VEGETATION DISTURBANCE AND MAINTENANCE OF DIVERSITY IN INTERMITTENTLY FLOODED CAROLINA BAYS IN SOUTH CAROLINA[1]

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Abstract. We manipulated the fire regime and soil disturbance in four grass-dominated Carolina bay wetlands during a prolonged drought period and examined vegetation composition and cover within dominant vegetation types prior to and after treatments. We used the seedling emergence technique to determine the role of the seed bank in the recovery process.

Burning did not affect richness, evenness, or diversity (all vegetation types combined); however, soil tillage increased diversity, including both evenness and richness. Percent similarity of the vegetation before and after disturbance was greater in the burning treatment than in the tillage treatment, probably due to greater disruption of the rhizomes of the perennial vegetation by tillage. Vegetation types varied in degree of recovery, although dominance was not altered by either treatment. Several native fugitive species increased following disturbance, indicating that species coexistence in these Carolina bay wetlands depends on the life history characteristics of residual vegetation, as well as that of seed bank species.

The seed bank (72 600 seedlings/m²) was larger and species richness (108 species) was greater than reported for most other freshwater wetlands. No differences in species richness, evenness, or diversity were detectable among the seed banks associated with different vegetation types in the bays. The floristic composition of the seed bank did not resemble the standing vegetation in patches dominated by large perennial grasses (*Panicum hemitomon, Leersia hexandra,* and *Andropogon virginicus*). In contrast, seed bank samples associated with vegetation dominated by an annual forb (*Iva microcephala*) or the small perennial grasses *Panicum wrightianum* or *P. acuminatum* var. *unciphyllum* more closely reflected the standing vegetation.

Species appear to persist with recurring and multiple disturbances because of seed banks, rhizomes, morphological plasticity during inundation, sexual reproduction following inundation, and perenniality coupled with early sexual maturity. Conservation management of intermittently inundated wetlands should incorporate techniques to foster maintenance of endemic species richness and the recruitment of rare species. During periods of drought, it may be desirable to disturb the aggressive perennial vegetation to allow recruitment of less common species.

Key words: biodiversity; Carolina bays; disturbance; rare plants; seasonal wetlands; seed bank; vegetation dynamics; wetland management.

INTRODUCTION

Studies of disturbance-related vegetation dynamics in freshwater wetlands have concentrated primarily on effects of temporal fluctuations in water level. Many of these studies have been conducted in freshwater wetlands that have been artificially flooded and drawn down to enhance waterfowl habitat (van der Valk and Davis 1978, Smith and Kadlec 1983, Smith and Kadlec

1985*a, b,* Welling et al. 1988). Natural intermittently flooded freshwater systems are less understood (Gerritson and Greening 1987, McCarthy 1987). In both natural and artificially controlled systems, recurring inundation and dry-down is a disturbance that permits periodic recruitment from the seed bank of species requiring specific water levels (usually low or dry conditions). Species that reproduce prior to recurrent disturbance replenish the seed bank of temporarily flooded wetlands. As a result, floristic richness may be closely linked with the disturbance regime and seed bank composition (Grubb 1977, van der Valk 1981, Pickett and White 1985, Grubb 1988, Gerritson and Greening 1989, Parker et al. 1989).

According to van der Valk's (1981, 1982) conceptual model, changes in floristic composition following flood disturbance are predicted from the life history char-

acteristics of individual species present in the seed bank. This model, however, may not be applicable to all wetlands (Parker and Leck 1985, Smith and Kadlec 1985, McCarthy 1987) or all types of disturbances in wetlands (Leck 1989), because the seed bank influences on vegetation dynamics depend on such additional factors as type and frequency of disturbance, persistence of remnant patches of live vegetation, seedling emergence conditions, and fresh seed input rate (Smith and Kadlec 1983, 1985, Pederson and Smith 1988, Gerritsen and Greening 1989, Leck 1989). If wetland restoration or management and conservation of rare species endemic to these habitats is to be based on sound ecological principles, we need a fundamental understanding of vegetation regeneration processes and conceptual models that can predict responses to perturbation in these wetlands (Keddy et al. 1989).

Carolina bays are common, elliptical, and geomorphically distinct depressions in the southeastern United States. Thousands of bays of various sizes are estimated to occur throughout the region; however, many of these wetlands have been drained or permanently filled for developmental or agricultural purposes (Sharitz and Gibbons 1982, Bennett and Nelson 1990). They typically have hydrologic regimes that fluctuate in response to rainfall or seasonal cycles of evapotranspiration (Sharitz and Gibbons 1982, Schalles and Shure 1989). In most years, Carolina bays are inundated in early spring (Schalles and Shure 1989). These intermittently flooded wetlands, particularly depression-meadows (bays dominated by grasses and sedges as opposed to trees and shrubs), provide habitat for several rare and/or endemic forbs (Bennett and Nelson 1990, Knox and Sharitz 1990).

Periods of low precipitation patterns in the Southeast may extend >10 yr and may recur in 30-yr cycles (Stahle et al. 1988). Natural cyclical patterns of vegetation change occur in bays in response to rainfall cycles (Kirkman 1992). During extended periods of drought, Carolina bays may be completely dry for more than a year. Fire may spread into the bays from upland areas, due to lightning or prescribed burning (Sharitz and Gibbons 1982). Other perturbations, such as mechanical discing and tilling or soil disturbance by animals (i.e., extensive rooting by hogs), are common when soil conditions are dry. Such drought-related disturbances are assumed to influence vegetation dynamics in these habitats; however, little is known about vegetation regeneration following such episodes.

To examine the mechanisms that maintain species and communities in these unpredictable environments, we applied experimental disturbance treatments to the vegetation of four Carolina bays during a prolonged drought. The primary objectives of this study were to: (1) determine the short-term effect of fire and soil disturbance on cover and abundance of dominant species and regionally rare taxa in depression-meadow bays; (2) compare the size and species composition of seed banks among dominant vegetation patch types; and (3) ascertain the role of seed banks in the regeneration process by comparing the seed bank flora with the field vegetation responding to drought-related disturbances.

