

THE EFFECT OF HERBIVORY BY WHITE-TAILED DEER AND ADDITIONALLY SWAMP RABBITS IN AN OLD-GROWTH BOTTOMLAND HARDWOOD FOREST

Margaret S. Devall, Bernard R. Parresol, and Winston P. Smith¹

Abstract—Forest openings create internal patchiness and offer different habitat qualities that attract wildlife, especially herbivores, that flourish along forest edges. But intense herbivory in these openings can reduce or eliminate herbaceous and woody species and thus influence local species composition and structure of the forest. This study in an old-growth bottomland hardwood forest in southeastern Arkansas compares plant colonization among experimental plots, which excluded white-tailed deer (*Odocoileus virginianus*), deer and swamp rabbits (*Sylvilagus aquaticus*), and control plots. After the third year, plant species composition and abundance were significantly affected by herbivores.

INTRODUCTION

Old-growth forests of various types, which had developed with only low-intensity human disturbance, occupied much of the presettlement landscape of Arkansas (Holder 1970). European exploration and settlement of Arkansas began in the 16th century. Although the forests provided a valuable source of wood to European settlers, they were an impediment to farming. Wetland forests were especially threatened because at the time of European colonization wetlands were considered useful only after they were drained. The Swamp Land Acts of 1849–1850 granted swamplands in Federal ownership to the States to be reclaimed and disposed of; thereafter, widespread destruction of forested wetlands proceeded at a rapid rate (Turner and Craig 1980). Since colonial times almost half of the wetlands in the United States have been destroyed, and until recently thousands of acres were lost each year (MacDonald and others 1979). As a result, while old-growth forests are becoming less common throughout the United States, old-growth forested wetlands are even scarcer.

Although much is unknown about old-growth forests, it is obvious that many of their characteristics are different from those of younger forests (Juday 1988, Runkle 1991). While numerous definitions of old-growth forests have been suggested, two features occur in many of these definitions: (1) trees die singly or in small groups, creating openings or gaps in which regeneration of seedlings can occur; and (2) large logs and snags account for many of the values of the forests (Runkle 1982, 1991). For example, they provide food, shelter, or germination sites for various plant and animal species (Harmon and others 1986). Conversely, in many younger eastern forests large-scale disturbances occur often enough to be the dominant influence on their structure and composition (Runkle 1982, 1991).

Increased densities of deer (*Odocoileus virginianus*) and other herbivores that thrive in fragmented forests can alter plant species composition and structure (Alverson and

others 1988). Swamp rabbits (*Sylvilagus aquaticus*) can be serious deterrents to the establishment of tree seedlings in wetlands. They clip seedlings at various heights above the ground and eat the tender parts (Blair and Langlinais 1960). Although there have been numerous studies of the effects of white-tailed deer on forests (Anderson and Loucks 1979, Alverson and others 1988, Griffin 1976, Richards and Farnsworth 1971, Ross and others 1970, Stewart and Burrows 1989), deer habitat and behavior vary considerably from one part of the country to another, and their effects on different plant species vary. Therefore, local studies are indispensable in answering questions about the effects of deer on a particular forest type (Strole and Anderson 1992). Moreover, the consequences of disturbance regimes and herbivory on old-growth bottomland hardwood forests are not well known because there have been few studies on the remaining old-growth wetland forests. The purpose of this study is to determine the effects of white-tailed deer and swamp rabbits on plant species diversity. Specific objectives include testing the hypotheses that species composition of tree regeneration is independent of white-tailed deer or combined white-tailed deer and swamp rabbit use of gap openings; and that plant species richness, abundance, and diversity within gaps are independent of white-tailed deer or white-tailed deer and swamp rabbit use.

The study area (Moro Bottoms) is a 40-ha old-growth bottomland hardwood forest located in Cleveland County, AR. It is part of a larger area owned by the Arkansas Natural Heritage Commission and the Arkansas Nature Conservancy. Dominant tree species at Moro Bottoms are oaks (*Quercus falcata* var. *pagodifolia* Ell., *Q. nigra* L., *Q. lyrata* Walt., *Q. alba* L., *Q. phellos* L., *Q. michauxii* Nutt., *Q. velutina* Lam.), sweetgum (*Liquidambar styraciflua* L.), and baldcypress [*Taxodium distichum* (L.) Rich.], with several hickory species [*Carya tomentosa* (Poir.) Nutt., *C. ovata* (Mill.) K. Koch and *C. cordiformis* (Wangenh.) K. Koch]. The small tree and shrub layer includes ironwood (*Carpinus caroliniana* Walt.), Carolina ash (*Fraxinus caroliniana* Mill.),

¹ Research Ecologist, USDA Forest Service, Southern Research Station, Stoneville, MS; Mathematical Statistician, USDA Forest Service, Southern Research Station, Asheville, NC; and Research Wildlife Biologist, USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, Juneau, AK, respectively.

and hollies (*Ilex opaca* Ait., *I. decidua* Walt.).² Moro Bottoms is an excellent example of a late transition bottomland hardwood forest becoming old growth through gap regeneration. Trees, especially sweetgum and cherrybark oak, are quite large (up to 149 cm)³ with exceptionally good form. Moro Bottoms provided an ideal opportunity to study the effects of large mammalian herbivores on biodiversity in wetland forest gaps. A severe windstorm during the late summer of 1989 caused windthrows, which created gaps in the overstory ranging from 0.1 to 0.5 ha. A cursory survey before the study suggested moderate use of the area by deer in late fall and greater use by swamp rabbits.⁴ Johnson and others (1995) noted that older forests generally provide the best foraging conditions for deer in fall and winter.

MATERIALS AND METHODS

Thirty paired plots consisting of herbivore exclosures and adjacent unmanipulated controls were installed within windthrow gaps. Each of the paired plots was randomly placed on one side of a north-south line located approximately through the center of each windthrow gap. Exclosures were approximately 2.5 by 4 m and were constructed of 5- by 10- cm welded wire fencing and 2.4-m metal posts. The fence was elevated 15 cm from the ground to allow entry of swamp rabbits. Within each exclosure ten 0.5- by 1.0-m quadrats were randomly located. These were fenced with 2.5- by 5-cm welded wire 0.6 m high to additionally exclude swamp rabbits. The remaining ten 0.5- by 1.0-m plots were available to swamp rabbits, but were protected from deer use. Adjacent to each exclosure was a control plot with three fence posts along one side. The control plot was divided into 10 contiguous 0.5- by 1-m quadrats. The exclosures were constructed in 1990 during winter prior to the growing season. While it would have been ideal to set up a separate set of fencing to exclude only swamp rabbits, and not to nest the rabbit exclosures inside the deer exclosures, operationally it would have been extremely difficult to accomplish. The logistics were such that the only practical course was to nest the treatments.

Data were collected during spring, summer, and fall of 1990, 1991, and 1992. Percent cover for herbaceous species (0 to 5, 6 to 15, 16 to 25, 26 to 35 . . . 95 to 100) and total percent cover were recorded in deer exclosures, deer-and-rabbit exclosures, and control plots. During 1990 and 1991 total cover of grasses and sedges were recorded in place of each

separate species, except for cane [*Arundinaria gigantea* (Walter) Muhl.], because of the difficulty of identifying these species when they were not fruiting or flowering; *Smilax* and *Vitis* totals also were recorded. During 1992 all herbaceous species were recorded separately. Duplicates of plant species in the plots were collected from areas nearby and identified; species not present in the exclosures were also collected.

During each visit the number and species of shrub and tree seedlings in each plot were recorded. All oak seedlings were recorded as *Quercus* spp. during 1990 and 1991, but the oaks were recorded by species during 1992. Oak seedling leaves can be quite variable so a few hard-to-determine seedlings were counted as red oak group. We were not able to distinguish separate hickory or blueberry (*Vaccinium* spp.) seedlings because of the difficulty of classifying seedlings and small nonfruiting specimens of these species, so these were recorded as *Carya* or *Vaccinium* spp. Plants were collected and identified, using Radford and others (1968), Little (1978), Steyermark (1963), Allen (1980), and Chabreck and Condrey (1979). "An Atlas and Annotated List of the Vascular Plants of Arkansas" (Smith 1988) was consulted to verify that the species identified occurred in Arkansas.

During the summer of 1991, exclosure and control plots 16 and 20 were destroyed by tree falls; exclosures 31 and 32 with controls were subsequently constructed to replace them. During the summer of 1992, falling trees destroyed plots 9 and 30.

