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wildlife management

Annual Fire Return Interval Influences Nutritional Carrying Capacity of White-Tailed Deer in Pine–Hardwood Forests

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Prescribed fire is a cost-effective habitat management tool in pine stands to enhance the quantity and quality of forage available for white-tailed deer (*Odocoileus virginianus*). Management recommendations typically suggest a 3- to 5-year burn rotation in mixed pine–hardwood stands to increase quality forage production, but as fire frequency increases, forb and legume biomass increases, and woody browse decreases. A more frequent burn rotation may be a viable management option for deer managers, but there is still a lack of information regarding preferred forage and nutritional carrying capacity response to prescribed fire at these intervals. We measured the production and nutritional quality of forage within mature pine–hardwood stands after a 1- or 2-year fire-return interval during three nutritionally stressful periods for deer on a 640-acre (259-hectare) enclosure located in east-central Alabama during 2014 and 2015. These stands had previously been burned annually for over 15 years, resulting in an abundance of herbaceous vegetation. We then compared forage class biomass, nutritional carrying capacity estimates, and digestible protein between burn treatments. A 1-year fire return interval improved habitat quality to a greater degree than a 2-year fire return interval by increasing the production of forage able to support greater nutritional planes. An annual burn rotation is an effective option for managers to increase protein availability in pine–hardwood stands, but other factors such as decreased cover availability and soft mast production should also be considered.

Keywords: nutritional carrying capacity, habitat management, nutrient availability, white-tailed deer, crude protein

Wildlife management requires a multifaceted approach to promote abundant, healthy wildlife populations, and habitat management is a facet that has received significant emphasis. Habitat management can provide wildlife species with a variety of food sources to meet their nutritional demands, and vegetative cover for escape, protection, bedding, and/or nesting. Although habitat management is important for all wildlife species, a considerable focus has been placed on managing habitat for white-tailed deer (*Odocoileus virginianus*). One of the main goals of habitat management for white-tailed deer is to provide forage capable of maintaining a high nutritional plane, because the nutritional quality of habitats that deer use is related to their overall productivity (Moen 1978, Parker et al. 2009, Hewitt 2011). Nutritional planes are characterized by the overall quantity and quality of resources deer are consuming (Green et al. 2017), and deer with access to an abundance of high-quality forage will be able to maintain a high nutritional plane, which has been shown to reduce gestation length and increase fawning rates in female deer and increase body weights and antler size in male deer (Verme 1965, Harmel et al. 1988). Therefore, providing a sufficient quantity of high-quality forages should be an integral component of any deer management plan.

Approximately 54 million acres (22 million hectares) of forest across the Southeast are composed of pine–hardwood stands (Thill 1984, Dickson and Sheffield 2001), and vegetation in these stands is a sustainable resource that can provide an abundance of nutritional forage (Halls 1970, Blair and Enghardt 1976, Edwards et al. 2004). However, these stands typically have a dense canopy cover and thick woody growth in the mid- and understory if left unmanaged, which leads to reduced vegetative production and nutritional carrying capacity (NCC, the maximum deer population a habitat can sustainably support given the amount of available resources over an extended period of time) (Halls and Alcaniz 1968, Blair and Brunett 1977, Sparks et al. 1998, Edwards et al. 2004, DeYoung 2011). Therefore, habitat manipulation techniques are commonly recommended in pine–hardwood stands to mitigate factors that lead to decreased forage productivity (Masters et al. 1993, Mixon et al. 2009, Iglay et al. 2010). Many forest-management techniques exist to improve forage quality, including thinning, clear cutting, mowing, and the use of herbicides (Kammermeyer and Thackston

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1995, Jacobson et al. 2011), but prescribed burning is one of the most commonly used techniques. Prescribed fire in pine–hardwood stands can help create an open understory suitable for growth of nutritious herbaceous forages by reducing forest floor litter and the competition and prevalence of undesired browse species such as sweetgum (*Liquidambar styraciflua*) in the midstory that shade out desirable herbaceous understories (Dale et al. 1989, Masters et al. 1993, Edwards et al. 2004).

Prescribed fire increases herbaceous forage production, and species richness and diversity, and decreases woody vegetation (Lay 1956, Lewis and Harshbarger 1976, Sparks et al. 1998). However, the effectiveness of prescribed burning is largely dependent upon the return interval of fire, because frequent fire implemented over a long period of time is needed to sustain open pine forests (Waldrop et al. 1992). A burn rotation of 3–5 years is generally the most common management recommendation to maintain quality forage production in pine–hardwood stands in the Southeast (Masters et al. 1996, Edwards et al. 2004, Iglay et al. 2010, Diefenbach and Shea, 2011), but as fire frequency increases, forb and legume biomass increases, and woody browse biomass decreases (Lay 1956, Buckner and Landers 1979, Waldrop et al. 1992, Masters et al. 1996). Thus, a more frequent burn rotation may be a viable management option for increasing production of quality forage. Along these lines, Buckner and Landers (1979) reported that legume abundance in a Georgia longleaf pine stand during the first growing season after a prescribed burn was approximately four times greater than in the same stands following 3 years of fire suppression. However, Masters et al. (1996) found that only forages of low preference and total woody biomass differed among pine–hardwood stands that were located in Oklahoma and treated with midstory removal during the first, second, or third growing season following prescribed fire. Whereas previous studies have determined the effects of different fire-return intervals on biomass production of different forage classes (e.g., grass, browse, legumes, and vines), there is a scarcity of information regarding the response of preferred forages or NCC (which may be better indicators of habitat quality) to prescribed fire (Hobbs and Swift 1985).

