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EFFECT OF CLIMATE FLUCTUATIONS ON LONG-TERM VEGETATION DYNAMICS IN CAROLINA BAY WETLANDS

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Abstract: Carolina bays and similar depression wetlands of the U.S. Southeastern Coastal Plain have hydrologic regimes that are driven primarily by rainfall. Therefore, climate fluctuations such as drought cycles have the potential to shape long-term vegetation dynamics. Models suggest two potential long-term responses to hydrologic fluctuations, either cyclic change maintaining open emergent vegetation, or directional succession toward forest vegetation. In seven Carolina bay wetlands on the Savannah River Site, South Carolina, we assessed hydrologic variation and vegetation response over a 15-year period spanning two drought and reinundation cycles. Changes in pond stage (water depth) were monitored bi-weekly to monthly each year from 1989–2003. Vegetation composition was sampled in three years (1989, 1993, and 2003) and analyzed in relation to changes in hydrologic conditions. Multi-year droughts occurred prior to the 1989 and 2003 sampling years, whereas 1993 coincided with a wet period. Wetland plant species generally maintained dominance after both wet and dry conditions, but the abundances of different plant growth forms and species indicator categories shifted over the 15-year period. Decreased hydroperiods and water depths during droughts led to increased cover of grass, upland, and woody species, particularly at the shallower wetland margins. Conversely, reinundation and longer hydroperiods resulted in expansion of aquatic and emergent species and reduced the cover of flood-intolerant woody and upland species. These semi-permanent Upper Coastal Plain bays generally exhibited cyclic vegetation dynamics in response to climate fluctuation, with wet periods favoring dominance by herbaceous species. Large basin morphology and deep ponding, paired with surrounding upland forest dominated by flood-intolerant pines, were features contributing to persistence of herbaceous vegetation. Drought cycles may promote directional succession to forest in bays that are smaller, shallower, or colonized by flood-tolerant hardwoods.

Key Words: depressional wetlands, drought cycles, hydrologic regime, succession

INTRODUCTION

The hydrologic regimes of depressional wetlands determine their ecological character. Because depression hydrology is driven mainly by rainfall and evapotranspiration, these wetlands are especially sensitive to climate variation. Depending upon local attributes such as basin size or topographic position, individual depressions within the same geographic region may have characteristic annual hydroperiods that are semi-permanent, seasonal, or temporary. The characteristic hydroperiod in turn shapes the typical dominant vegetation of each depression; however, drought or deluge periods can shift wetlands into a different hydroperiod or permanence class, thereby initiating vegetation change (Johnson et al. 2004). For example, in the semi-arid North American Great Plains region, multi-year drought and rewetting cycles typically promote cyclic shifts among different herbaceous cover types in prairie pothole and playa wetlands, which are herb-dominated and generally surrounded by non-

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forested uplands (van der Valk and Davis 1978, Kantrud et al. 1989, Poiani and Johnson 1991, Haukos and Smith 1994). Understanding such responses to present-day climate fluctuations is crucial for predicting the potential impacts of future climate change on depressional wetland systems (Poiani and Johnson 1991, Brooks 2004, Johnson et al. 2005).

In the humid and forested Southeastern Coastal Plain region, Carolina bays and similar depression wetlands have diverse ponding regimes and vegetation communities (Schalles and Shure 1989, Sharitz 2003, De Steven and Toner 2004). As in prairie potholes, annual hydroperiods may be semi-permanent (continuous ponding in most years) to seasonal or temporary (drying yearly), and they are influenced by periodic regional droughts. However, vegetation in Coastal Plain depressions differs from Northern Great Plains depressional vegetation and can range from open-water ponds to emergent marshes and forested swamps, and woody plants may play a greater role in climate-induced vegetation change. For herb-dominated depressions, Kirkman (1995) proposed a cyclic model of vegetation dynamics characterized by shifts from floating-aquatic vegetation during wet periods to an emergent marsh of characteristic grasses and sedges such as maidencane (*Panicum hemitomon*) and southern cutgrass (*Leersia hexandra*) during drier periods. Dry periods allow ephemeral wetland species to recruit from seed banks but also favor colonization by upland species and woody plants such as loblolly pine (*Pinus taeda*). Assuming that the upland and woody species are flooding-intolerant, the model predicted that reinundation would return the system to aquatic and emergent species.

This cyclic model is partially based on short-term studies that documented drought-induced shifts in vegetation zonation characterized by loss of aquatic plants, expansion of grass and sedge species more typical of drier conditions, and establishment of woody plants (Kirkman 1992, Mulhouse et al. 2005a, b). Few long-term data sets exist to evaluate the extent to which these short-term shifts are reversed following reinundation, as the cyclic model predicts, and how broadly the model applies. If more flood-tolerant hardwood trees such as swamp tupelo (*Nyssa biflora*) or sweetgum (*Liquidambar styraciflua*) establish successfully during drought, they may survive reinundation, shorten wetland hydroperiod through increased evapotranspiration, and promote further forest expansion. An aerial imagery change-detection study on the South Carolina Upper Coastal Plain (Kirkman et al. 1996) was suggestive in showing that some depressions maintained herbaceous plant cover after a 40-year period, while others developed closed forest cover. Succession to flood-tolerant hardwood forest is not generally reversed unless other disturbances intervene. Consequently, more comprehensive models have proposed that depression vegetation dynamics may follow either cyclic or directional pathways in response to hydroperiod change, depending upon topographic or landscape settings and upon other disturbances such as fire (Kirkman et al. 2000, De Steven and Toner 2004).

