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ABUNDANCE AND DISTRIBUTION OF HERBACEOUS ANGIOSPERMS IN GRASS-SEDGE MARSHES OF WEST-CENTRAL FLORIDA: THE EFFECT OF SEASONAL WATER-LEVEL FLUCTUATION

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ABUNDANCE AND DISTRIBUTION OF HERBACEOUS ANGIOSPERMS IN GRASS-SEDGE MARSHES OF WEST-CENTRAL FLORIDA: THE EFFECT OF SEASONAL WATER-LEVEL FLUCTUATION

by
Pamela S. Botts

A thesis submitted in partial fulfillment of the requirements
for the degree of Master of Science
in the Department of Biology in
the University of South Florida

August, 1987

Major Professor: Bruce C. Cowell

Graduate Council
University of South Florida
Tampa, Florida

CERTIFICATE OF APPROVAL

MASTER'S THESIS

This is to certify that the Master's Thesis of

Pamela S. Botts

with a major in Botany
has been approved by the examining committee
on 7/10/87 as satisfactory for the
Thesis requirement for the Master of Science degree.

Thesis Committee:
Major Professor: Bruce C. Cowell

Member: Clinton J. Dawes

Member: Earl D. McCoy

ACKNOWLEDGEMENTS

This research was funded in part by a grant from the Aquatic Plant Management Society. The Markborough Corporation graciously provided access to their property. The field assistance of K. Brewer, S. Kaczor, and E. Silver is gratefully acknowledged. K. Walters and W. Bros generously supplied computer programs and sorely needed expertise. E.D. McCoy and C.J. Dawes provided valuable input. I would particularly like to thank B.C. Cowell for his guidance, support, and advice during this study. Finally, without the constant support and encouragement of G. Botts and E. Silver, this study would have been impossible.

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IN GRASS-SEDGE MARSHES OF WEST-CENTRAL FLORIDA:
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An Abstract

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Grass-sedge marshes in west-central Florida were studied to determine the abundances and distributions of herbaceous angiosperms. Cluster analysis, reciprocal averaging, and a biotic boundaries technique were used to analyze the relationship between community composition and depth within the marsh. Shallow areas were dominated by Rhynchospora filifolia, Dichanthelium sabulorum, and Rhynchospora cephalantha. Abundances of the species fluctuated seasonally and varied between marshes. Deep areas of individual marshes differed markedly from shallow areas and from each other. A deep, well-drained marsh supported a monospecific stand of Juncus repens, while a less deep, but poorly drained marsh had a community dominated by Pontederia cordata. Similarities within marshes decreased when water levels were high. The importance of a depth gradient increased in December when conditions were wet and standing water was present in the marshes. Biotic boundaries within the marshes corresponded with water levels. Water level and drainage patterns explained up to 74% of the variation in the community in Marsh 3 and 41% of the variation in Marsh 4. In the shallow marshes no floristic gradients were detected.

Abstract approved:______________________
Major professor

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7-10-87
Date of Approval

INTRODUCTION

Determination of the factors controlling species abundance and distribution in a community is a two-step procedure. The first step is to make detailed and accurate descriptions of the organisms, their relationships to each other, and the relationships to the physical environment. This descriptive stage should result in hypothesis generation. The second step is to test experimentally the hypotheses generated (Harper 1982).

Wet meadows and sedge marshes have been well studied in Canada (Walker and Coupland 1968; Auclair *et al*. 1973, 1976; Lieffers 1984) and in north-central United States (van der Valk and Davis 1978; Dix and Smeins 1968). Water level fluctuation and drainage patterns in these wetlands have been shown to be responsible for differences in species composition, diversity, and distributions.

A number of investigators have suggested that disturbance also plays a major role in the regulation of marsh communities. Walker and Wehrhahn (1970) reported that disturbance in general, particularly grazing, fire, and mowing explained a significant amount of the variation in Saskatchewan marsh communities. Smith and Kadlec (1985a) reported a 48% reduction in productivity in *Typha latifolia* L. stands following fire and herbivory, but when they investigated the role of fire in regulating marsh seed banks, they determined that fire had little effect on seed banks (1985b). Vegetation changes in a Wisconsin

Carex wetland were reported when a cooling pond altered water levels and temperatures in the marsh (Bedford and Loucks 1986).

Population growth in west-central Florida has led to increasing development pressure on pine flatwood communities. Construction of residential developments, industrial complexes, and office parks has encroached upon these areas. Scattered throughout the pine flatwoods are small marshes and temporary ponds which inevitably will be affected by these developments. Because the pine flatwood community is characterized by a perched water table, drainage during times of heavy precipitation is frequently poor, and soil conditions alternate between dry in winter and spring and wet in summer and fall (Laessle 1942).

Currently, little is known regarding the species composition, biology, or ecology of these wetlands. This study was conducted to answer the following questions:

1. What is the most efficient way to sample the vegetation in the marshes and to analyze the data?
2. What are the species abundance and distribution in the marshes?
3. Does species abundance and distribution change seasonally?
4. Does elevation within the marsh affect species abundance and distribution?

