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HERBIVORY AND GAP REGENERATION IN SOUTHERN BOTTOMLAND HARDWOOD FORESTS

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Abstract: We conducted 2 experiments to examine the influence of herbivory by white-tailed deer (*Odocoileus virginianus*) and swamp rabbits (*Sylvilagus aquaticus*) on plant regeneration within canopy gaps in southern bottomland hardwood forests. One study was conducted at Moro Bottoms Natural Area in southern Arkansas in a bottomland forest containing windthrow gaps. The other was conducted at the Savannah River Site (SRS), South Carolina in a forest containing gaps created by group selection timber harvest. Herbivore exclosures and control plots were constructed in 30 gaps at Moro Bottoms and 36 gaps at the SRS. General patterns of deer use and effects on vegetation were similar for both sites. Counts of deer fecal pellet groups indicated little use of bottomland forests in spring and summer, with increased use during fall and winter when oak mast was available. Rabbit herbivory was not detected in the SRS gaps. Rabbits were more abundant in southern Arkansas, but apparent use of sampled vegetation in study plots was negligible. Plant abundance and diversity varied among gap sizes at the SRS, though these patterns likely were not influenced by deer herbivory. Differences in plant species diversity, richness, and number of unique plant species in the Arkansas gaps were not detected among treatments, but grasses and sedges were more abundant in plots available to deer. Landscape context may influence patterns of habitat use, so it may be necessary to index deer densities prior to timber harvest in some locations to assess their potential impacts on regeneration. We conclude that other factors, such as degree of inundation and soil disturbance from timber harvesting, were more important in determining the initial vegetative response than herbivory or gap size on these study areas.

Key words: bottomland hardwood forests, forest canopy gaps, herbivory, oak regeneration, *Odocoileus virginianus*, swamp rabbit, *Sylvilagus aquaticus*, white-tailed deer

Since European settlement, the extent of bottomland hardwood forests in the southeastern USA has decreased substantially. In the Lower Mississippi Alluvial Valley, 80% of the original forested acreage has been converted to cropland or cleared for development (MacDonald et al. 1979). Most remaining bottomland forests in the Southeast have experienced significant anthropogenic disturbance and no longer harbor the diversity of pre-settlement forest types (Rudis 1993). As total area and tract size of remaining forests decrease, plant communities may experience severe alteration. In particular, local extinction of sensitive plant and animal species may occur (Galli et al. 1976, Whitcomb et al. 1981, Freemark and Merriam 1986, Burdick et al. 1989, Robbins et al. 1989). In addition to anthropogenic disturbances, remnant old-growth bottomland forests have experienced natural disturbances at various scales. For example, as a forest ages, the probability increases that it will be impacted by a broad-scale disturbance, such as windstorm or fire (Spies and Franklin 1989, Whitmore 1989). Old-growth forests are characterized by large trees with closed canopies, resulting in lower light interception at the understory layer. Canopy gaps resulting from treefalls become principal areas for regeneration and can determine forest composition (Cho and Boerner 1991, Leemans 1991, Spies and Franklin 1989, Whitmore 1989). Thus, old-growth forests may be a mosaic of patches of different shapes, sizes, and in various phases of forest succession (Spies and Franklin 1989).

Regeneration within canopy gaps is influenced by a myriad of factors. The interaction of plant tolerances with opening characteristics, such as size and shape, may influence regeneration patterns (McClure and Lee 1993, Poulson and Platt 1989, Sipe and Bazzaz 1994, Whitmore 1989). A small gap disturbance regime may lead to little change in species composition if shade tolerant species dominate the canopy (Hara 1985), whereas larger gaps allow establishment of shade intolerant species (Barton 1984, McClure and Lee 1993, Whitmore 1989). Intolerant

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METHODS

Herbivory Estimates

Moro Bottoms.--We constructed fenced exclosures prior to the 1990 growing season within 30 windthrow gaps ranging from 0.1 - 0.5 ha. Gaps were selected to provide a range of canopy opening sizes. We constructed exclosures, approximately 2.5 x 4 m, of 5 x 10 cm welded-wire fencing and 8, 2.4 m metal posts. Fencing was raised 15 cm above ground to allow entry and exit by swamp rabbits. We randomly located 20, 0.5 x 1.0 m (0.5 m^2) vegetation sample plots within each exclosure. Of these, 10 were fenced with 2.5 x 5 cm welded wire 0.6-m high to exclude swamp rabbits. Immediately adjacent to each exclosure was a corresponding open control with 10, 0.5 m^2 sample plots. Controls had 3 fence posts along one side to duplicate the exclosures but had no fencing.

