WETLANDS, Vol. 18, No. 2, June 1998, pp. 230–241

LONG-TERM HYDROLOGIC EFFECTS ON MARSH PLANT COMMUNITY STRUCTURE IN THE SOUTHERN EVERGLADES

David E. Busch [1,3], William F. Loftus[2], and Oron L. Bass, Jr.[1]
[1] *National Park Service and* [2] *United States Geological Survey—Biological Resources Division*
Everglades National Park, Florida, USA

[3] *Present address: United States Geological Survey—Biological Resources Division*
Forest and Rangeland Ecosystem Science Center
Regional Ecosystem Office
P.O. Box 3623
Portland, Oregon, USA 97208

Abstract: Although large-scale transformation of Everglades landscapes has occurred during the past century, the patterns of association among hydrologic factors and southern Everglades freshwater marsh vegetation have not been well-defined. We used a 10-year data base on the aquatic biota of Shark Slough to classify vegetation and describe plant community change in intermediate- to long-hydroperiod Everglades marshes. Study area marsh vegetation was quantitatively grouped into associations dominated by 1) *Cladium jamaicense,* 2) a group of emergents including *Eleocharis cellulosa, Sagittaria lancifolia,* and *Rhyncospora tracyi,* 3) taxa associated with algal mats (*Utricularia* spp. and *Bacopa caroliniana*), and 4) the grasses *Panicum hemitomon* and *Paspalidium geminatum.* During the decade evaluated, the range of water depths that characterized our study sites approached both extremes depicted in the 40-year hydrologic record for the region. Water depths were near the long-term average during the mid-1980s, declined sharply during a late 1980s drought, and underwent a prolonged increase from 1991 through 1995. Overall macrophyte cover varied inversely with water depth, while the response of periphyton was more complex. An ordination analysis, based on plant species abundance, revealed that study area vegetation structure was associated with hydrologic patterns. Marsh plant community structure showed evidence of cyclic interannual variation corresponding to hydrologic change over the decade evaluated. Lower water depths, the occurrence of marl substrates, and high periphyton cover were correlated. These factors contributed to reduced macrophyte cover in portions of the study area from which water had been diverted.

Key Words: classification, Florida, hydroperiod, macrophyte, ordination, periphyton, Shark Slough, water depth

INTRODUCTION

Despite often-extreme environmental variability, the graminoid marsh communities of the Florida Everglades appear to have remained relatively stable with respect to structural change and species turnover. Contributing to this apparent stability may be a high degree of resistance and resilience to disturbances such as hurricanes, flooding, and fire (Craighead and Gilbert 1962, Herndon et al. 1991, Pimm et al. 1994). Time lags between physical change and vegetation response may also be responsible for a perceived lack of short-term change in Everglades plant community structure or composition (White 1994). Although Everglades graminoid vegetation has been thought to respond to hydrologic variation occurring over a one- to ten-year period, marsh plant associations showed no apparent correlation with hydrologic patterns at Everglades sites with differing hydrologic histories (Gunderson 1989, 1994). Indeed, the most obvious characteristic of communities dominated by sawgrass, *Cladium jamaicense,* was the absence of seasonal variation in plant structural and functional variables (Steward and Ornes 1975). Emergent plant communities in the northern Everglades responded only minimally to hydrologic variation in short-term (i.e., 2-year) investigations (Wood and Tanner 1990, Jordan et al. 1997). Accordingly, the response of Everglades marsh vegetation to a dynamic hydrologic system has been difficult to document over relatively short time periods or at a local scale. This implies that long-term investigations of the relationship between Everglades vegetation and hydrology may be required to adequately describe responses to wet periods or drought.

In spite of the apparent stability shown in short-term studies, there is little doubt that substantial change has occurred in the Everglades over the last century. Three of seven predrainage landscapes (custard apple forest, peripheral wet prairie, and cypress forest) have been completely lost from the Everglades ecosystem (Davis et al. 1994). More subtle shifts away from wet-prairie vegetation and toward *Cladium* and woody shrubs have occurred over a 15- to 25-year period of water and fire management (Kolipinski and Higer 1969). On a finer temporal and spatial scale, marl prairie vegetation of the southern Everglades has shown a decreasing abundance of *Muhlenbergia filipes* in relation to *Cladium* during a period of increased hydroperiod and water depth (T.V. Armentano, pers. comm.). However, it remains unclear how closely hydrologic variation is linked to vegetation change in intermediate- to long-hydroperiod Everglades marsh environments, in part because responses are complicated by nutrient, edaphic, or biotic interactions.

Understanding the interactions of plants with nutrient or hydrologic variation can facilitate understanding of structural aspects of the Everglades ecosystem (DeAngelis and White 1994). Nutrient additions clearly affect vegetation structure in oligotrophic Everglades marshes, although anthropogenic nutrient inputs are thought to be attenuated before they exert strong influence in the southern part of the Everglades (Urban et al. 1993, Craft et al. 1995, David 1996). While the hydrologic dynamics of the Everglades are thought to influence nearly all biotic aspects of the ecosystem (Rose and Rosendahl 1981), plant communities may respond in complex manners to hydrologic change at various temporal and spatial scales (Gunderson 1994). The intricacies of hydrologic variability are simplified somewhat by the finding that a number of variables relating to water depth and hydroperiod are highly intercorrelated, so that water depth may be used as a meaningful measure of the overall hydrologic regime in Everglades wetland communities (Gunderson 1989).

In addition to the macrophyte assemblage, algal mats are an important component of Everglades marsh vegetation. Algal mats are found on macrophyte stems (hence the name periphyton), at the water surface, and on the marsh bottom. Everglades periphyton is usually dominated by cyanobacteria, but following prolonged inundation, the proportion of diatoms and green algae may increase in the algal mat association (Browder 1981). Everglades algal mats often grow attached to floating stems of *Utricularia purpurea,* a vascular plant that is part of a periphyton-*Utricularia* complex (Ulanowicz 1995). Because of the direct influences of this complex on light, water, and nutrient acquisition by macrophytes, as well as indirect interactions with soil formation, physico-chemical changes, and trophic webs, algal mats must be considered a key component of Everglades marsh plant communities.

In general, previous investigations of Everglades marsh vegetation have evaluated communities over short intervals or have been based on qualitative descriptions of plant community structure. The availability of a decade-long data base on the aquatic biota of Everglades National Park made possible our inquiry into the nature of marsh macrophyte and periphyton responses to hydrologic variation. We examined marsh plant community responses occurring over annual precipitation cycles, as well as responses to prolonged drought and wet periods. Our objectives were to quantify plant community changes occurring in southern Everglades marsh vegetation during the 1985–1995 period and to evaluate those physical factors most likely to affect marsh plant community structure. We used plant community classification and ordination, together with an analysis of the effects of hydrologic change on the dominant species in four Everglades marsh plant associations, to isolate those ecological interactions contributing most clearly to community variation.

