Effects of dominant species on vegetation change in Carolina bay wetlands following a multi-year drought[1]

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MULHOUSE, J. M. (University of Georgia, Savannah River Ecology Laboratory, Drawer E, Aiken, SC 29802), D. DE STEVEN (USDA Forest Service, Southern Research Station, Center for Bottomland Hardwoods Research, P.O. Box 227, Stoneville, MS 38776), R. F. LIDE (Northwest Florida Water Management District, 81 Water Management Dr., Havana, FL, 32333), AND R. R. SHARITZ (University of Georgia, Savannah River Ecology Laboratory, Drawer E, Aiken, SC 29802). Effects of dominant species on vegetation change in Carolina bay wetlands following a multi-year drought. J. Torrey Bot. Soc. 132: 411–420. 2005.—Wetland vegetation is strongly dependent upon climate-influenced hydrologic conditions, and plant composition responds in generally consistent ways to droughts. However, the extent of species composition change during drought may be influenced by the pre-existing structure of wetland vegetation. We characterized the vegetation of ten herbaceous Carolina bay wetlands on the South Carolina Upper Coastal Plain during a period of average rainfall and again near the end of a four-year drought. We hypothesized that, as a group, bays dominated by less robust plant species (characteristic of open-water pond and depression meadow vegetation types) would show greater compositional change than bays dominated by dense, robust-form clonal graminoids (characteristic of grass and sedge marsh vegetation types). Aquatic species decreased during the drought in all wetlands, regardless of vegetation group. Compared to grass/sedge marshes, pond/meadow wetlands acquired more species, particularly non-wetland species, during the drought. Pond/meadow wetlands also had greater increases in the abundances of species that require unflooded conditions to establish. Prior to the drought, all wetlands were ponded almost continuously, but during drought the pond/meadow wetlands had shorter and more variable hydroperiods than the grass/sedge marshes. Thus, vegetation change may be partly confounded with hydrologic conditions that provide greater opportunities for species recruitment in pond/meadow bays. The results suggest that Carolina bay vegetation dynamics may differ as a function of dominant vegetation and climate-driven variation in wetland hydrologic condition.

Key words: Carolina bays, climate variation, depression wetlands, drought, plant colonization, succession, vegetation dynamics

In wetlands, plant composition is structured by the hydrologic regime, which in turn is influ-

enced strongly by climate (Mitsch and Gosselink 2000). For example, in prairie marshes and similar herbaceous wetlands, drought conditions have been shown to affect vegetation in generally consistent ways (van der Valk and Davis 1978, Greening and Gerritsen 1987, Kirkman 1995, Johnson et al. 2004). As water levels draw down, plant species favored by drier conditions establish and expand their distribution, while those that would be present under wetter conditions decline and perhaps disappear entirely. Re-flooding can generally reverse these changes; however, the signature of a prolonged drought could remain in a wetland community long after wetter conditions return if upland species survive in elevated refuges and colonizing woody species persist. Thus, depending on the wetland system, it has been suggested that droughts could drive a cyclic succession maintaining her-

baceous vegetation or promote directional change toward forest vegetation (van der Valk and Davis 1978, Kirkman 1995, Kirkman et al. 2000, De Steven and Toner 2004).

On the United States Southeastern Coastal Plain, Carolina bays are among the most prominent wetland systems. Ranging from Delaware through Georgia, bays are characterized by shallow elliptical basins generally oriented toward the northwest and by sandy, nutrient-poor soils (Sharitz 2003). Because basins generally have no surface inflows or outflows, hydrologic conditions are driven chiefly by precipitation inputs and evapotranspiration losses (Schalles and Shure 1989, Lide et al. 1995). Therefore, water depth and hydroperiod (ponding duration) fluctuate in response to climate variation, including periodic regional droughts. In Carolina bay ponds, the general pattern observed during water drawdowns is that aquatic plant species disappear while emergent species, particularly perennial grasses, expand (Kirkman 1995, Stroh 2004, Mulhouse et al. 2005). These changes result from interactions between wetland hydroperiod and the available species pool: dry conditions allow expansion of established species, but also permit recruitment of new species that emerge from seed banks or disperse onto exposed substrates. However, as relatively few bay sites have been studied, the potential variability among bays in response to drought conditions is unknown. Even during periods of normal rainfall, bays exhibit varied hydrologic patterns (Sharitz 2003, De Steven and Toner 2004), so one modifying factor on compositional change could be how severely a drought period affects the hydrologic regimes of individual bays.