We collected data from spring-fall 1990-92. We recorded percent cover for each herbaceous species and total percent cover for control and exclosure sample plots. During summer, we recorded percent cover for the entire exclosure and control, and for each sample plot. During 1990 and 1991, we recorded total percent cover of grass and sedge instead of each species, except for cane (*Arundinaria gigantea*), because of difficulty identifying grass and sedge species when they were not fruiting or flowering. During 1992, all herbaceous species were recorded separately.

We counted total number and species of shrubs and seedlings within each 0.5 m^2 sample plot during spring and autumn. During summer, we recorded number and species of seedlings in each sample plot, as well as totals for the entire exclosure or control. All oak seedlings were recorded as *Quercus* spp. during 1990 and 1991, but most were recorded by species in 1992.

Savannah River Site.—Thirty-six gaps in the forest canopy were created by a group selection timber harvest in December 1994. The 36 gaps represented 6 replicates of 6 sizes (7, 10, 14, 20, 29, and 40 m radius), resulting in an increasing range of canopy opening sizes. Trees were felled with mechanized harvesting equipment and grapple skidded to loading decks at the edge of the study area. Culls and undersized stems were manually felled before the first growing season, but no site preparation was performed.

We constructed fenced exclosures (6.5 x 3.5 m) in the center of each gap. The exclosures were constructed with welded-wire fencing and 2.4 m metal posts. We built deer exclosures with 1.5 m high fencing to exclude deer, but these were raised 20 cm to allow access by swamp rabbits. Deer and rabbit exclosures were built with the same 1.5 m fencing but were not raised so that both were excluded. We established controls without fencing immediately adjacent to the other exclosures. We did not place metal posts along the perimeter of control areas.

We established 12, 0.5 m^2 vegetation sample plots in each exclosure and control. Each month from April-September 1995-97 (except April 1997), we sampled 2 different plots from each exclosure type in each gap so that all plots were sampled during the 6-month period and each plot was sampled once per year. We recorded number and species of woody browse and estimated percent cover of all herbaceous species. We defined browse as twigs >1 cm in length and occurring <1.25 m above ground (Strole and Anderson 1992). We indexed browsing activity by recording the number of woody twigs and the percent cover of herbs apparently browsed by deer and rabbits. We only recorded twigs of woody species that had been browsed; herbaceous forage previously consumed by herbivores could not be estimated. Thus, our index of browsing activity is conservative.

Habitat Use

In both studies, we estimated seasonal use of forests by white-tailed deer from counts of fecal pellet groups (Eberhardt and Van Etten 1956). This technique requires that an observer remove or mark all pellets encountered along a transect, then return to that transect after a specified time has elapsed and record the number of pellet groups again. Total number of pellet groups recorded/m^2/day provided an index of deer density for each season. In both studies, transects were established to incorporate forested habitats and gaps in proportion to their occurrence across the study area.

In Moro Bottoms, we conducted bimonthly fecal pellet group surveys each year from 1990-92. Months were alternated between years so that a 2-year period included estimates from every month, recognizing that monthly estimates would be confounded by years. In the SRS study, we conducted surveys 4 times per year (spring, summer, fall, and winter) in 1995 and 1996. No fecal pellet group counts were conducted during 1997.

Statistical Analysis

We performed all analyses with SAS statistical software (SAS Institute 1989). We declared statistical significance at $P \leq 0.05$.

Table 1. Mean (±SE) percent total vegetative cover and mean percent cover of grasses, sedges, and other herbaceous vegetation per 0.5 m^2 plot for each season among herbivore exclosure types at Moro Bottoms Natural Area, Arkansas, 1990-92.