MATERIALS AND METHODS

Study sites

Four depression-meadow Carolina bays in South Carolina, USA, were selected for field disturbance treatments: Savannah River Site (SRS) bays 56 (33°17′40″ N, 81°33′10″ W), 57 (33°17′33″ N, 81°33′48″ W), and 58 (33°17′19″ N, 81°33′30″ W) in Barnwell County (see map, Schalles et al. 1989) and Groton Plantation Bay (32°49′43″ N, 81°23′38″ W) in Allendale County. The herbaceous vegetation is distinctly patchy, typical of depression-meadow bays in the region (Hodges, A., in Schalles et al. 1989; Tyndall et al. 1990, Kirkman 1992). We selected bays with distinct patches of herbaceous vegetation that are typical in the region.

Six vegetation types (each dominated by a single species) were recognized, but each bay contained only three or four of the six (Table 1). The vegetation types were Panicum hemitomon, Leersia hexandra, Panicum wrightianum, P. acuminatum var. unciphyllum, Andropogon virginicus (all Poaceae), and Iva microcephala (Asteraceae). All of the dominants were perennial grasses except for the annual I. microcephala. Infrequently occurring woody species were young (1–2 yr old) seedlings of Pinus taeda, Acer rubrum, Diospyros virginiana, and Cephalanthus occidentalis that had established in the previous dry years. Older (3–5 yr old) P. taeda were established along the outer edges of the bays, and isolated Nyssa sylvatica var. biflora and C. occidentalis were present within the interiors. In SRS bay 57, older P. taeda were also in the interior.

The bays varied in size, fire history, and flooding (Table 1). Regional rainfall over the previous decade was below average (Kirkman 1992) and all bays had been dry for at least 2 yr prior to the study. We determined previous fire history for each bay from U.S. Forest Service records for the SRS sites and by discussion with the Groton Plantation owner. Relative flooding responses to previous rainfall for these bays were determined from aerial photographs taken from 1938 to 1989. We ranked bays from driest to wettest and these rankings confirmed recent field observations following increased precipitation in 1991 and 1992.

Pre- and post-vegetation sampling and disturbance treatments

Each bay was divided into three wedge-shaped sections for experimental manipulations (each section including all vegetation types in the bay). In each section one of three treatments was assigned: (1) soil tillage, (2) burn, or (3) control (no manipulation). In early

TABLE 1. Characteristics of Carolina bay study sites.

Bay	Area (ha)	Vegetation types	Fire history (pre-study)	Hydro-logic response rank*	Surrounding landscape
SRS 56	1.49	*Leersia hexandra* *Panicum hemitomon* *Panicum wrightianum*	(no evidence of fire)	4	natural *Pinus taeda* and *P. palustris* forest
SRS 57	1.65	*Andropogon virginicus* *Panicum acuminatum* *Panicum hemitomon*	within past 10 yr	1	*P. taeda* plantation
SRS 58	1.41	*Andropogon virginicus* *Iva microcephala* *Panicum hemitomon* *Panicum wrightianum*	within past 2 yr	3	natural *P. taeda* and *P. palustris* forest
Groton	4.83	*Andropogon virginicus* *Iva microcephala* *Panicum hemitomon* *Panicum wrightianum*	6 mo prior to study	2	natural *P. palustris* forest

* Bays were ranked 1–4 based on apparent flooding response to rainfall (from aerial photography, 1938–1989); 1 = driest and 4 = wettest.

December 1989, a tractor with a disc-harrow was used to establish the soil disturbance treatment (depth of 15–20 cm) in SRS bay 57. Because soil conditions were too wet in the other three bays for the use of a tractor, we used a garden roto-tiller during winter 1989–1990. Savannah River Site bays 57 and 58 were burned in December 1989 using controlled backfires; bay 56 and Groton Bay were burned in March 1990. Increased rainfall in fall 1989 (during hurricane Hugo) temporarily inundated SRS bay 56. Surface water was pumped from this bay prior to burning.

Pre-disturbance vegetation was sampled in September–October 1989, the period in which most species reach maturity (see midsummer inventory below). Sample plots (1 × 1 m) within each of the treatment sections were stratified among dominant vegetation types and were randomly located. A total of 276 vegetation plots was established in the four bays; six plots per vegetation type were placed in each treatment section, with the exception of Groton Bay, where 12 plots per vegetation type were established in the burn treatment.

Percent cover in each 1-m² plot was estimated using a sampling frame in September–October 1989, prior to field manipulations. Percent cover categories were according to Braun-Blanquet (>75%, 50–75%, 25–50%, 5–25%, <5%, few, solitary) (Mueller-Dombois and Ellenberg 1974). Any additional species occurring within a 25-m² plot (5 × 5 m area including the 1-m² plot) were noted. The bays remained dry during the growing season of 1990. A midsummer (1990) inventory of species occurrence in each 25-m² plot was conducted to determine if species richness varied due to season. Post-treatment sampling of vegetative cover was conducted in September–October 1990. All plots were sampled as in pre-treatment sampling.

Voucher specimens of all species were collected and archived in the Savannah River Ecology Laboratory (SREL) herbarium. Nomenclature generally follows Godfrey and Wooten (1981), or if not included there, Radford et al. (1968). Exceptions are *Panicum* (Lelong 1986), and Asteraceae (Cronquist 1980). Questionable species identifications of *Panicum* and *Rhynchospora* were verified by M. Lelong (University of South Alabama) and R. Kral (Vanderbilt University), respectively.

Seed bank sampling and germination

Soil cores for seed bank studies were collected in December 1989 along the outside edge of the 1-m² vegetation sampling plots in the control (no disturbance treatment) sections of each of the four Carolina bays. At each plot, six evenly spaced cores were obtained with a metal soil sample can, 7 cm in diameter and 4.5 cm deep. The six replicate cores at each plot were combined into a single sample. Similar samples were obtained from December 1989 burned treatment plots in SRS bays 57 and 58. A total of 126 samples was collected.

