White-Tailed Deer Foraging Habitat in Intensively Established Loblolly Pine Plantations

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ABSTRACT Stand establishment techniques involving multiple herbicide applications are commonly used on industrial pine (*Pinus* spp.) plantations, raising concern over potential effects on white-tailed deer (*Odocoileus virginianus*) forage production. We tested effects of stand establishment intensity on deer forage in 1–5-year-old loblolly pine (*Pinus taeda*) plantations ($n = 4$) in the East Gulf Coastal Plain of Mississippi using forage biomass and 4 measures of nutritional carrying capacity that reflected crude protein or digestible energy requirements for body maintenance and lactation. We also assessed whether forage biomass combined with a deer use rating effectively indexed nutritional carrying capacity. Treatments were combinations of mechanical site preparation, chemical site preparation (CSP), and herbaceous weed control (HWC). Total forage biomass and forage biomass of grasses and forbs were reduced by broadcast HWC. Forage biomass of vines was reduced both by CSP and by multiple broadcast HWC applications. Maintenance-level carrying capacity estimates were reduced by broadcast HWC; lactation-level estimates were higher in moderate-intensity treatments. We believe the inherently low fertility of this region makes high-quality forage production a more important management priority than increasing forage quantity. Chemical or chemical and mechanical site preparation combined with banded HWC provided the best option for providing both forage quality and quantity in open-canopied, intensively managed pine plantations. Biomass-based indices may be suitable for indexing protein-based maintenance-level carrying capacity in this region, but our results indicated they were not useful for indexing other carrying capacity estimates. (JOURNAL OF WILDLIFE MANAGEMENT 73(4):488–496; 2009)

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Intensively managed pine (*Pinus* spp.) plantations play an important role in providing commercial wood products (Prestemon and Abt 2002). Industrial forest management strategies likely will continue to include increased use of herbicides (Wigley 2000). Management regimes may consist of chemical site preparation and ≥1 postplanting herbaceous weed control treatments. In 2002, approximately 286,000 ha of southern pine plantations received applications of herbaceous weed control, and 433,000 ha received chemical site preparation (Dubois et al. 2003), mostly relying on tank mixes of 2 or 3 herbicides (Shepard et al. 2004).

Maximizing timber yield often conflicts with maintaining habitat values for wildlife. Increases of up to 150% in timber volume are typical for pine species in the southeastern United States managed with herbicides (Wagner et al. 2004). However, increasing intensity of site preparation can reduce abundance and diversity of woody and herbaceous plants, depending on herbicide type (Miller et al. 1999), application rate (Zutter and Zedaker 1988), proportion of area receiving treatment (Schabenberger and Zedaker 1999), and additive effects of mechanical site preparation (Harrington and Edwards 1996).

The interval between planting and canopy closure often provides abundant white-tailed deer (*Odocoileus virginianus*) forage (Blair and Enghardt 1976, Johnson 1987). In previous research, single herbicide treatments generally had minor and temporary effects on plant communities (Zutter and Zedaker 1988, Miller et al. 1999). Studies comparing white-tailed deer habitat responses on chemically and mechanically prepared sites have consistently demonstrated that deer forage production was reduced for one growing season after site preparation, peaked 2–3 growing seasons posttreatment, and declined until canopy closure (Hurst and Warren 1980, Felix et al. 1986, Scanlon and Sharik 1986).

The silvicultural goal of intensive pine plantation establishment is to reduce vegetative competition with pine seedlings and shorten the time between planting and canopy closure, which may negatively affect habitat quality for white-tailed deer. We compared effects of 5 operational pine plantation establishment intensities on deer forage production and nutritional carrying capacity during years 1–5 postestablishment. We hypothesized that forage production and deer carrying capacity would decrease as treatment intensity increased. We also tested the utility of a carrying capacity index based on forage species biomass and deer use rating.

STUDY AREA

We studied deer forage on loblolly pine (*Pinus taeda*) plantations established at 4 industrial forest sites in George, Lamar, and Perry counties in the East Gulf Coastal Plain of Mississippi, USA (Bailey 1980). Stands were harvested during summer 2000–winter 2001 and averaged 66 ha. Common woody plants included sweetgum (*Liquidamabar styraciflua*), various oaks (*Quercus* spp.), common persimmon (*Diospyros virginiana*), various hollies (*Ilex* spp.), eastern baccharis (*Baccharis halimifolia*), *Vaccinium* spp., wax myrtle