Year	Season	Group	Deer	Deer and rabbit	Control
1990	Spring	Total	43.0 (2.4)B [a]	41.0 (3.0)B	52.0 (2.7)A
		Grasses	8.0 (1.1)	7.5 (1.0)	10.33 (1.4)
		Sedges	13.8 (1.5)B	16.3 (1.8)B	21.0 (1.9)A
		Other	23.1 (1.7)	20.0 (1.8)	21.3 (1.7)
	Summer	Total	48.0 (2.5)B	52.0 (2.6)A	56.3 (2.4)A
		Grasses	10.0 (1.1)	10.7 (1.2)	14.8 (1.3)
		Sedges	14.7 (1.2)B	13.7 (1.2)B	22.0 (1.8)A
		Other	24.0 (1.8)B	28.0 (1.9)A	20.5 (1.8)B
	Autumn	Total	48.0 (2.7)	50.3 (2.8)	52.7 (2.3)
		Grasses	10.3 (1.1)	10.17 (1.2)	9.5 (1.1)
		Sedges	14.0 (1.5)B	15.2 (1.6)B	21.3 (1.5)A
		Other	24.2 (1.9)	26.7 (1.9)	22.0 (1.5)
1991	Spring	Total	51.0 (2.9)	52.3 (2.8)	52.0 (2.3)
		Grasses	8.2 (1.0)	9.2 (1.1)	6.7 (0.5)
		Sedges	21.7 (3.8)B	19.3 (1.7)B	28.3 (2.0)A
		Other	22.0 (1.8)B	24.2 (1.6)A	17.5 (1.3)B
	Summer	Total	68.0 (2.5)	66.6 (2.6)	67.7 (2.1)
		Grasses	8.9 (1.6)B	8.8 (1.5)B	16.6 (2.0)A
		Sedges	13.2 (1.3)B	12.1 (1.2)B	20.4 (1.6)A
		Other	45.9 (3.0)A	45.9 (3.0)A	30.7 (2.1)B
	Autumn	Total	58.2 (2.2)	60.4 (2.3)	62.1 (1.9)
		Grasses	8.9 (1.1)B	8.8 (1.2)B	13.9 (1.5)A
		Sedges	12.0 (1.0)B	11.1 (1.1)B	17.1 (1.4)A
		Other	37.3 (2.1)A	40.5 (2.2)A	31.1 (1.7)B
1992	Spring	Total	67.7 (2.3)	67.8 (2.2)	71.6 (1.9)
		Grasses	6.9 (1.0)	5.9 (0.7)	10.2 (1.3)
		Sedges	21.2 (2.0)	17.4 (1.7)	28.8 (2.0)
		Other	39.6 (2.7)A	44.5 (2.8)A	32.6 (2.1)B
	Summer	Total	66.1 (2.3)B	68.0 (2.5)B	72.0 (2.0)A
		Grasses	10.9 (1.2)B	10.0 (0.9)B	15.4 (1.6)A
		Sedges	10.0 (1.0)B	9.1 (0.8)B	13.5 (1.4)A
		Other	45.2 (2.5)	48.9 (2.9)	43.2 (2.6)
	Autumn	Total	59.3 (1.8)B	62.1 (2.0)A	70.0 (1.8)A
		Grasses	13.0 (1.4)B	13.0 (1.7)B	18.2 (1.8)A
		Sedges	14.6 (1.2)	13.9 (1.3)	17.3 (1.4)
		Other	31.6 (1.7)	35.2 (2.1)	34.5 (1.8)

[a] Within a row, means followed by the same letter are not different at α=0.05.

Moro Bottoms.—We determined percent cover, plant species richness (mean number of species/plot), cumulative species (total number of unique species across all plots within a treatment category), and unique species (number of species that occurred in only one treatment category) for each exclosure treatment and control. Because controls were located immediately adjacent to exclosures, we analyzed data for comparisons between control versus deer exclosures and control versus deer and rabbit exclosures using a paired *t*-test (Sokal and Rohlf 1995). Due to the design of deer and rabbit exclosures, no statistically independent test could be constructed for comparing effects of rabbit versus deer exclosures. Any inference regarding the effects of rabbits were based on differences between deer and rabbit and deer exclosures. We used a Kruskal-Wallis test (Hollander and Wolfe 1973) to test for differences in seedling density among seasons, exclosure treatments, and canopy gap sizes because attempts to transform the response variables were unsuccessful. We used distribution-free multiple comparisons (Hollander and Wolfe 1973) to separate means when differences were detected with Kruskal-Wallis tests.

Savannah River Site.—We calculated plant species richness, diversity (Shannon Index), evenness (Shannon Evenness), relative abundance, and a browse index of woody and herbaceous species for each exclosure treatment and gap size. Relative abundance was expressed as the mean percent cover per plot of herbaceous plants and mean number of twigs per plot of woody species. Browsing index was the mean percent cover of herbaceous species browsed and mean number of browsed twigs of woody species. Because the residuals of the response variables met the required assumptions, we used analysis of variance (ANOVA) to test for differences among exclosure types and gap sizes. When ANOVA detected significant differences, we performed mean separation with Duncan's Multiple Range Test.