Soil samples were refrigerated (6°C) for ≥40 d, thoroughly mixed, and rhizomes and roots were removed by washing soil through several mesh sieves. Each sample was spread on top of 10 cm of potting soil in a 33 × 28.5 × 14 cm plastic tub, perforated to allow drainage. Tubs were randomly arranged on greenhouse benches under natural light. Temperatures were maintained close to outdoor ambient conditions, and soil was kept moist by watering once or twice a day.

We used seedling emergence to quantify the soil seed bank (Poiani and Johnson 1988, Gross 1990). Although this method underestimates the seed bank when germination requirements of all of the species present are not met (Roberts 1981, Baskin and Baskin 1989), it does provide an estimate of the readily ger-

TABLE 2. Median percent cover of species before and after treatment.†

Species	Annual/ Perennial	Till		Burn		Control	
		Before	After	Before	After	Before	After
Croton elliottii	A forb	0	2.5*	<1.0	<1.0*	<1.0	0
Diodia virginiana	P forb	0	2.5*	<1.0	2.5*	2.5	7.5
Euthamia minor	P forb	<1.0	15.0*	15.0	2.5*	2.5	1.4
Iva microcephala	A forb	0	15.0*	2.5	15.0	2.5	0*
Leersia hexandra	P grass	1.4	<1.0*	2.5	<1.0*	2.5	2.5
Panicum hemitomon	P grass	62.5	15.0*	15.0	15.0	37.5	26.3
Panicum wrightianum	P grass	37.5	15.0*	37.5	15.0*	37.5	37.5
Panicum verrucosum	P grass	2.5	15.0*	15.0	15.0	2.5	2.5
Panicum acuminatum	P grass	37.5	<1.0*	37.5	15.0*	62.5	37.5*
Pinus taeda	P woody	2.5	0*	2.5	0*	2.5	2.5*
Rhexia mariana	P forb	8.7	<1.0*	<1.0	2.5	1.4	15.0
Rhynchospora microcarpa	P sedge	<1.0	<1.0*	<1.0	<1.0*	<1.0	<1.0
Scleria reticularis	A sedge	0	0*	<1.0	0*	<1.0	0*
Stylisma aquatica	P forb	0	2.5*	<1.0	15.0*	<1.0	1.4
Viola lanceolata	P forb	1.4	2.5	2.5	<1.0	2.5	<1.0*

* Significant increase or decrease after treatment ($P < .05$) using Wilcoxon matched-pairs signed-rank test.
† Species shown here are those with relative frequency of occurrence in all plots >0.10.

minable fraction of the seed bank (Gross 1990). Seedlings were identified, censused, and removed throughout the course of the experiment (10 mo) on a 1–2 wk basis. Seedlings that could not be identified were transplanted to pots and grown to maturity. In August 1990, each sample (top 1-cm layer) was divided into two. Half of the sample was removed, mixed, and spread on a layer of potting soil in a separate, unperforated tub. These samples were then inundated to a depth of 3–4 cm above the soil for the remainder of the experiment (4 mo). The other half-sample was stirred and respread on the original potting soil, and seedling emergence was monitored as before. A final census of both treatments was made in December 1990. Voucher specimens were archived in the SREL herbarium.

Statistical analyses

Individual species cover changes were analyzed for significant differences in paired responses (i.e, response variable calculated for the same plot, before and after treatment) by treatment using the Wilcoxon matched-pairs signed-ranks test (Daniel 1990). Midpoints of cover classes were used as response variables. For cover classes of few or solitary, fractional values were assigned. Median values were obtained of the six plots within treatment types of each replicate bay. Percent similarity of vegetation in each sample plot before and after field manipulations was calculated using the Bray-Curtis distance coefficient (Ludwig and Reynolds 1988) and median values were obtained for the treatment plots in each bay. To determine differences in percent similarity by treatment, we used the Friedman two-way analysis of variance by ranks and multiple comparisons tests (Daniel 1990). Differences in percent similarity due to treatments within vegetation types were detected using the Kruskal-Wallis test (Daniel 1990).

Before- and after-treatment values for species di-

versity [Shannon-Wiener diversity index: $H' = \Sigma (p_i \ln p_i)$, where $p_i =$ (number of individuals of a species)(total number of individuals in sample)$^{-1}$]; evenness [Pielou evenness index: $H'/\ln S$)]; and richness ($S =$ number of species per plot) were calculated (Ludwig and Reynolds 1988) for each plot. Significant differences by treatment within initial (i.e., as designated prior to treatment) field vegetation types were examined using the Wilcoxon test (Daniel 1990).

The mean densities of seedling emergents in the seed bank samples, expressed as number per square metre, were compared by field vegetation type using a one-way ANOVA (SAS 1988). The response variable was a pooled value (median value of six seed bank samples from a vegetation type within a bay) replicated by bay. For each sample, species diversity, evenness, and richness were calculated and were analyzed for mean differences among vegetation types by a one-way ANOVA (SAS 1988).

RESULTS

Field manipulations

Significant changes in vegetative cover (before and after treatments) were apparent at the species level across all vegetation types. In the control plots, Iva microcephala, Panicum acuminatum, Scleria reticularis, Pinus taeda, and Viola lanceolata differed significantly in cover between 1989 and 1990 (Table 2). We show values for median percent cover, in addition to the results of analysis of ranked pairs. In some cases (e.g., Pinus taeda), the median percent cover value remained the same but the median differences of the ranked pairs differed significantly. Each of the dominant perennials declined following soil tillage, and Leersia hexandra, Panicum wrightianum, and P. acuminatum declined following burning. Two annuals that were large components of the seed bank, I. microceph-

TABLE 3. Median percent similarity of vegetation before and after treatment.*·†

Vegetation type	Till	Burn	Control
A. virginicus	49.9ᴬ	63.8ᴬ	72.1ᴬ
I. microcephala	48.4ᴬ	58.7ᴬ	32.4ᴮ
L. hexandra	26.8ᴬ	39.7ᴬ	32.9ᴬ
P. acuminatum	13.3ᴮ	72.9ᴬᴮ	95.6ᴬ
P. hemitomon	62.5ᴬ	66.0ᴬ	75.3ᴬ
P. wrightianum	44.0ᴮ	72.7ᴮ	84.0ᴬ
All vegetation	46.0ᶜ	67.8ᴮ	75.7ᴬ

* Rankings within all treatments were significantly different ($P < .05$) before and after treatment using Friedman's two-way analysis of variance with vegetation types as blocks.