Few field studies have described post-drought change following reinundation in order to validate these model pathways more fully. On the Savannah River Site, South Carolina, we examined longer-term vegetation dynamics by taking advantage of a study initiated in 1989 on seven large herb-dominated Carolina bay wetlands that were predicted to exhibit cyclic dynamics. From continuously maintained hydrologic monitoring and intermittent vegetation surveys, we synthesized data spanning a 15-year period (1989–2003) that included two drought and re-flooding cycles. We addressed three questions: 1) How did hydrologic conditions and vegetation composition change in response to drought and wet periods? 2) Did longer-term vegetation change suggest cyclic dynamics or directional succession? 3) What attributes of these wetlands might account for the observed vegetation dynamics?

METHODS

Study Site

The study was conducted on the U.S. Department of Energy Savannah River Site (SRS), an 80,000-ha National Environmental Research Park on the South Carolina Upper Coastal Plain. The seven Carolina bays in the study (Table 1) are part of protected lands set aside for research purposes and have remained relatively undisturbed since the 1950s (Hillestad and Bennett 1982, Workman and McLeod 1990). These bays were fairly large (4.5–12 ha) for depressions in the region and comprised nearly all the large herbaceous bays on the SRS. Four were located in Sandhills landscapes where deep sandy soils predominate, and three occurred on relict alluvial terrace or hilly uplands with finer-textured soils. Bay soils typically have sandy surface textures underlain at varying depths by denser sandy clay loam (Ogeechee and Williman soils; Typic and Arenic Endoaquults) or sandy clay (Rembert soil; Typic Endoaquult), except for the Rutlege soil (Typic Humaquept) that is sandy throughout. Based on a 1993 vegetation classification study (De Steven and Toner 2004), the seven bays were either ponds or emergent marsh/meadow wetlands and represented the wetter end of the hydrologic continuum for depressions. The bays were surrounded either by managed stands of pines (loblolly pine, *P. taeda*; slash pine, *P. elliottii* Engelm.; longleaf pine, *P. palustris* Mill.), or by mixed forest with pines and hardwoods such as sweetgum and oaks (*Quercus* spp.) (Table 1). The latter forest type is typically favored on finer-textured upland soils (Jones et al. 1984).

The regional climate is humid subtropical, with long, hot summers and short, mild winters. Annual precipitation averages about 1200 mm, but multi-year droughts recur on the order of decades (South Carolina State Climatology Office 2004). Between 1983 and 2003, periods of below-normal rainfall and drought occurred in 1984–1988 and 1999–2002 (Figure 1).

Vegetation Sampling

Bay vegetation was initially surveyed in 1989 (Keough et al. 1990). Resampling in 1993 and 2003 was prompted by changed climatic and hydrologic conditions. Although rainfall was slightly above normal in the 1989 sampling year, the wetlands were transitioning out of the 1984–1988 drought period (Figure 1). In contrast, the 1993 sampling year coincided with a multi-year wet period of normal or above-normal rainfall. In 2003, rainfall was well above normal, but the wetlands were again transitioning out of a four-year drought period.

Vegetation was sampled with a line-intercept method in August–September of each sampling year. In each bay, sample points were spaced at 10 m intervals (5 m in Woodward Bay) along eight transect radii originating from a permanent post in the bay center and spaced 45° apart. At each sample point, percent covers of all species intersecting a 1-m line segment were recorded. Transect locations were fixed, but transect lengths differed among years in response to changed conditions. In 1989, the transects were run from the center post outward until 100% cover of upland shrubs or small trees was encountered, at which point sampling was stopped and a permanent "margin" post was installed. Given limited prior knowledge at that time, the "upland" vegetation present at the posts was interpreted as indicating the maximum extent of the wetland. Transect lengths from center to margin post generally ranged between 50 m and 150 m. However, in the 1993 sampling year, bay water levels were found to extend beyond the posts; therefore, the original transects were extended further outward (upslope) until a more elevated basin perimeter and mature upland forest canopy were encountered. Depending upon bay size and shape, these extensions averaged from 10–40 m beyond the margin posts. In 2003, the entire extended transect lengths were re-sampled; the size stratum (seedling, sapling, canopy) of woody species at each sample point was also noted. We were unable to reach the deepest central areas of a few bays in 2003 because of excessive high water (depth $>$ 1.2 m), but we recorded qualitatively the few species present (typically water lily, *Nymphaea odorata*) in these deep-water areas.

Hydrologic Monitoring

Water-level monitoring was conducted by different methods and observers over the 15-year period. Beginning in May 1989, pond stage (water depth above ground surface) was measured continuously with a Stevens recorder placed at or near the center of each bay. After November 1990, pond stage was instead read manually from a staff gauge installed at the deepest central point in each bay and calibrated

Table 1. Locations and attributes of the seven study bays, including forest type of the surrounding uplands. Bay elevations are m above mean sea level. Data are from De Steven and Toner (2004) and the U. S. Forest Service–Savannah River.

