annual or biannual burning were dominated by herbaceous vegetation". To indicate that HT2 was still a majority herbaceous ANPP not equal as stated before.

Line 312: here and again at lines 346 and 356, revise statements to avoid the implication of a statistical difference – years were never analyzed together, right? Mb say, " we observed lower numerical values for grass cover in 2020 than 2019"?

Reworded line 312 to avoid this implication, cover results removed entirely and data placed in supplementary information,

Line 327: add comma after "2020".

This section was removed from the manuscript

Line 333-389: for functional groups, would be easier to follow if they are each addressed in separate paragraphs rather than having some on their own and some grouped.

This section was removed from the manuscript

Line 347: add the annual burn trtmts here parenthetically (HT1 and HNT1?) to remind readers.

This section was removed from the manuscript

Line 348: per previous comment, "forest treatments (CONT, HT, RRB)"

This section was removed from the manuscript

Line 385: add hyphen between cool and season here.

This section was removed from the manuscript

Line 402: shouldn't the reference here be to Table 6?

Changed reference to Table 6.

Line 409-410: For which spp - SPP? Per Table 6, comparisons are within rather than among spp.

Restructured this sentence and the one above it to make it easier to keep track of what spp. is being referenced.

Line 412: Significant difference was stated at $p<0.05$ (line 257). Please see comment below at line 531. Also line 419.

Added a new sentence at the end of the methods section to better clarify when effects are considered significant or marginally significant.

Line 419: PAN interaction has a P-value of 0.45, not even marginally significant as stated. Statement is true for SLZ only.

Changed to reflect showy partridge pea ($P = 0.096$) had a marginally significant response not panicum as stated previously.

Lines 429-430: delete, “. In particular,” and insert ”, which” after ANPP. (“…on understory ANPP, which was greatest…”) Mb put everything from “i.e.” onward in paren?

Changed all as suggested

Line 440-451: consider revising this material to be more concise and tie back to implications more directly

Restructured this paragraph as suggested, removing some redundant, or superfluous information and more directly linking to implications for deer.

Line 450: repetitive wording of “effects”

Sentence deleted.

Line 460: Is there any more recent work on this subject that could be cited?

Added some context to the older citations and a more recent citations on this topic.

Line 463: for consistency, use “interval” rather than “rotations”

Changed

Lines 470-471: replace veg community with “cover”

This section was removed entirely as part of larger changes to structure of the discussion section.

Line 479: add “which” before “likely”.

This section was removed entirely as part of larger changes to structure of the discussion section.

Line 488: do not start sentence with an abbreviation

This section was removed entirely as part of larger changes to structure of the discussion section.

Lines 500-501: Only 3 spp (ABB, PAN, and SPP) based on Table 6. DES was numerically greater in CONT, but not different than HT3. Could not see SUM or WGE in my version... Rephrase this statement to reflect this nuance.

Changed orientation of Table 6 to make all species visible. And added detail that only 3 were significantly different from all savanna treatments, but also highlighted the consistent trend of greater values in the forest treatments (10/11 species had had the greatest value in one or more forest treatments).

Lines 503-504: Can the authors speak to total CP produced - as opposed to concentration? This is an interesting point and would be worth expanding on.... Seems like simple multiplication of 2020 ANPP and CP per plant spp would get at this? Even if only a sentence or so here, would be of interest.

This is an interesting idea, but we are hesitant to make this calculation. Both CP and cover change throughout the year. We only have biomass for one point in time and have removed the results showing temporal variation in cover from the manuscript. Also, biomass data were collected at the functional group level and protein data at the species level estimates would be very crude at best. We hope that someone interested in making estimates could do so from the data we present.

Line 512: insert, “to our study” after “settings”.

Slightly changed sentence structure to accommodate this suggestion more smoothly.

Line 514-515: What was the reduced digestibility in fall compared to?

Changed this sentence, and added detail to more clearly illustrate digestibility of forages was likely not a concern, especially in the summer.

Lines 518-520: make this all past tense.

Changed as suggested

Lines 520-525: Great point re: phenology differences

Thank you!

Line 529: I do not think this work was conducted in GA. Please check reference.

Changed reference and the location of the study

Lines 531: Based on Table 5, only 2 (ABB and WGE) had a sig interaction. If SLZ and SPP are being included, make some sort of statement in M&M under Analyses to address the stated p-value being 0.10.