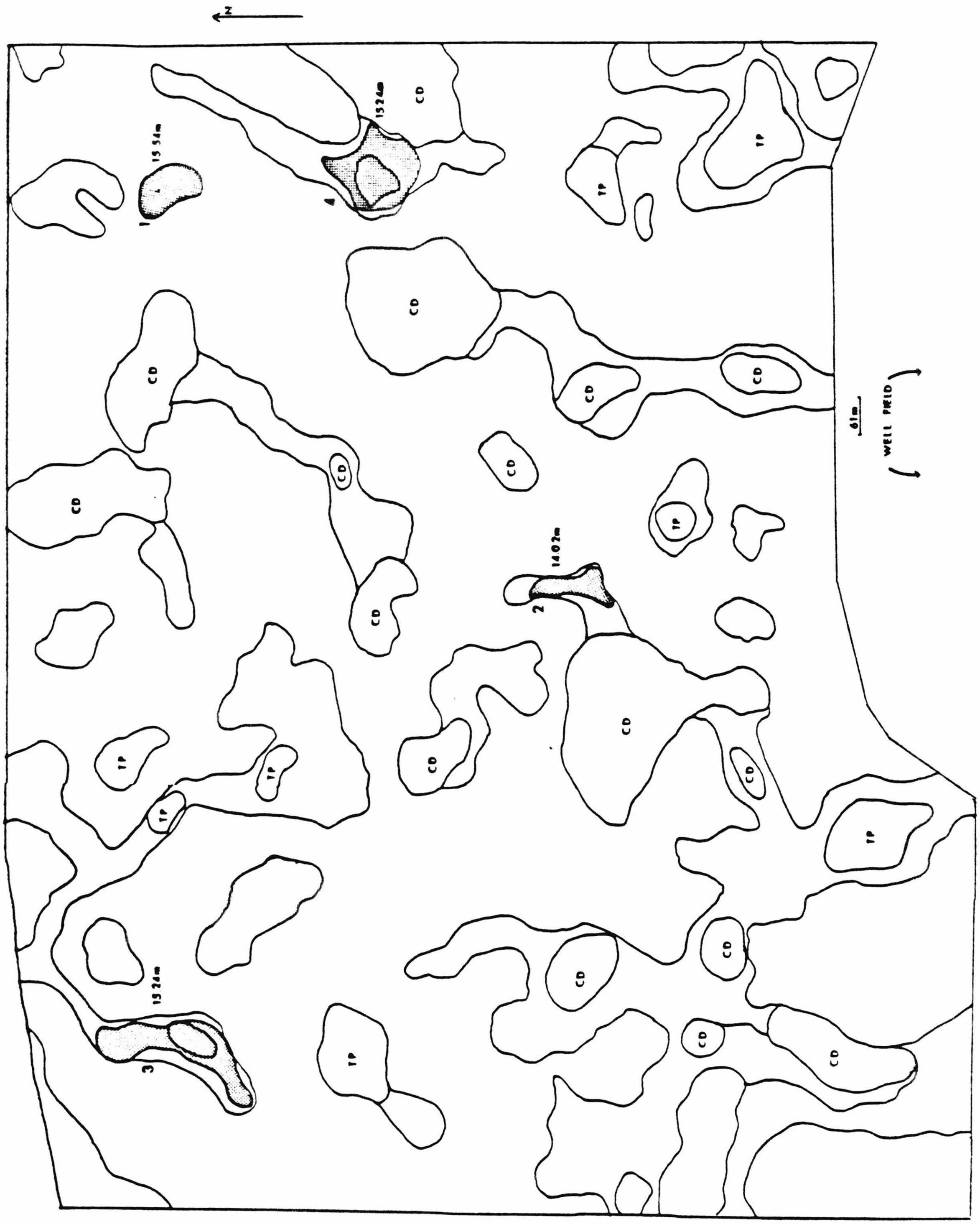
DESCRIPTION OF STUDY AREA

The Hunter's Green marshes are located in northeast Hillsborough County (28°11′ N Lat. and 82°17′ W Long.) eight km north of the city of Tampa, Florida. These marshes are palustrine, emergent wetlands which are grass-sedge dominated and seasonally flooded (Cowardin et al. 1979). The marshes are scattered through a pine flatwood community which currently is being used for cattle grazing. These marshes frequently are adjacent to cypress domes, and they are located in shallow depressions with an acidic sand substrate. In general, surface runoff is slow, but internal drainage is rapid unless the water table is high. Some of the marshes exhibit poor drainage regardless of the water table level.

The study site has an elevation gradient from north to south. The northern border is approximately 15.42 m above mean sea level, while the southern border is only 14.13 m above sea level. Furthermore, the southern edge is adjacent to the Morris Bridge well field and is subject to drawdown during periods of high water use (Fig. 1).

Rainfall patterns are seasonal. A summer wet season lasts from June to September and is characterized by frequent thunderstorms. Winter months tend to be drier; precipitation is less frequent and results from frontal storms. Daily mean temperatures range from 15.8°C in winter to 27.7°C in summer; average monthly precipitation ranges from 7.7 cm in winter to 17.8 cm in summer (N.O.A.A. 1986).

Figure 1. Map of the study area on the Hunter's Green property. Shaded areas represent the study marshes. Each study marsh is numbered, and elevation of the marsh (m above Mean Sea Level) is indicated to the right of the area. The Morris Bridge well field is adjacent to the lower border of this area. CD=Cypress Dome, TP=Temporary Pond.


N
CD
TP
15.54m
15.24m
14.02m
1
2
3
4
61m
WELL FIELD

METHODS

Marsh Locations and Features

Four marshes were chosen for detailed floristic analyses. Marsh 1 is a shallow, 0.74 ha, apparently homogeneous marsh located in the northeastern corner of the study site. A small stand of tupelo (*Nyssa sylvatica* Marsh) is located within the marsh (Fig. 2). Marsh 2 is 0.97 ha, located near the southern border of the property, and is connected to a cypress dome by a narrow extension. This marsh also has a small stand of tupelo which occupies the wettest area of the marsh. In general, the marsh is much drier than any of the others studied (Fig. 3). Marsh 3 is 1.8 ha in size and is located in the northwestern area of the study site; no trees are present. A large, circular depression in this marsh usually contains standing water, although it was dry early in the study (Fig. 4). Marsh 4 is a wet, 0.96 ha marsh on the eastern edge of the study site. One side of this marsh is adjacent to a cypress dome, and bald cypress (*Taxodium distichum* (L.) Rich.) is present in the marsh (Fig. 5).

Field and Laboratory Techniques

All marshes were surveyed in June, 1986 using a plane table and alidade (Welch 1952). Since there was no standing water in any of the marshes at the time of surveying, depths were measured using a Philadelphia rod. Four centimeter contour intervals were plotted on the

