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Influences of herbivory and canopy opening size on forest regeneration in a southern bottomland hardwood forest

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Abstract

We examined the effects of white-tailed deer (*Odocoileus virginianus*) browsing and canopy opening size on relative abundance and diversity of woody and herbaceous regeneration in various sized forest openings in a southern, bottomland hardwood forest over three growing seasons (1995-1997). We created 36 canopy openings (gaps), ranging from 7 to 40 m in radius, by group selection timber harvest in December 1994. Fenced exclosnres were constructed in the'center of each gap and vegetation was sampled monthly from April to September. Plant species richness, diversity, evenness, relative abundance, and a browsing index were calculated for each gap size and for each exclosure type. Herbaceous richness, diversity, or evenness did not differ among exclosure types in any year of the study. Browsing index was higher in the controls in 1996 and 1997. Browsing index for woody species was highest in the controls in 1995 and 1997. Relative abundance of herbaceous species was highest in the 29 m gap size. in 1997. Richness and diversity of woody species were lowest in the 29 m gap size in 1995 and 1996. Overall browsing rates on both woody and herbaceous vegetation were low throughout all the 3 years of the study. Low browsing rates reflect seasonal changes in habitat use by deer. Because of the low rates of browsing, vegetative differences among exclosure treatments and gap sizes likely are not attributable to deer herbivory. Other factors, such as soil disturbance, may have influenced the initial vegetative response more than herbivory or gap size.

Keywords: White-tailed deer; Herbivory; Croup selection; Bottomland hardwoods; Regeneration; South Carolina

1. Introduction

Clearcutting is the most efficacious method of harvesting and regenerating shade intolerant southern bottomland hardwood tree species (Clatterbuck and Meadows, 1993). However, clearcutting may not be acceptable in certain situations, particularly where

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aesthetics are a concern. In these situations, such as along important viewsheds or where streamside protection merits alternative methods, group selection may be more acceptable. Although not generally recommended for regenerating bottomland hardwoods (Meadows and Stanturf, 1997), group selection harvests can be successful, but require more attention and more frequent stand entry (Kellison and Young, 1997).

Regenerating stands to a desirable mid-tolerant tree species composition in bottomland hardwoods requires the development of advanced regeneration prior to harvest (Johnson and Krinard, 1976; Hodges and Janzen, 1987). Even if advanced regeneration is adequate, maintenance of the regeneration may be adversely impacted by herbivory. For example, in northern hardwood forests, browsing by white-tailed deer can impact regeneration of commercial species and result in profound changes in species composition (Hough, 1965; Ross et al., 1970; Anderson and Loucks, 1979; Marquis, 1981; Tilghman, 1989).

Canopy opening size can influence the dynamics and effects of deer herbivory. Regeneration in smaller harvest units created by group selection often is more susceptible to damage and can result in reductions in regeneration and changes in species composition (Curtis and Rushmore, 1958; Ripley and Campbell, 1960; Harlow and Downing, 1969). Deer and other mammalian herbivores can impact woody seedling growth directly by browsing stems, or indirectly by changing herb layer composition which can affect growth and survival (Tilghman, 1989).

Browsing by white-tailed deer also can impact noncommercial plant species. Ross et al., (1970) reported that common shrubs and herbs were more abundant inside a deer exclosure in north-central Minnesota. Shrubs and herbs may be more susceptible to herbivory because they never grow out of the reach of deer. Also, Miller et al. (1992) assessed the potential impacts of deer on threatened and endangered plant species and communities and suggested that higher deer densities and fragmented habitat make rare plants more apparent to deer. Plant apparency is well accepted as a mechanism which leads to increased levels of herbivory (Palo et al., 1993; Van de Koppel et al., 1996).

An understanding of the impacts of deer browsing is needed if the functions and attributes of southern bottomland hardwood forests are to be maintained through silvicultural manipulations. Accordingly, we examined the effects of white-tailed deer herbivory on relative abundance and diversity of woody and herbaceous regeneration within various sized forest openings created by group selection timber harvest. We also examined the effects of forest opening size on herbivory rates and on relative abundance and diversity of regeneration.

