



Management and Conservation Article

Deer Carrying Capacity in Mid-Rotation Pine Plantations of Mississippi

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ABSTRACT Herbicides, commonly used for vegetation management in intensively managed pine (*Pinus* spp.) forests of the southeastern United States, with and without fire, may alter availability of quality forage for white-tailed deer (*Odocoileus virginianus*; deer), an economically and socially important game species in North America. Because greater forage quality yields greater deer growth and productivity and intensively managed pine forests are common in the southeastern United States, forest managers would benefit from an understanding of fire and herbicide effects on forage availability to improve habitat conditions for deer. Therefore, we evaluated independent and combined effects of fire and herbicide (i.e., imazapyr) on forage biomass and deer nutritional carrying capacity (CC) on land owned and managed by Weyerhaeuser NR Company in east-central Mississippi, USA. We used a randomized complete block design of 6 pine plantations (blocks) divided into 4 10-ha treatment plots to each of which we randomly assigned a treatment (burn-only, herbicide-only, burn + herbicide, and control). We estimated biomass (kg/ha) of moderate- and high-use deer forage plants during July of 1999–2008, then estimated CC for diets to support either body maintenance (6% crude protein) or lactation (14% crude protein) with a nutritional constraints model. Herbaceous forages responded positively to fire and herbicide application. In most years, CC estimates for maintenance and lactation were greater in burn + herbicide than in controls. Maintenance-level CC was always greater in burn + herbicide than in controls, except at 1 year posttreatment. Burn + herbicide was 2.6–8.3 times greater ($\bar{x} = 4.0$) than control for lactation-level CC in 8 of 9 years posttreatment. We recommend fire and selective herbicides to increase high-quality deer forage in mid-rotation, intensively managed pine plantations.

KEY WORDS forest management, herbicide, intensive forestry, mid-rotation management, Mississippi, nutritional carrying capacity, *Odocoileus virginianus*, pine plantation, prescribed burning, vegetation management.

Intensively managed pine (*Pinus* spp.) forests cover an estimated 12.1 million ha in the southeastern United States, including 1.3 million ha in Mississippi (Munn 1997, Schultz 1997, Wear and Greis 2002). Saw-timber management typically includes even-aged management with a 27- to 32-year rotation followed by clear-cut harvest, site preparation, 1–2 commercial thinnings, and fertilization (Siry 2002). Understory plant management is limited to herbaceous and woody release following planting and then fertilization after commercial thinning (mid-rotation).

Prescribed burning and selective herbicide application can be used for midstory hardwood competition control and understory vegetation management during mid-rotation (postthinning) within pine stands throughout the southeastern United States (Edwards et al. 2004, Jones and Chamberlain 2004, Mixon et al. 2009). Both methods create a 2-tiered forest structure by reducing midstory hardwood and woody species and increasing understory coverage of semiwoody vines and herbaceous species (Mobley and Balmer 1981, Stransky and Harlow 1981). Many declining wildlife species of the southeastern United States are associated with this forest structure (Burger 2000, Hunter et al. 2001, Trani et al. 2001), and many game species including white-tailed deer (*Odocoileus virginianus*; hereafter, deer [Masters et al. 1996]), northern bobwhite (*Colinus virginianus*; Welch et al. 2004), and eastern wild turkey

(*Meleagris gallopavo silvestris*; Miller et al. 1999a) can benefit from such disturbance.

Control of woody species during mid-rotation is often not practiced by many landowners due to concerns regarding low timber-value returns on the investment in the southeastern United States (Sladek et al. 2008) and because postthinning fertilization may improve short-term (2-yr) pine tree growth regardless of fire or herbicide application (McInnis et al. 2004). However, competition control can have a greater influence on long-term pine tree growth (Fortson et al. 1996). Forest landowners, including those in forest industry, often also derive income from recreational hunting leases, providing incentive for landowners to manage habitat (Guynn and Marsinko 2003). Additionally, some forestry owners integrate hunt-lease programs into economic analyses and planning, which consequently connects wildlife and timber management objectives. Also, most forest industry lands are managed under sustainable forestry guidelines that require managing availability and diversity of wildlife habitat (Sustainable Forestry Initiative 2005).

Deer are the focus species for most land leased for hunting from forest industry and are an economically and socially important game species in the United States. Habitat management for deer is often designed to improve animal quality with forest management that increases deer forage quality, supporting greater deer growth and productivity, and may contribute to increased economic returns (Verme 1965, Ullrey et al. 1967, Demarais et al. 2000). Availability

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of high quality forage in spring and summer is important to deer to recover winter body mass losses, replace endogenous fat reserves, promote further body growth, and support lactation. Lactation requirements may be especially costly, because they come during a period of decreasing forage protein content that retards maternal recovery of body condition and may impair future breeding under food-limited conditions (Therrien et al. 2007, Jones et al. 2008). This period of nutritional stress is seen as a potential bottleneck for recruitment in deer and other cervids, where inadequate nutrition for lactation may lead to early weaning or even death of the fawn through starvation, compromised immunity, or greater vulnerability to predators (Landete-Castillejos et al. 2002, Lomas and Bender 2007, Therrien et al. 2007).

Deer have some capacity to forage selectively based on energy and protein content and should select forages based on nutritional demands associated with biological state (Berteaux et al. 1998, Parker et al. 2009). Protein demands for lactating females may be particularly heightened relative to energy requirements, because milk production relies on current dietary protein but may make use of endogenous fat reserves to supply necessary energy (Sadleir 1987, White 1992). Because nutritional quality of plants is typically related inversely to their abundance, carrying capacity (CC) models should integrate forage quality and quantity (White 1978, Mattson 1980, Breman and deWitt 1983, Hobbs and Swift 1985).