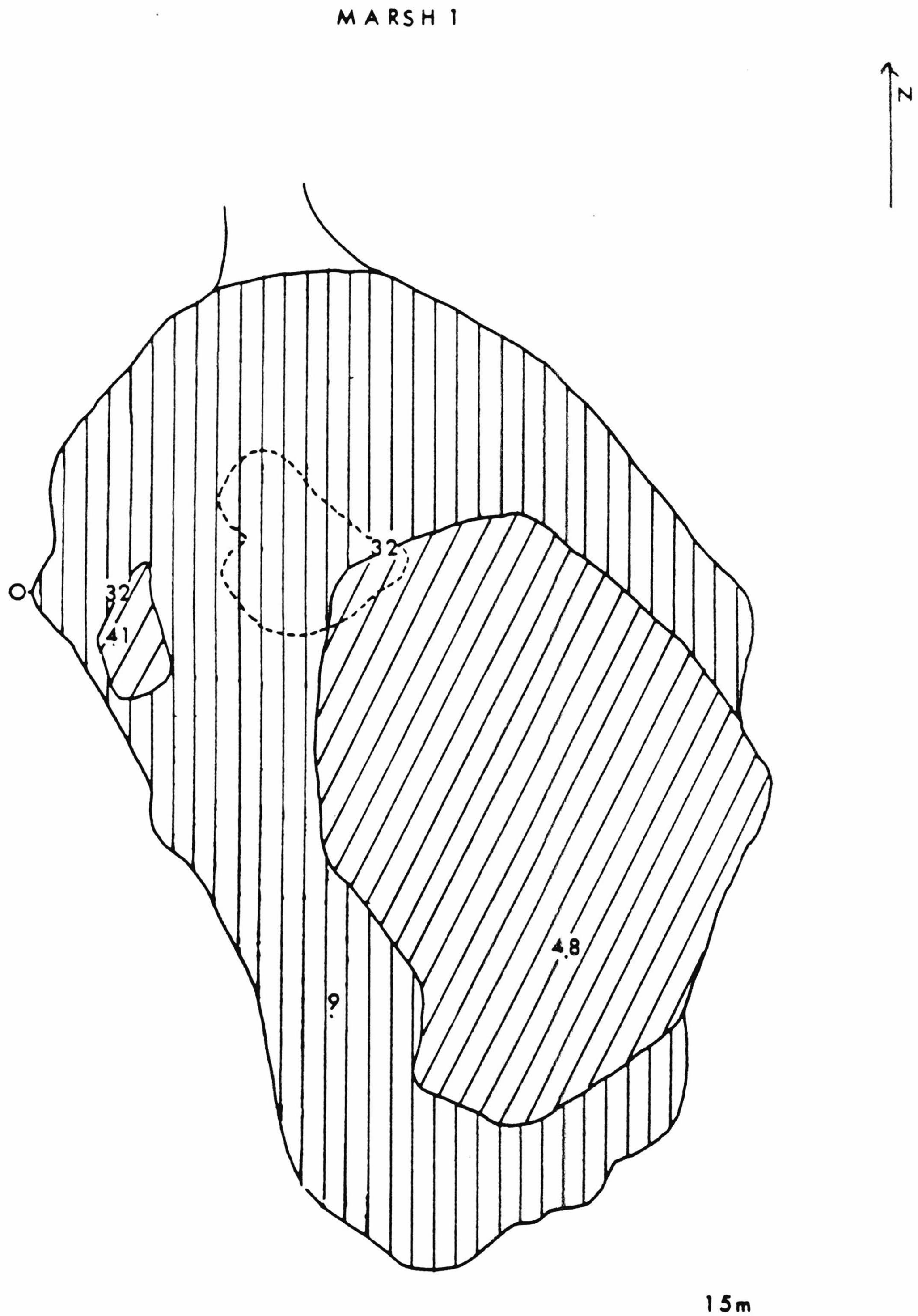


Figure 2. Contour map of Marsh 1, Hunter´s Green, Fl. Numbers represent centimeters of depth from the highest point in the marsh. Dotted lines represent the boundary of the stand of tupelo. (||)=Area 1A, (//)=Area 1B.