The structure of the existing vegetation could be another factor that affects how bays respond to drought. For example, herbaceous Carolina bays of the Upper Coastal Plain can be classed into one of four vegetation (bay) types based on characteristic dominant species (De Steven and Toner 2004). The pond vegetation type is characterized chiefly by open water and aquatic species such as *Nymphaea odorata* Ait. (water lily). The other three vegetation types are each dominated by different perennial graminoids: grass marshes by *Panicum hemitomon* J.A. Schultes. (maidencane), sedge marshes by *Carex striata* Michx. (peatland sedge), and depression meadows by *Leersia hexandra* Sw. (coastal plain cutgrass). All three species can expand clonally to form a vegetative matrix throughout a wetland. Both *P. hemitomon* and *C. striata* are tall, stout plants that can occur in dense and nearly monotypic stands, whereas *L. hexandra* is a slender and typically shorter species that may be found with a mix of other sedges, forbs, and grasses (including *P. hemitomon*). Given the contrasts in vegetation structure imparted by the dominant species, individual herbaceous bays could have different patterns of vegetation change during periods of water drawdown.

To examine these factors, we took advantage of a unique opportunity afforded by a prior study of Carolina bay depressions (De Steven and Toner 2004) and a recent severe regional drought in South Carolina (SC). At the end of a four-year drought period, we re-sampled 10 bays encompassing all four herbaceous vegetation types to determine if vegetation changes could be detected at the level of individual bays. We hypothesized that, as a group, open-water pond and depression meadow bays might show greater compositional change because their less robust vegetation offers more exposed substrates and weaker barriers to new species establishment. In contrast, grass and sedge marshes dominated by robust-form graminoids might be less susceptible to change during the drought if the denser stand structure inhibits the expansion or recruitment of other species. We also compared how the drought affected hydroperiods in bays of the two contrasting vegetation groups (pond/meadow versus grass/sedge marsh). Differences between the two vegetation groups would suggest that Carolina bay depressions have the potential for different successional trajectories as a consequence of climate-driven changes in wetland hydrologic conditions.

Methods. Site Description. The 10 study sites were herbaceous Carolina bays or bay-like depression wetlands located on the Savannah River Site (SRS), a 780 km^2 Department of Energy facility on the Upper Coastal Plain of SC, USA. The study sites represented most of the SRS herbaceous depressions included in the original De Steven and Toner (2004) study. We refer to all study wetlands as ''bays'', as there has been a lack of consensus as to what traits distinguish a Carolina bay from other depression wetlands, particularly when basin size is small (Lide 1997). All study bays were surrounded by managed pine (*Pinus taeda* L., *P. elliottii* Engl., *P. palustris* (Engl.) Miller) and mixed pine-hardwoods forests, which represent the predominant land use on the SRS. Bays encompassed all four herbaceous vegetation types described by De

Table 1.   Attributes of the 10 study bays on the Savannah River Site, including their classified vegetation type and the associated dominant species and hydrologic regime. Vegetation features are derived from a classification analysis of 57 Upper Coastal Plain bay wetlands (De Steven and Toner 2004).

Vegetation type	Dominant species	Typical hydroperiod[a]	Bay no.	Landscape position[b]	Bay area (ha)
Open-water pond	*Nymphaea odorata*	deep, semi-permanent	40	Uplands	7.5
			78	Uplands	4.5
Depression meadow	*Leersia hexandra*	shallow, variably seasonal	26	Terrace	1.2
			27	Terrace	2.3
			87	Uplands	1.8
			106	Uplands	2.5
Grass marsh	*Panicum hemitomon*	shallow, long-seasonal	9	Terrace	3.9
			127	Uplands	5.1
Sedge marsh	*Carex striata*	shallow, long-seasonal	136	Terrace	1.2
			165	Terrace	3.8

[a] Under normal rainfall conditions.
[b] ''Terrace'' is a relict alluvial terrace above the present-day Savannah River floodplain; ''Uplands'' include Sandhills and Loam Hills landscape settings (De Steven and Toner 2004).