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(*Myrica cerifera*), and American beautyberry (*Callicarpa americana*). Tungoil tree (*Vernicia fordii*) was common to 2 sites, which had previously been tungoil plantations. Common vines included lianas, such as poison ivy (*Toxicodendron radicans*), muscadine (*Vitis rotundifolia*), Virginia creeper (*Parthenocissus quinquefolia*), yellow jessamine (*Gelsemium sempervirens*), and various greenbriers (*Smilax* spp.), and early seral species such as sawtooth blackberry (*Rubus argutus*), southern dewberry (*R. trivialis*), and Japanese honeysuckle (*Lonicera japonica*). Herbaceous associates included threeawngrass (*Aristida* spp.), broomsedge (*Andropogon virginicus*), and various panic grasses (*Dicantheleum* spp.); forb communities were characterized by *Eupatorium* spp. and numerous asters (*Aster* spp., *Solidago* spp., and *Euthamia tenuifolia*). Two poorly drained sites had a strong sedge (*Carex* spp. and *Cyperus* spp.) and rush (*Juncus* spp.) component. The climate was subtropical, with mean annual temperature of 18.7° C and mean annual rainfall of 159 cm (National Oceanic and Atmospheric Administration 2008). Two soil associations occurred on the 4 stands (United States Department of Agriculture 1995). The McLaurin–Heidel–Prentiss association was common to 2 stands and was composed of gently sloping, well-drained sandy and loamy soils. The Prentiss–Rossella–Benndale association occurred on 2 stands and was characterized by poorly drained loamy and fine sandy loam soils.

Our selection of treatment elements was based on field conditions and silvicultural methods common to plantation management in the coastal southern United States. Drainage in this region is sometimes poor, and the rooting environment is often improved through mechanical site preparation using a combination plow to subsoil, disk, and bed (Morris and Lowery 1988, Smidt et al. 2005). The warm, moist environment promotes vigorous vegetative competition with planted pines, and herbicides are applied to target specific communities, as needed, to promote pine survival and long-term site dominance. Chemical site preparation typically targets residual woody species from the postharvest community (Shepard et al. 2004), although herbaceous plants are also impacted. Because each chemical has limited effectiveness, herbicides are often combined to ensure broad-spectrum control. Herbaceous weed control applications are typically made the spring after planting to reduce herbaceous competition and promote quick pine establishment (Shepard et al. 2004); application for multiple years has been shown to improve pine growth response (Miller et al. 2003).

METHODS

Study Design

Treatments were combinations of chemical site preparation (CSP), mechanical site preparation (MSP), and herbaceous weed control (HWC), designed to reflect the range of operational intensities used on industrial forests of the southeastern United States. We applied chemical site preparation at all sites during July–August 2001 (yr 0) using a mixture of 2.4 L/ha Chopper Emulsifiable Concentrate® (BASF Corp., Research Triangle Park, NC), 3.5 L/ha Accord® (Dow AgroSciences LLC, Indianapolis, IN), 3.5 L/ha Garlon 4® (Dow AgroSciences LLC), and 1% volume to volume ratio of Timberland 90® surfactant (UAP Timberland LLC, Monticello, AR) in a broadcast spray solution of 93.6 L/ha. We applied mechanical site preparation during September–December 2001 (yr 0) using a combination plow. We applied HWC during March–April 2002 (yr 1) and March–May 2003 (yr 2) consisting of 0.9 kg/ha Oustar® (E. I. du Pont de Nemours and Company, Inc., Wilmington, DE; sulfometuron methyl and hexazinone); we applied HWC either in a 1.5-m band over the tops of pine seedlings, resulting in 50% total coverage, or broadcast aerially over the entire experimental unit.

We associated treatment number with levels of herbicide use and mechanical disturbance during stand establishment to assign treatments ranging from least (treatment 1) to most (treatment 5) intensive. Treatment 1 consisted of MSP and 1-year banded HWC. Treatment 2 consisted of CSP and 1-year banded HWC. Treatment 3 combined both site preparation methods with 1-year HWC. Treatment 4 was identical to treatment 3 except that HWC was broadcast. Treatment 5 was identical to treatment 4 except for the addition of a second broadcast HWC treatment in year 2. We randomly assigned each treatment to an area $\geq$8 ha within each stand, creating a randomized complete block design with 4 replicates per treatment.

Apart from these treatments, management was standardized across all plots. Loblolly pines were planted on each site during winter 2001–2002 using 3.0- $\times$ 2.1-m spacing (1,551 trees/ha); each participating company used its own seedlings. Two sites were machine planted, and 2 sites were hand planted due to high coarse woody debris loads. All stands were fertilized in April 2002 with a broadcast application of di-ammonium phosphate at 280 kg/ha.