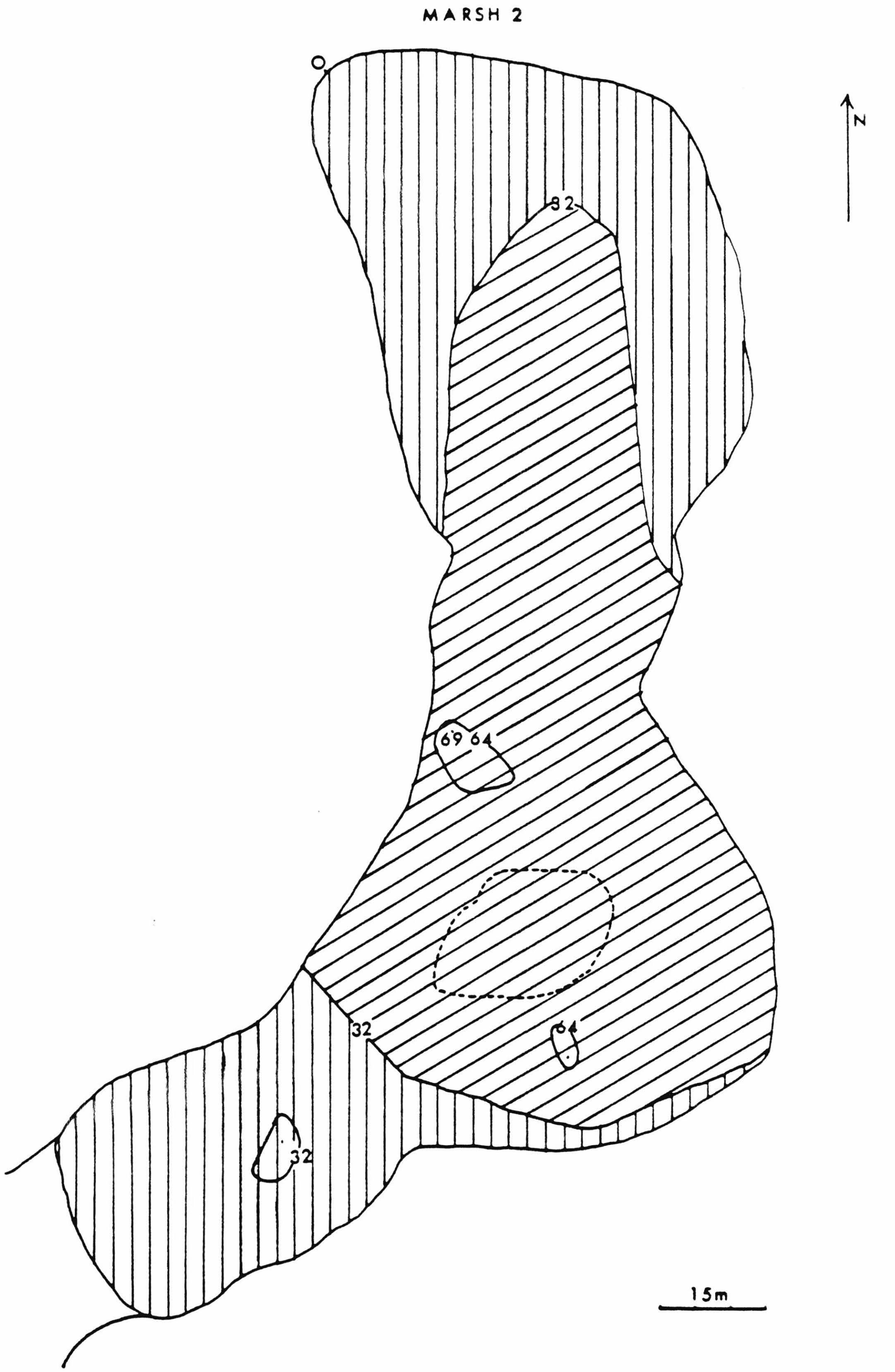


Figure 3. Contour map of Marsh 2, Hunter's Green, Fl. Numbers represent centimeters of depth from the highest point in the marsh. Dotted lines represent the boundary of the stand of tupelo. (| |)=Area 2A, (/ /)=Area 2B.

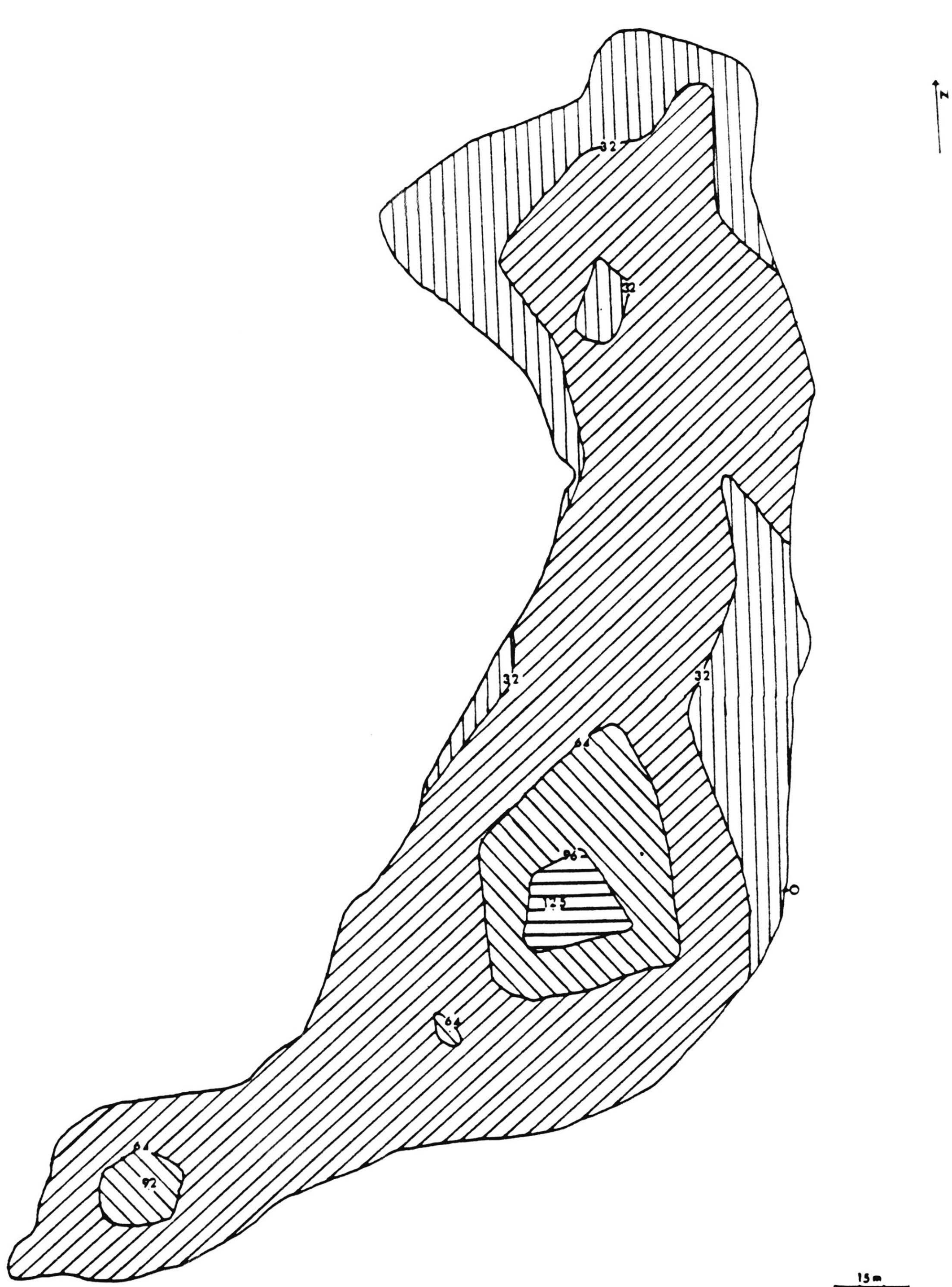


Figure 4. Contour map of Marsh 3, Hunter's Green, Fl. Numbers represent centimeters of depth from the highest point in the marsh. (||)=Area 3A, (//)=Area 3B, (\\)=Area 3C, (═)=Area 3D.