Added information to methods and results to indicate that given the consistent trend in CP response, marginally significant ($0.05 < P < 0.10$) results would be considered.

Line 538: Per Table 5, this is not an accurate statement (DES, SLZ, & SPP all declined); only SEZ remained stable. Revise this language to reflect the results in this table.

Revised this section to more accurately address the nuance of this topic.

Line: 543: insert “to” between our ability and study.

Added “to” as specified

Line 554: this is the first time that cattle have been mentioned. Perhaps bring it up, and find some previous work, to relate in the discussion first.

This section was removed as part of larger changes to the discussion

Line 559: But... per comment at line 504, is there more CP per acre (or at least per plot)?

Given the increase in ANPP total CP could be higher in savanna savanna, but this does not represent usable resources for wildlife as the concentration must be above a certain level otherwise the costs of searching for, consuming, and digesting food outweigh the nutritional benefit gained from it. This is especially true for selective browsers like deer.

Line 561: The life stages of deer were mentioned in the into and here, but the timelines were not. This would be important to highlight why some of your results for forage mass and CP are important throughout the seasons and then how land managers can provide during these times. Tie it into the discussion to round off the results into the overarching goals of the study.

Added to the intro, discussion and conclusions, better emphasizing this point and the importance of this idea to our findings.

Line 573: “growing-season fire”, not “growing season fire”

Added hyphen to “growing season fire”

Line 577: define NGO.

Spelled out “NGO”

Table 4: Could models have included year and functional groups? Could a statement be added at lines 255-256 and 258-259 be added explaining the authors choice?

Table 4 has been moved to supplementary information, models originally included year effects but including year resulted in many significant interactions with treatment and functional group most of these didn’t appear meaningful and only served to further complicate an already long section about cover results.

For Figures 2-4, make all y-axes scales the same.

Figure 2 moved to supplemental information, and figures updated.

Reviewer #2:

The authors of this manuscript have capitalized on a well-designed long-term experiment to evaluate how different combinations of habitat management (thinning and fire) influence the available forage base for white-tailed deer. The experimental nature of the authors' data facilitates stronger inference than many observational studies with similar objectives, and the results have important implications for management of deer habitat. I'm not convinced that those implications are presented as clearly as they could be, however, and I had a few other concerns about the manuscript as well. I hope my comments will be useful to the authors for crafting a revision.

Thank you for the positive comments. We improved the clarity of the manuscript based on your comments and those of Reviewer 1.

Major Comments

1. The Results section was very difficult to read, and so much information was presented that it was hard to make much sense of it. The manuscript would benefit a lot from a more concise summarization of key results from the study, and I have several suggestions that might help with that. My most general thought is that not all of the results are actually interesting or clearly relevant to the primary objective of white-tailed deer habitat management. One thing that would help to whittle things down into a more cohesive presentation would be to identify specific hypotheses and predictions in the Introduction that were then tested using the authors' data and results. Linking each result to a specific prediction would make the results and their relevance easier to keep track of. Moreover, any results that are tangential to the authors' core hypotheses and predictions could be removed. Along those lines, given the length and density of information in the manuscript,

We simplified objectives and results by removing cover and reframed objectives as a testable hypothesis.

I would strongly consider removing the cover analyses/results. Those results are almost entirely redundant with the productivity results (the authors make this point themselves in the Discussion), and thus they add considerable length and complexity to the manuscript with very little payoff in terms of the storyline. In many field studies of herbivore foraging ecology, cover data are collected in tandem with a smaller number of biomass estimates in a double-sampling scheme so that biomass can later be estimated from cover (because biomass is more directly relevant to herbivores, as the authors also point out). In this experimental study, however, the authors already have good biomass data, and the cover estimates don't add much to them in my opinion, so I would remove them and simplify the manuscript.

We removed cover section as suggested. We agree this will shorten and increase readability of the paper particularly the long results section and place greater attention on the more important (to deer) factors like CP and biomass. The cover data did have some interesting information regarding spring ephemerals and the effects of increased litter on biomass, but these do not warrant the length previously allocated to cover in the manuscript. We now include as supplementary information.

Another thing that made the Results difficult to read was the plethora of non-intuitive acronyms for the different treatments. These were impossible to keep track of, and although it
would require more characters, I think the authors could easily identify their treatments using a more intuitive naming scheme (e.g., Burn_Thin1).