† Values with different superscript letters (across rows) indicate that rankings within a vegetation type differed by treatment ($P < .05$) using Kruskal-Wallis test for multiple comparisons.

ala and Panicum verrucosum, increased significantly after soil disturbance. The percent cover of Croton elliottii, Stylisma aquatica, and Diodia virginiana increased in tilling and burning treatments.

At the patch level, dominance was not altered by either tilling or burning, although relative cover of some species was affected. Treatment effects were more pronounced in some vegetation types than in others (Table 3). In A. virginicus, L. hexandra, and P. hemitomon vegetation types, no differences were observed in before–after similarity. Before–after similarity was significantly lower in the tilled treatment than in control treatments for the P. acuminatum and P. wrightianum vegetation types. A significantly greater percent similarity of vegetation after burning than after control treatments was observed in the I. microcephala type. In L. hexandra and I. microcephala vegetation, the percent similarity of the control plots before and after were low relative to those of other vegetation types (Table 3). Percent similarity of the vegetation (all vegetation types combined) before and after treatments significantly differed among all treatments. The degree of change in vegetation due to treatment for both burn and control treatments was less than that of the soil disturbance treatment (Table 3).

Total species richness in SRS bays 56, 57, and 58 was similar with 56–58 species recorded in all 25-m² plots; however, Groton Bay had nearly twice as many species (Table 4) and about three times the area (Table 1). Typically, very few species were present in dense stands of P. hemitomon, L. hexandra, and P. acuminatum, whereas I. microcephala and P. wrightianum patches tended to have more associated species (Table 5a).

The control treatment had no significant changes between 1989 and 1990 in species diversity, evenness, or richness in any vegetation type (Table 5a). Burning caused a significant change in diversity only in vegetation dominated by I. microcephala, the decrease apparently reflecting changes in species abundances (Table 5a). Diversity, evenness, and richness by treatment

(all vegetation types combined) were unaffected by burning. However, each of these community parameters increased with soil disturbance. Species diversity increased following soil disturbance in all vegetation types except P. hemitomon and I. microcephala. Soil tillage in vegetation dominated by P. acuminatum var. unciphyllum increased both evenness and richness. In vegetation dominated by A. virginicus and P. wrightianum, the increase in diversity was due primarily to an increase in the evenness of abundance among species rather than a significant increase in species richness. Conversely, the significant change in diversity in L. hexandra vegetation following soil disturbance was due primarily to increased richness, usually involving the addition of I. microcephala and Acer rubrum. Although a small but significant increase in species richness due to soil disturbance in P. hemitomon stands was detected, the diversity measure did not increase significantly (Table 5a). Similarly, the species recruited were native wetland herbs or native woody species. Midsummer sampling of species presence/absence revealed a temporary seasonal increase in species richness in some plots. Overall, one additional taxon was recorded in the summer census.

Seed bank and relationship to vegetation

The seed bank flora totaled 108 species, with an average density of germinated seedlings of 419 per sample (equivalent to 72 600 seedlings/m²), and ≈20 species per sample. Nearly 70% of the seed bank flora was composed of perennial grasses and forbs (Fig. 1A) with similar distributions of annuals and perennials within associated vegetation types (Fig. 1B). Seedlings of woody species were absent in the seed bank except in a few samples from the P. hemitomon, A. virginicus, and L. hexandra vegetation types (Fig. 1A, B). Lists of all species recorded in the seedling emergence study and field plots are provided in Kirkman (1992).

Total species richness was remarkably similar across all vegetation types (17–19 species). No differences were detected among seed bank samples analyzed by vegetation types for diversity, evenness, richness, or seedling density (Table 5b). Species richness of seed bank samples was approximately twice that of the 25-m² vegetation plots (Tables 4, 5a and b). Total species richness of the seed bank was nearly equal to that of the vegetation in Groton Bay (Table 4).

TABLE 4. Total species richness by site (all vegetation types combined).

Site	Species richness (no. species/bay)		
	Field plots (1 × 1 m)	Field plots (5 × 5 m)	Seed bank
SRS Bay 56	20	58	83
SRS Bay 57	23	56	91
SRS Bay 58	22	58	79
Groton Bay	37	105	108

TABLE 5. Species diversity in field plots and seed bank.

a. Median values are given for species diversity, evenness, richness before and after treatments in each vegetation type.

Vegetation type	Diversity			Evenness			Richness		
	Till	Burn	Control	Till	Burn	Control	Till	Burn	Control
A. virginicus									
Before	0.704	0.976	1.169	0.502	0.574	0.608	4.0	7.5	6.0
After	1.246*	1.064	1.126	0.735*	0.559	0.569	5.5	8.0	6.0
I. microcephala									
Before	1.124	1.486	1.083	0.537	0.690	0.548	7.5	8.5	7.0
After	1.176	0.948*	1.264	0.544	0.449*	0.572	9.0*	8.0	9.0
L. hexandra									
Before	0.665	0.776	0.479	0.456	0.485	0.330	3.5	4.5	4.0
After	0.835*	1.071	0.959	0.566	0.672	0.727	5.5*	5.5	4.0
P. acuminatum									
Before	0.500	0.513	0.137	0.321	0.331	0.118	4.5	4.0	3.0
After	1.279*	0.774	1.137	0.653*	0.457	0.197	7.0*	5.0*	2.0
P. hemitomon									
Before	0.741	0.901	0.767	0.628	0.590	0.617	4.0	5.0	4.0
After	0.857	0.714	0.782	0.472	0.617	0.512	6.0*	5.0	4.0
P. wrightianum									
Before	1.052	1.203	1.048	0.468	0.522	0.513	8.5	9.0	8.0
After	1.371*	1.326	1.109	0.597*	0.619	0.518	10.0	8.5	7.0
All vegetation									
Before	0.854	1.051	0.982	0.507	0.578	0.582	5.0	7.0	5.0
After	1.110*	0.986	0.960	0.567*	0.556	0.544	8.0*	7.0	5.0

b. Comparison of species diversity, species evenness, species richness, and seedling density in soil seed banks by dominant field vegetation type (mean ± 1 SE). Densities refer to total density of seed bank of that vegetation type.