METHODS

Shark Slough is the principal drainage of the southern Everglades, with its hydrologic gradient trending southwestward across the lower Florida peninsula toward the Gulf of Mexico (Figure 1). The slough is a broad (average width = 10–16 km), slow-moving (ca. 1 cm/sec) watercourse bounded by wetlands of slightly higher elevation to the east and west. Shark Slough discharge is strongly influenced by the management of water-control structures along the interface between Everglades National Park and Water Conservation Areas 3A and 3B to the north. Three study areas were selected within wet-prairies in the northern portion of the slough in Everglades National Park. Our lowest elevation (1.3 m) study area was in central Shark Slough (CSS) and was characterized by relatively long hydroperiods and deep water. The second area, near the Shark Valley Road (SVR), was at a higher elevation (2.0 m) near the western edge of Shark Slough where hydroperiods were shorter and water depths lower. Since 1967, the northeastern segment of Shark Slough has been partially isolated hydrologically from the central slough by levees and by control of water deliveries. Typically, flows are managed by shunting water away from this section of the slough so that hydroperiods tend to be shorter and water depths lower than at similar elevations in the central slough (Loftus and Eklund 1994). Overall, our northeastern Shark Slough study area (NESS) was at an intermediate elevation (1.7 m) and experienced hydrologic conditions

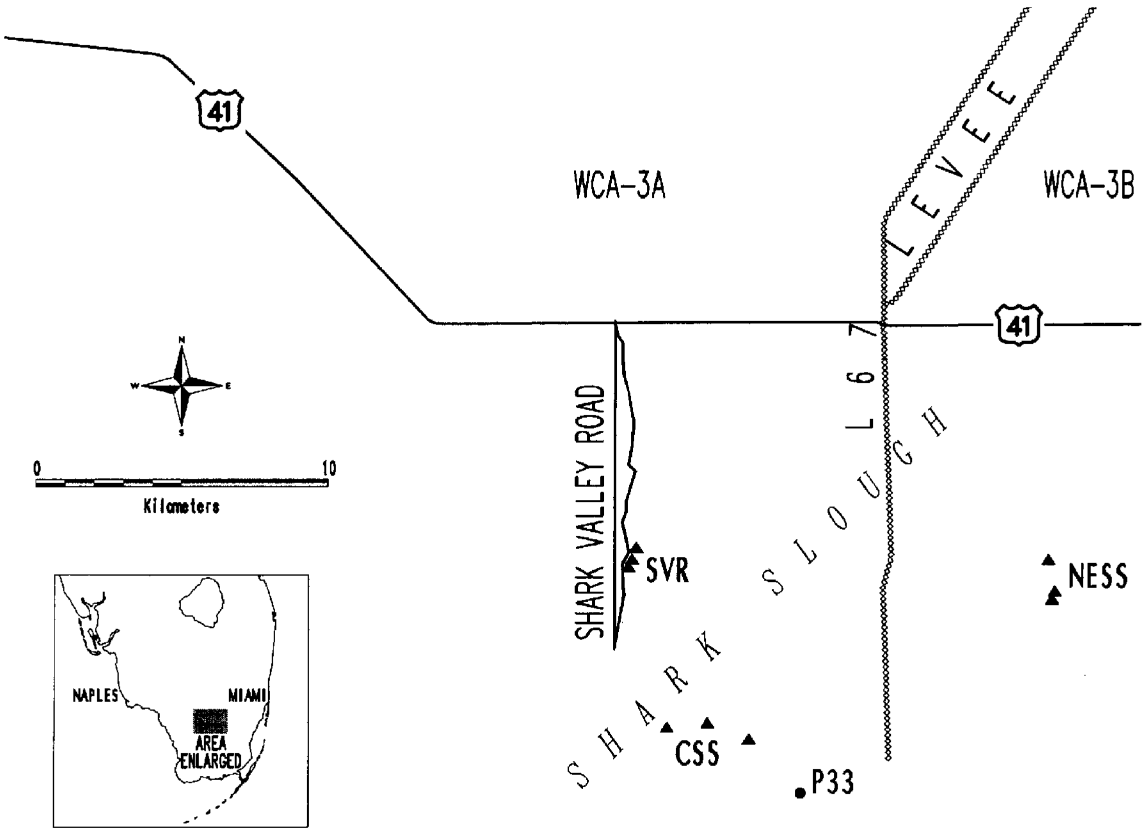

Figure 1. The southern Everglades showing plot locations at study areas in Shark Slough, including Central Shark Slough (CSS), Shark Valley Road (SVR), and Northeast Shark Slough (NESS). P-33 is a continuous hydrologic monitoring station in Shark Slough. U.S. Highway 41 (Tamiami Trail) is the location of a levee system (L-29) separating Water Conservation Areas (WCAs) 3A and 3B from Everglades National Park to the south.

that were intermediate between the CSS and SVR areas.

Substrate samples were taken at each study area and classified as peat, marl, or rock. All substrate samples from CSS were classified as peat. With one exception, all SVR substrate samples were classified as rock, although these samples typically had a shallow marl overlay. Of the 71 samples taken at NESS, 25 were classified as rock and 46 as marl.

Within each of the three study areas, three 100 × 100 m plots were established in wet prairie environments. Before each sampling period, seven coordinates were randomly selected within each plot from which data on aquatic biota and physical characteristics were collected. Samples were taken from quadrats bounded by a throw trap designed to sample aquatic biota by tossing it into the marsh (Kushlan 1981, Loftus and Eklund 1994). The throw trap consisted of a 1 × 1 m open horizontal frame with nylon mesh sides so that the 1-m^2 quadrats had variable vertical dimensions equivalent to the marsh water depth at the time of sampling. Information from each sampling location was later combined by averaging (in the case of continuous variables) or selecting modal values (in the case of ordinal variables) to derive data for each plot on each sample date.

Each site was sampled in February, April, July, October, and December during each year of our >10-year (1985–1995) study period. Sampling was not completed in February of 1988, April of 1990, and October of 1987, 1988, and 1990. Within each 1-m^2 quadrat, water depth was measured using a meter stick. Each site also had a permanent staff gauge from which water depth was recorded on each sample date. These discontinuous readings were regressed against hydrologic data from nearby continuous monitoring stations to estimate hydrologic parameters at each site. Water temperatures were recorded by submerging a thermometer to a depth of approximately 30 cm for 1 min. Estimates were made of the percent cover of each quadrat by macrophytes and by periphyton mats. Within each quadrat, stems of each emergent macrophyte were identified and counted. Separate estimates were made of periphyton and *Utricularia* cover in the periphyton-*Utricularia* complex. However, the two most common species of *Utricularia* (*U. purpurea* Walter and *U. fo-*

liosa L.) were not distinguished in the field. The abundance of periphyton, occurring as both floating and submergent forms and as a coating on vascular plant stems, was further quantified by measuring the total volume of the algal mat-*Utricularia* complex within each sample.