We agree the acronyms can be confusing at times. However, multiple previous publications used this naming system and maintaining consistency is necessary. To address this issue in the current manuscript, we modified table 1 and associated caption restructured the description of treatments in the methods, and made small changes to wording in the results.

2. In lines 518-523, the authors make the excellent point that phenological stage could have been an important driver of some of the differences in crude protein among treatments. This really is a critical point, and I'm wondering why it wasn't accounted for as part of the study design. It's well known that plant phenology is one of, if not the most important determinant of variation in forage quality. Take, for example, the proliferation of literature on 'green-wave' surfing by migratory ungulates over the past decade. For this reason, many of the ungulate forage-sampling studies that I'm aware of make it a point to compare samples across treatments or habitat types only within the same

phenological stage. I recognize that the authors can't likely go back and do that now, but at the very least I'd like to see a more detailed explanation of why they expect that their results would hold qualitatively if differences in phenology were accounted for.

This is an excellent point. However, it was beyond the scope of our study to measure frequently enough to assess the extent to which treatments may have caused differences in phenology related to leaf out, flowering, seed dispersal, and senescence. However, we speculate that the different microclimates created by the different treatments may have slightly altered timing to maturity within a given phenological stage for plants. During sampling, we did not note different phenological stages that would have been useful.

3. Some of the authors' main conclusions/recommendations seem to gloss over important aspects of deer foraging ecology. For example, there is a near-universal tradeoff between plant biomass and nutritional quality, and which is most limiting for an herbivore population depends on functional traits that scale with body size. Deer are relatively small-bodied and much more selective than many of their larger counterparts (e.g., elk), and are therefore much more likely to be limited by forage quality than forage biomass, except perhaps in extremely high-density populations. The authors seem to be suggesting (lines 570-571) that deer can have their cake and eat it too (so to speak) by getting their biomass from one type of habitat and their quality forage from another. This just isn't realistic. If deer are filling their rumens with low-quality, high-biomass forage, then supplementing that with small amounts of higher-quality forage from another habitat will be useless; thoverall quality of their diet will still be low. If deer are quality limited, then they'll need to consume the highest-quality forage they have access to most or all of the time, which is exactly what deer seem to do (see, for example, Lisa Shipley's work with captive deer). So, my point is that I think the authors need to carefully rethink their management implications/conclusions; deer don't benefit from consuming large amounts of low-quality forage, and this should be reflected in the authors' recommendations to managers.

Thank you for the helpful comments. We restructured the management implications to better illustrate how both savanna and forest treatments can provide value for deer without implying that deer will choose to forage in lower quality areas as was previously implied. We now better indicate forests with regular prescribed fire likely provide better quality forage in the growing season when needs are greatest for CP, but savannas particularly those with intermediate fire intervals, provide more forage when deer are limited by forage quantity and can provide resources to deer besides forage.

Minor Comments

1. Line 72: Is there a citation to support this statistic? Thirty percent seems surprisingly high given the large swaths of National Forest and private timberland managed by logging companies spread across many parts of the country.

This is from a US forest service technical report from 2018 cited as Butler et al. at the end of the paragraph, added additional citation to Butler et al. after the point about more than 30% family ownership of forests in the US. The same report indicated about 20% corporate ownership and about 30% federal ownership of forests.

2. Line 85: Why prescribed fire here specifically and not fire more generally?

Deleted “prescribed”

3. Line 91: 12.9 needs a dollar sign added.

added

4. Lines 97-98: It would be useful to give some examples (probably parenthetically) here of a few of these alternative management objectives to help contextualize the main point of this sentence.

Added some examples in text such as timber production or unmanaged areas.

5. Lines 114-115: Although the authors' points about crude protein here are true, I'm not sure they comprise a compelling justification for focusing solely on this one metric of quality. My understanding is that protein tends to be more limiting for ungulates at northern latitudes (e.g., the arctic and boreal forest), whereas energy is often more limiting in temperate zones. Do the authors have any evidence (anecdotal even) suggesting that protein might be limiting for deer in their study area, and thus that variation in crude protein is likely of importance to deer?

We made changes to this paragraph providing more support to CP being limiting to deer in the Southeast during the growing season. We also added into the discussion more information about the limitations of only looking at CP, the justification of doing so, and the potential value of further research on this topic at this site.