Given the importance of deer to many stakeholders and the prevalence of intensively managed pine forests in the southeastern United States, we investigated effects of prescribed fire and selective herbicide on deer nutritional CC and quality forage biomass to evaluate habitat management strategies in intensively managed pine stands of east-central Mississippi, USA. We hypothesized greater biomass of moderate- to high-use deer forages and concomitantly greater nutritional CC for maintenance and lactation requirements of deer on treated sites. Unlike past studies, we provided long-term side-by-side comparison of independent and combined effects of prescribed fire and selective herbicide.

STUDY AREA

We conducted our research in mid-rotation pine plantations on land owned and managed by Weyerhaeuser NR Company in Kemper County, Mississippi, USA in the Interior Flatwoods Soil Resource Region (Pettry 1977). Our study sites were located within a 9,700-ha area composed of managed pine (70%), mature pine-hardwood (17%), mature hardwoods (10%), and nonforested areas (3%). Soils were clay to sandy loam with poor to imperfect drainage. Climate was subtropical with mean annual temperatures of 17.4° C and mean annual precipitation of 149 cm (National Oceanic and Atmospheric Administration 2009).

METHODS

We divided 6 mid-rotation, intensively managed pine plantations (60–120 ha, 18–22 yr old), commercially

thinned to approximately 296 trees/ha, 2–5 years prior to project initiation, into 4 10-ha (286 × 350-m) plots. A treatment buffer ≥ 50 m wide separated plots. We randomly assigned a treatment (burn-only, herbicide-only, burn + herbicide, control) to each plot, creating a randomized complete block design with 6 replicates. During September 1999, we applied one treatment of imazapyr herbicide (Arsenal®; BASF Corp., Research Triangle Park, NC) at Weyerhaeuser NR Company's recommended rate of 0.87 L/ha (BASF Corporation 2006) and 0.5% volume:volume ratio of Timbersurf90® surfactant (Timberland Enterprises, Inc., Monticello, AR) in a broadcast spray solution of 187 L/ha via skidder. Weyerhaeuser NR Company's operational herbicide rate was lower than that recommended for quality vegetation management (1.17 L/ha; Edwards et al. 2004) and label prescriptions for controlling target species (0.94–1.87 L/ha; BASF Corporation 2006). However, we used this rate because it met operational needs of Weyerhaeuser NR Company at a lower cost. We conducted prescribed burns using drip torches to light strip-flanking fires during January 2000 and 2003 and January–March 2006 under conditions of 24–55% relative humidity, 7–22% fuel moisture, 0.0–6.9 km/hour in-stand wind speeds, and 3.3–27.2° C in-stand temperatures. Following standard silvicultural practices, we aerially fertilized all sites according to soil tests with diammonium phosphate (127–283.5 kg/ha, \bar{x} = 153.4 kg/ha) and (or) urea (381–448 kg/ha, \bar{x} = 222.8 kg/ha) immediately after commercial thinning and again in winter 2001.

We composed a list of potential moderate- and high-use deer forages from the literature (Warren and Hurst 1981, Miller and Miller 1999) and input from deer biologists with Mississippi Department of Wildlife, Fisheries and Parks. We estimated biomass (kg/ha) of these forages ≤ 2 m above ground level in July 1999–2000 using 10 1-m² hoops/plot placed systematically following a random starting point; we increased sampling intensity to 20 hoops/plot in 2001–2008 to reduce our coefficient of variance. We conducted all sampling ≥ 50 m from plot boundaries to avoid edge effects. We clipped and weighed leaves and growing stem tips to represent consumable plant portions for each species, dried samples at 60° C in a forced-air oven for 72 hours, then extrapolated dry matter biomass (kg/ha) for each forage.

Important summer deer forages in Mississippi show greater variability in crude protein (CP) content than in digestible energy, so we assumed lactating females would tend to select forages by CP rather than energy content (P. Jones, Mississippi State University, unpublished data). We collected representative samples of each forage species in 2007 and had these evaluated for CP by the Mississippi State University Animal Nutrition Laboratory using the Kjeldahl procedure (Jurgens 2002). Nutritional CC estimates provide a relative comparison of foraging environment comparable to an index. We estimated growing season nutritional CC at 2 levels of diet quality using an explicit nutritional constraints model (Hobbs and Swift 1985). We used a target diet quality of 6% CP to represent maintenance requirements and 14% CP to represent minimum require-

Table 1. Interaction and main effects of burn and herbicide treatments with white-tailed deer carrying capacity at 14% and 6% crude protein, biomass by growth form of species used in protein analysis, and species richness of important deer forages in intensively managed mid-rotation pine plantations in Kemper County, Mississippi, USA, summers 1999–2008 with summer 1999 as pretreatment.

| Variable | Pretreatment | | Treatment | | Yr | | Treatment × yr | |
|--------------------------|-----------------------|-----------------|-----------|-----------------|----------|-----------------|----------------|-----------------|
| | <i>F</i> ^a | <i>P</i> -value | <i>F</i> | <i>P</i> -value | <i>F</i> | <i>P</i> -value | <i>F</i> | <i>P</i> -value |
| Carrying capacity | | | | | | | | |
| 14% crude protein | 0.16 | 0.692 | 16.84 | ≤0.001 | 9.36 | ≤0.001 | 1.67 | 0.040 |
| 6% crude protein | 0.15 | 0.704 | 21.68 | ≤0.001 | 20.56 | ≤0.001 | 4.04 | ≤0.001 |
| Forage class | | | | | | | | |
| Forb | 0.07 | 0.799 | 4.24 | 0.017 | 3.14 | 0.004 | 1.89 | 0.015 |
| Grass | 0.00 | 1.000 | 17.66 | ≤0.001 | 8.06 | ≤0.001 | 2.78 | ≤0.001 |
| Herbaceous vine | 0.35 | 0.558 | 1.29 | 0.287 | 3.41 | ≤0.001 | 1.93 | 0.008 |
| Legume ^b | 0.76 | 0.390 | 5.99 | 0.001 | 11.08 | ≤0.001 | 1.63 | 0.047 |
| Semiwoody vine | 7.50 | 0.019 | 21.20 | ≤0.001 | 12.45 | ≤0.001 | 2.36 | ≤0.001 |
| Woody plant ^b | 0.04 | 0.844 | 1.19 | 0.339 | 8.02 | ≤0.001 | 2.65 | ≤0.001 |
| Woody vine | 1.46 | 0.237 | 6.17 | 0.003 | 19.34 | ≤0.001 | 2.09 | 0.005 |
| Species richness | 2.77 | 0.106 | 7.16 | ≤0.001 | 86.0 | ≤0.001 | 1.83 | 0.019 |

^a We determined df using Kenward–Roger.