The marsh vegetation data base consisted of 368 samples within which 30 plant taxa were identified. Relative frequencies were calculated by dividing the number of occurrences of each taxon in the data set by 368. Overall means were calculated and plotted for water depth, macrophyte cover, and periphyton cover for each sampled month within the decade-long study period. These variables, as well as periphyton volume, were separately compared across study areas using a repeated-measures analysis of variance (ANOVA) with the arcsine transformation applied to cover percentages (Zar 1984, Potvin et al. 1990) . Where ANOVA indicated there was a significant ($p < 0.05$) probability that at least two means were different, the Student-Newman-Keuls (SNK) test was used to determine which categories differed significantly for each variable.

Detrended correspondence analysis (DCA, Hill 1979a) was used to ordinate study area macrophyte density information from the Shark Slough vegetation data matrix. The DCA procedure for downweighting rare species was employed to reduce the possibility that infrequent taxa in our data set would distort this analysis. Mean values were calculated for DCA axis loadings of each study area in each study year. These data were plotted against DCA axes 1 and 2 to help interpret between-area community variation, as well as the trajectories of change within areas during the study period. Correlation analysis was used to evaluate the association of abiotic and biotic variables with the marsh community variation as described by four DCA axes.

Two-way indicator species analysis (TWINSPAN, Hill 1979b) was employed to classify the Shark Slough marsh-plant community based on the abundance of taxa in vegetation samples. A hierarchical arrangement was derived using TWINSPAN and displayed for a graphical examination of the tentative associations among plant taxa. Additional analyses were used to examine the relationships of dominant taxa from our prospective plant associations with study-area environmental variation. Repeated-measures ANOVA and SNK tests were performed on square-root transformed data (Zar 1984) to evaluate between-area differences in the density (stems/m^2) of 7 dominant macrophyte taxa and to test for inter-area differences in cover (using the arcsine transformation) of *Utricularia* in periphyton mats. The chi-square (χ^2) test was employed for among-site comparisons of the frequencies of the eight most common taxa. Expected frequencies for the χ^2 analysis were derived by multiplying the total frequency of each taxon in all samples by the proportion of samples that were taken at each area. Correlation analysis was used to evaluate the associations of biotic and abiotic variables with density or cover of the dominant taxa across all study areas.

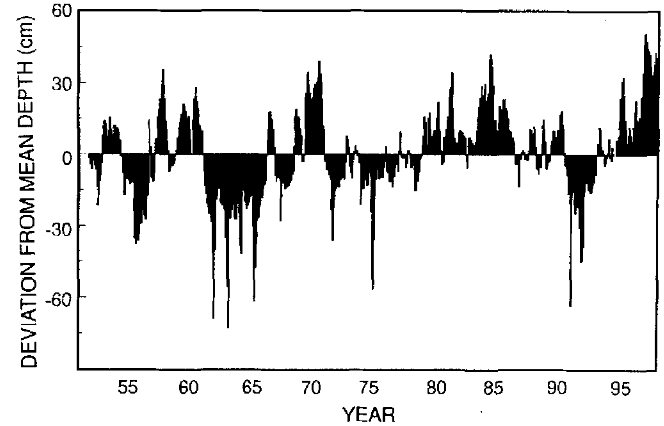

Figure 2. Deviations of monthly mean water depths from the overall mean for the 43-year period of record at Everglades National Park hydrologic monitoring station P-33 in Shark Slough.

RESULTS

Water depths on the study areas correlated closely with water depths at Everglades National Park hydrologic monitoring stations ($r = 0.97$, $p < 0.001$). An analysis of the deviations of mean monthly water depths from the water depth grand mean for the 40-year period of record at hydrologic monitoring station P-33 (Figure 1) indicated that, during the decade evaluated (1985–1995), hydrologic conditions were highly variable (Figure 2). Water depths during the evaluation period encompassed both extremes in the long-term record and were, therefore, considered representative of the overall range of Shark Slough hydrologic variation. Information from regression models linking measured study area water depths with continuous monitoring station data indicated that hydroperiods varied from an average of 343 days at CSS, to 312 days at NESS, to 294 days at SVR.

On the study areas, water depths approached the long-term average during the early part of the evaluation period. During the drought years of the late 1980s, average water depths varied between approximately 10 and 40 cm on the study areas (Figure 3a). Following this dry period was a sustained period of increasing wetness from 1991 through 1995, where average water depth ranged between about 30 and 80 cm. In response to annual precipitation patterns, there was

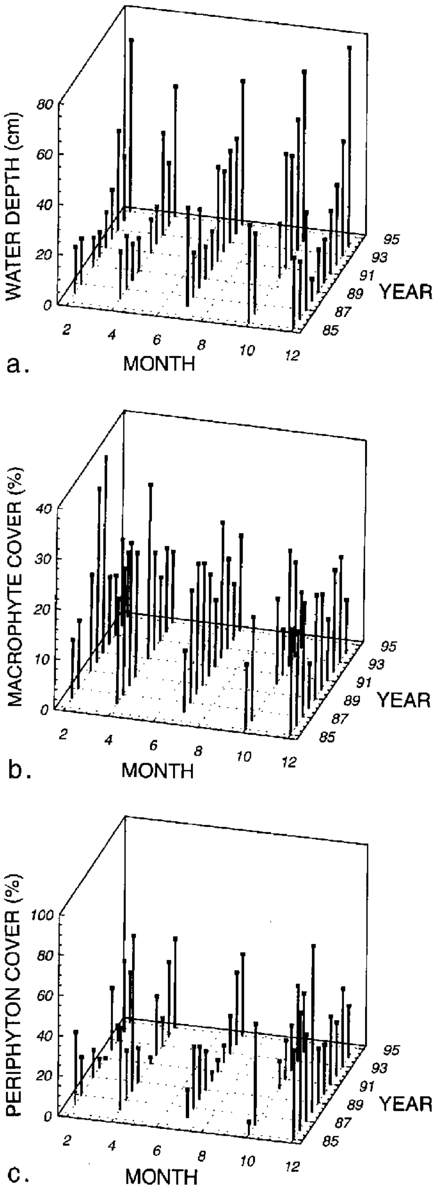

Figure 3. Water depth (a), macrophyte cover (b), and periphyton cover (c) at Shark Slough study areas.

a tendency for late dry-season water depth (April range ca. 10–50 cm) to be lower than late wet-season water depth (October range ca. 20–70 cm). However, interannual variation was characteristically greater than within-year variation.