6. Lines 548-549: Could the authors provide some additional detail here? How large of a percentage are we talking? Do these grasses still count as potential forage if they're rarely consumed by deer? What are the management implications (e.g., are there ways that managers could influence community composition in addition to just ANPP)?

This sentence was significantly changed as part of a larger reworking of the management implications section.

7. Table 6: This table was too wide for portrait formatting and needs to be landscape.

Changed orientation

8. Figure 1 and others: Treatment types should be spelled out in the figure caption so readers can more easily interpret the results.

Changed figure captions.

Highlights

•Forest thinning and prescribed fire increase the production of understory plants

• Forage crude protein concentration decreases with increased fire frequency

• A fire return interval of 3-years or less required to maintain savanna conditions

•The effects of forest management on deer forage are greatest when deer are most in need of nutrient rich forages

Forage Quantity and Protein Concentration Changes Across a Forest-Savanna Gradient with Management Implications for White-Tailed Deer

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Highlights

- **Forest thinning and prescribed fire increase the production of understory plants**
- **Forage crude protein concentration decreases with increased fire frequency**
- **A fire return interval of 3-years or less required to maintain savanna conditions**
- **The effects of forest management on deer forage are greatest when deer are most in need of nutrient rich forages**

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.

KEY WORDS crude protein, nutrition, *Odocoileus virginianus*, Oklahoma, prescribed fire, savanna, wildlife, understory productivity

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. 1993, Reich et al. 2001, Feltrin et al. 2016, Adhikari et al. 2021a).

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. 1993, 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, Lewis et al. 1982, Masters et al. 1993b). In contrast, woody browse is the largest component of deer forage and is consumed throughout the year (Short 1971, Johnson et al. 1995, Jenks et al. 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 8-12% (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 ^{o}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 (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 7-12 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 hours at 85 $^{\circ}$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 (NFTA, 1993).

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. 1993). 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) (**Figure 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 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 less than 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**).

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, Figures 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 (**Figures 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**, **Figure 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 2004, Lashley et al. 2011, Adhikari et al. 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 et al. 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 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 Figure 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 et al. 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 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 et al. (2021a) found that herbaceous understory ANPP was generally greatest during the growing season after burning.

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 1998).

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 x 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-Governmental Organizations, 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 litter layer. Our results reinforce that heterogeneity benefits wildlife objectives by providing a variety of different forage and browse species, qualities, and timing of availabilities.

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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

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	0.2 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
			2020			
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 3 P values for treatment, season, and treatment x 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.

Commented [A1]: Changed all references to acronym for showy partridge pea to SHP, to avoid confusion when referencing groups of plant species (I.e. *Quercus* spp.)

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

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	10.5 b	9.3 ab	13.8 b	13.3	11.0 b	8.6 b	9.5	9.7	10.6 b	9.9	10.5 ab
HT2	10.5 b	8.3 b	13.1 b	13.1	11.9 ab	8.6 b	10.6	9.3	11.3 b	10.9	10.2 b
HT3	11.6 b	9.7 ab	14.7 ab	12.3	12.7 a	9.0 b	11.1	9.8	11.3 b	11.2	10.9 ab
HT4	11.8 b	8.9 ab	13.0 b	13.6	11.1 b	9.7 ab	11.4	10.3	10.6 b	11.3	11.8 a
RRB	12.7 b	10.4 a	15.2 ab	12.9	11.5 b	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	11.5 b	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 $p < 0.05$