Vegetation type	n†	Diversity	Evenness	Richness	Density (seedlings/m²)
A. virginicus	2	0.1059 ± 0.04	0.0382 ± 0.02	19.2 ± 3.7	89 311 ± 17 863
I. microcephala	2	0.1241 ± 0.06	0.0458 ± 0.03	18.0 ± 4.5	79 155 ± 37 043
L. hexandra	1	0.1850	0.0640	19.0	40 522
P. acuminatum	1	0.1331	0.0465	18.0	76 170
P. hemitomon	4	0.0903 ± 0.01	0.0320 ± 0.00	17.0 ± 2.0	72 036 ± 10 871
P. wrightianum	3	0.0737 ± 0.01	0.0262 ± 0.00	18.0 ± 3.0	76 165 ± 16 659

* Indicates significant increase or decrease after treatment ($P < .05$) using Wilcoxon matched-pairs signed-rank test.

† n = number of bays in which vegetation type is sampled (i.e., replicates); median of six plots per vegetation type per bay used to calculate mean. *Leersia hexandra* and *Panicum acuminatum* were excluded from analysis. Mean values are not significantly different by vegetation type ($P > .5$) using Duncan's Multiple Comparisons Test.

Although both the seed bank and standing vegetation in all the bays were dominated by perennial species (Fig. 1A), there was little resemblance in floristic composition or abundance between the seed banks and vegetation types. Species dominance in the seed bank was heterogeneous among vegetation types (Table 6a). Most species occurred in the seed bank at low relative densities (Table 6b). Highest densities of *I. microcephala* and *P. wrightianum* were found in seed bank samples from vegetation types dominated by these species. The seed bank flora contained few seedlings of the perennial species that strongly dominated the vegetation types, including *A. virginicus* (Tables 6a, 7a) and *L. hexandra* (relative density < 0.03 and relative frequency < 0.50). No *P. hemitomon* seedlings were observed. The annual grass, *P. verrucosum,* was abundant in the seed banks of *L. hexandra* and *P. hemitomon* vegetation. Although relative densities were low,

more species had high relative frequencies of occurrence (Table 7a) than intermediate frequencies (Table 7b). *Iva microcephala, Rhynchospora microcarpa, P. verrucosum,* and *P. wrightianum* had high relative frequencies in the seed bank across all vegetation types (Table 7a). The seed bank was dominated by plants that are wetland-dependent rather than terrestrial weedy species (Kirkman 1992). Of the terrestrial weedy species, only *Andropogon virginicus, Eupatorium capillifolium,* and *Gnaphalium purpureum* occurred with relatively high frequency in the seed bank (Table 7a).

No significant differences were detected in mean values of diversity, evenness, or richness of the seed bank between burn (data not shown) and control treatments. No species in the seed bank consistently increased or decreased in density due to experimental burning. Flooding of the seed banks resulted in emergence of an additional five species that did not emerge under
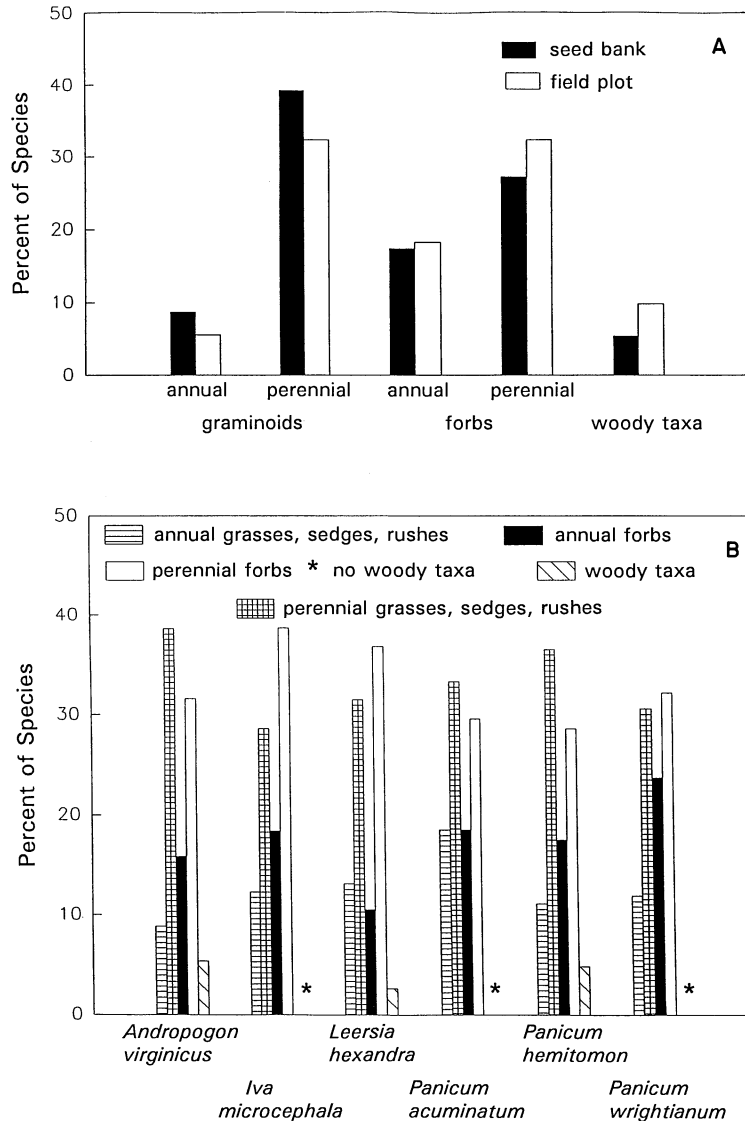
FIG. 1. (A) Composition of total seed bank (all four bays combined) and field vegetation based on life history characteristics. (B) Composition of seed bank in associated vegetation types.

unflooded conditions: *Sagittaria isoetiformis, Echinodorus parvulus, Eleocharis tricostata, Potamogeton diversifolius,* and *Xyris* sp. (Kirkman 1992).