2. Study area and methods

2.1. Study area

The study was conducted on the Savannah River Site (SRS) in west-central South Carolina, in the Upper Coastal Plain physiographic province. The SRS, designated as a National Environmental Research Park, is a 780 km^2 nuclear production facility that has been maintained by the Department of Energy since 1950. Approximately 700 km^2 of the site is forested with habitat types consisting of planted pine, upland hardwoods, bottomland hardwoods, and swamp forests (Whipple et al., 1981). Deer populations are maintained at moderate densities (3.0-7.0 deer/km*) through annual harvests (Leberg and Smith, 1993).

The study area was a 120 ha, 70-year-old, bottomland hardwood stand located 1.5 km East of the Savannah River. Soils were primarily Rembert sandy loam with a small area of Smithboro loam. Shallow flooding occurred on parts of the area during the winter but typically dried during the growing season. Common overstory species were swamp chestnut oak (*Quercus michauxii*), laurel oak (Q. *laurifolia*), cherrybark oak (Q. *falcata var. pagodaefolia*), loblolly pine (*Pinus taeda*), and sweetgum (*Liquidambar styraciflua*) at a basal area of 33 m^2/ha (Pauley et al., 1996). The Society of American Foresters forest classification was Type 91, swamp chestnut oak-cherrybark oak (Shropshire, 1980).

2.2. Methods

During November-December 1994, 36 openings (gaps) in the forest canopy were created by a group selection timber harvest. The 36 gaps included six replicates of six sizes (7, 10, 14, 20, 29, 40 m radius). Trees were felled with mechanized harvesting equipment and grapple skidded to loading decks. Culls and undersized stems were felled manually before the first growing season but no additional site preparation was performed.

Fenced deer exclosures (6.5 x 3.5 m) were constructed in the center of each gap. Swamp rabbits (*Sylvilagus aquaticus*) were the only other potential mammalian herbivore. Thus exclosures designed to exclude both deer and rabbits also were constructed to assess herbivory other than deer. Controls that excluded neither deer nor rabbits were established adjacent to the other exclosure types. The exclosures were constructed using welded wire fencing and 2.4 m metal posts. The deer exclosures were built with 1.5 m high fencing to exclude deer but raised 20 cm to allow free movement of swamp rabbits underneath. The deer/rabbit exclosures were built with the same 1.5 m fencing but were not raised. The control replicates were unfenced.

We established twelve (0.5 m^2) vegetation sample plots in each exclosure type. Each monthfrom April to September of 1995, 1996 and 1997 (excluding April 1997), we sampled two of the plots from each exclosure type in each gap so that all the plots were sampled during the 6-month period. We recorded the number and species of browsable woody twigs and estimated the percent cover of all herbaceous species. Browsable twigs are defined as twigs >1 cm in length and occurring <1.25 m from the ground. Browsing activity was measured by recording the number of woody twigs and the percent cover of herbs browsed by deer and rabbits. Since we only recorded twigs of woody species that had been browsed, individual leaves that were taken could have been missed during sampling. In addition, ephemeral herbaceous species that were browsed during spring may have no longer been apparent during late summer sampling. Thus, our estimate of browsing activity is best viewed as a conservative browsing index.

Species richness, Shannon diversity and evenness, relative abundance, and a browse index were determined for each exclosure type and for each gap size. Relative abundance is expressed as the mean percent cover of herbaceous species and mean number of twigs of woody species. The browsing index is the mean percent cover browsed of herbaceous species and mean number of twigs browsed of woody species. Two-way analysis of variance was used to test for differences among exclosure types and gap sizes. Statistical significance was accepted at a = 0.05. Where significant differences were detected, mean separation was performed with Duncan's Multiple Range Test. Duncan's is less conservative than other tests and uses a variable level dependent on the number of means involved at any stage (Steel et al., 1997).