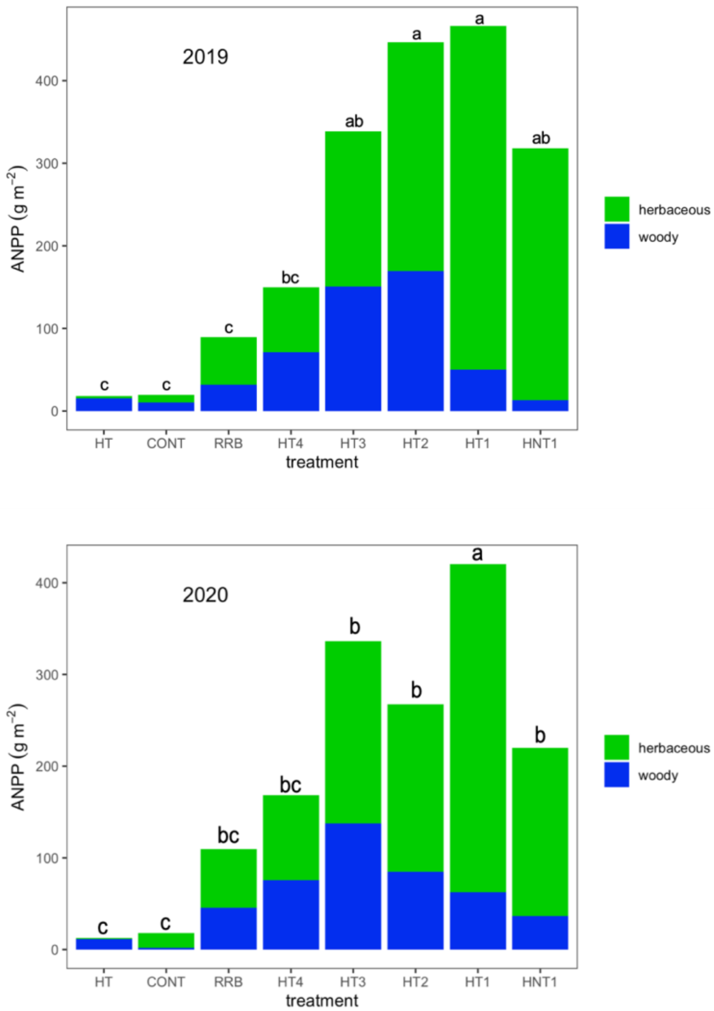

Figure 1 Herbaceous and understory woody aboveground net primary production (ANPP) for eight treatments on the FHRA in 2019 and 2020. Within each year, letters indicate significant differences based on total ANPP (woody + herbaceous) at $p < 0.05$. See Table 1 for definition of treatments.

