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Rapid responses of vegetation to hydrological changes in Taylor Slough, Everglades National Park, Florida, USA

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Abstract

We analyzed the dynamics of freshwater marsh vegetation of Taylor Slough in eastern Everglades National Park for the 1979 to 2003 period, focusing on cover of individual plant species and on cover and composition of marsh communities in areas potentially influenced by a canal pump station ("S332") and its successor station ("S332D"). Vegetation change analysis incorporated the hydrologic record at these sites for three intervals: pre-S332 (1961–1980), S332 (1980–1999), post-S332 (1999–2002). During S332 and post-S332 intervals, water level in Taylor Slough was affected by operations of S332 and S332D. To relate vegetation change to plot-level hydrological conditions in Taylor Slough, we developed a weighted averaging regression and calibration model (WA) using data from the marl prairies of Everglades National Park and Big Cypress National Preserve. We examined vegetation pattern along five transects. Transects 1–3 were established in 1979 south of the water delivery structures, and were influenced by their operations. Transects 4 and 5 were established in 1997, the latter west of these structures and possibly under their influence. Transect 4 was established in the northern drainage basin of Taylor Slough, beyond the likely zones of influence of S332 and S332D. The composition of all three southern transects changed similarly after 1979. Where muhly grass (*Muhlenbergia capillaris* var. *filipes*) was once dominant, sawgrass (*Cladium jamaicense*), replaced it, while where sawgrass initially predominated, hydric species such as spikerush (*Eleocharis cellulosa* Torr.) overtook it. Most of the changes in species dominance in Transects 1–3 occurred after 1992, were mostly in place by 1995–1996, and continued through 1999, indicating how rapidly vegetation in seasonal Everglades marshes can respond to hydrological modifications. During the post-S332 period, these long-term trends began reversing. In the two northern transects, total cover and dominance of both muhly grass and sawgrass increased from 1997 to 2003. Thus, during the 1990's, vegetation composition south of S332 became more like that of long hydroperiod marshes, but afterward it partially returned to its 1979 condition, i.e., a community characteristic of less prolonged flooding. In contrast, the vegetation change along the two northern transects since 1997 showed little relationship to hydrologic status.

Introduction

The marsh vegetation communities of the Everglades are critical components in the biodiversity of the region, both for the structure they provide in support of other biota, and for the intrinsic values of their constituent plant species assemblages. Taylor Slough is an important southeastern Everglades drainage that provides a hydrologic link among the major uplands, freshwater wetlands, and estuaries of the region. Returning Taylor Slough as nearly as possible to its pre-disturbance condition is a goal of a federal/state partnership established to bring about ecological restoration of the greater Everglades (USACE & SFWMD, 1999). Plans for restoration assume that providing the "right" hydrology will produce the desired mixture of marsh communities along the hydrological gradient that connects the interior and coastal ecosystems of the Everglades. However, while the ecology of these marshes is inextricably bound to their hydrology, they remain complex ecosystems driven by multiple variables, both physical and biological that could delay or modify the trajectories intended by hydrologic restoration. One way to assess the likelihood that hydrologic restoration can succeed is to determine how rapidly vegetation has responded to hydrology in recent decades. In other wetlands, researchers have reported that the time course of measured vegetation change in response to hydrologic changes varies widely depending on local conditions, disturbance types and intensity, and details of hydrologic change (Craft et al., 2002; Warren et al., 2002). In this paper, we examine the temporal and spatial co-variation of vegetation and hydrology in seasonally flooded marshes, focusing specifically on the middle and upper reaches of Taylor Slough during the period 1979–2003.

Over the last half century or so, vegetation dynamics in Everglades marshes have been addressed frequently, usually in the context of variation in water stage, flooding duration, or water quality (e.g., Kolipinski & Higer, 1969; Davis et al., 1994; David, 1996; Olmsted & Armentano, 1997; Busch et al., 1998; Newman et al., 1998; Nott et al., 1998; Ross et al., 2000, 2003a). Prompting much of this work has been recognition of the major influence of human intervention upon the natural hydrology of the Everglades. In several other studies, sources of variation in plant community structure other than hydrology, particularly fire and nutrients, are recognized (Jensen et al., 1995; Doren et al., 1997; Childers et al., 2003; Lockwood et al., 2003; Ponzio et al., 2004). These studies demonstrate or at least support the notion that water management changes that have occurred frequently during recent decades can induce major vegetation responses in receiving basins. However, the time frame in which these responses may be expected to run their course is yet unclear.

Two studies describe repeated point observations at annual or sub-decadal frequencies in short hydroperiod marshes in Everglades National Park (ENP) and/or Big Cypress National Preserve (Nott et al., 1998; Armentano et al., 2000). Both suggest that substantial changes in vegetation may be realized within a few years, a conclusion that we evaluate more thoroughly. Our objectives were to analyze the complete vegetation and hydrological databases for Taylor Slough in order to examine whether any temporal or spatial trends in marsh vegetation were strongly related to hydrologic variation. Thus in this paper we describe vegetation changes within a permanent plot network over a 24-year period, in light of a continuous hydrologic record of more than 40 years.

Study area

Taylor Slough, the second largest flow-way for surface water in ENP, is a 409 km^2 freshwater wetland that originates along the eastern boundary of the park and stretches nearly 30 km to Florida Bay (Fig. 1). The slough is a relatively narrow, sediment-filled channel that broadens southward, flanked by areas 10–30 cm higher that are much broader than the slough itself. Even prior to development, the headwaters of Taylor Slough were poorly defined, originating north of the slough in the Rocky Glades, a slightly elevated outcropping of oolitic limestone west of the Miami Rock Ridge, which forms the southern extent of the Atlantic Coastal Ridge. Under natural conditions during wet years, overflow from the much larger Shark Slough to the northwest reached Taylor Slough by flowing southward across the Rocky Glades. Taylor Slough also regularly channeled water drained off adjacent uplands and marl prairies. When sufficiently hydrated, water in the central channel flowed south to the mangrove forests bordering Florida Bay. Water levels probably were once distinctly higher than today, judging from reports that it was possible to navigate Taylor Slough by skiff all the way from Long Pine Key to its outlet at Little Madeira Bay around 1900 (Craighead, 1971). At present, Taylor