Bay Name	Landscape Setting	Elevation (m)	Wetland Area (ha)	Wetland Soil Series	Wetland Type	Upland Forest Stand Type
Dry	Terrace	46	7.3	Williman[a]	open-water pond	pine/hardwood
Ellenton	Terrace	43	12.1	Rutledge	open-water pond	pine/hardwood
Flamingo	Loam Hills	94	11.2	Rembert[a]	pond/grass marsh	pine/hardwood
Mona	Sandhills	85	11.7	Ogeechee	depression meadow	pines
Sarracenia	Sandhills	79	4.5	Ogeechee	open-water pond	pines
Thunder	Sandhills	61	8.6	Ogeechee[a]	open-water pond	pines
Woodward	Sandhills	85	9.5	Ogeechee	depression meadow	pines

[a] Incomplete survey; other series may be present.

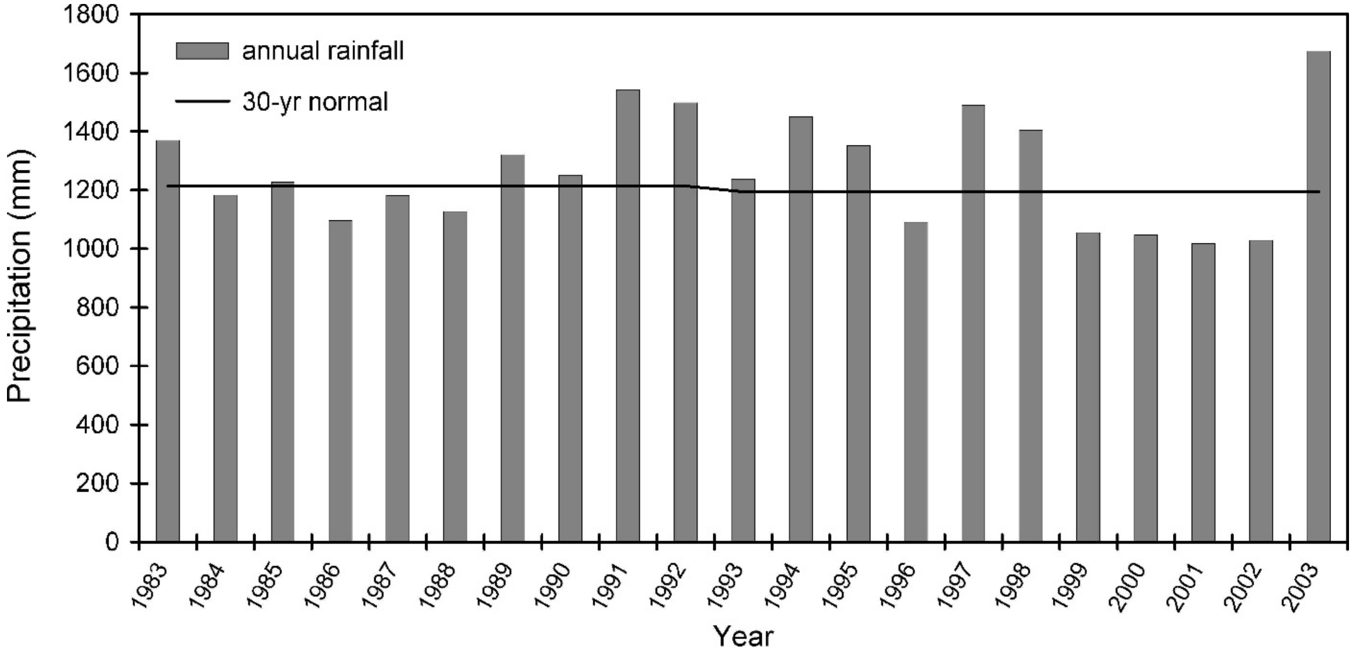

Figure 1. Average annual precipitation at the Savannah River Site from 1983–2003 (n = 7 SRS rain stations), compared to the 30-year normal at a nearby NOAA weather station in Blackville, SC. Periodic recalculation of the normal value occurred in 1993, hence deviation in line.

to the elevation of the Stevens recorder gauge. To facilitate long-term data collection, additional staff gauges were added at shallower depths and calibrated to center gauge elevation. Water levels at the staff gauges were recorded weekly from May 1989 to May 1990, weekly to biweekly or monthly from June 1990 to June 1997, and biweekly to monthly from August 1997 to December 2003. The varying intervals partly reflected adjustments for hydrologic conditions; that is, gauges were read less frequently when bays were completely dry during extended periods without rain. Recorder and staff gauge data sets were combined and cross-calibrated to give a single 15-year water-level record at each bay center. Elevations of all 1989 vegetation sample points had been surveyed with a laser level, and we used the average elevation difference between the center and margin posts to estimate a comparable 15-year record of water-level change at the shallower margins of each bay.