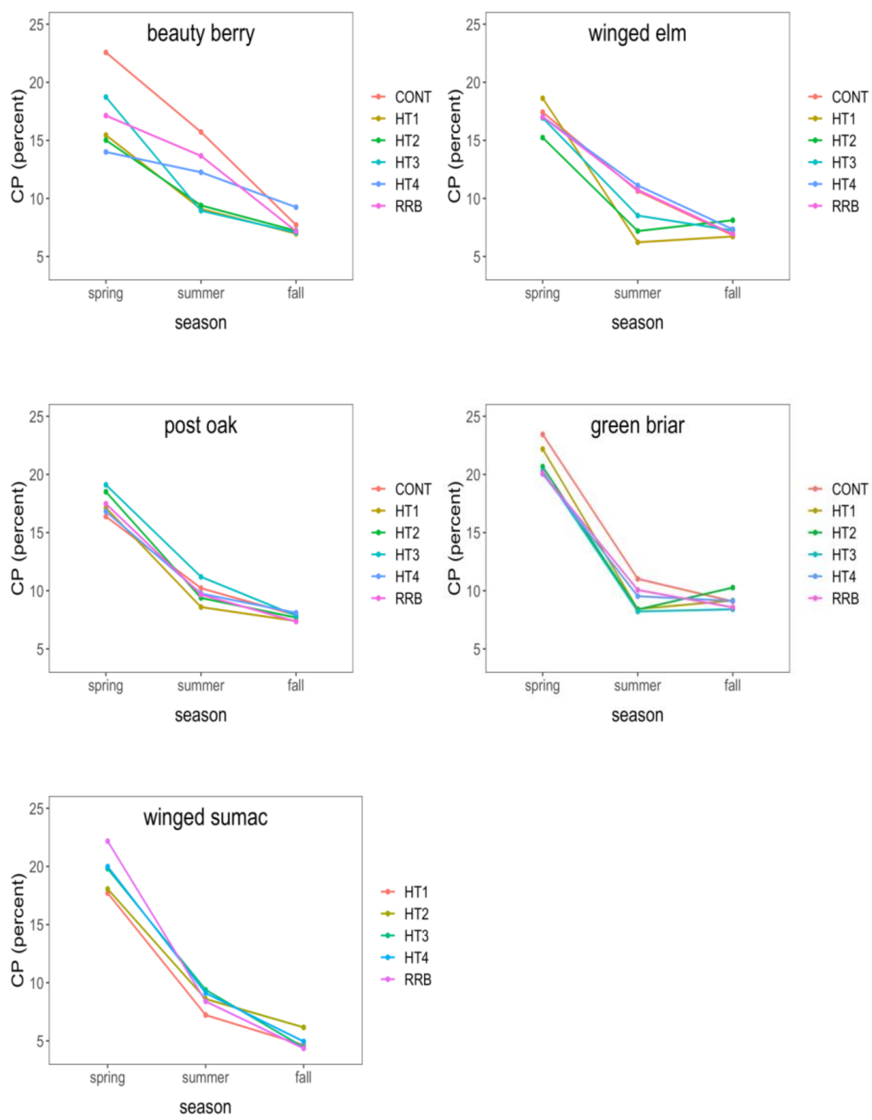

Figure 2 Crude protein (CP) concentration for woody species throughout the 2020 growing season at the FHRA. See Table 1 for definition of treatments.

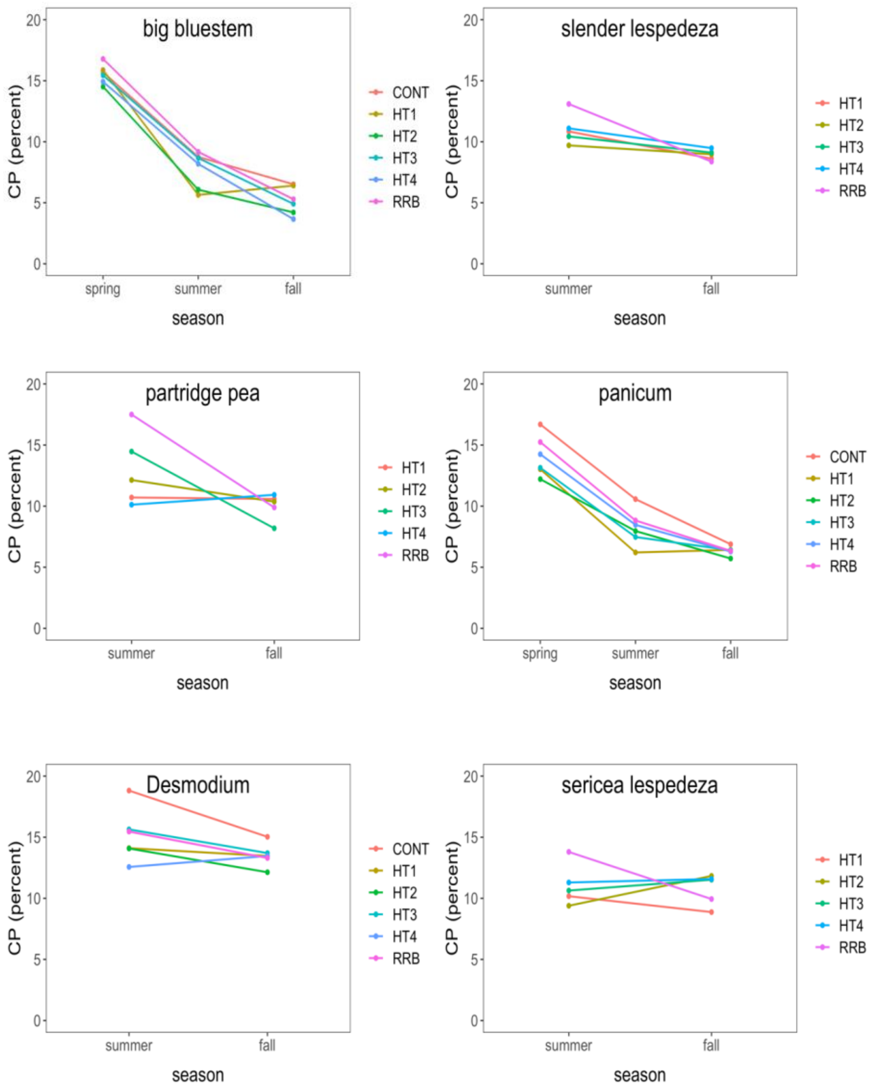

Figure 3 Crude protein (CP) concentration for herbaceous plants throughout the 2020 growing season at the FHRA. Big bluestem and panicum are grasses and sericea lespedeza, *Desmodium* spp. slender lespedeza and partridge pea are legumes. See Table 1 for definition of treatments.