Sampling

We composed a list of potential deer forages from the literature (Warren and Hurst 1981, Miller and Miller 1999) and Mississippi Department of Wildlife, Fisheries and Parks biologists, ranking forages from 1 (limited use) to 4 (high use). We randomly placed 20 1-m^2 exclosures (Harlow 1977) within each experimental unit to sample production of forages with rankings of 3 or 4. We placed exclosures by 1 April and sampled during July 2002–2006, excluding a 30-m buffer zone along treatment boundaries to ensure uniformity; we sampled all treatments within each block within a 5-day period. We clipped and weighed leaves and growing stem tips to represent consumable plant portions for each species and collected 3 known-weight field samples of $\geq$30 g for each species. We dried these samples in a forced-air oven at 60° C for 72 hours, averaged resulting wet:dry ratios, and extrapolated dry weight biomass on a kg/ha basis for each species. We assigned species to forage classes and calculated dry weight forage biomass for forbs (non-leguminous), grasses, legumes, vines, woody species, and total forage.

Composite samples of each forage species were processed by the Mississippi State University Animal Nutrition Laboratory for crude protein (CP) and digestible energy (DE). Crude protein was determined using the Kjeldahl procedure (Helrich 1990). Gross energy was determined using a bomb calorimeter and digestibility by in vitro dry matter disappearance (Cherney et al. 1997) using rumen fluid from a fistulated steer. We calculated DE as the product of gross energy and digestibility. We report all nutritional values on a dry matter basis.

We used an explicit nutritional constraints model (Hobbs and Swift 1985) to determine treatment effects on nutritional carrying capacity by estimating deer-days of foraging capacity during the growing season at 2 levels of diet quality. We assumed a daily dry matter intake (DMI) of 1,360 g (Edwards et al. 2004), which is within the range of intake rates of white-tailed deer in the southern United States (Fowler et al. 1967, Asleson et al. 1996, Campbell and Hewitt 2005). For each treatment, we calculated 4 measures of nutritional carrying capacity based on maintenance requirements and lactation demands for DE and CP. For DE, we considered a target diet quality of 2.2 kcal DE/g DMI as sufficient for maintenance, based on a requirement of 159 kcal/kg$^{0.75}$/day (Hellickson and DeYoung 1997, McCall et al. 1997) for a 50-kg deer and a requirement of 3.25 kcal DE/g DMI as sufficient for a lactating female with one fawn (Campbell et al. 2002, adjusted for DMI). For CP-based estimates, we set target diet quality at 6% CP for maintenance (French et al. 1956, McEwen et al. 1957, Asleson 1996) and 14% CP to support a lactating female with one fawn (Verme and Ullrey 1984). Both lactation-level requirements should be more than adequate to support antler growth in males (Robbins 1993, Asleson 1996). We assumed that CP and DE content of forages provided an accurate relative comparison of forage quality among treatments. Although plant secondary compounds such as tannins can influence digestibility (Hanley et al. 1992), we assumed that any such effects were consistent among treatments and study areas.

To quantify a treatment's capacity to produce preferred deer forage, we calculated a total forage value (TFV) by multiplying projected biomass × use rating for each forage species rated 3 or 4, then summing the products within each experimental unit to yield one value (Jones et al. 1993). We compared these values with the nutritional carrying capacity estimates to determine their potential use as a carrying capacity index.

Data Analysis

We used a repeated measures, mixed model analysis of variance to test for main effects of year, treatment, and year × treatment interaction for biomass in each forage class, nutritional carrying capacity estimates, and TFV. We compared means among treatments ($n = 5$) and years ($n = 5$) using SAS PROC MIXED (SAS Institute, Cary, NC). We treated stand (i.e., block, $n = 4$) as the random effect, year as the repeated effect, and treatment × stand as the subject. For each analysis, we selected the best combination of data transformation, use of the random statement, and covariance structure, choosing the combination that minimized Akaike's Information Criterion corrected for small sample size (AIC_c; Littell et al. 2006, Gutzwiller and Riffell 2007). This is not a case of mixing analytical paradigms as warned against in Anderson et al. (2001); we analyzed only one a priori model and we did not use AIC_c to rank models, but rather to determine which analysis procedure made best use of the data. We determined whether log or square-root transformation improved AIC_c and used it accordingly. We selected the best covariance structure from among 1) autoregressive with treatment as a group, 2) autoregressive without treatment as a group, and 3) unstructured. We used the Kenwardroger adjustment in denominator degrees of freedom for repeated measures and small sample sizes (Littell et al. 2006, Gutzwiller and Riffell 2007). We considered differences significant if $P < 0.10$ (Tacha et al. 1982). We used LSMEANS SLICE to identify a treatment effect within years after a significant interaction (Littell et al. 2006). When main effects were significant, we conducted pairwise tests using Fisher's protected least significant difference (Carmer and Swanson 1973). For ease of data interpretation, we present actual means although we conducted most analyses on transformed data.