Data Analysis

Annually, pond stage in these depression wetlands typically rises to a spring high and then declines through the year at varying rates as growing-season evapotranspiration increases. For analysis, we chose ponding duration (hydroperiod) and maximum water depth as the two depression hydrologic properties most relevant to plant species presence and vegetation composition. For bay centers and margins, we calculated an annual hydroperiod index (hereafter, "hydroperiod") as the proportion (percentage) of water level readings each year with water depth > 0. Periodic measures can give reasonable estimates of annual hydroperiod (Shaffer at al. 2000), particularly when there is a fairly predictable seasonal pattern. We estimated annual maximum depth for centers and margins from the highest recorded depths each year (typically in early spring); these maxima determine the ponding conditions that plants encounter as the growing season begins. We then tested the correlations between yearly precipitation and mean hydrologic variables (annual hydroperiod and maximum water depth) using one-tailed Pearson's r tests, with transformed values for hydroperiod (arcsine square root). Retrospectively, we discovered that the Stevens recorders had not been placed initially at the deepest point in three bays (Thunder, Sarracenia, and Flamingo). This problem was eliminated when the recorders were replaced by staff gauges, but we could not fully correct a few truncated center water-level readings during brief dry periods in 1989 and 1990, when other bays contained no surface water. Therefore, in those two years, average hydroperiod at bay centers is likely overestimated.

For vegetation analysis, we defined the original 1989 transect lengths as representing a wetland "interior" zone, and the 1993 transect extensions as representing a shallower "margin" zone subject to greater water-level change. Vegetation data were divided into interiors and margins, where interiors included all sample points from the center to (but excluding) the margin posts, and margins encompassed all sample points from the margin posts outward. This allowed for a limited estimation of margin plant composition in 1989 based on the post sample points. For each zone (interior, margin) in each bay, we calculated species richness (total number of species observed), the proportion of species in various growth forms (aquatic, grass, sedge/rush, forb, or woody), and the proportion of species in three wetland indicator categories (classing OBL and FACW as "wetland" species, FAC as "facultative", and FACU and UPL as "upland"; Reed 1988). To evaluate changes in absolute abundance over time in each zone, we calculated the average percent cover of each species (over sample points), and then summed the mean species covers to give total plant cover, percent cover of species growth forms, and percent cover of wetland indicator categories. As there were few upland or forb species represented in the data, we combined facultative and upland species for analysis of indicator categories, and for growth form analysis we combined forbs with sedges/rushes as representing a "meadow" species group indicative of shallow-water or drawdown conditions. Taxon nomenclature generally followed Radford et al. (1973). A few species that were uncommon or indistinguishable in form were grouped at the generic level to simplify data presentation, but this did not affect the analyses.

As the bays shared similar relative size and wetness traits (see Study Site), we used a statistical approach to test for generalized trends in vegetation response to climate fluctuations. With the seven bays as replicates, we tested for differences in the vegetation variables of each zone across years using repeated-measures ANOVA, with model validation by Greenhouse-Geiser statistics. To improve normality and variance homogeneity, we applied arcsine square root transformations to species proportion data and log transformations to absolute cover data. Differences within wetland interiors were tested across all three sampling years. However, because sampling of wetland margins had been truncated in 1989 based on the presence of woody species, the calculations of margin species richness, total cover, and woody plant cover were most likely underestimated in that year. Therefore, we mainly tested margin differences between 1993 and 2003 only; but for variables where underestimation was less problematic, we also indicate whether tests indicated a significant difference between 1989 and 1993. Analyses were performed with SYSTAT software (SPSS, Inc. 1999).

RESULTS

Temporal Hydrologic Variation

All seven bays exhibited the potential to pond deeply (> 1 m), but the duration and depth of ponding varied with precipitation inputs (Figures 1 and 2). Over the 15-year period, mean annual hydroperiod was positively correlated with annual rainfall ($r = 0.77$ and 0.66 at bay centers and margins, respectively; $df = 13$; both $P < 0.01$). Hydroperiods at the shallower margins were more sensitive to decreased rainfall, based on larger average differences between centers and margins in drier years (Figure 2A). For example, bay hydroperiods averaged 100% and 95% at centers and margins in the wet year of 1992, compared to averages of 58% and 18% in the dry year of 2001. Maximum annual water depths were also correlated with annual rainfall ($r = 0.58$ and 0.54 for centers and margins; both $P < 0.05$). Central water depths exceeded 1 m in wetter years, but drought periods (e.g., in 1989 and 2000–2002) reduced center depth maxima to averages of less than 0.6 m and margin depth maxima to less than 0.3 m (Figure 2B).

Individual bays differed somewhat in long-term hydrologic behavior. Annual hydroperiods averaged $\geq 80\%$ over the 15-yr period in all bays except Woodward, which was more variable (long-term mean = 35%). Most bays remained permanently ponded (100% duration) centrally except during drought periods, but Mona and especially Woodward exhibited some degree of central drying in most years.