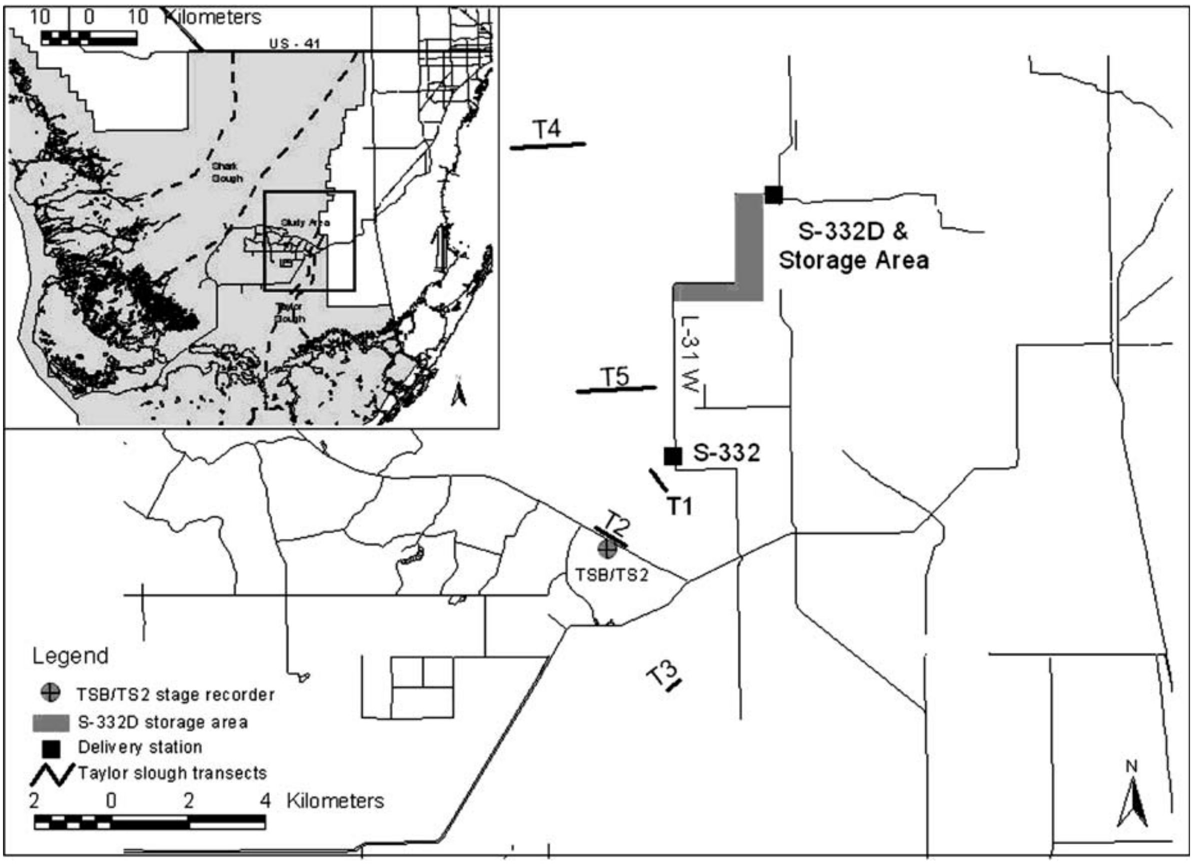

Figure 1. Location of Taylor Slough vegetation sampling transects, S332 and S332D water control structures, Stage recorder TSB/TS2, and storage area on the eastern boundary of Everglades National Park.

Slough is clogged with freshwater emergent vegetation in its upper and middle segments and by mangroves in its lower segments, a condition consistent with chronically lowered water levels.

Ecological observations made in the Taylor Slough basin are consistent with a long-term trend of lowered water tables. The encroachment of exotic tree species (principally *Schinus terebinthifolius* Raddi, and *Casuarina glauca* Sieb. ex Spreng.), along with apparent expansion of native woody and herbaceous species into higher Taylor Slough and Rocky Glades marshes, has been reported over the past several decades (Hofstetter & Hilsenbeck, 1980; Wade et al., 1980). These changes are believed to be responses to reduced water levels brought about by water management policies (Hofstetter & Hilsenbeck, 1980) The dynamics of the situation are complicated by the role of fire (Lockwood et al., 2003). In the higher areas of the Taylor Slough drainage basin, depressed water tables and arson have altered natural fire regimes, increasing the frequency and area burned (Curnutt et al., 1998).

The history of water management in the southern Everglades is well documented. As South Florida developed as an agricultural and population center during the last half of the 20th Century, inflows to Shark Slough from the Water Conservation Areas to the north were reduced and regulated by water control structures along US 41 (Fig. 1). In Taylor Slough, the South Dade Conveyance System along the park's eastern boundary was authorized in 1968 to, among several purposes, improve the supply and distribution of water to ENP, but its operations were strongly constrained by demands for flood control east of the park. Comparison of Taylor Slough discharges from 1960 to 1981 reveals the significant flow reductions that occurred after canal construction in 1968 (Rose et al., 1981).

Continuing the engineering of the system, the L-31 canal was realigned and the L-31W canal was added in 1971, thus severing Taylor Slough from its headwaters outside of ENP boundaries. In 1980, pump station S332 began to deliver water from the L-31W to Taylor Slough, partially replacing flows that once originated from the Slough's upper reaches. Since 1981, ground water stages in the headwaters of Taylor Slough have been significantly lowered for flood protection east of the park, causing large water losses from the Taylor Slough marshes (Van Lent et al., 1993). Adjustments of deliveries since 1993 have partly reversed this loss, without, however, restoring most of the overland flows into Taylor Slough from the north. These hydrologic alterations have led to reductions of the water table of 1.2 m or more as measured in a well located ca. 10 km east of Taylor Slough (Craighead, 1971).

Regulations controlling the operation of S332 thus have changed several times during the past 25 years, in response to various environmental concerns (Van Lent et al., 1993, 1999). Most recently, operation of S332 was replaced in 1999 by a new station at S332D (Fig. 1). The purposes included changing flow pattern from delivery through a gate to sheet flow, and raising water levels in marl prairies near northern Taylor Slough while reducing flooding in marl prairies west of Shark Slough, thereby improving habitat for a federally endangered bird. Over the last 3–4 decades, then, water management in Taylor Slough has taken an uneven course, the ecological results of which are the subject of this paper.

Three vascular plant species are characteristic of the Slough and appear to have some value as indicators of hydrological conditions. Sawgrass (*Cladium jamaicense* Crantz; hereafter *Cladium*) is the freshwater marsh dominant throughout most of the Everglades including large portions of Taylor Slough. It occurs in marshes which reportedly range in hydroperiod (annual flooding duration) from 2 to 9 months and typically dominate marshes exposed to 5 to 9 months of annual flooding (Wade et al., 1980; Doren et al., 1997; Olmsted & Armentano, 1997). Muhly grass (*Muhlenbergia capillaris var. filipes* (M.A. Curtis) Chapm. ex Beal; hereafter *Muhlenbergia*) characterizes marl prairies that are reportedly flooded for approximately 2 to 4 months per year but sometimes up to six months (Olmsted et al., 1980; Werner & Woolfenden, 1983). The scientific literature is unclear on whether *Muhlenbergia*-dominated prairie is a natural feature of the Everglades or represents a response to artificial drainage and fires (Craighead, 1971; Werner & Wolfenden, 1983). The species receives little mention in the earlier papers describing south Florida vegetation (e.g., Davis, 1943, Egler, 1952). Spikerush (*Eleocharis cellulosa* Torr.) often is found in wet prairies that are annually flooded on average about six to nine months (Gunderson & Loftus, 1993; Olmsted & Armentano, 1997). All three species show considerable plasticity in adaptation to environmental conditions and thus the hydroperiod ranges suggested herein are best considered as approximations; in all of the cited examples, there is little information on patterns extending over more than several years.

Materials and methods

Vegetation sampling

Vegetation data were collected along five transects of *ca.* 2 km length: two in the headwaters of Taylor Slough (Transects 4 and 5), two in Upper Taylor Slough (Transects 1 and 2), and one in Middle Taylor Slough (Transect 3) (Fig. 1). The three lower transects were established by Olmsted and colleagues in 1979 (Olmsted et al., 1980). The same plots were resampled in 1992 (Transect 2), 1995 (Transects 1 and 2), and 1996 (Transect 3) (Armentano et al., 2000). To broaden the sampling domain, Transects 4 and 5 were established and sampled in 1997, and all five transects were resampled in 1999 and 2003.