Fecal pellet group counts (Bennett et al., 1940) were used to index seasonal deer densities on the study area. Counts were conducted four times per year (spring, summer, fall, and winter) in 1995 and 1996 by walking established transect lines and removing all pellet groups within 2 m on each side of the line. The lines were walked again approximately 7 days later and the number of pellet groups encountered were recorded. In 1996, a sample of pellet groups was marked with stand-up flags to examine the effect of dung beetles on persistence. The marked groups were examined after 7 days and the condition of each was noted..

3. Results

3.1. Herbivore exclosures

No browsing activity by swamp rabbits was identified, so all browsing (excluding insects) was attributed to deer. Overall browsing rates were low in all years of the study. Total mean percent browsed of herbaceous species was 0.002, 0.004, and 0.005% for years 1995–1997, respectively. Total mean number of twigs browsed of woody species was 0.008, 0.016, and 0.016% for years 1995-1997, respectively.

Herbaceous richness, diversity, evenness, relative abundance, and browse index did not differ among exclosure types in 1995 (Table 1). In 1996, relative abundance was higher (p = 0.005) in the deer + rabbit exclosures than in other exclosure types. Browse index was highest in the controls in 1996 (p = 0.01) and 1997 (p = 0.02).

Browse index of woody species was greater in the controls than in other exclosure types in 1995 (p = 0.002) and 1997 (p = 0.0001). In 1996, browse index of woody species also differed (p = 0.0001)

Table 1
Plant species richness, diversity, evenness, relative abundance, and browse index per 0.5 m^2 plot (mean ± SE) among herbivore exclosure types at the Savannah River Site, South Carolina, 1995-1997

Group	Index[a]	Deer	Deer + Rabbit	Control
1995 Herbaceous	*n*	13.72 (0.90)	14.03 (.80)	13.28 (0.81)
	H'	1.89 (0.07)	1.89 (0.07)	1.84 (0.08)
	E	0.74 (0.02)	0.73 (0.01)	0.74 (0.02)
	RA	0.20 (0.03)	0.22 (0.02)	0.20 (0.03)
	BI	0.00	0.00	0.00
1995 Woody	*n*	12.97 (0.90)	14.14 (0.89)	13.14 (0.82)
	H'	2.19 (0.08)	2.25 (0.08)	2.21 (0.07)
	E	0.88 (0.01)	0.88 (0.01)	0.88 (0.01)
	RA	0.29 (0.04)	0.45 (0.10)	0.28 (0.05)
	BI	0.00B[b]	0.00B	0.01 (0.01)A
1996 Herbaceous	n	13.08 (0.50)	13.17 (0.56)	13.72 (0.51)
	H'	1.84 (0.05)	1.83 (0.05)	1.92 (0.05)
	E	0.72 (0.01)	0.72 (0.01)	0.74 (0.01)
	RA	0.68 (0.03)B	0.82 (0.04)A	0.65 (0.04)B
	BI	0.00B	0.00B	0.01 (0.01)A
1996 Woody	*n*	12.83 (0.75)	13.28 (0.62)	13.50 (0.69)
	H'	2.20 (0.07)	2.24 (0.06)	2.28 (0.05)
	E	0.88 (0.01)	0.88 (0.01)	0.89 (0.01)
	RA	0.57 (0.07)	0.57 (0.07)	0.55 (0.07)
	BI[c]	0.00	0.00	0.02 (0.01)
1997 Herbaceous	*n*	18.28 (0.60)	17.28 (0.61)	19.78 (0.65)
	H'	2.34 (0.04)	2.29 (0.04)	2.45 (0.05)
	E	0.81 (0.01)	0.81 (0.01)	0.82 (0.01)
	RA	0.59 (0.03)	0.61 (0.03)	0.65 (0.04)
	BI	0.00B	0.00B	0.02 (0.01)A
1997 woody	n	13.94 (0.66)	14.08 (0.57)	14.00 (0.64)
	H'	2.35 (0.05)	2.37 (0.04)	2.37 (0.04)
	E	0.91 (0.003)	0.91 (0.003)	0.91 (0.004)
	RA	0.71 (0.07)	0.76 (0.07)	0.62 (0.06)
	BI	0.00B	0.00B	0.04 (0.01)A

[a] n-mean number of species per plot; K-Shannon index; E-Shannon evenness; RA-mean percent cover for herbaceous species and mean number of twigs for woody species; BI-mean percent cover browsed for herbaceous species and mean number of twigs browsed for woody species.
[b] Within a row, means followed by the same letter are not different at $a = 0.05$.
[c] Significant interaction with gap size.

among exclosure types but there was a significant (p = 0.0003) interaction with gap size. Browse index was higher in the controls in the 7, 10, 14, 20 m gaps but was not different among exclosure types in the 29 or 40 m gaps.

