VEGETATION CHANGE IN HERBACEOUS CAROLINA BAYS OF THE UPPER COASTAL PLAIN: DYNAMICS DURING DROUGHT

by

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(Under the Direction of REBECCA R. SHARITZ)

ABSTRACT

While hydrologic condition is not the only driver of plant species composition in herbaceous wetlands, it is considered to exert the strongest influence on species composition. The vegetation of thirteen herbaceous Carolina bay wetlands of the South Carolina Upper Coastal Plain was sampled during inundation; the seed bank of four of these bays was also sampled. In 2002, toward the end of a multi-year drought, vegetation was re-sampled and compared to the previous data sets. Bays generally had higher species richness by 2002, but the increase was not significant. All bays lost aquatic species while grasses increased dramatically in occurrence. Woody plants also established. Results were consistent with cyclic models of Carolina bay vegetation dynamics. There was little relationship between species that were in the vegetation and their occurrence in the seed bank. The vegetation of herbaceous Carolina bays appears to be resilient, cycling as climate-driven wetland conditions oscillate.

INDEX WORDS: Carolina bays, Depression wetlands, Drought, Plant colonization, Succession, Vegetation dynamics, Vegetation type

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DEDICATION

I dedicate this thesis to my family for their unconditional support, encouragement, and assistance.

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CHAPTER ONE

INTRODUCTION AND LITERATURE REVIEW

One of the chief goals of plant ecology is to understand the relationship between physical conditions and processes in the landscape and patterns of species composition, particularly over time. The more refined our understanding of how environmental variables influence the establishment, persistence, disappearance, or extirpation of plant species, the better our ability to predict species composition for given environmental parameters. Wetlands, given the complex array of legal issues attending their removal, construction, and protection, illustrate the necessity of understanding how the environment, often modified by humans, impacts an ecosystem. Knowledge of how wetland species interact with the environment and each other is crucial if society is to effectively balance development with the restoration and preservation of these systems. As developers and preservationists meet in court and tens of thousands of dollars are spent on individual mitigation projects, it remains important to continually further our understanding of what functional wetland ecosystems should "look like," and how to recreate characteristic, and clearly dynamic, vegetation composition.

To make ecologically sound decisions, we must have a strong foundation for illustrating how the vegetation of a natural wetland system is structured. Only then can we begin to make predictions about the results of disturbance, both natural and manmade, creative and destructive. However, it is important to act swiftly as by the 1980's wetland acreage in the U.S. had already decreased by 53% relative to pre-settlement figures, with particularly high losses in the South

(Johnson 1994). It is within the landscape of the southeastern U.S. that Carolina bays, an endemic depression wetland type, are found. There are perhaps 10,000 to 20,000 Carolina bays along the southeastern seaboard (Richardson and Gibbons 1993) and, like so many other wetland ecosystems, they are increasingly under threat from human development.

Carolina bays

Naturally disconnected from streams and adjacent basins, Carolina bays and similar depression wetlands are found on the Atlantic Coastal Plain of the southeastern United States from Delaware through Georgia. They can be as large as 3,600 hectares or smaller than a hectare (Sharitz and Gibbons 1982, Sharitz and Gresham 1998). There has not always been consensus regarding what traits distinguish a Carolina bay from other Coastal Plain depression wetlands, particularly when basin size is small (Lide 1997). Nevertheless, there is general agreement that larger Carolina bay basins are elliptical and curiously oriented from the northwest to the southeast. Sand rims often occur along the eastern and southeastern edge of basins, leading to speculation that strong prevailing winds and wave action may have been responsible for much of their development after the late Pleistocene (Kaczorowski 1977). However, the true nature of their origin remains unclear and, in fact, all bays may not have been formed contemporaneously (Soller and Mills 1991).

It has been reported that 97% of the Carolina bays in South Carolina have been disturbed, often by agriculture, sometimes by logging operations, and occasionally by both activities (Bennett and Nelson 1991). Many bays were drained with the advent of mechanical means of drainage in the late 1940’s and federal incentives existed for conversion of wetlands to croplands. Nineteen fifty-one aerial photography indicated that a majority (66%) of nearly 300

Carolina bays on the Savannah River Site (SRS), a 780 km^2 Department of Energy facility near Aiken, South Carolina, USA, were ditched (Kirkman et al. 1996). After widespread loss of wetlands in the Southeast, mirroring a national trend, federal programs such as the Farm Bills of the mid-eighties and early nineties began to offer incentives for the conservation of wetland areas. Yet, the vast majority of Carolina bays bear the imprint of human activity.

Soils

The soils of Carolina bays are frequently sand or sandy loam and may be underlain by clay at a depth of a meter or more (Gamble et al. 1977, Hodge 1985, Lide et al. 1995). Bays may burn during dry periods and thus much of the organic matter that accumulates on the surface is often lost, compounding their nutrient-poor character. However, in those bays that have not been exposed to frequent fire, an organic surface horizon may exist, sometimes at depths of greater than a meter, in the center of a basin (Frey 1950, Newman and Schalles 1990). Thus, some bay soils can be highly organic (>10%) and will retain nutrients when their relatively low pH is raised to 5.0 or higher (Clemson University 1982).

Even relatively small bays are not homogenous in terms of soil type and character (Reese and Moorhead 1996). Soil properties change along gradients of elevation and may be related to patterns in vegetation, as well as hydrologic condition. These spatial patterns can be at a rather fine scale and likely vary from bay to bay (Reese and Moorhead 1996).

Hydrology

Carolina bays, and depression wetlands in general, are largely dependent on seasonal and annual precipitation inputs and evapotranspiration losses (Schalles and Shure 1989). Bays may occasionally have a permanently flooded character that is in line with a lacustrine classification, but are more typically palustrine (Cowardin et al. 1979, Sharitz and Gresham 1998). Bays on the Upper Coastal Plain often hold the highest volume of water in the early spring with continual drawdown occurring throughout the summer. By early fall a bay may be completely dry. However, this regime is highly variable amongst bays and subject to wide climatic variation (Lide *unpublished data*). Some bays appear to be connected to shallow groundwater (Chmielewski 1996); there may be inflow when the water table rises to intersect the basin or there may be outflow as seepage during drier periods (Lide et al. 1995). It has been noted that the thick clayey layer underlying many bays may act as an aquiclude, rendering a bay a perched hydrologic system, isolated from the influence of groundwater. In contrast, Lide et al. (1995) reported that in at least one bay such a layer remained saturated and did not appear to fully restrict interaction with shallow groundwater. There remains a need for a more comprehensive understanding of the hydrology of Carolina bays, particularly the potential influence of shallow groundwater.

Water chemistry

In a study of 49 Carolina bays, Newman and Schalles (1990) reported that waters were generally soft (median Ca=1.69 mg/l) and acidic (median pH=4.6). Dissolved organic carbon concentrations averaged just over 17 mg/l and solute concentrations were considered to be low (1.07 meq/l). Further, this low solute concentration indicated that bays were receiving minerals chiefly from the atmosphere and not from weathering of substrate. However, Newman and Schalles (1990) also reported wide variability among bays and noted the variety of potential mineral sources in individual bays.

Vegetation

Carolina bays on the Upper Coastal Plain can be divided into two broad vegetation classes: woody and herbaceous. Woody systems are dominated by large, flood-tolerant trees such as *Nyssa sylvatica* Marsh., *Nyssa sylvatica* var. *biflora* (Walt.) Sarg., *Taxodium* spp., and *Liquidambar styraciflua* L. Herbaceous bays are often dominated by grasses, including *Panicum hemitomon* J. A. Schultes., *Leersia hexandra* Sw., and a variety of *Dichanthelium* spp. or additional *Panicum* spp. *Carex striata* Michx. can also be a large component of some herbaceous bays, as can *Nymphaea odorata* Ait., which is characteristic of wetter sites. Beyond this categorization, there have been several attempts to further divide bays, both within and amongst sites, based largely on plant composition (Schalles 1979; Hodge 1985; Schalles et al. 1989; Tyndall et al. 1990; Kirkman et al. 1996; De Steven and Toner 1997, 2004; Sharitz 2003).

Kirkman et al. (1996) described five types of bays on the SRS, identifiable from aerial photographs: herbaceous, pine forest, hardwood forest, mixed forest, and shrub systems. Herbaceous bays, which included occasional trees, encompassed wet meadow and floating aquatic habitats as well. Hardwood forest wetlands had a canopy of at least 95% hardwood species. Pine forest wetlands contained at least 95% pine species and may have been planted. Mixed forest wetlands had a canopy of pine greater than 50%, but less than 95%. Shrub wetlands appeared texturally distinct from forested basins in the aerial photographs, although they may have contained saplings of tree species. Approximately 40% of 299 bays identified in 1951 aerial photography of the SRS were herbaceous (Kirkman et al. 1996). Forested bays, less than 25% of all bays, were associated with former agricultural fields. By 1992, 67% of the bays were forested, many were highly disturbed, and some may have ceased to function as wetlands (Kirkman et al. 1996).

De Steven and Toner (1997, 2004) described six distinct bay vegetation types in bays on the Upper Coastal Plain, emphasizing the influence of hydrologic condition and designating a single characteristic or “diagnostic” species. Associated species, those that occurred in at least 75% of the wetlands of a particular type and/or at high relative abundances, were also noted. Open-water ponds were the largest systems, remaining wet throughout the year. *Nymphaea odorata* was considered to be the diagnostic species in this type and associated species included *Panicum hemitomon*, *Leersia hexandra*, and *Nyssa sylvatica* var. *biflora*, among others. Grass marshes were smaller and shallower than open-water ponds, but remained flooded for at least most of the year. The diagnostic species in grass marshes was *Panicum hemitomon*, co-occurring with *Nyssa sylvatica* var. *biflora*, *Rhexia* spp., and *Leersia hexandra*. Depression meadows had a variable hydrologic condition, remaining flooded some years and drying down in others. In these systems, soils were very sandy, organic matter content was low, and at least occasional groundwater inputs were suspected in some of the basins. The diagnostic species was considered to be *Leersia hexandra* with associated species including *Eleocharis melanocarpa* Torr., *Rhexia* spp., and *Bidens* spp. Wet forests were defined by the presence of *Nyssa sylvatica* var. *biflora* and characterized by shallow flooding for most of the year. These bays were often found at lower elevations, indicating potential groundwater inputs. Associated species in these systems included *Taxodium* spp. and *Cephalanthus occidentalis* L. Sedge marshes were morphologically similar to wet forests, although they tended to occur on river terraces and were slightly larger with sandier soils. In addition to the diagnostic *Carex striata*, *Nyssa sylvatica* var. *biflora*, *Cephalanthus occidentalis*, and *Panicum hemitomon* were associated species. Finally, mesic forests, defined by the presence of *Liquidambar styraciflua*, typically dried down by late May or early June. Similar to floodplain forests, these systems were thought to receive only surface water input, had clayey soils, and a high likelihood of past disturbance by farming or other means. Other woody species associated with these systems included *Acer rubrum* L., *Smilax* spp., and *Ulmus americana* L.

De Steven and Toner (1997, 2004) pointed out that these descriptions were approximations and may represent a snapshot in time of a successional sequence. For instance, bays may change vegetative character as hydrologic condition changes. Yet, the categorizations developed by De Steven and Toner (1997, 2004) are useful and characterize definite and recognizable vegetation types under given hydrologic and soil conditions.

General within-bay classifications are somewhat problematic given the wide range of habitat variability in individual bays. Several studies have reported that the influence of elevation and hydrologic condition can result in broadly definable zones (Kelley and Batson 1955, Hodge 1985, Tyndall et al. 1990). For example, Hodge (1985) found seventeen different species associations in eight Carolina bays with one bay, Craig's Pond, located on the boundary of the SRS, containing six distinct types. In Craig's Pond, Hodge (1985) described, from an upland pine border, successive associations of 1.) *Andropogon virginicus* L.-*Aristida affinis* (Schult.) Kunth., 2.) *Rhynchospora tracyi* Britt.-*Lobelia boykinii* T. & G., 3.) *Nymphaea odorata*.-*Eleocharis robbinsii* Oakes, 4.) *Eleocharis equisetoides* (Ell.) Torr.-*Nymphaea odorata*, 5.) *Panicum hemitomon*-*Pontedaria cordata* L., and 6.) *Nymphaea odorata*-*Brasenia schreberi* Gmel. At a second site, Ellenton Bay, Hodge, proceeding from a shrub border to a *Decodon verticillatus* (L.) Ell.-*Panicum hemitomon* center, noted adjacent *Panicum hemitomon*-*Panicum hirsutum* Sw., *Nymphaea odorata*-*Leersia hexandra*, and *Juncus canadensis* J. Gay ex Laharpe-

Nymphaea odorata associations. By 1990, Kirkman (1992) noted differences in the associations mapped by Hodge in Craig's Pond and Ellenton Bay, as the wet period during which Hodge sampled in the late 1970's and very early 1980's had been succeeded by several years of below average precipitation.

Tyndall et al. (1990) also characterized zones of distinct composition using ordination techniques in six Carolina bays in Maryland. Sites tended to have higher, perimeter zones dominated by *Leucothoe racemosa* (L.) Gray, adjacent areas characterized by grasses such as *Panicum hemitomon* and *Panicum verrucosum* Muhl., and interiors dominated by *Rhexia virginica* L. *Carex striata* occurred in the lowest portions of some bays, but in other instances was found along the perimeter.

Vegetation and seed bank characteristics

Species richness in the vegetation of Carolina bays has been reported as comparable to that of other wetland types, typically between 10 and 35 taxa (Keough et al. 1990; Poiani and Dixon 1995; De Steven and Toner 1997, 2004). However, in three bays, Kirkman (1992) and Kirkman and Sharitz (1994) observed around 60 species and, in another, which was burned routinely, 105. Bay seed banks are thought to have the highest species richness of any freshwater wetland type; Kirkman (1992) and Kirkman and Sharitz (1994) observed 107 species in one bay and 71-91 in three other sites. While the richest bay was burned prior to sampling, even the richness of the seed banks of the other three wetlands was markedly high. Poiani and Dixon (1995) found somewhat fewer species in bay seed banks, from 16 to 35 taxa, but reported little resemblance between the composition of the seed bank and extant vegetation, consistent with Kirkman (1992) and Kirkman and Sharitz (1994). Germination from the seed bank, and resultant richness in the vegetation, appears to be highest in Carolina bays when hydrologic condition is fluctuating and lower during absolutely wet or dry conditions (Collins and Battaglia 2001, Battaglia and Collins *in review*).

Vegetation Dynamics

Studies have verified that hydrologic condition is the main driver influencing species composition in Carolina bays, resulting in distinct differences amongst wetlands (De Steven and Toner 1997, 2004; Collins and Battaglia 2001). Therefore, bay vegetation is a function of the interaction of annual and seasonal meteorological patterns and the physical features of a basin; the resultant hydrologic regime largely defines the vegetation of the six bay types described by De Steven and Toner (1997, 2004).

Yet, the plant species composition of bays is also related to landscape-level factors such as soil type (De Steven and Toner 1997, 2004). Deep sandy soils may increase throughflow of water, resulting in a drier basin and an increased frequency of upland vegetation, while a clay hardpan facilitates water retention and the existence of hydrophytic species. Basin size and landscape setting are also related to composition, influencing hydrologic condition at within-bay and regional levels and determining the available species pool (De Steven and Toner 1997, 2004). Finally, disturbance, both natural and human-induced, can shuffle composition or alter it completely (Kirkman 1995). Fire, for example, is a critical factor in removing woody species from bays, creating opportunities for the establishment of herbaceous vegetation. In many cases, human-induced disturbance such as drainage is the most dramatic driver of species composition and, indeed, is often responsible for the complete loss of wetland vegetation.

Within-bay shifts in vegetation patterns

The first study describing how climatic cycles might alter vegetation patterns within Carolina bays was by Kirkman (1992, 1995). By interpreting aerial photos, Kirkman was able to map vegetation patterns in four bays. Contour maps and water depth data made it possible to closely correlate vegetation type with hydrologic condition. Kirkman was then able to compare maps of vegetation patterns in 1990, following ten years of below-average precipitation, to maps developed by Hodge (1985) in 1978. It was found that vegetation had changed in similar ways in all four sites. First, floating aquatic species such as *Nymphaea odorata* and *Brasenia schreberi* declined sharply. Second, upland species, particularly *Pinus taeda* L. and *Rubus* spp., had moved into the basins as conditions became drier. Finally, the position of dominant grass species within basins changed, as did their abundances. *Panicum hemitomon*, for example, moved into deeper parts of two basins and declined in the others. *Leersia hexandra* generally declined and was replaced by either *Panicum hemitomon* or, in one bay, *Manisuris rugosa* (Nutt.) Kuntze.

Based on her observations, Kirkman (1992, 1995) envisioned a cyclic model of vegetation dynamics in Carolina bays. In such a model, bays that are flooded for long duration and to a depth of >1.5m will be dominated by aquatic species that can germinate under water such as *Potomogeton* spp. and *Nymphaea odorata*. As bays dry and water depth declines to 1.0-1.5 m, *Leersia hexandra,* which is better able to elongate its stem above high water than other perennial grasses, particularly *Panicum hemitomon*, may become dominant. *Panicum hemitomon* will dominate *Leersia hexandra* as water level continues to decrease, as will *Manisuris rugosa*, where present. Overall species richness is predicted to increase during drawdown as recruitment from the seed bank increases and previously submerged soil is exposed. Drought-related disturbance such as fire can also contribute to greater richness. Later, if drier conditions continue, woody species such as *Pinus taeda* and upland successional species, including *Andropogon virginicus*, will encroach. Upon re-inundation, the system is predicted to "reset" to a system dominated by distinct zones of perennial grasses and aquatic species. It should be noted that additional disturbance, including drainage, might act to alter the successional cycle.