Steven and Toner (2004), and occurred within both of the major landscape positions (uplands and relict alluvial terrace) on the SRS (Table 1). The range of bay sizes was similar within each vegetation group (pond/meadow bays: 1–7 ha; grass/sedge marshes: 1–5 ha) (*t*-test not significant).

The climate of the SC Upper Coastal Plain is humid subtropical, with long, hot summers and short, mild winters. Mean temperature is 7.3 °C in January and 25.6 °C in July. Annual precipitation averages 1217 mm, chiefly as rainfall during the spring and summer months. Precipitation patterns are cyclic, with major droughts occurring on the order of decades (National Oceanic and Atmospheric Administration 2003). Rainfall was generally above average from 1991–1998, but below average during 1999–2002 (Figure 1).
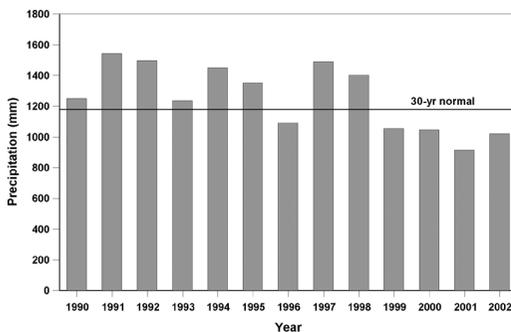

Fig. 1.   Mean annual precipitation at the Savannah River Site (SRS), relative to 30-year normals at a nearby NOAA weather station in Blackville, SC (National Oceanic and Atmospheric Administration 2003). Data are averaged over 7 rain stations distributed across the SRS.

Drought conditions became evident in 1999, and by August 2002 the drought had been designated as ''extreme'' throughout all of SC (SC Department of Natural Resources 2003).

FIELD METHODS. Beginning in April–May 1995, water depth was measured via staff gauges placed in the deepest point of each bay. Gauges were read weekly through 1998, then monthly until 2001, and bi-monthly beginning in April 2001. The less frequent monitoring over time was partly a function of the dry conditions in many wetlands during the drought period.

Data on pre-drought vegetation composition were taken from the study of De Steven and Toner (2004). They used a modified line-intercept method with transects spanning the entire depression basin to obtain representative sampling of the dominant vegetation composition. In each bay, one transect was placed across the long axis and two additional transects were sampled across the width of each site, trisecting the long axis. At 10-m intervals along each transect, all plant species intersecting the vertical projection of a 1-m line segment were recorded, including any taller woody species if present. Incidental species observed outside of sampling locations were also noted. This sampling design provided species frequencies that are proportional to their overall abundance (coverage) in each wetland, and so we used these frequencies as a measure of abundance. Seven study bays had been surveyed in 1993 and three in 1995; both years had above-normal rainfall and similar ponding conditions (Figure 1; De Steven and Toner 2004). These data will be referred to collectively as the ''1993'' (pre-drought) survey.

In 2002, the fourth year of the drought, vegetation in the 10 study bays was re-surveyed in late July and early August according to the methods of De Steven and Toner (2004). Although transects had not been permanently marked in 1993, the starting points of each were replicated from field notes as closely as possible. This resulted in slight differences in the number of sample points in each wetland between the two years. Species vouchers collected during the 2002 survey were deposited in the University of Georgia Herbarium. Taxonomy followed Radford et al. (1968) and Godfrey and Wooten (1981). In a few cases, taxa difficult to distinguish in one or both years were grouped at the generic level (*Eupatorium*, 2 spp.; *Rhexia*, 3 spp.; *Rhynchospora*, 2 groups of 3 spp.; *Taxodium*, 2 spp.; *Triadenum*, 2 spp.; *Utricularia*, 3 spp.); *Sphagnum* moss was also recorded as one taxon. For simplicity, we used these groups as species for tabulating species richness, since it was rare that more than one member of a group occurred in the same wetland.