The average macrophyte cover on marsh study areas appeared to have an inverse relationship with water depth (Figure 3a and 3b). Following the 1988–1990 dry period, average macrophyte cover approached 40 percent. Later in the study period, average macrophyte cover decreased to the 10–20 percent range, coincident with increased water depth during this time. Examination of within-year macrophyte cover differences indicated decreasing cover between the middle of each

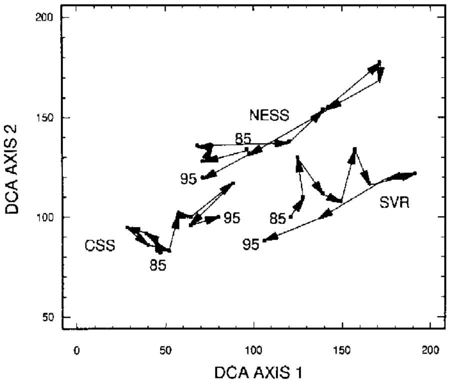

Figure 4. Detrended Correspondence Analysis (DCA) ordination of vegetation samples for Shark Slough study areas in each study year from 1985 through 1995. Arrows show the direction of change in annual means for each study area in relation to DCA axes 1 and 2.

dry period (February) and the latter portions of the subsequent wet period (October). Responses of algal-mat cover to hydrologic variation are more difficult to discern (Figure 3c). In general, it appeared that periphyton cover was least during periods of water recession (1989–91) and increased with increasing water depth. During most of the study years, December (early dry season) periphyton cover was high in relation to the other months examined.

Differences in plant frequency and cover among the three study sites governed the between-site gradation shown along four detrended correspondence analysis (DCA) axes. DCA axis 1 described 33% of the variance in the plant community data set. The relative position of study sites along DCA axis 1 described a hydrologic transition from the Central Shark Slough (CSS) to the Northeast Shark Slough (NESS) and Shark Valley Road (SVR) study areas (Figure 4). Additionally, annual changes in the loadings along this axis for each area portrayed a pattern of increase during the middle years of the study followed by decreases during the wet latter years of the study. Interannual variation was less pronounced relative to DCA axis 2, which accounted for an additional 30 percent of the community data variance. Between-site plant community differences along DCA axis 2 separated central and western Shark Slough sites (CSS and SVR) from the hydrologically-isolated northeastern portions of the slough (NESS). Third and fourth DCA axes described 19 and 18 percent of the plant community variance, respectively.

Correlations among the biotic and physical factors that are likely to govern the plant community variation described by our ordination are summarized in Table 1. DCA axis 1 was inversely correlated with macrophyte cover, periphyton cover and volume, and water

Table 1. Correlations among Detrended Correspondence Analysis axes, environmental, and biotic variables. Correlation coefficients (r) are presented with statistical significance denoted as * where $p < 0.05$ and ** where $p < 0.001$.

	Axis 1	Axis 2	Axis 3	Axis 4	Year	Macrophyte Cover	Periphyton Cover	Periphyton Volume	Water Depth	Water temperature
Macrophyte Cover	−0.34**	−0.24**	0.04	0.12*	−0.12*	—				
Periphyton Cover	−0.17*	0.08	0.11*	−0.13*	−0.08	−0.01	—			
Periphyton Volume	−0.15*	0.01	0.08	−0.04	−0.16*	−0.18*	0.79**	—		
Water Depth	−0.27**	−0.20**	−0.04	0.11*	0.46**	0.02	−0.02	0.02	—	
Water Temperature	−0.28**	−0.10	0.11*	−0.05	−0.80**	0.09	0.16*	0.24**	−0.21*	—

temperature and depth. DCA axis 2 was inversely correlated with macrophyte cover and water depth, while DCA axis 3 was correlated with periphyton cover and water temperature. DCA axis 4 was correlated with macrophyte cover and water depth, and inversely correlated with periphyton cover. The study year was inversely correlated with macrophyte cover, periphyton volume, and water temperature. Year was positively associated with water depth. Periphyton volume was inversely correlated with macrophyte cover. Periphyton cover and volume were positively correlated. Water temperature showed positive associations with periphyton cover and volume, and was inversely correlated with water depth.

The three study areas were not uniform over the decade evaluated in terms of their macrophyte cover, periphyton abundance, and water depth (Table 2). Average CSS macrophyte cover was greater than that at NESS and SVR. Conversely, algal mat cover was greater at NESS than at CSS and SVR. Periphyton volume tended to be lowest at CSS, intermediate at SVR, and greatest at NESS. Evidence for the influence of hydrology on such between-site variation comes from the hydrologic differences among CSS (greatest average water depth and longest hydroperiod), NESS (intermediate), and SVR (shallowest on average with shortest hydroperiod).

Thirty-two vegetation categories were identified on the three study areas over the ten-year study period (Table 3). Of these, eight taxa appeared in more than 100 of the 368 plots (relative frequencies all ≥ 0.3) and were considered as dominants in our determination of plant associations. The other 24 taxa were infrequent in study plots (relative frequencies all ≤ 0.17).

Two-way indicator species analysis (TWINSPAN) resulted in an ordering of the 32 taxa found on study plots in a seven-level classification dendrogram (Figure 5). The second level of this classification revealed a separation of the taxa into four plant associations that can be considered typical of Shark Slough marsh vegetation. The largest of these groups included 14 taxa; of these, only *Cladium jamaicense* was among the eight dominant species on the study plots. A second association included the dominant aquatic emergents *Eleocharis cellulosa, Sagittaria longifolia,* and *Rhyncospora tracyi.* The third association identified using TWINSPAN was characterized by *Utricularia* sp. and *Bacopa caroliniana,* species with affinities to the Everglades algal mat community. A fourth association included the dominant grasses *Panicum hemitomon* and *Paspalidium geminatum.*

The *Paspalidium-Panicum* association had negative values on DCA axis 1, low positive values on DCA axis 2, and low to intermediate values on DCA axis 3

Table 2. Repeated-measures analysis of variance results for differences among sites in macrophyte cover, periphyton cover, periphyton volume, and water depth. All F-values were statistically significant at the $p < 0.05$ level. Data presented are factor means averaged over the study period ± one standard error. Different superscripts indicate significant differences among means using the Student-Newman-Keuls test.

Factor	Site			F-value
	CSS	SVR	NESS	
Macrophyte cover (%)	26.0 ± 1.3^a	11.4 ± 1.5^b	15.5 ± 1.4^b	24.6
Periphyton cover (%)	24.1 ± 1.7^a	23.3 ± 1.9^a	36.7 ± 1.3^b	38.1
Periphyton volume (ml)	1689 ± 192^a	2555 ± 258^b	3415 ± 273^c	13.5
Water depth (cm)	41.9 ± 1.6^a	21.8 ± 1.8^b	28.9 ± 1.7^b	35.8

(data not shown). The *Cladium* association tended to have higher values on all three DCA axes. The association including *Utricularia* and *Bacopa* had intermediate values on DCA axis 1 and a broad range on DCA axis 3. Likewise, the association that includes *Eleocharis, Rhyncospora,* and *Sagittaria* was centrally located in relation to the ordination axes.

Table 3. Relative frequency of plant taxa in Shark Slough aquatic vegetation plots (n = 368). Species with only a single occurrence in the data set are indicated with dashes.

