

Linking hydroperiod and vegetation response in Carolina bay wetlands

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Received 13 February 2004; accepted in revised form 23 September 2005

Key words: Carolina bay, Depressional wetland, Gradient, Plant community, Vegetation, Zonation

Abstract

Hydrology filters propagule bank expression in herbaceous Carolina bays, but the strength of this filter's effects on community composition at different points along the hydrologic gradient of these southeastern U.S. depressional wetlands is unknown. We used an experimental approach to determine the pattern of vegetation expression from propagule banks of Carolina bays exposed to different hydrologic conditions and gradients. Propagule banks of sediment cores collected from six Carolina bays were placed in bins, each of which was allocated to one of three hydrologic treatments: moist soil (MS), mid-summer drawdown (DD), or flooded (FL). After one season of vegetation development (1995) in the hydrologic treatments, half of the bins were left flat and the remaining were sloped to produce a finer moisture gradient within each bin. We compared taxa richness, community composition based on cover, and cover patterns of eight abundant species that developed in bins over the season (1996) after sloping. Species richness was significantly higher in the moist soil treatment and in sloped bins. Community composition, however, was affected by the hydrologic treatment only and not the finer-scale flooding gradient produced by sloping. Under flooded conditions, floating-leaved and submerged aquatics had higher cover; vegetation converged on simpler, less variable communities dominated by obligate wetland species, with species exhibiting different patterns of abundance over small changes in water depth. Emergent species typically had higher cover in moist soil and drawdown treatments. These results confirm a tight mechanistic link between hydrology and vegetation patterns within Carolina bays, but suggest that the strength of this link is not uniform across the gradient. The linkage weakens with drier conditions as both facultative wetland and upland species recruit into the standing vegetation.

Introduction

Carolina bay elliptical depression wetlands are unique features throughout much of the Atlantic Coastal Plain and are most abundant in the Carolinas (Sharitz and Gibbons 1982; Bennett and Nelson 1991; Richardson and Gibbons 1993; Sharitz and Gresham 1998; Taylor et al. 1999; Sharitz 2003). These isolated wetlands provide habitat for many aquatic and semi-aquatic animal

and plant species in an upland landscape matrix, and thus contribute to overall landscape diversity (Kirkman et al. 1999). Historically, bays were often drained and converted to farmland or timber, or ditched to receive water and maintained as farm ponds (Bennett and Nelson 1991).

Bays are similar to other isolated wetlands such as prairie potholes (Euliss and Mushet 1996) and vernal pools (Zedler 2003) in that they are characterized by spatial and temporal variation in

hydroperiod. Typical Carolina bays fill over winter, are maximally full in spring, and dry down over summer (Schalles and Shure 1989). The rate and extent of filling and drying, however, varies among bays and is influenced by a number of factors. These include rainfall and evaporation (Sharitz and Gibbons 1982; Schalles and Shure 1989), degree of isolation from the water table (Lide et al. 1995), basin morphology, and surrounding landscape (Brinson 1993). Bays range from pond-like wetlands, characterized by relatively stable hydroperiod, to flashy bays that can dry partially or completely at intervals during summer (Kirkman and Sharitz 1994; Poiani and Dixon 1995; Collins and Battaglia 2001).

Vegetation patterns within and among bays reflect successive filters on propagule bank composition, recruitment, and plant survival. Although the surrounding landscape (Poiani and Dixon 1995; Kirkman et al. 1996; De Steven and Toner 2004), soil disturbance (Kirkman and Sharitz 1994), and fire history (Kirkman and Sharitz 1994) can be additional influences, hydrology is a primary filter on recruitment of vegetation from the propagule bank (Poiani and Dixon 1995; Sharitz and Gresham 1998; DeSteven and Toner 2004). This filter acts as an environmental sieve that interacts with life history characteristics of plant species to produce compositional patterns in plant communities (van der Valk 1981; Gerritsen and Greening 1989; Keddy 2000). As in other wetlands, germination of some species is inhibited by inundation (Kozlowski 2002; Ahn et al. 2004), whereas others require it (Leck 1996). A combination of lower germination, as well as physiological stress from flooding on seedlings (Kozlowski 2002), can lead to lower plant densities with increasing water depth (Seabloom et al. 1998).

Fluctuating water in bays is often associated with unzoned seed banks and vegetation dominated by annuals and small perennial species that recruit from the seed bank (Kirkman and Sharitz 1994; Poiani and Dixon 1995; Collins and Battaglia 2001). When or where drying events are rare, wetland vegetation tends to be dominated by long-lived clonal species that rarely recruit from the seed bank (van der Valk 1981; Poiani and Dixon 1995; Collins and Battaglia 2001). In six herbaceous Carolina bays, linkages between vegetation expression and propagule banks were related to

basin shape and hydrology (Collins and Battaglia 2001). Vegetation within bays became richer and more dissimilar from bay centers toward the margins, with greatest richness in the zone of fluctuating water. Species richness was lowest in experimental bins placed in flooded treatments, and communities became more similar with degree of inundation (Collins and Battaglia 2001).

One gap in our understanding is the strength of the linkage between hydrology and vegetation expression. Do very small changes in hydrology translate to changes in vegetation composition or species abundances? Does the linkage change at different points along the hydrologic gradient? These questions address two important issues in wetland management and restoration: propagule bank contribution to vegetation and hydrology needed to maintain desired vegetation. If linkages with vegetation expression are strong, hydrology and factors that influence it, such as basin slope and morphology, will strongly influence community recovery. If linkages are weak, tolerances for factors that affect hydrology would be expected to be less critical for bay conservation or for successful restoration or wetland creation projects.