Although providing adequate nutritional resources for deer on a year-round basis is important, nutritional demands and forage quality and abundance fluctuate throughout the year, creating nutritional stress periods during which meeting nutritional demands becomes more difficult (Short 1975, Thill and Morris Jr. 1983, Asleson et al. 1997, Hewitt 2011). In parts of the Southeast, these periods occur during the summer and early fall when forage quality is declining, females are entering the final trimester of gestation and then beginning lactation, and males are in the crucial stages of antler development (Blair and Halls 1967, Asleson et al. 1997, Hewitt 2011). Numerous factors constitute forage quality, including palatability and digestibility, but forage quality is typically most often referred to in terms of nutrient content. Although protein and energy are both important during antler growth, gestation, and lactation, protein is generally more limited in terrestrial ecosystems and is required to a greater degree than energy for these processes for deer in southern climates (White 1993, Asleson et al. 1996, Barboza and Parker 2008, Lashley et al. 2011). Crude protein requirements for antler growth and lactation are over 1.5 and 2.5 times that of maintenance requirements, respectively (Holter et al. 1979, Verme and Ullrey 1984, Asleson et al. 1996). Therefore, it is important to determine the effects of prescribed burning on forage quality and quantity during specific nutritional stress periods to help deer meet their nutritional demands.

Considering the importance of providing deer with adequate nutrition and the significance of prescribed fire as a habitat management tool, our goal was to examine the effects of prescribed fire on production of quality forage for deer. Extensive research has been conducted to determine the effects of prescribed fire, but there is still a lack of information regarding preferred deer forage and NCC response when prescribed fire is used at a 1- or 2-year fire-return interval. Our specific objective was to determine whether a 1- or 2-year fire-return interval was more suitable to increase NCC and the production of preferred deer forages during select stress periods for deer in pine–hardwood habitats in the Southeast. Information regarding how frequent burn rotations influence quality forage production would allow managers to better provide resources during key nutritional stress periods.

Methods

Study Area

Three Notch Wildlife Research Foundation (Three Notch) was located in Bullock County, approximately 6 miles (10 km) east of Union Springs, Alabama, United States, and encompassed 639 ac (259 hectares) that had been enclosed by a 9.8-ft. (3-m) high deer-proof fence since 1997. Approximately 16 ac (6.5 hectares) and 9 ac (3.5 hectares) of food plots were planted year round in alfalfa (*Medicago sativa*) and Ladino clover (*Trifolium repens*), respectively, and 2.5 ac (1 hectares) of winter rye (*Secale cereale*) was planted during the cool season. An extensive irrigation system supplemented natural precipitation on all alfalfa and clover plots. High-protein supplemental feed (20 percent protein; Purina Antlermax, St. Louis, MO) was provided ad libitum at 12 permanent feeding troughs throughout the year. The average annual rainfall was approximately 55 in. (1.4 m), and temperatures varied from an average annual high of 75.6°F (24.2°C) to an average annual low of 50.7°F (10.4°C) (National Climatic Data Center 2010). The topography of the area was primarily flat with a few gently sloping hills and an elevation of 541 ft. (165 m) above sea level. Predominant soils on the property included gently and strongly to moderately sloping,

Management and Policy Implications

Treating pine–hardwood stands annually with prescribed fire is an effective option for managers to increase protein availability of the habitat during nutritional stress periods for deer. Although these stands were dominated by warm season grasses, they were also characterized by a variety and abundance of legume biomass, which provided a substantial amount of high-quality forage. However, managers should also consider other factors such as increased cost to burn annually, the availability of suitable cover, decreased fruit production, and negative impacts on other components of the forest ecosystem when determining the preferred fire-return intervals for their property. If deer densities are relatively low, and food plots or supplemental feed are also available, less of the total pine–hardwood habitat of a property may need to be maintained on an annual burn rotation, and the remainder could be maintained on a longer fire-return interval for cover and soft mast production (Lashley et al. 2015a).

moderate to well-drained, loamy sand soils (Soil Survey Staff and National Resource Conservation Service 2013).