Rare taxa

Several regionally uncommon species emerged in the seed bank samples but were not present in field plots (Table 8). Of the species listed in South Carolina as rare, only *Croton elliottii* occurred in both the seed bank and in the field plots. *Scleria reticularis, Iva microcephala,* and *Ludwigia suffruticosa* also occurred both in the seed bank and in the field plots. These species are not listed as threatened or endangered in South Carolina but are of interest for protection in

adjacent states with similar Carolina bay habitats. *Hedyotis boscii* and *Iva microcephala* occurred in the seed bank with both high relative densities and frequencies (Tables 6a, 7a). Both of these species had notably higher frequencies of occurrence in the seed banks from the three bays that had a pre-study occurrence of fire (Table 8). Although *Ludwigia spathulata* and *Scleria reticularis* had lower relative densities, both species frequently occurred in the seed bank (Table 7a). In Groton Bay, several *Eulophia ecristata* plants (a candidate for federal listing as an endangered species) were noted, although the species was not observed to germinate from the seed bank. Similarly, *Balduina uniflora* was present in Groton Bay but was not observed in the seed bank.

TABLE 6. Relative densities of seed bank.

		Vegetation type					
Species	Annual/ Perennial	*Andropogon virginicus* (*n* = 18)	*Iva micro- cephala* (*n* = 12)	*Leersia hexandra* (*n* = 6)	*Panicum acumi- natum* (*n* = 6)	*Panicum hemitomon* (*n* = 24)	*Panicum wright- ianum* (*n* = 18)
a. Dominant seed bank taxa (taxa with relative density ≥0.15 in one or more vegetation types).							
Cyperus erythrorhizos	A sedge	0.01	<0.01	0.04	0.15	0.02	0.01
Hedyotis boscii	P forb	0.15	0.01	0.01	0.10	0.10	<0.01
Iva microcephala	A forb	0.02	0.24	0.21	0.06	0.05	0.02
Panicum acuminatum	P grass	0.04	<0.01	0.02	0.17	0.01	0.0
Panicum verrucosum	A grass	0.04	0.07	0.22	0.01	0.19	0.07
Panicum wrightianum	P grass	0.15	0.11	0.05	0.02	0.02	0.32
Rhynchospora microcarpa	P sedge	0.03	0.20	0.13	0.07	0.07	0.14
b. Less dominant seed bank taxa (taxa with relative density ≥0.03–0.14 in one or more vegetation types).							
Andropogon virginicus	P grass	0.03	0	0	0.01	<0.01	<0.01
Bacopa sp.	P forb	<0.01	0.04	0	0	0.04	<0.01
Eupatorium capillifolium	P forb	0.02	0.03	0.01	<0.01	0.03	0.03
Eleocharis sp.	P sedge	0.01	0.01	0.03	0.04	0.01	0.02
Gnaphalium obtusifolium	A forb	0.01	0.04	<0.01	<0.01	0.06	0.01
Hedyotis uniflora	A forb	0.05	<0.01	0	0.04	<0.01	<0.01
Linaria canadensis	A forb	0	<0.01	0	0.02	0.03	<0.01
Manisuris rugosa	P grass	0.04	<0.01	0	0	0	<0.01
Polypremum procumbens	P forb	0.12	0.01	<0.01	0.05	0.06	0.04
Psilocarya nitens	A sedge	0.04	0.05	<0.01	0	0.03	0.05
Rhexia mariana	P forb	0.05	0.04	0.07	0.03	0.02	0.07
Rhexia virginica	P forb	0.01	0.05	<0.01	0	0.03	0
Rhynchospora filifolia	P sedge	0.02	0.02	<0.01	0	<0.01	0.03
Rotala ramosior	A forb	0.02	0.01	0.07	0.06	0.03	<0.01
Scleria reticularis	A sedge	<0.01	0.01	0.01	0.06	0.01	0.03
Viola lanceolata	P forb	0.01	0.01	0	0.04	0	0.02
Xyris sp.	P forb	0.02	<0.01	0.01	<0.01	<0.01	0.04
Other species (78)[1]	· · ·	0.14	0.07	0.10	0.01	0.16	0.11

[1] Species of relative density <0.03.

DISCUSSION

Changes in regional land use have greatly reduced the number of bays and altered their hydrology, flora, and fauna. Development of management options and strategies for Carolina bay wetlands has been constrained by the lack of information about vegetation processes. Efforts to conserve biodiversity might include restoration of natural hydrologic regimes, and restoration of disturbances, particularly those associated with periodic droughts. The latter is indicated from our experimental study.

Species responses and mechanisms of persistence

Our results suggest that establishment and survival factors such as persistent seed banks, perenniality coupled with early sexual maturation, and favorable response to disturbance are clearly involved in maintaining the flora of these wetlands. Two important features that emerge from this study are that some dominant perennials persist vegetatively following disturbance with an apparent absence in the seed bank and that less common species are recruited from the seed bank. The short-term responses to burning and soil disturbance were more evident at the species level than in community structural changes. However, over a longer period, under repeated disturbances and coupled with recurrent inundation, individual species' responses may promote longer term community trends.