The objectives of our research were to determine if vegetation expression from propagule banks of Carolina bays exhibits fine-scale responses to hydrology, and if the strength of response differs over the flooding gradient. We compared vegetation and species distributions that developed from bay sediments in experimental mesocosm bins that were placed in three hydrologic treatments: moist soil (MS), midsummer drawdown (DD), and flooded (FL). To investigate finer-scale responses to hydrology, bins within each hydrologic treatment were either (1) sloped to form a water level gradient within the bin or (2) left unsloped (flat) to form homogeneous hydrologic conditions. We hypothesized that richness would be greater in sloped bins compared to flat bins if species exhibit fine-scale species sorting in response to hydrology. We also hypothesized that stronger community turnover with small changes in water depth would lead to simpler and more similar assemblages at the wetter end of the hydrologic gradient, while weaker linkages between hydrology and vegetation expression would lead to more individualistic species distributions and less pattern in the vegetation at the drier end of the gradient.

Methods

Mesocosm study of bay propagule banks and vegetation

Our research builds upon an initial mesocosm study of vegetation and propagule bank expression within and among six herbaceous Carolina bays on the Savannah River Site (SRS) near Aiken, SC (Figure 1; Collins and Battaglia 2001). These bays are 'set aside' from management activities, and five of the six are bordered by upland forest. The sixth, Ellenton Bay, is surrounded by an old-field, which was abandoned approximately 50 years ago. Four of the bays are in the sandhills region of the SRS, and are underlain by deep sands. Two are on a terrace of the Savannah River.

Sediments were taken from each bay along transects that ran N, S, E, and W from bay center to the margin. Basin morphology was used to establish sampling locations along each transect that represented 10, 25, 50 and 75% of full basin or maximum water depth. In this way, sampling was matched to water depth within each bay and the four transects around the bay served as replicates of each flooding level within the bay. Further, the flooding regime and hydrology effects on vegetation expression could

be compared among the six bays (Collins and Battaglia 2001).

Three sediment cores (8 cm diam. × 10 cm deep) were removed from within a 1 m radius around each sampling point during late winter 1994–1995 when the bays were maximally full for the season. Each core was homogenized and then spread over 15 cm sand in a plastic bin (25 cm × 30 cm × 12 cm deep) in late February; bins were allocated among three hydrology treatments: flooded (FL), mid-summer drawdown (DD), or moist soil (MS). Hydrology treatments were established by placing the sediment bin inside a larger bin (36 cm × 51 cm × 22 cm deep). Holes were drilled in the sides of the outer bin, and it was flooded to provide 10 cm (FL and DD treatments) or 0 cm (MS treatment) water depth over the top of the sediment bin. Midsummer drawdown in early July was accomplished by drilling holes in the outer bins to drop the water level from 10 to 0 cm cover (for more information, see Collins and Battaglia 2001).

Sloped and flat bin comparisons

In March 1996, one year after the mesocosm study was established, we randomly selected half

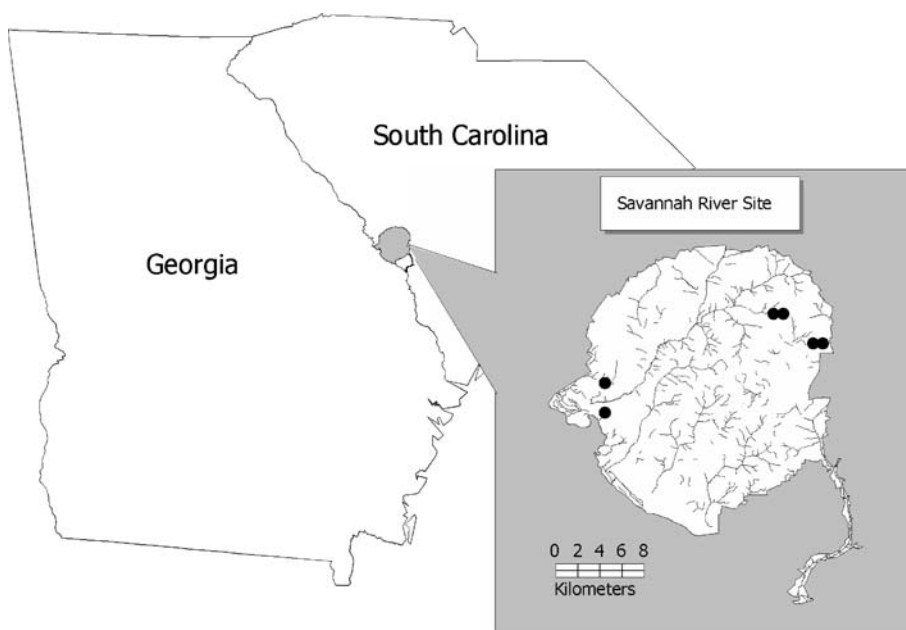


Figure 1. Map of the Savannah River Site near Aiken, SC, showing locations of the six selected herbaceous Carolina bays. Bays are represented by black circles.

(144) of the sediment bins within each bay [6]×sampling location (water level in bay) [4]×1995 hydrology treatment [3] combination, using two of the four replicates (transect directions) in each combination. Selected bins were sloped approximately 45° inside the external container by placing a small block under each sediment bin (Figure 2). The remaining bins ($n=144$) were left flat (Figure 2). Original hydrology treatments (assigned in 1995) were maintained, and plant communities were allowed to develop in sloped and flat bins throughout the 1996 growing season. The aim of the ‘sloping’ treatment was to superimpose a fine-scale gradient in water depth on the hydrologic treatments. Sloping the bins resulted in ‘new’ elevations, or hydrologic conditions, in the moist soil treatment (the ‘dry’ elevation (dy); Figure 2) and the flooded treatment (the ‘flooded deeply’ elevation (fd); Figure 2). These ‘new’ elevations are not represented in the flat bins.