Species	Relative frequency
Eleocharis cellulosa Torrey	1.00
Rhyncospora tracyi Britton	0.79
Sagittaria lancifolia L.	0.71
Utricularia spp.	0.67
Panicum hemitomon Schultes	0.63
Paspalidium geminatum Forsskal	0.39
Bacopa caroliniana (Walter) B.L. Robinson	0.37
Cladium jamaicense Crantz	0.30
Chara sp.	0.17
Nymphaea odorata Aiton	0.10
Utricularia cornuta Michaux	0.10
Potamageton illinoensis Morong	0.08
Nymphoides aquatica (J.F. Gmilin) Kuntze	0.07
Justicia ovata (Walter) Lindau	0.04
Pontederia lanceolata Nuttall	0.02
Aeschynomene pratensis Small	0.02
Typha domingensis Persoon	0.02
Hymenocallis latifolia (Miller) Roemer	0.01
Oxypolis filiformis (Walter) Britton	0.01
Unknown	0.01
Sarcostema clausum (Jacquin) Schultes	0.01
Mikania scandens (L.) Willdenow	0.01
Ipomea sagittaria Poiret	0.01
Filamentous green algae	—
Rhyncospora inundta (Oakes) Fernald	—
Phyla nodiflora (L.) Greene	—
Thalia geniculata L.	—
Muhlenbergia filipes M.A. Curtis	—
Rhizophora mangle L.	—
Valisineria sp.	—
Rhyncospora sp.	—
Myrica cerifera L.	—

Although *Cladium* density was high at SVR relative to the other sites, density did not differ significantly across sites (Table 4). However, the frequency of *Cladium* occurrence was greatest on SVR plots (Table 5). *Eleocharis* was present on all plots sampled but occurred in the greatest densities on CSS plots. *Rhyncospora* density and frequency were greatest at SVR and NESS. *Panicum* density and frequency were greatest at CSS, with SVR intermediate, and NESS showing the lowest values for both parameters. *Sagittaria* density and frequency did not vary significantly among areas. *Paspalidium* was encountered most frequently on CSS plots, but its densities were low at all three sites. *Utricularia* cover and frequency tended to be high at CSS relative to SVR and NESS. *Bacopa* occurred commonly in samples taken at SVR and CSS, but its densities were greatest at SVR.

The occurrences of the eight most common species in relation to various environmental factors are more closely evaluated in Table 6. *Cladium* and *Sagittaria* densities were inversely correlated with water depth, providing evidence of affinities for relatively drier environments. This pattern was reversed for *Eleocharis*. The densities of *Eleocharis, Panicum, Utricularia,* and *Paspalidium* were all positively associated with macrophyte cover, while *Rhyncospora* density was inversely correlated with this factor. *Utricularia* cover was correlated with algal mat cover and periphyton volume. *Panicum* and *Paspalidium* were both negatively associated with the volume of periphyton on our sites. With the exception of *Rhyncospora,* the common species were inversely correlated with study year or showed no association with this variable.

DISCUSSION

Community Classification

Classification of Shark Slough vegetation provided a depiction of the communities investigated in this

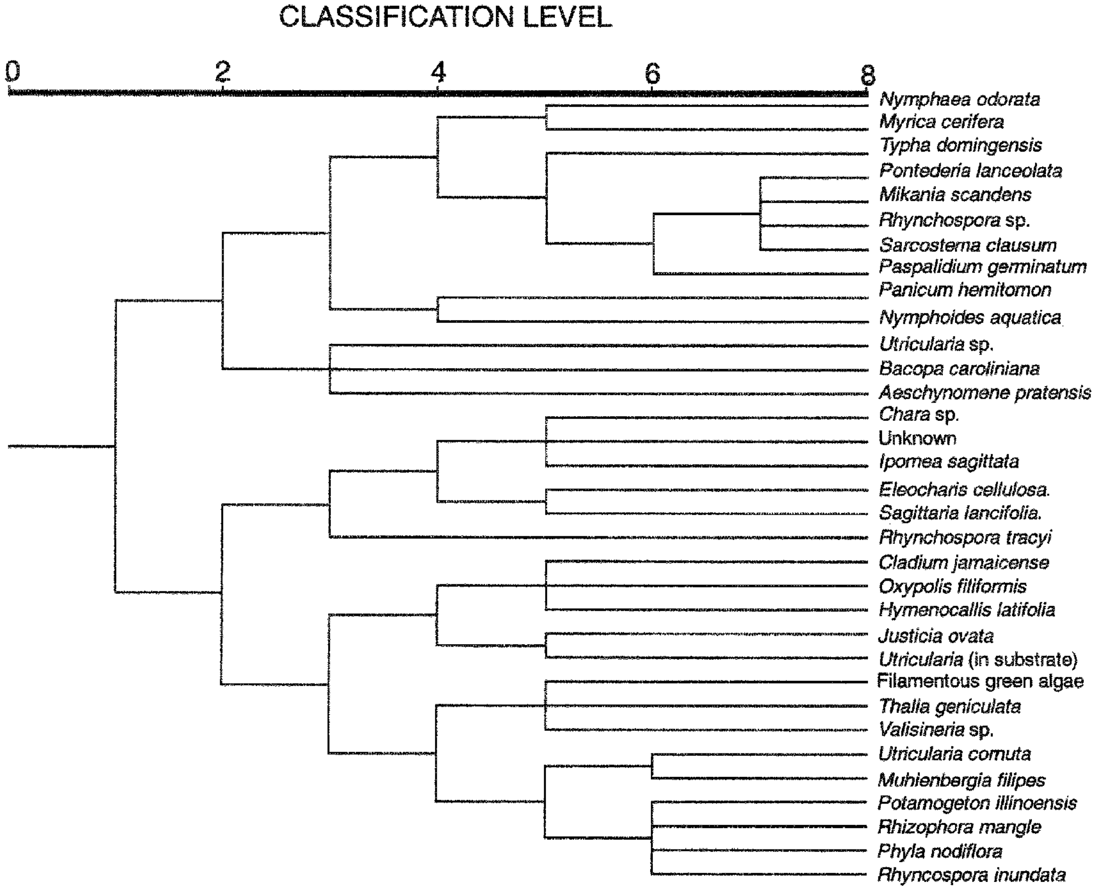

Figure 5. Hierarchical representation of two-way indicator species analysis (TWINSPAN) results for Shark Slough marsh vegetation.

study. The four plant associations, derived quantitatively by applying TWINSPAN to our matrix of plots and species, correspond well with previous qualitative descriptions of Everglades marsh communities. Past

Table 4. Between-site comparisons of stem density and cover for eight dominant taxa in Shark Slough marsh vegetation. Test statistic values from repeated measures ANOVA are presented with the degree of statistical significance for each comparison (* = $p < 0.05$ and ** = $p < 0.001$). Significant differences among sites (SNK test) are noted with different letter superscripts.