Seed bank density in this study was much greater than previously reported in other wetland systems (van der Valk and Davis 1976, 1978, Nicholson and Keddy 1983, Smith and Kadlec 1983, Leck 1989) with few exceptions (van der Valk and Davis 1978, Walker et al. 1986). Total species richness of the seed bank was also considerably greater than that in other freshwater wetlands (van der Valk and Davis 1979, Smith and Kadlec 1983, Schneider and Sharitz 1986, Leck 1989). Consistent with commonly reported findings is the lack of resemblance of the composition of the vegetation and associated seed bank (McCarthy 1987, Gerritson and Greening 1989, Matlack and Good 1990).

The dominant perennial grasses apparently use several strategies to persist in an environment with recurring disturbances. *Leersia hexandra* and *Panicum hemitomon* primarily reproduce vegetatively. *Panicum hemitomon* was unaffected by fire or soil tillage of the intensity used in this study. Fire tolerance of *P. hemitomon* has been substantiated in experimental growth studies (Kirkman and Sharitz 1993) and in field observations (Van Arman and Goodrick 1979, Wade et al. 1980). The robust aboveground and belowground

TABLE 7. Relative frequencies of seed bank.

Species	Annual/ Perennial	Andro- pogon virginicus	Iva micro- cephala	Leersia hexandra	Panicum acumi- natum	Panicum hemitomon	Panicum wright- ianum
a. Most frequent seed bank taxa (relative frequency ≥0.81 in one or more vegetation types).							
Andropogon virginicus	P grass	0.89	0	0	1.00	0.17	0.11
Bulbostylis ciliatifolia	P sedge	0.22	0.08	0	1.00	0.25	0.05
Cyperus erythrorhizos	P sedge	0.61	0.25	1.00	0.83	0.58	0.22
Eleocharis sp.	P sedge	0.67	0.58	0.67	0.83	0.54	0.72
Eupatorium capillifolium	P forb	0.33	0.50	0.83	0.67	0.42	0.56
Gnaphalium purpureum	A forb	0.56	0.67	0.17	1.00	0.63	0.44
Hedyotis boscii	P forb	0.33	0.75	0.83	0.83	0.92	0.17
Iva microcephala	A forb	0.61	1.00	1.00	1.00	0.83	0.83
Ludwigia spathulata	P forb	0.50	0.58	0.83	0.17	0.79	0.28
Panicum acuminatum	P grass	0.61	0.08	0.17	1.00	0.17	0.11
Panicum verrucosum	A grass	0.72	0.92	0.83	0.33	0.83	0.78
Panicum wrightianum	P grass	1.00	0.75	0.83	0.50	0.63	1.00
Psilocarya nitens	A sedge	0.44	0.67	0.67	0.83	0.63	0.67
Rhexia mariana	P forb	0.83	0.83	1.00	0.50	0.58	0.89
Rhynchospora microcarpa	P sedge	1.00	1.00	1.00	0.66	0.75	0.89
Rotala ramosior	A forb	0.44	0.50	1.00	1.00	0.67	0.05
Scleria reticularis	A sedge	0.56	0.50	0.50	1.00	0.25	0.72
Viola lanceolata	P forb	0.56	0.58	0	1.00	0.46	0.67
b. Less frequent seed bank taxa (relative frequency ≥0.51–0.80 in one or more vegetation types).							
Cyperus sp.	? sedge	0.28	0	0.67	0.33	0.38	0.44
Leersia hexandra	P grass	0	0.58	0.50	0	0.21	0
Ludwigia sphaerocarpa	P forb	0.05	0.42	0.67	0	0.17	0.05
Ludwigia suffruticosa	P forb	0.22	0	0	0.67	0	0.11
Polypremum procumbens	P forb	0.67	0.25	0.67	0.50	0.54	0.50
Rhynchospora filifolia	P sedge	0.56	0.42	0.17	0.50	0.08	0.39
Xyris sp.	P forb	0.44	0.17	0.17	0.33	0.13	0.67

organs of this species permit aggressive vegetative reproduction, particularly during dry periods or periods of shallow, fluctuating water levels (Kirkman 1992). Due to its stature and the density of stands, few species can become established beneath it.

The low numbers, or absence, of seedlings of *L. hexandra* and *P. hemitomon* may have been due to a lack of seed production by these perennial dominants, which once established, primarily reproduce vegetatively. Because seed production by these two perennial grasses may be stimulated by inundation (Kirkman and Sharitz 1993), their seeds may not occur in the seed bank following several years of dry conditions. Alternatively, seeds may have been present in the soil samples, but suitable conditions for germination in the greenhouse did not occur (Poiani and Johnson 1988, Gross 1990). In addition to stimulation of flowering, inundation during the growing season promotes stem elongation of *P. hemitomon,* maintaining leaves above the water surface. The spatial distribution of this species within a bay is dynamic as a result of its wide tolerance to fluctuating water levels (Kirkman 1992). Thus, re-establishment by seed is probably not critical to the success of this perennial grass, because it probably can survive somewhere along the hydrologic gradient.

Leersia hexandra, which occurred as a dominant in only one of the study bays, decreased in dominance during the extended dry-down, presumably a result of

lower drought tolerance than competing species (Kirkman and Sharitz 1993). Disturbances such as fire or tilling may severely limit its presence under dry conditions, with essentially no opportunity for seed bank recruitment. Like *P. hemitomon, L. hexandra* also flowers and elongates under inundated conditions and can survive depths >1.5 m. It remains unclear, however, how this species persists during extended dry periods that completely eliminate standing stems and rhizomes; more experimental work is necessary to determine if seed germination of *L. hexandra* occurs under flooded conditions.

Panicum wrightianum was less resilient to fire than *P. hemitomon.* The re-establishment of *P. wrightianum* following either disturbance appeared to be from seedling recruitment. This species was abundantly represented in the seed bank. Our greenhouse observations and those of other investigators (Nicholson and Keddy 1983, Gunther et al. 1984, McCarthy 1987) indicate that this species (= *P. spretum* in other studies) can reproduce sexually in the same year it germinates. The abundant seed bank permits this species to re-establish following dry-down and to quickly replenish the seed bank.