Kirkman's (1992, 1995) study of Upper Coastal Plain systems again points out the way by which vegetation and hydrologic regime are inextricably linked in Carolina bays. Focusing on vegetation maps developed from air photos and detailing the response of a few important perennial grass species, Kirkman's study laid the groundwork for a more descriptive investigation of vegetation dynamics within bays. By utilizing floristic inventories and a comprehensive analysis of how a variety of species behave over time, our understanding of how bay vegetation responds to hydrologic variation can be deepened.

Vegetation-environment relationships across Carolina bays

In 1993 and 1995 De Steven and Toner (1997, 2004) surveyed 57 depression wetlands to determine patterns of vegetation composition, explore environmental factors that might influence species composition, and assess the potential predictive value of landscape setting as related to key environmental factors. Bays were selected quasi-randomly, yet were between 0.4 ha and 20 ha in size. Also, each basin had to contain a functional wetland that exhibited characteristic vegetation and hydrologic conditions. Sites were categorized according to soil type and landscape position within the sandhills, loam hills, or river terrace environments of the South Carolina Upper Coastal Plain. Bays were also grouped according to hydroperiod; in 1995, when the majority of the vegetation sampling was completed, annual rainfall was 26% above average (1506 mm). While species dominance was most related to hydrologic condition, soil type, basin size, prior disturbance, and landscape setting all had some correspondence with vegetation. Expanding on Kirkman (1992, 1995), a chiefly cyclic model was described, although directional succession was considered possible in mesic systems in which hardwoods established.

The De Steven and Toner (1997, 2004) study is a valuable examination of the way a variety of factors, but most importantly hydrologic condition, determines vegetation composition in Carolina bays. This work can be used in conjunction with current inventories of previously sampled basins to quantify how dominant species have changed during a climatic shift from a relatively wetter period to one of prolonged drought. Such information can be used to better understand how vegetation types of Carolina bays change with hydrologic variation.

Current study

Precipitation patterns in South Carolina are cyclic, with major droughts occurring on the order of decades. For example, yearly deficits of more than 250 mm relative to average annual precipitation occurred in the mid-1920's, the early-1930's, and the mid-1950's (National Oceanic and Atmospheric Administration 2003). In June 1998, South Carolina entered a continuous drought that, lasting into the fall of 2002, was quite prolonged (Kiuchi 2002). During this time Carolina bays on the SRS were under a hydrologic regime that left them much drier than normal. In fact, nearly all Carolina bays on the SRS were dry by the fall of 2001. By comparing previous surveys of the vegetative composition of selected Carolina bays with surveys conducted during the 2002 field season, it was possible to better understand the impact of specific hydrologic regimes and, in particular, how the cyclic nature of climate impacts vegetation dynamics.

In the summer of 2002, a subsample of 10 bays on the SRS used by De Steven and Toner (1997, 2004) in their initial study was selected. Only predominantly herbaceous bays were included and all sites had to be free of recent disturbance within or near the basin. Five sites (Bays 9, 26, 27, 136, and 165) were located within the river terrace landscape, three (Bays 78, 87, and 106) were in the sandhills, and two (Bays 40 and 127) were in the loam hills. According to the vegetation categories assigned by De Steven and Toner (1997, 2004), four bays (Bays 26, 27, 87, and 106) were classified as depression meadows, two (136 and 165) were sedge marshes, two (Bays 9 and 127) were grassy marshes, and two (40 and 78) were open-water ponds. Thus, there was a cross-section of bay types and landscapes, enabling an investigation into the effect of drought within vegetation types as described by De Steven and Toner (1997, 2004).

In 1999, one year after drought began, Burbage (2004) sampled the vegetation in four large herbaceous Carolina bays [Bay 3 (Flamingo Bay), Bay 31 (Dry Bay), Bay 78 (Sarracenia Bay), and Bay 176 (Ellenton Bay)] on the SRS along permanent transects to determine what factors were influencing the pattern and distribution of species across and among basins. At the time of sampling, all four bays held considerable water, though one (Bay 78) was rapidly drying. In spring 2000, Burbage sampled the seed bank of each study bay extensively, monitoring germination well into 2001. In 2002, a revisiting of the bays sampled by Burbage provided vegetation data over a four-year interval during which bays were drawing down as drought conditions worsened. The combination of these three data sets allowed an investigation into the relationship between extant vegetation across wet and dry periods and the role the seed bank played in determining vegetation composition at either end of the hydrologic spectrum.

Objectives

The first chapter of this thesis is an investigation of vegetation change within vegetation types of ten herbaceous Carolina bays of the Upper Coastal Plain during drought. Specifically, analyses addressed these questions: 1.) How had the composition of herbaceous Carolina bay vegetation types responded to the drought? 2.) Did patterns of change vary with initial vegetation types? 3.) Can the response of vegetation types be generalized as a tool for prediction of change in bay vegetation during dry periods?

The second chapter examines the relationship between extant vegetation and the seed bank throughout wet and dry hydrologic regimes. Questions included: What was the response of vegetation in herbaceous Carolina bays through a period of fluctuating hydrologic conditions? Were species observed in the vegetation in 1999 well-represented in the seed bank of 2000? What role did the seed bank play in influencing the vegetation of bays during the 2002 drought?

Together, these chapters provide a useful framework for determining what the range of vegetation composition of a particular Carolina bay might be, how the seed bank interacts with vegetation, and how species composition can be expected to change if hydrologic condition is altered. Only by gaining such an understanding of vegetation dynamics can management of herbaceous Carolina bays of the Upper Coastal Plain proceed on a sound ecological footing.

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CHAPTER TWO

VEGETATION DYNAMICS IN HERBACEOUS CAROLINA BAYS OF THE SOUTH CAROLINA UPPER COASTAL PLAIN: CHANGES WITHIN VEGETATION TYPES FOLLOWING A MULTI-YEAR DROUGHT[1]

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INTRODUCTION

The general effects of dry conditions on the plant community composition of herbaceous wetlands are well-documented (van der Valk and Davis 1978, van der Valk 1981, Greening and Gerritsen 1987, Kirkman 1992, Kirkman et al. 2000). In herbaceous wetlands, as water levels draw down, plant assemblages shift as species that can tolerate lower water availability establish and expand while those that would be present under wetter conditions decline and perhaps disappear entirely. In the most extreme cases, dry conditions can permanently alter an entire ecosystem, initiating or speeding hydrarch succession and resulting in the eventual loss of wetland vegetation (Vogl 1969, Winkler 1988). However, even when less severe, the signature of an extended drawdown may be seen in a wetland plant community years after wetter conditions return as upland species remain in dry refuges and tree seedlings that established during the drought persist (Kirkman 1992).

Since wetland plant composition is influenced greatly by hydrologic condition (van der Valk 1981; Schalles and Shure 1989; Mitsch and Gosselink 2000; Collins and Battaglia 2001; De Steven and Toner 1997, 2004), it may be hypothesized that changes in the composition of wetland plant communities during drought can be predicted. Indeed, Weiher and Keddy (1995) reported that, of several environmental variables, water depth and fluctuation (i.e. flooding duration) were of primary significance in affecting experimental wetland plant community development and composition (although soil fertility and leaf litter were also of some importance). Climatic drought, then, as an agent of disturbance in wetlands, alters plant communities in quantifiable ways (Keddy 2000). However, relatively little information exists regarding drought-related change in herbaceous Carolina bays of the southeastern Coastal Plain.

Carolina bays

Naturally disconnected from streams and adjacent basins, Carolina bays and similar shallow elliptical depression wetlands are found on the Atlantic Coastal Plain of the southeastern United States from Delaware through Georgia. These depressions can be as large as 3,600 hectares or smaller than a hectare (Sharitz and Gibbons 1982, Sharitz and Gresham 1998). There has not always been consensus regarding what traits distinguish a Carolina bay from other Coastal Plain depression wetlands, particularly when basin size is small (Lide 1997).

Bays are largely dependent on seasonal and annual precipitation inputs and evapotranspiration losses (Schalles and Shure 1989) and thus their hydrologic condition may fluctuate. On the Upper Coastal Plain, bays often hold the highest volume of water in the early spring with continual drawdown occurring throughout the summer. By early fall a bay may be completely dry. Yet, there remains a need for a more comprehensive understanding of the hydrology of Carolina bays, particularly the potential influence of shallow groundwater.

Climatic oscillation

Precipitation patterns in the Upper Coastal Plain, and South Carolina in particular, are cyclic, with major droughts occurring on the order of decades. For example, yearly deficits of more than 250 mm relative to average annual precipitation occurred in the mid-1920’s, the early-1930’s, and the mid-1950’s (National Oceanic and Atmospheric Administration 2003). Other, less severe deficits were recorded in the late-1930’s, the late-1970’s, and the late-1980’s. While the mid-1990’s was a time of somewhat higher than average precipitation, particularly during the El Niño event of 1997 and early 1998, from June 1998 through the duration of the present study (September 2002), South Carolina was in a continuous drought (Kiuchi 2002). By August 2002, the drought had been designated as “extreme” throughout all of South Carolina (Figure 2.1; South Carolina Department of Natural Resources 2003).

Previous studies

The first attempt to describe how climatic cycles might alter vegetation patterns in Carolina bays was by Kirkman (1992, 1995) in grass-dominated herbaceous systems of the Upper Coastal Plain. In 1990, following ten years of below-average precipitation, Kirkman utilized aerial photos, contour maps, and water depth data to relate vegetation type to hydrologic condition in four bays ranging from 4.9-86.6 ha in area on the Savannah River Site (SRS), a 780 km^2 Department of Energy facility near Aiken, South Carolina, USA (Figure 2.2). Kirkman envisioned a cyclic model of vegetation dynamics in these herbaceous Carolina bays. In the model, as a bay dried and water depth decreased, floating and submersed aquatics declined and *Leersia hexandra* Sw., which had survived prolonged deep inundation by elongating its stem above water, expanded to become dominant. With continued drying, *Leersia hexandra* declined and other perennial grasses, particularly *Panicum hemitomon* J. A. Schultes, became dominant. Overall species richness was predicted to increase with drying as recruitment from the seed bank increased and previously submerged soil was exposed. Related disturbance such as fire could also contribute to greater richness. If drought ensued, woody species such as *Pinus taeda* L. and upland successional species, including *Andropogon virginicus* L., encroached. Once wetter conditions returned, species that could not tolerate inundation disappeared and aquatics re-established. This model, while specific to grass-dominated herbaceous systems of the Upper Coastal Plain, provided a useful illustration of bay vegetation dynamics.

In 1993 and 1995, De Steven and Toner (1997, 2004) surveyed 57 depression wetlands on the Upper Coastal Plain, 35 of which were on the SRS, encompassing a range of vegetation community types. Precipitation was 120 mm below average in 1993, but 210 mm above average in 1992, following an El Niño event (Figure 2.1; Southeastern Regional Climate Center); as rainfall had been above average in 1995, all bays remained flooded during the vegetation surveys (De Steven and Toner 1997, 2004). Sites could be differentiated by relatively few species, with the wettest dominated by the aquatic *Nymphaea odorata* Ait. Specific clonal grasses or sedges characterized herbaceous bays that held less water. Based on these patterns, De Steven and Toner (1997, 2004) confirmed that dominant species most closely corresponded to hydrologic regime and described systems that ranged from deeply flooded open-water ponds to drier shallow grass and sedge marshes and depression meadows (Table 2.1).

De Steven and Toner (1997, 2004) suggested a model that expanded upon that of Kirkman (1992, 1995) and Kirkman et al. (2000) in which, unless there was widespread establishment of hardwoods during drought, the vegetation of herbaceous bays cycled continuously with variability in hydroperiod. Subsequent fluctuations in climate have provided an opportunity to confirm and refine these cyclic models and increase our understanding of how Carolina bay vegetation responds to drought, particularly within the vegetation types established by De Steven and Toner.

Current study

In July and August 2002, the vegetation of 10 herbaceous bays on the SRS used in the De Steven and Toner (1997, 2004) study was re-sampled. The resultant long-term data set, encompassing periods of average hydrologic conditions and drought, was analyzed to address these questions: 1.) How had the composition of herbaceous Carolina bay vegetation types responded to the drought? 2.) Did patterns of change vary with initial vegetation types? 3.) Can the response of vegetation types be generalized as a tool for prediction of change in bay vegetation during dry periods?

METHODS

Site description

The South Carolina Upper Coastal Plain receives an average of 1217 mm of precipitation per year, chiefly as rainfall during the spring and summer months (National Oceanic and Atmospheric Administration 2003). The climate is humid subtropical, with long, hot summers and short, mild winters. Average temperature is 7.3° C in January and 25.6 C° in July (National Oceanic and Atmospheric Administration 2003).

The ten study sites were Carolina bay wetlands located on the SRS. Bays were dominated primarily by herbaceous vegetation, ranged in area from 1.2-7.5 ha, and were undisturbed by recent fire or logging operations within or near the basins (Table 2.1). Seven of the bays in the study had been sampled in early-July to mid-August of 1993 (Bays 9, 40, 78, 87, 127, 136, and 165) and three in July of 1995 (Bays 26, 27, and 106). Hereafter this data set will be designated “1993.”

Field methods

Water depth was measured via staff gauges placed in the deepest point of each bay. These gauges were read at weekly intervals from April 1995 to December 1998, then monthly until 2001, and bi-monthly beginning in April 2001. Due to sampling omission, the total number of water level measurements differs among bays. While the vegetation of the bays in the De Steven and Toner (1997, 2004) study was surveyed prior to the start of this comprehensive monitoring, it was extrapolated that inundated conditions had been present for an extended period; cumulative rainfall was 4% above average from 1990-1993, as it was from 1995-1998 (Figure 2.1; Southeastern Regional Climate Center 2003) when bays remained flooded (Lide *unpublished data*)

Bay vegetation was surveyed in late-July and early-August 2002 following the protocols employed by De Steven and Toner (1997, 2004). A modified line-intercept sampling method across an entire basin ensured that most potential vegetative zones were included. One transect was placed across the longest axis of a bay 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 a 1 m line segment were recorded. The 1 m sampling length was extended vertically to encompass mid-story and canopy tree cover. Incidental species observed outside of sampling locations were also recorded. Disparities in measuring sampling distances resulted in differences in the overall number of sampling points between 1993 (*n*=404) and 2002 (*n*=370).

In accord with the De Steven and Toner (1997, 2004) study, several species were combined at the generic level. These included *Diodia*, *Erianthus*, *Eupatorium*, *Hypericum*/*Triadenum*, *Pinus*, *Rhexia*, and *Rhynchospora* (three separate groups of this genus were created: large, robust species; small, obligate wetland species; and small, facultative wetland species). In the present study, no distinction was made between *Nyssa sylvatica* Marsh. and *Nyssa sylvatica* Marsh. var. *biflora* (Walt.) Sarg. as many individuals of this genus were small seedlings and difficult to distinguish. Taxonomy followed Radford et al. (1968) and

Godfrey and Wooten (1981). Species vouchers collected during the 2002 vegetation survey were deposited in the University of Georgia Herbarium.

Data analyses

Bays were grouped by herbaceous vegetation type based on dominant species in 1993 and included open-water pond, grass marsh, depression meadow, and sedge marsh (Table 2.1; De Steven and Toner 1997, 2004). The number and percent of months that a bay contained standing water in the deepest point was calculated for each bay for each year and summarized for the period prior to (1995-1998) and during (1999-2002) the drought; a mean for each vegetation type was determined for both periods. Significant differences between the percent of months of record for which a bay was flooded prior to and during the drought were tested using a Wilcoxon rank sign test.

Mean monthly water depth was determined for each bay for each year and an overall mean calculated for each bay for the total pre-drought and drought record. Significant differences in mean monthly water depth in each period were determined via rank sign test. An overall mean monthly depth for the bays in each vegetation type during each period was also calculated.

For each study year, the number of species present in each bay was determined and the mean within vegetation types calculated. Differences in species richness between years were tested by rank sign test. The percent of species in both 1993 and 2002 was also determined for each bay. Finally, the total number of species within bays of a particular vegetation type was determined for 1993 and 2002 and the number and percent of the total taxa observed in both years calculated for each type.

Percent frequency of each species was calculated for each site by dividing the number of sampling locations at which a species was observed by the total number of sampling locations in a bay. Incidental species were assigned an arbitrary percent frequency designation of 0.2% for a site (De Steven and Toner 1997, 2004). Because vegetation types were represented by relatively few bays, sampling points from all bays within a vegetation type were compiled and overall species frequencies calculated. Species occurring at high frequencies within a vegetation type were determined by calculating the percent of total sampling points within a type at which a species was recorded. For each study period, species that occurred with a frequency of ≥15% in each vegetation type were listed, as were species that had increased or decreased in frequency by at least 15% of sampling points within a type by 2002. National Wetland Indicator (NWI) category was assigned to each of these species, and vegetation change relative to the indicators characterized within vegetation types.

For both study years, species lists were combined for each possible pair of vegetation types and the number and percent of common taxa calculated. Chi-square tests were performed to determine if the number of shared species between pairs of vegetation types was significantly higher or lower by 2002 than expected, indicating convergence or divergence during the drought.

Trends in species composition across sites and years were explored using non-metric multidimensional scaling (NMDS). NMDS depicts objects (i.e. bays) in a manner by which their distances from one another correspond with their rank-order dissimilarities while minimizing stress, the disparity between those distances in the ordination and the calculated rank-order dissimilarities (Kruskal 1964). Species with fewer than two occurrences in the data set were removed and each remaining species was standardized to its maximum frequency across all bays to prevent the most frequent species from swamping the ordination. Dissimilarities were then calculated using the Bray-Curtis index (Bray and Curtis 1957). The combination of standardizing to species maxima in conjunction with Bray-Curtis dissimilarities is considered to be one of the most effective techniques for ordination of community data (Faith et al. 1987, Sandercock 1997, Battaglia et al. 2002). The species compositions of all sites in both 1993 and 2002 were ordinated together (n=20).