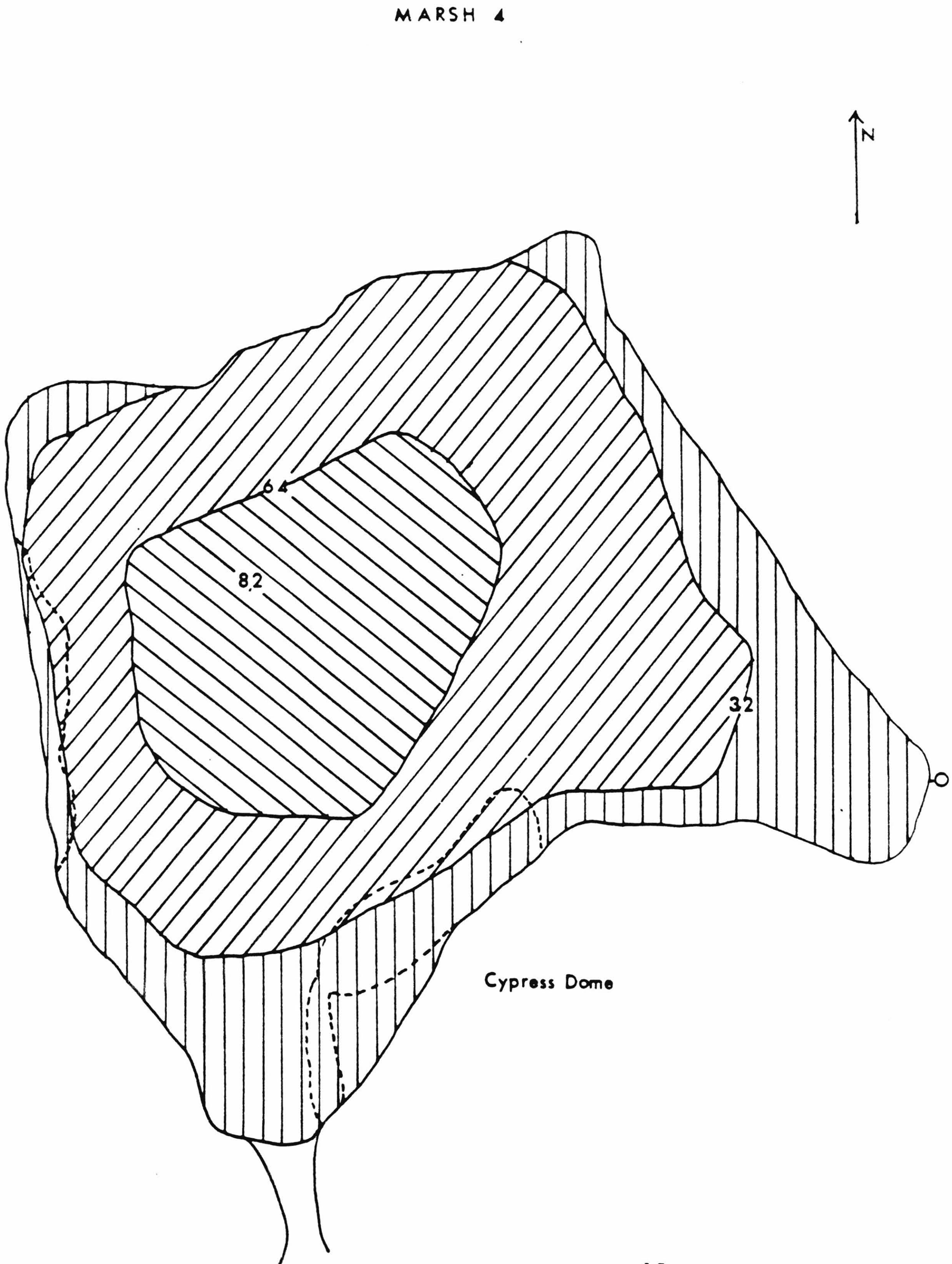


Figure 5. Contour map of Marsh 4, Hunter's Green, Fl. Numbers represent centimeters of depth from the highest point in the marsh. Dotted lines represent the boundaries of the stands of bald cypress trees. (||)=Area 4A, (//)=Area 4B, (\\)=Area 4C.

maps, and planimetry was used to calculate the total area of each marsh and the area of each contour. A 5 m grid system was established so that the location of quadrats could be defined on the maps.

Marshes were subdivided arbitrarily into areas corresponding to depth intervals of 32 cm (Figs. 2,3,4, and 5) and sampling was stratified within these intervals. Twenty randomly placed 1 m^2 quadrats were located within each 32 cm interval in each marsh. Since deeper contours tended to have smaller areas, this resulted in higher sampling intensity in these areas.

Sampling was conducted in June/July 1986 and December 1986/January 1987. Presence or absence of each species in each quadrat was recorded and cover values for each were estimated using the Domin scale, a modified Braun-Blanquet scale (Kershaw 1985) (See Table 1). All species identifications were according to Wunderlin (1982), and voucher specimens have been deposited with the University of South Florida herbarium.

During the June sampling period, soil samples to a depth of 20 cm were collected from a random location in each quadrat. These samples subsequently were mixed and subsampled. Percent moisture was determined by drying samples for 24 h at 105°C in a drying oven and reweighing. Samples were then ashed for 4 h at 510°C and percent organic matter was determined.

At bimonthly intervals, water depth at the deepest point in each marsh was recorded. Temperature and precipitation data were obtained from the National Oceanic and Atmospheric Administration records for Florida (N.O.A.A. 1986, 1987).

Table 1. Domin scale (Kershaw 1985) used for estimating percent cover for plant species within 1 m^2 quadrats in the Hunter's Green marshes (1986).

Symbol	Cover Value
r	isolated
1	scarce, cover small
2	very scattered, cover small
3	individuals numerous, cover low
4	abundant, 5%
5	abundant, 20%
6	25-33%
7	33-50%
8	50-75%
9	>75%
10	100%

Analyses

Czechanowski's Quantitative Index of Community Similarity (Field and MacFarlane 1969) was used to calculate similarities between the vegetation in each 32 cm contour interval. This index measures similarities between communities based on some quantitative measure of the species which occur in both stands. The index weights each species in the community by its abundance and can be used with frequency data (Greig-Smith 1983).

An area x area similarity matrix was constructed using Czechanowski's index to compare communities within each 32 cm interval, and cluster analyses were performed for June and December. The clustering technique was hierarchical, and areas were grouped in order of decreasing similarity; thus, the more similar areas were grouped, similarities were recalculated, and clustering then was performed again using the new values until all areas had been incorporated into the dendrogram. Direct comparisons cannot be made between areas that did not cluster together.

Reciprocal averaging (Hill 1973) was used to extract a single floristic gradient for each marsh. This technique produces stand ordinations based on weighted species averages and species ordinations based on weighted stand averages. Floristic gradients are presented linearly on the first axis, thereby facilitating interpretation of the data when a single strong environmental gradient exists. Results are presented as a regression of quadrat loading on quadrat location. Since quadrats are entered in order along a depth gradient, the r^2 values and probability statements reflect the amount of variation in the vegetation that is explained by depth within a marsh.