Hydrologic conditions in each vegetation survey year (1989, 1993, and 2003) were influenced by current-year rainfall and by prior-year conditions (Figure 2). In 1993, after several years of above-normal rainfall, the wetlands were ponded for an average of 95% (centers) and 86% (margins) of the year, with high water depths averaging > 1.5 m. However, conditions in 1989 and 2003 reflected each previous drought period. Rainfall in 1989 was above normal, but hydroperiods averaged only 78% (centers) and 29% (margins), and central water depths were shallow (mean 0.6 m). Similarly, despite high rainfall in 2003 (Figure 1), hydroperiods averaged 98% in the centers but only 69% at the margins, and central water depths were 20–30 cm shallower than in 1993. Thus, vegetation in 1989 and

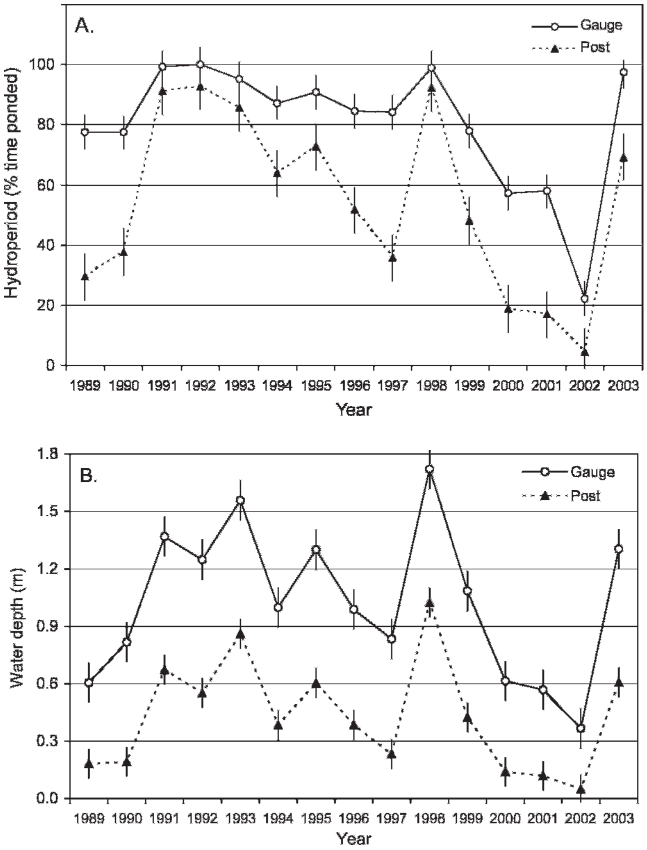

Figure 2. A) Mean annual hydroperiod and B) mean maximum water depth at centers (gauge) and margins (post) of seven Carolina bays from 1989–2003. Vertical lines represent 1 ± SE. Mean central hydroperiod in 1989 was an overestimate (see Methods).

2003 experienced ponding conditions that were transitional between drydown and full reinundation.

Vegetation Change in Wetland Interiors and Margins

Vegetation change in the bay interiors represented the dynamics of the largest portions of the wetlands. Mean species richness in the interiors was greater in 1989, when wetlands were driest, than in the two years with greater ponding (Table 2); richness in 2003 was likely reduced by heavy late-summer rains that flooded the bays and reduced total vegetative cover. Wetland species predominated in all three sampling years (averaging > 80% of all species), but facultative/upland species and emergent "meadow" species (rushes/sedges/forbs) were more prevalent in 1989. Grass species were more prevalent in the years following drought (e.g. 2003), whereas the fewest aquatic species occurred in 1989. Plant abundance (cover) showed similar changes (Table 2). Wetland species (e.g., *Panicum*/*Sacciolepis, Leersia hexandra, Nymphaea odorata*; Table 3) dominated the vegetative cover of bay interiors in all years (62%–110% mean cover), but facultative/upland species averaged greater cover (nearly 20%) in the driest year of 1989. Cover of wet meadow species and grasses (e.g., beaksedges, *Rhynchospora* spp.; meadow beauties, *Rhexia* spp.; witch-grasses, *Dichanthelium* spp.; Table 3) was also greater in 1989, whereas cover of aquatic plants (e.g., water lily, *N. odorata*; watershield, *Brasenia schreberi*; bladderworts, *Utricularia* spp.; Table 3) was greatest (averaging nearly 50%; Table 2) in the wet period represented by 1993. Woody plants contributed only minor cover (< 10%) in any year (Table 2); these were typically wetland species such buttonbush (*Cephalanthus occidentalis*) and swamp tupelo (*Nyssa biflora*).

As the bay margin zones represent a hydrologically dynamic ecotone with the surrounding uplands, margin vegetation reflected the generally shorter hydroperiods and shallower ponding depths. Wetland species still predominated in number and cover (Table 2); however, facultative and upland species were more prevalent (averaging 15%–24% of all species) and had higher average cover (23%–32%) compared to their abundance in wetland interiors (5%–17% of species and 1%–17% mean cover). Woody plant cover was also substantially higher, averaging 23%–53% (Table 2).