Plant communities that developed in bins were sampled in July 1995 [the first season of growth and the year before sloping; see Collins and Battaglia (2001)] and, after the sloping treatment was imposed, in June, August, and September 1996.

Cover of each taxon was estimated to the nearest 1% in each bin. Sloped bins were subdivided into three elevation zones (25 cm×10 cm) using a wooden sampling frame, and cover data were collected separately in each. Figure 2 shows the position of sloped bin elevations relative to water level and the corresponding flat bins in each hydrologic treatment.

Data analyses

Bins were considered experimental units. Sloping half of the bins within each bay×sampling location×hydrology treatment combination allowed us to assess the effects of imposing a finer-scale gradient (i.e., compare flat and sloped bins) in each hydrology treatment. Previous analyses indicated that there were no differences among bays, transect direction, or sampling locations; therefore, we were able to pool bins across these factors, resulting in 48 bins for each sloped – no slope [2]×hydrology treatment [3] combination. All bays and all flooding regimes within a bay were represented in each sloping×hydrology treatment combination.

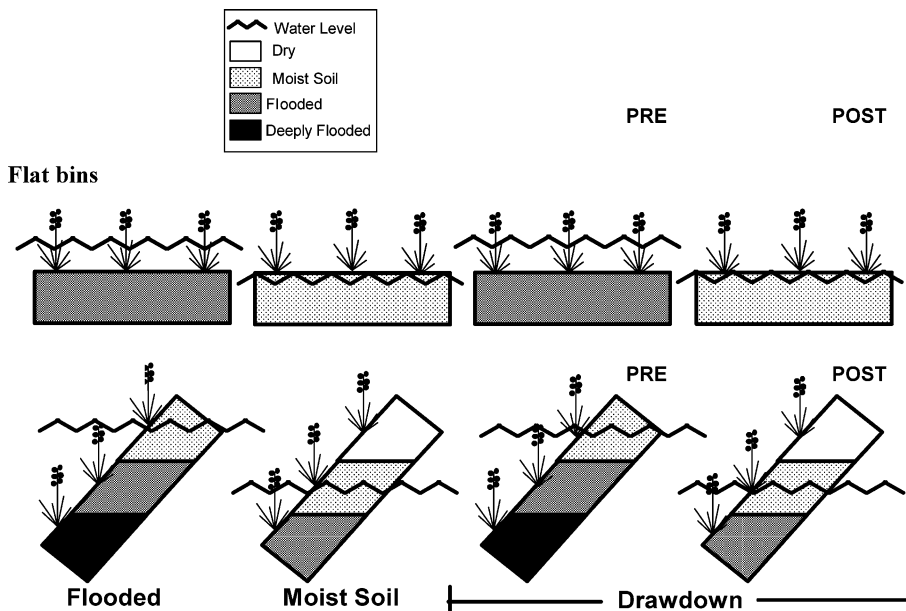


Figure 2. Schematic of wetland mesocosm experiment. Sloped and flat bins were assigned to one of three hydrology treatments: flooded (FL), mid-summer drawdown (DD), or moist soil (MS). In the DD treatment, both pre- and post-drawdown states are shown. Each elevation class in the sloped bins is shaded according to the flat bin hydrology treatment it most resembles. For clarity, elevation names are always in lowercase, and hydrologic treatments are always in uppercase. dy (upper end of MS & upper end of post-DD) and fd (lower end of FL & lower end of pre-DD) elevations are not represented in the flat bins.

Comparisons of species richness (number of distinct taxa per bin) were made using two-way analysis of variance (PROC GLM, SAS v. 8.1) on square-root transformed data. We compared richness between sloped and flat bins and among hydrologic treatments in 1996. In a separate one-way ANOVA that included sloped bins only, we compared richness among elevations by hydrologic treatment. Treatment means were compared using Bonferroni *t*-tests.

To examine trends in species composition, we used non-metric multidimensional scaling (NMDS), a technique that has been shown to be robust and effective for ordination of community data (Minchin 1987). The percentage cover data were standardized by species maxima, and dissimilarities were calculated using the Bray–Curtis index (Bray and Curtis 1957). This combination of standardization and dissimilarity index is one of the most effective for community ordination (Faith et al. 1987, Sandercock 1997). We performed NMDS in one to six dimensions, in each case using 50 random initial configurations. The DECODA package (Minchin 1989) was used for the NMDS ordination analysis.

Distance-based MANOVA was used to test whether there were significant effects of hydrologic treatments, sloping treatments, or their interaction, on species composition. This is a relatively new technique that was developed to allow the use of appropriate dissimilarity measures for community data and to use permutation tests to assess statistical significance of treatment main effects and interactions (Legendre and Anderson 1999; Anderson 2001a, b; McArdle and Anderson 2001). The use of an appropriate dissimilarity measure for community data (e.g. Bray–Curtis) and permutation tests avoids many of the stringent assumptions of traditional MANOVA (that are often violated with community data), making this method more effective for analyzing multivariate community responses in designed experiments. XMATRIX, DISTLM v.5, and PERMDISP (Anderson 2003; 2004a, b) were used for the distance-based MANOVA.