Forested habitat on the property ranged from upland areas of mature, open pine–hardwood stands to dense hardwood stands along creek drainages. Common pine species on the property were loblolly (*Pinus taeda*) and shortleaf (*Pinus echinata*), and common hardwood species included white oak (*Quercus alba*), water oak (*Quercus nigra*), hickory (*Carya* spp.), sweetgum, and yellow poplar (*Liriodendron tulipifera*). Pine–hardwood, pine, and mature hardwood stands made up approximately 40 percent, 10 percent, and 30 percent of the total habitat within the study area, respectively. The mean basal area of the pine–hardwood stands was 83.11 ft^2/ac (19.08 m^2/hectare), and the mean tree density was approximately 98 trees/ac (240 trees/hectare). Approximately 250–300 ac (100–120 hectares) of mature pine/pine–hardwood habitat had been treated with prescribed fire annually for over 15 years in late February to mid-March to improve the availability of natural vegetation for deer and aid in the detection of shed antlers. Extremely selective harvest, low hunting pressure limited to archery, and ample nutritious food sources facilitated a high population density within the enclosure. A mark–recapture camera survey (Jacobson et al. 1997) in 2007 estimated a density of at least one deer per 4.2 ac (1.7 ha), three times that normally found in the region, and a sex ratio (M:F) of 2.64:1 (McCoy et al. 2011).

Data Collection

Each year, we identified eight mature upland pine–hardwood stands previously managed under a 1-year fire regime and ranging in size from 0.9 to 2.8 ac (0.38–1.14 ha) to be used for vegetation sampling. To ensure our pine–hardwood stands were similar for comparison, we measured the basal area and tree density of each stand. To calculate the basal area, we measured the dbh of all trees >4 in (10.16 cm) within a 0.10-ac (0.04-hectare) plot with a diameter tape (Forestry Suppliers, Jackson, MS), repeated for a total of five plots, and then averaged across the five plots. We then averaged the basal areas across the five 0.10-ac (0.04-hectare) plots. We also calculated the mean number of trees within the five plots for each stand. We used an analysis of variance and Tukey's HSD post hoc test to test for differences in basal area and tree density among stands. Four of our eight stands were treated with head fires in late February to mid-March during the year of sampling, and four did not receive prescribed fire to compare forage production during the first and second growing season after the fire (1- and 2-year fire return interval). We established new stands for the second year of data collection, and prescribed burning treatments were repeated. We constructed seven 5 ft. × 5 ft. × 4.5 ft. (1.52 m × 1.52 m × 1.37 m) exclosures in each pine–hardwood stand during April and May to measure biomass production. We randomly generated exclosure locations within each stand in ArcMap 10.1 (Environmental Systems Research Institute, Inc., Redlands, CA). We built exclosures large enough to enable three separate, primary-growth samples per year. To avoid stand edge bias, exclosures were >50–65 ft. (15–20 m) from stand edges (Mueller-Dombois and Ellenberg 1974, Masters et al. 1993).

We sampled vegetation for 7–10 days at the beginning of June, July, and September in conjunction with peak antler growth, gestation, and lactation, respectively, for the region. Rapid antler growth for males in this region occurs during June and July (Jacobson and Griffin 1983, Demarais and Strickland 2011). Although breeding in most parts of the country occurs in November, peak breeding across portions of the Southeast is often as late as the end of January (Gray et al. 2002, Diefenbach and Shea 2011). With an approximately 200-day gestation length (Ditchkoff 2011) and the greatest demands of gestation occurring during the third trimester (Pekins et al. 1998, Hewitt 2011), the greatest nutritional demands for gestation are during June and July at our study area. Females bred in late January give birth to fawns in August, and because peak milk production is approximately 10–37 days after birth (National Resource Council 2007, Hewitt 2011), the greatest nutritional demands for lactation are early September.

We composed a list of 25 preferred species that deer commonly consume based on the literature (Miller and Miller 2005) and relative abundance (e.g., visual inspection of the property during the 3 months prior to the study) of each plant at the study area (Table 1). All other species found at the study site that were high-quality forages of deer were present in such small quantities that their inclusion in the analysis would have been negligible. During each sampling period, we sampled all seven exclosures in each stand using the destructive harvest method with 2.7 ft^2 (0.25 m^2) quadrats. We placed quadrats at the corners of each exclosure approximately 6 in. (15 cm) from the edge. We clipped all current annual woody and herbaceous vegetation 1 in. (2.54 cm) above the ground and up to 5 ft. (1.5 m) in height within each quadrat (Bonham 1989, Masters et al. 1993), and we separated vegetation individually into brown paper bags for the 25 preferred species. We grouped all other vegetation not found on the list of 25 preferred species into a grass, forb, or browse category. We assumed that the nutrient content of forages was the same across the entire property regardless of habitat or burn rotation (Stransky and Halls 1976, Wood 1988, Edwards et al. 2004).

At the end of each sampling day, we placed samples in a forced-air drying oven at 122°F (50°C) for 48 h (Tilley and Terry 1963, Goering and Van Soest 1970). We then weighed samples to obtain a dry-matter biomass weight. We saved samples for each of the 25 preferred forages and browse and forb categories until 10–15 g of each was obtained for nutritional analysis and then discarded thereafter. We collected additional biomass opportunistically from the property if sampling failed to produce the required quantities of 0.4–0.5 ounces (10–15 g) dry weight needed for nutritional analysis. We failed to identify smooth ticktrefoil (*Desmodium laevigatum*) in our prestudy survey of the site, and it was added to our list of preferred species (bringing the total to 25) after the June sampling period of the first year of data collection. This species was added to the list because we recognized it to be an influential species that would potentially impact our models of carrying capacity.