For herbaceous species, many temporal changes in the bay margins paralleled the interior changes. For example, the percentage and cover of aquatic plants was lowest, and that of grass cover highest, in the driest year of 1989 (Table 2). Likewise, facultative species such as witch-grasses (*Dichanthelium* spp.) and broomsedge (*Andropogon virginicus*) were more abundant in 1989, but were greatly reduced after reflooding (Table 3). Woody plants exhibited a different pattern. Woody cover in the bay interiors changed little over time, but woody plants in the margins were affected markedly by drydown and reinundation (Table 2). In 1989, woody cover was probably higher than estimated because transect sampling was truncated when woody plants were encountered (see Methods). However, the tree species contributing to high marginal woody cover in 1993 (e.g., loblolly pine, sweetgum, swamp tupelo; Table 3) were generally saplings or seedlings that had established during the 1980s drought but had been undersampled in 1989. Dying and dead saplings of loblolly pine were noted in 1993, indicating that reinundation was reducing this flooding-sensitive species. By 2003, total woody cover in the margins had declined (Table 2). Only stumps remained of the pine saplings that had established in the 1980s, and new pine seedlings that

Table 2. Means (± SE) of vegetation composition variables averaged over seven bays, and ANOVA F statistics for differences among years. Significance levels are indicated by: + $P \leq 0.10$; * $P \leq 0.05$; ** $P \leq 0.01$. Mean annual hydroperiod for each location and year is also noted.

	Wetland Interior				Wetland Margin			
Variable	1989	1993	2003	F[a]	1989	1993	2003	F[b]
Mean annual hydroperiod (% time ponded)	78[c]	95	98	–	29	86	69	–
Species richness (number of species)	17 (1)	11 (2)	9 (2)	11.1**	10 (2)[d]	13 (1)	13 (2)	0.1
Percent wetland species	83 (5)	95 (3)	92 (5)	4.5*	76 (6)	85 (3)	78 (5)	0.4
Percent facultative/upland species	17 (5)	5 (3)	8 (5)	–	24 (6)	15 (3)	22 (5)	–
Percent aquatic species	11 (5)	32 (4)	26 (6)	8.8**	**4 (4)***	18 (3)	18 (5)	0.1
Percent grass species	33 (5)	27 (3)	40 (5)	5.5*	45 (11)+	24 (3)	30 (4)	3.0
Percent rushes/sedges/forbs	45 (5)	30 (7)	26 (4)	4.5*	35 (7)	27 (6)	18 (5)	2.5
Percent woody species	11 (3)	10 (4)	8 (3)	0.7	16 (8)[d]	31 (6)	34 (6)	0.7
Total plant cover (%)	129 (7)	110 (13)	68 (9)	12.6**	131 (12)[d]	138 (10)	87 (12)	14.2**
Cover of wetland species (%)	110 (11)	109 (12)	62 (10)	8.0**	94 (16)+	113 (10)	64 (17)	8.7*
Cover of facultative/upland species (%)	17 (6)	1 (0.6)	6 (4)	10.2**	32 (10)	25 (2)	23 (10)	2.2
Cover of aquatic plants (%)	16 (5)	47 (9)	18 (10)	6.8*	**3 (3)***	30 (8)	13 (8)	3.8+
Cover of grasses (%)	74 (10)	39 (12)	43 (9)[e]	5.0*	**88 (12)***	39 (9)	44 (7)[e]	1.1
Cover of rushes/sedges/forbs (%)	32 (10)	18 (8)	2 (1)	6.9**	16 (7)	17 (5)	2 (1)	9.0*
Cover of woody plants (%)	7 (4)	6 (4)	5 (4)	0.6	23 (10)[d]	53 (11)[e]	28 (9)[e]	4.7+

[a] For interiors, F test compares all years, with df = 2, 12.

[b] For margins, F test compares 1993 and 2003, with df = 1, 6; 1989 means differing from 1993 at $P \leq 0.05$ are noted in boldface.

[c] Value is overestimate; see Methods.

[d] Values are underestimated (see Methods); differences from 1993 not tested.

[e] Dead cover also present.

had established during the 1999–2002 drought were also showing signs of flooding stress and die-back. Cover of the facultative sweetgum declined between 1993 and 2003; similarly, upland blackberry shrubs (*Rubus* spp.) also decreased from 1989 and showed evidence of die-back in 2003 (Table 3). The more flood-tolerant tupelo (*Nyssa biflora*) showed less change between 1993 and 2003.

Forest composition of the surrounding uplands appeared to influence woody plant dynamics in the bay margins. In four bays surrounded by pine stands (Mona, Sarracenia, Thunder, and Woodward; Table 1), pine colonization and die-off were more evident (across all years, mean pine cover = 18% vs. mean hardwood cover = 3%). In three bays surrounded by stands of pine-hardwood or pine-oak mixes (Dry, Ellenton, and Flamingo), establishment of hardwoods such as sweetgum and swamp tupelo was more evident (mean hardwood cover = 46% vs. mean pine cover = 5%).

DISCUSSION

Hydrologic Variation and Vegetation Response

Except for the more seasonally ponded Woodward Bay, these wetlands generally exhibited semi-permanent hydroperiods and were ponded deeply (> 1 m) in most years. However, annual hydroperiod and water depth of all bays fluctuated with annual rainfall variation, confirming the importance of precipitation inputs and climate variability (Schalles and Shure 1989, Lide et al. 1995, Brooks 2004, Johnson et al. 2004). Shallower bay margins experienced more frequent water-level change (see also Collins and Battaglia 2001), but even the deepest wetlands dried completely during prolonged drought. When drought conditions ended, it appeared that more than a year was required for water levels to recover completely. The controlling factors on individual depression hydrology are still poorly understood. Depressions with small or shallow basins may be more seasonal or dry more often than larger and deeper wetlands (Schalles and Shure 1989, Brooks and Hayashi 2002, De Steven and Toner 2004), but hydrologic behavior can be complicated by local groundwater inputs that may prolong hydroperiods (Lide et al. 1995, Chmielewski 1996). Detailed study of water balance and water budgets in relation to basin morphology, soils, and local topography (e.g., Brooks and Hayashi 2002, Sun et al. 2006) are needed to identify causes of variation among wetlands.