	Density (stems/m^2)			
	Area			
Species	CSS	SVR	NESS	F-value
Cladium jamaicense	2.9^{a}	15.8^{a}	3.8^{a}	15.0
Eleocharis cellulosa	137.9^{a}	46.1^{b}	55.9^{b}	24.6*
Rhyncospora tracyi	14.4^{a}	44.5^{b}	37.2^{b}	77.2**
Panicum hemitomon	12.9^{a}	5.8^{ab}	2.5^{b}	20.1*
Sagittaria longifolia	4.5^{a}	6.9^{a}	9.6^{a}	0.8
Paspalidium geminatum	3.8^{a}	0.6^{a}	0.8^{a}	10.1
Bacopa caroliniana	4.2^{ab}	12.2^{a}	0.5^{b}	19.1*
	Cover (percent)			
Utricularia sp.	24.9^{a}	3.9^{b}	18.1^{c}	1673.7**

Table 5. Between-site comparison of frequency for eight dominant taxa in Shark Slough marsh vegetation. Test statistic values from χ^2 analyses are presented with the degree of statistical significance for each comparison (* = $p < 0.05$ and ** = $p < 0.001$). Significant differences among sites are noted with different letter superscripts.

	Frequency (n)			
	Area			
Species	CSS	SVR	NESS	χ^2
Cladium jamaicense	24^{a}	58^{b}	28^{a}	27.8**
Eleocharis cellulosa	136^{a}	111^{a}	122^{a}	1.0
Rhyncospora tracyi	60^{a}	109^{b}	121^{b}	32.7**
Panicum hemitomon	133^{a}	72^{b}	26^{c}	60.1**
Sagittaria longifolia	96^{a}	68^{a}	98^{a}	3.2
Paspalidium geminatum	114^{a}	22^{b}	9^{b}	109.4**
Utricularia sp.	118^{a}	55^{b}	74^{b}	13.7*
Bacopa caroliniana	61^{a}	72^{a}	3^{b}	65.1**

Table 6. Correlations of species cover or density with biotic and abiotic variables at Shark Slough marsh vegetation study areas. Correlation coefficients and indications of statistical significance for $p < 0.05$ (*) or $p < 0.001$ (**) are presented.

	Factor				
Species	Macrophyte Cover	Periphyton Cover	Periphyton Volume	Water Depth	Year
Cladium jamaicense	−0.02	−0.04	0.05	−0.12*	0.02
Eleocharis cellulosa	0.63**	0.04	−0.02	0.15*	−0.32**
Rhyncospora tracyi	−0.11*	0.02	0.02	−0.10	0.12*
Panicum hemitomon	0.41**	−0.09	−0.15*	0.00	−0.11*
Sagittaria longifolia	−0.01	−0.07	0.00	−0.18**	−0.05
Utricularia sp.	0.16*	0.49**	0.37**	−0.09	−0.22**
Paspalidium geminatum	0.31**	−0.07	−0.16*	0.04	−0.22**
Bacopa caroliniana	−0.05	−0.02	0.00	−0.05	−0.01

categorizations tended to group herbaceous Everglades marsh vegetation into communities dominated by 1) *Cladium jamaicense* growing in dense stands or more sparsely in marl prairie habitats, 2) *Eleocharis cellulosa* found in wetter slough environments and often interspersed with areas dominated by *Panicum hemitomon* or *Rhyncospora,* and 3) a matrix in which the periphyton-*Utricularia* complex is dominant (Gunderson 1989, 1994, Wood and Tanner 1990, Browder et al. 1994, Davis et al. 1994, Jordan et al. 1997). These classes correspond well with our quantitatively-derived classification of Everglades marsh vegetation into plant associations dominated by 1) *Cladium,* 2) *Eleocharis, Rhyncospora,* and *Sagittaria,* 3) *Panicum* and *Paspalidium,* and 4) *Utricularia* and *Bacopa.* Similar communities were discernable in LANDSAT imagery used to map the Everglades (Rose and Rosendahl 1981, Gunderson et al. 1986). Thus, the hierarchical clustering of marsh species agrees with independent depictions of Everglades vegetation derived from multispectral scanner data and helps justify our classification as a system to provide context for depicting community change.

Hydrology-Macrophyte Interactions

The density and frequency of the eight most common species at the three study sites, as well as their tendencies to associate with the parameters measured on study plots, permit further evaluation of the relationships of these species with environmental factors. The most common taxa on our plots were those characteristic of long hydroperiod, deeper water environments. *Eleocharis* was found on every plot sampled, while *Rhyncospora tracyi, Panicum hemitomon,* and *Sagittaria* were present on the majority of plots analyzed. In contrast, *Cladium* had the lowest relative frequency of the taxa that were common on our plots. Other species such as *Nymphaea odorata* may be good indicators of either plant associations or the hydrologic responses of marsh vegetation, but such species were not well-represented in our samples. Accordingly, our design produced a depiction of the wetter end of the hydrologic gradient in Everglades graminoid marshes wherein taxa with affinities for shorter hydroperiod environments were a secondary floristic component.

Cladium's relationship to DCA axes 1 and 2, and the correlation of these axes with water depth, demonstrate its association with relatively drier conditions. *Cladium* frequency and density were greatest at SVR, the site with the greatest elevation and shortest hydroperiod. Although *Cladium* was less abundant in wet prairie vegetation at NESS and CSS, it was still present at these areas in stands flanking the lower elevation marshes studied. *Cladium* density was also inversely correlated with water depth. Other studies have demonstrated *Cladium*'s association with shorter hydroperiod environments (Herndon et al. 1991, David 1996, Jordan et al. 1997). Although our data come from the wetter end of this species' inundation-tolerance range, the absence of a correlation with study year meant that there was no evidence for reductions in *Cladium* abundance over the 10-year study period in Shark Slough.

Eleocharis abundance strongly influenced overall macrophyte community structure in long-hydroperiod marshes. *Eleocharis* was found in the greatest densities at CSS, confirming its tendency to dominate sites with greater mean water depth and longer inundation periods (Gunderson 1994, David 1996, Jordan et al. 1997). *Eleocharis* was also the only species associated positively with water depth, indicating an affinity for wetter environments. In contrast, the density and frequency of *Rhyncospora* were greatest at NESS and SVR, a response that could not be attributed to hydrologic or biotic factors due to its relatively weak correlations with water depth and macrophyte cover. *Rhyncospora* was the only species to associate positively with study year, an indication of a general density increase during the 1985–1995 period. The inverse correlation of *Sagittaria* density with water depth may reflect a response time-lag for colonization of marsh habitats from refugia in substrate depressions that hold water during dry periods. An inhibition of germination during periods of inundation is one mechanism that would explain such a time-lag. In any case, the tendency of *Rhyncospora* and *Sagittaria* to associate with *Eleocharis* under wetter conditions was not absolute.