Upland forest stands on the SRS are managed by thinning and periodic clearcutting, which could affect bay vegetation during droughts if weedy successional species colonize from adjacent harvested uplands. Site records were checked to determine if there had been any cutting in the upland stands surrounding each study bay during the study period. Only one bay (a grass marsh) had any nearby harvest activity between 1993 and 2002, thus there was little potential for this management disturbance to influence the vegetation of most bays over the study period.

DATA ANALYSES. Mean annual hydroperiod (percent of time ponded at staff gauge) and mean annual water depth were determined for each year for each vegetation group (open-water ponds/depression meadows and grass/sedge marshes), and overall means were calculated for the cumulative pre-drought (1995–1998) and drought (1999–2002) periods. Mean plant species richness (total number of species observed) in each vegetation group was tabulated for each survey year (1993, 2002). The mean percentage of all observed species common to both survey years was also calculated for each vegetation group. Abundance of each species was calculated as percent frequency, i.e., the percent of sampling locations in which the species occurred in each bay. Mean species abundance in each of the four vegetation types was calculated for each

survey year, and the number of species with a net increase or decrease in abundance of > 10% between 1993 and 2002 was tabulated for each type. National Wetland Indicator (NWI) categories for Region 2 (Southeast) were assigned to each species (Reed 1988), and species were grouped into three indicator classes: wetland (OBL and FACW species), facultative (FAC+ and FAC species), and upland (FAC-, FACU, and UPL species). FAC- species were classed as ''upland'' because they are considered to have less than 50% probability of occurring in wetlands and thus are not indicators of wetland vegetation for jurisdictional purposes (Environmental Laboratory 1987, Reed 1988). The relative abundances of species in the three indicator classes were then calculated for each bay in each survey year.

For all variables, differences between the pre-drought and drought periods, or between survey years, were tested across bays using paired *t*-tests. Differences between the two vegetation groups (pond/meadow bays and grass/sedge bays) were tested by two-sample *t*-tests, using the separate-variances option as appropriate. Because landscape position can potentially influence bay hydrologic condition (Chmielewski 1996), differences in hydrologic variables between bays in the uplands versus terrace were also tested with the two-sample *t*-test. SYSTAT® was used for all analyses (SPSS 1999). Most variables were normally distributed, but some were transformed (log or square root) to achieve normality where needed. Tests with $P \leq 0.05$ were considered statistically significant; however, as bays are generally variable and the number of study bays was small, *P*-values in the marginal range of 0.05–0.10 were noted as indicating positive trends.

In addition to the above analyses, multiple response permutation procedures (MRPP) were used to test whether bays of each vegetation group changed in overall species composition between survey years. MRPP was performed on species abundance data in PC-ORD© (McCune and Mefford 1995), with bays as a block factor. A distance-based ordination (non-metric multidimensional scaling; Minchin 1989) was also run to confirm the MRPP results visually; the ordination graph is not presented here for purposes of brevity.

Results. On average, all bays were ponded nearly continuously through the pre-drought period (mean hydroperiod = 96%). Hydroperiods

Table 2. Mean annual hydroperiods (percent of months ponded) and mean water depths (m) from 1995–2002 for each vegetation group. Cumulative pre-drought and drought means are also shown. The pre-drought period was March 1995 to December 1998; drought period was January 1999 to August 2002.