The rationale for plot selection in Transects 1–3 and 4–5 differed. In 1979 the objective was to establish a baseline for determining the effects of the future operation of the S-332 station on two distinct community types – one dominated by *Cladium* and the other by *Muhlenbergia.* Therefore, half of the plots established along Transects 1–3 were subjectively located in *Cladium* stands (C-plots), and half in *Muhlenbergia* stands (M-plots). Furthermore, data from the 1979 survey were only available in summarized form, as means among all C- or M-plots. In contrast to Transects 1–3, the plot locations established in Transects 4 and 5 in 1997 were not selected on the basis of existing cover types, but rather were placed at 100 m intervals along the transect.

To facilitate direct comparison of the sequential surveys, vegetation sampling protocols initiated by Olmsted and colleagues in 1979 (Olmsted et al., 1980) were maintained throughout the study. The corners of twenty 1 m × 5 m plots were permanently marked along each transect, with each plot divided into five 1 × 1 m quadrats. Cover (% of the ground surface covered in a vertical projection) was estimated for all vascular plants in each quadrat. Data were averaged at the level of the plot (5 m^2), i.e., 100 quadrat estimates were used to generate 20 plot estimates per transect. Areas covered by periphyton or devoid of vascular plant material were recorded separately as "open". All observers were trained and tested in visual estimation by the senior investigator, such that there were common participants through the entire 1992–2003 period. The spatial unit for which cover was estimated was 0.25 m^2, or 4 units per quadrat. A frame subdivided into quarters with string defined the observational unit. Blind testing of observer differences showed that discrepancy of species cover estimates among individuals was primarily 15% or less where cover was in the 50% range or above and smaller at lower cover. With rare exception, all individuals beyond the cotyledon stage were identified in the field.

On Transects 1–3, a single elevation was determined for the middle quadrat of each plot with a laser Topcon leveler tied to a permanent benchmark established by professional surveyors. On Transects 4–5, elevations along the transects and at each quadrat per plot were determined by surveying with an auto-level from an established benchmark.

We reviewed the fire frequency records for the transect areas for the 1979 to 2003 period because of the well-known role of fire in modifying vegetation in the fire-adapted marl prairie community. If recent fires burned through some plots but not others, cover estimates could be differentially affected. In 1995 a fire burned the far western edge of Transect 5, but fell short of the majority of plots. In 1991, fire burned the eastern 60% of the same transect. In 1985, widespread fires burned over the entire area of Transect 4 and 5, and portions of Transect 3, but this was more than a decade before sampling. Transect 5 also burned in 1983, Transect 3 in 1982 and Transect 4 in 1981. The effects of the 1991 and earlier fires on marsh vegetation along these transects are believed to be unimportant given the capacity of *Muhlenbergia* and *Cladium* to recover from fire within 2–3 years (Herndon & Taylor, 1986; Herndon et al., 1991).

Analytical methods

Hydrologic models

Multiple linear regression models were developed to examine changes in water level in relation to rainfall and management-related activities, including deliveries from S332 and S332D. The period for which both water level and rainfall data were available was divided into 3 sub-periods: (1) pre-S332 period (1961–1980); (2) S332 period (1980–1999); (3) post-S332 period (1999–2002). For a brief transitional period from 1999 to 2000, water was delivered into Taylor Slough through both structures S332 and S332D. Stage data from ENP hydrologic stations TSB and TS2 (25° 24′ N, 80° 36′ 25″ W) were used to calculate daily mean water level in Taylor Slough during dry (November through May) and wet (June through October) seasons between 1961 and May 2003. Rainfall data from ENP climatic station RPL (2 km southeast of TSB) were used to calculate total seasonal rainfall during the period. Mean daily flow (cubic meters/sec) through S332 and S332D was used to calculate monthly mean volume of water (million cubic meters/month) delivered to Taylor Slough through these structures in dry and wet seasons during the S332 and post-S332 periods.

Six seasonal models were developed to predict the seasonal mean for water level at TSB (Taylor Slough Bridge). Models 1A and 2A (wet and dry season, respectively) were based on data from the pre-S332 period. The primary predictor in these models was total rainfall (cm) during that period. Inclusion in the models of a term representing water level present at the end of the previous season, i.e., mean daily water level during the prior May or October, resulted in improved model performance during the pre-S332 period (Models 1B and 2B). However, Models 1B and 2B were not appropriate for predicting during the delivery period, because the value of the "one-month lag" variable would itself have been affected by delivery, which was not included as an independent variable in these models. Instead, Model 1A and 2A were substituted for the S332 and post-S332 periods, in order to predict the water levels that would have occurred during 1980–2002 in the absence of delivery. Models 3 and 4, based on the period 1980–2001, included terms for rainfall and separate terms for volume of water delivered through S332 and S332D during wet and dry seasons. However, S332D delivery and rainfall were not significant in predicting water level in dry and wet season, respectively, and thus were not included in the final models. These models were used to predict water level during the S332 and post-S332 periods. Models 3 and 4 were also not improved by including a one-month lag term as an additional predictor.

Vegetation dynamics

We applied a non-metric multidimensional scaling (NMS) ordination (Kruskal, 1964), using PC-ORD software (McCune & Mefford, 1999), to visualize temporal changes during the study period. The NMS procedure involves an iterative search to position sites along a limited number of axes, such that the rank order of among-site dissimilarities in vegetation composition is replicated as closely as possible (McCune & Grace, 2002). For these analyses, the Bray-Curtis distance metric was used as a measure of dissimilarity among sites. To minimize the effects of rare species on the ordination, species present in less than 5% of plots were eliminated from the analysis. Cover data were standardized to site total by dividing each species' cover by the total abundance of all species within the plot. To be consistent with the level of integration of the 1979 vegetation data, the ordinations for Transects 1–3 were applied to data summarized across all C- or M-plots (classification of individual plots was retained throughout the study, regardless of any shift in composition). Site ordinations for Transects 4 and 5 were calculated on a plot-level basis.

Differences in plant communities among sampling years were also examined quantitatively through Analysis of Similarity (ANOSIM), a nonparametric multivariate analysis used to test for difference in community composition among two or more entities, such as treated and untreated plots (Clarke, 1993). An R-statistic is generated based on the difference of mean rank among groups. When R is near 0, differences between places or times are no larger than one replicate to another in any place or time. When R is near 1, there are likely to be real differences in samples from differing locations and/or times. The analysis requires replication within groups; in our case, this meant plots within years. Therefore, on Transects 1–3, we analyzed post-1979 data only, testing within M- and C-plots separately. On Transects 4 and 5, we tested for temporal differences among all sample years.

Weighted averaging models for calculation of vegetation-inferred hydroperiod

Weighted averaging (WA) regression and calibration models (Birks et al., 1990) were used to better understand vegetation responses to apparent hydrological conditions at the plot level. The models were developed in two steps. In the regression step, species optima and tolerances for hydroperiod were estimated on the basis of their abundances and observed hydroperiods at 91 locations along three transects, which included Transects 4 and 5 from this study and a transect from an independent study of marl prairies located west of Shark Slough in the vicinity of the ENP-Big Cypress National Preserve border (Ross et al., 2003b). In these plots, vegetation was surveyed in the winter and spring of 2003, and hydroperiods were estimated from mean plot elevations and water level records from the 1996 to 2001 water years at ENP recorders CR-2, NTS-1 and NP-205. The WA species optimum for hydroperiod was calculated by averaging hydroperiods for plots in which a species was present, weighted by the species' relative abundance in each plot and tolerance for each species was estimated as the weighted standard deviation of hydroperiods (Ter Braak & Looman, 1995). We used the C^2 program of Juggins (2003) to calculate species optima and tolerances, and we selected the models that minimized the root mean square error of prediction (RMSE) of 100 bootstrapped estimates from the data set.