Raup and Crick (1979) developed a probabilistic technique to determine whether the species in a community are randomly distributed. Monte Carlo techniques are used to generate random assemblages of the species found in an area. From these assemblages, the probability of two areas having a particular number of species in common is calculated. The actual number of species common to both areas is then compared to the expected number to determine whether the number of species that pairs of quadrats have in common is greater or less than that expected by chance alone. McCoy *et al*. (1986) extended this concept to the placement of boundaries along environmental gradients. A matrix of quadrat-quadrat similarities is generated using the Raup and Crick technique, and this matrix is examined for clusters of quadrats between which differences are greater or smaller than expected. The McCoy *et al*. technique examines all possible boundaries between pairs of consecutive locations along an environmental gradient. The best boundary location is selected when the similarities among the locations on either side of the boundary or the differences among the locations on opposite sides of the boundaries are maximized.

This boundary technique was applied to the marsh data. Quadrats were grouped within 4 cm contours, but spatial location was not considered in ordering quadrats within a contour. Since this technique examines all possible boundaries between all quadrats on either side of a proposed boundary, the ordering of quadrats can have a potential effect on the results of the analysis. This is particularly true if more than one gradient is present. In those marshes which were found to have internal boundaries, transect lines were drawn through the marsh to include as much variation in depth and vegetation as possible. Quadrats falling with 10 m of the line were selected and the data for each transect was subjected to the analysis. Boundaries along each transect were located and were plotted on the contour maps. The transect boundaries were connected to construct continuous boundaries that enclosed discrete vegetation associations.

RESULTS

Soil and Water

Water levels in the marshes fluctuated markedly on a seasonal basis, but patterns of change followed precipitation patterns recorded for the area (Fig. 6). The spring season was unusually dry (see Appendix I), and all marshes were dry at the start of the study. In July, following a period of frequent summer storms, water levels increased rapidly, but the magnitude of the increase varied from marsh to marsh; deeper marshes retained more water than the shallow marshes. From September to December, a comparatively dry period, water levels dropped in all marshes except Marsh 4. Water depth in Marsh 4 increased during this interval, possibly reflecting poor drainage. Marsh 2, on the other hand, lost water more rapidly (earlier in the season) than the others and was dry by October. A period of heavy precipitation in late December and January was followed by increased water levels in all marshes.

Soil moisture was measured in June when there was no standing water in the marshes. The substrate in Marsh 4, however, was noticeably soggy. Soil moisture in Marshes 1 and 2 ranged from 5% to 24% and from 1% to 21% respectively, and showed no relationship to depth (r^2=0.06, $p>0.05$ and r^2=0.01, $p>0.05$), while moisture in Marshes 3 and 4 (0% to 27% and 2% to 59%) was strongly related to depth within the marsh (r^2=0.66, $p<0.001$ and r^2=0.37, $p<0.001$), reflecting a slower or more

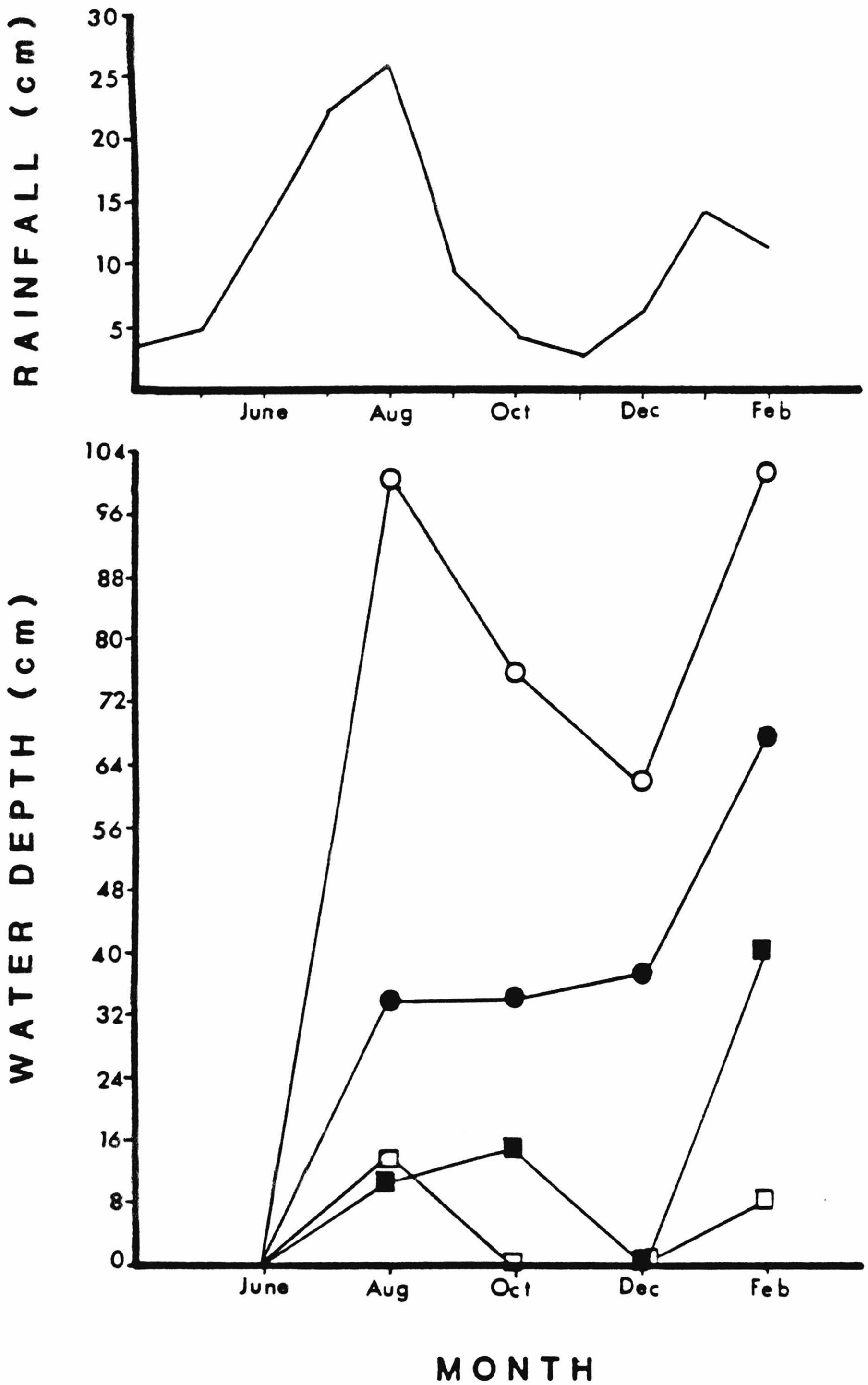


Figure 6. The lower figure is a graph of water depth (cm) measured at the deepest area of each marsh and plotted by month. (-■-)=Marsh 1, (-□-)=Marsh 2, (-○-)=Marsh 3, (-●-)=Marsh 4. The upper figure is a graph of monthly precipitation (cm) totals recorded at St. Leo, Fl. in 1986 and 1987.

recent loss of standing water in the deeper areas (Fig. 7).