To supplement the distance-based MANOVA, we used Analysis of Similarities or ANOSIM (Clarke 1993), which provides a way to test statistically whether there is a significant difference in community composition between two or more *a priori* groups in a one-way design. If there are

differences between groups, the between-group dissimilarities should be greater than the within-group dissimilarities. To test this hypothesis, the test statistic *R* is computed and its statistical significance is then tested using a random permutation procedure which simulates the null hypothesis of no real difference among the groups. ANOSIM operates directly on the same Bray–Curtis dissimilarity matrix computed for the NMDS ordination and distance-based MANOVA. ANOSIM cannot be used in two-way designs because it does not test interactions terms, but we did use it in conjunction with the other analytical methods, specifically to conduct pairwise comparisons (analogous to multiple means tests following a significant univariate ANOVA) where significant main effects warranted further comparisons.

We also examined responses of select individual species to provide insight into their environmental preferences. Species representing a range of flood tolerance and life history characteristics with sufficient sample sizes were selected for further analyses. We calculated relative frequencies of 15 individual species' occurrences in each slope-no slope [2]×hydrologic treatment [3] combination. Finally, we selected eight of those 15 species (*Eleocharis robbinsii* Oakes, *Fuirena squarrosa* Michaux, *Juncus repens* Michx., *Leersia hexandra* Swartz, *Nymphaea odorata* Aiton, *Panicum hemitomon* Schultes, *Rhynchospora microcarpa* Baldw. Ex. Gray, and *Utricularia purpurea* Walt.) for individual analyses of cover patterns. Nomenclature follows Radford et al. (1968). For each species in each bin, we averaged percent cover over the three sampling dates (June–September). We compared average percent cover of each species among elevations in sloped bins and across sloping and hydrologic treatments using PROC GENMOD (SAS v. 8.1). Pairwise comparisons of least-squares means were made for significant main effects or interactions.

Results

In 1996, richness (number of taxa) differed significantly between sloped and flat bins ($p < 0.0001$; Figure 3); sloped bins were consistently richer than flat bins. Richness also differed among hydrologic treatments ($p < 0.0001$; Figure 3). Richness was significantly higher in the Moist Soil (MS) treatment

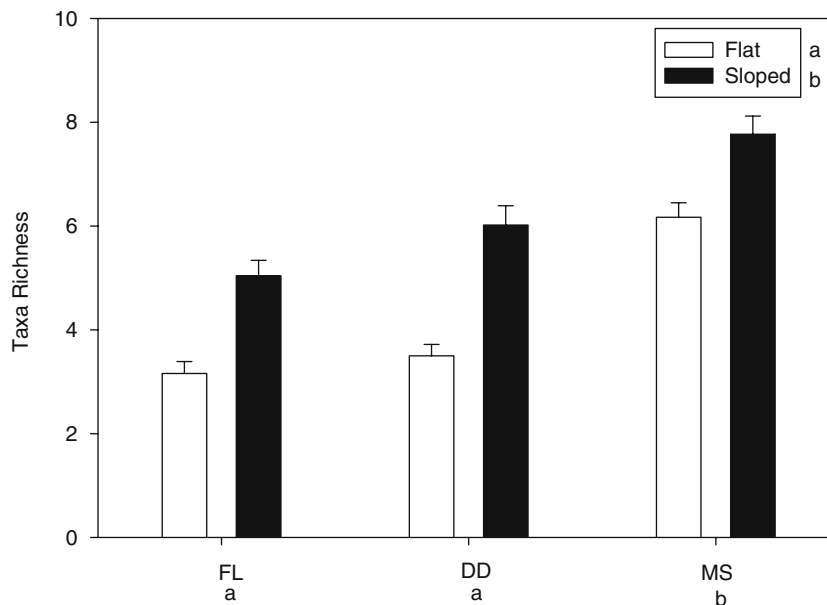


Figure 3. Mean richness (± 1 Standard Error) of flat and sloped bin communities in flooded (FL), drawdown (DD), and moist soil (MS) hydrology treatments in 1996. Means with the same letters do not differ significantly.

than in the Flooded (FL) and Drawdown (DD) treatments, which did not differ from each other. Greater species richness in sloped compared to flat bins (Figure 3) resulted from a number of taxa that were infrequent and had low abundance. These included *Eupatorium capillifolium*, *Gnaphalium purpureum*, *Hypericum* spp., *Ludwigia leptocarpa*, *Pontederia cordata*, and *Rubus* spp. (Figure 5). None of these taxa was present in the 1995 vegetation. In contrast, *Typha latifolia* was present in flat bins only, but this was likely an artifact of its presence in the 1995 vegetation in these bins. *T. latifolia* was present in the same bins in both years.

Species richness differed across elevation categories in the sloped bins, but only in the FL and DD hydrologic treatments (Figure 4). In those treatments, there was a consistent and significant loss in richness from the drier ends of the bins to the wetter ends. In the MS bins, however, richness was relatively high and did not vary across the small-scale moisture gradient in the bins.

A scree-plot (minimum stress vs. number of dimensions) for the NMDS ordination of the entire data set (not shown) indicated that a minimum of two dimensions was needed to adequately display the community variation (stress=0.2856). Based on a visual examination of the ordination in

which we coded the bins according to the applied hydrologic treatment, we found that species composition was quite variable in the DD and MS treatments, and no clear separation between these groups was evident (not shown). Although species composition of the FL bins did overlap to some degree with the other two treatments, it appeared that they occupied a more restricted (upper, left) portion of the ordination space and that the variability among FL bins was much lower. Re-coding the bin symbols in the ordination according to sloped vs. non-sloped status did not reveal any distinct patterns (not shown).