We assumed a priori there would be seasonal differences and reasonably expected to have yearly differences, so we dispensed testing for these effects. The most expedient analyses for comparing treatments at each measuring period were, therefore, simple paired t-tests. Hence, paired t-tests were used to analyze the percent-cover data with the following comparisons: deer exclusion versus control and deer and rabbit exclusion versus control. Due to the nested nature of rabbit exclosures with deer exclosures, no statistically independent test could be constructed for comparing the effects of rabbit exclosures versus deer exclosures. Nonparametric analysis of variance (Kruskal-Wallis test) was employed to evaluate the seedling data. A probability of < 0.05 was accepted as statistical justification for rejecting a null hypothesis.

RESULTS

One hundred and fifty-six vascular plant species were present in the plots. Thirty-eight of these were tree or shrub species. Twelve grass (*Graminae* spp.) species, 10 sedge (*Cyperaceae* spp.) species, and 73 other herbaceous species were recorded in the plots. Also, there were 13 woody vines (*Vitaceae* spp.), 8 nonwoody vines, and 2 ferns.

The number of plant species encountered varied considerably among treatments. There was no clear pattern of treatment effects across sampling periods on plant diversity as reflected by species richness (mean number of species per unit area), cumulative species (total number of species across all plots in a treatment category), or number of unique species (species that occurred in only one treatment category) (fig. 1A–C).

² Peacock, Lance. 1983. Moro Bottoms site (preserve) summary. Little Rock, AR: Arkansas Nature Conservancy. 7 p. Unpublished report. On file with: The Nature Conservancy, Arkansas Field Office, 601 N. University Avenue, Little Rock, AR 72205.

³ Devall, Margaret S. 1998. Dendroecological study of Moro Bottoms Natural Area. 10 p. Unpublished data. On file with: U.S. Department of Agriculture, Forest Service, Southern Research Station, Center for Bottomland Hardwoods Research, P.O. Box 227, Stoneville, MS 38776.

⁴ Smith, Winston P.; Toliver, John R.; Devall, Margaret S.; Parresol, Bernard R. 1990. Windthrow gaps in an old-growth bottomland hardwood forest: wildlife use and consequent influence on forest composition. 16 p. Study plan. On file with: U.S. Department of Agriculture, Forest Service, Southern Research Station, Center for Bottomland Hardwoods Research, P.O. Box 227, Stoneville, MS 38776.

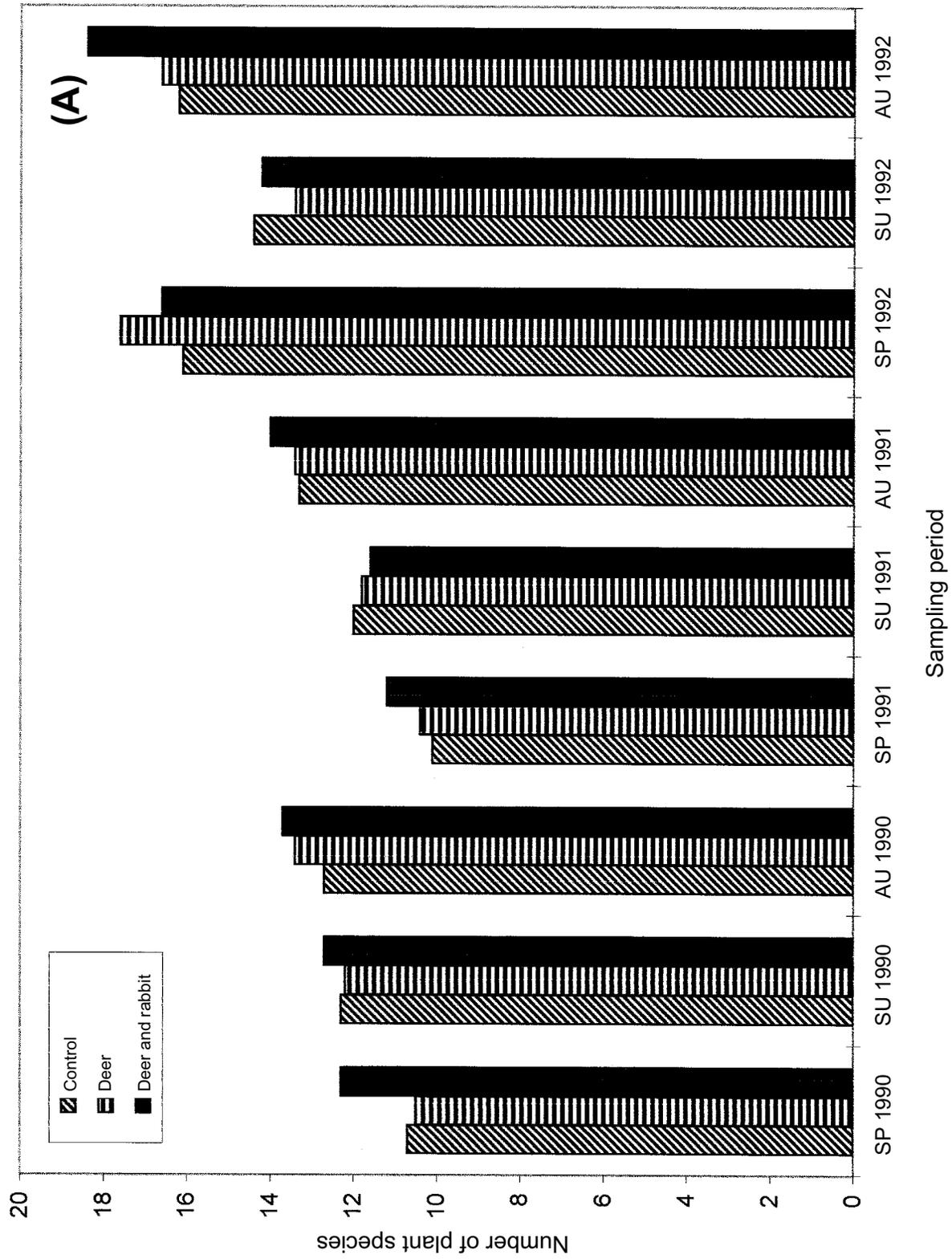


Figure 1A—Mean number of species per plot recorded seasonally in 5-m² plots (species richness). Moro Bottoms Natural Area (SP = spring, SU = summer, AU = autumn).