In the calibration step, we applied the best WA model to the historical and current vegetation data from the five Taylor Slough transects. WA techniques are usually applied to infer the level of an environmental variable in data sets in which it is unknown but species composition is known. Our usage in this case was somewhat different. Here, we examined temporal changes in the vegetation-inferred estimates, to shed light on the responsiveness of the plant communities to annual or longer-term hydrologic variation. Relative changes in vegetation-inferred hydroperiod over the sampling period would support the hypothesis that vegetation in Taylor Slough changed in response to short-term hydrological changes. The differences in inferred-hydroperiods among years were analyzed with the use of repeated-measures analysis of variance (repeated-ANOVA) using STATISTICA, Version 6.0 (StatSoft, Inc., Tulsa, OK, USA).

Results

Hydrological changes in Taylor Slough

During the pre-S332 period (1961–1980), mean daily water level in Taylor Slough in both dry and wet seasons correlated significantly with rainfall. In addition, the water level present at the end of the previous season, i.e., mean daily water level during the prior May or October, also related significantly to the water level in wet and dry seasons, respectively, and including this term improved the performance of the respective predictive models (Table 1; Figs. 2 and 3). When the precipitation-only model derived from data from the pre-S332 period was used to estimate water levels during the S332 (1980–1999) and post-S332 (1999–2003) periods, predicted water levels were much lower than observed water levels. This incongruity indicated that water management activities were apparently raising water levels substantially over what they would have been in a precipitation-driven system.

Water levels in the slough during 1980–2003 were primarily driven by the volume of water delivered from pumping stations. Water delivery was much less during 1980–1992 (3.8 million m^3) than during 1992–2003 (13.6 million m^3), and much higher (but less variable) in the wet season than the dry season (Figs. 2 and 3). Once delivery was initiated, rainfall contributed significantly to prediction of water level only during dry seasons in the S332 period, when delivery from the pumping station was lowest (R^2 of 2-factor model = 0.764, $p_{\text{rainfall}} = 0.032$) (Table 1). Rainfall was not significant in predicting water level in the wet season during S332 & post-S332 periods. Once pumping to Taylor Slough through S332 or S332D began, the 1-month lag term also became non-significant in the water level predictions, and therefore was excluded from Models 3 & 4 (Table 1).

In general, mean daily water levels during the S332 period were about 30–40 cm higher than in the pre-S332 period, and were much higher in the 1990's than in the 1980's. Subsequently, during the post-S332 period, mean daily water levels in Taylor Slough declined slightly, primarily because less water was delivered from S332D compared to S332, which ceased operation in 2000.

Vegetation patterns along and across the transects

Vegetation composition along Transects 1–3 changed substantially between 1979 and 2003. The NMS ordination indicated that by 1995, M-plots (i.e., dominated by *Muhlenbergia* in 1979) on

Table 1. Linear regression models for the relations of water level to rainfall, S332 and S332D delivery and 1-Month Lag

Period	Season	Model	R^2	Standard error of estimate
Pre-S332	Wet	(1A) WL = 58.09 + 2.11*Rainfall	0.382	13.47
		(1B) WL = 63.20 + 1.51*Rainfall + 0.23*1-Month Lag	0.705	9.60
	Dry	(2A) WL = 19.04 + 5.41*Rainfall	0.544	13.12
		(2B) WL = −34.33 + 4.95*Rainfall + 0.51*1-Month Lag	0.713	10.74
S332 &	Wet	(3) WL = 102.80 + 1.35*S332-Del + 1.23*S332D Del	0.631	8.16
post-S332 Period	Dry	(4) WL = 53.02 + 2.57*Rainfall + 2.51*S332-Del	0.764	10.98

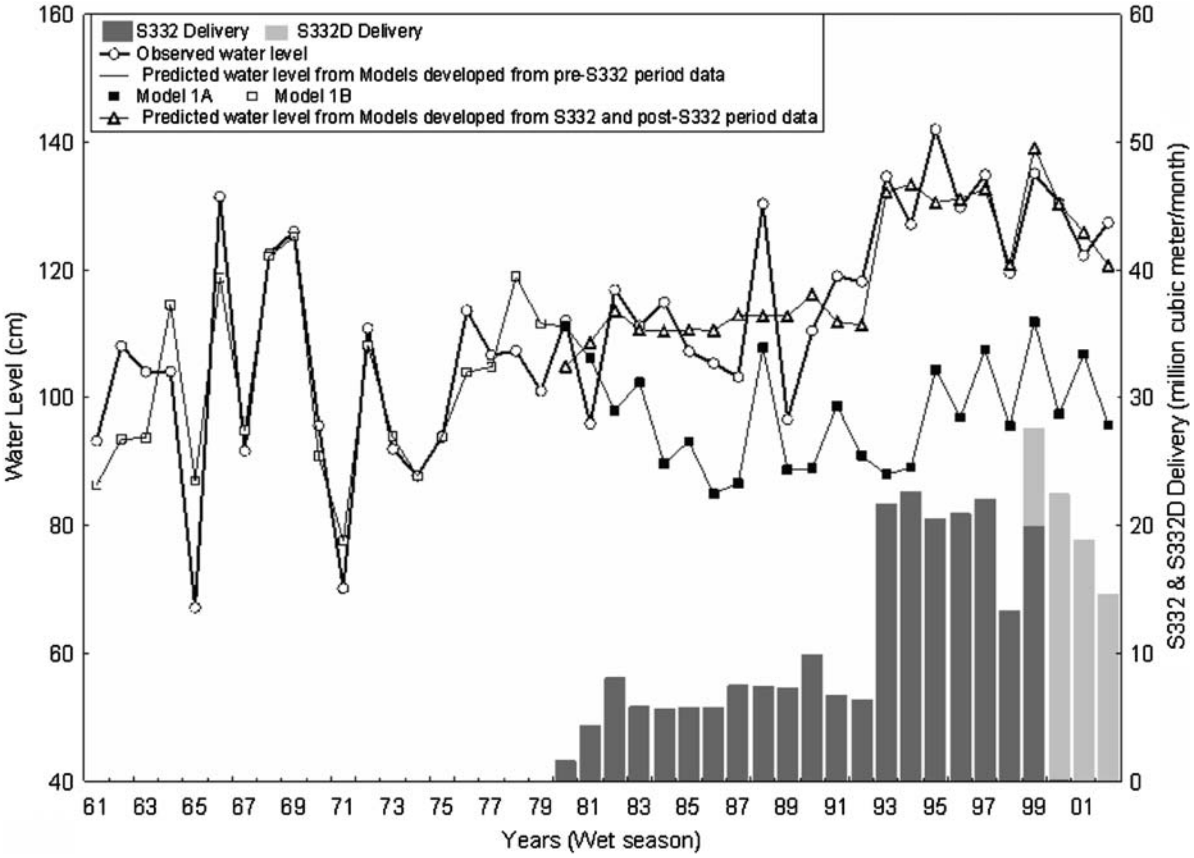

Figure 2. Observed and predicted water level and water flow through S332 and S332D into Taylor Slough during the 1961–2002 wet seasons. See Table 1 for details of the models.

Transect 1 resembled 1979 C-plots (dominated by *Cladium*), a trend that continued through 2003 (Fig. 4). Similar patterns occurred in Transects 2 and 3. However, along the Transect 2, partial reversion of the C-plots towards the community present in 1979 apparently occurred during the post-S332 period. This recent change suggested that vegetation was responding to the decrease in Taylor Slough water levels associated with S332D operations.