RESULTS

Herbivory Experiments

Moro Bottoms.—Swamp rabbits were present on the study area but their browsing on vegetation within study plots was negligible. We detected no differences in plant species richness, cumulative species, or unique species among treatments, seasons, or years. However, there appeared to be a general pattern of encountering more plant species as the growing season proceeded.

Total percent vegetative cover was affected by exclusion during the first and third years of the study (Table 1). Total percent cover in control plots was greater than in deer and deer and rabbit exclosures in spring 1990 ($P < 0.014$). In summer 1990, total percent cover was greater in control plots than in the deer exclosures ($P = 0.017$) but was not different from deer and rabbit exclosures. By autumn 1990, however, no differences were detected ($P \geq 0.315$) in total percent cover among control and exclosure plots. In summer and autumn 1992, total percent cover in control plots was again greater ($P < 0.006$) than in deer and deer and rabbit exclosures. No differences in total percent cover were detected among exclosure treatments in 1991.

When we grouped percent vegetative cover into grasses, sedges, and other herbaceous vegetation and compared each among exclosure treatments, 2 general patterns emerged. First, vegetative cover of grasses and sedges was generally highest in control plots. Percent cover of grasses was greater in controls than deer and deer and rabbit exclosures in summer and autumn 1991 and 1992 ($P < 0.04$; Table 1). Percent cover of sedges was greater in controls in all seasons 1990-91 and summer 1992 when compared to deer and deer and rabbit exclosures ($P < 0.04$). Second, percent vegetative cover of other herbaceous species was generally lowest in controls. Deer and rabbit exclosures had greater percent cover of other herbaceous species than controls during summer 1990 and spring 1991 ($P < 0.006$). During summer and autumn 1991 and spring 1992, percent cover of other herbaceous species was greater ($P < 0.05$) in both exclusion treatments as compared to controls, but the effect appeared to diminish as no differences were detected in summer or autumn 1992.

Total number of woody seedlings did not differ among treatments or seasons throughout the study. Comparisons of selected woody species revealed that only ironwood (*Carpinus caroliniana*) differed among exclosure treatments. Density of ironwood seedlings was greater in controls than deer exclosures during spring 1990 and spring and summer 1991 ($P < 0.04$). The pattern was reversed in 1992, with a greater density of ironwood seedlings in deer and rabbit exclosures than controls in spring and summer ($P < 0.05$).

Canopy gap size appeared to have no effect on seedling density throughout the study. Comparisons of total seedling density, as well as specific comparisons of oaks, sweetgum, red maple, and ironwood, revealed no differences among gap sizes. Additionally, seedling density among herbivore exclosure treatments did not differ among gap sizes.

Savannah River Site.—During the study, no browsing was positively identified as swamp rabbit, so all browsing was assumed to be deer based on characteristic shredded appearance of vegetation browsed upon by deer. Overall, browsing rates were low in every year of the study. Total mean percent of herbaceous species and total mean number of woody species browsed was <0.02% in 1995-97.

We detected no differences among exclosure treatments in herbaceous plant species richness, diversity, evenness, relative abundance, or browse index in 1995 (Table 2). In 1996, relative abundance was greater in the deer and rabbit exclosures than other exclosure types ($P = 0.005$). Browse index of herbaceous species was highest in the controls in 1996 ($P = 0.010$) and 1997 ($P = 0.020$). Woody species had a higher browse index in the controls than in exclosure treatments in 1995 ($P = 0.002$) and 1997 ($P \leq 0.001$). In 1996, browse index of woody species interacted with gap size ($P \leq 0.001$). Browse index was higher in the controls in the 7, 10, 14, and 20 m gaps ($P \leq 0.001$) but was not different among exclosure types in the 29 or 40 m gaps.