Results of the distance-based MANOVA confirmed our interpretation of the ordination results. Hydrologic treatment had a significant effect on species composition, but neither the sloping treatment nor the hydrologic*sloping interaction was significant (Table 1). Although we could not test for an interaction term in the ANOSIM analyses, we found that comparisons of composition among hydrologic treatments and between sloping treatments supported the previous results (significant hydrologic effect, $R=0.0667$, $p<0.0001$; no sloping effect, $R=0.0031$, $p=0.2191$). Pairwise comparisons among the hydrologic treatments indicated that composition in the FL bins differed from the MS ($R=0.1241$,

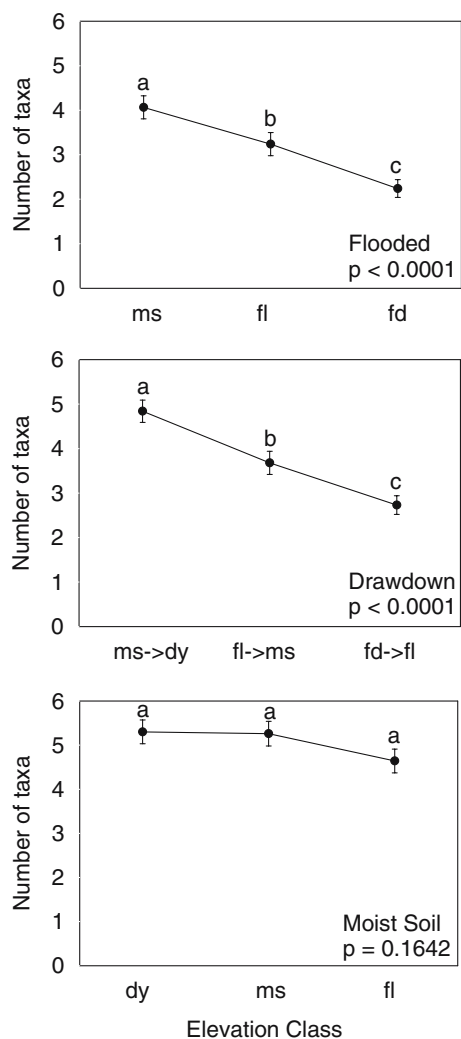


Figure 4. Average taxa richness among elevation classes within sloped bins in flooded (FL), drawdown (DD), and moist soil (MS) hydrologic treatments in 1996. Hydrologic treatment and elevation abbreviations follow those in Figure 2. In the DD treatment, we have indicated a mid-summer switch in conditions within each elevation. Means with the same letters do not differ significantly.

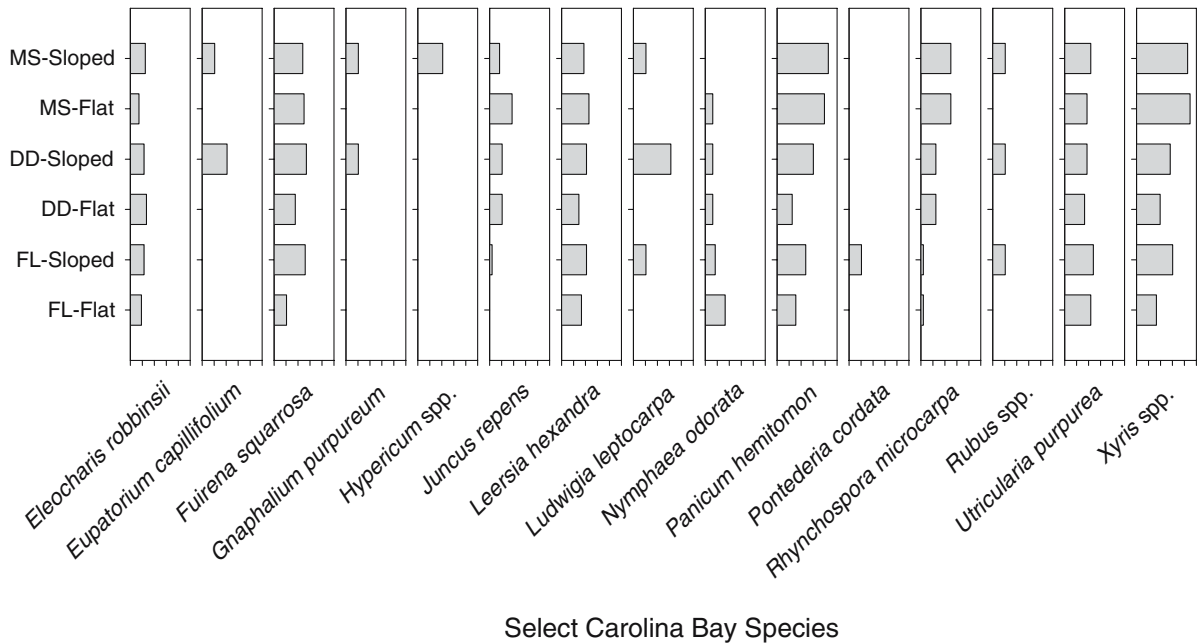
$p < 0.0001$) and DD ($R = 0.0788$, $p < 0.0001$) bins, which did not differ from each other ($R = 0.0101$, $p = 0.0842$).