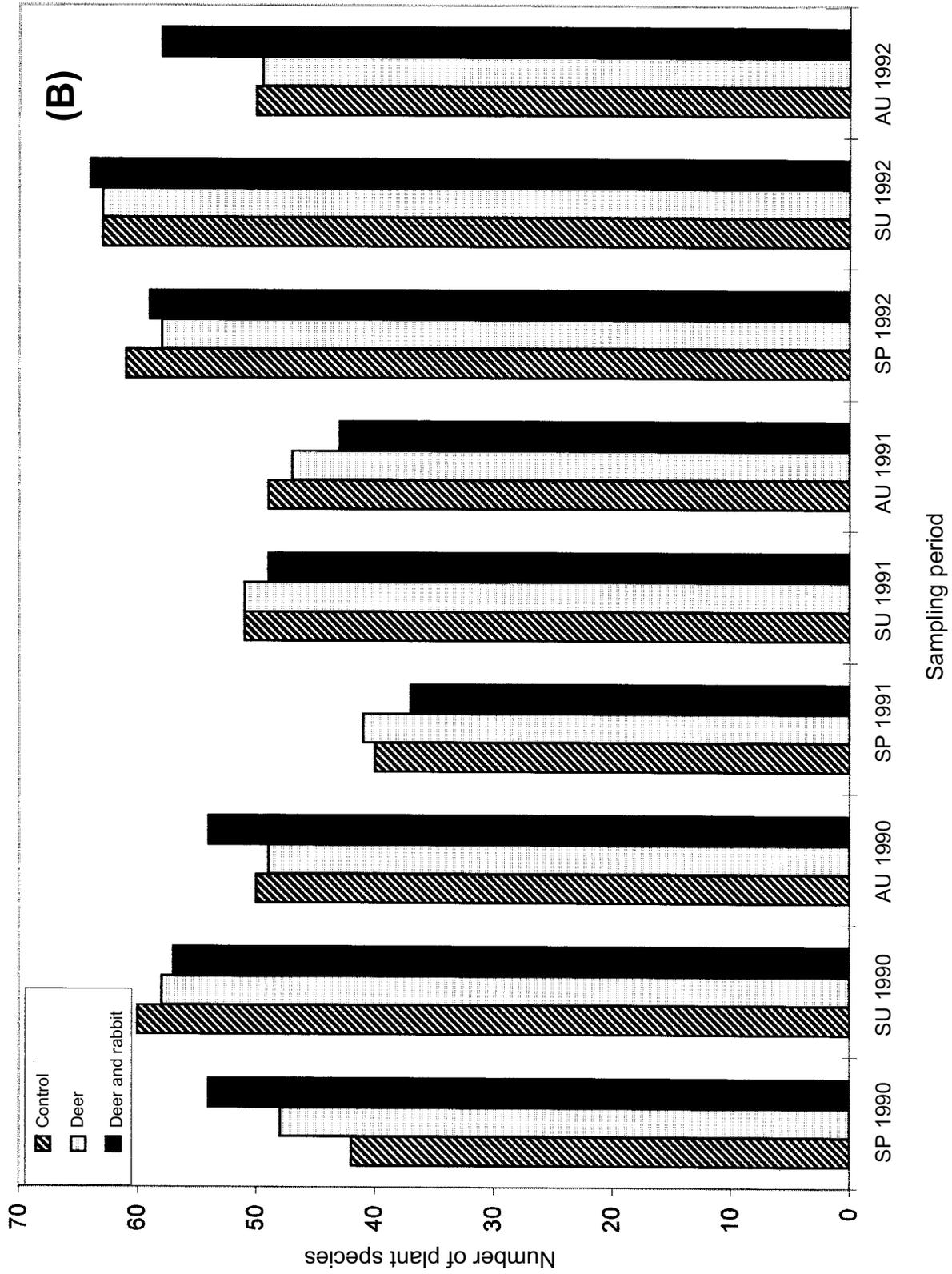


Figure 1B—Number of species across all plots within a treatment category for each period (cumulative species). Moro Bottoms Natural Area (SP = spring, SU = summer, AU = autumn).

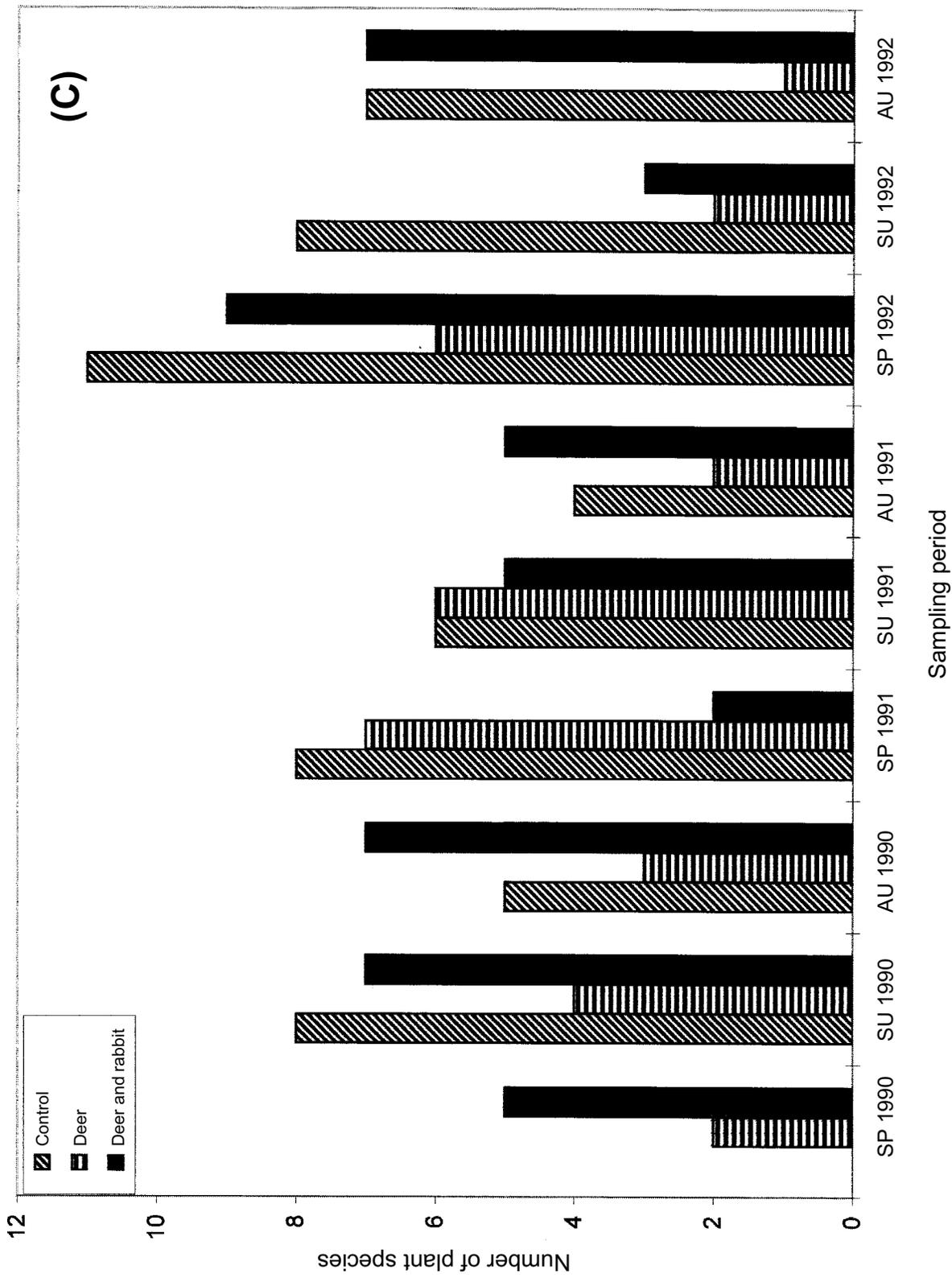


Figure 1C—Number of species found only in one treatment category for each period (unique species). Moro Bottoms Natural Area (SP = spring, SU = summer, AU = autumn).

Eighty plant species were present in the deer and in the deer-and-swamp-rabbit exclosures in 1992, and 82 in the controls. The number of species occurring in a plot ranged from 9 to 25 in the deer exclosures, 9 to 31 in the deer-and-swamp-rabbit exclosures, and 9 to 23 in the controls.

Percent cover of herbaceous vegetation recorded among treatment and control plots during 1990–92 is summarized in figure 2. Percent cover in the controls ranged from 15 to 100 with standard deviations ranging from 16 to 25; in the deer exclusion plots, cover ranged from 5 to 100 with standard deviations of 16 to 26; cover in the deer-and-rabbit plots varied from 5 to 100 with standard deviations of 18 to 28. Percent cover of vegetation in the deer and in the deer-and-rabbit exclosures was significantly less than that in the control plots in the spring of 1990 (table 1). The control versus deer comparison also was significant in the summer of 1990. Significant differences did not occur again until the summer of 1992, and in the fall of 1992 control versus deer exclusion and control versus deer-and-rabbit exclusion were both highly significant.

Means of percent cover of grasses, sedges, and other herbaceous vegetation are presented in figure 3 A–C. In general, percent cover of grasses and sedges was higher in

Table 1—Paired comparisons of percent cover of herbaceous vegetation in the Moro Bottoms exclosures

Date	Variable	Mean	Standard error	T	Prob > T
Spring 1990	C vs. D	.08	.03	2.64	.01 ^a
	C vs. DR	.11	.03	3.17	0 ^a
Summer 1990	C vs. D	.08	.03	2.53	.02 ^b
	C vs. DR	.04	.03	1.61	.12
Fall 1990	C vs. D	.05	.03	1.61	.12
	C vs. DR	.02	.02	1.02	.32
Spring 1991	C vs. D	.01	.03	.29	.78
	C vs. DR	-0	.02	-.15	.88
Summer 1991	C vs. D	-0	.02	-.15	.88
	C vs. DR	.01	.03	.38	.70
Fall 1991	C vs. D	.04	.02	1.83	.08
	C vs. DR	.02	.02	.82	.42
Spring 1992	C vs. D	.04	.02	1.69	.10
	C vs. DR	.04	.02	1.73	.09
Summer 1992	C vs. D	.06	.02	3.04	.01 ^a
	C vs. DR	.08	.02	3.47	0 ^a
Fall 1992	C vs. D	.11	.22	4.67	0 ^a
	C vs. DR	.08	.02	3.47	0 ^a

Vs. = versus; mean and standard error = standard error of differences in percent cover; T = student's t statistic; Prob >|T| = associated probability from paired t-test; C vs. D = control versus deer; C vs. DR = control versus deer-and-swamp rabbit.

^a P = 0.01.

^b P = 0.05

control plots than in deer or in deer-and-rabbit plots, while coverage of other herbaceous species was higher in deer and in deer-and-rabbit plots. Paired comparisons (t statistic) of percent cover of grasses, sedges, and other herbaceous vegetation between control and treatment plots demonstrated that the observed pattern often reflected significant variation among treatments (table 2).

The sum of woody seedlings of all species ranged from a low of 138 in the deer exclosures in spring 1991 to a high of 761 in the deer-and-swamp-rabbit exclosures in 1992 (table 3). The total numbers of woody seedlings were similar (P > 0.05) among treatments during the 3 years of the study (table 4). Although not significant, 1992 results showed smaller probability values than the 1990 and 1991 data.