Comparisons among gap sizes revealed higher herbaceous species richness in the 10, 14, and 20 m gaps and lowest richness in the 7 and 29 m gaps in 1995 ($P = 0.002$; Table 3). Diversity of herbaceous species was highest in the 10, 14, 20, and 40 m gaps and lowest in the 29 m gaps ($P = 0.01$). Relative abundance also differed among gap sizes, being highest in the 14, 20, and 40 m gaps and lowest in the 7 m gaps ($P = 0.006$). In 1996, neither species richness, diversity, evenness, relative abundance, nor browse index differed among gap sizes ($P \geq 0.05$). In 1997, relative abundance of herbaceous species was higher in the 29 m gaps than in other gap sizes ($P = 0.04$). Woody species richness was lowest in the 29 m gaps ($P = 0.01$) while all other

Table 2. Mean (±SE) species richness ( ), diversity (H'), evenness (E), relative abundance (RA), and a browse index (BI) per 0.5 m^2 plot for woody and herbaceous plant species among herbivore exclosure types at the Savannah River Site, South Carolina, 1995-97.

Group	Index	Deer	Deer and rabbit	Control
1995		13.3 (0.9)	14.0 (0.8)	13.3 (0.8)
Herbaceous	H'	1.9 (0.07)	1.9 (0.07)	1.8 (0.1)
	E	0.7 (0.02)	0.7 (0.01)	0.7 (0.02)
	RA	0.2 (0.03)	0.2 (0.02)	0.2 (0.03)
	BI	0.0	0.0	0.0
1995		12.9 (0.9)	14.1 (0.9)	13.1 (0.3)
Woody	H'	2.2 (0.1)	2.3 (0.1)	2.2 (0.1)
	E	0.9 (0.01)	0.9 (0.01)	0.9 (0.01)
	RA	0.3 (0.04)	0.5 (0.1)	0.3 (0.1)
	BI	0.0B [a]	0.0B	0.01 (0.01)A
1996		13.1 (0.5)	13.2 (0.6)	13.7 (0.5)
Herbaceous	H'	1.8 (0.1)	1.8 (0.1)	1.9 (0.1)
	E	0.7 (0.01)	0.7 (0.01)	0.7 (0.01)
	RA	0.7 (0.03)B	0.8 (0.04)A	0.7 (0.04)B
	BI	0.00B	0.00B	0.01 (0.01)A
1996		12.8 (0.8)	13.3 (0.6)	13.5 (0.7)
Woody	H'	2.2 (0.1)	2.2 (0.1)	2.3 (0.1)
	E	0.9 (0.01)	0.9 (0.01)	0.9 (0.01)
	RA	0.6 (0.1)	0.6 (0.1)	0.6 (0.1)
	BI [b]	0.0	0.0	0.02 (0.01)
1997		18.3 (0.6)	17.3 (0.6)	19.8 (0.7)
Herbaceous	H'	2.3 (0.04)	2.3 (0.04)	2.5 (0.05)
	E	0.8 (0.01)	0.8 (0.01)	0.8 (0.01)
	RA	0.6 (0.03)	0.6 (0.03)	0.7 (0.04)
	BI	0.0B	0.0B	0.02 (0.01)A
1997		13.9 (0.7)	14.1 (0.6)	14.0 (0.6)
Woody	H'	2.4 (0.1)	2.4 (0.04)	2.4 (0.04)
	E	0.9 (0.003)	0.9 (0.003)	0.9 (0.004)
	RA	0.7 (0.1)	0.8 (0.1)	0.6 (0.1)
	BI	0.0B	0.0B	0.01 (0.01)A

[a] Within a row, means followed by the same letter are not different at _=0.05.

[b] Significant interaction with gap size.

sizes were similar in 1995. Diversity was highest in the 7, 14, 20, and 40 m gaps and lowest in the 29 m gaps (P = 0.002). Evenness was lowest in the 10 m gaps (P = 0.002) while all other sizes were similar. In 1996, woody species richness was highest in the 7 and 20 m gaps and lowest in the 29 m gaps ($P = 0.05$). Woody plant diversity was highest in the 7, 20, 40 m gaps and lowest in the 29 m gaps (P = 0.02). As previously mentioned, browse index of woody species interacted with exclosure type ($P \leq 0.001$). In 1997, relative abundance of woody species was higher in the 10, 14, and 20 m gaps while lowest in the 7 and 29 m gaps ($P \leq 0.001$). Browsing index was greater in the 20 m gaps than in all other gap sizes ($P = 0.008$).

HABITAT USE

Moro Bottoms.—The index of white-tailed deer density in the old-growth stand varied considerably among bi-monthly sampling periods. Examining the density index (number of pellet groups/m^2/day x 10^{-5}) by season (winter, spring, summer, and autumn), deer appeared to use the area more during autumn and winter than in spring and summer. Values ranged from 0.0 in spring 1991 to 22.5 in autumn 1991. Although no pellet groups were encountered along the transects in spring 1991, deer occurred on the study area as evidenced by visual observations.