An analysis of similarity (Clarke 1993) was performed to determine if groups of sites within the NMDS ordination were significantly different. This analysis tests whether the compositional dissimilarity within supposed groups in an ordination is significantly smaller than that between groups. A permutation procedure (1000, in this instance) was performed to determine whether a test statistic, Clarke's R, was significantly different from zero, the null hypothesis of no dissimilarity between groups (Minchin 1989, Clarke 1993). This analysis was done by assuming that the vegetation types defined by De Steven and Toner (1997, 2004) represented distinct bay groups in the ordination. Each of the four groups of vegetation types included the composition of a site in both 1993 and 2002 to increase the number of "objects" in each group and determine if vegetation types remained compositionally distinct over time. *P*-values for individual pairwise tests among vegetation types were Bonferroni-corrected to reduce the likelihood of spurious significant results, although this technique has been considered extremely conservative (Perneger 1998). Thus, to achieve a level of significance of α=0.05, *p*-values had to be ≤0.008 (α=0.05/n; n=number of pairwise comparisons).

The percent of months with standing water and the average water depth were used as potential explanatory variables for vector fitting in the NMDS ordination. Vector fitting is a multiple regression technique that finds the direction across an ordination with which sample variables have the highest correlation with axis scores (Dargie 1984, Faith and Norris 1989, Kantvilas and Minchin 1989). Random permutation of variables simulates the null hypothesis of no trend and tests the significance of the correlation. When presented within an ordination, vector lengths are proportional to the values of the correlation coefficient (r). Further, angles between vectors indicate whether variables are correlated, with 0° representing complete correlation and 90° no correlation. The percent of months a bay was flooded and the average water depth during the pre-drought period were assigned to the species composition in 1993 and calculations for those variables during the drought assigned to the 2002 composition. Ordination, analysis of similarity tests, and vector fitting were done using DECODA (Minchin 1989).

RESULTS

All bays were flooded for more than 91% of the months prior to the drought (1995-1998), but two bays were dry for more than half of the drought period (1999-2002); three bays were dry throughout 2002 (Table 2.2). The difference in the percent of months flooded between these periods was significant (rank sign test p=0.002). Open-water ponds held water for the greatest mean percent of months pre-drought (99%), yet even the driest types, sedge marshes and depression meadows, were wet for nearly all of the record (Table 2.2). During the drought, grass and sedge marshes contained water for roughly 70% of the months while open-water ponds and depression meadows were wet for approximately half the record.

Mean water depth amongst bays pre-drought ranged from 0.35 m to 1.65 m and dropped to between 0.10 m and 0.66 m during the drought; only three bays retained a mean depth ≥10 cm at the deepest point by 2002 (Table 2.3). The mean depth between these periods was significantly different (rank sign test p=0.002). Open-water ponds had the highest mean water depth (1.16 m) prior to the drought while grass marshes and depression meadows had the lowest (0.50 m; Table 2.3). During the drought, open-water ponds still had the highest mean depth (0.46 m) and depression meadows the lowest (0.17), but mean depth was more similar among vegetation types.

In 1993, species richness per bay ranged from 7-33 (mean=18); by 2002 the range was 13-39 (mean=23; Table 2.4). Some bays exhibited substantial increases in richness, but this trend was not significant overall (rank sign test p=0.131). The percent of species observed in both years ranged from 12-42% with a mean of 25% (Table 2.4). Within vegetation types, depression meadows had the most species (49) in 1993, while open-water ponds had the fewest (27). By 2002, the combined species richness of all depression meadows was still 49, although only about one-quarter of these species was present in 1993 (Table 2.4). Open-water ponds had accumulated the most additional species (21) during the drought and had a total richness of 48. Sedge marshes had the fewest species (25) by 2002 (Table 2.4). Across the study period, sedge marshes retained the highest percentage of species (36%) between years, while open-water ponds had the lowest (23%).

Floating aquatic species disappeared from all bays between 1993 and 2002, although the species lost were sometimes unique to the vegetation type (Table 2.5). By 2002, in open-water ponds, *Panicum hemitomon* was the most frequent species, observed at 72% of sampled points. Other grasses, particularly *Panicum verrucosum* Muhl., *Andropogon virginicus*, and *Dichanthelium wrightianum* (Scribn.) Freckmann, recorded at one-fifth to one-half of sampled locations by 2002, also increased markedly (Table 2.5). In grass marshes, *Panicum hemitomon* declined somewhat, yet remained the most frequent species throughout the drought, detected at 80% of points. Woody species, including *Pinus taeda*, *Cephalanthus occidentalis* L., and

Liquidambar styraciflua, became more frequent and were found at one-fifth to one-quarter of sampled points, although only *Pinus taeda* increased substantially (Table 2.5). Grass marshes lost *Sphagnum* sp. and *Juncus canadensis* J. Gay ex Laharpe, both previously frequent, while *Panicum verrucosum* and a forb, *Triadenum* sp., increased by 16% of sampled locations. In depression meadows, *Leersia hexandra* declined by 27% of points during the drought, yet remained the second most frequent species, while *Panicum verrucosum* established and became most frequent, detected at 63% of sampled points (Table 2.5). *Pinus taeda*, *Rhexia* sp., and *Andropogon virginicus* increased by approximately one-third of locations and were among the most frequent species overall, as was *Dichanthelium wrightianum*. Vegetation in the sedge marshes was relatively stable, with *Carex striata* Michx. and *Nyssa sylvatica* remaining among the most frequent species (75% and 34% of sampling points, respectively, by 2002; Table 2.5). With the exception of *Utricularia* sp., no species substantially increased or decreased in sedge marshes.

Across all vegetation types, 11 of the 13 records of frequent species in 1993 for which NWI category could be assigned were obligate wetland species. Since the same species might be frequent in more than one vegetation type, this represented seven different taxa (Table 2.5). By 2002, only five of the 19 records of frequent species were obligate wetland plants (four taxa). Of six species that increased by ≥15% of sampled locations, only one was a wetland obligate, *Panicum hemitomon*, in open-water ponds (Table 2.5). Other species establishing or increasing were a variety of facultative and facultative wetland species. Aside from the non-vascular *Sphagnum* sp., each of the eight records (four taxa) of a species declining by ≥15% of points within a vegetation type during the drought was an obligate wetland species (Table 2.5).

In 1993, grass and sedge marshes had by far the highest percentage (36%) of shared species, although not the highest number (16); open-water ponds and sedge marshes had the lowest number (10) and percentage (20%) (Table 2.6a). By 2002, grass marshes and depression meadows shared the most species (23; 36%), while sedge marshes shared the fewest with both open-water ponds (14; 21%) and depression meadows (13; 21%) (Table 2.6b). Yet, no pair of vegetation types had more or fewer species in common by 2002 than would be expected ($\chi^2<3.84$ for all pairs; Table 2.7).

A two-dimensional NMDS ordination (stress=0.21) was obtained from ten out of ten random starts and selected for analysis (Figure 2.3). A three-dimensional ordination did not substantially decrease stress (0.12) or aid interpretation. Prior to the drought, bays appeared at the top of the ordination (Figure 2.3). Bays shifted downward by 2002, with all but one below any bay in 1999.

Significant differences between groups, which included species compositions in both 1993 and 2002 for bays in each vegetation type, were found within the ordination for half of the six possible pairs of vegetation types (Clarke's R=0.50, $p<0.001$). The dissimilarities between depression meadows and all other vegetation types were significant at the Bonferroni-corrected value of $\alpha=0.008$ (Table 2.8). There were no significant differences between the other vegetation types.

Vector fitting showed a significant correlation across the ordination for percent of months flooded (r=0.78, $p<0.001$) and average water depth (r=0.58, $p=0.013$; Figure 2.3). The angle between these vectors was 14.8°, indicating high correlation between the two variables themselves. Shifts in bay positions in the ordination during the drought were approximately parallel to these vectors (Figure 2.3).

DISCUSSION

Given that Carolina bays are subject to seasonal drawdown, the duration of flooding prior to the drought, even before the El Niño event, was surprisingly high in all vegetation types. However, despite being flooded for nearly the entire pre-drought period, open-water ponds and depression meadows were flooded for considerably fewer months during the drought than grass and sedge marshes. This suggests that the open-water ponds and depression meadows were less hydrologically stable. Open-water ponds had the greatest mean water depth during the drought, but this was a result of high water levels early in the record, just after the El Niño. Depression meadows had the lowest mean water depth during the drought, consistent with their more variable flooding duration.

Generally, the number of species per bay increased during the drought, in accord with the predictions of Kirkman regarding Carolina bays (1992), findings of McCarthy (1987) in intermittent ponds, and reported trends in wetland seed bank germination in prairie potholes (van der Valk and Davis 1978). However, this increase was not significant overall. In one bay, species richness increased three-hundred-fold during the drought, but in three bays richness decreased, though declines in two were modest (one species). Although the line-intercept surveying method may not detect all species present, and thus render low richness estimates, the number of species recorded in this study was not vastly different from that in most studies of Carolina bays in the Upper Coastal Plain that utilized more intensive line-intercept protocols (Keough et al. 1990) or plot-based methods (Burbage 2004, Mulhouse et al. *in prep.*). It was unclear if, in the early stages of the drought, richness might have increased significantly, then decreased as drawdown progressed and the drought became extreme. Within vegetation types, trends in species richness varied during the drought. Open-water ponds and grass marshes exhibited increases, sedge marshes showed a decrease, and depression meadows, which had the highest overall richness in both 1993 and 2002, showed no change.

Seed bank studies in Carolina bays have shown decreased richness in seed bank expression in flooded or dry conditions relative to a gradual hydrologic gradient (Battaglia and Collins *in review*). Further, in a New England salt marsh, plant species richness was highest in an intermediate upper middle intertidal zone, where physical conditions were mitigated (Hacker and Bertness 1999); and Mitchell and Niering (1993) found little difference in species richness in a topogenic bog prior to and during extensive flooding. Thus, previous descriptions of substantial increases in richness under drier conditions (i.e. van der Valk and Davis 1978, McCarthy 1987, Kirkman 1992) may be more generally applicable to intermittent drawdown or the early stages of hydrologic change. Yet, low species richness has been documented in bay communities dominated by *Panicum hemitomon* or *Carex striata* regardless of hydrologic regime (Tyndall et al. 1990).

Even though the increase in species richness for all bays combined was not significant during the drought, species turnover was considerable. Less than 50% of species sampled in any bay were present in both 1993 and 2002. Within vegetation types, less than one-third of species were common to both years. This change in composition demonstrates that a majority of the potential species pool may be unable to persist throughout a complete hydrologic cycle. Yet, species that disappear from the standing vegetation in the absence of a suitable environment may remain in the seed bank (van der Valk 1981, Mulhouse et al. *in prep*). van der Valk and Davis (1978) also reported substantial shifts in prairie pothole vegetation during drawdown and subsequent reflooding; only about 25% of species germinating in moist or submersed treatments survived in both.

It was not surprising that of the most frequently detected species in 1993, aquatics such as *Utricularia* sp. and *Nymphaea odorata* disappeared from every vegetation type during the drought. However, dominant emergent grasses were present both years and consistently among the most frequent species. For example, *Panicum hemitomon* or *Leersia hexandra* were among the most frequent species in both study years in every vegetation type except sedge marshes. As predicted by Kirkman (1992, 1995), *Leersia hexandra* declined where it had been most frequent, the depression meadows. However, *Leersia hexandra* still occurred frequently in depression meadows by 2002 and its decline could not be attributed to competition with *Panicum hemitomon* (Kirkman 1992, 1995), which remained infrequent. Additional grasses, including *Panicum verrucosum*, *Andropogon virginicus*, and *Dichanthelium wrightianum*, all became among the most frequently occurring species in one or more types during the drought. In sedge marshes, *Carex striata*, also a graminoid, was frequent both years.

Woody species, often observed as seedlings, were dynamic during the drought and influential in all but open-water ponds. Prior to the drought, *Nyssa sylvatica*, observed in sedge marshes, was the only woody species occurring frequently in any vegetation type. By 2002, *Pinus taeda* and *Liquidambar styraciflua*, amongst other woody species, became frequent in grass marshes and depression meadows, while *Nyssa sylvatica* increased in sedge marshes.

Overall, nearly all the most frequent species during the drought and ten of fifteen instances of species increasing by ≥15% of sampled points were grass or woody species. Similarly, shifts in important taxa in a northeastern bog during flooding could be attributed to a few aquatic, woody, shrub, and herb/moss species, including graminoids (Mitchell and Niering

1993). van der Valk and Davis (1978) described shifts in aquatic, emergent, and mud-flat species groups to illustrate vegetation cycling driven by changing hydrologic conditions in a prairie pothole, yet each group was comprised of several species and life-forms.

While aquatic, grass, and woody species were most dynamic within all bay vegetation types, species varied among types. In 1993, the percent of species in common between vegetation types was low and no pair of vegetation types shared even 40% of species. By 2002, there was no evidence of convergence among vegetation types. These results would suggest that the majority of species that accumulated in each vegetation type during the drought were unique to that type. Yet, it must be remembered that this was based on analysis of the full floras, and thus influenced by rare and infrequent species. In fact, several of the most frequent species during the drought were common among vegetation types. *Panicum verrucosum, Andropogon virginicus*, and *Dichanthelium wrightianum*, largely absent in 1993, were frequent in two or more vegetation types by 2002. Similarly, a study of six Carolina bays in Maryland described five distinct zonal community types, yet some of these shared several of the most dominant species (Tyndall et al.1990).

Some of the similarity in frequent species among vegetation types was likely directly attributable to hydrologic regime. The less hydrologically stable open-water ponds and depression meadows, on average, contained standing water for just over half the drought record while grass and sedge marshes were flooded 70% of that time. Thus, pronounced drawdown in open-water ponds and depression meadows provided an opportunity for species, including upland grasses, to become established. Similarly, van der Valk and Davis (1978, 1979) reported that, in prairie potholes, large areas of substrate exposed during drawdown were often colonized by a variety of species not seen prior to drying. Further, Kirkman (1992, 1995) noted the influence of dispersal and seed bank response in species establishment during drawdown in ponded Carolina bays. In contrast, grass and sedge marshes, with relatively wetter regimes during the drought, had the highest percentage of persistent species. This suggests that even a small degree of stability in the hydrologic condition of a bay might stabilize species composition. However, the life-history of *Carex striata*, a dense, clonal perennial, may also confer stability, as might landscape setting, since these systems were exclusively in lower, wetter areas.

It should be noted that trends within a vegetation type might not be indicative of all the individual bays within that type, nor is the hydrologic fluctuation of all bays within a vegetation type necessarily different from that of other types. For example, in two depression meadow bays, the percent of months flooded during the drought record was much higher than for the two other bays of that type and more similar to that of grass and sedge marshes. Further, while depression meadows as a type had the highest number of species, some of the individual bays within that type had rather low richness. Thus, a larger sample size would be needed to generalize further about species dynamics as related to average hydrologic characteristics within vegetation types.

The shift in sites between years in the NMDS ordination reflected the comparable ways in which species composition shifted. Notably, *Utricularia* sp. disappeared in every vegetation type, and *Panicum* spp. established or increased in frequency in all but the sedge marshes. But composition during the drought was clearly not independent of the initial vegetation types. For example, De Steven and Toner (1997, 2004) characterized depression meadows, which remained distinct from other vegetation types throughout the study, by *Leersia hexandra* and this was the only type in which the grass was frequent by 2002. Statistically, sedge marshes were not significantly different from other vegetation types, yet they were visually distinguishable in both years due to the widespread dominance of *Carex striata*. In this case, a larger sample size might have yielded significant differences between other vegetation types. However, in open-water ponds, following the loss of the dominant *Nymphaea odorata* (Table 2.1; De Steven and Toner 1997, 2004), *Panicum hemitomon* became most frequent, as it was in grass marshes throughout the study. Moreover, *Panicum verrucosum* became frequent in both vegetation types during the drought. Thus, during drier conditions, open-water ponds and grass marshes may become largely indistinguishable. De Steven and Toner (1997, 2004) considered these two vegetation types to have a successional relationship. That changes in species composition in the ordination paralleled vectors for flooding duration and depth is further evidence of the eminence of hydrologic condition in driving composition (van der Valk 1981, Schalles and Shure 1989, Mitsch and Gosselink 2000, Collins and Battaglia 2001, De Steven and Toner 2004).

Summary

The response of herbaceous Carolina bays of the Upper Coastal Plain to drought can perhaps be predicted at a species-level only within the context of the above-described vegetation types. Keddy (2000) noted the difficulty of predicting the occurrence of individual species and suggested the use of broader functional groups. van der Valk (1981) considered life history traits rather than individual species when attempting to conceptualize vegetation change in prairie potholes. While the current study does not explicitly consider functional or life history groups, in general, it could be said that in herbaceous Carolina bays aquatic species disappear and signature grasses, changing in identity and extent based on the severity of drawdown, establish and/or expand during drought. Within these matrices of grasses may be found woody seedlings and scattered herbs such as *Rhexia* spp. and *Triadenum* spp. The sedge marsh vegetation type is an exception in that it remains almost totally dominated by *Carex striata*.

Of future interest is whether vegetation change is truly cyclic (i.e. given a return to a wetter hydrologic regime, bays return to a composition that approximates that seen in 1993). There is precedent for vegetation cycling in other wetland systems, including van der Valk's (1981) description of cyclic dynamics in prairie potholes and Mitchell and Niering's (1993) assertion that unidirectional succession in northeastern bogs was unlikely. Together with Kirkman's (1992, 1995) findings during drought ten years previous and the De Steven and Toner (1997, 2004) model, the current results certainly reinforce the conception that the vegetation of herbaceous Carolina bays does cycle over time. Yet, Kirkman (1995) and Kirkman et al. (2000) also described the importance of fire, now almost totally removed from the landscape at the SRS, in maintaining a cyclic dynamic. In herbaceous Carolina bays, fire removes woody species, stimulates seed bank response and, depending on when inundation occurs relative to a burn, can drastically alter the dynamics of dominant grasses, including *Panicum hemitomon* (Kirkman 1993, 1995). The present study does not explore the impact of fire or other disturbance that may occur during drought conditions, and only with additional long-term data sets can the resilience of herbaceous Carolina bay vegetation and composition cycling in relation to climate, be verified.