The distribution (frequency) of select species over experimental water levels supports, to some degree, the decline in species richness and convergence of bin communities with increase in water depth (Figure 5). Primarily obligate and facultative wetland taxa capable of vegetative growth, including *Eleocharis robbinsii*, *Fuirena squarrosa*,

Leersia hexandra, *Nymphaea odorata*, *Panicum hemitomon*, and *Utricularia purpurea* were found in the FL bins. These species extended into the deepest (fd) part of the water level gradient in sloped bins, and with the exception of *N. odorata*, they also extended into the driest (dry) end of the water level gradient. Thus, there was a decline in richness and convergence on these species at the wettest end of the gradient, creating a simpler assemblage that was largely a subset of the ones found at the drier end of the gradient. *Eupatorium capillifolium*, *Gnaphalium purpureum*, *Hypericum* spp., *Ludwigia leptocarpa*, *Pontederia cordata*, and *Rubus* spp. only occurred in sloped bins (Figure 5).

Some of the eight species selected for cover analyses (see methods) exhibited changes in abundance in response to the hydrologic and sloping treatments (Table 2). A significant interaction between hydrologic and sloping treatments influenced percent cover of two emergent species: *F. squarrosa* and *P. hemitomon* (Table 2, Figure 6). In flat bins, *P. hemitomon* cover was highest in the FL treatment and lowest in the MS treatment. *Panicum* showed the opposite pattern in sloped bins: cover was highest in the MS treatment and lowest in the FL treatment. *Fuirena* cover was highest in the MS treatment in flat bins, but lowest in that treatment in sloped bins. Further, of the eight taxa examined, only *F. squarrosa* differed in cover among the elevations within sloped bins. *Fuirena* cover decreased as water level increased within the flooded treatment only ($p = 0.0001$). The same trend was evident in the drawdown treatment, but was not significant ($p = 0.44$).

Hydrologic treatment, but not sloping, had significant effects on cover of the emergents *J. repens* and *R. microcarpa*, as well as *U. purpurea* (Table 1, Figure 7). The two emergent taxa increased in cover with each level of decreasing water depth. In contrast, *U. purpurea*, which has both floating and submerged parts, had significantly higher cover in FL bins compared to the DD and MS treatments. Both hydrology and sloping significantly affected cover of the floating-leaved species *N. odorata* (Table 2). Among hydrologic treatments, cover was higher in FL bins than in DD ($p = 0.0037$) and MS ($p = 0.0071$) treatments, which did not differ from each other ($p = 0.5007$). Flat bins supported higher *N. odorata* cover than sloped bins ($p = 0.045$). Cover of the remaining species, *E. robbinsii* and *L. hexandra*, did not differ



Select Carolina Bay Species

Figure 5. Frequency (number of bins with species/total number of bins) of selected species in each hydrologic and sloped/flat treatment combination. Frequencies (on the x axis) of *Eleocharis robbinsii*, *Fuirena squarrosa*, *Panicum hemitomon*, *Utricularia purpurea*, and *Xyris* spp. range from 0 to 1.0. Frequencies of *Juncus repens*, *Leersia hexandra*, *Nymphaea odorata*, and *Rhynchospora microcarpa* range from 0 to 0.5. Frequencies of *Eupatorium capillifolium*, *Gnaphalium purpureum*, *Hypericum* spp., *Ludwigia leptocarpa*, *Pontederia cordata*, and *Rubus* spp., range from 0 to 0.1. FL = flooded, DD = drawdown, and MS = moist soil hydrologic treatments.

Table 1. Results of distance-based MANOVA. The response variable in this analysis was dissimilarity in species composition.

Source	df	SS	MS	pseudo- F	p
Hydrology	2	36886.3	18443.1	4.49	0.0001
Sloping	1	6008.5	6008.5	1.46	0.0807
Hydrology*	2	6562.8	3281.4	0.80	0.8120
Sloping					
Residual	274	1124872.0	4105.4	—	—
Total	279	1174224.8	—	—	—

between sloping, or among, hydrologic treatments (Table 1).

Discussion

Results of our research confirm a link between hydrology and vegetation patterns within Carolina bays, and suggest the linkage is strongest at the wettest end of our experimental gradient. Declining richness and convergence of species composition in the FL treatment and at the wetter end of the gradient in sloped bins led to a simpler assemblage that

Table 2. Explanatory variables included in models (generalized linear model, logit distribution) of percent cover of eight herbaceous Carolina bay species.

Species	Main effect	Change in deviance prob. $> \chi^2$
<i>Eleocharis robbinsii</i>	—	—
<i>Fuirena squarrosa</i>	Hydrology	0.7381
	Sloping	0.0081
	Hydrology*Sloping	0.0096
<i>Juncus repens</i>	Hydrology	< 0.0001
<i>Leersia hexandra</i>	—	—
<i>Nymphaea odorata</i>	Hydrology	< 0.0001
	Sloping	0.0327
<i>Panicum hemitomon</i>	Hydrology	0.9823
	Sloping	0.4038
	Hydrology*Sloping	0.0351
<i>Rhynchospora microcarpa</i>	Hydrology	< 0.0001
<i>Utricularia purpurea</i>	Hydrology	0.0011

For each species, we report the variables that produced a significant reduction in deviance and the corresponding p -value based on the χ^2 distribution. Dashes in cells indicate that neither hydrologic nor sloping treatment was significant. When inclusion of the hydrology*sloping interaction term significantly reduced deviance, the full model was retained.