RESULTS

Forage Biomass

We detected treatment differences in 3 of 5 forage classes and in total forage biomass (Table 1). Broadcast HWC reduced biomass of forage grasses by 87% compared with treatments with banded HWC. Similarly, total forage biomass was 2 times greater in treatments with banded HWC than in treatment 5, which represented 2 broadcast HWC applications.

Year × treatment interactions for forb and vine forage biomass indicated treatment effects varied in relation to time since treatment. Broadcast HWC reduced forage biomass of forbs by 89% compared with banded HWC during the first growing season after establishment. During year 2, forb biomass was 1.9 times greater in treatments 3 and 4 than in treatments 1, 2, and 5. Vine biomass tended to reflect the treatment intensity gradient. Treatment 1 produced the greatest vine biomass in years 1–4, due to retention of residual vines from the preharvest stand and greater biomass of blackberry and dewberry (*Rubus* spp.). During year 1, treatment 1 produced 4 times more forage vine biomass than treatments 2, 4, and 5, with intermediate effects under treatment 3. After the second broadcast HWC application in year 2, vine biomass under treatment 1 was 62 times greater than under treatment 5 and nearly 3 times greater than under treatments 2–4. Effect size gradually decreased through years 3 and 4 until all treatments were equivalent in year 5.

Carrying Capacity Estimates and TFV

We estimated nutritional carrying capacity using biomass and nutritional parameters from 71 forage species, including 30 forbs, 2 grasses, 9 legumes, 12 vines, and 18 woody species. Crude protein values ranged from 3.4% to 19.4%,

Table 1. Consumable biomass (kg/ha) of moderate- to high-use white-tailed deer forages available in 1–5-year-old loblolly pine plantations established using 5 levels of intensity ranging from low (treatment 1) to high (treatment 5) in the Mississippi East Gulf Coastal Plain, USA, 2002–2006.[a]

		Treatment (trt)[b]												
		1		2		3		4		5		*P*-values[c]		
Forage class	Yr	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	Yr	Trt[d]	Yr × trt
Forb	1	110A	42	106A	69	138A	111	3B	2	23B	16	0.002	0.004	0.019
	2	76B	53	80B	61	178A	60	211A	87	150B	122		0.011	
	3	67	45	99	64	45	27	88	40	85	62		0.769	
	4	65	20	62	37	92	35	56	12	29	11		0.659	
	5	22	6	36	23	47	13	29	6	15	6		0.802	
Grass	All	51A	16	52A	17	44A	15	6B	3	7B	3	0.174	0.049	0.241
Legume	All	4	2	4	1	7	2	9	3	3	1	0.369	0.772	0.910
Vine	1	152A	34	64BC	30	92AB	49	26C	21	32BC	17	≤0.001	0.013	≤0.001
	2	448A	26	159B	36	222B	78	122B	40	7C	5		≤0.001	
	3	511A	128	280B	66	282B	72	183B	58	73C	22		≤0.001	
	4	395A	65	243B	16	258AB	28	177B	37	155B	35		0.034	
	5	199	30	132	11	156	25	144	27	98	15		0.532	
Woody	1	59	28	68	26	12	9	16	10	7	6	≤0.001	0.153	0.035
	2	47	14	54	23	93	36	92	40	82	41		0.872	
	3	50	12	88	35	119	68	56	22	77	31		0.829	
	4	154	36	99	35	75	24	101	50	112	29		0.613	
	5	80	22	83	28	92	16	96	28	136	51		0.900	
Total	1	335	71	319	156	366	222	48	23	66	16	≤0.001	0.021	0.268
	2	601	76	337	73	516	131	436	88	242	97			
	3	744	163	550	122	487	146	344	67	244	62			
	4	659	96	447	86	464	39	360	48	315	47			
	5	373	54	280	42	318	29	281	22	261	58			
	All	542A	54	367AB	47	430AB	56	294BC	38	226C	31			