We measured *in vitro* dry matter digestibility (IVDMD) in duplicate for all samples (Tilley and Terry 1963, Goering and Van Soest 1970) using rumen fluid obtained from a rumen-fistulated dairy cow (*Bos taurus*). Crude protein analysis was conducted by the Auburn University School of Forestry and Wildlife Science's Elemental Analysis Laboratory using a 2400 Series Perkin Elmer elemental analyzer (PerkinElmer, Waltham, MA). We then calculated crude protein by multiplying the nitrogen content of each sample by 6.25 (Robbins 1993).

We used nutritional constraints models (Hobbs and Swift 1985) to calculate the mean biomass production (lbs/ac) for deer to attain

Table 1. List of 25 forages sampled and their associated crude protein content (%) within pine–hardwood stands after a 1- (*n* = 8) or 2-year (*n* = 8) fire return interval during 3 periods in 2014 and 2015 at Three Notch Wildlife Research Foundation in east-central Alabama, United States.

	Crude protein (%)					
	2014			2015		
Species	June	July	Sept.	June	July	Sept.
Legume						
Atlantic pigeonwings (*Clitoria mariana*)	14.9	17.3	13.3	17.9	17.4	13.8
Butterfly pea (*Centrosema virginianum*)	15.1	14.0	13.2	17.7	15.7	15.9
Chinese lespedeza (*Lespedeza cuneata*)	12.9	7.9	11.5	15.8	10.6	10.5
Creeping lespedeza (*Lespedeza repens*)	14.2	11.1	11.6	11.9	9.9	12.4
Fuzzy bean (*Strophostyles umbellata*)	18.5	15.8	16.3	13.9	14.0	13.9
Hairy small-leaf ticktrefoil (*Desmodium ciliare*)	12.9	8.4	8.1	13.7	11.3	11.0
Hoary pea (*Tephorsia spicata*)	16.8	15.7	9.3	17.7	13.7	9.9
Milk pea (*Galactia volubilis*)	15.4	16.5	13.6	16.3	11.7	13.0
Nuttall's ticktrefoil (*Desmodium nuttallii*)	12.3	9.8	11.4	13.6	11.8	11.1
Partridge pea (*Chamaecrista nictitans*)	18.6	15.5	14.6	18.0	17.5	13.9
Pencil flower (*Stylosanthes biflora*)	17.8	12.1	16.4	18.0	16.3	9.4
Pinebarren ticktrefoil (*Desmodium strictum*)	13.7	14.0	9.4	14.9	10.4	12.8
Rabbit bells (*Crotalaria rotundifolia*)	14.5	12.9	13.4	14.0	12.8	11.8
Slender lespedeza (*Lespedeza virginica*)	11.4	8.5	8.2	11.2	10.1	10.3
Smooth ticktrefoil (*Desmodium laevigatum*)	–	11.2	10.8	12.9	11.4	11.9
Vine						
Blackberry (*Rubus* spp.)	7.6	5.0	4.6	8.7	7.4	6.8
Grape (*Vitis* spp.)	11.3	7.5	6.9	10.2	8.5	5.9
Greenbrier (*Smilax* spp.)	10.7	10.3	10.8	12.8	11.2	7.3
Japanese honeysuckle (*Lonicera japonica*)	8.1	7.3	9.9	9.4	9.6	9.5
Partridgeberry (*Mitchella repens*)	7.6	8.7	9.1	8.7	9.1	9.7
Poison ivy (*Toxicodendron radicans*)	10.8	9.9	10.4	14.2	13.0	11.0
Trumpet creeper (*Campis radicans*)	12.1	11.0	7.0	10.8	9.4	11.0
Virginia creeper (*Parthenocissus quinqefolia*)	10.7	8.6	9.3	13.5	11.3	11.2
Yellow jessamine (*Gelsemium sempervirens*)	9.7	3.8	7.7	9.0	6.4	6.8
Browse						
Chinese privet (*Ligustrum sinense*)	13.1	11.1	12.2	14.9	13.4	13.4
Other browse*	9.4	7.1	6.6	10.2	8.4	8.0
Forb†	10.6	7.1	5.7	9.9	7.4	6.2
Grass‡	8.1	5.6	6.2	7.5	9.8	5.4

* All remaining browse species that were sampled but not individually separated.
† All remaining forb species that were sampled but not individually separated.
‡ All grass species sampled were grouped into a single category for crude protein analysis.

nutritional planes of 10–18 percent CP, at 1 percent intervals. We used 1 percent intervals because we wanted to compare varying forage quantities across a gradient of nutritional levels that may be desirable to various land managers with different management goals. We chose 10–18 percent CP because this range covers the recommended CP levels to support antler growth, gestation, and lactation (Verme and Ullrey 1984, Harmel et al. 1988, Asleson et al. 1996), but also represents a greater nutritional plane for trophy management (17 percent and 18 percent CP). These models provide a quantifiable method to determine habitat quality by incorporating forage quality, quantity, and diet selection (Hobbs and Swift 1985, McCall et al. 1997). An abundance of vegetation may be produced for consumption, but animals will be unable to meet their dietary needs if it is primarily of low quality (Hobbs and Swift 1985). Therefore, the quantity and quality of each forage must be accounted for individually rather than as a mean value (Hobbs et al. 1982, Hobbs and Swift 1985).