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Table 2.1. Study bay characteristics, including basin size, vegetation type, and dominant species as defined by De Steven and Toner (1997, 2004). Dominant species were those occurring at high abundance in ≥90% of wetlands in that vegetation type. Species designations were derived from a larger group of wetlands (*n*=57) than used in the current study.

Bay	**Size (ha)**	**Vegetation type**	**Dominant species**
9	3.9	Grass marsh	*Panicum hemitomon*
26	1.2	Depression meadow	*Leersia hexandra*
27	2.3	Depression meadow	*Leersia hexandra*
40	7.5	Open-water pond	*Nymphaea odorata*
78	4.5	Open-water pond	*Nymphaea odorata*
87	1.8	Depression meadow	*Leersia hexandra*
106	2.5	Depression meadow	*Leersia hexandra*
127	5.1	Grass marsh	*Panicum hemitomon*
136	1.2	Sedge marsh	*Carex striata*
165	3.8	Sedge marsh	*Carex striata*

Table 2.2. The percent and number (*n*) of months flooded for each year for each of the study bays. Due to sampling omission the monthly record for each year does not always equal 12 and the months of record can vary amongst bays. Overall pre-drought and drought calculations are also shown. Pre-drought record was from March 1995 to December 1998. Drought record was from January 1999 through August 2002. Means±standard errors for the pre-drought and drought record are given for each vegetation type.

Vegetation type	**1995**	**1996**	**1997**	**1998**	**Pre-drought ’95-‘98**	**1999**	**2000**	**2001**	**2002**	**Drought ‘99-‘02**
Open-water pond										
Bay 40	100 (10)	100 (12)	100 (12)	100 (11)	**100 (45)**	73 (8)	40 (4)	57 (4)	0 (0)	**50 (16)**
Bay 78	100 (9)	100 (12)	92 (11)	100 (11)	**98 (45)**	73 (8)	50 (5)	71 (5)	25 (1)	**59 (19)**
Mean±s.e.					**99±1**					**55±5**
Grass marsh										
Bay 9	100 (9)	100 (12)	100 (12)	82 (9)	**95 (42)**	73 (8)	60 (6)	71 (5)	50 (2)	**66 (21)**
Bay 127	100 (10)	100 (12)	100 (11)	100 (11)	**100 (45)**	100 (11)	70 (7)	83 (5)	50 (2)	**81 (25)**
Mean±s.e.					**98±2**					**73±8**
Depression meadow										
Bay 26	100 (9)	92 (11)	92 (11)	100 (11)	**95 (42)**	91 (10)	90 (9)	71 (5)	25 (1)	**78 (25)**
Bay 27	100 (9)	92 (11)	92 (11)	100 (11)	**95 (42)**	73 (8)	70 (7)	57 (4)	50 (2)	**66 (21)**
Bay 87	100 (8)	100 (12)	83 (10)	100 (11)	**95 (41)**	55 (6)	10 (1)	14 (1)	0 (0)	**25 (8)**
Bay 106	100 (8)	100 (12)	92 (11)	82 (9)	**93 (40)**	36 (4)	30 (3)	57 (4)	0 (0)	**35 (11)**
Mean±s.e.					**95±0.5**					**51±13**
Sedge marsh										
Bay 136	100 (9)	100 (12)	100 (12)	100 (11)	**100 (44)**	100 (11)	70 (7)	71 (5)	50 (2)	**78 (25)**
Bay 165	100 (8)	100 (12)	92 (11)	73 (8)	**91 (39)**	55 (6)	50 (5)	100 (7)	50 (2)	**63 (20)**
Mean±s.e.					**95±5**					**70±8**

Table 2.3. The means±standard errors of water depths (m) for each year for each of the study bays. Overall pre-drought and drought means are also shown. Periods of record were the same as in Table 2.2. Means for the pre-drought and drought record are also given for each vegetation type.

Vegetation type	**1995**	**1996**	**1997**	**1998**	**Mean ’95-‘98**	**1999**	**2000**	**2001**	**2002**	**Mean ‘99-‘02**
Open-water pond										
Bay 40	1.83±.05	1.52±.05	1.35±.03	1.96±.08	**1.65±.05**	1.10±.02	.48±.20	.63±.22	0±.0	**.66±.12**
Bay 78	.88±.03	.55±.08	.35±.05	.94±.08	**.66± .05**	.38±.08	.20±.07	.25±.07	.08±.08	**.26±.04**
Mean±s.e.					**1.16±.42**					**.46±.39**
Grass marsh										
Bay 9	.41±.02	.32±.04	.34±.03	.38±.08	**.35± .02**	.18±.05	.12±.04	.21±.06	.04±.03	**.15±.03**
Bay 127	.73±.05	.46±.04	.42±.04	.98±.10	**.64± .05**	.40±.05	.23±.05	.38±.08	.10±.06	**.30±.04**
Mean±s.e.					**.50±.20**					**.23±.13**
Depression meadow										
Bay 26	.54±.03	.33±.06	.36±.04	.73±.08	**.48± .04**	.31±.05	.25±.04	.27±.08	.05±.05	**.25±.03**
Bay 27	.47±.04	.22±.05	.32±.04	.77±.09	**.43± .04**	.25±.06	.20±.05	.21±.08	.08±.05	**.20±.03**
Bay 87	.61±.06	.34±.06	.34±.08	1.07±.12	**.58± .06**	.30±.10	.08±.08	.09±.09	0±0	**.15±.05**
Bay 106	.61±.02	.45±.05	.40±.06	.66±.13	**.52± .04**	.08±.04	.08±.04	.20±.08	0±0	**.10±.03**
Mean±s.e.					**.50±.16**					**.17±.10**
Sedge marsh										
Bay 136	.71±.02	.58±.03	.69±.03	.67±.03	**.70± .01**	.53±.05	.37±.09	.43±.12	.13±.09	**.41±.05**
Bay 165	.58±.03	.55±.06	.46±.06	.58±.14	**.54± .04**	.20±.06	.16±.06	.61±.08	.18±.10	**.28±.05**
Mean±s.e.					**.62±.16**					**.34±.19**

Table 2.4. The number of species recorded in each bay by study year and vegetation type as a whole, and the percent of total taxa observed in both years. The mean±standard error of the number of species per bay is shown for each vegetation type in each study year and for all vegetation types combined. The mean±standard error of the percent of total taxa observed in both study years is also presented for all vegetation types combined.

Vegetation type	**1993**	**2002**	**Taxa observed in both years**
Open-water pond			
Bay 40	17	25	24%
Bay 78	15	32	21%
Within type	27	48	23%
Mean±s.e.	16±1	29±4	
Grass marsh			
Bay 9	24	23	42%
Bay 127	7	22	12%
Within type	28	38	32%
Mean±s.e.	16±8	23±1	
Depression meadow			
Bay 26	11	15	24%
Bay 27	19	18	19%
Bay 87	10	18	22%
Bay 106	33	39	18%
Within type	49	49	26%
Mean±s.e.	18±8	23±8	
Sedge marsh			
Bay 136	12	13	39%
Bay 165	30	20	28%
Within type	32	25	36%
Mean±s.e.	21±9	17±4	
Total			
Mean±s.e.	18±3	23±3	25%±3%

Table 2.5. Percent frequency of species occurring at 15% or more of sampled points within vegetation types in 1993 and 2002 and their National Wetland Indicator category. Also shown are species that expanded or declined by at least 15% of sampled points within vegetation types by 2002. Percentages in bold represent species completely established within or absent from a vegetation type by 2002.

Vegetation type	**National Wetland Indicator**	**1993**	**2002**	**Increased by ≥15% of sampling locations**	**Declined by ≥15% of sampling locations**
Open-water pond					
Andropogon virginicus	FAC-		25%	**25%**	
Dichanthelium wrightianum	NI		19%	**19%**	
Nymphaea odorata	OBL	67%			**67%**
Panicum hemitomon	OBL	44%	72%	28%	
Panicum verrucosum	FACW	+	52%	48%	
Scleria reticularis Michx.	FACW+	+	18%	15%	
Utricularia sp.	OBL	66%			**66%**
Grass marsh					
Acer rubrum L.	FAC	+	17%		
Cephalanthus occidentalis	OBL	+	19%		
Juncus canadensis	OBL	19%			**19%**
Liquidambar styraciflua	FAC+	+	18%		
Panicum hemitomon	OBL	89%	80%		
Panicum verrucosum	FACW		16%	**16%**	
Pinus taeda	FAC	+	25%	21%	
Pontedaria cordata	OBL	19%			**19%**
Sphagnum sp.		47%	+		38%
Triadenum sp.		+	20%	16%	
Utricularia sp.	OBL	42%			**42%**
Depression meadow					
Andropogon virginicus	FAC-		31%	**31%**	
Dichanthelium wrightianum	NI		21%	**21%**	
Diospyros virginiana L.	FAC	18%	22%		
Leersia hexandra	OBL	75%	47%		27%
Liquidambar styraciflua	FAC+	+	19%		
Panicum verrucosum	FACW		63%	**63%**	
Pinus taeda	FAC	+	37%	34%	
Rhexia sp.		+	35%	33%	
Rhynchospora sp. a			25%	**25%**	
Rhynchospora sp. b			19%	**19%**	
Utricularia sp.	OBL	56%			**56%**
Sedge marsh					
Carex striata	OBL	66%	75%		
Nyssa sylvatica	FAC	29%	34%		
Pinus taeda	FAC	+	16%		
Utricularia sp.	OBL	73%			**73%**

NI Species for which no National Wetland Indicator has been assigned. This species was considered as FAC or drier for calculations.
\+ Species present in a survey year but at <15% frequency.

Table 2.6a. The number and percent (*p*) of species common between vegetation types in 1993.

	Open-water pond	**Grass marsh**	**Depression meadow**	**Sedge marsh**
Open-water pond	27 (100)			
Grass marsh	11 (25)	28 (100)		
Depression meadow	17 (29)	17 (28)	49 (100)	
Sedge marsh	10 (20)	16 (36)	14 (21)	32 (100)

Table 2.6b. The number and percent (*p*) of species common between vegetation types by 2002.

	Open-water pond	**Grass marsh**	**Depression meadow**	**Sedge marsh**
Open-water pond	48 (100)			
Grass marsh	21 (32)	38 (100)		
Depression meadow	22 (29)	23 (36)	49 (100)	
Sedge marsh	14 (21)	14 (29)	13 (21)	25 (100)

Table 2.7. Chi-square values for the number of shared species by 2002 relative to 1993 for all pairs of vegetation types (df=1, α=0.5, χ^2=3.84). None are significant.

	Open-water pond	**Grass marsh**	**Depression meadow**
Grass marsh	0.676		
Depression meadow	0.004	0.819	
Sedge marsh	0.011	0.644	0.003

Table 2.8. Analysis of similarity results to determine if groups of vegetation types within the non-metric multidimensional scaling ordination were significantly different from one another. Groups included sites in 1993 and 2002. Clarke's R and *p*-values, in parentheses, are provided for each pair of classifications, with R representing a number from -1 – +1 and a significant *p*-value indicating that R is different than zero. Note that a significant difference between vegetation types is based on a Bonferroni-corrected α of 0.05/*n* or 0.008. The null hypothesis is R=0 (i.e. groups are not different).

	Grass marsh	**Depression meadow**	**Open-water pond**
Depression meadow	0.55 (0.001)*		
Open-water pond	0.10 (0.324)	0.44(0.006)*	
Sedge marsh	0.64 (0.028)	0.67 (0.002)*	0.53 (0.022)

* $p < 0.008$.

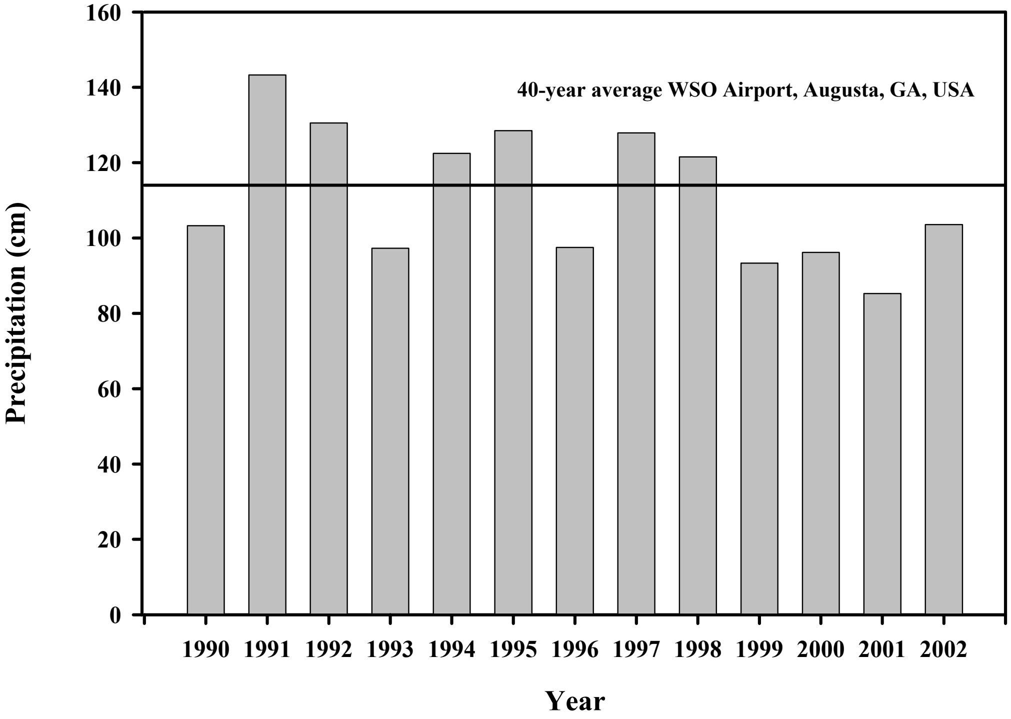

Figure 2.1. Yearly precipitation in Augusta, GA throughout the study period relative to the 40-year average (Southeastern Regional Climate Center 2003).

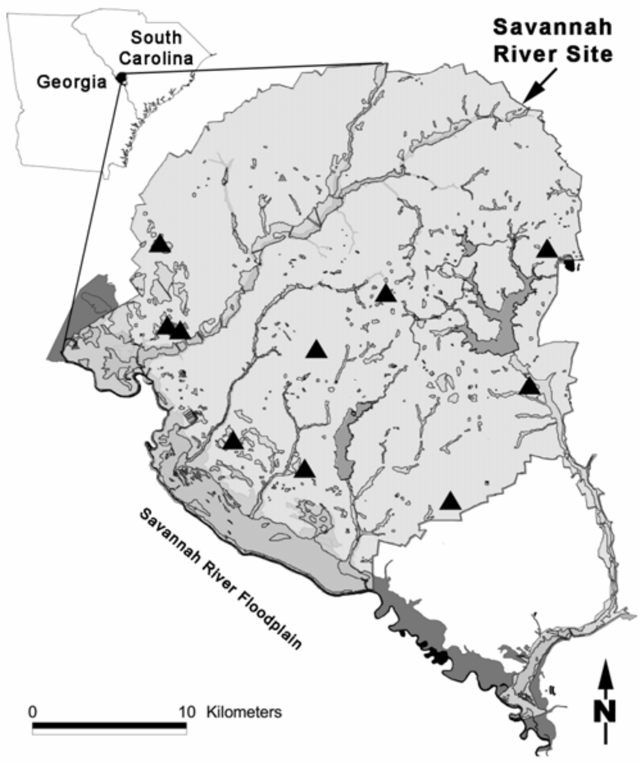

Figure 2.2. The Savannah River Site (SRS) in Aiken, South Carolina, USA, within which all study bays, indicated by triangles, were located. Center latitude: 33°14’44.79”; longitude: 081°37’58.33”.

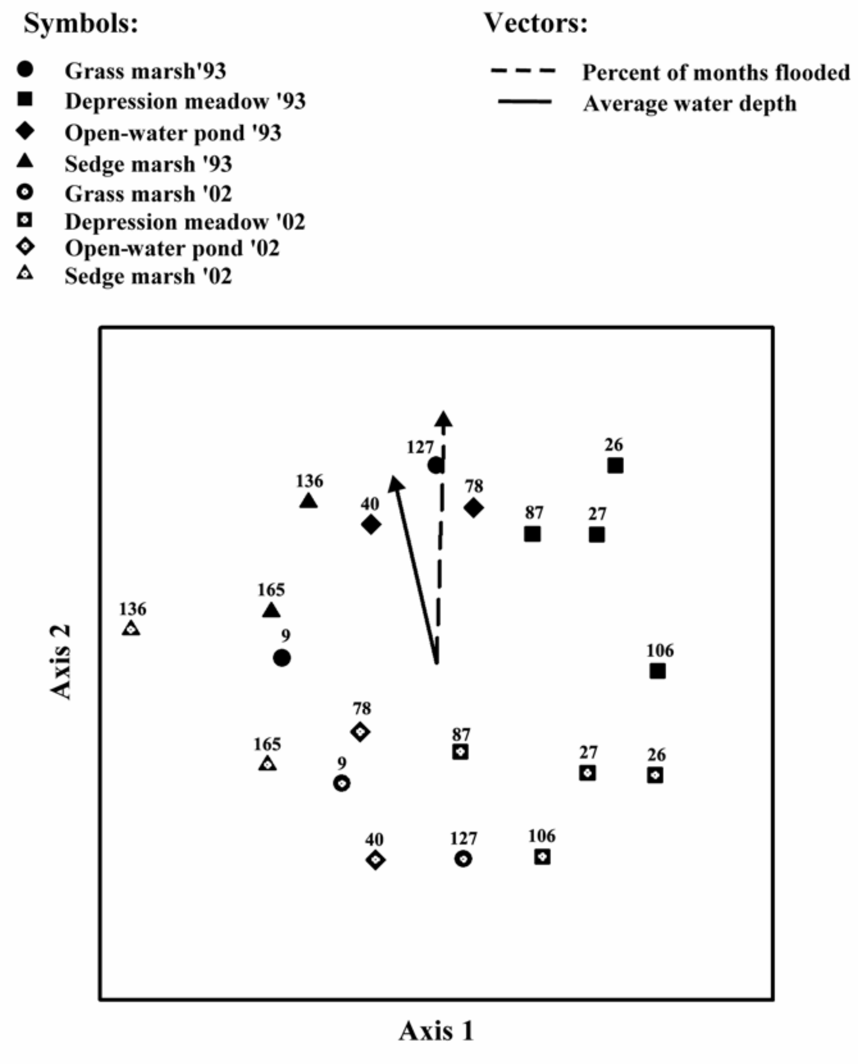

Figure 2.3. Two-dimensional non-metric multidimensional scaling ordination of species composition of bays in both 1993 and 2002 (stress=0.21). Vector variables were significantly correlated with site coordinates; vector lengths are proportional to correlations. The angle between vectors=14.8º, indicating correlation between variables.