Variable	1995	1996	1997	1998	Pre-drought (1995–1998)	1999	2000	2001	2002	Drought (1999–2002)
Annual hydroperiod (%):										
Pond/meadow mean (s.e.)	100	97	92	97	**96 (1)**[a]	67	48	54	17	**52 (8)**[b]
Grass/sedge mean (s.e.)	100	100	98	89	**96 (2)**[a]	82	62	81	50	**72 (4)**[b]
Overall mean (s.e.)	100	98	94	94	**96 (1)**[c]	73	54	65	30	**60 (6)**[c]
Mean water depth (m):										
Pond/meadow mean (s.e.)	0.82	0.57	0.52	1.00	**0.72 (0.2)**[d]	0.40	0.22	0.28	0.04	**0.27 (0.1)**[e]
Grass/sedge mean (s.e.)	0.61	0.48	0.48	0.65	**0.56 (0.1)**[d]	0.33	0.22	0.41	0.11	**0.29 (0.1)**[e]
Overall mean (s.e.)	0.74	0.53	0.50	0.87	**0.66 (0.1)**[f]	0.37	0.22	0.33	0.07	**0.28 (0.1)**[f]

[a] Two-sample t-test of difference between vegetation groups pre-drought, P not significant.
[b] Two-sample t-test of difference between vegetation groups during drought, $P = 0.07$.
[c] Paired t-test of pre-drought versus drought hydroperiod for all bays, $P < 0.001$.
[d] Two-sample t-test of difference between vegetation groups pre-drought, P not significant.
[e] Two-sample t-test of difference between vegetation groups during drought, P not significant.
[f] Paired t-test of pre-drought versus drought water depth for all bays, $P < 0.001$.

were significantly shorter during the drought, particularly by 2002 when bays were ponded for only 30% of the year (Table 2). In the drought period, pond/meadow wetlands tended to have shorter hydroperiods than grass/sedge marshes (means of 52% and 72%, respectively); the difference was especially prominent in 2002 (Table 2). Prior to the drought, bay hydroperiods did not differ significantly between landscape positions (uplands versus terrace), but during the drought an apparent trend was for hydroperiods of upland bays to be shorter and more variable (upland mean = 50%, SE = 10; terrace mean = 70%, SE = 3; not significant). Three of the four grass/sedge marshes, which generally had longer hydroperiods during the drought, were located in terrace landscape positions (Table 1).

Prior to the drought, mean water depths ranged from 0.48 to 1.00 m (overall mean = 0.66 m) (Table 2). Mean depths appeared higher in the pond/meadow group (0.72) than in grass/sedge bays (0.56), but the average for the former is somewhat skewed because pond bays typically flood more deeply (mean depths > 1 m) than either meadow or marsh bays (De Steven and Toner 2004); hence, mean depths did not differ significantly between the two vegetation groups. During the drought period, mean water depths were significantly lower in all bays (overall mean = 0.28 m) and were nearly identical between vegetation groups, given that nearly all bays eventually dried down completely (Table 2). Mean bay water depths did not differ between landscape positions, either in the pre-drought or drought periods (both $P > 0.10$).

As indicated by MRPP tests, overall vegetation composition changed between 1993 and 2002, but the change was apparently greater in pond/meadow bays ($P = 0.008$) and less in grass/sedge marsh bays ($P = 0.03$). Species richness increased in pond/meadow bays by 2002 ($P = 0.03$), but did not change significantly in grass/sedge marshes (Table 3). The percentage of species observed in a bay in both years ranged between 12–42%, but was fairly low overall (mean = 25%) and did not differ significantly between vegetation groups (Table 3). Across all bays, there were fewer total wetland

Table 3. Species richness (number of species observed) in each survey year, and the percent of taxa observed (shared) in both years. Means are averaged over bays in each vegetation group.

Vegetation group	1993	2002	Mean percent of taxa shared	Range of percent taxa shared
Pond/meadow mean (s.e.)	18 (3)[a]	25 (5)[a]	21 (1)[c]	18–26
Grass/sedge mean (s.e.)	18 (5)[b]	20 (2)[b]	31 (7)[c]	12–42
Overall mean (s.e.)	18 (3)	23 (3)	25 (3)	12–42

[a] Paired t-test of difference between years for ponds/meadows; $P = 0.03$.
[b] Paired t-test of difference between years for grass/sedge marshes, P not significant.
[c] Two-sample t-test of difference between vegetation groups, P not significant.

Table 4.   Relative abundance (% frequency) of species by indicator class for each vegetation group in 1993 and 2002, and net change in abundance between years. Data are means (SE) averaged over bays in each vegetation group.