As documented in previous studies (Kirkman 1995, Mulhouse et al. 2005a), vegetation composition shifted with short-term reductions in ponding depth and duration. Wetland drying reduced aquatic

Table 3. Average cover (%) of common species in interiors and margins of the seven bay wetlands in each survey year, with taxa ordered by wetland indicator class and growth form. Common species were present in at least four bays and had ≥ 10% cover in two or more bays. Species averaging ≥ 10% mean cover in a given year are highlighted in boldface. Mean annual hydroperiod for each location and year is also noted below.

Species	Indicator class	Growth form	Wetland Interior			Wetland Margin		
			1989	1993	2003	1989[a]	1993	2003
Brasenia schreberi Gmel.	wetland	aquatic	1.3	**10.9**	1.0	–	**12.7**	0.9
Nymphaea odorata Ait.	wetland	aquatic	**10.3**	**22.4**	**15.0**[a]	–	4.1	6.3
Sagittaria spp. (mostly *S. graminea* Mich.)	wetland	aquatic	1.7	1.5	–	0.9	2.4	–
Utricularia spp.	wetland	aquatic	0.5	**11.1**	2.1[a]	–	8.7	2.9
Erianthus sp.	wetland	grass	1.3	0.7	0.2	3.9	0.5	0.5
Leersia hexandra Sw.	wetland	grass	**15.7**	**13.4**	3.0	**16.3**	4.2	5.5
Panicum hemitomon Schult., *Sacciolepis striata* (L.) Nash[c]	wetland	grass	**32.6**	**24.5**	**31.9**[a]	**33.9**	**29.5**	**27.7**
Paspalum laeve Michx.	wetland	grass	**10.0**	–	0.7	6.7	1.6	0.5
Rhexia spp. (*R. mariana* L., *R. virginica* L.)	wetland	forb	0.4	–	–	1.3	0.1	0.3
Eleocharis spp.	wetland	sedge	5.9	**10.0**	–	4.4	**10.3**	0.4
Rhynchospora spp.	wetland	sedge	**12.0**	0.6	0.3	3.1	0.1	0.1
Cephalanthus occidentalis L.	wetland	woody	1.9	2.4	2.8[e]	7.0	7.7	2.0[e]
Nyssa biflora (Walt.) Sarg., *N. sylvatica* Marsh	wetland	woody	2.6	2.5	1.4	7.5	**12.7**	**10.0**
Andropogon virginicus L.	facultative	grass	4.2	–	4.9[e]	7.4	0.2	5.8[e]
Dichanthelium spp.	facultative	grass	8.1	–	0.6	**14.7**	0.1	1.6
Liquidambar styraciflua L.	facultative	woody	0.2	–	–	–[b]	7.7	0.9
Pinus taeda L.	facultative	woody	2.3	0.2	0.5	7.1[b]	**16.1**[e]	**11.2**[e]
Eupatorium capillifolium (Lam.) Small	upland	forb	0.9	–	–[e]	0.1	0.1	-[e]
Rubus spp.	upland	woody	0.1	0.6	< 0.1[e]	1.8[b]	0.1	0.1[e]
Mean annual hydroperiod (% time ponded)	–	–	78[d]	95	98	29	86	69

[a] Estimated from partial sampling.
[b] Values are likely underestimated; see Methods.
[c] Species indistinguishable in vegetative form.
[d] Value is overestimate; see Methods.
[e] Dead cover also present.

plant cover but allowed expansion of perennial emergent grass and meadow species. Species richness increased during drought periods, as species dependent upon water drawdowns emerged from seed banks or from incoming seeds. In particular, the presence of facultative and upland species increased during droughts, and woody plants colonized the shallower margin areas. From aerial photographs spanning the time period before and after the 1980s drought, Kirkman (1992) detected this pine and hardwood expansion in Mona, Thunder, and Ellenton bays. Many woody species do not form persistent seed banks and must disperse from bordering habitats (Kirkman and Sharitz 1994). Their ability to establish successfully depends upon wetland drydowns coinciding with times of seed dispersal, germination, and early growth. Thus, multi-year drought periods particularly favor successful colonization by facultative tree species such as loblolly pine and sweetgum.

Our longer-term observations built upon earlier studies by documenting vegetation response to reinundation. As conditions of prolonged and deep ponding returned in 1993, cover of aquatic species increased and cover of other species groups declined. A similar trend was apparent in 2003, after the second drought period; increased aquatic plant dominance is likely if several more wet years follow. The rate of vegetation change is affected by species sensitivity to the anoxic conditions of prolonged flooding. After the 1999–2002 drought, flood-intolerant facultative and upland grass species were dying in the first year of reinundation. In contrast, woody species may endure several years of stress before elimination, depending upon tree size and flooding duration (Hook 1984). We found standing dead sapling and seedling pines in 1993, and Kirkman (1992) noted stressed and dying pines in 1992, several years after the end of the 1980s drought.