Percent organic matter of the soil was highly correlated with percent moisture in Marshes 1, 3 and 4, but not in Marsh 2 (Fig. 8). Soil organic content ranged from 1% to 11% in Marsh 1, from 2% to 11% in Marsh 2, from 1% to 15% in Marsh 3, and from 1% to 20% in Marsh 4. In Marsh 1, the area with the highest soil moisture was found under a stand of trees where decaying wood and leaves were present. A similar situation occurred in Marsh 2; but in addition, this marsh was heavily grazed by cows. The deeper areas of Marsh 3 were covered by dense mats of live *Juncus repens* and dead *Eleocharis* sp. In Marsh 4, the deeper, more moist areas had large amounts of decaying vegetation on the soil.

Species Abundance and Distribution

Dichanthelium sabulorum, *Rhynchospora filifolia*, and *Rhynchospora cephalantha* were ubiquitous in the drier areas of all marshes (see Appendix II for a complete list of all plant species encountered in the marshes)(see Table 2 for frequency and cover values for the common species in the marshes). Percent frequency of *Dichanthelium sabulorum* was lowest in Marsh 4 (8% and 3% in June and December, respectively) where it was.present in a narrow shallow band at the periphery of the marsh. Although this species occurred commonly, its cover value within a quadrat was consistently less than 5%. *Rhynchospora filifolia* was abundant in all marshes. Ranges of cover values were between 5% and 20% in June but increased to between 25% and >75% in December. *Rhynchospora cephalantha* was more abundant in December than in June and was found closer to the edges of marshes than *Rhynchospora filifolia*.

A number of species were common to all marshes (Table 2). Two

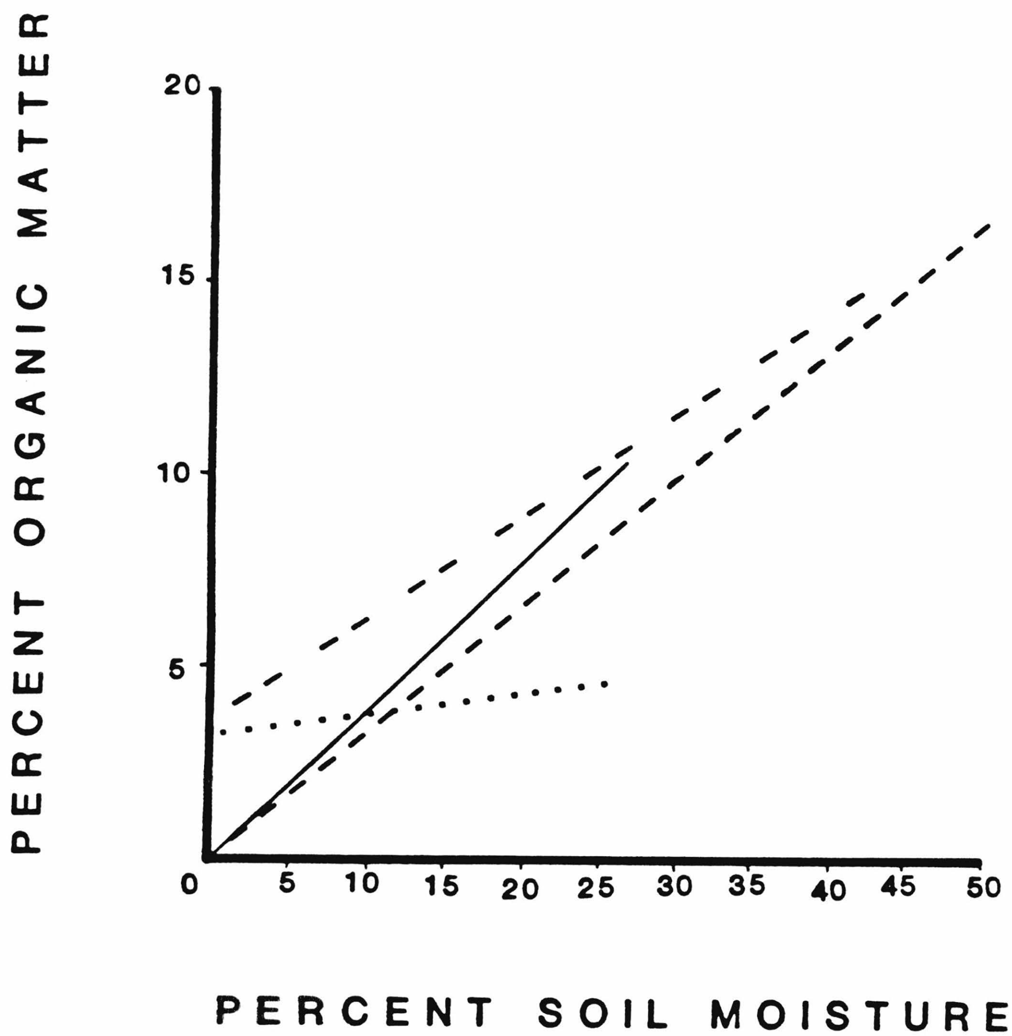


Figure 7. Regression of percent soil moisture in the upper 20 cm of soil vs. depth (cm) of the quadrat. (——)=Marsh 1, (· · ·)=Marsh 2, (- - -)=Marsh 3, (– –)=Marsh 4.

Marsh 1: $Y = 13.5 - 0.08\ X$, $r^2 = 0.06$, $p > 0.05$.

Marsh 2: $Y = 11.8 + 0.03\ X$, $r^2 = 0.01$, $p > 0.05$.

Marsh 3: $Y = 1.06 + 0.22\ X$, $r^2 = 0.66$, $p < 0.001$.

Marsh 4: $Y = 9.89 + 0.35\ X$, $r^2 = 0.37$, $p < 0.001$.