Statistical Analysis

We calculated the mean production (lbs/ac [kg/hectare], dry-matter basis) of seven forage classes for each treatment (browse, grass, forb, vine, legume, preferred species, and total biomass). These forage classes included species from our list of 25 preferred species and those not included in that list. We also calculated mean digestible protein production (Edwards et al. 2004), by summing the products of each species' biomass, CP, and IVDMD percentage.

We used a mixed-effects, general linear model to compare means between 1-year ($n = 8$) and 2-year ($n = 8$) fire return intervals for each forage class during each stress period ($n = 3$), with burn rotation and year as fixed effects and stand as a random effect. To compare NCC biomass production at each diet level interval and digestible protein production, we used a general linear model with burn rotation and year as fixed effects. To ensure normality, we square-rooted and log-transformed the data to determine whether either transformation improved the fit by reducing Akaike's Information Criterion score of the model (AIC_c, which corrects for small sample size) (Anderson and Burnham 2002, Jones et al. 2009). We used log transformation in all analyses because it improved AIC_c the greatest in all cases, but actual means are presented for interpretation purposes. We performed statistical tests in R, version 3.1.1 (R Core Team, Vienna, Austria, 2013), and α was set to 0.05.

Results

The mean basal area and tree density of the pine–hardwood stands were 83.1 ft^2/ac (19.1 m^2/hectare) and 98 trees/ac (242 trees/hectare), respectively (Table 2). All stands had similar basal areas, but two stands from 2014 that received a 2-year fire return interval had significantly greater tree densities from some of the other stands. However, because stands selected for each treatment were determined randomly, we decided to keep these two stands for analysis because pine–hardwood forests can be highly variable (Hurst et al. 1979), and these stands captured the natural variation represented in this forest type.

The mean total biomass production did not differ between the 1- and 2-year fire return intervals during June (P = .524), July (P = .410), or September (P = .927; Table 3). Mean biomass production of grass, forb, browse, or preferred species also did not differ during any stress period. However, legume biomass production in 1-year stands was nearly 4 times greater in June (P = .012), two times greater in July (P = .023), and three times greater in September (P = .038) than in 2-year burn plots. The opposite trend was seen for vine biomass production which was at least 2.5 times greater in June (P = .042) and September (P = .034) in 2-year stands than in 1-year stands.

Crude protein values of the 25 preferred species used to calculate the NCC estimates ranged from 3.8 percent to 18.6 percent (Table 1). Biomass at 14 percent (P = .031) and 15 percent CP (P = .022) was at least three times greater in 1-year stands than 2-year stands during June, and similar results were found in July (Table 4). However, differences in biomass production at CP diet qualities ≥14 percent between burn treatments were not found in September but were found at each CP diet quality ≤13 percent. Although CP tended to be greater in 1-year stands, digestible protein did not differ between burn treatments during June (P = .974), July (P = .237), or September (P = .217) (Table 5).

Table 2. Estimates of basal area (ft²/ac [m²/hectare]) and tree density (trees/ac [trees/hectare]) in pine–hardwood stands after a 1- (*n* = 8) or 2-year (*n* = 8) fire return interval in 2014 and 2015 at Three Notch Wildlife Research Foundation in east-central Alabama, United States.

	1-year		2-year	
	Basal area	Tree density	Basal area	Tree density
Stand	$\bar{X}$	$\bar{X}$	$\bar{X}$	$\bar{X}$
1	73.5 (16.9)	94 (232)	70.3 (16.1)	66 (163)
2	57.6 (13.2)	52 (128)	90.4 (20.8)	190 (470)
3	106.4 (24.4)	124 (306)	84.3 (19.4)	84 (208)
4	82.7 (19.0)	74 (183)	96.3 (22.1)	278 (687)
5	55.9 (12.8)	84 (208)	81.1 (18.6)	56 (138)
6	71.0 (16.3)	54 (133)	100.3 (23.0)	76 (188)
7	110.2 (25.3)	88 (217)	72.5 (16.6)	46 (113.7)
8	93.0 (21.4)	74 (183)	84.5 (19.4)	126 (311)

Discussion

Production of forage able to support quality antler growth and gestation (14 percent and 15 percent CP; Verme and Ullrey 1984, Asleson et al. 1996) during June and July in pine–hardwood stands was greater during the year following prescribed fire than during the second year following fire. These improvements in forage production were detected despite results indicating that total biomass did not differ between fire return intervals. Although 1-year stands were largely composed of numerous grass species, which deer primarily do not consume, legume biomass was also substantial, similar to results from other studies evaluating forage composition in stands under a repeated annual burn regiment (White et al. 1990). Differences in legume and vine biomass production between return intervals were the forage classes that primarily contributed to greater forage quality in 1-year stands. Legumes and vines are both important and nutritious forage sources for deer (Miller and Miller 2005), but legume production was greater in 1-year stands, and vine

Table 3. Forage class biomass production (lbs/ac [kg/hectare]) in pine–hardwood stands after a 1-year (*n* = 8) or 2-year (*n* = 8) fire return interval during three periods in 2014 and 2015 at Three Notch Wildlife Research Foundation in east-central Alabama, United States.