The tendency for *Panicum* and *Paspalidium* to be associated with each other seems to be substantive. Both species occurred at greater densities and frequencies at CSS where water depths were greatest, supporting Gunderson's (1994) description of a *Panicum* marsh community in Everglades slough environments. These taxa were also found near the wetter end of an apparent hydrologic gradient that was demonstrated in species ordinations and correlations of DCA axes with water depth. Despite this, neither species' density was directly correlated with water depth. Similar to *Eleocharis*, both *Paspalidium* and *Panicum* were positively associated with overall macrophyte cover in DCA and correlation analyses. Unlike *Eleocharis*, these species tended to be negatively associated with periphyton volume. Thus, *Panicum*, *Paspalidium*, and *Eleocharis* apparently respond similarly to hydrologic variation, but interactions with the marsh algal mat community may play different roles in the responses of these species.

Decreasing *Utricularia* cover and frequency corresponded with the pattern of decreasing average water depth from CSS to NESS and SVR. This finding is in agreement with those of others who found that the abundance of *Utricularia* increases with increasing water depth and inundation frequency (David 1996, Jordan et al. 1997). *Utricularia* cover was also associated with overall periphyton cover and volume, consistent with the hypothesis that the *Utricularia*-periphyton assemblage operates via a positive feedback mechanism wherein *Utricularia* serves as a periphyton substrate as well as a carnivorous consumer of zooplankton periphyton grazers in what has been termed a "self-organizing unit" (Browder et al. 1994, Ulanowicz 1995). *Bacopa* density and frequency were greatest at the driest area, SVR, but no clear hydrologic relationship was evident because its abundance was intermediate at the wettest site, CSS, and low at NESS.

Decreases in the abundance of four dominant species over time were consistent with the inverse relationship of study year and overall macrophyte cover. Along with the positive association of study year and water depth, this would lead to the prediction that marsh plant abundance declines as a function of water depth. The correlation of macrophyte cover and water depth was not, however, statistically significant. This apparent anomaly may be explained by the importance of *Eleocharis* as a determinant of overall macrophyte cover and the positive association that was demonstrated between *Eleocharis* and water depth.

Community Interactions

Ordination analysis highlighted several meaningful associations of community pattern and environmental variables. Study area locations relative to DCA axes 1 and 2 described a wet-dry hydrologic transition from CSS to NESS and SVR that was supported by the associations of these axes with water depth. Annual trajectories of study area positions relative to DCA axis 1 and 2 indicate that the marsh communities at NESS and SVR changed substantially over the decade evaluated but returned to an overall structure similar to the mid-1980s by the study's conclusion in 1995. Although plant community structure at CSS appeared more stable than the other areas during the decade evaluated, all of the study areas showed directional change away from the hydrophytic extremes depicted in the ordination until about 1991. From approximately 1992 through 1995, wetter conditions produced a three-year reversal in community structure that was most pronounced at SVR and NESS. This cyclical nature of vegetation response over time demonstrates that studies based on data collected at only a few discrete temporal points could draw incorrect conclusions as to the degree and direction of long-term community change. Moreover, our findings indicate that Shark Slough plant community change is strongly influenced by hydrologic variation at the site and species level.

A simple direct relationship between water depth or hydroperiod and marsh plant community structure is unlikely. In addition to the hydrologic relationships that were demonstrated, DCA axes had significant positive and negative associations with macrophyte cover, periphyton abundance, and water temperature. During the decade evaluated, our southern Everglades study areas experienced general increases in water depth and decreases in macrophyte density and periphyton abundance. Direct correlations of water depth with macrophyte or periphyton abundance were lacking, however. Shade or mechanical interference could result in the observed negative association of periphyton volume and macrophyte cover. Correlation of Everglades marsh community attributes with water temperature supports an association of these attributes with periphyton abundance. Water temperature, which was measured near the surface, was positively correlated with periphyton abundance, while water depth and water temperature were inversely related. Water depth and temperature did not seem to directly affect overall macrophyte cover, but interrelationships among macrophyte cover, periphyton volume, and water depth and temperature indicate that Everglades marsh vegetation responds to hydrologic patterns at least partly via factors mediated by periphyton.

While the three study areas were arrayed along DCA axis 1 in relation to an indirect hydrologic gradient, community attributes relative to DCA axis 2 highlighted a separation of NESS from the other two areas. Compared to the other sites, NESS was intermediate with respect to water depth, hydroperiod, and macrophyte cover, while periphyton cover and volume were greatest at this area. The characteristics of Everglades algal mat communities are interrelated with sediment attributes wherein calcitic mud substrates, calcareous periphyton, and limestone outcroppings tend to co-occur (Browder et al. 1994). Thus, the presence of rocky substrates and marl soils at NESS, and to a lesser extent SVR, helps to explain the higher periphyton volume at these areas. Although the differences between NESS and CSS macrophyte communities may be partially attributable to hydrologic variation, the influence of algal mats and associated interrelationships with the edaphic factors leading to marl formation also seem to explain differences in community structure between NESS and the central slough.

Hurricanes can be a potent form of disturbance to Everglades plant communities, but their effects have been more pronounced in forest than in marsh macrophyte communities (Craighead and Gilbert 1962, Armentano et al. 1995). Nonetheless, floating periphyton-*Utricularia* mats have been subject to disruption from wind and waves in past hurricanes (Craighead and Gilbert 1962, Roman et al. 1994). The north eyewall of Hurricane Andrew, which passed directly over our study area in August, 1992, had winds among the most intense recorded for hurricanes in south Florida but also had relatively light rainfall (Pimm et al. 1994). Water depth on our study areas increased an average of 14 cm between July and September of 1992, but this fluctuation was typical of other two- to three-month intervals in the hydrologic record. Shark Slough water-depth increases occurring during 1992 were part of a high precipitation period that ran through the study's conclusion. Macrophyte cover decreased slightly following the hurricane, but this change did not stand out in the long-term record. Periphyton cover increased from a relatively low value following Hurricane Andrew, but again, this increase was typical of the late wet season in other study years. Accordingly, the 1992–1995 changes in Shark Slough macrophyte and periphyton abundance are more likely attributable to the extended wet period rather than any short-duration meteorological disturbance.

In summary, it is clear that Everglades marsh vegetation responded to hydrologic change. However, this response could be complicated by temporal and edaphic factors and by the interrelationships of macrophytes and periphyton. Interactions among the environmental processes important to the structure of Everglades plant communities may contribute to results that seem, at least partially, contradictory (Gunderson 1994). The finding that overall macrophyte cover was not related to water depth *per se* is similar to previous results (Gunderson 1989) showing that marsh plant associations were unrelated to differing hydrologic histories among sites. We feel that this points not to the lack of a relationship, but to the need to consider community structural change and indirect relationships. Our decade-long data base enabled us to show how dominant Everglades marsh plants responded to hydrologic factors. *Eleocharis* contributed to high macrophyte abundance at wetter sites, while the negative relationships of other taxa with water depth may have resulted in a decline in macrophyte cover in response to increasing water depth. Ordinations showing trajectories of community structure, as well as general comparisons of macrophyte cover and water depth, provide evidence for pronounced, but partly indirect, hydrologic influences on Everglades marsh plant communities.