Long-term Vegetation Dynamics

The changes observed over the 15-year period generally confirmed a pattern of cyclic vegetation dynamics in these wetlands. The bays maintained overall dominance by wetland and herbaceous plant species through dry and wet periods. Historical aerial photography from 1951 also suggests that nearly all seven study wetlands have remained herb-dominated for some time (Kirkman et al. 1996). Flamingo Bay has persistent marginal areas of flood-tolerant hardwoods (principally swamp tupelo), but deep and nearly permanent ponding has historically maintained an open central area (Taylor and Brooks 1994). Only Woodward Bay, with a shorter and more variable hydroperiod, shows evidence of successful pine encroachment. Because pine trees greatly increase evapotranspiration rates (Sun et al. 2001), their presence may accelerate wetland drying and eventually promote succession toward forest in this bay.

While cyclic dynamics in these bays appeared to be controlled mainly by long hydroperiods and deep ponding, adjacent forest management and landscape setting may have also played a role (Kirkman et al. 2000, De Steven and Toner 2004). Wetlands in Sandhills landscapes, with droughty sand soils and pine-dominated uplands, were colonized primarily by flood-intolerant pines, whereas wetlands in Terrace and Loam Hills landscapes were more likely to have hardwood trees colonize from surrounding hardwood-pine forests. In these large and deep bays, hardwood trees such as sweetgum, tupelos, and red maple (*Acer rubrum* L.) did not generally show increases in cover over time; rather, it appeared that prolonged inundation was limiting their inward expansion.

Morphological and physiological characteristics of the dominant plants contributed to stabilizing vegetation composition over time. Although unable to persist aboveground during droughts, aquatic species such as water lily can readily re-establish from tuberous rhizomes and seeds after reflooding. The dominant wetland grasses (*P. hemitomon, L. hexandra*) have stems that can elongate through water depths of roughly 1 m to maintain shoot and root aeration; their leaf stomatal control and rhizomatous growth habit allow persistence through drought and rapid recovery in wetter conditions (Kirkman and Sharitz 1993, 1994). Conversely, the facultative and upland woody and grass species that established during droughts generally lack features for surviving long and deep inundation during establishment (Cronk and Fennessey 2001). Even in more flood-tolerant species such as swamp tupelo, seedlings may be sensitive to flooding stress while tolerance increases with tree age and size (Hook 1984, Jones and Sharitz 1998).

Other types or sizes of depression wetlands are predicted to exhibit different vegetation responses to climate fluctuations. In smaller seasonally ponded depressions, moderately flood-tolerant hardwoods could survive and become well-established, eventually altering wetland hydroperiod and promoting succession toward forest communities (Kirkman et al. 1996, De Steven and Toner 2004). Whether vegetation change is cyclic or directional may also depend on the role of fire, which particularly reduces the cover of fire-sensitive hardwoods (Kirkman et al. 2000, De Steven and Toner 2004, Casey and Ewel 2006). Upland pine stands on the Savannah River Site are managed by prescribed burning, but the general practice has been to prevent the fires from moving into the adjoining wetlands. Drought periods offer the greatest potential for fire spread into bays, but such conditions paradoxically can restrict prescribed burning activity because of greater fire hazards. Thus, it is uncertain whether fires affected the observed vegetation changes in the study bays, though their deep ponding and longer hydroperiods make it unlikely. In general, opportunities for fire impact would likely be greater in depressions with seasonal or temporary ponding (Kirkman et al. 2000).

Over the next 30 to 60 years, it is predicted that South Carolina may experience climatic shifts that are likely to affect wetland habitat dynamics and distribution (South Carolina State Climatology Office 2004). The regional climate models do not agree on whether annual precipitation will rise or decrease, but they have predicted that annual temperatures — and potentially drought frequency — will increase. Understanding how Carolina bays and similar depressional wetlands respond to current drought cycles can help predict how the systems might be impacted by future climate change. For example, hydrologic simulations for shallow prairie pothole depressions in the semi-arid Northern Great Plains region predicted that temperature increases of 3°C would result in earlier seasonal drawdowns and wetlands that remain dry with greater frequency and duration. Depending upon how temperature-induced changes interacted with precipitation changes, simulations predicted that habitat suitability for waterfowl would change dramatically at a region-wide scale (Johnson et al. 2005). Similarly, in Carolina bays and other Southeastern depressions, more frequent drought would likely cause more immediate hydrologic change in small shallow bays that are naturally more prone to drying. Shifts to shorter hydroperiods would favor forest succession in more wetlands and thus alter the landscape distribution of plant community types (De Steven and Toner 2004). The herpetofaunal and aquatic invertebrate communities of depressional wetlands are influenced by hydroperiod and vegetation structure (Semlitsch and Bodie 1998, Golladay et al. 1999, Taylor et al. 1999, Russell et al. 2002); therefore, long-term hydrologic changes could affect the fauna of individual wetlands and alter landscape patterns of faunal diversity as well. Additional hydrologic and modeling studies are needed to address these issues.

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