^b Legume and woody plant treatment × yr interactions were for differences within a treatment(s) across yr.

ments for a lactating female with one fawn (French et al. 1956, McEwen et al. 1957, Verme and Ullrey 1984, Asleson et al. 1996). We assumed dry-matter intake of 1.36 kg/deer/day (French et al. 1956, Fowler et al. 1967, Edwards et al. 2004). Although secondary compounds of plants, such as condensed tannins, can reduce protein digestibility and, thus, potentially invalidate CC estimates based on unadjusted CP, deer with access to a variety of forages are unlikely to be materially affected (Hodgman et al. 1996, Jones et al. 2010). Given the variety of forages available in managed pines and our sites specifically (see Results), we assumed that any impact of condensed tannins was negligible and similar across treatments (Warren and Hurst 1981, Edwards et al. 2004, Jones et al. 2009, Mixon et al. 2009).

Because ours was a designed manipulative study, we used a mixed-models, repeated-measures analysis of covariance in SAS Proc Mixed (SAS Institute Inc., Cary, NC) to examine main effects of treatment, year, and treatment × year interactions for nutritional CC estimates and biomass by forage class (forb, grass, herbaceous vine, legume, semiwoody vine, woody plant, woody vine). We used 4 levels of treatment main effect (burn, herbicide, burn + herbicide, control), random effect of plantation ($n = 6$), repeated measures of year ($n = 9$; 2000–2008), and subject of plantation × treatment to test the hypothesis of no difference in forage species richness, mean biomass by forage class, and nutritional CC among treatments within years (Littell et al. 2006). We used pretreatment year (1999) biomass as a baseline covariate (Milliken and Johnson 2002). Because our data followed a time series, we selected the appropriate covariance structure from among the following: 8-banded Toeplitz, heterogeneous compound symmetry, heterogeneous auto-regressive, and first-order auto-regressive. For each analysis, we selected the covariance structure that minimized Akaike's Information Criterion corrected for small sample size (Littell et al. 2006, Gutzwiller and Riffell 2007). We used the Kenward–Roger correction in

denominator degrees of freedom for repeated measures to avoid inflated Type I error (Littell et al. 2006, Gutzwiller and Riffell 2007). We used the LSMEANS SLICE option to identify a treatment effect within years following a significant interaction, and we used LSMEANS PDIF to conduct pair-wise comparisons among treatments when there was no interaction (Littell et al. 2006). We used an a priori significance level of $\alpha = 0.05$ for all tests.

RESULTS

Significant treatment × year interactions occurred in all 7 forage classes and species richness (Table 1). Our pretreatment covariate was significant for semiwoody vines but not for other forage-class biomass and species-richness estimates. Grass and semiwoody vine biomass was consistently greater in burn + herbicide plots than control plots during years 3–9 (Table 2). Grass biomass in herbicide-only and burn-only plots was similar to burn + herbicide plots in years 5 and 6, respectively. Semiwoody vine biomass in herbicide-only plots was similar to burn + herbicide plots in years 1, 2, 4, 6, and 7, controls and burn-only plots in years 1, 2, 5, 6, and 8, and burn-only plots in year 9. Forb biomass was greatest in burn + herbicide plots in years 1 ($\bar{x} = 33$ kg/ha vs. $\bar{x} = 6$ kg/ha) and 4 ($\bar{x} = 92$ kg/ha vs. $\bar{x} = 13$ kg/ha). Forb biomass within herbicide-only plots was similar to all other treatments in years 2, 3, and 5–9. Biomass of herbaceous vines differed among plots in 3 of 9 years, but there was no consistent pattern and biomass was low (≤ 5 kg/ha) across all years and treatments. Biomass of legumes was greater in burn + herbicide ($\bar{x} = 13$ kg/ha) than burn-only and control ($\bar{x} = 2.5$ kg/ha) plots in year 3 and greater in burn + herbicide and burn-only than herbicide-only ($\bar{x} = 42$ kg/ha vs. $\bar{x} = 14$ kg/ha) plots in year 9. Legume biomass within herbicide-only plots was similar to controls in all years. Herbicide application reduced woody plant biomass relative to controls in year 1, with burn-only plots intermediate. Woody plant biomass switched response by year 7 in which woody plant biomass ($\bar{x} = 36$ kg/ha) in

Table 2. Least-square mean biomass estimates (kg/ha) of important white-tailed deer forages from intensively managed pine plantations following mid-rotation treatments of prescribed fire (yr 1, 4, and 7) and imazapyr herbicide (yr 0) in Kemper County, Mississippi, USA, 2000–2008.