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Declaration of interests

☒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.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Author Contributions

C. M. McKinney: Conceptualization, Methodology, Formal Analysis, Investigation, Data Curation, Writing - Original Draft**,** Writing - Review & Editing **R.E. Masters:** Conceptualization, Resources, Writing - Review & Editing, Supervision **A. Adhikari:** Conceptualization, Investigation, Writing - Review & Editing,
B. Mishra: Conceptualization, Investigation, Writing - Review & Editing **O. Joshi:** Conceptualization, Funding acquisition, Writing - Review & **C. B. Zou:** Conceptualization, Funding acquisition, Writing - Review & Editing **R. E. Will:** Conceptualization Funding acquisition Project administration, Writing - Original Draft**,** Writing - Review & Editing,

Percent cover 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 20 × 50 cm Daubenmire frame (Daubenmire 1959). Percent cover sampling was conducted along the two previously established 100 m transects in each unit (Masters 1991a, b). Ten samples were taken along each transect at random intervals for a total of 20 sampling points for each unit on each sampling date. Data were collected monthly during the growing season (March-October) and once during the dormant season to capture seasonal changes in plant communities that make up important components of deer forage. The same transects were used each sampling period, but the individual frame locations were at different points each month. When conducting the Daubenmire sampling, ground cover was separated into the following functional groups: woody, panicum grasses, other grasses, non-legume forb, sedge, legume, litter, bare ground, and rock. Only understory woody vegetation less than 1.4 m in height was sampled. The functional groups were estimated using the following eight categories (0.01<1.5%, 1.5<3.5%, 3.5<7.5, 7.5<17.5%, 17.5<37.5%, 37.5<62.5%, 62.5<85%, 85<97.5%) that covered a range of percentages, and the midpoint of each class was used for analysis.

Vegetation percent cover results

For percent cover, all functional groups showed significant treatment differences ($P < 0.05$) except sedge in 2019 (**Table 3**). However, the treatment effects were not consistent for all sampling periods. There were significant interactions between treatment and month for grass and legumes in 2019 ($P < 0.0001$) and 2020 ($P = 0.0001$), for panicum in 2019 ($P < 0.0001$), and for woody in 2020 ($P = 0.023$). These interactions occurred primarily because all treatments had similarly low coverage in the dormant-season and early spring samplings, and then coverage diverged during the middle of the growing-season (**Figure 2**). As treatments were largely consistent in rank during the growing season, main effects are discussed below. However, treatments burned before a given growing season (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 C4 grasses was greatest ($P<0.05$) in the savanna treatments (HNT1, HT1, HT2, HT3) with 41.9% to 50% in 2019 and 24.1% to 39.7% in 2020 (**Table 4**). However, coverage in the HT3 treatment was lower than annual burn treatments in 2020. In 2019, grass coverage in the HT4 treatment was greater than all other forest treatments at 21.5%. The coverage of 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 both 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 and 1.5% to 13.6% in 2020 (**Table 4**). Woody plant coverage was significantly greater in treatments with longer fire return intervals (HT2, HT3, HT4, and RRB), and declined with annual burning or in the absence of burning. 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 (**Table 4**). Coverage was the greatest in treatments burned that year (HNT1, HT1, HT2) and RRB. Forb coverage was the lowest in HT along with CONT and HT3 treatments. In 2020, forb coverage ranged from 2.3% in the RRB treatment to 0.1% in the HT.

In 2019, legumes ranged from 9.4% in the HNT1 treatment to 0.1% in the HT treatment (**Table 4**). 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. The HNT1 treatment had legume coverage significantly greater than the forested treatments, the 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.

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 compared to the other treatments in 2020 especially in the fall (**Table 4, Figure 2**). 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) (**Table 4**). Percent cover for litter decreased with shorter fire intervals, ranging from 87.7% for the HT treatment in 2020 to 11.5% in 2019 for the HT1 treatment (**Table 4**). Trends for percent bare ground and rock were generally opposite those for litter coverage because fires tended to expose soil and surface rock.

For all functional groups, coverage varied by month (**Table 3**). 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 2).** Grasses, legumes, and woody plants reached maximum coverage in June or July in both years. In contrast, 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.

Percent cover figures and tables

Supplemental table 1. P values from 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 and 2020 at the FHRA. Effects were considered significant at p < 0.05. See Table 1 for definition of treatments.

				2019					
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
				2020					
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

Supplemental table 2. Means for percent coverage of the nine functional groups or ground covers for the eight treatments sampled in 2019 and 2020 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	litter	bare	rock
					2019				
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
					2020				
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

Supplemental figure 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.