[a] Actual means presented; we performed analysis on square-root transformed data.
[b] Within-yr treatment means followed by the same uppercase letter are not significantly different ($\alpha = 0.10$). Treatment differences correspond to least square means.
[c] *P*-values correspond to least square means. Degrees of freedom were as follows: $Yr_{Forb} = 4, 54.7$; $Trt_{Forb} = 4,20$; $Yr \times trt_{Forb} = 16, 55.4$; $Yr_{Grass} = 4, 30.5$; $Trt_{Grass} = 4, 7.28$; $Yr \times trt_{Grass} = 16, 31.6$; $Yr_{Legume} = 4, 60.3$; $Trt_{Legume} = 4, 21.2$; $Yr \times trt_{Legume} = 16, 59.9$; $Yr_{Vine} = 4, 59.8$; $Trt_{Vine} = 4, 18.4$; $Yr \times trt_{Vine} = 16, 59.2$; $Yr_{Woody} = 4, 60.3$; $Trt_{Woody} = 4, 19.6$; $Yr \times trt_{Woody} = 16, 59.7$; $Yr_{Total} = 4,12$; $Trt_{Total} = 4, 15$; $Yr \times trt_{Total} = 16, 17.9$.
[d] When Yr × trt is significant; trt *P*-values are for within-yr comparisons.

and DE ranged from 0.81 kcal/g to 3.73 kcal/g. Treatments resulted in more differences in protein-based estimates than in energy-based estimates at both maintenance and lactation levels (Tables 2–5).

Maintenance-level carrying capacity estimates based on CP responded negatively to increasing treatment intensity (Table 2). Estimates under treatment 1 were double those under treatments 4 and 5, with intermediate estimates under treatments 2 and 3. Broadcast HWC was primarily responsible for the reduction, although only treatment 1 differed from both treatments 4 and 5, indicating that CSP was also a factor. The second broadcast HWC in treatment 5 did not prevent estimates from increasing in year 2; however, the increase was not as great as in treatment 4, which did not receive the additional HWC application. Similarly, broadcast HWC seemed to be the primary factor influencing the year 4 treatment difference in DE-based carrying capacity (Table 3), where treatment 1 yielded estimates 2.3 times greater than treatments 4 and 5.

Unlike maintenance-level estimates, lactation-level carrying capacity estimates were generally greater under moderate-intensity treatments, indicating these treatments produced more nutritious forage than treatments 1 and 5. Within treatments 2–4, production of forage with greater CP was delayed by increasing management intensity, so that carrying capacity estimates peaked earlier in less intensive treatments (Table 4). In year 1, estimates were 5 times greater under treatment 2 than under other treatments. In year 2, treatment 3 produced estimates 16 times greater than did treatments 1, 4, and 5. In year 3, estimates under treatment 4 were 7 times greater than treatments 1, 2, and 5. Estimates for DE-based carrying capacity during year 1 were 13 times greater under treatments 2 and 3 than under other treatments (Table 5).

Response of TFV was negatively correlated with treatment intensity (Table 6). Because CP-based maintenance estimates used 99% of available forage biomass, TFV seemed to effectively index this estimator. The DE-based maintenance estimator averaged 64% use of available biomass and was less effectively indexed by TFV. The lactation-level estimators averaged 4% (CP) and 7% (DE) biomass incorporation and were not correlated with TFV.

DISCUSSION

Forage Development

Our treatment design facilitated comparisons between treatments with one differing component, clarifying effects of individual treatment elements. Mechanical site preparation worked in concert with chemical site preparation to suppress woody forages in year 1. Chemical site preparation

Table 2. Estimates of white-tailed deer carrying capacity (deer-days/ha) based on a mean diet quality of 6% crude protein in 1–5-year-old loblolly pine plantations established using 5 levels of intensity ranging from low (treatment 1) to high (treatment 5) in the Mississippi East Gulf Coastal Plain, USA, 2002–2006.[a]

		Treatment (trt)[b]					*P*-values[c]		
Yr		1	2	3	4	5	Yr	Trt	Yr × trt
1	$\bar{x}$	245	230	261	31	49	<0.001	0.021	0.257
	SE	52	111	162	16	10			
2	$\bar{x}$	440	248	377	321	176			
	SE	56	54	96	64	72			
3	$\bar{x}$	547	405	358	253	179			
	SE	120	89	108	49	46			
4	$\bar{x}$	484	329	340	264	231			
	SE	70	63	28	36	34			
5	$\bar{x}$	272	200	232	205	191			
	SE	39	27	22	16	43			
All	$\bar{x}$	397A	282ABC	313AB	215BC	165C			
	SE	40	34	41	28	23			

[a] Actual means presented; we performed analysis on square-root transformed data.
[b] Treatment means followed by the same uppercase letter are not significantly different ($\alpha = 0.10$). Treatment differences correspond to least square means.
[c] *P*-values correspond to least square means. Degrees of freedom were 4, 12 for yr; 4, 15 for treatment; and 16, 17.9 for interaction.

is typically applied to control remnant woody vegetation that may compete with planted pines; however, suppression of this woody component may also release the site for herbaceous plants (Miller et al. 1995, Edwards 2004, Mihalco 2004), increasing the opportunity for establishment of nutritious forbs and legumes.