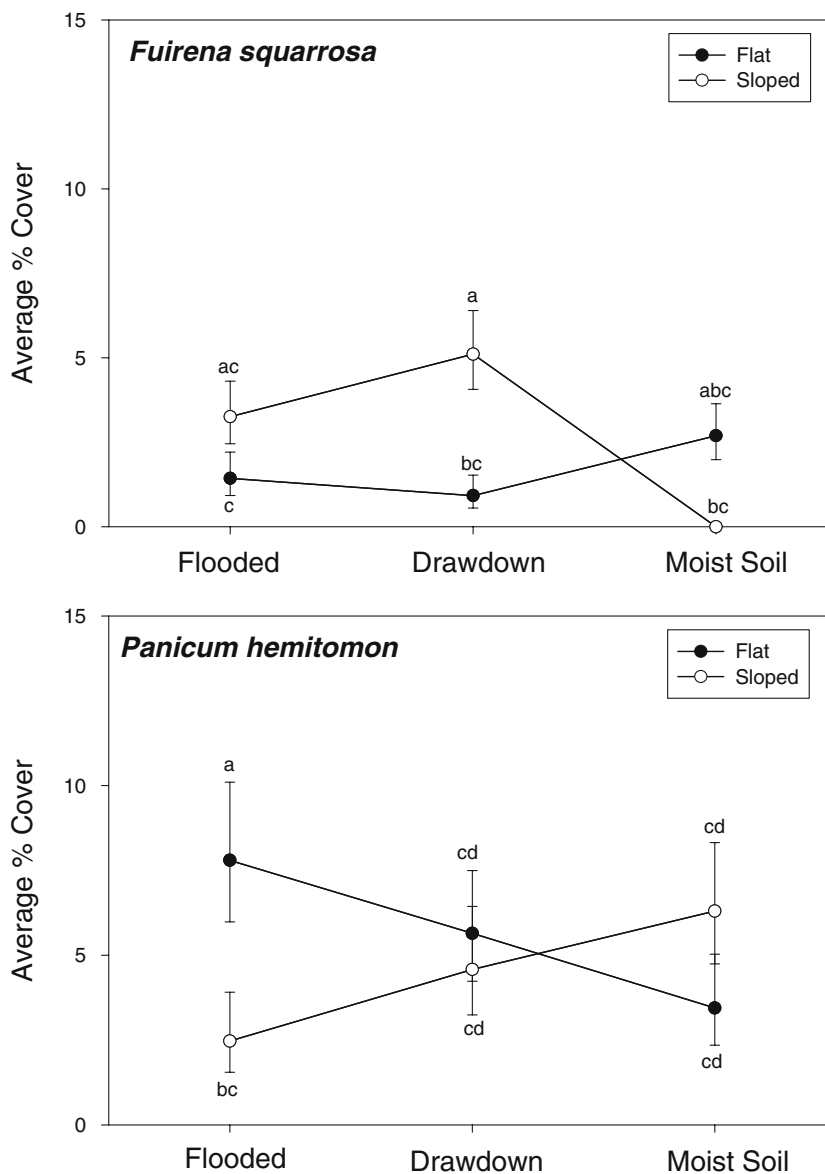


Figure 6. Average percent cover of *Fuirena squarrosa* and *Panicum hemitomon* across sloping and hydrologic treatments. See Figure 2 caption for explanation of treatments and abbreviations. Means with the same letters are not significantly different.

was largely a subset of those found at the drier end of the gradient. Collectively, the results illustrate that even small-scale changes in the water depth gradient can affect richness patterns and species-specific responses in Carolina bay vegetation.

Over the MS, DD, and FL hydrology treatments, sloping bins to create new elevations and a water depth gradient resulted in greater species richness. This trend in sloped bins, which included greater variation in water depth than flat bins,

suggests that more species can coexist by finely partitioning water depth variation (Vivian-Smith 1997). In particular, the flooded sloped bins supported the highest number of species (18) not found in flat bins of the same hydrologic treatment. Although richness gains were sufficiently small and the identity of species gained sufficiently inconsistent that differences in community composition over the gradients in sloped bins were not statistically significant, the results suggest turnover