CHAPTER THREE

SEED BANK-VEGETATION RELATIONSHIPS IN HERBACEOUS CAROLINA BAYS OF THE SOUTH CAROLINA UPPER COASTAL PLAIN: RESPONSES TO CLIMATIC VARIABILITY[1]

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[1] Mulhouse, J.M., L.E. Burbage, and R.R. Sharitz. To be submitted to *Wetlands*.

INTRODUCTION

Hydrologic condition has long been recognized as the main driver of plant species composition in wetlands (van der Valk 1981, Mitsch and Gosselink 2000, Collins and Battaglia 2001, De Steven and Toner 2004). Variability in the depth and duration of inundation observed in a wetland will cause the composition of species in the vegetation to shift as conditions become favorable for some species and prohibitive to others (van der Valk and Davis 1978; van der Valk 1981; Schalles and Shure 1989; Kirkman 1992, 1995; Kirkman et al. 2000; Battaglia and Collins *in review*). In herbaceous, precipitation-driven, depression wetlands, this phenomenon is most marked at the extremes of the climatic cycle. For instance, during times of high precipitation, when water levels rise, species suited to inundation such as aquatic and emergent wetland species may thrive, while grasses and forbs unable to tolerate flooding are not prevalent (van der Valk and Davis 1978, Kirkman et al. 2000, Mulhouse et al. *in prep*). Conversely, during drought, it is the aquatic species that are unable to persist while upland species, including trees, may colonize (Kirkman 1992, Mulhouse et al. *in prep*). Yet, despite this straightforward understanding of the mechanisms by which species composition shifts as climate alters hydrologic condition, relatively little detailed empirical information exists to document the changes and species-level fluctuations that occur in shallow, precipitation-driven, herb-dominated wetlands.

In the absence of disturbance or potential barriers to establishment such as salinity or deep litter (Smith and Kadlec 1983, 1985b; Galinato and van der Valk 1986), the interaction between the species pool (i.e. standing vegetation, propagule bank, and dispersal inputs) and hydrologic condition has been considered to provide a substantial explanation of vegetation composition as environment changes (van der Valk 1981). In some studies of herbaceous wetland communities, including prairie potholes (van der Valk and Davis 1978), brackish marshes (Smith and Kadlec 1983), freshwater tidal marshes (Parker and Leck 1985, Leck and Simpson 1987), and Carolina bays (Kirkman and Sharitz 1994, Poiani and Dixon 1995), the seed bank has contained more species than were seen in the vegetation at a particular time. Presumably, at least some of the species in the seed bank not expressed in the vegetation would germinate if more favorable hydrologic conditions were present (van der Valk 1981, Smith and Kadlec 1983, Gerritsen and Greening 1989). On the other hand, some studies of temporary ponds (McCarthy 1987), lakeshores (Keddy and Reznicek 1982), and prairie potholes (Galatowitsch and Biederman 1998) have found fewer species in wetland seed banks than were observed in the extant vegetation. In such cases, nearly all common species in the vegetation may be represented in the seed bank (Keddy and Reznicek 1982, Galatowitsch and Biederman 1998) and dispersal must be the means by which additional species establish in the vegetation. Moreover, the species detected at the highest densities in the seed bank are frequently not those observed at the highest abundances in the vegetation (Keddy and Reznicek 1982, McGraw 1987, Ungar and Woodell 1996) and species rare in the seed bank may be those most abundant in the vegetation (Galatowitsch and Biederman 1998). Thus, the relationship between the seed bank and vegetation is complex and predictions of standing vegetation based on seed bank composition and hydrologic fluctuations have been elusive. In Carolina bay wetlands, it remains largely unknown how the interrelation of seed bank, vegetation, and hydrologic condition might specifically influence vegetation as climate cycles through wet and dry periods.

Carolina bays

Found on the Atlantic Coastal Plain of the southeastern United States from Delaware through Georgia, Carolina bays are shallow, elliptical depression wetlands that are usually unconnected to other sources of surface water. Bays may be as large as 3,600 hectares, but some bay-like depressions may be smaller than one hectare (Sharitz and Gibbons 1982, Sharitz and Gresham 1998), and up to several meters deep, usually reaching peak water volume in the early spring and drying down throughout the summer. Precipitation and evapotranspiration are the chief hydrologic drivers in bays (Schalles and Shure 1989), however, there may be some inflow from shallow groundwater when the water table is high and seepage when low (Lide et al. 1995).

Few Carolina bays have escaped alterations by agriculture, through cultivation, drainage, or both. Of 2,651 bays of >0.8 ha in South Carolina, 97% have been disturbed (Bennett and Nelson 1991). Johnson (1994) reported that by the 1980's wetland acreage in South Carolina was 25-49% of what it had been in the 1780's and noted that this loss had resulted in a lower density of wetlands, increasing the distance between basins and drastically reducing travel between systems by animals (Semlitsch and Bodie 1998) and dispersal by plants.

Current study

Drought in the South Carolina Upper Coastal Plain is cyclic, and notable rainfall deficits occur approximately every decade. Substantial yearly deficits of 250 mm or more below average were observed in the mid-1920's, the early-1930's, and the mid-1950's (National Oceanic and Atmospheric Administration 2003). Droughts of somewhat less severity were recorded in the late 1930's, 1970's, and 1980's (National Oceanic and Atmospheric Administration 2003).

From December 1997-April 1998, South Carolina experienced an El Niño event with precipitation nearly 65% above the 100-year average for that period (South Carolina Department of Natural Resources 2003). Yet, by June 1998, rainfall was below average and drought was incipient (Kiuchi 2002). Annual precipitation remained low from 1999-2002, with 2001, when rainfall was >320 mm below average, the third driest year on record in the state (National Oceanic and Atmospheric Administration 2003). By August 2002, drought status was designated "extreme" in every county in South Carolina (South Carolina Department of Natural Resources 2003); many shallow Carolina bays were completely dry by fall 2001, if not earlier (Lide *unpublished data*).

Vegetation surveys of four herbaceous Carolina bays during the drought in 2002, in conjunction with a prior survey in 1999, provided an opportunity to investigate how species composition shifted over a short period with a climate-driven hydrologic change. Further, seed bank samples taken in spring 2000 enabled an examination of the interaction between climate, established vegetation, and the seed bank. Questions included: What was the response of vegetation in herbaceous Carolina bays through a period of fluctuating hydrologic conditions? Were species observed in the vegetation in 1999 well-represented in the seed bank of 2000? What role did the seed bank play in influencing the vegetation of bays during the 2002 drought?

METHODS

Site description

The climate of the South Carolina Upper Coastal Plain is humid subtropical, characterized by long, hot summers and short, mild winters. In January, the average temperature is 7.3° C and in July it is 25.6° C (National Oceanic and Atmospheric Administration 2003). The average yearly precipitation is 1217 mm, most of which falls during the spring and summer (National Oceanic and Atmospheric Administration 2003).

Four predominantly herbaceous bays located on the Savannah River Site (SRS), a 780 km^2 Department of Energy facility on the Upper Coastal Plain of South Carolina, USA (Figure 3.1), were chosen based on the following criteria: 1.) functional wetlands historically, as determined by aerial photographs taken in 1951; 2.) free of natural or man-made disturbance, including recent ditching and fire; and 3.) part of an existing hydrologic monitoring effort. Sites used were SRS Bay 3 (Flamingo Bay; 11.2 ha; basin relief: 110 cm), SRS Bay 31 (Dry Bay; 7.3 ha; basin relief: 110 cm), SRS Bay 78 (Sarracenia Bay; 4.5 ha; basin relief: 110 cm), and SRS Bay 176 (Ellenton Bay; 12.1 ha; basin relief: 150 cm).

Water depth sampling

Water depth was measured via staff gauges installed at the deepest point of each bay. Gauges were read monthly during the 1999 growing season (March through November) and bi-monthly during the growing season of 2002 (Lide *unpublished data*).

Vegetation sampling

In 1999, a transect was established from the deepest point of each bay to the perimeter along the longest axis. A second transect was run perpendicular to the first from the deepest point to the perimeter along the shortest axis. To capture abrupt changes in elevation along each transect, PVC poles were installed at intervals of 10 cm of elevational change or 20 m of distance from the previous pole, whichever occurred first. Each pole represented the center of a 2 x 4 m plot that was divided into eight 1 x 1 m sub-plots (Figure 3.2). Plot elevations were measured from the deepest point of each bay using a Spectra-Physics Laserplane leveling system.

The herbaceous vegetation layer, defined as non-woody and woody plants less than 1 m tall (woody plants greater than 1 m tall were not considered in this study), was sampled in four 1 x 1 m sub-plots in every plot in a bay (Figure 3.2). In 1999, vegetation was sampled from mid-July through August, except for one transect in one bay sampled in late September. In 2002, all bays were re-sampled in mid-August and sampling protocol followed that of 1999, utilizing all original plots. Abundance measurements of percent cover in each sub-plot followed a modified Braun-Blanquet scale (i.e. 6=95-100%; 5=75-95%; 4=50-75%; 3=25-50%; 2=5-25%; 1=<5%; +=few individuals, little cover; r=one individual, little cover). Taxonomy followed Radford et al. (1968) and Godfrey and Wooten (1981) and species vouchers collected during the 2002 vegetation survey were deposited in the University of Georgia Herbarium.

Seed bank sampling

In March 2000, two soil cores were taken with a 6.35 cm diameter auger to a depth of 10 cm from the center of the two 1 x 1 m subplots adjacent to each pole and previously sampled for vegetation (Figure 3.2). These cores were kept from 3-123 days at 4° C before being selected by plot for processing. The four subplot samples were mixed by hand and cleaned of roots and rhizomes. The cleaned, composited samples were then divided into four subsamples and placed into four 12 x 17 cm flats over a substrate of 1-2 cm of sand. Flats were randomly arrayed on greenhouse benches. Two subsamples from each plot received a moist treatment and were watered daily while the other two were submerged to a constant depth of 1-2 cm. Subsamples receiving different treatments were separated by partitions. Greenhouse temperature ranged between 21-32° C in summer and 16-24° C in winter under a natural photoperiod. Flats were monitored for seedling emergence and, upon identification, seedlings were removed to prevent maturation and seed development. Control plots of sand were used to monitor potential seed contamination in the greenhouse. All samples were observed for 445-480 days, when apparent germination had ceased, at which time any remaining unidentified seedlings were marked and allowed to mature to facilitate identification. All seedlings were counted and identified to the most precise taxonomic level possible, usually species. Taxonomy followed Radford et al. (1968), Godfrey and Wooten (1981), Taylor et al. (1993), and Crow and Hellquist (2000).

Data analyses

The mean water depth and the percent and number of months the bays were flooded, defined as the months during which there was a measurable depth of water, were calculated for the 1999 and 2002 growing seasons. Differences between the pre-drought and drought hydrologic measurements were tested with a paired t-test.

Prior to vegetation and seed bank analyses, occurrences of plants that could not be identified to genus were removed from the data sets. In 1999, approximately 1-8% of the occurrences in a bay could not be identified to genus; in 2002, no more than 3% of occurrences were unknown. Fewer than 1-3% of seedlings from the seed bank of a bay were unidentifiable.

Identifications to genus only were retained if there was no possibility of the plant being identified to species in another data set; these included observations in the vegetation of *Bidens* sp., *Carex* sp., and two *Panicum* spp. that clearly did not appear in the seed bank. *Juncus* sp. and *Polygonum* sp. were removed from the seed bank data as possibly being one of several species identified in the vegetation. *Utricularia* and *Psilocarya* species were combined at the genus level in all data sets because they were difficult to identify to species in the seed bank.

In both vegetation surveys, observations receiving a cover of "r", indicating the presence of only a single individual, within a sub-plot, were dropped from all analyses as inconsequential. In 1999, no more than seven species were removed from any bay and two bays lost no species (see: Appendix). One to five herbaceous species per bay were removed in 2002; a comparable number of woody species were also removed (see: Appendix). *Utricularia* spp., *Lemna valdiviana* Phil., and *Eleocharis acicularis* (L.) Roemer & J.A. Schultes could not be clearly counted as individuals in the seed bank and were assigned an arbitrary count of 0.5 per record to represent their relatively small size. Overall, the approach was conservative, rendering species richness lower and data sets more similar to each other.

The number of species present in the vegetation of each bay in each survey year and the number and percent of total species occurring in both years combined was determined. The difference in species richness between years was tested via a Wilcoxon signed rank test. The total number of seed bank species in each bay was determined by combining observations of the moist and submerged treatments. The number and percent of species present in both the vegetation and the seed bank was calculated for 1999 and 2002, as was the number of species observed in the seed bank of a bay and never recorded in the vegetation. Also, the number of species present in both the 2000 seed bank and 2002 vegetation that were not in the 1999 vegetation was determined (i.e. new seed bank germinants by 2002).

For each bay, the mean number of species per 8 m^2 plot was calculated for both years of vegetation sampling and differences between years tested by signed rank test. Mean richness of germinating seeds per plot was also calculated, as was the mean number of germinating seeds per m^2.

In each bay, the frequency of occurrence of each species was determined as the percent of 8 m^2 plots in which it was present. An average abundance value for each species was calculated for each 8 m^2 plot as the mean of the mid-points of the cover classes for the four subplots. Observations of "few" individuals (+ cover class) were assigned an arbitrary value of 0.1. Plot averages were summed for all species within a bay and the relative abundance of each species calculated by dividing its abundance by the sum total abundance of all species. Relative abundance in the seed bank was calculated by bay for each species by dividing the number of germinating seeds of a species by the total number of germinating seeds in a bay. Tables of species frequency and relative abundance were sorted by National Wetland Indicator (NWI) category.

To investigate potential dispersal inputs, species found in the vegetation but not in the seed bank were assigned NWI categories and tabulated. Occurrences of small trees (<1 m), shrubs, and woody vines in the vegetation were not included in this analysis, as the woody contribution to wetland seed banks has been considered largely unimportant (Gunther et al. 1984, Leck 1989).

For each bay, the absolute cover of species in an 8 m^2 plot in 1999 and 2002 was compared and Bray-Curtis dissimilarity values (Bray and Curtis 1957) calculated between years for each plot. Bray-Curtis dissimilarity values were also computed between the relative abundances of species in the vegetation in a plot in each year and the relative abundances of species in the seed bank of that plot. Mean dissimilarity values for a bay were determined for each of the three comparisons. Differences in dissimilarities between the vegetation and the seed bank prior to and during the drought were tested by signed rank test.

RESULTS

Hydrology

Though the drought began in June 1998 (Figure 3.3; Kiuchi 2002), water levels in the study bays were high following the 1997-98 El Niño event and remained elevated during 1999 (Table 3.1; Southeastern Regional Climate Center 2003, Lide *unpublished data*). In 1999, all bays were flooded ≥78% of the months of the growing season, and three remained flooded throughout (Table 3.1). By 2002, the percent of months flooded during the growing season ranged from 0-25%. Mean water depth during the 1999 growing season ranged from 0.39-0.89 m (Table 3.1). During the drought, the range was 0-0.14 m, and all bays were dry by June 2002, if not earlier (Lide *unpublished data*). There were significant differences between the pre-drought and drought periods in percent of months bays were flooded (p=0.004) and mean water depth (p=0.012).

Vegetation

In 1999, richness of the vegetation was between 15 and 24 species per bay; by 2002 it ranged from 18-32 (Table 3.2), but the difference between years was not significant (p=0.250). Between 8 and 13 species, or 18-50% of a bay's flora, were observed in both years. Species richness in the 2000 seed bank was between 55 and 80 (Table 3.2). The number of species in the vegetation in 1999 also found in the seed bank ranged from 5 to 17, a third to nearly threequarters of the taxa. By 2002, 9-18 species in the vegetation were in the seed bank, comparable to 1999, although the percent was generally not as high (42-56%; Table 3.2). Thirty-nine to 61 species (61-76%) in the seed bank of a bay were not recorded in the vegetation of that bay in either study year. Of the species in the seed bank expressed in the 2002 vegetation, 0-11, or 0-85%, were not observed in the 1999 vegetation (Table 3.2).

In 1999, the mean number of species in a plot was between 3 and 4, while in 2002 it ranged from 3-5; the difference was not significant (p=0.500; Table 3.3). Mean species richness per plot in the seed bank was between 11 and 18 and the mean density of germinating seeds ranged from 9152-13949 per m^2 (Table 3.3).