| Forage class | Yr | P-values ^a | Treatment | | | | SE |
|-----------------|----------------|-----------------------|-----------|-----------|------------------|---------|-----------------|
| | | | Burn | Herbicide | Burn + herbicide | Control | |
| Forb | 1 ^b | ≤0.001 | 15 B | 1 B | 33 A | 2 B | 5 ^c |
| | 2 | 0.034 | 66 B | 218 AB | 692 A | 18 B | 164 |
| | 3 | 0.787 | 10 | 9 | 13 | 3 | 7 |
| | 4 | 0.004 | 30 B | 6 B | 92 A | 4 B | 17 |
| | 5 | 0.054 | 6 | 2 | 30 | 4 | 8 |
| | 6 | 0.077 | 37 | 8 | 51 | 5 | 14 |
| | 7 | 0.108 | 86 | 5 | 89 | 33 | 28 |
| | 8 | 0.200 | 33 | 9 | 41 | 18 | 11 |
| | 9 | 0.675 | 23 | 5 | 11 | 15 | 10 |
| Grass | 1 | 0.203 | 26 | 1 | 6 | 24 | 10 |
| | 2 | 0.154 | 22 | 13 | 82 | 7 | 25 |
| | 3 | ≤0.001 | 23 BC | 67 B | 123 A | 10 C | 16 |
| | 4 | 0.021 | 43 B | 43 B | 97 A | 27 B | 16 |
| | 5 | 0.036 | 11 B | 31 AB | 60 A | 7 B | 13 ^c |
| | 6 | 0.031 | 108 AB | 66 B | 143 A | 33 B | 26 |
| | 7 | 0.006 | 68 B | 29 B | 133 A | 38 B | 21 |
| | 8 | 0.007 | 94 B | 45 B | 222 A | 40 B | 38 |
| | 9 | ≤0.001 | 58 B | 21 C | 114 A | 14 C | 12 |
| Herbaceous vine | 1 | 0.999 | 0 | 0 | 0 | 0 | 1 |
| | 2 | 0.009 | 1 B | 1 B | 1 B | 5 A | 1 |
| | 3 | 0.002 | 3 AB | 0 B | 0 B | 5 A | 1 |
| | 4 | 0.160 | 1 | 1 | 3 | 0 | 1 |
| | 5 | 1.000 | 0 | 0 | 0 | 0 | 1 |
| | 6 | 0.293 | 1 | 1 | 3 | 1 | 1 |
| | 7 | 0.005 | 1 B | 1 B | 5 A | 1 B | 1 |
| | 8 | 0.983 | 0 | 0 | 0 | 0 | 1 |
| | 9 | 1.000 | 0 | 0 | 0 | 0 | 1 |
| Legume | 1 | 0.146 | 9 | 0 | 1 | 2 | 3 |
| | 2 | 0.481 | 3 | 1 | 1 | 1 | 1 |
| | 3 | 0.032 | 2 C | 11 AB | 13 A | 3 BC | 3 |
| | 4 | 0.629 | 4 | 2 | 4 | 2 | 1 |
| | 5 | 0.065 | 28 | 7 | 20 | 8 | 6 ^c |
| | 6 | 0.076 | 47 | 11 | 37 | 16 | 11 |
| | 7 | 0.412 | 25 | 14 | 37 | 15 | 11 |
| | 8 | 0.222 | 36 | 9 | 30 | 11 | 11 |
| | 9 | 0.019 | 45 A | 14 B | 39 A | 17 AB | 8 |
| Semiwoody vine | 1 | 0.701 | 82 | 86 | 104 | 101 | 17 |
| | 2 | 0.543 | 160 | 160 | 181 | 116 | 33 |
| | 3 | ≤0.001 | 88 C | 174 B | 271 A | 78 C | 21 ^d |
| | 4 | 0.002 | 74 B | 170 A | 210 A | 70 B | 28 ^d |
| | 5 | 0.002 | 43 B | 72 B | 121 A | 44 B | 15 |
| | 6 | 0.041 | 147 AB | 149 AB | 225 A | 92 B | 31 |
| | 7 | ≤0.001 | 66 B | 138 A | 157 A | 60 B | 17 |
| | 8 | 0.002 | 90 B | 83 B | 139 A | 50 B | 15 ^d |
| | 9 | ≤0.001 | 56 BC | 62 B | 127 A | 26 C | 13 |
| Woody plant | 1 | 0.031 | 31 AB | 10 B | 3 B | 46 A | 10 |
| | 2 | 0.710 | 50 | 53 | 51 | 23 | 21 |
| | 3 | 0.328 | 41 | 32 | 15 | 40 | 11 |
| | 4 | 0.503 | 10 | 6 | 14 | 10 | 4 |
| | 5 | 0.539 | 33 | 18 | 18 | 26 | 9 |
| | 6 | 0.052 | 44 | 29 | 26 | 7 | 9 |
| | 7 | 0.011 | 32 AB | 36 A | 17 BC | 11 C | 6 |
| | 8 | 0.057 | 57 | 50 | 26 | 21 | 11 |
| | 9 | 0.075 | 39 | 72 | 52 | 23 | 13 |
| Woody vine | 1 | 0.003 | 46 A | 2 B | 2 B | 27 AB | 8 ^c |
| | 2 | 0.174 | 27 | 18 | 13 | 34 | 7 |
| | 3 | ≤0.001 | 69 A | 23 B | 10 B | 74 A | 11 |
| | 4 | 0.029 | 74 AB | 39 B | 35 B | 96 A | 15 ^c |
| | 5 | 0.456 | 33 | 16 | 23 | 23 | 7 |
| | 6 | 0.002 | 99 A | 69 A | 33 B | 83 A | 11 |
| | 7 | 0.197 | 47 | 61 | 29 | 63 | 12 |
| | 8 | 0.295 | 86 | 72 | 46 | 66 | 15 |
| | 9 | 0.538 | 78 | 58 | 60 | 80 | 14 |

^a P-values are for within-yr treatment comparisons.

^b Within yr, treatments with the same letter do not differ significantly ($P > 0.05$).