3.2. Gap size

In 1995, herbaceous species richness was highest (p = 0.002) in the 10, 14, and 20 m gaps (Table 2). The 7 and the 29 m gaps had the lowest richness. Diversity of herbaceous species was highest (p = 0.01) in the 10, 14, 20, and 40 m gaps while lowest in the 29 m gaps. Relative abundance also differed (p = 0.006) among gap sizes, being highest in the 14, 20, and 40 m gaps and lowest in the 7 m gaps. In 1996, species richness, diversity, evenness, relative abundance, or browse index did not differ among gap sizes. In 1997, relative abundance of herbaceous species was higher (p = 0.04) in the 29 m gap sizes than in other gap sizes. In 1995, woody species richness was lowest (p = 0.01) in the 29 m gaps while all other sizes did not differ (Table 2). Diversity was highest (p = 0.002) in the 7, 14, 20, and 40 m gaps and lowest in the 29 m

Table 2
Plant species richness, diversity, evenness, relative abundance, and browse index per 0.5 m^2 plot (mean ± SE) among gap sizes (m radius) at the Savannah River Site, South Carolina, 1995-1997

Group/Year	Index[a]	7	10	14	20	29	40
1995 Herbaceous	*n*	11.44 (0.90)B[b]	15.66 (1.01)A	15.22 (1.27)A	15.77 (1.11)A	10.33 (1.25)B	13.61 (0.94)AB
	H'	1.80 (0.09)AB	2.06 (0.07)A	1.96 (0.11)A	1.93 (0.08)A	1.54 (0.13)B	1.96 (0.09)A
	E	0.75 (0.02)	0.76 (0.01)	0.73 (0.02)	0.71 (0.02)	0.71 (0.03)	0.76 (0.02)
	RA	0.10 (0.03)B	0.19 (0.03)AB	0.28 (0.05)A	0.29 (0.03)A	0.18 (0.04)AB	0.21 (0.04)A
	BI	0.00	0.00	0.00	0.00	0.00	0.00
1995 Woody	*n*	14.17 (0.86)A	13.33 (1.22)A	13.55 (1.11)A	16.44 (1.33)A	9.72 (1.34)B	13.27 (1.03)A
	H'	2.33 (0.06)A	2.12 (0.10)AB	2.27 (0.09)A	2.44 (0.08)A	1.85 (0.15)B	2.28 (0.08)A
	E	0.89 (0.01)A	0.84 (0.01)B	0.89 (0.01)A	0.89 (0.01)A	0.88 (0.02)A	0.90 (0.01)A
	RA	0.23 (0.03)	0.36 (0.07)	0.31 (0.05)	0.52 (0.10)	0.22 (0.09)	0.41 (0.16)
	BI	0.01 (0.01)	0.00	0.00	0.00	0.00	0.00
1996 Herbaceous	*n*	11.88 (0.94)	14.22 (0.51)	14.44 (0.76)	12.88 (0.69)	13.33 (0.84)	13.17 (0.52)
	H'	1.82 (0.09)	1.91 (0.06)	1.90 (0.07)	1.79 (0.06)	1.87 (0.08)	1.91 (0.05)
	E	0.76 (0.01)	0.72 (0.02)	0.71 (0.02)	0.70 (0.01)	0.73 (0.02)	0.75 (0.01)
	RA	0.60 (0.07)	0.68 (0.06)	0.83 (0.07)	0.75 (0.04)	0.74 (0.04)	0.72 (0.05)
	BI	0.00	0.00	0.01 (0.01)	0.00	0.00	0.00
1996 Woody	n	14.33 (0.52)A	13.27 (1.08)AB	13.11 (1.12)AB	14.77 (0.85)A	10.55 (1.11)B	13.16 (0.81)AB
	H'	2.38 (0.04)A	2.19 (0.09)AB	2.23 (O.lO)AB	2.38 (0.05)A	1.99 (0.13)B	2.28 (0.06)A
	E	0.90 (0.01)	0.86 (0.01)	0.89 (0.01)	0.89 (0.01)	0.87 (0.02)	0.90 (0.01)
	RA	0.44 (0.09)	0.67 (0.11)	0.62 (0.09)	0.73 (0.11)	0.41 (0.07)	0.50 (0.09)
	BI[c]	0.00	0.01 (0.01)	0.02 (0.01)	0.00	0.00	0.00
1997 Herbaceous	*n*	17.79 (0.92)	19.33 (0.94)	18.08 (0.86)	17.67 (0.59)	18.91 (0.69)	19.00 (0.62)
	H'	2.33 (0.06)	2.40 (0.06)	2.30 (0.06)	2.37 (0.04)	2.37 (0.05)	2.38 (0.05)
	E	0.82 (0.01)	0.82 (0.01)	0.80 (0.01)	0.83 (0.01)	0.81 (0.01)	0.81 (0.01)
	RA	0.55 (0.04)B	0.60 (0.03)AB	0.62 (0.03)AB	0.56 (0.04)B	0.71 (0.04)A	0.63 (0.03)AB
	BI	0.00	0.01 (0.01)	0.00	0.01 (0.01)	0.00	0.00
1997 Woody	*n*	13.75 (0.61)	14.33 (0.76)	14.46 (0.89)	15.67 (0.63)	12.46 (0.81)	14.04 (0.72)
	H'	2.38 (0.04)	2.36 (0.05)	2.38 (0.07)	2.47 (0.04)	2.25 (0.07)	2.38 (0.05)
	E	0.92 (0.01)	0.90 (0.01)	0.91 (0.01)	0.90 (0.004)	0.91 (0.01)	0.91 (0.004)
	RA	0.50 (0.06)B	0.85 (0.09)A	0.82 (0.08)A	0.87 (0.08)A	0.53 (0.07)B	0.67 (0.08)AB
	BI	0.01 (0.002)C	0.03 (0.01)AB	0.01 (0.004)ABC	0.03 (0.01)A	0.01 (0.004)BC	0.01 (0.002)C