	1-year		2-year		
Forage class	$\bar{X}$*	SE	$\bar{X}$	SE	P
June					
Grass	401.5 (450.0)	45.5 (51.0)	366.6 (410.9)	56.5 (63.3)	0.594
Forb	111.6 (125.1)	21.8 (24.4)	88.1 (98.7)	17.4 (19.5)	0.452
Browse	370.4 (415.2)	59.2 (66.3)	845.2 (948.0)	125.3 (140.4)	0.107
Legume	152.8 (171.3)	31.9 (35.7)	40.2 (45.1)	8.4 (9.4)	0.012
Vine	37.3 (41.8)	14.5 (16.3)	101.2 (113.4)	30.2 (33.9)	0.042
Preferred†	188.8 (211.6)	34.0 (38.1)	141.1 (158.2)	30.2 (33.9)	0.649
Total	1,072.3 (1,201.9)	92.1 (103.2)	1,441.7 (1,615.9)	130.3 (146.1)	0.524
July					
Grass	581.7 (652.0)	69.9 (78.3)	553.9 (620.8)	88.8 (99.5)	0.861
Forb	229.2 (256.9)	52.3 (58.6)	143.1 (160.4)	32.0 (35.9)	0.155
Browse	845.4 (947.6)	142.3 (159.5)	1,159.3 (1,299.4)	159.4 (178.7)	0.127
Legume	217.6 (243.9)	32.5 (36.4)	127.5 (142.9)	39.4 (44.2)	0.023
Vine	41.4 (46.4)	10.6 (11.9)	119.3 (133.7)	26.1 (29.3)	0.059
Preferred*	258.8 (290.1)	33.5 (37.5)	246.7 (276.5)	49.4 (55.4)	0.824
Total	1,915.3 (2,146.8)	180.0 (201.8)	2,103.1 (2,357.3)	184.0 (206.2)	0.410
September					
Grass	664.5 (744.8)	75.6 (84.7)	496.0 (555.9)	77.8 (87.1)	0.240
Forb	239.7 (268.7)	34.6 (38.8)	152.7 (171.1)	26.5 (29.7)	0.427
Browse	823.5 (923.0)	192.4 (215.7)	1,074.6 (1,204.5)	199.0 (223.1)	0.151
Legume	266.3 (298.5)	45.2 (50.7)	97.3 (109.1)	18.1 (20.3)	0.038
Vine	34.3 (38.4)	9.3 (10.4)	109.9 (123.2)	30.4 (34.1)	0.034
Preferred†	304.1 (340.8)	47.9 (53.7)	207.1 (232.1)	35.2 (39.5)	0.480
Total	2,031.8 (2,277.3)	209.4 (234.7)	1,930.5 (2,163.8)	199.2 (223.3)	0.927

* Actual means presented. Analyses were conducted using log-transformed data.
† Composed of 25 native forage species known to be preferred by deer and abundant at the study area.

Table 4. Estimates of nutritional carrying capacity (lbs/ac [kg/hectare]) based on crude protein production in pine–hardwood stands after a 1- (*n* = 8) or 2-year (*n* = 8) fire return interval during three periods in 2014 and 2015 at Three Notch Wildlife Research Foundation in east-central Alabama, United States.

	1-year		2-year		
Crude protein (%)	$\bar{X}$*	SE	$\bar{X}$	SE	*P*
June					
18	9.8 (11.0)	5.4 (6.1)	3.7 (4.2)	2.6 (2.9)	0.243
17	79.9 (89.5)	49.9 (55.9)	13.6 (15.2)	5.4 (6.0)	0.089
16	102.9 (115.3)	59.6 (64.6)	19.4 (21.8)	8.0 (9.0)	0.064
15	153.6 (172.2)	66.1 (74.1)	29.8 (33.4)	12.4 (13.9)	0.022
14	209.3 (234.6)	82.3 (92.2)	47.8 (53.6)	15.2 (17.0)	0.031
13	255.0 (285.8)	81.9 (91.8)	74.1 (83.1)	18.6 (20.8)	0.047
12	319.6 (358.2)	84.9 (95.2)	121.2 (135.9)	29.3 (32.8)	0.085
11	348.0 (430.4)	84.4 (94.6)	254.2 (284.9)	72.4 (81.2)	0.410
10	451.2 (505.7)	86.6 (97.1)	494.1 (553.8)	129.7 (145.4)	0.826
July					
18	0.0	0.0	0.0	0.0	---
17	91.7 (102.8)	51.6 (57.8)	17.3 (19.4)	7.6 (8.5)	0.349
16	131.8 (147.7)	64.0 (71.7)	29.4 (32.9)	9.5 (10.7)	0.240
15	174.6 (195.7)	72.4 (81.1)	39.0 (43.7)	11.2 (12.5)	0.018
14	213.4 (239.2)	84.3 (94.5)	62.7 (70.3)	12.5 (14.0)	0.038
13	263.9 (295.8)	98.6 (110.5)	88.1 (98.8)	19.3 (21.6)	0.051
12	316.3 (354.5)	111.0 (124.4)	114.9 (128.8)	26.2 (29.4)	0.056
11	375.8 (421.2)	110.6 (124.0)	155.5 (174.3)	36.6 (41.0)	0.057
10	464.0 (520.1)	113.8 (127.5)	239.5 (268.4)	60.5 (67.8)	0.080
September					
18	0.0	0.0	0.0	0.0	---
17	0.0	0.0	0.0	0.0	---
16	7.6 (8.5)	5.2 (5.8)	6.4 (7.2)	3.8 (4.3)	0.737
15	35.0 (39.2)	11.9 (13.3)	15.4 (17.3)	6.9 (7.7)	0.077
14	127.1 (142.5)	43.7 (49.0)	40.2 (45.0)	15.2 (17.0)	0.057
13	223.8 (250.8)	58.8 (65.9)	83.6 (93.7)	17.5 (19.6)	0.026
12	296.5 (332.3)	76.4 (85.6)	115.4 (129.3)	22.5 (25.2)	0.023
11	382.5 (428.7)	99.7 (111.7)	150.6 (168.8)	29.4 (32.9)	0.027
10	488.6 (547.6)	115.6 (129.6)	212.4 (238.1)	42.6 (47.7)	0.035