^c SE differed in one treatment/forage class within designated yr as follows: burn + herbicide_{forb} = 4, control_{grass} = 14, control_{legume} = 7.

herbicide-only plots was greater than woody plant biomass ($\bar{x} = 14$ kg/ha) in burn + herbicide plots and woody plant biomass in controls. Woody plant biomass in burn and burn + herbicide treatments was similar in all years. Woody vine biomass differed among treatments in years 1, 3, 4, and 6 and was consistently greater in control and burn-only ($\bar{x} = 71$ kg/ha) than in burn + herbicide ($\bar{x} = 20$ kg/ha) treatments but was significantly greater only in years 3, 4, and 6 for control and years 1, 3, and 6 for burn-only. Species richness among moderate- to high-use deer forages differed among treatments in years 2–3 and 6–9. Species richness in burn-only plots was greater than herbicide-only plots each year and controls in years 6–9 but always similar to species richness in burn + herbicide plots. Herbicide treatments (herbicide-only and burn + herbicide) were similar in years 2, 6, and 7. By years 8 and 9, burn treatments had the greatest species richness.

We analyzed protein content for 66 important deer forage species out of 390 species we collected across all treatment plots and years. Nearly all (65 of 66 species) were used in at least one lactation-level estimate (Table 3). Both diet quality levels had treatment \times year interactions (Table 1). For lactation-level estimates, nutritional CC averaged 4 times greater in burn + herbicide ($\bar{x} = 275$ deer-days/ha) than control ($\bar{x} = 69$ deer-days/ha) plots in every year except year 5 (Table 4). Neither herbicide-only nor burn-only treatments consistently improved CC relative to controls. Carrying capacity in herbicide-only plots was greater than controls in year 3 and was greater in burn-only plots than controls in years 8 and 9. Maintenance-level estimates produced a similar pattern. In years 2–9, CC in burn + herbicide ($\bar{x} = 376$ deer-days/ha) plots was 2 times greater than controls ($\bar{x} = 141$ deer-days/ha). Likewise, CC in herbicide-only plots was greater than controls in years 3 and 6 and greater in burn-only plots than controls in years 6, 8, and 9.

DISCUSSION

Prescribed fire and herbicide had a synergistic effect on deer nutritional CC, increasing it more consistently than either fire or herbicide alone. Burning alone resulted in hardwood midstory reduction, but treatment with fire in combination with herbicide created a well-defined, 2-tiered vegetation structure through more effective removal of midstory hardwoods (R. B. Iglay, Mississippi State University, unpublished data). This improved midstory control by herbicide treatment promoted development of important understory deer forages and increased CC. Maintenance-level CC clearly reflected overall forage biomass, because virtually all species were of sufficient quality to be included in CC models, similar to results from other studies (Hobbs and Swift 1985, McCall et al. 1997, Jones et al. 2009). Demands of lactation were supported primarily by greater

protein forbs and legumes and also by large amounts of sawtooth blackberry (*Rubus argutus*). Woody vines that comprised roughly 66% of forage biomass in control plots had generally lesser protein content and, thus, contributed less to the lactation diet. Thus, lactation CC estimates did not correspond as well with forage-class biomass.

Hurst et al. (1979), in Mississippi, USA, pine plantations, reported a positive correlation between an established hardwood midstory and overall woody biomass. Fire and herbicide reduced hardwood midstory trees on our sites (Thompson 2002; Woodall 2005; R. B. Iglay, unpublished data), possibly releasing an herbaceous understory of forbs, grasses, and semiwoody vines. Additionally in our study, herbicide treatments (herbicide-only and burn + herbicide) substantially reduced biomass of woody plants and woody vines immediately following initial treatment application. However, the effect on woody plant biomass was short-lived, possibly due to resprouting shrubs and trees and the low application rate of imazapyr. Fire may have prolonged herbicide effects by maintaining a 2-tiered vegetation structure with resprouting stems restricted to the bottom tier. Without fire, resprouting stems could eventually cover shade-intolerant, high-use forage species.

Forbs and legumes had limited responses to our treatments but were important contributors to deer CC estimates. Prescribed fire in pine stands has been shown to release forbs and legumes, but most studies focused on overall understory plant response, not only moderate- to high-use deer forage species (Masters et al. 1996, Brennan et al. 1998, Edwards et al. 2004, Welch et al. 2004). Although we did not detect overall treatment effects on legume biomass, burned plots tended to have a greater legume biomass than unburned plots during years 5–9. Additionally in our study, forb biomass increased immediately following the initial herbicide application and second and third burns but then decreased steadily, possibly due to canopy closure (R. B. Iglay, unpublished data). Prescribed fire may have stimulated these forage classes more than herbicide by providing multiple seed-catchment opportunities through mineral soil exposure and seed scarification (Brennan et al. 1998). Prescribed fire also caused increased species richness of moderate- to high-use deer forages.

Semiwoody vines and grasses were the only forage classes with consistent responses to treatments. Both responded well to prescribed fire and low-rate imazapyr herbicide but also were dominated by a few species. Semiwoody vine biomass used for lactation-level CC estimates was mostly (96.5%) composed of *Rubus* spp. and Japanese honeysuckle (*Lonicera japonica*). Slender woodoats (*Chasmanthium laxum*), variable panicgrass (*Dichantheium commutatum*), and open flower rosette grass (*D. laxiflorum*) contributed 90.7% of grass biomass. All of these species are uncontrolled by low-level imazapyr application (BASF Corporation

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^d Semiwoody plant SE differed across treatments/designated yr as follows: control_{year 3} = 22, control_{year 5} = 17, herbicide_{year 9} and control_{year 9} = 17.

^e Woody vine SEs differed across treatments/designated yr as follows: burn-only_{year 1} and herbicide-only_{year 1} = 9, burn-only_{year 4} = 16.