The analysis of similarity (ANOSIM) of post-1979 data showed significant inter-annual variation within both M- and C-plots on all three transects. Furthermore, most comparisons between successive sampling years indicated significant differences in composition. The only exceptions were 1995–1999 or 1996–1999 comparisons, which were non-significant within both M-and C-plots on Transect 1, and C-plots on Transect 3 (Table 2).

In 1979, mean total plant cover ranged from a low of 14.5% on Transect 3 to 49.3% on Transect 1 (Fig. 5). In the M-plots, *Muhlenbergia* dominated, with a relative cover of 90, 77 and 59% on Transects 1, 2 and 3, respectively. In those plots, *Cladium*, the next most abundant species, was the only other one with an absolute cover >1%. In the C-plots, *Cladium* was most abundant, with relative cover values of 34, 47 and 85% on Transects 1, 2, and 3, respectively. *Muhlenbergia* was absent from C-plots on Transects 1 and 2, but had the second highest cover (6%) in C-plots on Transect 3. *Eleocharis*, a major component of long hydroperiod prairies in the Everglades, was absent from M-plots on all three transects, and from C-plots on Transects 2 and all but one plot on Transect 3. *Eleocharis* was present in 56% of the C-plots of Transect 1, though its cover averaged only 0.6%.

By 1995, changes in vegetation composition along Transects 1, 2 and 3 became apparent.

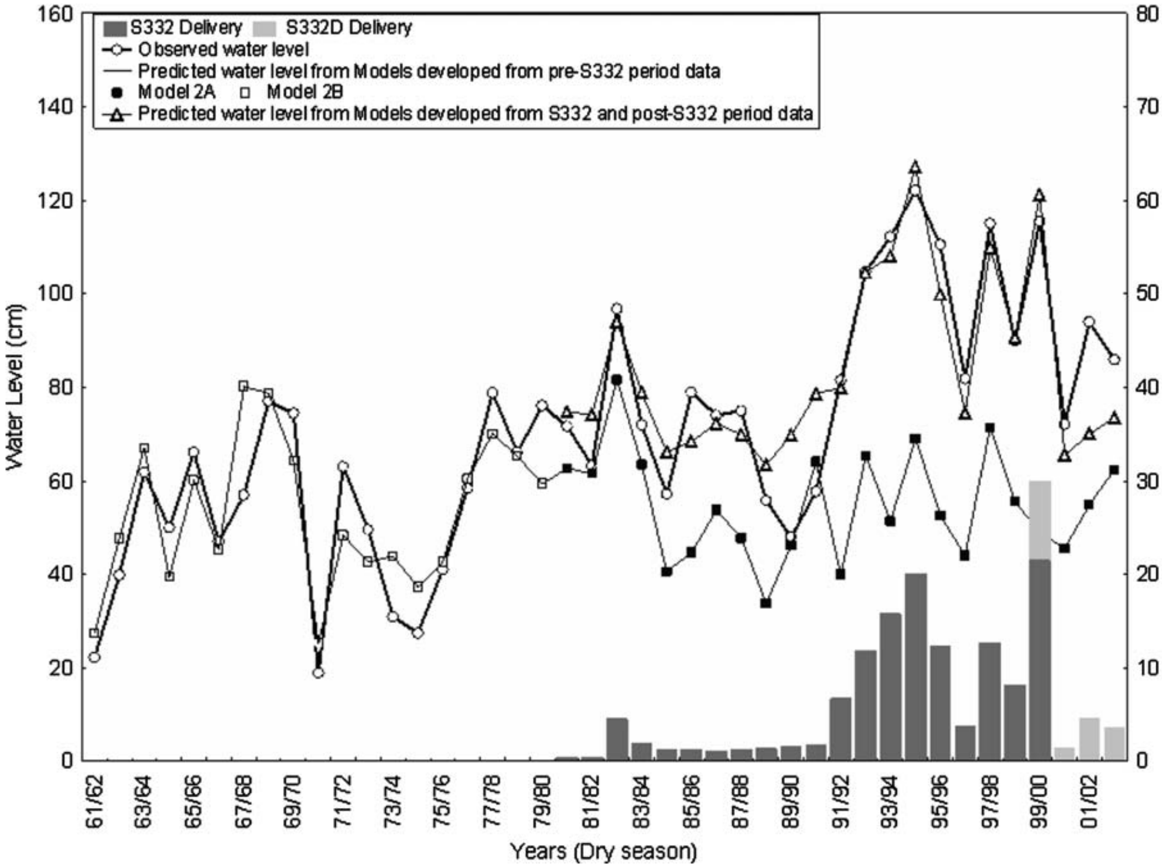

Figure 3. Observed and predicted water level and water flow through S332 and S332D into Taylor Slough during the 1961–2002 dry seasons. See Table 1 for details of the models.

Cover of *Muhlenbergia* had substantially decreased while *Cladium* cover increased on the M-plots and decreased on the C plots (Fig. 5). Changes in cover of the two species in both plot types were most dramatic on Transect 1. Here, the absolute cover of *Muhlenbergia* in the M-plots on Transect 1 decreased by 1700% by 1995, compared to 400% and 300% on Transect 2 and 3, respectively (Fig. 5). Parallel decreases in *Cladium* cover in C-plots also occurred. In contrast, *Cladium* cover increased significantly in M-plots over the sampling period. *Eleocharis*, absent in M -plots of Transect 1 in 1979, established in M-plots on Transect 1 and 3 by 1995, while becoming a major species in C-plots on all three transects.

Vegetation trends between 1979 and 1995 continued through 1999, though the changes in *Muhlenbergia* and *Cladium* cover were smaller. However, during this period, the cover of *Eleocharis* increased in the M-plots on Transect 1 and in the C-plots on all three transects (Fig. 5). *Eleocharis* was the most abundant species in M- and C-plots on Transect 1, with an absolute cover of 11.3% and 16.6%, respectively. Its average cover reached 10% in C-plots on Transect 3, and, at 40%, reached its highest abundance in the C-plots on Transect 2.

The compositional trend between 1999 and 2003 contrasted with trends prevailing prior to 1999. Cover of *Muhlenbergia* and *Cladium* increased in M- and C-plots, respectively (Fig. 5), and cover of *Eleocharis* in these plots decreased considerably. *Eleocharis* was virtually absent (mean cover <0.1%) in the M-plots of Transect 2 and 3, as well as the C-plots of Transect 3. However, cover of *Cladium* in the M-plots continued to increase through 2003. Total cover of all species increased sharply in M-plots in all three transects, and in C-plots in Transects 1 and 3, but not Transect 2.

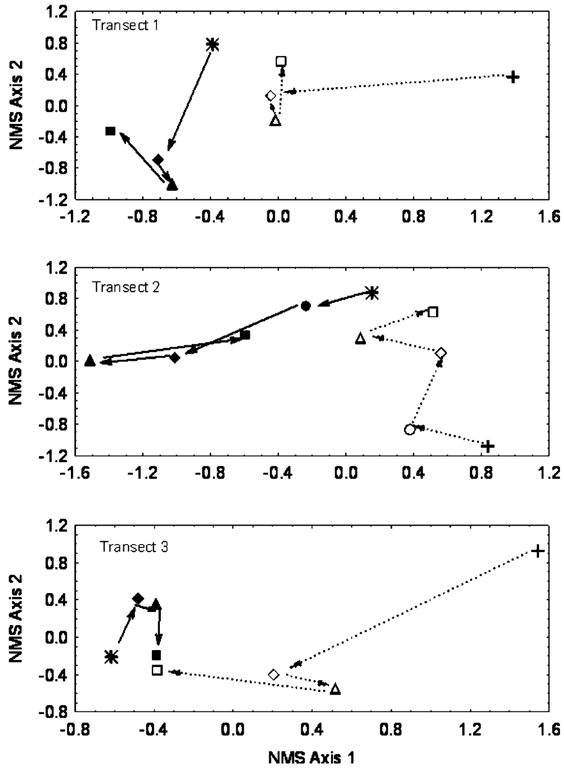

Figure 4. Site scores from NMS ordination, based on relative cover averaged across all *Muhlenbergia* (M; open symbol, dashed line) and all *Cladium* (C; closed symbol, solid line) plots on Transects 1, 2 and 3 (Stress = 1.15, 7.63 and 0.02, respectively) sampled in 1979 (+M-plots, ✱C-plots), 1992 (circle), 1995 or 1996 (diamond), 1999 (triangle) and 2003 (square).