Savannah River Site.—We observed a pattern of habitat use by deer at SRS similar to that at Moro Bottoms. Deer density estimates on the study area were highest during fall and winter and lowest in spring and summer. Values ranged from 0.0 in spring and summer 1995 to 24.8 in winter 1995. Although high and low values occurred in 1995, this pattern of habitat use was consistent during both 1995 and 1996.

Table 3. Mean (±SE) species richness ( ), diversity (H'), evenness (E), relative abundance (RA), and browse index (BI) per 0.5 m^2 plot for herbaceous and woody plant species among gap sizes (m radius) at the Savannah River Site, South Carolina, 1995-97.

		Gap size (radius, m)					
Group	Index	7	10	14	20	29	40
1995		11.44 (0.90)B [a]	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
Herb	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		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
Woody	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		11.88 (0.94)	14.22 (0.51)	14.44 (0.76)	12.88 (0.69)	13.33 (0.84)	13.17 (0.52)
Herb	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		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
Woody	H'	2.38 (0.04)A	2.19 (0.09)AB	2.23 (0.10)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 [b]	0.00	0.01 (0.01)	0.02 (0.01)	0.00	0.00	0.00
1997		17.79 (0.92)	19.33 (0.94)	18.08 (0.86)	17.67 (0.59)	18.91 (0.69)	19.00 (0.62)
Herb	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		13.75 (0.61)	14.33 (0.76)	14.46 (0.89)	15.67 (0.63)	12.46 (0.81)	14.04 (0.72)
Woody	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] Within a row, means followed by the same letter are not different at α=0.05.

[b] Significant interaction with herbivore exclosure type.

DISCUSSION

In both studies, use of bottomland hardwoods by deer varied seasonally with the greatest use occurring during autumn and winter. We suspect this pattern of seasonal habitat use was in part related to the landscape habitat composition of the study areas. Moro Bottoms Natural Area is part of a narrow, riparian corridor that dissects a landscape of intensively managed timberland, mostly even-aged stands of loblolly pine. Likewise, the study area at SRS is surrounded by upland habitats, primarily pine plantations and utility right-of-ways.

The patterns of seasonal use in both studies were probably typical of deer inhabiting minor bottoms surrounded by upland habitats in the Southeast. Although deer densities were highest on both study areas during fall and winter, we found little evidence from spring vegetation surveys to indicate that deer had browsed woody twigs during winter. This finding was not surprising because hardened woody twigs typically constitute only a small portion of deer diets during winter in the Southeast (Cushwa et al. 1970, Harlow and Hooper 1972, Johnson et al. 1995). Woody twigs are browsed primarily in spring and summer when succulent 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. Perhaps the most likely explanation of increased use during fall and winter was the availability of acorns. Deer were likely attracted to the bottoms during fall to exploit acorns because they represent a high-energy food source.

We observed no obvious herbivory impact by white-tailed deer on plant diversity among seasons at Moro Bottoms. We did, however, observe greater percent cover of grasses and sedges in controls and greater percent cover of other herbaceous vegetation in deer and deer and rabbit exclosures. These results suggest that deer or rabbits may have selectively browsed herbs and avoided grasses and sedges. This seems likely because sedges and grasses rarely occur in the diet of deer (Harlow and Hooper 1972, Murphy and Noble 1972, Newsom 1984) but herbs, such as *Aster* spp., are preferred food for white-tailed deer in bottomland hardwood forests (Murphy and Noble 1972). Our results concur with other previously published studies which suggest that deer or rabbit herbivory can represent a strong selective force and can cause and maintain shifts in plant species composition (Harper 1977, Alverson et al. 1988, Hjältén 1991, Strole and Anderson 1992).

Variation in microtopography and periods of inundation may have influenced regeneration and development of the understory vegetation. Periods of inundation can substantially reduce local seedling densities of small-seeded species because of seed redistribution that often accompanies typical riparian flooding (Streng et al. 1989). Thus, microtopography may affect patterns of seed dispersal, seedling mortality, and consequently overall seedling establishment (Huenneke and Sharitz 1986, Streng et al. 1989). Moro Bottoms experienced frequent, and occasionally, extreme flooding events with fluctuations as great as 2 m in a 24-hr period. In some years, water remained on a large portion of the study area during the growing season, as late as June. During these flooding events, movement of water through the study area was apparently rapid and powerful as suggested by the amount and size of woody debris that accumulated along the exclosures. Thus, the patterns in understory vegetation we observed may have been influenced by microtopography and hydrology.