Species indicator class	Vegetation group	1993[a]	2002[a]	Net change[b]
Wetland	pond/meadow	89 (4)	63 (8)	−26 (9)
	grass/sedge	84 (7)	67 (9)	−17 (5)
Facultative	pond/meadow	11 (4)	25 (6)	14 (6)
	grass/sedge	16 (7)	30 (11)	14 (7)
Upland	pond/meadow	0.4 (0.4)	12 (4)	12 (4)
	grass/sedge	0.4 (0.4)	4 (3)	3 (3)

[a] Paired t-tests of difference between years for each indicator class: all $P < 0.01$.
[b] Two-sample t-tests of difference between vegetation groups for each indicator class: P not significant for wetland species or facultative species, $P = 0.08$ for upland species.

species in 2002 (45, vs. 60 in 1993), but more facultative and upland species (34 vs. 14). Per bay, the average number of wetland species did not decrease significantly in either vegetation group, but the increase in facultative and upland species was significant in pond/meadow bays (paired t-test, $t = 4.1$, $P = 0.01$).

Collectively, the relative abundance of wetland species declined significantly during the drought, while the relative abundance of facultative and upland species increased significantly (Table 4). Upland species showed significantly greater increases in pond/meadow bays (mean change = 12%) than in grass/sedge marshes (mean change = 3%; Table 4).

Changes in the abundance of individual species during the drought also were apparent. The most abundant species in 1993 were consistent with the expected dominants for each vegetation type (see Table 1), while emergent grasses and sedges generally became more prevalent by 2002 (see Appendix). Differences in mean abundance of 10% or more in a vegetation type between 1993 and 2002 were taken to indicate a true net change (Table 5). *Panicum verrucosum* Muhl., an annual wetland grass, exhibited a mean net increase of approximately 50% in pond/meadow bays, compared to an increase of 15% in grass/sedge marshes. Similarly, two upland and facultative grasses (*Andropogon virgin-*

Table 5.   Change in mean abundance (% frequency), by vegetation type, for species with net increases or decreases of > 10% between 1993 and 2002. A + or − indicates species as present but with net change of < 10%; and boldface indicates species that newly appeared or disappeared by 2002. OW = open-water pond; DM = depression meadow; GM = grass marsh; SM = sedge marsh.

Species	Indicator class	Net increase (%)				Net decrease (%)			
		OW	DM	GM	SM	OW	DM	GM	SM
Andropogon virginicus	upland	**25**	**31**	+					
Dichanthelium wrightianum	facultative	**19**	**21**	+					
Eupatorium spp.	upland		11	+					
Juncus canadensis	wetland							**−19**	−
Leersia hexandra	wetland					−	−27		
Liquidambar styraciflua	facultative		14	12		−			−
Nymphaea odorata	wetland					**−67**	−		−
Panicum hemitomon	wetland	28	+		+			−	
Panicum verrucosum	wetland	48	**63**	**16**	**14**				
Pinus taeda	facultative	13	34	21	13				
Pontedaria cordata	wetland							**−19**	−
Psilocarya nitens	wetland	**22**							
Rhexia spp.	wetland	+	33	13	+				
Rhynchospora spp. a	wetland		25					−	
Rhynchospora spp. b	wetland	+	**19**	+					
Scleria reticularis	wetland	15	13		+				
Sphagnum spp.	wetland					−	−38		
Triadenum spp.	wetland	+		16					
Utricularia spp.	wetland					**−66**	**−56**	**−42**	**−73**
Total species with > 10% change		7	9	5	2	2	1	4[a]	1

[a] Number of species decreasing may have been influenced by a prescribed burn that impacted one site in 2000.