Besides *Muhlenbergia, Cladium* and *Eleocharis*, 26 species exceeded 1% cover in M- or C-plots on Transect 1–3 during sampling years. In general, the cover of species with an optimum hydroperiod between 150 and 180 days expanded in the M-plots on Transects 1 and 2 over the sampling period. Many of these short hydroperiod species were present in the C-plots, but their cover was low (<1%) or they were absent in subsequent years. In contrast, species with optimum hydroperiods >210 days increased in cover on both transects and plot-types between 1979 and 1999, then decreased during the post-S332 period.

Since Transect 4 and 5 plots were not grouped into M and C categories, vegetation composition on these transects was analyzed at the plot level. Similar to the other three transects, composition on Transects 4 and 5 changed substantially over the 6-year sampling period. ANOSIM showed that vegetation composition in 1997, 1999 and 2003 differed significantly from one another (Table 2). The plots were likewise grouped by year in the NMS diagram, indicating a directional change in vegetation along an unidentified gradient (Fig. 6).

Vegetation dynamics on Transects 4 and 5 during 1997–2003 demonstrated a marked increase in total cover that paralleled cover trends already noted in Transects 1–3 in 1999–2003, a period of relatively low water level in Taylor Slough. This increase was concentrated particularly among the two major species, *Cladium* and *Muhlenbergia* (Fig. 7). In the six-year study period, the mean cover of *Cladium* increased from 3.7% to 37.8% and from 2.8% to 22.3% on Transects 4 and 5, respectively. The cover of *Muhlenbergia* also increased more than 7-fold on these transects (Fig. 7).

At the beginning of the 1997–2003 period, species other than *Cladium* and *Muhlenbergia* contributed about two thirds of the total cover on Transects 4 and 5, but no single species stood out. Two species, *Centella asiatica* (L.) Urban and *Phyla nodiflora* (L.) Greene exceeded 1% on Transect 4, while five species (*C. asiatica*, *Dichanthelium dichotomum* (L.) Gould, *Eragrostis elliottii* S. Wats., *Panicum tenerum* Beyr. ex Trin. and *Solidago stricta* Ait.) did so on Transect 5. The proportion of total cover contributed by species other than *Cladium* and *Muhlenbergia* decreased significantly by 2003, more so during the post-S332 period (1999–2003) than in the first two years (1997–1999) (Fig. 7).

Total species number recorded along the transects varied during the study period (Table 3). On Transects 1–3, species number decreased between 1979 and 1995, then remained almost stable through 1999. During 1999–2003, the number of species increased in the M- and C-plots on Transect 1, and in the C-plots of Transects 2 and 3. Increase in the number of species at the transect level was also observed on Transect 5 during this period, though the same pattern was not observed at the plot level. The total number of species present along Transect 4 remained nearly stable over the 6-year study period.

Vegetation-hydrology relationships

The species cover patterns generally suggest that higher water levels in Taylor Slough after 1992

Table 2. R-statistics and p-values from analysis of similarity (ANOSIM) testing for among-year differences in species composition along Transects 1–5, 1992–2003. Plots along Transects 1–3 were grouped in M-plots (*Muhlenbergia capillaris var. filipes*-dominated) and C-plots (*Cladium jamaicense*-dominated)

Transect	Plots	Comparisons	R-Statistic	p-value
T1	C-plots	Among all years	0.208	0.001
		1995, 1999	0.048	0.172
		1995, 2003	0.262	0.003
		1999, 2003	0.317	0.002
	M-plots	Among all years	0.212	0.001
		1995, 1999	0.036	0.268
		1995, 2003	0.302	0.002
		1999, 2003	0.292	0.002
T2	C-plots	Among all years	0.568	0.001
		1992, 1995	0.670	0.001
		1992, 1999	0.913	0.001
		1992, 2003	0.785	0.001
		1995, 1999	0.132	0.032
		1995, 2003	0.470	0.001
		1999, 2003	0.425	0.001
	M-plots	Among all years	0.454	0.001
		1992, 1995	0.581	0.001
		1992, 1999	0.628	0.001
		1992, 2003	0.647	0.001
		1995, 1999	0.158	0.020
		1995, 2003	0.464	0.001
		1999, 2003	0.268	0.002
T3	C-plots	Among all years	0.237	0.002
		1996, 1999	0.004	0.371
		1996, 2003	0.380	0.002
		1999, 2003	0.336	0.004
	M-Plots	Among all years	0.474	0.001
		1996, 1999	0.389	0.002
		1996, 2003	0.495	0.001
		1999, 2003	0.583	0.001
T4		Among all years	0.382	0.001
		1997, 1999	0.074	0.034
		1997, 2003	0.561	0.001
		1999, 2003	0.493	0.001
T5		Among all years	0.675	0.001
		1997, 1999	0.621	0.001
		1997, 2003	0.726	0.001
		1999, 2003	0.750	0.001

considerably affected the vegetation composition along Transects 1, 2 and 3. To examine this possibility quantitatively, we applied the WA model to the sequential vegetation data from the five Taylor Slough transects, estimating vegetation-inferred hydroperiods for each sampling year after 1980 (Figs. 8 and 9). Because 1979 vegetation data were available only in summarized form at the transect level, plot-level inferred hydroperiods were not estimated for that year.

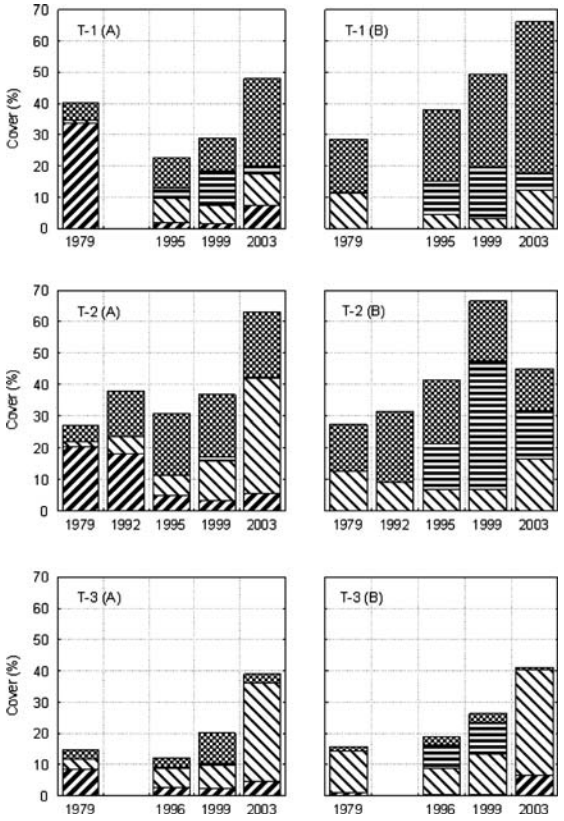

Figure 5. Absolute cover (%) of major species averaged across all *Muhlenbergia* (a) and *Cladium* (b) plots on Transects 1, 2 and 3, 1979–2003 ▧. *Cladium jamaicense* ☰ *Eleocharis cellulosa* ▨ *Muhlenbergia capillaris* var *filipes* ▩ *Other species*.