Species frequencies in vegetation: In 1999, obligate wetland species and grasses were the only species occurring frequently in the bays. *Nymphaea odorata* Ait. was observed at frequencies of 59-79% in three bays, and *Utricularia* spp. was found at about 70% frequency in two bays (Table 3.4). *Panicum hemitomon* J.A. Schultes, a perennial obligate wetland grass, was frequent in all four bays (43-66%). *Panicum verrucosum* Muhl., an annual facultative wetland grass, the only frequent non-obligate species, was frequent in one bay (55%; Table 3.4).

By 2002, aquatic species had disappeared and a wider variety of grasses occurred frequently. *Panicum hemitomon* was the first or second most frequent species in every bay, observed in 41-83% of plots (Table 3.4). *Panicum verrucosum* was found in >50% of plots in three bays. *Leersia hexandra* Sw. and *Sacciolepis striata* (L.) Nash, obligate wetland grasses, occurred frequently in one bay (40-45%; Table 3.4). Two upland grasses, *Andropogon virginicus* L. and *Dichanthelium wrightianum* (Scribn.) Freckmann, also appeared frequently in one bay, detected in 59-73% of plots. *Scleria reticularis* Michx. (45%) was the only frequent species in one bay that was not a grass (Table 3.4). In two bays, all frequent species were grasses.

Species abundances in vegetation: Each of the species that occurred frequently in 1999 was also abundant. *Nymphaea odorata* was the most abundant species in three bays (35-69%; Table 3.4). *Panicum hemitomon*, while not always as abundant as other obligate species, was abundant in every bay (5-21%). *Utricularia* spp. was abundant in three bays (5-22%; Table 3.4). In one bay, *Brasenia schreberi* J.F. Gmel. (44%) and *Pontederia cordata* L. (11%), obligate species that were not frequent, were abundant. Two *Panicum* species and *Dichanthelium wrightianum* were three of four non-aquatic species observed at ≥5% relative abundance in one bay, the fourth being *Scleria reticularis* (14%; Table 3.4).

Grasses comprised the vast majority of species with high relative abundances during the drought. In 2002, *Panicum hemitomon* was observed in all bays at abundances of 19-70%, and *Panicum verrucosum* was abundant in three bays (16-27%; Table 3.4). *Panicum dichotomiflorum* Michx. (40%) and *Sacciolepis striata* (11%) were each abundant in one bay. *Dichanthelium wrightianum* (22%) and *Andropogon virginicus* (19%) were abundant in one bay, in which five of six most abundant species were grasses (Table 3.4). *Cyperus odoratus* (14%), a facultative wetland species, was the only species abundant in one bay other than *Panicum hemitomon*. In one bay, grasses were the only abundant species (Table 3.4).

Seed bank

There were 2-7 times more species occurring at a frequency of ≥40% in the 2000 seed banks of bays than in the 1999 or 2002 vegetation. Some frequent seed bank species also were frequent in the vegetation in at least one year such as *Panicum verrucosum*, frequent in the seed bank of every bay (63%-95% of plots), and *Panicum hemitomon*, frequent in the seed bank of two bays (52-71% of plots; Table 3.4). *Scleria reticularis* was also frequent in both the seed bank (86% of plots) and 2002 vegetation of one bay. However, many other species, including *Chamaesyce serpens* (Kunth) Small, a non-wetland herb, and *Psilocarya* spp., each observed in 49-90% of plots in nearly every bay, were rare or absent in the vegetation (Table 3.4). *Fuirena breviseta* (Coville) Coville, *Juncus acuminatus* Michx., *Bacopa caroliniana* (Walt.) B. L. Robins., *Eriocaulon compressum* Lam., and *Xyris smalliana* Nash, among others, were all frequent in only the seed bank of one or more bays (59-100% of plots).

Overall, there were 31 occurrences of species with a seed bank frequency of ≥40% but a seed bank abundance of <5% in a bay. *Chamaesyce serpens* and *Panicum hemitomon*, both frequent, did not occur at high relative abundances (Table 3.4). *Nymphaea odorata* and *Scirpus cyperinus* (L.) Kunth. were also not abundant in the two bays in which they were frequent. Conversely, *Panicum verrucosum*, abundant in three bays (5-17%), was frequent in each, as was *Psilocarya* spp. (6-15%; Table 3.4). Also, *Juncus effusus* L. and *Juncus acuminatus* tended to remain abundant (6-25%) in bays in which they were frequent. A few species were infrequent yet abundant, including *Oldenlandia uniflora* L. in two bays (5-6%; Table 3.4).

Eleven herbaceous species, most of which were obligate wetland perennials, were observed in the vegetation surveys of bays in 1999, but not detected in the seed bank (Table 3.5a). Of these, only one, *Brasenia schreberi*, in one bay, occurred in the vegetation at a relative abundance ≥5%. The vegetation survey of 2002 recorded nearly twice as many species in the vegetation that were not in the seed bank (21) and, while their NWI categories varied, most were perennials (Table 3.5b). Yet, only two species, *Andropogon virginicus* and *Sacciolepis striata*, occurred at relative abundances ≥5% (Table 3.5b).

The mean Bray-Curtis dissimilarity between the vegetation of a plot sampled in 1999 and that of that same plot by 2002 was high (0.84-0.94) and very close to that between the vegetation and the seed bank in 1999 (0.89-0.97) and 2002 (0.86-0.93; Table 3.6). By 2002, the vegetation of a plot was not significantly more or less dissimilar than the seed bank than it was in 1999 (p=0.297).

DISCUSSION

The number of species reported in the extant vegetation of herbaceous Carolina bays of the southeastern Upper Coastal Plain has been comparable to that in other wetland types such as prairie potholes (van der Valk and Davis 1978, Galatowitsch and van der Valk 1996, Galatowitsch and Biederman 1998), freshwater tidal marshes (Parker and Leck 1985, Leck and Simpson 1987), and temporary ponds (McCarthy 1987). However, seed bank richness in these bays has been reported to be the highest among freshwater wetlands (Kirkman and Sharitz 1994, Kirkman 1995). Typically, from 10-35 species have been observed in the vegetation of herbaceous bays, as in the current study (Keough et al. 1990; Poiani and Dixon 1995; De Steven and Toner 1997, 2004), although Kirkman and Sharitz (1994) reported about 60 species at three sites and a fourth, regularly burned, contained 105. The seed bank of the burned site Kirkman and Sharitz (1994) sampled contained 108 species and had a seed density of 72,600 per m^2. While burning has not always been shown to increase seed bank germination (Smith and Kadlec 1985a), some species require fire for establishment (e.g. Nuzzo et al. 1996) or seed bank augmentation (Wellington and Noble 1985). Other bays in the Kirkman (1992) study had between 79-91 species in the seed bank, equal to or just slightly higher than found here.

In accord with predictions by Kirkman (1992), the number of species in the vegetation of a bay generally increased during the drought, although the increase was not significant; at the plot level, the increase was even less pronounced. Further, the number of species observed in both the vegetation and seed bank by 2002 was higher in only one bay, providing no clear evidence of an increase in germination from the seed bank. This was consistent with the findings of Battaglia and Collins (*in review*), who reported an increase in germination associated with a zone of hydrologic variability, but no difference in species richness between wholly flooded or dry conditions. The results of van der Valk and Davis (1978), who did report an increase in germination in an Iowa marsh during artificial drawdown, may not pertain to climatological drought, which would inhibit the establishment and survival of many wetland plants.

In the current study, the majority of species in the seed bank were never recorded in the vegetation of any bay. Seed bank composition was obviously influenced by vegetation history but, given the longevity of many seeds (see: Leck 1989), the relevant history may be on the order of several years or even decades, not simply the previous season. Also, while the number of species present in both the vegetation and seed bank was generally not higher by 2002, in three bays 44-85% of species in both were not observed in 1999. Although this result was not completely consistent (there was no change in taxa in one bay, only a decline in overall response), species did germinate from the seed bank and establish during the drought even as some 1999 germinants disappeared.

In 1999, *Nymphaea odorata*, *Panicum hemitomon*, and *Utricularia* spp. were, with one exception, the only species observed at a frequency of ≥40% in the bays. Grasses, with three exceptions, were the only species frequent in any bay by 2002. *Panicum hemitomon* was ubiquitous, but other grasses were also frequent in individual bays during the drought. This preeminent position of aquatics and grasses in the dynamics of species composition in herbaceous bays was even more obvious when relative abundance was considered. In 1999, 35-83% of the vegetation cover in any bay was aquatic species. Together, aquatics and grasses represented 69-91% of vegetation cover. *Panicum hemitomon*, *Panicum dichotomiflorum*, and *Panicum verrucosum* had all established and/or expanded substantially by 2002; together they comprised 37-70% of the vegetation cover in any bay. Several grass species were already present in 1999, yet others such as *Andropogon virginicus* and *Panicum dichotomiflorum* were colonizers during the drought.

The species dynamics observed were consistent with a cyclic vegetation model proposed by Kirkman (1992, 1995) in which, during drawdown, aquatics disappeared and grasses expanded toward the center of a basin. If dry conditions persisted, upland species such as *Andropogon virginicus* were predicted to establish. Thus, much of the change in vegetation in these herbaceous Carolina bays during wide hydrologic fluctuation can be ascribed to essentially two species groups. Likewise, Keough et al. (1990) observed that the floras of 12 herbaceous Carolina bays of the Upper Coastal Plain, encompassing hydrologic regimes ranging from standing water throughout the growing season to continuously dry, were often dominated by one or two species, usually grasses. Keough et al. (1990) found *Panicum hemitomon* in every bay but one, at greater than 85% frequency in four, and co-dominant in another four. *Leersia hexandra* and *Paspalum laeve* Michx., both grasses, were also considered dominant species in additional bays. In other wetland types such as prairie potholes and a Great Salt Lake marsh, a larger array of species groups has been required to describe change during drawdown (see: van der Valk and Davis 1978 and Smith and Kadlec 1983).

Several of the most frequently occurring species in the vegetation of bays were also frequent in the seed bank. For example, *Panicum hemitomon* was frequent in the seed bank of some bays. Galatowitsch and Biederman (1998) also reported an apparent correspondence between the extant vegetation and seed bank in prairie potholes when species were considered by frequency of occurrence. However, in the current study, exceptions included some aquatic species and grasses such as *Leersia hexandra* and *Andropogon virginicus*, both infrequent in the seed bank. Moreover, there were always at least two to three times more species occurring frequently in the seed bank than in the vegetation, and several of the most frequent seed bank species were rare or absent in the aboveground vegetation in both years.

It is possible that certain species germinated disproportionately under greenhouse conditions, as reported for prairie pothole species (van der Valk and Pederson 1989), resulting in a disparity between the vegetation and seed bank. Yet, Poiani and Dixon (1995) found 20-60% more species in the seed bank than the vegetation of seven Carolina bays, many of which were infrequent. Similar incongruities between the species composition of standing vegetation and the seed bank have been reported for Carolina bays (Kirkman 1992), prairie potholes (Galatowitsch and Biederman 1998), and a brackish wetland (Smith and Kadlec 1983). McGraw (1987) also noted that the dominant species in the seed bank of a sphagnum bog might not be those in the extant vegetation and remarked on the difficulty of establishing a direct relationship between the vegetation and seed bank.

The discrepancy between the standing vegetation and seed bank was even more striking when relative species abundances were compared. Generally, species observed at a relative abundance of $\geq$5% in the vegetation in either 1999 or 2002 were not found at a comparable abundance in the seed bank. *Panicum verrucosum* was found at a high abundance in three bays by 2002 and was abundant in the seed banks of those bays, yet this was an exception. Other studies have reported that perennial grasses that reproduce vegetatively such as *Panicum hemitomon* (frequent in some seed banks in the current study, but not abundant) and *Leersia hexandra* may be rare or absent in the seed banks of wetlands in which they otherwise represent the dominant vegetation (Kirkman 1995).

By 2002, there was nearly twice the number of species in the vegetation that were not observed in the seed bank as in 1999, all but two of which had established during the drought. Yet, other than *Erechtites hieraciifolia* (L.) Raf. Ex DC, which colonized two bays, these species were not annuals known for long-distance dispersal. It is not known whether the other additional species were missed in the seed bank, did not germinate in the assay, or were dispersed by wind, water, or animals; whatever the case, their establishment did not result in high abundance. Two grasses, *Andropogon virginicus* and *Sacciolepis striata*, were the only exceptions, as they became relatively abundant in two bays. Overall, dispersal, particularly in fragmented landscapes, may not be a significant source of propagules for many Carolina bays, despite the establishment opportunity presented by substrate exposed during drawdown (van der Valk and Davis 1978, Burke and Grime 1996).

Even though percent dissimilarities between 1999 and 2002 were high, it was likely that only a small number of aquatic and grass species were driving the dynamics. High percent dissimilarities between the seed bank and the extant vegetation of either year reflected vast differences between both the number and abundance of species, even at the same point on the landscape (Kirkman and Sharitz 1994). Spatial dissimilarity between the seed bank and adult plants is not surprising, as fluctuating water levels transport seeds throughout a basin, often at a distance from the populations from which they were set (van der Valk and Davis 1976).

However, it remains that the majority of seed bank species in a plot were never seen in the vegetation of that plot.

Weiher and Keddy (1995) experimentally tested the effects of water depth, flooding duration, leaf litter, soil surface texture, growing season, and an invasive species on community composition in freshwater microcosms and reported that hydrologic variables were most strongly significant. It is possible that studies in Carolina bays undertaken during a moderate climate, when individuals are not drowned or drought-stressed, might observe different relationships between the seed bank and extant vegetation. Yet, Weiher and Keddy (1995) also reported that fertility and leaf litter could significantly influence communities in some instances and, clearly, factors other than hydrologic condition contribute to species composition. In these bays it may be that dense, clonal grasses prevented germination from the seed bank or establishment by other species (Kirkman and Sharitz 1994), as has been suggested for *Phalaris arundinacea* L. and *Leersia oryzoides* (L.) Sw. in prairie pothole wetlands (Galatowitsch and van der Valk 1996). Also, the role of disturbance, particularly fire, which was historically a part of the landscape and is now almost totally suppressed, in altering vegetation dynamics was not investigated in this study. Kirkman (1992) and Kirkman and Sharitz (1994) considered fire integral to bay vegetation dynamics, removing woody species and changing the dynamics of grasses, including *Panicum hemitomon*, when followed by winter inundation (Kirkman and Sharitz 1993, Kirkman 1995). There is evidence that fire stimulates the establishment of some herbaceous bay species (Kirkman 1995), and the extent to which fire alters the relationship between the seed bank and vegetation in herbaceous Carolina bays warrants further research.

The high dissimilarity between the seed bank and vegetation throughout the study makes it difficult to predict vegetation composition based on the species pool. van der Valk (1981) described a model of succession in prairie potholes that posited that if the seed bank composition and the conditions under which those species would germinate were known, then species present in the vegetation could be predicted for a given environment. Thus, the environment acted as a sieve, removing species unsuited to the conditions present and enabling others to establish. However, in Carolina bays, there are vastly more species in the seed bank than the vegetation, many of which have similar life histories as defined by van der Valk (1981). Further, seed bank species often occur at low abundance and, therefore, it is extremely difficult to forecast which will be expressed at a given time.

Knowledge of the range of plant species composition observed in relatively undisturbed herbaceous Carolina bays is crucial if we are to assess, restore, and manage these isolated wetlands effectively. In prairie pothole systems, the plant species composition of restored wetlands has been shown not to approximate that of natural wetlands (Mulhouse and Galatowitsch 2003), yet little information describing species composition has been available to facilitate such comparisons in Carolina bays. This study provides a template for determining what the vegetation of herbaceous bays might be throughout a range of hydrologic conditions and illustrates the complex way in which the seed bank influences composition (see also: De Steven and Toner 2004). Such information may aid those involved in the monitoring and restoration of bays.

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Table 3.1. The percent and number (*n*) of months flooded and water depth (mean±standard error) during the growing season (March-November) for both years vegetation was sampled. There were only four months of record for 2002 due to sampling omission.

Bay	**1999 mo. flooded**	**2002 mo. flooded**	**1999 depth (m)**	**2002 depth (m)**
3	100 (9)	25 (1)	.89±.09	.14±.12
31	100 (9)	25 (1)	.61±.04	.05±.05
78	78 (7)	25 (1)	.39±.25	.08±.07
176	100 (9)	0 (0)	.78±.05	0±0

Table 3.2. Summaries and comparisons of 1999 and 2002 vegetation surveys and 2000 seed bank survey. See notes for detailed descriptions.

Bay	**Veg. Rich-ness (‘99)**	**Veg. rich-ness (‘02)**	**Spp. in both ’02 and ’99 veg.[+]**	**Seed bank rich-ness (’00)**	**Spp. in both ’99 veg. and seed bank[†]**	**Spp. in both ’02 veg. and seed bank[‡]**	**New species from seed bank by ‘02.[Φ]**	**Seed bank spp. never in veg.[Ψ]**
3	21	32	8 (18)	80	13 (62)	13 (42)	6 (46)	61 (76)
31	15	29	9 (25)	55	5 (33)	13 (45)	11 (85)	39 (71)
78	21	18	13 (50)	63	15 (71)	9 (50)	0 (0)	48 (76)
176	24	32	11 (22)	67	17 (71)	18 (56)	8 (44)	41 (61)

+ The number and percent (*p*) of species in total bay flora observed in both 1999 and 2002.
† The number and percent (*p*) of species in 1999 vegetation also observed in seed bank.
‡ The number and percent (*p*) of species in 2002 vegetation also observed in seed bank.
Φ The number and percent (*p*) of species in both the 2002 vegetation and the seed bank not observed in 1999 vegetation.
Ψ The number and percent (*p*) of species in the seed bank not observed in vegetation in either survey year.

Table 3.3. The mean±standard error of the number of species per plot in the 1999 and 2002 vegetation surveys and the 2000 seed bank. Mean±standard error seed bank densities are also presented.