Table 3. Biomass (kg/ha) and crude protein (CP) of species used for lactation-level (14% CP) white-tailed deer carrying-capacity estimates in intensively managed pine plantations of Kemper County, Mississippi, USA, treated with factorial arrangements of prescribed fire and imazapyr herbicide, 1999–2008.

| Forage class | Species | Biomass | | | | CP | |
|--|---|--|-----------|------------------|---------|------|-----|
| | | Burn | Herbicide | Burn + herbicide | Control | | |
| Forb | American burnweed (<i>Erechtites hieraciifolia</i>) | 152 | 1,001 | 1,290 | 117 | 16.6 | |
| | American pokeweed (<i>Phytolacca americana</i>) | 195 | 139 | 97 | 120 | 11.0 | |
| | Anisescented goldenrod (<i>Solidago odora</i>) | 4 | 6 | 33 | 0 | 9.7 | |
| | Blackeyed Susan (<i>Rudbeckia hirta</i>) | 0 | 0 | 8 | 0 | 8.2 | |
| | Blue Ridge horsebalm (<i>Collinsonia serotina</i>) | 4 | 11 | 19 | 6 | 14.2 | |
| | Canada goldenrod (<i>Solidago altissima</i>) | 577 | 63 | 1,012 | 28 | 20.1 | |
| | Carolina vetch (<i>Vicia caroliniana</i>) | 26 | 7 | 35 | 4 | 17.2 | |
| | Carolina wild petunia (<i>Ruellia caroliniensis</i>) | 8 | 1 | 17 | 3 | 8.9 | |
| | Common ragweed (<i>Ambrosia artemisiifolia</i>) | 472 | 149 | 2,722 | 20 | 19.2 | |
| | Common sneezeweed (<i>Helenium autumnale</i>) | 12 | 15 | 5 | 5 | 9.6 | |
| | Common yellow oxalis (<i>Oxalis stricta</i>) | 29 | 6 | 35 | 2 | 11.5 | |
| | Downy lobelia (<i>Lobelia puberula</i>) | 2 | 1 | 1 | 0 | 13.6 | |
| | Greater tickseed (<i>Coreopsis major</i>) | 5 | 0 | 0 | 0 | 6.8 | |
| | Hairy white oldfield aster (<i>Symphotrichum pilosum</i>) | 22 | 5 | 24 | 9 | 13.2 | |
| | Lateflowering thoroughwort (<i>Eupatorium serotinum</i>) | 121 | 73 | 731 | 149 | 20.3 | |
| | Lesser snakeroot (<i>Ageratina aromatica</i>) | 0 | 0 | 10 | 0 | 10.2 | |
| | Maryland meadowbeauty (<i>Rhexia mariana</i>) | 10 | 2 | 17 | 4 | 15.1 | |
| | Seedbox (<i>Ludwigia alternifolia</i>) | 3 | 0 | 40 | 7 | 10.0 | |
| | Swamp smartweed (<i>Polygonum hydropiperoides</i>) | 0 | 12 | 57 | 21 | 20.6 | |
| | Violet (<i>Viola</i> spp.) | 0 | 0 | 1 | 0 | 7.7 | |
| | Woodland sunflower (<i>Helianthus divaricatus</i>) | 54 | 2 | 18 | 6 | 13.2 | |
| | Total forb | | 1,696 | 1,493 | 6,172 | 501 | |
| | Grass | Cypress panicgrass (<i>Dichanthelium dichotomum</i>) | 19 | 0 | 16 | 2 | 8.7 |
| Hairy crabgrass (<i>Digitaria sanguinalis</i>) | | 0 | 0 | 34 | 0 | 9.4 | |
| Openflower rosette grass (<i>Dichanthelium laxiflorum</i>) | | 138 | 27 | 377 | 0 | 8.7 | |
| Rosette grass (<i>Dichanthelium aciculare</i>) | | 0 | 0 | 5 | 0 | 8.3 | |
| Slender woodoats (<i>Chasmanthium laxum</i>) | | 107 | 4 | 456 | 34 | 9.2 | |
| Variable panicgrass (<i>Dichanthelium commutatum</i>) | | 19 | 21 | 487 | 0 | 8.3 | |
| Vasey's grass (<i>Paspalum urvillei</i>) | | 93 | 0 | 2 | 0 | 5.7 | |
| Total grass | | 376 | 52 | 1,374 | 36 | | |
| Herbaceous vine | Man of the earth (<i>Ipomoea pandurata</i>) | 41 | 25 | 82 | 68 | 14.7 | |
| Legume | Atlantic pigeonwings (<i>Clitoria mariana</i>) | 10 | 6 | 15 | 9 | 23.9 | |
| | Boykin's clusterpea (<i>Dioclea multiflora</i>) | 1,017 | 304 | 935 | 381 | 18.3 | |
| | Creeping lespedeza (<i>Lespedeza repens</i>) | 88 | 38 | 19 | 26 | 14.7 | |
| | Slender lespedeza (<i>Lespedeza virginica</i>) | 1 | 0 | 21 | 0 | 13.1 | |
| | Smooth ticktrefoil (<i>Desmodium laevigatum</i>) | 20 | 23 | 34 | 0 | 11.0 | |
| | Trailing lespedeza (<i>Lespedeza procumbens</i>) | 17 | 5 | 15 | 0 | 10.7 | |
| | Total legume | | 1,153 | 376 | 1,039 | 416 | |
| Semiwoody vine | Evening trumpetflower (<i>Gelsemium sempervirens</i>) | 34 | 17 | 11 | 4 | 13.3 | |
| | Japanese honeysuckle (<i>Lonicera japonica</i>) | 805 | 588 | 940 | 189 | 10.4 | |
| | Northern dewberry (<i>Rubus flagellaris</i>) | 138 | 3 | 465 | 6 | 8.9 | |
| | Sawtooth blackberry (<i>Rubus argutus</i>) | 2,666 | 4,868 | 6,782 | 2,079 | 14.1 | |
| Total semiwoody vine | | 3,643 | 5,476 | 8,198 | 2,278 | | |
| Woody plant | American beautyberry (<i>Callicarpa americana</i>) | 501 | 694 | 624 | 146 | 15.2 | |
| | American black elderberry (<i>Sambucus nigra</i>) | 7 | 27 | 13 | 10 | 21.0 | |
| | Bitternut hickory (<i>Carya cordiformis</i>) | 9 | 47 | 0 | 1 | 11.5 | |
| | Blackgum (<i>Nyssa sylvatica</i>) | 12 | 0 | 33 | 0 | 9.1 | |
| | Carolina rose (<i>Rosa carolina</i>) | 0 | 4 | 5 | 0 | 5.0 | |
| | Cherrybark oak (<i>Quercus pagoda</i>) | 13 | 0 | 0 | 16 | 9.6 | |
| | Chinese privet (<i>Ligustrum sinense</i>) | 0 | 2 | 0 | 31 | 17.0 | |
| | Eastern baccharis (<i>Baccharis halimifolia</i>) | 39 | 41 | 43 | 11 | 20.1 | |
| | Elliot's blueberry (<i>Vaccinium elliotii</i>) | 1 | 4 | 4 | 0 | 9.8 | |
| | Farkleberry (<i>Vaccinium arboreum</i>) | 0 | 20 | 27 | 0 | 4.8 | |
| | Green ash (<i>Fraxinus pennsylvanica</i>) | 1 | 0 | 13 | 2 | 12.9 | |
| | Partridgeberry (<i>Mitchella repens</i>) | 0 | 3 | 5 | 0 | 15.5 | |
| | Pignut hickory (<i>Carya glabra</i>) | 64 | 83 | 43 | 20 | 14.4 | |
| | Red buckeye (<i>Aesculus pavia</i>) | 112 | 120 | 29 | 12 | 13.9 | |
| | Red maple (<i>Acer rubrum</i>) | 90 | 184 | 98 | 12 | 10.0 | |
| | Southern red oak (<i>Quercus falcata</i>) | 0 | 0 | 0 | 7 | 8.2 | |
| | St. Andrew's cross (<i>Hypericum hypericoides</i>) | 7 | 9 | 36 | 1 | 12.4 | |
| | Winged elm (<i>Ulmus alata</i>) | 16 | 74 | 39 | 63 | 21.2 | |
| | Winged sumac (<i>Rhus copallinum</i>) | 51 | 0 | 2 | 0 | 8.9 | |
| | Total woody plant | | 923 | 1,312 | 1,014 | 332 | |