Significant differences among deer and deer-and-swamp-rabbit exclosures and controls were not demonstrated during spring, summer, or fall of any year for selected species that were thought to be favorite deer foods: sweetgum, greenbriars, red maple (*Acer rubrum* L.), and oak species, and for ironwood, which is eaten by deer, but is low choice (Halls 1977).

Diversity of the stands was investigated using the Shannon diversity index. Values of the Shannon index ranged from a low of 3.15 to a high of 3.70 (fig. 4).

DISCUSSION

We studied the vegetation occurring in forest gaps, but did not collect quantitative data beyond the gaps. Nevertheless, some comparisons to other older bottomland hardwood forests can be made. Moro Bottoms is in the west gulf Coastal Plain. Other sites located in the Mississippi River alluvial floodplain have different soils, stand origin, and possible disturbance history. Robertson and others (1978) studied woody species in two stands on Horseshoe Lake Island in Alexander County, IL, one relatively undisturbed and one recovering from disturbance in the late 1800's or early 1900's. Trees with the highest importance value in the 35-ha old-growth stand were sweetgum, red maple, and green ash (*F. pennsylvanica* Marsh.). Sugar maple (*A. saccharum* Marsh.), sweetgum, tupelo gum (*Nyssa aquatica* L.), bitternut hickory, American elm (*Ulmus americana* L.), northern red oak (*Q. rubra* L.), and sassafras [*Sassafras albidum* (Nutt.) Nees] were dominants in the secondary stand. In the old-growth shrub-sapling stratum, 22 woody species were encountered, with pawpaw [*Asimina triloba* (L.) Dunal], red buckeye (*Aesculus pavia* L.), buttonbush (*Cephalanthus occidentalis* L.), grapes (*Vitis* spp.), and silver maple (*A. saccharinum* L.) the dominant species. There were 20 species in the secondary forest. In the seedling stratum, 46 and 45 species of trees, shrubs, and vines occurred in the old growth and secondary areas, respectively, compared to 51 at Moro Bottoms. Pawpaw, red buckeye, green ash, tupelo gum, and bitternut hickory dominated seedlings in the secondary forest. The forests seem similar to that at Moro Bottoms, except that the secondary forest at Horseshoe Lake Island contained more fast-growing, short-lived species.

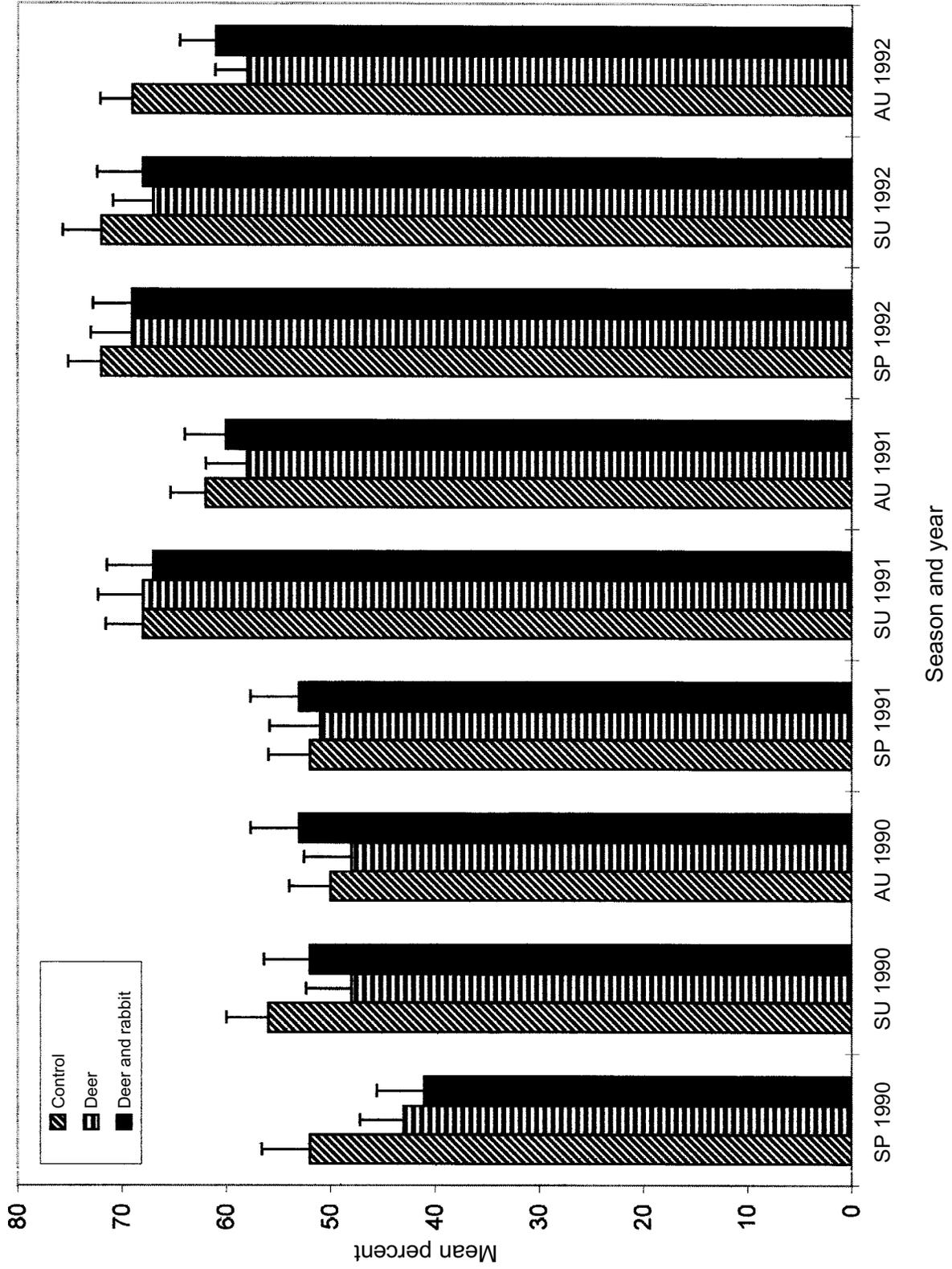


Figure 2—Mean of percent ground cover of herbaceous vegetation within control, deer exclusion, and deer-and-rabbit exclusion plots, Moro Bottoms Natural Area. (SP = spring, SU = summer, AU = autumn).