Andropogon virginicus is an early old-field successional species and was not abundant in the seed bank, even within the *A. virginicus*-dominated vegetation. Because *A. virginicus* is a common upland wind-dis-

TABLE 8. Relative frequency of occurrence [(number of samples) ÷ (total samples)] of rare species in seed bank samples of each bay.

Rare species*	Annual/ Perennial	Bay				Rarity status†·‡			
		SRS 56	SRS 57	SRS 58	Groton	Geor- gia	North Caro- lina	South Caro- lina	USA
Balduina uniflora*	P forb	0	0	0	0	···	···	S?	···
Croton elliottii**	A forb	0.17	0	0.08	0	S2	···	S?	3C
Echinodorus parvulus	A or P forb	0.04	0.40	0	0	···	S1	S2	···
Eleocharis melanocarpa*	P sedge	0	0	0	0	S?	S?	···	···
Eulophia ecristata* (=Ptereglossapsis ecristata)	P forb	0	0	0	0	S1	SX	S2	C2
Hedyotis boscii (=Oldenlandia boscii)	P forb	0	0.89	0.33	0.42	S1	S1	···	···
Iva microcephala**	A forb	0.05	0.94	0.75	0.83	···	S1	···	···
Ludwigia linifolia	P forb	0	0	0.13	0.13	···	S1	···	···
Ludwigia spathulata	P forb	0	0.44	0.42	0.58	···	···	S?	···
Ludwigia suffruticosa**	P forb	0.11	0.39	0	0.08	···	S2	···	···
Sagittaria isoetiformis	P forb	0.13	0	0.08	0	···	S2	S2	C2
Scleria reticularis**	A sedge	0.05	0.67	0.75	0.29	···	S?	···	···
Stylisma aquatica**	P forb	0.05	0	0.08	0	···	S1	···	···

* Indicates species was present in field plots, but not in seed bank flora; ** indicates species was present in both field plots and seed bank flora.

† S1 = critically imperiled; S2 = imperiled; S? = status uncertain; SX = probably extirpated; C2 = candidate for federal listing; 3C = former candidate for federal listing; ··· = not listed in state or federal list.

‡ Sources: Georgia Freshwater Wetlands and Heritage Inventory (1991), South Carolina Heritage Trust (1991), Weakly (1991).

persed species, invasion of Carolina bay wetlands is probably by dispersal into them during dry periods, rather than recruitment from a persistent seed bank.

The invasion by woody species into bays dominated by herbaceous plants is restricted to periods of drought. The significant changes in cover of *Pinus taeda* are also best explained by the similarity to old-field invasions (Oosting 1942, Keever 1950). The species was not recruited in the vegetation following disturbance. Seed sources surround the bays but pine seedlings rarely emerged from the seed bank. Seeds of *P. taeda* have low viability after 1 yr (Wahlenberg 1960). Decline in abundance following disturbance is due to fire intolerance of the young seedlings and to physical removal by tilling.

In seasonal wetlands, such as temporary ponds and Carolina bays, inundation is usually not of sufficient depth or duration to kill all the emergent vegetation (McCarthy 1987; L. K. Kirkman, *personal observation*). Thus, annuals such as *I. microcephala, P. verrucosum,* and *C. elliottii,* which require exposed soil for germination, may depend on drought-related disturbance for recruitment from the seed bank.

Our results suggest that *I. microcephala* requires disturbance for successful establishment. Its decline in the absence of disturbance was significant. Some control plots that were dominated by *I. microcephala* had few or none 1 yr later. It also increased in cover following soil disturbance, and had high density and frequency in the seed bank. Although a significant increase in cover was not detected for this species following burning, a positive trend was observed. Also, the two bays

that had large uniform patches of *I. microcephala* had both recently been burned.

Several regionally rare taxa persist in the seed bank during unfavorable environmental conditions (usually high water levels). The optimal frequency and amplitude of water level fluctuations and the life-span of buried seeds probably vary by species. During extended periods of drought, competitive perennials may preclude establishment of rare, less competitive species (McCarthy 1987, Keddy et al. 1989). *Croton elliottii,* a rare species, responded favorably to both burning and soil tillage. Thus, for some species of concern (e.g., *Croton elliottii* and *Iva microcephala*), prescribed burning or soil disturbance could be implemented to enhance seedling recruitment.

Rare plant conservation efforts may require control of probable competitors such as *Panicum hemitomon.* Because *P. hemitomon* tolerates a wide range of flooding depths during the growing season, deep and prolonged winter flooding would probably be necessary to eliminate or reduce this species (Kirkman and Sharitz 1993). Alternatively, this species might be controlled by burning off or cutting dead stems prior to winter inundation to a depth of 1–2 dm (Kirkman and Sharitz 1993), similar to the management of *Typha angustifolia* in waterfowl habitats (Sale and Wetzel 1983, Jordon and Whigham 1988).

Disturbance and community regeneration

Drought-related disturbances of burning and soil tillage had significant effects on the community structure 1 yr after treatment, although community dominance

patterns did not change. As a whole, soil tillage increased richness, evenness, and diversity and had a greater effect than did burning. Soil disturbances by pig activity are common when these wetlands become dry, and the effects may be quite similar to that of the soil tillage treatments. Although both soil tillage and burning significantly decreased the cover of dominant perennials, their live rhizomes remained and recolonization is likely, providing that conditions remain dry.

Although hydrologic regimes primarily drive vegetation changes of these wetlands, disturbances enhance species coexistence, permitting recruitment of fugitive species, and thus maintaining species richness. Maximum species richness in these wetlands is probably balanced by disturbance and local successional dynamics. We recommend that conservation management goals should focus on mechanisms for enhancing endemic species richness and the maintenance of fugitive and sometimes rare species. In the absence of naturally occurring disturbances, such strategies should consider episodic disturbance events associated with prolonged drought periods as a desirable component in the preservation of Carolina bay wetlands.

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