icus L. and *Dichanthelium wrightianum* (Scribn.) Freckmann) and a weedy upland forb (dogfennel, *Eupatorium* spp.) increased substantially in pond/meadow bays but not in grass/sedge marshes (Table 5). Wetland sedges such as *Scleria reticularis* Michx., *Psilocarya nitens* (Vahl) Wood, and *Rhynchospora* spp. also showed net increases only in the pond/meadow group. Loblolly pine (*P. taeda*) increased in abundance by 2002 in all vegetation types, generally as newly-recruited seedlings, but showed the greatest net change in abundance (34%) in depression meadows (Table 5). Overall, the number of species increasing in abundance was significantly higher in pond/meadow bays (mean = 9, SE = 1) than in grass/sedge marshes (mean = 4, SE = 1) (t = 3.8, P = 0.01). In contrast, floating aquatic species (*Nymphaea*, *Utricularia*) disappeared from all vegetation types by 2002 and comprised the majority of species with large net decreases in abundance (Table 5). The average number of species with net decreases did not differ between pond/meadow bays (mean = 3, SE 1) and grass/sedge marshes (mean = 2, SE = 1) (P > 0.10).

Discussion. Changes in vegetation composition through the drought were detectable at the level of individual bays. As a group, wetland plant species declined, whereas facultative and upland species increased. The declining species were mostly aquatic plants; few other types of wetland species consistently decreased in abundance. Rather, overall compositional change was characterized mainly by increases in the number and abundance of various emergent herbaceous and woody species.

Disturbance and vegetation structure are among the factors thought to influence the susceptibility of plant communities to entry of new species (Johnstone 1986, Crawley 1987). Our results supported the initial hypothesis that vegetation dominated by less robust or smaller-statured species (such as *N. odorata* and *L. hexandra* in ponds/meadows) would be more susceptible to change than would vegetation dominated by robust-form clonal species (such as *P. hemitomon* and *C. striata* in grass/sedge marshes). Pond/meadow bays had larger changes in species richness, species abundance, and species composition during drought. Increasing species included facultative/upland grasses and forbs, wetland sedges, wetland grasses, and loblolly pine. The exposed substrates associated with drying in ponds/meadows permitted these

additional species to establish from soil seed banks or by dispersal into the bays (Mulhouse et al. 2005). Similarly, in prairie pothole wetlands, substrates exposed during drawdown were colonized by a variety of species not seen prior to drying (van der Valk and Davis 1978, 1979).

In contrast to ponds/meadows, the robust graminoid cover in grass/sedge marshes appeared to provide fewer opportunities for new species establishment or expansion. Instances of species increasing only in grass/sedge marshes were uncommon, though several hardwood tree species (*Acer rubrum* L., *Liquidambar styraciflua* L., *Nyssa* spp.) had net increases in abundance of 7–12% in the grass marshes. Low plant species diversity in bay communities dominated by *P. hemitomon* or *C. striata* also has been documented elsewhere (Tyndall et al. 1990). However, species absent in the standing vegetation because of unfavorable conditions may persist in the seed bank (van der Valk 1981, Kirkman 1995, Collins and Battaglia 2001, Mulhouse et al. 2005). Seed banks in grass/sedge marshes could be relatively diverse, but the persistent and dense graminoid cover may limit recruitment without physical disturbances that create areas of open substrate (Kirkman and Sharitz 1994).

Although the data are consistent with the hypothesis that vegetation structure influences species dynamics in herbaceous Carolina bays during drought, the results may be somewhat confounded with differences in hydrologic behavior. Though all wetlands were flooded during the pre-drought period, during drought both ponds and meadow bays tended to have shorter and more variable hydroperiods than did grass/sedge bays. This was true even though pond bays typically flood more deeply than meadow bays. The differences in hydroperiods between the two vegetation groups may have been partly influenced by wetland location. The grass/sedge marsh bays of this study were located chiefly in the terrace landscape, where bays may flood for longer periods because of potential groundwater influence in this lower landscape position (Chmielewski 1996). Generally, species that recruited or increased in abundance require unflooded substrates to establish successfully. Thus, the grass/sedge marshes may have shown less species change both because the dominant vegetation inhibited species recruitment and because unflooded conditions were of shorter duration than in ponds/meadows. Since persistent flooded conditions also appear to favor dominance by *P. hemitomon* and *C. striata* (De Stev-

en and Toner 2004), vegetation structure and hydrologic regime are inevitably linked in affecting how individual bays respond to drought.