ACKNOWLEDGMENTS

Reviews by T.V. Armentano, S. Galatowitsch, L.H. Gunderson, M.A. Huston, W.B. Robertson, and J.C. Trexler contributed to this manuscript. We were assisted by many able field workers, especially E.A. Bennett, J.D. Chapman, A.-M. Eklund, L.D. Oberhofer, and J. Schmidt. Analytical and graphical expertise was provided by M.A. Alvarado, M.J. Lounsbury, D.A. Sikkema, and B.E. Wood.

LITERATURE CITED

Armentano, T.V., R.F. Doren, W.J. Platt, and T. Mullins. 1995. Effects of Hurricane Andrew on coastal and interior forests of southern Florida: overview and synthesis. Journal of Coastal Research 21:111–144.

Browder, J.A. 1981. Perspective on the ecological causes and effects of the variable algal composition of southern Everglades periphyton. U.S. National Park Service, Homestead, FL, USA. Report T-643.

Browder, J.A., P.J. Gleason, and D.R. Swift. 1994. Periphyton in the Everglades: spatial variation, environmental correlates, and ecological implications. p. 379–418. *In* J. Ogden and S. Davis (eds.) Everglades: the Ecosystem and Its Restoration. St. Lucie Press, Delray Beach, FL, USA.

Craft, C.B., J. Vymazal, and C.J. Richardson. 1995. Response of Everglades plant communities to nitrogen and phosphorus additions. Wetlands 15:258–271.

Craighead, F.C. and V.C. Gilbert. 1962. The effects of Hurricane Donna on the vegetation of southern Florida. Quarterly Journal of the Florida Academy of Sciences 25:1–28.

David, P.G. 1996. Changes in plant communities relative to hydrologic conditions in the Florida Everglades. Wetlands 16:15–23

Davis, S.M., L.H. Gunderson, W.A. Park, J.R. Richardson, and J.E.

Mattson. 1994. Landscape dimension, composition, and function in a changing Everglades ecosystem. p. 419–444. *In* J. Ogden and S. Davis (eds.) Everglades: the Ecosystem and Its Restoration. St. Lucie Press, Delray Beach, FL, USA.

DeAngelis, D.L., and P.S. White. 1994. Ecosystems as products of spatially and temporally varying driving forces, ecological processes, and landscapes: a theoretical perspective. p. 9–27. *In* J. Ogden and S. Davis (eds.) Everglades: the Ecosystem and Its Restoration. St. Lucie Press, Delray Beach, FL, USA.

Gunderson, L.H., D.P. Brannon, and G. Irish. 1986. Vegetation cover types of Shark River Slough, Everglades National Park, derived from LANDSAT thematic mapper data. National Park Service. Everglades National Park. Homestead, FL, USA. SFRC-86/03.

Gunderson, L.H. 1989. Historical hydropatterns in wetland communities of Everglades National Park. p. 1099–1111. *In* R.R. Sharitz and J.W. Gibbons (eds.) Freshwater Wetlands and Wildlife. U.S. Department of Energy. Oak Ridge, TN, USA.

Gunderson, L.H. 1994. Vegetation of the Everglades: determinants of community composition. p. 323–340. *In* J. Ogden and S. Davis (eds.) Everglades: the Ecosystem and Its Restoration. St. Lucie Press, Delray Beach, FL, USA.

Herndon, A., L. Gunderson, and J. Stenberg. 1991. Sawgrass (*Cladium jamaicense*) survival in a regime of fire and flooding. Wetlands 11:17–28.

Hill, M.O. 1979a. DECORANA, a FORTRAN program for detrended correspondence analysis and reciprocal averaging. Microcomputer Power, Ithaca, NY, USA.

Hill, M.O. 1979b. TWINSPAN, a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Microcomputer Power, Ithaca, NY, USA.

Jordan, F., H.L. Jelks, and W.M. Kitchens. 1997. Habitat structure and plant community composition in a northern Everglades wetland landscape. Wetlands 17:275–283.

Kolipinski, M.C. and A.L. Higer. 1969. Some aspects of the effects of the quantity and quality of water on biological communities in Everglades National Park. U.S. Geological Survey, Tallahassee, FL, USA. Open File Report 69007.

Kushlan, J.A. 1981. Sampling characteristics of enclosure fish traps. Transactions of the American Fisheries Society 110:557–562.

Loftus, W.F. and A.M. Eklund. 1994. Long-term dynamics of an Everglades small-fish assemblage. p. 461–483. *In* J. Ogden and S. Davis (eds.) Everglades: the Ecosystem and Its Restoration. St. Lucie Press, Delray Beach, FL, USA.

Pimm, S.L., G.E. Davis, L. Loope, C.T. Roman, T.J. Smith III, and J.T. Tilmant. 1994. Hurricane Andrew. BioScience 44:224–229.

Potvin, C., M.J. Lechowicz, and S. Tardiff. 1990. The statistical analysis of ecophysiological response curves obtained from experiments involving repeated measures. Ecology 71:1389–1400.

Roman, C.T., N.G. Aumon, J.C. Trexler, R.J. Fennema, W.F. Loftus, and M.A. Soukup. 1994. Hurricane Andrew's impact on freshwater resources. BioScience 44:247–255.

Rose, P.W., and P.C. Rosendahl. 1981. Landsat hydrobiological classification for an inland fresh water marsh within Everglades National Park. American Water Resources Association, Minneapolis, MN, USA.

Steward, K.K. and W.H. Ornes. 1975. The autecology of sawgrass in the Florida Everglades. Ecology 56:162–171.

Ulanowicz, R.E. 1995. *Utricularia's* secret: the advantage of positive feedback in oligotrophic environments. Ecological Modelling 79: 49–57.

Urban, N.H., S.M. Davis, and N.G. Aumen. 1993. Fluctuations in sawgrass and cattail densities in Everglades Water Conservation Area 2A under varying nutrient, hydrologic, and fire regimes. Aquatic Botany 46:203–223.

White, P.S. 1994. Synthesis: vegetation pattern and process in the Everglades ecosystem. p. 445–458. *In* J. Ogden and S. Davis (eds.) Everglades: the Ecosystem and Its Restoration. St. Lucie Press, Delray Beach, FL, USA.

Wood, J.M. and G.W. Tanner. 1990. Graminoid community composition and structure within four Everglades management areas. Wetlands 10:127–149.

Zar, J.H. 1984. Biostatistical Analysis. Prentice-Hall. Englewood Hills, NJ, USA.

Manuscript received 24 February 1997; revisions received 2 October 1997 and 22 December 1997; accepted 19 February 1998.