Table 3. Continued.

| Forage class | Species | Biomass | | | | |
|--------------|---|---------|-----------|------------------|---------|------|
| | | Burn | Herbicide | Burn + herbicide | Control | CP |
| Woody vine | Alabama supplejack (<i>Berchemia scandens</i>) | 13 | 30 | 16 | 25 | 10.4 |
| | Cat greenbrier (<i>Smilax glauca</i>) | 67 | 64 | 29 | 24 | 11.8 |
| | Eastern poison ivy (<i>Toxicodendron radicans</i>) | 1,232 | 531 | 277 | 878 | 12.5 |
| | Muscadine grape (<i>Vitis rotundifolia</i>) | 469 | 353 | 550 | 265 | 11.1 |
| | Saw greenbrier (<i>Smilax bona-nox</i>) | 22 | 0 | 21 | 1 | 9.2 |
| | Summer grape (<i>Vitis aestivalis</i>) | 69 | 9 | 52 | 8 | 10.2 |
| | Virginia creeper (<i>Parthenocissus quinquefolia</i>) | 61 | 66 | 209 | 6 | 9.8 |
| | Total woody vine | 1,933 | 1,053 | 1,154 | 1,207 | |

2006). Had these species not been important deer forages, our nutritional CC results could have been much different. Special care is needed when choosing a selective herbicide if undesirable plants could gain a competitive advantage. Although releasing these species was not our intention, our application rate was consistent with Weyerhaeuser NR Company policy and recommended based on hardwood midstory control and support of wildlife-friendly plants.

Treatment response delay, community composition, shade tolerance, and fertilization may have impacted high-use deer forage response after prescribed fire or imazapyr. Immediately following initial treatment application, most treatment plots experienced a delay (2 yr) in plant response similar to that reported by Mixon et al. (2009). Herbicide, with and without prescribed fire, did not substantially reduce plant biomass until the second growing season posttreatment. Plant community composition was strongly influenced by dominance of common ragweed (*Ambrosia artemisiifolia*) in one burn + herbicide plot in year 2, affecting estimates of forb biomass. Forb biomass in burn-only and herbicide-only

plots may have been more comparable to burn + herbicide without this extreme observation. As with semiwoody vines and grasses, biomasses of other forage classes were comprised mostly of a few species. Poison ivy (*Toxicodendron radicans*) and muscadine grape (*Vitis rotundifolia*) dominated (85.2%) woody vine biomass similar to common ragweed (34.1%) and American burnweed (*Erechtites hieraciifolia*: 25.96%) for forbs and American beautyberry (*Callicarpa americana*: 54.87%) for woody plants. Slender woodoats, poison ivy, muscadine grape, and American beautyberry are shade-tolerant, enabling them to thrive under a closing canopy, unlike semiwoody vine and forb species in our study plots. Shade-tolerant plants could thrive in all treatment plots regardless of canopy coverage if unaffected by treatments. Maintaining an open canopy, which was enhanced by heavy thinning in our study plots (see below), is another contribution of the combined treatment for increased biomass of greater CP forbs and semiwoody vines. Fertilization effects from our 2001 application seemed to have had a time-limited impact on understory plant growth

Table 4. Least-square mean estimates (SE) of white-tailed deer nutritional carrying capacity (deer-days/ha) based on mean diet qualities of 14% and 6% crude protein in intensively managed pine plantations treated with prescribed fire (yr 1, 4, and 7) and imazapyr herbicide (yr 0) in Kemper County, Mississippi, USA, 2000–2008.