Our results provide some short-term evidence for two possible trajectories in herbaceous Carolina bays during drought. In ponds/meadows, drought results in establishment and expansion by additional species as a result of more open vegetation structure and a more variable hydrologic condition. Grass/sedge marshes acquire fewer species, at least in the short term, given their denser vegetation structure and somewhat longer hydroperiods. Of future interest is whether vegetation change is cyclic in the long term, such that after reflooding, wetland composition will again resemble that seen in 1993. Models and some data provide support for cyclic dynamics in pond and depression meadow bays (Kirkman 1995, Stroh 2004), where pine and other flood-intolerant species that establish during drought are killed when high water levels return. Other models incorporating additional factors, such as fire and anthropogenic disturbance, predict that herbaceous bays, particularly grass/sedge marshes, might exhibit directional change under some conditions (Kirkman et al. 1996, 2000; De Steven and Toner 2004). For example, in the absence of fire, herbaceous Carolina bays could undergo succession toward forested wetlands if hydrologic conditions allow flood-tolerant hardwood trees to establish.

In the southeastern United States, major droughts occur with periodicities on the order of decades (National Oceanic and Atmospheric Administration 2003). Continued studies are needed to set the observed short-term responses within the framework of possible long-term vegetation trajectories. Both hydroperiod and vegetation are known to affect the habitat suitability of Carolina bays for semi-aquatic animal species (e.g., Taylor et al. 1999, Semlitsch 2000, Snodgrass et al. 2000). Thus, understanding the drivers of vegetation dynamics in these wetlands can provide a basis for better-informed vegetation management; further, long-term datasets can provide input to models assessing the potential impacts of future climate change on these important wetland habitats (e.g., Johnson et al. 2004).

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Appendix

Abundance (% frequency) of species observed at an average of > 10% of sample points in each study year, where NWI is species National Wetland Indicator category and OW = open-water pond, DM = depression meadow, GM = grass marsh, SM = sedge marsh. + indicates presence in a survey year but at < 10% frequency.

Species	NWI	1993				2002			
		OW	DM	GM	SM	OW	DM	GM	SM
Acer rubrum L.	FAC	+	+	+	+	+		17	+
Andropogon virginicus L.	FAC−					25	31	+	
Cephalanthus occidentalis L.	OBL	+	+	12	+	11	+	19	+
Carex sriata Michx.	OBL				66				75
Dichanthelium wrightianum (Scribn.) Freckmann	FAC		18			19	21		
Diospyros virginiana L.	FAC	+			+		22	+	
Eupatorium spp. (capillifolium (Lam.) Small, compositifolium Walter)	FAC−/FACU		+				12	+	
Juncus canadensis J. Gay ex La Harpe	OBL			19	+				
Leersia hexandra Sw.	OBL	+	75			+	47	18	
Liquidambar styraciflua L.	FAC+	+	+	+	12		19		+
Nymphaea odorata Ait.	OBL	67	+		+				
Nyssa sylvatica (v. sylvatica Marsh., biflora (Walt.) Sarg.)	FAC/OBL	11	+	+	29	15	+	12	34
Panicum hemitomon J. A. Schultes.	OBL	44	+	89	+	72	+	80	+
Panicum verrucosum Muhl.	FACW	+				52	63	16	14
Pinus taeda L.	FAC	+	+	+	+	14	37	25	16
Pontedaria cordata L.	OBL			19	12				+
Psilocarya nitens (Vahl.) Wood	OBL					22			
Rhexia spp.	OBL/FACW		+	+		+	35	13	+
Rhynchospora sp. a	OBL/FACW			+			25		
Rhynchospora sp. b	OBL/FACW					+	19	+	
Scleria reticularis Michx.	FACW+	+	+	47		18	14		+
Sphagnum spp.	OBL	+	+				+	+	
Taxodium spp. (ascendans Brogngn., distichum (L.) Rich.)	OBL	+		+		12			
Triadenum spp.	OBL	+	+	+		+		20	
Utricularia spp.	OBL	66	56	42	73	+			+