* Actual means presented. Analyses were conducted using log-transformed data.

Table 5. Digestible protein production (lbs/ac [kg/hectare]) in pine–hardwood stands after a 1- (*n* = 8) or 2-year (*n* = 8) fire return interval during three periods in 2014 and 2015 at Three Notch Wildlife Research Foundation in east-central Alabama, United States.

	1-year		2-year		
Month	$\bar{X}$*	SE	$\bar{X}$	SE	*P*
June	35.0 (39.2)	6.7 (7.5)	35.0 (39.2)	8.7 (9.8)	0.974
July	49.2 (55.1)	7.0 (7.8)	37.2 (41.7)	9.5 (10.7)	0.237
Sept.	45.7 (51.2)	7.1 (8.0)	29.4 (33.0)	4.6 (5.2)	0.217

* Actual means presented. Analyses were conducted using log-transformed data.

production was greater in 2-year stands. The nutritional quality of legumes is typically much greater than vines (Mixon et al. 2009, Iglay et al. 2010), resulting in increased quality forage production in stands that were burned annually. Buckner and Landers (1979) reported that legume density was over 2 times greater in longleaf (*Pinus palustris*) pine stands that were burned annually in South Carolina than in stands during the second growing season following prescribed fire. Waldrop et al. (1992) also found that vine abundance was reduced considerably in South Carolina loblolly pine stands treated annually with prescribed fire. Therefore, increased production of higher quality legumes in pine–hardwood stands maintained on a 1-year fire-return interval increased the amount of biomass able to support antler growth and gestation. Mixon et al. (2009) similarly reported that increased forb production in midrotation loblolly pine stands treated with prescribed fire and herbicides contributed a greater amount of biomass to NCC estimates at 14 percent CP than lower-quality vines, even though vine production was high. These differences also help explain why improvements in NCC estimates were found in 1-year stands, despite the inability to detect differences in biomass production between treatments.

Overall declines in forage quality and plant senescence resulted in a substantial decrease in forage production able to meet nutritional requirements during September, regardless of treatment. However, forage production to support lactation (14 percent; Verme and Ullrey 1984) tended to be more than three times greater in 1-year than 2-year burn stands. Although forage quality generally declined during this time period, the CP content of certain legumes at our study site was still high enough to contribute to a nutritional plane of 14 percent CP, and legume production was nearly 3 times greater in 1-year stands during September than 2-year stands. Considering that endogenous resources are often used by females to meet the high demands of lactation (Oftedal 1985, Hewitt 2011), the beginning of September is a critical period in some regions (Gray et al. 2002) to provide adequate nutritional resources to help females meet these demands. September is also an important time to provide for the high demands of fawn growth in other parts of the Southeast where breeding occurs earlier (Diefenbach and Shea 2011). Although an annual burn rotation was important for increasing habitat quality during June and July to support antler growth and gestation, it became increasingly important during September to help support the high demands of lactation at our study site.

Comparisons of our results to similar studies with longer fire return intervals (3–5 years) have also shown that a 1-year fire return interval increases NCC for deer. There are only three analogous studies that report NCC estimates in response to prescribed fire (Edwards et al. 2004 Mixon et al. 2009, Iglay et al. 2010), two of which (Edwards et al. 2004, Mixon et al. 2009) only used a combination of fire, herbicides, and/or fertilizers, making it difficult to compare directly. Further, Mixon et al. (2009) did not report estimates for a fire return interval greater than 2 years. Iglay et al. (2010) reported average NCC estimates at 14 percent CP in Mississippi midrotation pine plantations during a 3-year fire return interval were 58 deer days/ac (144 deer days/hectare) compared with our 1-year return interval of 71 deer days/ac (175 deer days/hectare) in July. However, the estimates of NCC in mature loblolly pine stands in Mississippi at 12 percent CP in August 3 years after treatment reported by Edwards et al. (2004) were 129 deer days/ac (318 deer days/hectare) compared with our 1-year estimate of 105 deer days/ac (260 deer days/hectare) in July, but their treatment also included herbicide and fertilizer.