Broadcast herbaceous weed control seemed to impact total forage biomass more than other treatment elements, but impacts were mostly confined to the year of application, similar to reports from other studies (Blake et al. 1987, Keyser et al. 2003, Keyser and Ford 2006). It is likely that banded HWC also reduced total forage production in year 1 compared with no HWC (Blake et al. 1987), but we had no opportunity to make this comparison. Broadcast HWC virtually eliminated forage grasses; forbs were similarly affected, but recovered the year after the application, similar to results from Blake et al. (1987). Because forage vines included both lianas and early seral species, they were sensitive to the combination of broadcast HWC and CSP.

Carrying Capacity Estimators

Treatment impacted both quantity of forage produced and distribution of forage quality. Maintenance-level carrying capacity estimates responded similarly to forage biomass because diet requirements were low enough to include most forage biomass in the models. Similarly, measures of forage biomass in Texas yielded carrying capacity rankings identical to those derived from nutritional constraints analysis at the maintenance level (McCall et al. 1997). Hobbs and Swift (1985) reported similar results for low-quality diets on burned vs. unburned range for mule deer (*Odocoileus hemionus*), but rankings reversed as target diet quality was increased due to non-equivalent distribution of high-quality forages. Likewise, lactation-level estimates in our study were not correlated with forage biomass, and treatment differ-

Table 3. Estimates of white-tailed deer carrying capacity (deer-days/ha) based on a mean diet quality of 2.2 kcal/g digestible energy in 1–5-year-old loblolly pine plantations established using 5 levels of intensity ranging from low (treatment 1) to high (treatment 5) in the Mississippi East Gulf Coastal Plain, USA, 2002–2006.[a]

		Treatment (trt)[b]					*P*-values[c]		
Yr		1	2	3	4	5	Yr	Trt[d]	Yr × trt
1	$\bar{x}$	117	162	88	11	33	<0.001	0.145	0.066
	SE	58	77	48	7	12			
2	$\bar{x}$	99	125	198	178	82		0.392	
	SE	32	55	73	42	17			
3	$\bar{x}$	185	293	197	130	103		0.654	
	SE	54	124	112	33	45			
4	$\bar{x}$	428A	305AB	315A	191B	179B		0.055	
	SE	79	74	30	54	42			
5	$\bar{x}$	197	198	212	167	158		0.701	
	SE	61	37	27	24	59			

[a] Actual means presented; we performed analysis on $\log_{10}$-transformed data.
[b] Treatment means followed by the same uppercase letter are not significantly different ($\alpha = 0.10$). Treatment differences correspond to least square means.
[c] *P*-values correspond to least square means. Degrees of freedom were 4, 12 for yr; 4, 15 for treatment; and 16, 17.9 for interaction.
[d] Treatment values are within-yr; yr and interaction values are overall.

Table 4. Estimates of white-tailed deer carrying capacity (deer-days/ha) based on a mean diet quality of 14% crude protein in 1–5-year-old loblolly pine plantations established using 5 levels of intensity ranging from low (treatment 1) to high (treatment 5) in the Mississippi East Gulf Coastal Plain, USA, 2002–2006.[a]

		Treatment (trt)[b]					*P*-values[c]		
Yr		1	2	3	4	5	Yr	Trt[d]	Yr × trt
1	$\bar{x}$	5.3B	32.2A	3.2B	3.2B	14.6B	0.542	0.070	0.025
	SE	4.1	19.1	2.0	2.9	14.4			
2	$\bar{x}$	2.0BC	18.2AB	26.6A	2.7BC	0.3C		0.072	
	SE	1.5	16.5	2.7	2.4	0.3			
3	$\bar{x}$	3.7B	5.5B	11.7AB	27.8A	2.8B		0.078	
	SE	1.6	4.9	6.0	10.1	2.6			
4	$\bar{x}$	4.0	9.7	13.1	15.7	4.8		0.655	
	SE	2.0	8.0	7.0	7.1	3.5			
5	$\bar{x}$	8.1	5.3	1.2	7.4	4.1		0.842	
	SE	4.7	4.3	0.5	3.4	1.8			