Bay	**1999 Vegetation**	**2002 Vegetation**	**2000 Seed bank**	**Seed bank density (seeds/m^2)**
3	3±0.4	3±0.4	15±0.8	11705±1691
31	3±0.2	3±0.4	11±0.9	13723±2801
78	4±0.4	5±0.8	15±0.6	9152±1142
176	3±0.2	5±0.3	18±0.6	13949±1549

Table 3.4. Percent frequency (and number of plots) of species occurring at ≥40% in the 1999 and 2002 vegetation and percent relative abundance of species observed at ≥5%. Also shown is the percent frequency (and number of plots) of species occurring at ≥40% in the 2000 seed bank and percent relative abundance of species observed at ≥5%. Species are arrayed by National Wetland Indicator category.

Bay 3 ***Species***	**Veg. freq. 1999**	**Veg. freq. 2002**	**Veg. abun. 1999**	**Veg. abun. 2002**	**Seed bank freq. 2000 (plots)**	**Seed bank abun. 2000 (seeds)**
OBL						
Bacopa caroliniana	+		+		65 (24)	5 (266)
Brasenia schreberi	+		44			
Decodon verticillatus					84 (31)	8 (435)
Isoetes sp.					49 (18)	5 (296)
Juncus acuminatus					46 (17)	+
Leersia hexandra Sw.	+	+	5	+	+	+
Ludwigia palustris (L.) Ell.					57 (21)	+
Nymphoides cordata (Ell.) Fern.	+		+		59 (22)	5 (270)
Panicum hemitomon	43 (16)	41 (15)	21	19	+	+
Polygonum hydropiperoides Michx.	+	+	+	+	43 (16)	+
Pontederia cordata	+		11		+	+
Psilocarya spp.					76 (28)	6 (367)
Rhynchospora decurrens Chapman					+	6 (356)
Sagittaria filiformis J. G. Sm.	+		+		57 (21)	+
Utricularia spp.	+		5		+	+
FACW+						
Rhexia virginica		+		+	65 (24)	16 (926)
FACW						
Panicum dichotomiflorum		+		40	+	+
Panicum verrucosum		51 (19)		27	78 (29)	11 (613)
FACW-						
Oldenlandia uniflora					+	5 (302)
FAC+						
Chamaesyce serpens					49 (18)	+
FACU						
Eupatorium capillifolium	+		+		62 (23)	+
Oxalis corniculata L.					51 (19)	+

+ Species present, but below designated threshold.

Table 3.4 (cont'd).

Bay 31 ***Species***	**Veg. freq. 1999**	**Veg. freq. 2002**	**Veg. abun. 1999**	**Veg. abun. 2002**	**Seed bank freq. 2000 (plots)**	**Seed bank abun. 2000 (seeds)**
OBL						
Juncus acuminatus					62 (18)	9 (452)
Juncus repens					45 (13)	+
Micranthemum umbrosum					+	7 (351)
Nymphaea odorata	62 (18)		61		41 (12)	+
Panicum hemitomon	66 (19)	83 (24)	5	70	52 (15)	+
Psilocarya spp.		+		+	+	6 (276)
Scirpus cyperinus		+		+	45 (13)	+
Utricularia spp.	69 (20)		22		+	+
FACW+						
Juncus effusus	+	+	6	+	55 (16)	25 (1222)
FACW						
Cyperus odoratus		+		14	72 (21)	18 (888)
Panicum verrucosum		+		+	66 (19)	+
FACW-						
Oldenlandia uniflora					+	6 (273)
FAC+						
Chamaesyce serpens					69 (20)	+

+ Species present, but below designated threshold.

Table 3.4 (cont'd).

Bay 78 ***Species***	**Veg. freq. 1999**	**Veg. freq. 2002**	**Veg. abun. 1999**	**Veg. abun. 2002**	**Seed bank freq. 2000 (plots)**	**Seed bank abun. 2000 (seeds)**
OBL						
Bacopa caroliniana					73 (16)	+
Drosera rotundifolia	+		+		+	10 (246)
Eriocaulon compressum	+	+	+	+	73 (16)	+
Nymphaea odorata	59 (13)		35		+	+
Leersia hexandra		45 (10)	+	+	+	+
Panicum hemitomon	45 (10)	73 (16)	8	21	+	+
Psilocarya spp.					86 (19)	11 (272)
Utricularia spp.	+		+		41 (9)	+
Xyris jupicai					50 (11)	11 (277)
Xyris smalliana					59 (13)	+
FACW+						
Scleria reticularis	+	45 (10)	14	8	86 (19)	+
Eleocharis tricostata Torr.					41 (9)	+
FACW						
Panicum verrucosum	55 (12)	55 (12)	9	16	95 (21)	17 (445)
FACW-						
Oldenlandia uniflora					41 (9)	+
FAC+						
Chamaesyce serpens					77 (17)	+
FAC-						
Andropogon virginicus		73 (16)		19		
FACU						
Oxalis corniculata					55 (12)	+
NO						
Dichanthelium wrightianum		59 (13)	17	22	50 (11)	6 (147)
Panicum sp.		+		7		

+ Species present, but below designated threshold.
NO Species for which an indicator was not applicable. In both cases, species were considered to occur chiefly in a non-wetland environment.

Table 3.4 (cont'd).

Bay 176 ***Species***	**Veg. freq. 1999**	**Veg. freq. 2002**	**Veg. abun. 1999**	**Veg. abun. 2002**	**Seed bank freq. 2000 (plots)**	**Seed bank abun. 2000 (seeds)**
OBL						
Decodon verticillatus	+	40 (19)	5	19	46 (22)	+
Fuirena breviseta	+		+		100 (48)	8 (723)
Juncus acuminatus	+		+		85 (41)	6 (496)
Juncus canadensis		+		+	67 (32)	+
Nymphaea odorata	79 (38)		69		48 (23)	+
Panicum hemitomon	50 (24)	67 (32)	15	28	71 (34)	+
Polygonum densiflorum		+		6	54 (26)	5 (424)
Psilocarya spp.		+		+	90 (43)	15 (1231)
Sacciolepis striata		40 (19)		11		
Scirpus cyperinus		+		+	73 (35)	+
Utricularia spp.	71 (34)		7		+	+
Xyris jupicai					50 (24)	+
FACW+						
Juncus effusus	+	+	+	+	71 (34)	24 (2076)
FACW						
Cyperus odoratus		+		+	81 (39)	+
Panicum verrucosum	+	52 (25)	+	18	63 (30)	5 (415)
FAC+						
Chamaesyce serpens					56 (27)	+
FACU						
Eupatorium capillifolium	+	40 (19)	+	+	40 (19)	+

+ Species present, but below designated threshold.

Table 3.5a. Relative abundances of herbaceous species found in the vegetation in 1999, but not in the 2000 seed bank, for each of the four bays. The bold number is a species occurring at a relative abundance of ≥5% in 1999. Species are ordered by National Wetland Indicator category and assigned appropriate life form (A=annual; P=perennial). Woody species and lianas were excluded from tabulation.

Species	**Life-form**	**Bay 3**	**Bay 31**	**Bay 78**	**Bay 176**
OBL					
Brasenia schreberi	P	**43.55**			
Hydrocotyle ranunculoides L. f.	P				0.16
Hydrocotyle verticillata Thunb.	P				0.13
Lachnanthes caroliana (Lam.) Dandy	P			2.08	
Myriophyllum sp.	P	0.90			
Nelumbo lutea Willd.	P	0.51			
Sagittaria filiformis	P		0.44		
FACW					
Bidens discoidea (Torr. & Gray) Britt.	A	1.54	0.08		
Centella asiatica (L.) Urban	P			3.81	
Galium tinctorium	P				0.001
FAC+					
Solidago fistulosa P. Mill.	P				0.02

Table 3.5b. Relative abundances of herbaceous species found in the vegetation by 2002, but not in the 2000 seed bank, for each of the four bays. Identifications to genus were considered to be unique species based on a comparison of species already observed in the field to those in the seed bank (i.e. if all species of a genus in the seed bank were found at a bay, additional unique species in the extant vegetation that could not be fully identified were considered to represent new taxa). Bold numbers are species occurring at a relative abundance of ≥5% by 2002. Species are ordered by National Wetland Indicator category and assigned appropriate life form (A=annual; P=perennial; AP=annual/perennial). Woody species and lianas were excluded from tabulation.

Species	**Life-form**	**Bay 3**	**Bay 31**	**Bay 78**	**Bay 176**
OBL					
Carex comosa Boott.	P				0.18
Lachnanthes caroliana	P			1.47	
Ludwigia leptocarpa (Nutt.) Hara	AP		0.28		
Ludwigia sphaerocarpa Ell.	P	0.25			
Lycopus uniflorus Michx.	P				0.005
Sacciolepis striata	P	2.82			**11.24**
FACW+					
Boehmeria cylindrica (L.) Sw.	P	0.63			
Polygonum punctatum Ell.	AP	0.54			
FACW					
Centella asiatica	P			0.01	
Eleocharis melanocarpa Torr.	P			0.01	
Erianthus giganteus (Walt.) Pers.	P		0.05		1.03
Rhynchospora globularis (Chapman) Small	AP	0.003			0.005
FAC-					
Andropogon virginicus	P	0.04	0.05	**18.91**	0.39
Erechtites hieraciifolia	A	0.50			0.41
Eupatorium compositifolium	P	0.002	0.002		0.18
NA					
Bidens sp.		0.13			
Carex sp.	P	0.003			
Eupatorium altissimum L.	P			0.01	
Panicum sp. 1		1.03		6.85	
Panicum sp. 2					0.44
Polygonum caespitosum Blume	A	0.01			

Table 3.6. The means±standard errors of the Bray-Curtis dissimilarities between the 1999 and 2002 vegetation, 1999 vegetation and 2000 seed bank, and 2002 vegetation and 2000 seed bank for each study bay as computed for each plot for each bay. Vegetation comparisons were based on the absolute abundances of species in the vegetation in a given plot in each study year while calculations between the vegetation and seed bank were based on relative abundances.

Bay	**‘99 veg. and ‘02 veg.**	**‘99 veg. and seed bank**	**’02 veg. And seed bank**
3	0.84±0.05	0.97±0.01	0.91±0.02
31	0.94±0.02	0.90±0.03	0.86±0.05
78	0.90±0.03	0.89±0.03	0.93±0.02
176	0.86±0.03	0.97±0.01	0.91±0.02

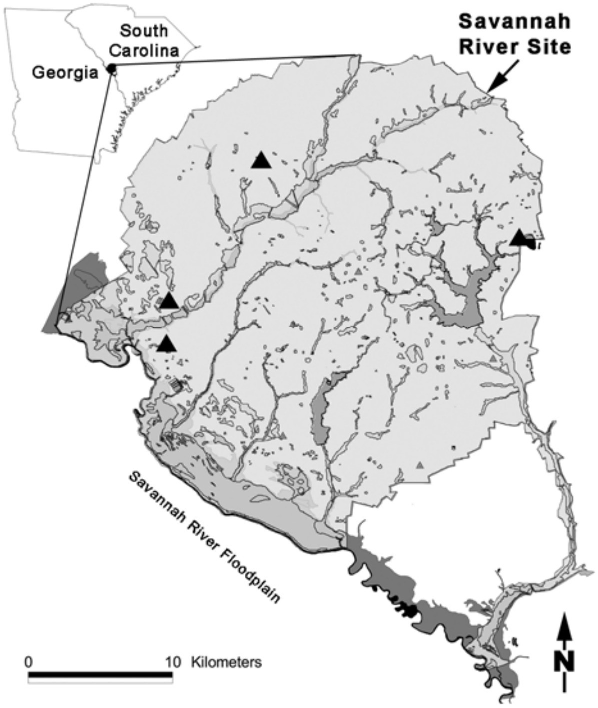

Figure 3.1. The Savannah River Site (SRS) in Aiken, South Carolina, USA, within which all study bays, indicated by triangles, were located. Center Latitude: 33°14’44.79” Longitude: -081°37’58.33”.

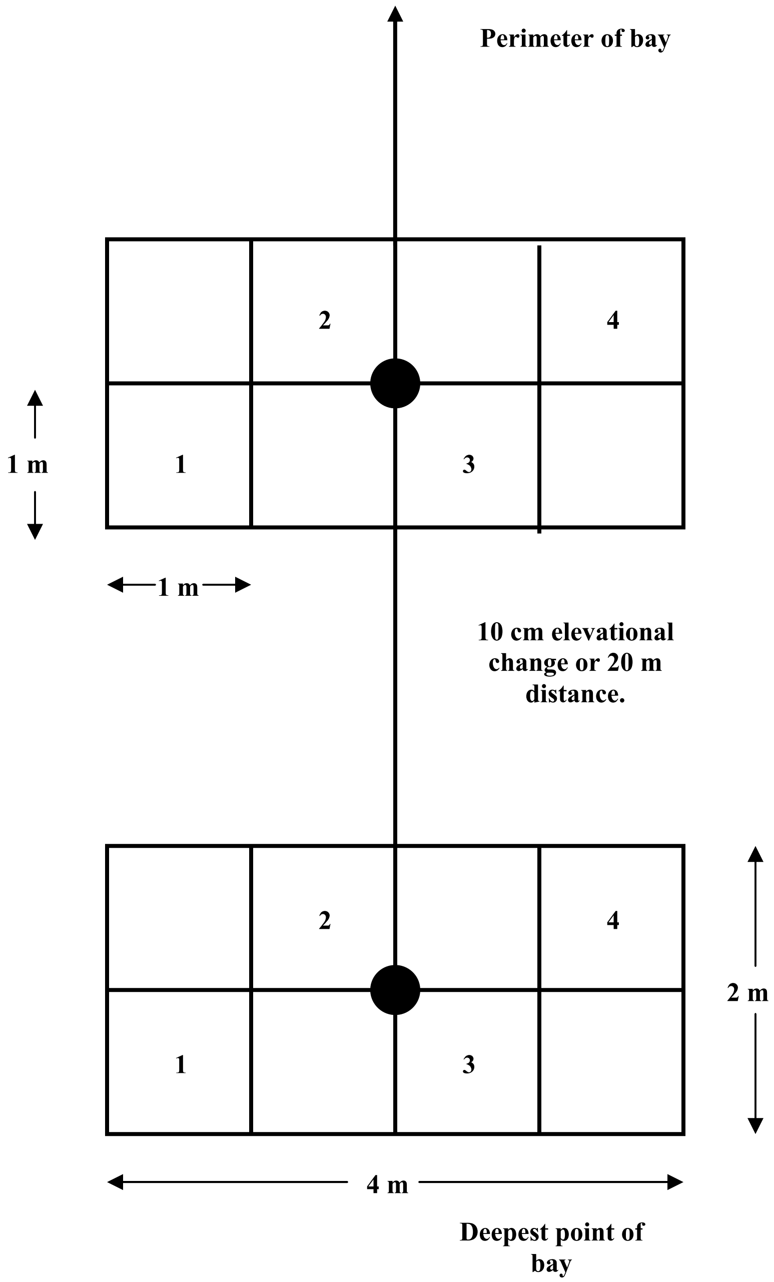

Figure 3.2. Layout of sampling plots used in seed bank and vegetation surveys. Subplots 1, 2, 3, and 4 were used for vegetation sampling in 1999 and 2002. Subplots 2 and 3 were used for seed bank sampling in 2000.

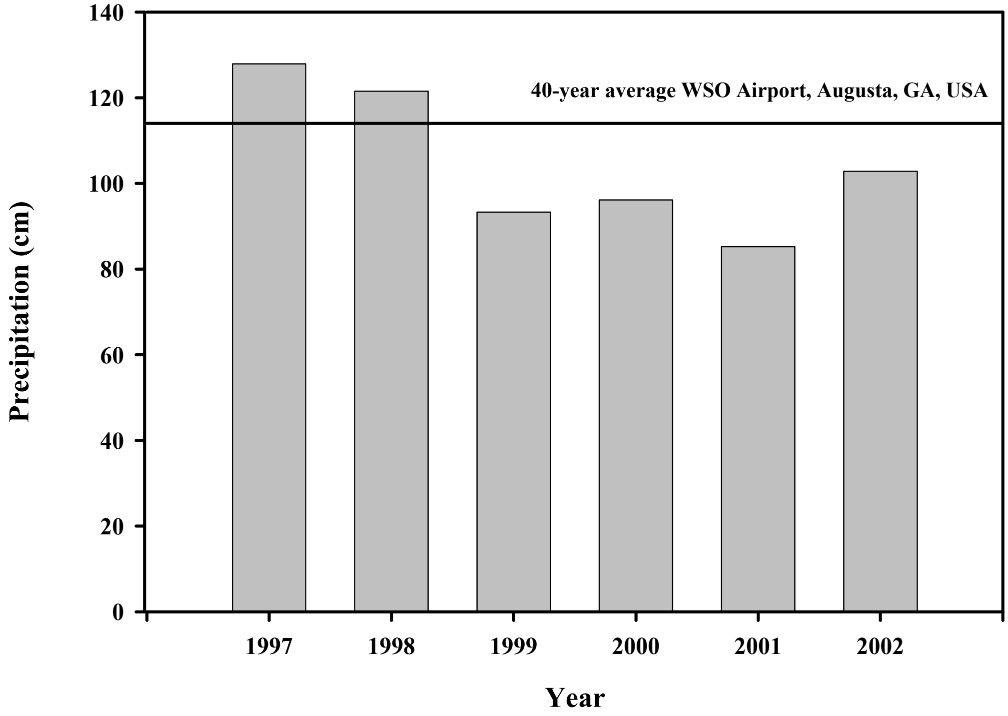

Figure 3.3. Yearly precipitation in Augusta, GA throughout the study period relative to the 40-year average (Southeastern Regional Climate Center 2003).