At the SRS, we observed differences in plant species richness, diversity, evenness, relative abundance, or browsing index among gap sizes and exclosure treatments during every year of the study. Because of low browsing rates, however, these differences may not be attributable to herbivory. In every circumstance where the browse index was different among exclosure treatments, the values were extremely low. So, while statistically significant, these differences probably have no biological significance relative to deer herbivory. Additionally, there appeared to be no lasting effects of gap size on regeneration. Herbaceous plant species richness, diversity, and relative abundance differed among gap sizes in 1995 but not in 1996 or 1997, suggesting that effects of gap size on herbaceous growth diminished after the first growing season.

We suspect that soil disturbance caused by logging equipment during timber harvest, or an interaction between soil disturbance and gap size, was the major influence on the initial vegetative response. The various gap sizes were arranged randomly across the study area connected by skid trails, with 2 loading decks located in the adjacent uplands. As a result, logs were skidded through gaps enroute to the loading decks. The smaller gaps were barely wider than the skid trail and received repeated equipment traffic that resulted in extensive soil disturbance. In larger gaps, the skid trail covered a smaller portion of the gap and the remainder of the gap received less disturbance. This variation in intensity of soil disturbance 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 but not statistically significant, except for relative abundance in 1997.

One trend that emerged during the study was the lower woody plant species richness and diversity in the 29 m gaps during the first 2 years of the study. This was unexpected because plant species richness typically increases with canopy opening size (Smith 1981, Phillips and Shure 1983). Soil disturbance also may explain these differences. Two of the 29 m gaps were randomly located near loading decks. Consequently, logs from all of the other gaps were skidded through these gaps repeatedly, causing extensive soil disturbance. Richness and diversity of herbaceous plant species appeared to recover from this disturbance by the second growing season, but values for woody species remained low until the third growing season. Life-history strategies of light seeded, annual, herbaceous species may allow them to recover from soil disturbance more quickly than woody species. For example, thoroughworts (*Eupatorium* spp.) were common and comprised a majority of the herbaceous cover in some gaps.

MANAGEMENT IMPLICATIONS

Results from two independent experiments examining gap regeneration in bottomland hardwood forests of different regions in the Southeast were similar. At both sites, herbivory had little effect on gap regeneration, apparently due to seasonal changes in habitat use by deer and rabbits. The location of our study sites relative to other nearby habitats and food resources likely influenced habitat use by deer. Results of these studies may be applicable to bottomland hardwood forests that are a small part of a predominantly upland landscape, as would be encountered throughout much of the Atlantic and Gulf Coastal Plains. In areas such as the Lower Mississippi Alluvial Valley, where bottomland habitats occupy most of the landscape, our results may not be applicable. In more expansive floodplain forests where there are few or no nearby upland habitats to provide spring and summer forage, effects of deer herbivory may be more significant. The extent of deer and rabbit herbivory in these more extensive bottomland habitats remains unclear and warrants further study. Nonetheless, it would be prudent to index deer densities prior to timber harvest to assess potential impacts on regeneration.

We conclude that there are multiple factors that influence abundance and distribution of herbaceous and woody plant species in regenerating bottomland hardwood forests. It is likely that frequency and depth of inundation were responsible for much of the variation observed at Moro Bottoms. This was not surprising because it is one feature that clearly distinguishes bottomland forests from other forests. Unless hydrology has been altered by anthropogenic disturbances, differential flooding regimes are a natural feature of hardwood bottomlands. Thus, the observed patterns of regeneration may be typical of old-growth bottomland forests in response primarily to hydrology. At the SRS study site, soil disturbance during timber harvesting appeared to be the primary influence on regeneration. The effects of gap size likely were influenced more by soil disturbance than herbivory. Non-standard methods of tree removal, such as helicopter-logging or horse-logging, cause less soil disturbance than log skidders and may deserve consideration in some circumstances. Nevertheless, effects on richness and diversity of both herbaceous and woody species appeared to have a short-term effect in our study. Long-term implications are still unclear and deserve further study, as do effects on individual plant species that may be locally extirpated by disturbance.

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