[a] *n*–mean number of species per plot; H'-Shannon index; E-Shannon evenness; RA-mean percent cover for herbaceous species and mean number of twigs for woody species; BI-mean percent cover browsed for herbaceous species and mean number of twigs browsed for woody species.
[b] Within a row, means followed by the same letter are not different at $\alpha = 0.05$.
[c] Significant interaction with herbivore exclosure type.

gaps. Evenness was lowest ($p = 0.002$) in the 10 m gap size while all other sizes did not differ. In 1996, woody species richness differed ($p = 0.05$) among gap sizes. Richness was highest in the 7 and 20 m gaps and, as in 1995, was lowest in the 29 m gaps. Woody diversity was highest ($p = 0.02$) in the 7, 20, 40 m gaps and lowest in the 29 m gaps. Browse index also differed ($p = 0.004$) among sizes but, as explained above, interacted significantly ($p = 0.0003$) with exclosure type. In 1997, relative abundance was higher ($p = 0.0001$) in the 10, 14, and 20m gaps while lowest in the 7 and 29 m gaps. Browsing index was higher ($p = 0.008$) in the 20 m gaps than in all other gap sizes.

3.3. Fecal pellet group counts

Fecal pellet group counts indicated seasonal changes in habitat use by deer (Table 3). Deer use of the bottomland study area were highest during fall and winter and lowest during spring and summer. This pattern of habitat use was consistent during 1995 and 1996. No fecal pellet group counts were conducted during 1997.