CHAPTER FOUR

CONCLUSIONS

Response of vegetation during the drought

Herbaceous Carolina bay plant communities of the Upper Coastal Plain clearly, and not surprisingly, changed considerably in response to drought. Yet, whether considered in terms of vegetation type (chapter 1) or at a within-bay level (chapter 2), much of the change in species composition was driven by the total disappearance of aquatic species and the dynamics of a few grasses. Additionally, there was an increase in seedlings of woody species. Although grass species differed among vegetation types (chapter 1), their overarching importance in establishment and expansion during the drought was unquestionable.

Following the universal loss of aquatic species, particularly *Utricularia* spp., vegetation types responded differently to drought if change was considered at the species level. Open-water ponds and depression meadows exhibited the most striking decreases in duration of flooding and mean water depth, with establishment of upland grasses in both types. Open-water ponds also accumulated the most species, likely as a result of the substrate exposed as water depth declined. Yet, depression meadows retained *Leersia hexandra* as a frequently occurring species, while *Panicum hemitomon* was frequent by 2002 in open-water ponds. Since *Panicum hemitomon* remained frequent in grass marshes, open-water ponds and grass marshes may have become indistinguishable during the drought, particularly as *Panicum verrucosum* became frequent in both. De Steven and Toner (1997, 2004) suggested that grass marshes and open-water ponds might have a successional relationship. The bays examined in chapter two, in which *Nymphaea odorata* and *Panicum hemitomon* were generally the most frequent and/or abundant species in 1993, could be categorized as open-water ponds; *Panicum hemitomon* and *Panicum verrucosum* had expanded or established in most of these bays by 2002. Sedge marshes, dominated by *Carex striata*, were unique in that composition did not fluctuate appreciably. With relatively high flooding duration and mean water depth throughout the drought, sedge marshes may be the most hydrologically stable systems; such hydrologic stability could also stabilize species composition. The life-history of *Carex striata*, a dense, clonal perennial, may also confer stability, as might landscape setting, since these systems were found exclusively in low, wet areas. However, Tyndall et al. (1990) reported low species richness in bays in Maryland dominated by *Carex striata* regardless of hydrologic condition and *Carex striata*, in the absence of disturbance, may be an effective barrier to the establishment of other species.

The dynamics of the aquatic, grass, and woody species in both studies were remarkably similar to predictions by Kirkman (1992, 1995), who used aerial photos as well as field sampling to determine vegetative cover. De Steven and Toner's cyclic model (1997, 2004), an expansion upon Kirkman (1992, 1995) developed within the context of vegetation types, is also consistent with the current findings. Additional studies have described wetland vegetation dynamics as influenced largely by changes in a few species. Mitchell and Niering's (1993) investigation of beaver flooding in a topogenic bog summarized vegetation change using only four broad species groups, each including a few predominant taxa. Yet, some work, such as van der Valk and Davis's (1978) description of vegetation dynamics in prairie potholes, has incorporated more diverse species groups and a larger number of individual species.

Seed bank-vegetation relationships

Overall, there was little similarity between the vegetation of either 1999 or 2002 and the 2000 seed bank (chapter 2). Species frequent and/or abundant in the vegetation were generally not found at commensurate levels in the seed bank. *Panicum hemitomon* was extremely abundant in each of the bays, yet frequent in seed banks of only two. Other abundant grasses such as *Leersia hexandra* and *Andropogon virginicus* were rare or absent in seed banks. Further, more than 60% of the species in the seed banks were never detected in the vegetation. Therefore, although seed bank composition was obviously influenced by vegetation history, given the longevity of many seeds (see: Leck 1989), the relevant history may be on the order of several years or even decades, not simply the previous season.

Perhaps during flooded or very dry conditions the seed bank does not play a large role as an extreme environment prevents recruitment. A study undertaken during a more moderate climate shift than occurred in this study period might observe different relationships between the seed bank and extant vegetation. In the current study, as previously reported for other wetlands, including Carolina bays, knowledge of the seed bank conferred very little power to predict vegetation change (Smith and Kadlec 1983, McGraw 1987, Poani and Dixon 1995, Ungar and Woodell 1996, Galatowitsch and Biederman 1998).

van der Valk (1981) described a model of succession in prairie potholes that posited that if the seed bank composition and the conditions under which those species would germinate was known, then species present in the vegetation could be predicted for a given hydrologic environment. Thus, the environment acted as a sieve, removing species unsuited to the conditions present and enabling others to establish. However, in Carolina bays, there are likely too many species in the seed bank relative to the vegetation, many of which have similar life histories and occur at low seed bank abundance, to forecast of which will be expressed at a given time. Chapter two presents evidence that many of these species may germinate infrequently, and it is unclear under what conditions most might be present in the standing vegetation. The dominance of robust, fast-spreading, clonal grasses and sedges such as *Panicum hemitomon* and *Carex striata* that can tolerate wet and dry conditions, may further prevent establishment of seedlings in Carolina bays.

Predictions of vegetation response during fluctuating hydrologic conditions

The response of herbaceous Carolina bays to drought can perhaps be predicted at a species-level only within the context of vegetation types (chapter 1). Even then, the fullest extent of prediction may be in stating to what degree a particular grass species might expand or how frequent seedlings of a certain woody species might become. Keddy (2000) noted the difficulty of predicting the occurrence of individual species and suggested the use of broader functional groups. van der Valk (1981) also considered life history traits rather than individual species when attempting to conceptualize vegetation change in prairie potholes. While the current studies do not explicitly consider functional or life history groups, in general, it could be said that in herbaceous Carolina bays aquatic species disappear and signature grasses, changing in identity and extent based on the severity of drawdown, establish and/or expand during drought. Within these grasses may be found woody seedlings and scattered herbs such as *Rhexia* spp. and *Triadenum* spp., but it is the matrix of grasses that is most dynamic. The exception to this is the sedge marsh vegetation type (chapter 1), which, even as some species disappear and others establish, remains almost totally dominated by *Carex striata* and, on the periphery of bays, *Nyssa sylvatica*.

Future research

Of future interest is whether, given a return to a wetter hydrologic regime, bay vegetation resembles that seen during previous periods of inundation, both individually and in the context of vegetation types. There is precedent for vegetation cycling in other wetland systems, including van der Valk's (1981) description of cyclic vegetation dynamics in prairie potholes and Mitchell and Niering's (1993) assertion that unidirectional succession in northeastern bogs is unlikely. Together with Kirkman's (1992, 1995) findings during drought ten years previous and the De Steven and Toner model (1997, 2004), the current study reinforces the conception that the vegetation of herbaceous Carolina bays cycles over time. De Steven and Toner (1997, 2004) predicted that if hardwoods were persistent in bays there might be directional succession toward forested systems in some instances. However, widespread establishment by hardwoods was not observed in the current study.

Kirkman (1995) also described the importance of fire, now almost totally removed from the landscape surrounding the bays in this study, in maintaining a cyclic dynamic. In herbaceous Carolina bays, fire removes woody species, stimulates seed bank response and, depending on when inundation occurs relative to a burn, can drastically alter the dynamics of dominant grasses, including *Panicum hemitomon* (Kirkman 1995). The extent to which fire alters the relationship between the seed bank and vegetation warrants further research. The present studies do not explore the impact of fire or other disturbances, and only with additional long-term data sets can we be sure that the perspective that herbaceous Carolina bays of the Upper Coastal Plain are resilient systems, with vegetation composition cycling in relation to climate, is correct.

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APPENDIX

Appendix: Plant species observed in the 1999 and 2002 vegetation and 2000 seed bank.

	’99 Vegetation				**‘02 Vegetation**				**‘00 Seed bank**			
Bay	**3**	**31**	**78**	**176**	**3**	**31**	**78**	**176**	**3**	**31**	**78**	**176**
Species												
Acer rubrum L.		X		X	X†	X		X				
Ampelopsis arborea (L.) Koehne		X										
Andropogon virginicus					X	X	X	X				
Antennaria fallax Greene										X		
Baccharis halimifolia L.						X						
Bacopa caroliniana	X								X	X	X	X
Bidens discoidea	X	X										
Bidens sp.					X							
Boehmeria cylindrica					X							
Brasenia schreberi	X			X						X		X
Campsis radicans (L.) Seem. ex Bureau						X						
Carex albolutescens Schwein.				X		X			X	X	X	X
Carex comosa								X				
Carex lurida Wahlenb.									X			X
Carex sp. 1						X‡						
Carex sp. 2					X							
Celtis laevigata Willd.					X							
Centella asiatica			X				X		X			
Cephalanthus occidentalis L.	X	X			X	X			X			X
Chamaesyce serpens									X	X	X	X
Conyza canadensis (L.) Cronq.						X	X†	X	X	X	X	X
Croton elliottii Chapman			X				X				X	
Cyperaceae							X‡					
Cyperus compressus L.									X		X	
Cyperus globulosus Aublet.									X	X	X	X
Cyperus haspan L.									X	X	X	X
Cyperus odoratus L.						X		X	X	X	X	X
Cyperus polystachyos Rottb.									X	X		X
Decodon verticillatus				X				X	X		X	X
Dicanthelium wrightianum			X		X		X		X		X	
Digitaria sanguinalis (L.) Scop.									X		X	X
Diodia teres Walt.					X†							
Diospyros virginiana L.			X	X	X	X†	X†	X				
Drosera rotundifolia			X						X		X	X
Echinodorus parvulus Engelm.									X			
Eleocharis acicularis									X	X	X	
Eleocharis elongata Chapman									X		X	

† Species removed from analyses as only occurring as a single individual in subplots (“r” cover).
‡ Species removed from analyses as incomplete identification potentially confounded with other species.
Φ Species combined at genus level.

Appendix (cont’d).

	‘99 Vegetation				**‘02 Vegetation**				**‘00 Seed bank**			
Bay	**3**	**31**	**78**	**176**	**3**	**31**	**78**	**176**	**3**	**31**	**78**	**176**
Species												
Eleocharis equisetoides (Ell.) Torr.			X				X		X		X	
Eleocharis melanocarpa							X					
Eleocharis obtusa Willd. J.A. Schultes			X					X	X	X	X	X
Eleocharis tricostata Torr.											X	X
Eleocharis vivipara Link									X		X	X
Erechtites hieraciifolia					X	X†	X†	X				
Erianthus giganteus						X		X				
Eriocaulon compressum Lam.			X				X				X	
Eupatorium altissimum							X					
Eupatorium capillifolium	X			X		X		X	X	X	X	X
Eupatorium compositifolium					X	X		X				
Eupatorium sp.							X†					
Fimbristylis autumnalis (L.) R. & S.									X	X	X	X
Fuirena breviseta				X					X	X	X	X
Fuirena pumila (Torr.) Spreng				X								X
Galium tinctorium				X								
Gnaphalium spicatum Lam.									X	X	X	
Gratiola ramose Walt.									X		X	
Habenaria repens Nutt.				X								X
Hibiscus moscheutos L.	X				X				X			
Hydrocotyle ranunculoides L. f.				X								
Hydrocotyle verticillata Thunb.				X								
Hypericum canadense L.									X	X		X
Hypericum denticulatum Walt.									X		X	X
Hypericum gymnanthum Engelm. & Gray					X†							
Hypericum hypericoides (L.) Crantz									X	X		
Hypericum mutilum L.									X	X	X	X
Isoetes sp.									X	X	X	X
Iva microcephala Nutt.											X	
Ilex opaca Ait.					X†		X†					
Juncus acuminatus				X					X	X	X	X
Juncus canadensis								X		X		X
Juncus dichotomus Ell.									X	X	X	X
Juncus effusus		X		X		X		X		X	X	X
Juncus elliottii Chapman									X	X	X	X
Juncus marginatus Rostk.									X	X		X
Juncus repens										X		X
Juncus tenuis Willd.									X			
Juncus sp.										X‡		X‡
Lachnanthes caroliana			X				X					
Leersia hexandra	X		X	X	X		X	X	X		X	X

† Species removed from analyses as only occurring as a single individual in subplots (“r” cover).
‡ Species removed from analyses as incomplete identification potentially confounded with other species.
Φ Species combined at genus level.

Appendix (cont’d).

	‘99 Vegetation				**‘02 Vegetation**				**‘00 Seed bank**			
Bay	**3**	**31**	**78**	**176**	**3**	**31**	**78**	**176**	**3**	**31**	**78**	**176**
Species												
Lemna valdiviana	X	X								X		
Lindernia anagallidea (Michx.) Pennell									X	X	X	X
Liquidambar styraciflua		X			X†	X	X†		X			
Ludwigia decurrens Walt.												X
Ludwigia leptocarpa						X		X	X			X
Ludwigia palustris (L.) Ell.									X	X	X	X
Ludwigia sphaerocarpa					X			X†				
Ludwigia spathulata Torr. & Gray									X			
Lycopus uniflorus								X				
Mayaca fluviatilus Aubl.									X		X	
Micranthemum umbrosum									X	X		
Myrica cerifera								X		X		
Murdannia keisak (Hassk.) Hand.-Maz.									X			
Myriophyllum sp.	X											
Nelumbo lutea	X											
Nymphaea odorata	X	X	X	X			X†		X	X	X	X
Nymphoides cordata	X								X	X	X	X
Nyssa sylvatica	X	X	X		X	X	X	X†				
Oldenlandia boscii (DC.) Chapman									X			X
Oldenlandia uniflora									X	X	X	X
Oxalis corniculata									X	X	X	X
Panicum dichotomiflorum					X				X	X	X	X
Panicum hemitomon	X	X	X	X	X	X	X	X	X	X	X	X
Panicum longifolium Torr.									X	X		
Panicum verrucosum			X	X	X	X	X	X	X	X	X	X
Panicum sp. 1					X		X					
Panicum sp. 2								X				
Paspalum acuminatum Raddi									X		X	
Pinus taeda	X		X	X	X	X†	X					
Pluchea foetida (L.) DC.										X		
Pluchea odorata (L.) Cass.								X†				X
Polygonum caespitosum					X							
Polygonum densiflorum					X			X	X			X
Polygonum hirsutum Walt.				X				X				X
Polygonum hydropiperoides	X				X	X		X	X	X		X
Polygonum punctatum Ell.					X							
Polygonum sp.									X‡			
Polypremum procumbens L.									X	X	X	X
Pontedaria cordata	X								X	X		
Potamogeton diversifolius Raf.									X			X
Psilocarya nitens (Vahl) Gray					X†	X		X	X$^{\Phi}$	X$^{\Phi}$	X$^{\Phi}$	X$^{\Phi}$

† Species removed from analyses as only occurring as a single individual in subplots (“r” cover).
‡ Species removed from analyses as incomplete identification potentially confounded with other species.
Φ Species combined at genus level.

Appendix (cont'd).

	'99 Vegetation				**'02 Vegetation**				**'00 Seed bank**			
Bay	**3**	**31**	**78**	**176**	**3**	**31**	**78**	**176**	**3**	**31**	**78**	**176**
Species												
Psilocarya scirpoides (Torr.) Gray											X$^{\Phi}$	X$^{\Phi}$
Psilocarya sp.									X$^{\Phi}$	X$^{\Phi}$	X$^{\Phi}$	X$^{\Phi}$
Quercus nigra L.							X†	X				
Quercus phellos L.		X				X						
Quercus sp.					X†							
Rhexia mariana L. *var. mariana*				X	X	X	X†	X	X	X	X	X
Rhexia virginica			X		X				X	X	X	X
Rhus copallinum L.					X†				X			X
Rhus radicans L.					X							
Rhynchospora decurrens			X						X	X	X	X
Rhynchospora filifolia Gray									X		X	
Rhynchospora globularis					X			X				
Rhynchospora gracilenta Gray											X	
Rhynchospora tracyi Britt.											X	
Rotala ramosior (L.) Koehne	X								X	X	X	X
Rubus sp.					X	X	X	X				
Sacciolepis striata					X			X				
Sagittaria filiformis	X	X							X		X	
Sagittaria isoetiformis J.G. Sm.									X		X	
Salix nigra Marsh.						X			X			X
Saururus cernuus L.					X†							
Scirpus cyperinus						X		X	X	X	X	X
Scleria reticularis			X			X	X		X	X	X	X
Smilax rotundifolia L.	X	X	X		X	X						
Solidago fistulosa				X								
Sphagnum sp.					X							
Stachys hyssopifolia Michx. *var hyssopifolia*									X			
Taxodium distichum (L.) L.C. Rich		X				X						
Triadenum walteri (J.G. Gmel.) Gleason				X	X†			X		X		X
Typha latifolia L.						X						
Typha sp.									X	X		
Utricularia biflora L.									X$^{\Phi}$	X$^{\Phi}$	X$^{\Phi}$	X$^{\Phi}$
Utricularia subulata L.										X$^{\Phi}$	X$^{\Phi}$	X$^{\Phi}$
Utricularia (*purpurea* Walt. & *biflora* L.)	X$^{\Phi}$	X$^{\Phi}$	X$^{\Phi}$	X$^{\Phi}$								
Vaccinium elliottii Chapman								X†				
Vaccinium sp.						X†						
Viola lanceolata L.			X		X		X		X		X	X
Vitis rotundifolia Michx.						X						
Xyris jupicai									X	X	X	X
Xyris platylepis Chapman											X	X
Xyris smalliana									X		X	X

† Species removed from analyses as only occurring as a single individual in subplots ("r" cover).

‡ Species removed from analyses as incomplete identification potentially confounded with other species.

Φ Species combined at genus level.

Appendix (cont'd).

	'99 Vegetation				**'02 Vegetation**				**'00 Seed bank**			
Bay	**3**	**31**	**78**	**176**	**3**	**31**	**78**	**176**	**3**	**31**	**78**	**176**
Species												
Unk. seedling 1					X†‡							
Unk. seedling 2							X†					
Unk. tree seedling								X‡				

† Species removed from analyses as only occurring as a single individual in subplots ("r" cover).
‡ Species removed from analyses as incomplete identification potentially confounded with other species.
Φ Species combined at genus level.