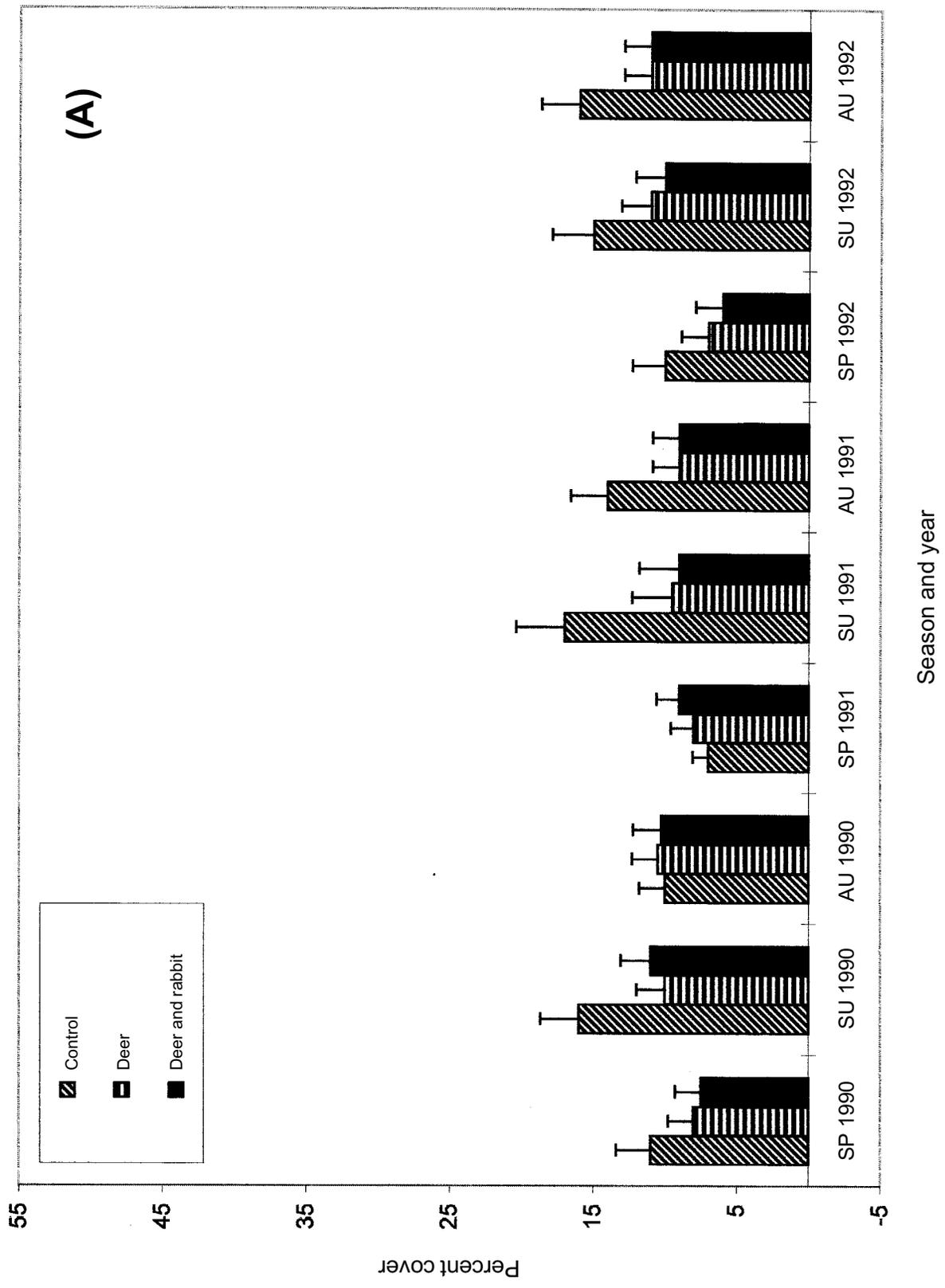


Figure 3A—Mean of percent ground cover of grasses and sedges at Moro Bottoms Natural area. (SP = spring, SU = summer, AU = autumn).

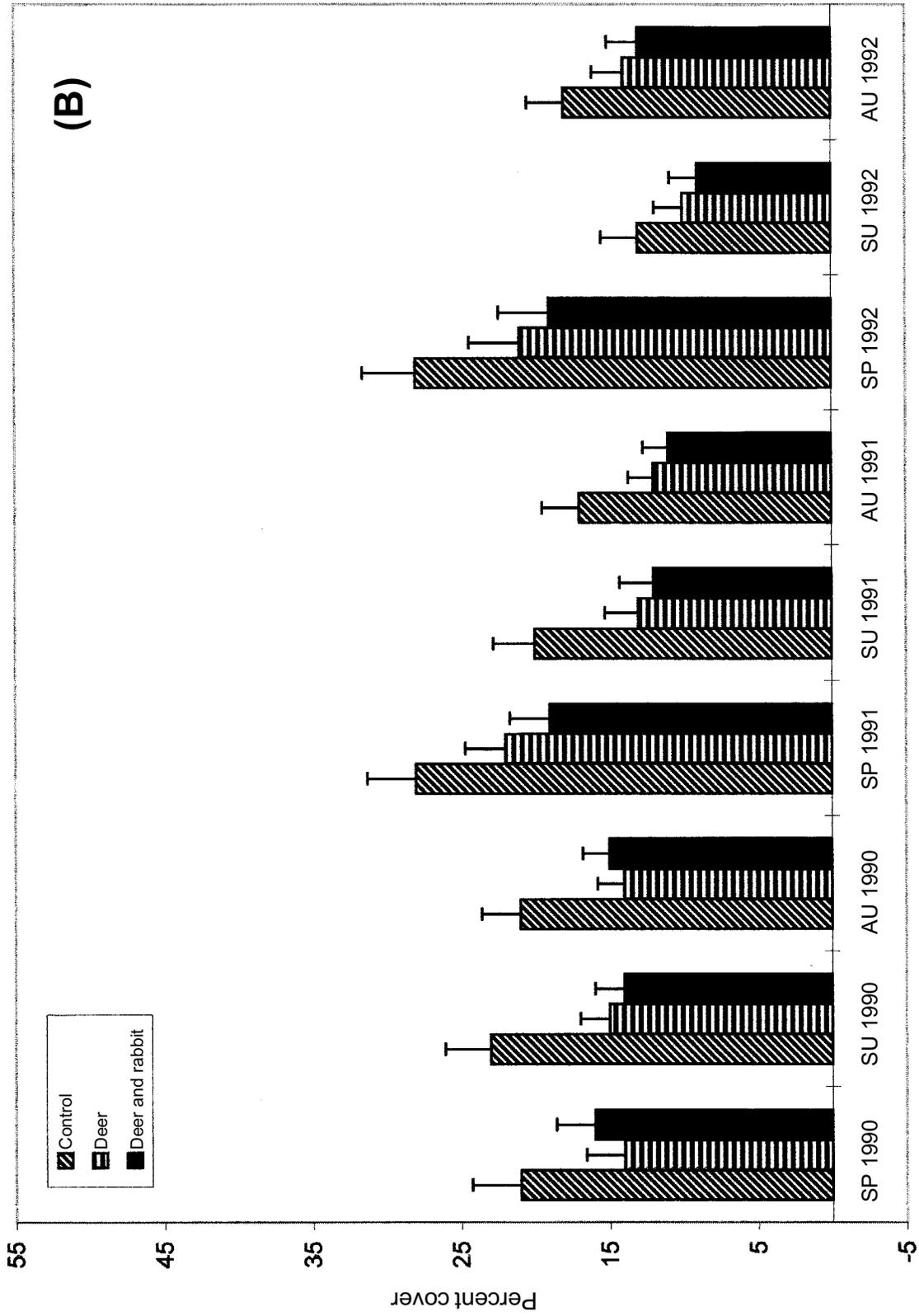


Figure 3B—Mean of percent ground cover of grasses and other herbaceous vegetation at Moro Bottoms Natural Area. (SP = spring, SU = summer, AU = autumn).

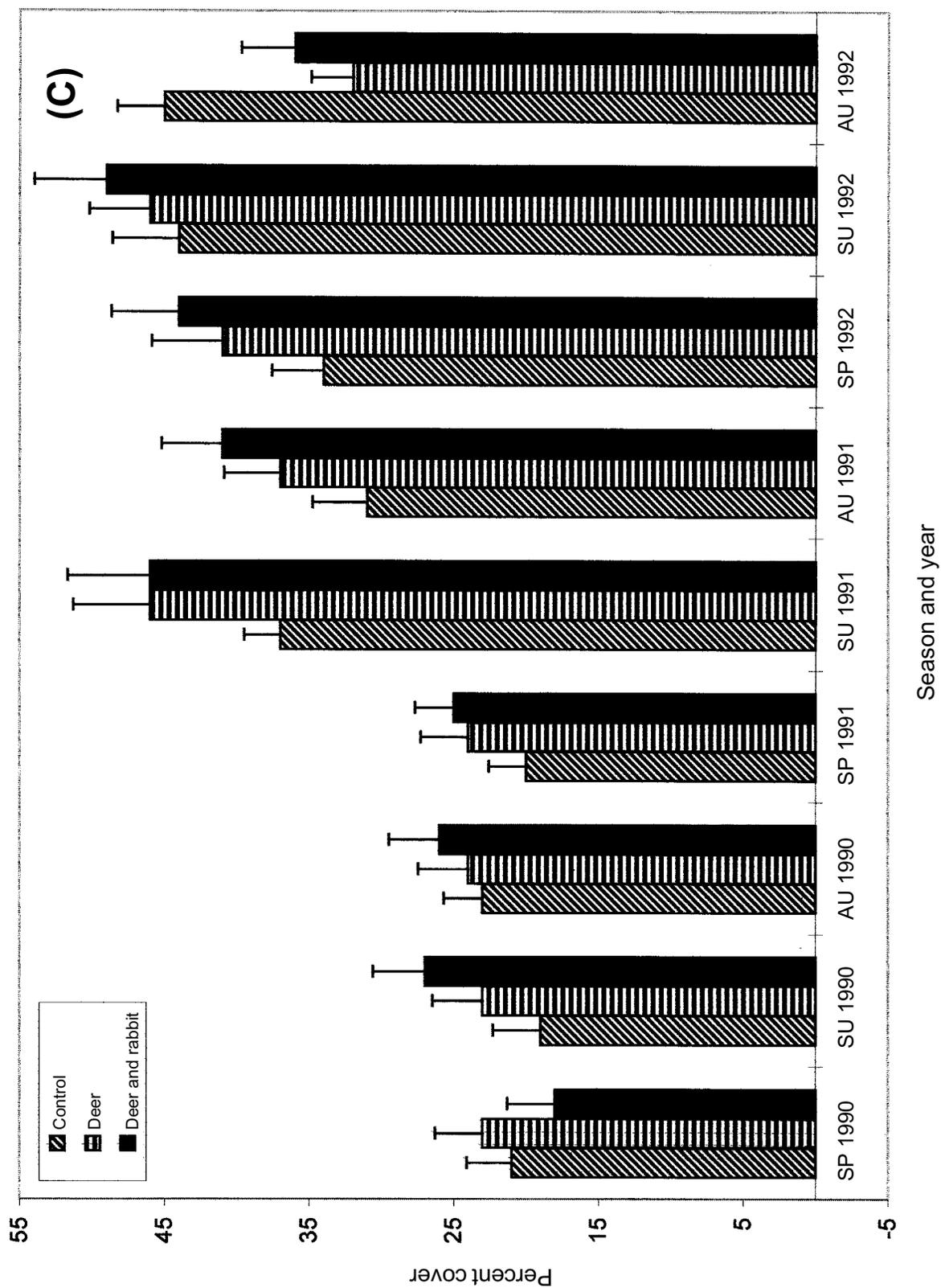


Figure 3C—Mean of percent ground cover of grasses within control, deer exclusion, and deer-and-rabbit exclusion plots at Moro Bottoms Natural Area. (SP = spring, SU = summer, AU = autumn).