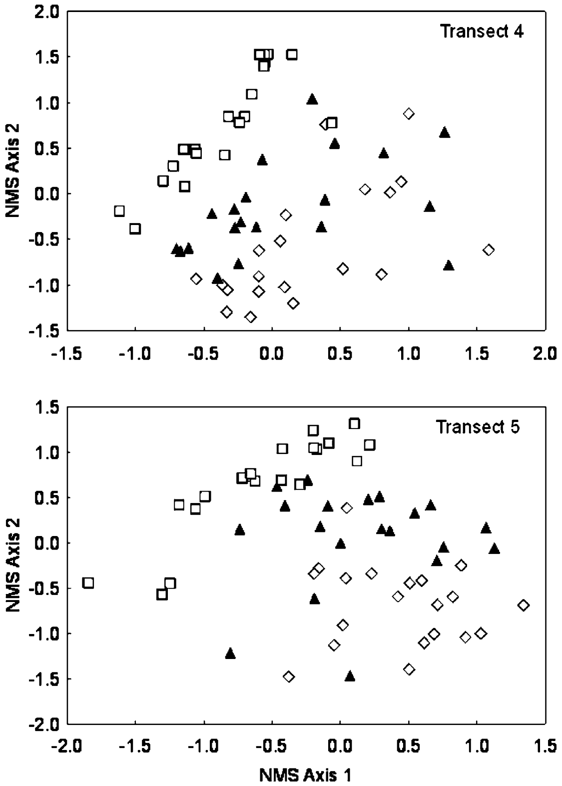

Figure 6. Site scores from 2-axis NMS ordination, based on relative cover in plots on Transects 4 and 5 (Stress = 11.5 and 15.6, respectively) sampled in 1997 (diamond), 1999 (closed triangle) and 2003 (square).

Temporal changes in vegetation-inferred hydroperiods were substantial, especially on Transects 2 and 3 (Fig. 8). On Transect 1, inferred hydroperiods did not differ significantly between 1995 and 1999 (consistent with the ANOSIM results presented in Table 2), but inferred hydroperiods in 2003 were shorter than in 1999, particularly in the M-plots (Fig. 8a; Table 4). On Transect 2, inferred hydroperiods were significantly longer in 1995 and 1999 than in 1992 (M- and C-plots) and 2003 (C-plots only) (Fig. 8b). Inferred hydroperiods along Transect 3 did not differ significantly between 1996 and 1999, but were shorter in 2003 than either of the previous years, mainly in the C-plots. The shorter inferred hydroperiods on all three transects in 2003 in comparison to 1995 and 1999 (Fig. 8c) indicated that the decrease in Taylor Slough water levels during the post-S332 period (Fig. 2 and 3) resulted in vegetation characteristic of drier conditions within 4 years or less. The Transect 2 data from 1992 and 1995 indicate that, in the presence of marked hydrological changes, turnover in species dominance can occur within three years.

On Transect 4 and 5, among-year differences in inferred hydroperiods were non-significant (Table 4; Fig 9). In conjunction with the ANOSIM results, which did indicate significant among-year differences in vegetation, these analyses suggest that factors other than hydrology were responsible for vegetation change in the headwater portions of Taylor Slough.

Discussion

In Taylor Slough prairies, temporal variation in plant species composition related closely to hydrologic changes which, in ENP, are driven

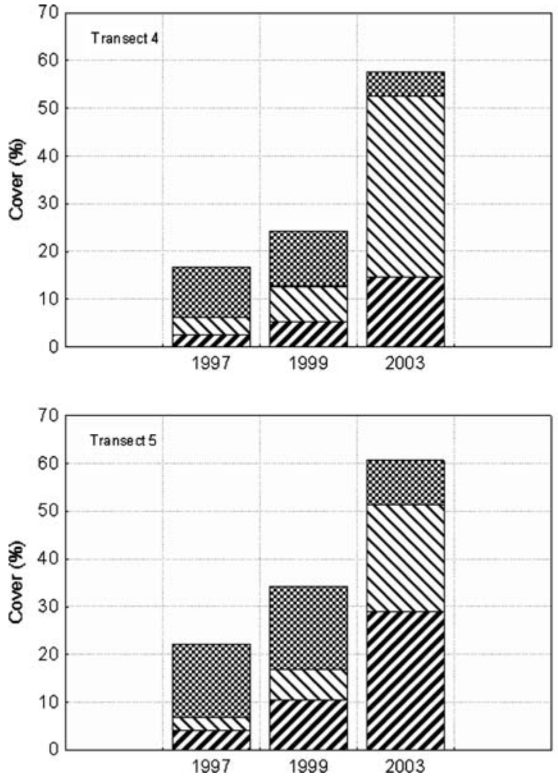

Figure 7. Absolute cover (%) of major species in plots on Transect 4 and 5 sampled in 1997, 1999 and 2003 ▧. *Cladium jamaicense* ☰ *Eleocharis cellulose* ▨ *Muhlenbergia capillaris var filipes* ▩ *Other species.*

more by water management activities than by natural processes (Figs. 2 and 3; see also Leach et al., 1971; McIvor et al., 1994). The management-induced hydrological regimes have changed vegetation structure and composition in Everglades landscapes over periods ranging from a few years to decades (Gunderson, 1994; David, 1996; Busch et al., 1998; Nott et al., 1998). Generally, how quickly hydrological changes induce wetland community changes depend on the magnitude of the hydrologic alteration and the nature of the affected communities (Craft et al., 2002; Warren et al., 2002). In Taylor Slough, visible changes in plant community dominance in response to hydrological change occurred within no more than 3 or 4 years of management intervention.

Modification of water management operations since 1980 raised Taylor Slough marsh water levels above those of the previous two decades. During 1993–1999, water deliveries by S332 were much higher than previously, reflecting both high rainfall in several of the years, and operational choices. In fact, water deliveries were 3–4 times higher in the wet season and up to 30 times higher in the dry season, elevating water levels in most years by 30–40 cm over levels of previous decades. During the post-S332 period, water levels in Taylor Slough dropped slightly in response to altered delivery protocols. A lag term representing carryover from the previous season was not significant in our water level model during the S332 and post-S332 periods, suggesting that storage was not an important element in the hydrologic budget under this management regime.

That conspicuous shifts in species dominance could occur within 3 or 4 years is perhaps surprising given that the dominant species are long-lived perennials and that *Cladium* and *Eleocharis* spread primarily through rhizomes. Seedling establishment, which in some species can lead to rapid vegetation change, appears to be rare in the three species in the absence of disturbance such as

Table 3. Total numbers of species sampled on Transects 1–5, 1979–2003

Transect/Plot-type	1979	1992	1995/96/97	1999	2003
T1-C	41		22 (9)	19 (9)	21 (9)
T1-M	46		29 (12)	28 (12)	35 (15)
T2-C	47	36 (15)	33 (14)	25 (14)	30 (13)
T2-M	49	30 (12)	35 (14)	36 (14)	36 (14)
T3-C	21		18 (4)	19 (6)	25 (7)
T3-M	28		15 (7)	25 (11)	25 (9)
T4			49 (16)	46 (15)	46 (14)
T5			40 (18)	50 (19)	55 (15)

Numbers inside parentheses are mean numbers of species per 5 m^2 plot. *Muhlenbergia* (M) and *Cladium* (C) plot-types on Transects 1–3 are summarized separately.