[a] Actual means presented; we performed analysis on square-root transformed data.
[b] Treatment means followed by the same uppercase letter are not significantly different ($\alpha = 0.10$). Treatment differences correspond to least square means.
[c] *P*-values correspond to least square means. Degrees of freedom were 4, 55.6 for year; 4, 14.8 for treatment; and 16, 55.9 for interaction.
[d] Treatment values are within-yr; yr and interaction values are overall.

ences were primarily attributable to differences in availability of high-quality forages.

At the lactation level, DE- and CP-based carrying capacity estimates ranked treatments differently, which contrasted with expectations, because protein and energy contents are often assumed to be closely correlated in forage plants (Westoby 1974, Robbins 1993). In our study, forage CP and DE were not correlated; thus, CP- and DE-based models often incorporated different species. Of the 71 species we tested, only 4 exceeded target diet quality for DE, 11 for CP, and no species exceeded both, which may have been partly attributable to low soil fertility in the East Gulf Coastal Plain of Mississippi (Pettry 1977, Jacobson 1984), which reduces protein content of individual forage species relative to more fertile regions of the state (Jones et al. 2008). In regions of greater fertility, we would expect to include a greater proportion of forage biomass in lactation-level models, possibly improving the correlation between the CP- and DE-based methods.

Deer often select forest clearings with greater biomass of high-quality forage (Bechwith 1964), even if overall forage biomass is lower than other areas (Stewart et al. 2000). Although greater forage biomass was produced without CSP, the lack of CSP reduced the opportunity for establishment of higher quality forages, particularly forbs. In treatments with CSP, using broadcast HWC eliminated most forb biomass in the year of application. In this region of limited soil nutrients, nutritional needs for lactating females were better served by combining CSP with banded HWC only.

Timing of peak forage value is important information for land managers. Maintenance-level carrying capacity estimates in all treatments typically peaked in years 2–3, similar to other studies of forage development in pine plantations, whether treated with MSP (Lewis et al. 1984, Johnson 1987), CSP (Blake et al. 1987, Gassett et al. 2000), or HWC (Keyser and Ford 2006). Lactation-level estimates were less comparable. Energy-based estimates

Table 5. Estimates of white-tailed deer carrying capacity (deer-days/ha) based on a mean diet quality of 3.25 kcal/g digestible energy in 1–5-year-old loblolly pine plantations established using 5 levels of intensity ranging from low (treatment 1) to high (treatment 5) in the Mississippi East Gulf Coastal Plain, USA, 2002–2006.[a]

		Treatment (trt)[b]					*P*-values[c]		
Yr		1	2	3	4	5	Yr	Trt[d]	Yr × trt
1	$\bar{x}$	0.5C	15.9A	13.0AB	0.1C	3.1BC	<0.001	0.014	0.091
	SE	0.3	8.0	8.7	0.1	2.9			
2	$\bar{x}$	5.4	1.0	2.8	0.3	3.8		0.614	
	SE	4.8	0.7	2.0	0.3	2.1			
3	$\bar{x}$	27.1	25.4	21.5	5.4	5.3		0.276	
	SE	13.2	21.5	13.7	0.4	2.5			
4	$\bar{x}$	90.6	23.1	44.9	19.6	19.0		0.152	
	SE	38.8	8.6	13.6	8.9	7.4			
5	$\bar{x}$	54.2	33.1	41.3	15.3	20.3		0.684	
	SE	40.0	13.6	16.4	4.8	5.6			

[a] Actual means presented; we performed analysis on $\log_{10}$-transformed data.
[b] Treatment means followed by the same uppercase letter are not significantly different ($\alpha = 0.10$). Treatment differences correspond to least square means.
[c] *P*-values correspond to least square means. Degrees of freedom were 4, 57.5 for yr; 4, 18.6 for treatment; and 16, 57.3 for interaction.
[d] Treatment values are within-yr; yr and interaction values are overall.

Table 6. Mean total forage value for 5 levels of establishment intensity in 1–5-year-old loblolly pine plantations established using 5 levels of intensity ranging from low (treatment 1) to high (treatment 5) in the Mississippi East Gulf Coastal Plain, USA, 2002–2006.