Table 2—Mean and standard error of differences in percent cover of grasses, sedges, and other herbaceous vegetation between control and deer exclusion and between control and deer-and-rabbit exclusion, Moro Bottoms Natural Area

Date	Plant group	Sample size	Variable	Mean	Standard error	T	Prob > t
Spring 1990	Grasses	30	C vs. D	2.33	2.44	.96	.35
			C vs. DR	2.83	2.42	1.17	.25
	Sedges	30	C vs. D	7.17	2.68	2.68	.01 ^a
			C vs. DR	4.67	1.74	2.68	.01 ^a
	Other	30	C vs. D	-1.38	3.15	-.44	.66
			C vs. DR	1.55	3.20	.49	.63
Summer 1990	Grasses	30	C vs. D	4.83	2.80	1.72	.09
			C vs. DR	4.16	2.65	1.57	.13
	Sedges	30	C vs. D	7.33	2.09	3.52	0 ^a
			C vs. DR	8.33	1.92	4.33	0 ^a
	Other	30	C vs. D	-3.50	2.67	-1.31	.20
			C vs. DR	-7.50	3.28	-2.29	.03 ^b
Fall 1990	Grasses	30	C vs. D	-.83	1.78	-.47	.64
			C vs. DR	-.66	1.85	-.36	.72
	Sedges	30	C vs. D	7.33	2.21	3.32	0 ^a
			C vs. DR	6.17	1.31	4.72	0 ^a
	Other	30	C vs. D	-2.17	2.42	-.90	.38
			C vs. DR	-4.31	2.48	-1.74	.09
Spring 1991	Grasses	30	C vs. D	-1.50	1.68	-.89	.38
			C vs. DR	-2.50	1.90	-1.32	.20
	Sedges	30	C vs. D	6.67	3.16	2.11	.04 ^b
			C vs. DR	9.00	2.63	3.42	0 ^a
	Other	30	C vs. D	-4.50	2.94	-1.53	.14
			C vs. DR	-6.67	2.63	-2.94	.01 ^a
Summer 1991	Grasses	28	C vs. D	7.68	3.38	2.27	.03 ^b
			C vs. DR	7.86	3.21	2.45	.02 ^b
	Sedges	28	C vs. D	7.14	2.46	2.90	.01 ^a
			C vs. DR	8.21	2.52	3.26	0 ^a
	Other	28	C vs. D	-15.18	4.55	-3.34	0 ^a
			C vs. DR	-15.18	4.38	-3.47	0 ^a
Fall 1991	Grasses	28	C vs. D	5.00	2.04	2.45	.02 ^b
			C vs. DR	5.18	2.42	2.14	.04 ^b
	Sedges	28	C vs. D	5.18	2.25	2.30	.03 ^b
			C vs. DR	6.07	2.48	2.44	.02 ^b
	Other	28	C vs. D	-6.25	2.72	-2.30	.03 ^b
			C vs. DR	-9.46	3.68	-2.57	.02 ^b
Spring 1992	Grasses	29	C vs. D	3.28	1.89	1.73	.09
			C vs. DR	4.31	1.93	2.23	.03 ^b
	Sedges	29	C vs. D	7.59	3.40	2.23	.03 ^b
			C vs. DR	11.38	3.24	3.51	0 ^a
	Other	29	C vs. D	-7.07	3.36	-2.10	.04 ^b
			C vs. DR	-11.90	3.80	-3.13	0 ^a
Summer 1992	Grasses	27	C vs. D	4.44	1.65	2.69	.01 ^a
			C vs. DR	5.37	2.05	2.62	.01 ^a
	Sedges	27	C vs. D	3.52	1.92	1.83	.08
			C vs. DR	4.44	2.02	2.20	.04 ^b
	Other	27	C vs. D	-2.04	2.79	-.73	.47
			C vs. DR	-5.74	3.23	-1.78	.09
Fall 1992	Grasses	28	C vs. D	5.18	1.95	2.66	.01 ^a
			C vs. DR	5.18	2.28	2.27	.03 ^b
	Sedges	28	C vs. D	2.68	1.77	1.51	.14
			C vs. DR	3.39	1.76	1.92	.07
	Other	28	C vs. D	2.86	2.32	1.23	.23
			C vs. DR	-.71	2.89	-.25	.80

SE = standard error; T = student's t statistic; Prob > |t| = associated probability from paired t-test of means; C vs. D = control versus deer exclusion; C vs. DR = control versus deer-and-rabbit exclusion.

^a P=0.01.

^b P=0.05.

Table 3—Density values of woody seedlings occurring in the plots at Moro Bottoms

Species	Plot type	1990			1991			1992		
		SP	SU	F	SP	SU	F	SP	SU	F
----- Number of seedlings -----										
All species	D	281	485	356	138	287	307	548	500	540
	DR	358	392	431	197	369	370	720	683	761
	C	309	526	473	159	400	360	493	609	697
Oaks ^a	D	178	240	232	48	160	173	336	295	333
	DR	220	288	253	73	202	225	417	402	443
	C	197	318	312	27	222	211	320	393	484
Red maple	D	26	19	3	5	5	2	25	12	14
	DR	14	27	10	5	1	4	92	35	35
	C	7	11	10	2	3	2	24	25	18
Sweetgum	D	11	18	11	12	12	12	10	18	15
	DR	13	21	23	10	19	18	18	25	24
	C	12	20	15	11	18	14	15	19	16
Ironwood	D	36	56	52	16	31	32	82	76	90
	DR	60	67	69	59	42	25	106	101	134
	C	40	78	68	59	55	29	63	86	78

SP = spring; SU = summer; F = fall; D = deer exclusion plots, DR = deer-and-swamp rabbit plots; C = control.

^aOaks = water oak, overcup oak, white oak, willow oak, black oak, cherrybark oak.

Table 4—Kruskal-Wallis test of number of woody seedlings present in the Moro Bottoms deer, deer-and-swamp rabbit, and control exclosures

Date	Chi-square	Degrees of freedom	Prob. > chi-square
Spring 1990	2.85	2	0.24
Summer 1990	1.34	2	.51
Fall 1990	1.38	2	.50
Spring 1991	1.20	2	.55
Summer 1991	.83	2	.66
Fall 1991	.92	2	.63
Spring 1992	4.36	2	.11
Summer 1992	1.56	2	.46
Fall 1992	4.92	2	.09

Devall (1982) studied the Beauvais tract (42 ha) at Cat Island, a bottomland swamp in West Feliciana Parish, LA, where timber has been selectively cut, but old trees are also present (oldest 450 years), and there is some gap regeneration. Twenty-two tree species occurred in this forest. Sugarberry (*Celtis laevigata* Willd.) had the highest importance value, followed by cypress and green ash. Many of the trees and woody vines occurring at Moro Bottoms were also present at Cat Island. The midstories were dissimilar, with sugarberry, green ash, and American elm common at Cat Island. Fifty-one species (herbs and woody seedlings) occurred in 1-m quadrats (not located in gaps), 18 of which were present at Moro Bottoms, and 75 species were collected outside of quadrats, 13 of these at Moro Bottoms. Grass and sedge species were much more important at Moro Bottoms, and herbaceous diversity was greater.

There are few exotic species present in Moro Bottoms. In addition to Mariana maiden fern [*Thelypteris torresiana* (Gaud.) Alston] reported by Orzell and Bridges,⁵ Japanese

⁵ Orzell, Steve; Bridges, Edwin. 1990. Moro Creek Bottoms, Arkansas. 4 p. Unpublished report. On file with: Arkansas Natural Heritage Commission, 1500 Tower Building, 323 Center Street, Little Rock, AR 72201.