Table 4. p-values from repeated-measures ANOVA testing for effects of plot-type (M- and C-plots, on Transects 1–3), Transects (T4 & T5) and year (1992–2003) on vegetation-inferred hydroperiod

Transect	Transect/Plot	Year	Transect/ Plot × Year
1	<0.001	0.005	0.015
2	<0.001	<0.001	0.049
3	0.005	<0.001	<0.001
4 & 5	0.003	0.902	0.139

fires. The direction and rate of vegetation change in response to management intervention is of course highly dependent on the type and intensity of treatment as well as a range of ecosystem variables. In wetlands, the rates of change in response to hydrologic operations vary widely, depending on species composition, disturbance types and intensity, and details of hydrologic change. For instance, plant community biomass in created marshes in the Pamlico River estuary approached reference marsh conditions within 3–15 years depending on tidal flooding duration (Craft et al., 2002). Warren et al. (2002) found that salt marshes cut off from tidal exchange for decades replaced *Phragmites communis* marshes at a rate of 5–7%/yr where tidal exchange was fully restored but only at a rate of 0.5%/yr where flood frequency was still partially restricted.

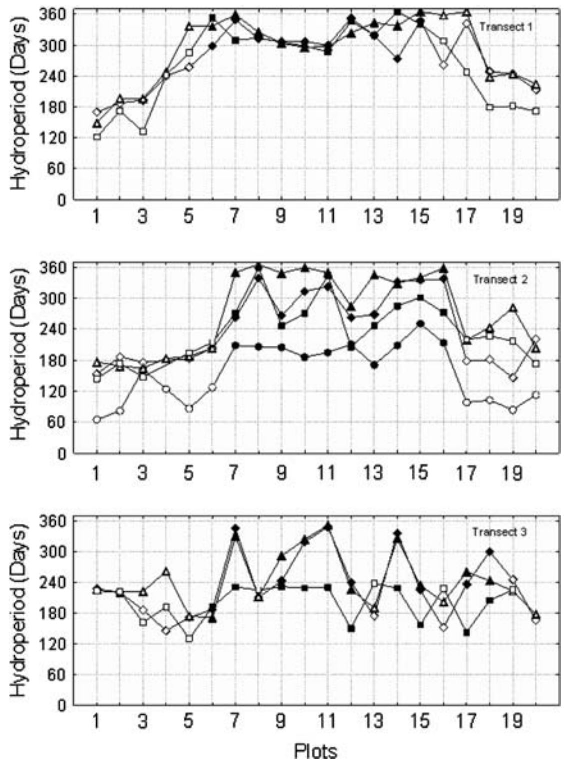

Figure 8. Plot level vegetation-inferred hydroperiods estimated in *Muhlenbergia* (open symbol) and *Cladium* (closed symbol) plots along the Transects 1, 2 and 3 in 1992 (●), 1995 (Transects 1 and 2) or 1996 (Transect 3; ♦), 1999 (▲) and 2003 (■).

Besides hydrological conditions, fire and nutrient availability are known to be major influences on wetland vegetation in the Everglades (Doren et al., 1997; Childers et al., 2003; Lockwood et al., 2003). Fire records indicate that the Taylor Slough wetlands were burned patchily in space and irregularly in time, with no burning taking place since the mid-1980's in the transects subject to water delivery, and only four of twenty plots in Transect 4 affected by a 1999 fire. Thus, the occurrence of fire had little to do with the compositional changes attributed to hydrology in this study.

Given the proximity of Transect 1 to the L-31W canal some nutrient enrichment might be expected, resulting in increased biomass and altered species composition in comparison to marsh areas far from the canal. However, there are several reasons why the cover patterns that we observed are unlikely to have resulted from nutrient enrichment. First, the concentration of total phosphorous, the chief limiting nutrient in Everglades freshwater marshes, averaged only 11.6 ppb in water entering Taylor Slough at S-332 in the 1986–1996 period, a value slightly above natural background levels of 5–10 ppb or less (Rudnick et al., 1999). The total phosphorus concentrations at Taylor Slough Bridge, near Transect 2 and about 2 km from the pump station, were reduced to 6.1 ppb over the same period, presumably through marsh uptake. However most of the uptake presumably occurred within the slough channel rather than in the higher marl prairies because surface water is confined to the channel until it reaches levels high enough to flood the prairies. Furthermore, where phosphorous is limiting, uptake is preferentially restricted to microbial and periphyton communities rather than macrophytes (Childers et al., 2002). Finally, observed increases in total species cover during the

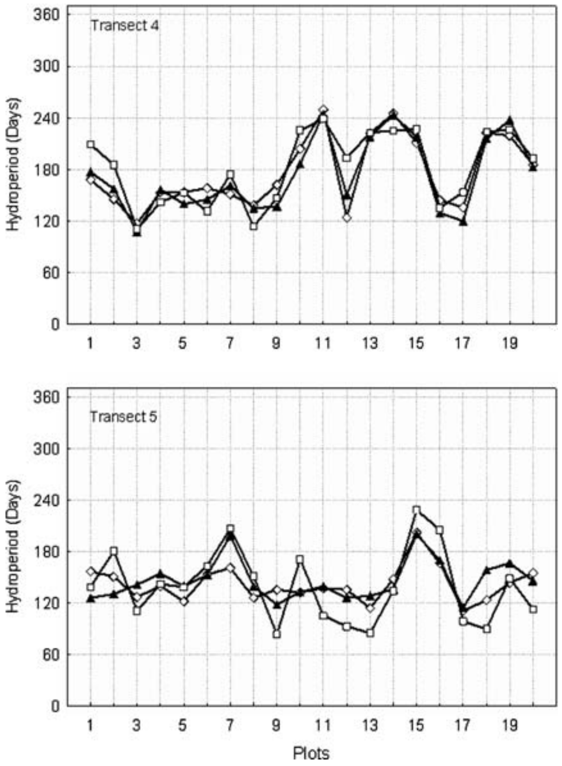

Figure 9. Plot level vegetation-inferred hydroperiods estimated along the Transects 4 and 5 in 1997 (◇), 1999 (▲) and 2003 (□).

period of record were not restricted to transects adjacent to the L31W canal or downstream from the delivery structures, but also included Transects 4 and 5, which were remote from discharge effects.

Our data indicate that under some conditions hydrologic manipulation can substantially and promptly affect plant species diversity, an emergent ecosystem property that is a prime objective of many restoration efforts. In this study, the long-term wetting trend in Taylor Slough in the S332 period led to a decrease in the number of species at the plot and transect levels, a trend that was partially reversed in some transects during the post-S332 period. These temporal changes took place along a spatial gradient in which herb species diversity increases with decreasing duration of flooding in south Florida fresh water wetlands (Busch et al., 1998; Ross et al., 2003b). In this context, higher plant richness is not necessarily a valid ecosystem goal. Rather, restoring the greater Everglades ecosystem has more to do with habitat (γ) diversity (Whittaker, 1972) than the local diversity measures we were able to quantify here. Within Taylor Slough, the objective should be to maintain prairie, marsh, and slough habitats in their characteristic structure and composition, and in proportions commensurate with their pre-development condition.

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