Table 3
Deer density index (pellet groups/m²/day x 10^{-5}) from seasonal fecal pellet group counts at the Savannah River Site, South Carolina. 1995 and 1996

Season	1995		1996	
	Area sampled (ha)[a]	Density index	Area sampled (ha)	Density index
Winter	4.5	24.8	3.0	17.1
Spring	6.2	0.0	6.0	1.9
Summer	6.2	0.0	4.6	0.0
Fall	6.1	3.8	5.2	8.8

[a] Area sampled varied depending on the amount of flooding on the study area.

4. Discussion

The low browsing rates we observed likely were due to seasonal changes in habitat use by deer. There was little use of the study area during the growing season but the use increased during fall and winter when oak mast was available. This same trend was observed in other studies of deer use of southern bottomland hardwood forests (Smith et al., 1995). Even though deer were present during fall and winter, hardened woody twigs usually constitute only a small portion of deer diets during the winter in the Southeast (Harlow and Hooper, 1972; Johnson et al., 1995). Typically, woody twigs are browsed only in spring and summer when the succulent, rapidly growing twigs are taken with green leaves (Johnson et al., 1995). Most herbaceous species present in the gaps were warm season annuals and were not present during fall and winter.

We detected few differences among exclosure types during the study. The differences detected in browse index, while statistically significant, probably have no biological importance because of the low browsing rates. In contrast, richness, diversity, evenness, relative abundance, and/or browsing index differed among gap sizes during every year of the study. However, since the browsing index only differed among gap sizes in 1997 and browsing rates were extremely low in every year, we conclude that these differences likely were biologically insignificant. Additionally, there were few trends that emerged throughout the study to suggest that gap size had a major effect on regeneration. For example, herbaceous richness, diversity and relative abundance differed among gap sizes in 1995 but did not differ in 1996 or 1997. Relative abundance of herbaceous species also differed among gap sizes in 1995 and 1997 but not in 1996. The effects of gap size on herbaceous growth appeared to diminish after the first growing season. Herbaceous richness, diversity and relative abundance differed among gap sizes in 1995 but there were no differences in 1996 and only relative abundance differed in 1997. These results suggest that there may be a relationship between herbaceous response and gap age. Moore and Vankat (1986) reported that gap age influenced the herb layer in natural forest gaps in Ohio. There was an increase in total herbaceous cover after gap formation with subsequent decrease in coverage with increasing gap age. However, these gaps were a result of a single-tree fall and, therefore, were smaller than the gaps in this study.

Soil disturbance caused by logging equipment during harvest, or a combination of soil disturbance and gap size, likely were the major influence on the initial vegetative response. The various gaps sizes were arranged randomly across the study area and connected by skid trails to two loading decks in uplands adjacent to the study area. As a result, logs were skidded through gaps en route to the loading decks. The smaller gaps were marginally wider than the skid trail and received repeated equipment traffic that resulted in extensive soil disturbance. In the larger gaps, the skid trail covered only a small portion of the gap and the remainder of the gap received less disturbance. This variance in disturbance intensity of the soil may explain the difference in vegetative response among gap sizes. The 7 m gaps, which received extensive soil disturbance, had lower herbaceous richness, diversity, and relative abundance than other sizes in 1995. Values were generally lower in 1996 and 1997 though not statistically significant with the exception of relative abundance in 1997.

Our results demonstrate that deer herbivory had little effect on regeneration in this bottomland forest. The spatial arrangement of habitats on the SRS may influence habitat use by deer, and therefore, may have been a major influence on our results. The upland habitats consisting of pine plantations and utility right-of-ways that surrounded the study area provided abundant forage in the spring and summer. In other areas, such as the Mississippi Alluvial Valley, where bottomland habitats are more extensive, nearby upland habitats may not be available to provide forage during spring and summer. As a result, the effects of herbivory may be more significant in these area. Thus, it may be necessary to index spring/summer deer densities prior to harvest to assess potential impacts on regeneration. The effects of gap size appeared to have a short term effect on herbaceous and woody species. The effects on herbaceous species were no longer evident after the first growing season. The effect on woody species was still evident after 2 years but appeared to recover by the third growing season. Soil disturbance during harvesting of bottomland stands appears to influence regeneration more than herbivory or gap size.

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