The pine–hardwood habitat at our study area had been treated annually with prescribed fire for over 15 years, resulting in an abundance of herbaceous vegetation because of reduced mid- and understory growth of undesired browse species and litter on the forest floor. After 40 years of annual burning in loblolly pine stands located in South Carolina, Waldrop et al. (1992) similarly reported an understory dominated by a variety of forb, grass, and legume species. However, prescribed fire will be far less productive in mature pine stands where management has been nonexistent or used sparingly (Waldrop et al. 1992, Edwards et al. 2004). Pine stands in the absence of management are typically characterized by increasingly dense hardwood and woody shrub growth in the mid- and understory (Martin et al. 1975, Waldrop et al. 1992, Sparks et al. 1998), which negatively impacts production of herbaceous vegetation. Waldrop et al. (1987) found that hardwood species in the understory exceeding 4–6 in (10–15 cm) dbh could not be reduced with prescribed fire alone, even if implemented annually. Additional management actions such as thinning and herbicide use, in addition to fire, might initially be necessary in poorly managed stands to reduce browse and shrub species in the mid- and understory (Hodgkins 1958, Edwards et al. 2004). Prescribed burning during the dormant season versus growing season should also be considered because the timing of prescribed burning can have an influence on the composition of understory vegetation (Waldrop et al. 1992, Sparks et al. 1998, Hiers et al. 2000, Lashley et al. 2015b). Waldrop et al. (1992) reported that whereas both growing and dormant-season burns in South Carolina loblolly pine stands resulted in an abundance of herbaceous plant species, woody vegetation was less resistant to dormant-season burns, and thus more persistent. Additionally, they reported that sweetgum was particularly resistant to dormant-season burning, which was also abundant in the pine–hardwoods stands at our study site. Growing-season burns may have effectively reduced sweetgum abundance, resulting in greater herbaceous vegetation growth, but also reduce the availability of vegetation temporarily following fire during an important nutritional stress period for deer.

Our study area had been enclosed by a high fence and sustained a high density of deer for over 15 years, so it is possible that forage production may not have been reflective of similar pine habitat in free-ranging conditions where deer densities are typically much less. High-density deer populations can cause over-browsing, eventual depletion of natural forage, and negative plant community changes (Waller and Alverson 1997, Côté et al. 2004, Thiemann et al. 2009). However, estimates of NCC in our study area were similar to values reported from other studies in free-ranging habitat (Mixon et al. 2009, Iglay et al. 2010). Although differences would be expected between studies because of regional variation, stand conditions, and past management history (Waldrop et al. 1992, Jones et al. 2008, Mixon et al. 2009), our results indicate that forage production at our study area was similar to that of other areas. The high availability of alternative food sources (e.g., food plots and supplemental feed) in our study area may explain the apparent lack of over-browsing of forages within pine–hardwood stands.

Whereas annual burning increased production of quality forage, it has been shown also to have negative effects on other stand characteristics or wildlife species. Lashley et al. (2015b) found that lactating deer were more likely to use longleaf pine stands treated with prescribed fire as the fire return interval in those stands increased and speculated that this was because of increased cover as the fire return interval increased. Lactating females prefer dense cover to decrease fawn predation risk (Kie and Bowyer 1999, Lashley et al. 2015b), but prescribed fire is generally used to open the understory, and thus eliminates many species that provide adequate cover for fawns. A decrease in cover may also negatively affect other species such as certain songbirds (Dickson and Wigley 2001). Annual burn rotations can also negatively impact soft mast production. Lashley et al. (2017) found that fruit production was reduced by 99 percent in longleaf pine stands maintained on a 1- or 2-year regime compared with stands maintained on a 3-year regime. Van Lear and Harlow (2002) also reported that soft mast production was greatest 2–4 years after burning, which could negatively impact species that are dependent upon these fruits if a more frequent fire interval is prescribed. Repeated implementation of prescribed burning that does not vary in fire return interval, season, or fire weather conditions can also create homogenous habitats, thus reducing overall biodiversity on a landscape scale (Sparks et al. 1998, Lashley et al. 2014). Liechty and Hooper (2016) found that long-term frequent prescribed fire may negatively impact forest floor nutrient levels, including nitrogen levels, but also noted there was no indication that nutrient loss was significant enough to alter productivity. Other studies (Knelman et al. 2017, Akburak et al. 2018, James et al. 2018) also suggest that repeated fire impacts physical and chemical properties of soil, and that some of the greatest impacts may occur in the organic layer (Certini 2005). Because of the impact of the organic layer on vegetative production, there is considerable potential for frequent fire to impact vegetative communities via soil alteration. Additionally, whereas pine species are generally resistant to the effects of fire, prescribed fire may have a negative effect on pine growth. Boyer (1987) reported that in 14-year-old longleaf pine stands in Alabama, pine volume growth was reduced over 20 percent in stands biennially burned compared with nonburned stands. Therefore, land managers must take into account the tradeoff between increasing production of quality forage for deer and the possible negative impacts an annual fire regime may have on the ecosystem as a whole when determining the optimal fire regime for their property.

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