| Protein | Yr | P-values ^a | Treatment | | | | | | | |
|---------|----------------|-----------------------|-----------|-----|-----------|-----|------------------|-----|-----------|-----------------|
| | | | Burn | | Herbicide | | Burn + herbicide | | Control | |
| | | | \bar{x} | SE | \bar{x} | SE | \bar{x} | SE | \bar{x} | SE |
| 14% | 1 ^b | 0.031 | 68 AB | 21 | 60 B | 20 | 107 A | 20 | 38 B | 19 ^c |
| | 2 | 0.002 | 158 B | 115 | 338 B | 115 | 750 A | 115 | 90 B | 115 |
| | 3 | 0.002 | 66 B | 26 | 147 A | 25 | 178 A | 25 | 53 B | 25 |
| | 4 | 0.007 | 86 B | 43 | 120 B | 43 | 256 A | 43 | 39 B | 43 |
| | 5 | 0.184 | 82 | 28 | 71 | 27 | 124 | 27 | 47 | 28 |
| | 6 | 0.049 | 218 AB | 48 | 134 B | 48 | 272 A | 48 | 99 B | 47 |
| | 7 | 0.030 | 164 B | 40 | 125 B | 39 | 256 A | 39 | 98 B | 39 |
| | 8 | 0.013 | 178 AB | 32 | 113 BC | 31 | 203 A | 31 | 74 C | 31 |
| | 9 | 0.006 | 148 AB | 26 | 101 BC | 25 | 176 A | 25 | 60 C | 25 |
| 6% | 1 | 0.004 | 152 A | 18 | 79 B | 18 | 110 AB | 18 | 145 A | 18 |
| | 2 | 0.004 | 242 B | 112 | 345 B | 112 | 752 A | 112 | 146 B | 112 |
| | 3 | ≤0.001 | 172 C | 24 | 236 B | 23 | 327 A | 24 | 152 C | 24 |
| | 4 | 0.008 | 172 B | 39 | 201 B | 39 | 336 A | 39 | 150 B | 39 |
| | 5 | 0.012 | 112 B | 27 | 111 B | 27 | 201 A | 27 | 76 B | 29 |
| | 6 | 0.011 | 354 A | 47 | 250 A | 47 | 381 A | 47 | 171 B | 47 |
| | 7 | 0.008 | 238 B | 37 | 214 B | 36 | 344 A | 37 | 158 B | 37 |
| | 8 | 0.003 | 291 AB | 41 | 202 BC | 41 | 372 A | 41 | 149 C | 41 |
| | 9 | 0.001 | 219 B | 28 | 174 BC | 28 | 296 A | 28 | 125 C | 28 |

^a P-values are for within-yr treatment comparisons.

^b Within yr, treatments with the same letter do not differ significantly ($P > 0.05$).

^c SE differed across treatments for both protein levels/designated yr as follows: burn + herbicide_{year 5} = 27 and herbicide-only_{year 5} = 27.

with increased growth only evident in the year of application. Although fertilization can influence CP content, such effects are generally short-lived, and we assumed that crude protein values in our year 8 samples were not influenced by fertilization (Kinard 1977, Wood 1986, Hafley et al. 1987).

Overstory thinning practices also influence deer carrying capacity by impacting amount of sunlight penetrating to the forest floor (Blair and Enghardt 1976, Conroy et al. 1982, Masters et al. 1995, Peitz et al. 1999), similar to hardwood midstory canopy reduction by fire and imazapyr herbicide (Waldrop et al. 1987, Van Lear 2000, Sladek et al. 2008). However, hardwood canopies typically reduce forest-floor sunlight more than pine canopies, and thinning effects are short-lived (Guo and Shelton 1998, Miller et al. 1999b, Peitz et al. 1999). Regardless, Weyerhaeuser NR Company thins heavily (12.3–15.9 m²/ha postthin) to promote growth of sawtimber-class trees. Larger canopy openings associated with reduced overstory basal area may increase positive impacts of fire and herbicide by providing greater opportunity for herbaceous understory plant growth (Thompson et al. 1991). Integration of fire and herbicide with heavy thinning regimes may further improve deer nutritional carrying capacity in intensively managed pine stands by supporting increased herbaceous growth.

MANAGEMENT IMPLICATIONS

Mid-rotation pine management using fire and herbicide in an intensively managed system can increase deer nutritional CC through production of deer forages with greater CP content. Prescribed fire and herbicide by themselves are not as effective. Initial plant response (≤ 2 yr posttreatment) following herbicide and fire may not reflect long-term results, and a consistent fire return interval may extend combination treatment effects. Prescribed fire has been associated with reduced pine growth, but growth restrictions are caused typically by crown scorch (Waldrop et al. 1992, McInnis et al. 2004). Following carefully designed fire prescriptions can avoid crown scorch in mid-rotation pine plantations (Wade and Lunsford 1989, Bessie and Johnson 1995, Schimmel and Granstrom 1997). Managers may prefer not to burn because of smoke management issues, limited number of burning degree days, and liability concerns, but benefits of fire to white-tailed deer and numerous other wildlife species of the southeastern United States merit its use. We strongly encourage managers to use prescribed fire in mid-rotation intensively managed pine plantations wherever possible to promote plant species richness and promote habitat management to support sustainable forestry concepts. Herbicide and fire effects may vary by site characteristics including soil type, seed bank, and topography (Wade and Lunsford 1989, Miller and Miller 2004). Overall treatment response patterns in southeastern pine plantations are expected to be similar to our results and those of past studies in that combining fire and herbicide can increase herbaceous biomass and improve deer foraging environment. Therefore, within pine stands with a well-established hardwood midstory (>3 – 5 yr

postthin in most cases), we recommend a one-time imazapyr application coupled with dormant season prescribed fire on a 3-year return interval to improve nutritional CC for deer in intensively managed, thinned mid-rotation pine stands of the southeastern United States.

ACKNOWLEDGMENTS

We thank Weyerhaeuser NR Company, National Council for Air and Stream Improvement, BASF Corporation, Mississippi State University Forest and Wildlife Research Center, the National Wild Turkey Federation (NWTf), and the Mississippi Chapter of NWTf for their funding and support for this project.

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Associate Editor: Hall.