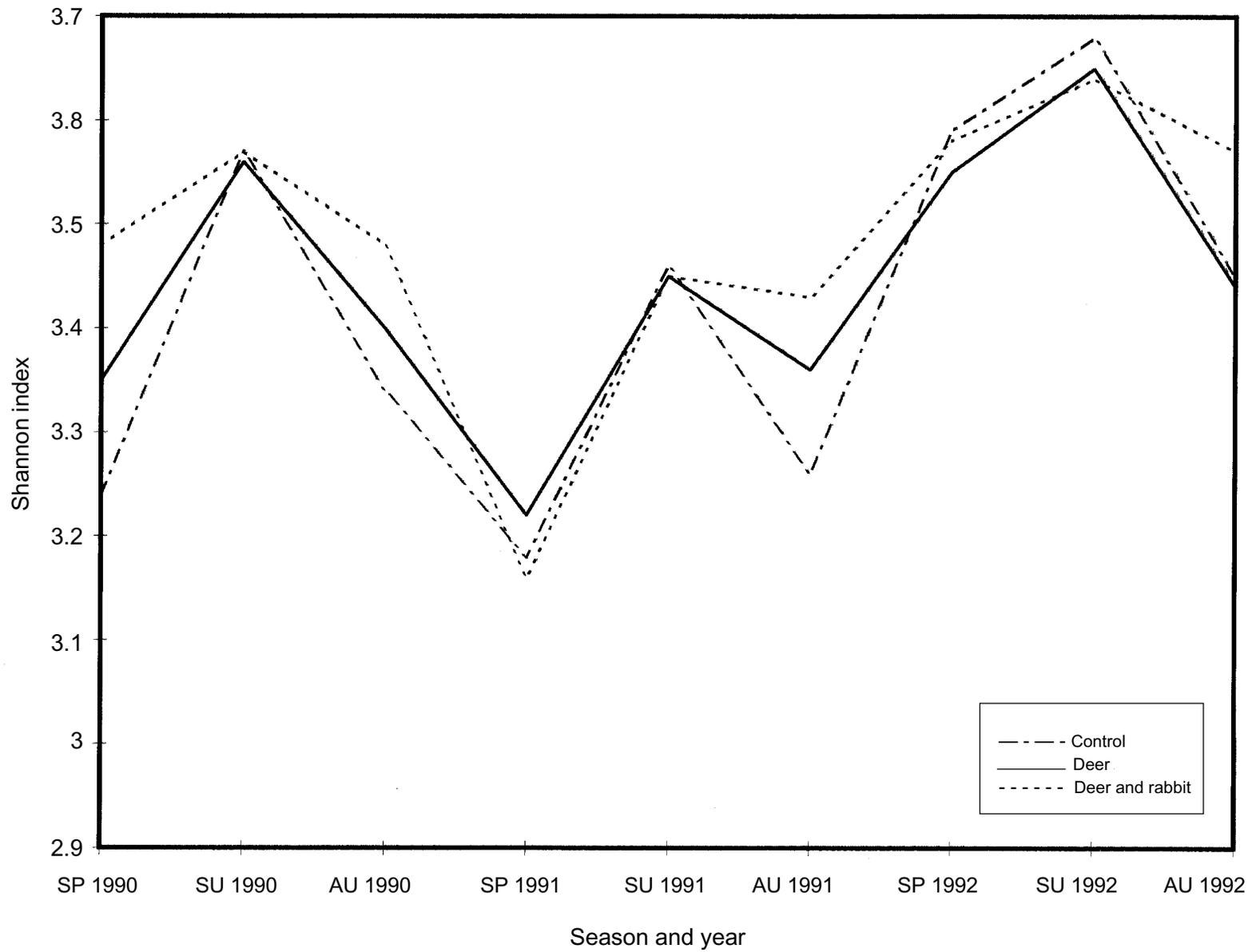


Figure 4—Values of the Shannon diversity index for herbaceous vegetation within control, deer exclusion, and deer-and-rabbit exclusion plots at Moro Bottoms Natural Area. (SP = spring, SU = summer, AU = autumn).

honeysuckle (*Lonicera japonica* Thunb.) was noted in and near plot 21. Although Orzell and Bridges (see footnote 5) mentioned damage by feral pigs, we did not note evidence of feral pigs during the study.

It was somewhat surprising that species richness, total cumulative species, and number of unique species were apparently not affected by herbivory of white-tailed deer or swamp rabbits (fig. 1A–C). Deer density varied considerably in different seasons, from < 1 deer per square kilometer in spring to 21.8 deer per square kilometer in autumn.⁶ Alverson and others (1988) reported that herbivory prevented regeneration of common woody species such as Canada yew (*Taxus Canadensis* Marsh.), eastern hemlock [*Tsuga Canadensis* (L.) Carr.], and white cedar (*Thuja occidentalis* L.) even at deer densities as low as four deer per square kilometer, reduced reproductive success, or caused local extirpation of several herbaceous species indigenous to northern hemlock-hardwood forests. Tilghman (1989) reported analogous results for comparable deer densities in Pennsylvania. In other cases, comparable deer populations have caused severe damage to the understory (Hough 1965). Similar to our results, Balgooyen and Waller (1995) found that percent cover of several herbaceous species declined significantly in areas with higher historic and recent deer densities. In spite of these effects, deer densities did not seem to be directly related to the overall number of herbaceous species, the Shannon-Weaver index of diversity, or vegetative cover.

Perhaps the initial shock of exclusion accounted for the differences in percent cover of herbaceous vegetation in 1990, because all evidence of treatment effects disappeared by autumn 1990. It seems that the intensity of browsing pressure was not sufficient to cause apparent impacts until the end of the third year of exclusion of deer and rabbits. At that time we began to detect differences in the percent cover of total vegetation in the control versus deer exclosures, and by the fall of 1992 there were differences between the control versus deer and control versus deer and swamp rabbits, although not in the direction one might expect. The control plots had greater percent cover of vegetation than the exclosure plots. Perhaps deer and swamp rabbits kept the vegetation trimmed, so some species did not grow large and shade others, or grazing stimulated growth.

We observed that the percent cover of grasses and sedges was consistently greater and the percent cover of other herbaceous vegetation regularly less in control plots than in exclosure plots. Although there was some variation, sedges were clearly more abundant in control plots than in deer-exclusion plots, and the effect was even more pronounced in the deer-and-rabbit plots. Deer rarely eat sedges and grasses (Harlow and Hooper 1972, Murphy and Noble 1973, Newsom 1984); deer in bottomland forests prefer herbs such

as *Aster* spp. (Murphy and Noble 1973). Little published information exists regarding the food preferences of swamp rabbits, but such features as digestibility that are attractive to ungulates are also important to rabbits (Hjaltén 1991). Thus, the pattern of cover that we observed was probably a consequence of deer and/or rabbits avoiding grasses and sedges and selectively browsing other herbs.

Deer browsing has been shown to reduce plant biodiversity (Dzieciolowski 1980, Strole and Anderson 1992) and can bring about inconspicuous changes in species composition, even when deer are not very abundant (Anderson and Loucks 1979, Stewart and Burrows 1989, Strole and Anderson 1992). Treatment effects may occur slowly; recovery, if deer are excluded, can require several growing seasons (Ross and others 1970). Neither deer nor swamp rabbits appeared to be very numerous at Moro Bottoms, but by the third year of deer and swamp rabbit exclusion (summer 1992), the effects of herbivory became apparent. Many of the previous studies mentioned recount vegetation responses after five or more growing seasons; the effects of herbivory at Moro Bottoms may become more pronounced with time. The long-term consequences of herbivory on the biological diversity of this old-growth bottomland hardwood forest can only be determined through further study.

Few cypress, hickory, or holly seedlings occurred in the plots. Although acorns are a favorite deer food (Halls 1977), oak seedlings were not scarce (fig. 3). Ironwood and red maple seedlings were also numerous (fig. 3). It was apparent from the larger number of seedlings present in spring and fall that many seedlings did not survive the summer (evidently new seedlings germinated after rains). We did not monitor survival of particular seedlings, but few of the oaks, ironwood, red maple, cypress, and hickory appeared to be more than 1 year old until 1992, when more older oak seedlings were present, especially willow oak (*Q. phellos* L.) and water oak. Sweetgum seedlings were not as numerous as the oak species, but appeared to survive the summers better (dead willow oak and water oak seedlings were present in the fall, although new oak seedlings had germinated).

Balgooyen and Waller (1995) noted differences in the effects of deer grazing on herbaceous and woody plants. The gaps at Moro Bottoms were created by a windstorm in late summer of 1989, thus most of the vegetation we measured germinated no earlier than the spring of 1990, when the study began. Delayed oak germination can occur in the fall, as well. Perhaps herbaceous species are affected sooner by grazing than woody species, and the effects of herbivory by deer and rabbits on woody species will become apparent later.