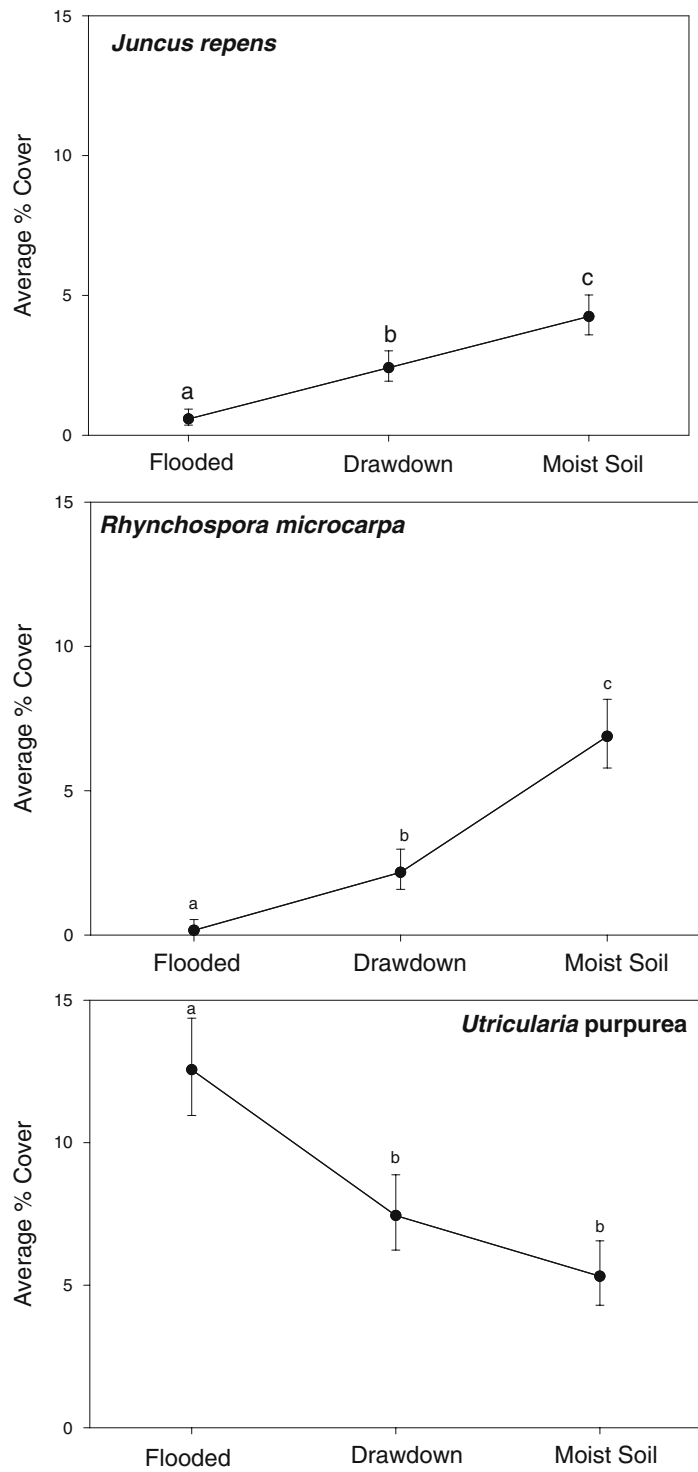


Figure 7. Average percent cover of *Juncus repens*, *Rhynchospora microcarpa*, and *Utricularia purpurea* across hydrologic treatments. See Figure 2 caption for explanation of treatments and abbreviations. Means with the same letters do not significantly differ.

of species along water table gradients in the field may account for the zonation patterns commonly reported in bays (Sharitz 2003). In addition, as we hypothesized, the wet end of the gradient appears to be 'biologically steep' compared to the drier end, with higher species turnover accompanying small changes in water depth. Toward the wetter end of the gradient in sloped bins, and among the three hydrologic treatments in flat bins in both 1995 (Collins and Battaglia 2001) and 1996, elimination of upland, flood-intolerant species such as *Andropogon virginicus* led to reduced species richness and convergence on a community of obligate and facultative wetland species.

Carolina bays may have large patches of vegetation that are low in richness, zoned vegetation driven by species turnover across small differences in water depth, or a combination of these patterns (Collins and Battaglia 2001; DeSteven and Toner 2004). Although vegetation patterns are driven largely by the interaction between basin morphology and hydrology, the chance occurrence of a species in the propagule bank and its capability of responding play a large role. Decreasing abundance of emergents such as *J. repens* and *R. microcarpa* and increasing abundance of floating-leaved plants such as *N. odorata* and *U. purpurea*, which reproduce vegetatively and can form large clones, with flooding in the bins support field observations of bay vegetation (Tyndall et al. 1990; Collins and Battaglia 2001; Sharitz 2003). In addition, species that occurred only in sloped bins may have been responding to the rapid water table change incurred in the dormant season when we sloped the bins and may not have occurred in our study had we not sloped the bins. Four of the six taxa, *Eupatorium capillifolium*, *Gnaphalium purpureum*, *Hypericum* spp., and *Rubus* spp., are common in old fields and are known to respond to disturbances (Collins and Pinder 1990). It is possible that other species were present in the propagule banks, but we did not meet their exact establishment requirements.

Vegetation patterns appeared affected less by species tolerances at the drier end of the hydrologic gradient. It is likely that vegetation patterns in less stressful areas are driven more by biotic factors such as dispersal, longevity and assimilation into the seedbank, and competition (Grace and Wetzel 1981). The losses of flood-intolerant species sometimes coincided with increased

abundance or relative frequency of occurrence of more flood-tolerant species, such as *F. squarrosa* and *N. odorata*, respectively. Although beyond the scope of our study, it is possible that release from competition played a role in obligate wetland species responses (Grace and Wetzel 1981). Persistence of the flood-tolerant plants along with the less flood-tolerant species produced species-rich and compositionally variable vegetation. Extant vegetation patterns in the six herbaceous Carolina bays also showed this pattern: vegetation became richer and more dissimilar from bay centers toward the margins (Collins and Battaglia 2001), presumably as less flood-tolerant species overcame species-specific thresholds of tolerance to flooding.

Results of our research have implications for conservation and restoration of Carolina bays and other isolated wetlands. DeSteven and Toner (2004) suggest four reference vegetation types to guide restoration of herbaceous Carolina bays. These include sedge meadows, depression meadows, grass marshes, and open-water ponds, which were discriminated in part by hydroperiod and water depth. Our results suggest that desired richness, species composition, and vegetation pattern can be achieved to some extent in restoration efforts and guided toward one or more of these targets by site selection that matches basin characteristics and landscape setting to the appropriate hydrologic conditions (Keddy and Reznicek 1986; Zampella and Laidig 2003). Mesocosm and field-based experiments will continue to help us improve our understanding of species-specific and community level responses to hydrology, thereby enabling us to fine-tune our control of recovery trajectories.

Acknowledgements

This research was partially funded by a grant from the SREL Set-Aside program. Additional funding was by Financial Assistance Award Number DE-FC09-96SR18546 between the U.S. Department of Energy and the University of Georgia. We thank Peter Minchin for assistance with the distance-based MANOVA. Also, we acknowledge Emily Cantonwine for field help and Pamela Weisenhorn for assistance with figures.

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