		Treatment (trt)[a]					*P*-values[b]		
Yr		1	2	3	4	5	Yr	Trt	Yr × trt
1	$\bar{x}$	1,189	1,080	1,190	158	232	<0.001	0.038	0.201
	SE	236	568	729	70	53			
2	$\bar{x}$	2,126	1,131	1,754	1,492	804			
	SE	273	241	415	296	291			
3	$\bar{x}$	2,693	1,958	1,695	1,146	827			
	SE	620	431	517	196	211			
4	$\bar{x}$	2,395	1,597	1,608	1,272	1,121			
	SE	343	291	141	202	170			
5	$\bar{x}$	1,292	986	1,097	984	909			
	SE	175	156	94	70	212			
All	$\bar{x}$	1,939A	1,350ABC	1,469AB	1,010BC	779C			
	SE	199	169	188	129	105			

[a] Treatment means followed by the same uppercase letter are not significantly different ($\alpha = 0.10$). Treatment differences correspond to least square means.
[b] *P*-values correspond to least square means. Degrees of freedom were 4, 12 for yr; 4, 15 for treatment; and 16, 17.9 for interaction.

tended to be greater in years 4 and 5 and protein-based estimates in moderately intensive treatments peaked during years 1–3.

None of the treatments in our study provided sustained high-quality foraging options for deer. Managers in this region should therefore incorporate landscape-scale considerations to enable deer to maintain a nutritional plane adequate for seasonal needs. Traditional management techniques, such as prescribed fire, retention of mast-producing hardwoods, and supplemental forage production should be implemented to create and maintain diverse foraging habitat (Yarrow and Yarrow 1999). Within pine stands, thinning increases ground-level production of important forage plants (Peitz et al. 1999), and use of selective herbicide and prescribed fire can increase availability of high-quality forage in both mid-rotation (Iglay et al. 2006, Ragsdale and Demarais 2006) and mature pine stands (Edwards et al. 2004).

The nutritional constraints model has prevented over-estimating carrying capacity by explicitly addressing diet quality, not just nutrient availability (Hobbs and Swift 1985). In our study, lactation-level carrying capacity estimates averaged only 7% those of maintenance-level, emphasizing the discrepancy between the ability of these sites to produce bulk versus high-quality forage. Had we required even marginally greater diet quality for lactating deer, carrying capacity estimates would have approached zero. Previous work comparing stand establishment regimes in the South has focused on forage quantity (Stransky and Halls 1978, Blake et al. 1987, Chamberlain and Miller 2006, Keyser and Ford 2006). Our results indicate such a focus may not sufficiently characterize the potential impact of pine plantation establishment regimes on deer, particularly in areas of limited soil fertility. Comparisons of nutritional carrying capacity should be made in other soil regions to test if plant communities resulting from various management regimes will provide similar levels of nutritional support for deer.

TFV

The simple vegetation sampling procedure used in the biomass-based TFV makes this approach easier than the more intensive process of gathering data to populate a nutritionally explicit carrying capacity model. Forage surveys are commonly used in management of ungulates because of an assumed relationship between forage measurement(s) and carrying capacity (Mackie 2000, Higgins et al. 2005). Edwards (2004) found neither forage coverage nor species richness were reliable indicators of differences in carrying capacity estimates calculated using a diet quality of 12% CP in the Mississippi East Gulf Coastal Plain. In our study, CP-based maintenance-level estimates were successfully indexed by TFV because most forage species met or exceeded the target diet quality of 6% CP. However, the wide range of forage digestibilities sharply reduced the correlation of TFV with DE-based estimates. Because high-quality forage did not represent a constant proportion of overall forage across treatments, TFV was not correlated with lactation-level estimates. With the exception of maintenance-level CP-based estimates, it seems unlikely that measures of forage biomass can be used as an informative index of nutritional carrying capacity in this region.

MANAGEMENT IMPLICATIONS

Access to high-quality forage may be limited in the East Gulf Coastal Plain of Mississippi and early seral stage pine plantations may represent a significant foraging option for deer. As such, managers should attempt to meet the requirements of the greatest seasonal demand, which is lactation. Although management options may be limited on ownerships where wood production is the primary objective, our results demonstrate that commonly employed pine management strategies may yield a considerable range of potential outcomes. Strategies that depend on producing bulk rather than quality forage may reduce deer habitat values in young plantations in this region of limited soil fertility. Superior levels of both lactation-level and maintenance-level carrying capacity were provided in chemically site-prepared stands followed by banded HWC. Therefore, we recommend combining CSP or CSP and MSP with, at most, banded HWC during pine plantation establishment to maximize the value of young plantations for high quality deer forage production in this region.

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