The gaps are at different elevations, but all are covered with 1 m or more of water most years for varying periods during spring, and they may be flooded briefly after hard rains at other times of the year. While inundation no doubt had an effect on the vegetation at Moro Bottoms, periodic flooding occurred during the time that herbs and woody species growing at Moro Bottoms became adapted to conditions there, thus they should have adapted to withstand submersion (Noble and Murphy 1975).

⁶ Smith, Winston P.; Devall, Margaret S.; Parresol, Bernard R. 1995. Windthrow gaps, mammalian herbivores, and diversity of old-growth bottomland hardwood forests. 122 p. Completion report. On file with: U.S. Department of Agriculture, Forest Service, Southern Research Station, Center for Bottomland Hardwoods Research, P.O. Box 227, Stoneville, MS 38776.

Except as noted above, seedlings occurring in the exclosures reflected the composition of the overstory, suggesting that gap processes could have been operating when the existing canopy developed (Runkle 1991). This also suggests that without outside influence, the forest will remain stable in the near future and will not change in composition. Succession to a different forest type does not appear to be occurring. During the time the study was conducted, occasional trees fell, creating new gaps or increasing the size of existing ones; Runkle (1991) states that repeated death of canopy trees in eastern old-growth forests is common. In older forests, crown sizes are large enough to provide opportunities for seedling and sapling growth.

ACKNOWLEDGMENTS

We thank the Arkansas Natural Heritage Commission and the Arkansas Field Office of The Nature Conservancy for allowing us to carry out the study on their preserve. A USDA Forest Service Research Cost-Share Grant (Dendroecological history of old-growth bottomland hardwood forest in southern Arkansas; Agreement SRS-33-CC-98-458 dated January 01, 1998) with cost-share support provided by Arkansas Forestry Commission, Arkansas Game and Fish Commission, Arkansas Game and Fish Foundation, and Arkansas Natural Heritage Commission funded the study. We appreciate the help with plant identifications by Eric Sundell, Seth Barnes, Michael Lelong, Danny Skojac, and Allen Moore.

LITERATURE CITED

- Allen, Charles M.** 1980. Grasses of Louisiana. Lafayette, LA: The University of Southwestern Louisiana. 358 p.
- Alverson, William S.; Waller, Donald M.; Solheim, Stephen L.** 1988. Forests too deer: edge effects in northern Wisconsin. *Conservation Biology*. 2(4): 348-358.
- Anderson, R.C.; Loucks, O.L.** 1979. White-tail deer (*Odocoileus virginianus*) influence of structure and composition of *Tsuga canadensis* forests. *Journal of Applied Ecology*. 16: 855-861.
- Balگوoyen, Christine P.; Waller, Donald M.** 1995. The use of *Clintonia borealis* and other indicators to gauge impacts of white-tailed deer on plant communities in northern Wisconsin, USA. *Natural Areas Journal*. 15(4): 308-318.
- Blair, Robert M.; Langlinais, Murphy J.** 1960. Nutria and swamp rabbits damage baldcypress plantings. *Journal of Forestry*. 58: 388-389.
- Chabreck, R.H.; Condrey, R.E.** 1979. Common vascular plants of the Louisiana marsh. Baton Rouge: Louisiana State University Center for Wetland Resources. 116 p.
- Devall, Margaret S.** 1982. Cat Island Swamp: an ecological and phenological study in West Feliciana Parish, Louisiana. New Orleans: University of New Orleans. 82 p. M.S. thesis.
- Dzięciolowski, R.** 1980. Impact of deer browsing upon forest regeneration and undergrowth. *Ekologia Polska*. 28: 583-599.
- Griffin, J.R.** 1976. Regeneration in *Quercus lobata* savannas, Santa Lucia Mountains, California. *American Midland Naturalist*. 95: 422-435.
- Halls, Lowell K.** 1977. Southern fruit-producing woody plants used by wildlife. Gen. Tech. Rep. SO-16. New Orleans: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station. 235 p.
- Harlow, Richard F.; Hooper, Robert G.** 1972. Forages eaten by deer in the Southeast. In: Proceedings annual conference of the Southeastern Association of Game and Fish Agencies; 1971 October 17-20; Charleston, SC. Columbia, SC: Southeastern Association of Game and Fish Commissioners. 25: 18-47.
- Harmon, M.E.; Franklin, J.F.; Swanson, F.J. [and others].** 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research*. 15: 133-302.
- Hjältén, Joakim.** 1991. Food selection by small mammalian herbivores and its impact on plant populations. Rep. 21. Umeå, Sweden: Swedish University of Agricultural Sciences, Institutionen for Viltökologi. 31 p.
- Holder, T.H.** 1970. Disappearing wetlands in eastern Arkansas. Little Rock, AR: Arkansas Planning Commission. 72 p.
- Hough, A.F.** 1965. A twenty year record of understory vegetational changes in a virgin Pennsylvania forest. *Ecology*. 46(3): 370-373.
- Johnson, A.S.; Hale, P.E.; Ford, W.M. [and others].** 1995. White-tailed deer foraging in relation to successional stage, overstory type and management of Southern Appalachian forests. *American Midland Naturalist*. 133: 18-35.
- Juday, Glenn Patrick.** 1988. Old-growth forests and natural areas: an introduction. *Natural Areas Journal*. 8(1): 3-6.
- Little, Elbert L., Jr.** 1978. Checklist of United States trees (native and naturalized). Agric. Handb. 541. Washington, DC: U.S. Department of Agriculture, Forest Service. 375 p.
- MacDonald, P.O.; Frayer, W.E.; Clauser, J.K.** 1979. Documentation, chronology, and future projections of bottomland hardwood habitat loss in the lower Mississippi Alluvial Plain. State College, PA: HRB Singer, Inc. 133 p. Vol. 1.
- Murphy, Patrick K.; Noble, Robert E.** 1973. The monthly availability and use of browse plants by deer on a bottomland hardwood area in Tensas Parish, Louisiana. In: Proceedings of the annual conference of the Southeastern Association of Game and Fish Agencies; 1972 October 22-25; Knoxville, TN. Columbia, SC: Southeastern Association of Game and Fish Commissioners. 26: 39-57.
- Newsom, John D.** 1984. Coastal Plain. In: Halls, Lowell K., ed. White-tailed deer. Ecology and management. Harrisburg, PA: Stackpole Books: 367-380.
- Noble, Robert E.; Murphy, Patrick K.** 1975. Short term effects of prolonged flooding on understory vegetation. *Castanea*. 40: 228-238.
- Radford, Albert E.; Ahles, Harry E.; Bell, C. Ritchie.** 1968. Manual of the vascular flora of the Carolinas. Chapel Hill, NC: The University of North Carolina Press. 1,183 p.
- Richards, N.A.; Farnsworth, C.E.** 1971. Effects of cutting level on regeneration of northern hardwoods protected from deer. *Journal of Forestry*. 69: 230-233.
- Robertson, Philip A.; Weaver, George T.; Cavanaugh, James A.** 1978. Vegetation and tree species patterns near the northern terminus of the southern floodplain forest. *Ecological Monographs*. 48: 249-267.

- Ross, B.A.; Bray, J.R.; Marshall, W.H.** 1970. Effects of long-term deer exclusion on a *Pinus resinosa* forest in north-central Minnesota. *Ecology*. 51: 1088–1093.
- Runkle, James R.** 1982. Patterns of disturbance in some old-growth mesic forests of Eastern North America. *Ecology*. 63(5): 1533–1546.
- Runkle, James R.** 1991. Gap dynamics of old-growth eastern forests: management implications. *Natural Areas Journal*. 11(1): 19–25.
- Smith, Edwin B.** 1988. An atlas and annotated list of the vascular plants of Arkansas. Fayetteville, AR: University of Arkansas at Fayetteville. 489 p.
- Stewart, G.H.; Burrows, L.E.** 1989. The impact of white-tailed deer (*Odocoileus virginianus*) on regeneration in the coastal forests of Stewart Island, New Zealand. *Biological Conservation*. 49: 275–293.
- Steyermark, Julian A.** 1963. *Flora of Missouri*. Ames, IA: Iowa State University Press. 1,728 p.
- Strole, Todd A.; Anderson, Roger C.** 1992. White-tailed deer browsing: species preferences and implications for central Illinois forests. *Natural Areas Journal*. 12(3): 139–144.
- Tilghman, Nancy G.** 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. *Journal of Wildlife Management*. 53(3): 524–532.
- Turner, R.E.; Craig, N.J.** 1980. Recent areal changes in Louisiana's forested wetland habitat. *Louisiana Academy of Science*. 3: 48–55.