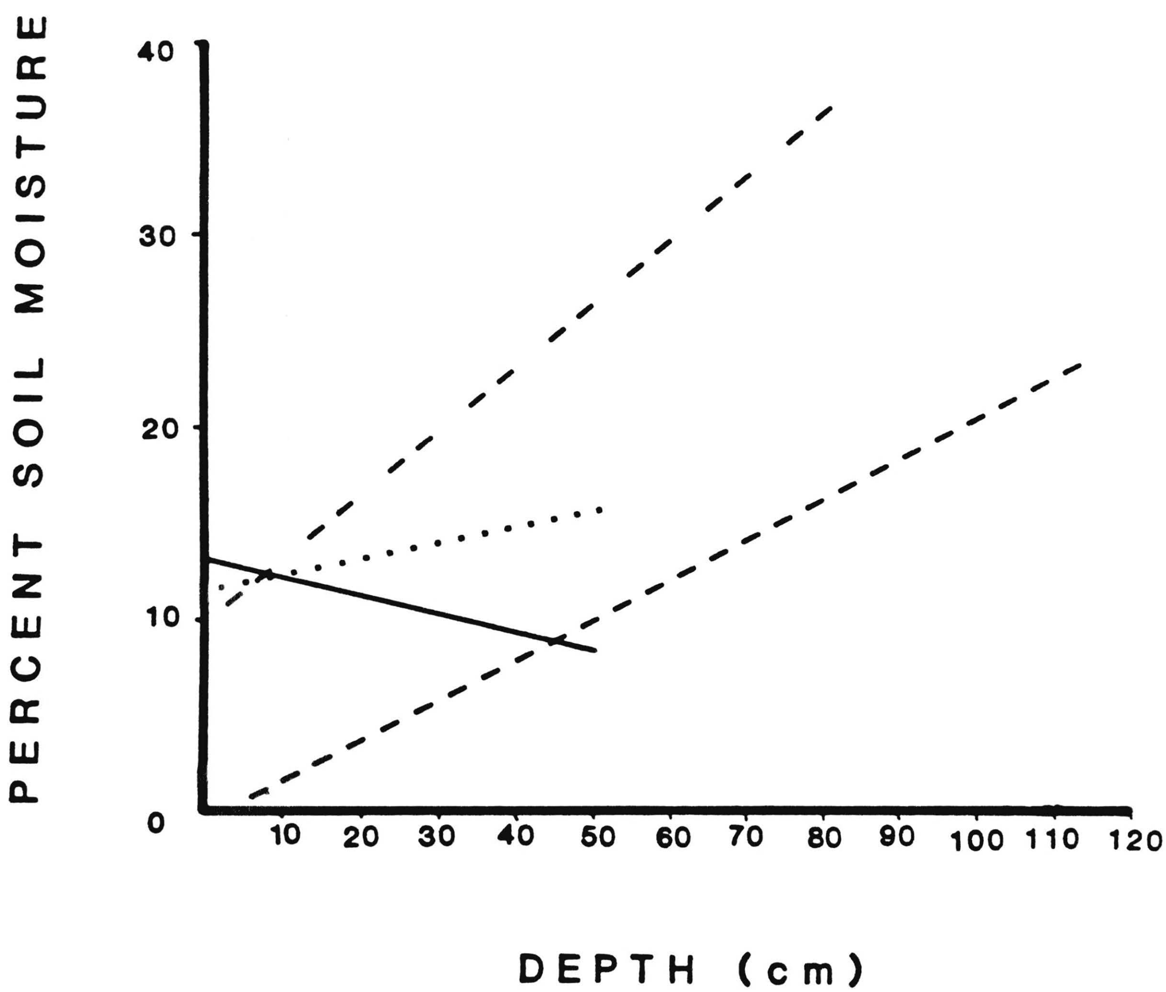


Figure 8. Regression of percent organic matter in the upper 20 cm of soil vs. percent soil moisture. Symbols as in Fig. 7.
Marsh 1: $Y = 0.05 + 0.35\ X$, $r^2 = 0.56$, $p<0.05$.
Marsh 2: $Y = 3.40 + 0.12\ X$, $r^2 = 0.06$, $p>0.05$.
Marsh 3: $Y = 0.21 + 0.33\ X$, $r^2 = 0.42$, $p<0.05$.
Marsh 4: $Y = 3.70 + 0.25\ X$, $r^2 = 0.76$, $p<0.05$.

Table 2. Percent frequency and cover values for the common species of angiosperms in the Hunter's Green marshes, J=June 1986, D=December 1986. Freq=the number of quadrats occupied by a species divided by the total numer of quadrats. Cov=average cover value for a species over all quadrats.

Taxon	Marsh 1				Marsh 2				Marsh 3				Marsh 4			
	Freq		Cov		Freq		Cov		Freq		Cov		Freq		Cov	
	J	D	J	D	J	D	J	D	J	D	J	D	J	D	J	D
Alismataceae																
Sagittaria graminea	0	18	11	1	0	0	0	0	0	25	0	3	17	63	3	7
Poaceae																
Andropogon virginicus	0	30	0	4	2	10	1	3	0	15	0	3	0	10	0	3
Aristida stricta	10	0	3	0	20	22	6	6	4	11	7	7	0	0	0	0
Axonopus furcatus	0	0	0	0	39	0	5	0	1	1	r	2	4	0	5	0
Dichanthelium sabulorum	78	55	4	4	39	49	1	3	41	40	4	4	8	3	1	3
Eragrostis elliottii	0	13	0	2	0	12	0	2	0	21	0	2	0	2	0	2
Panicum sp.1	50	30	4	3	78	0	5	0	36	1	4	2	15	0	4	0
Panicum hemitomon	0	10	0	3	0	0	0	0	0	18	0	3	57	68	5	7
Paspalum notatum	0	2	0	2	0	6	0	3	53	18	4	2	8	13	3	2
Paspalum setaceum	15	0	3	0	20	59	6	6	2	4	1	3	12	5	1	2
Cyperaceae																
Eleocharis baldwinii	0	2	0	3	0	31	0	3	30	13	5	5	0	3	0	2
Rhynchospora cephalantha	3	18	3	5	39	59	5	0	0	15	0	3	0	13	0	5
Rhynchospora fasicularis	40	2	5	1	5	0	4	0	27	0	6	0	18	0	3	0
Rhynchospora filifolia	45	78	5	9	37	16	5	6	37	34	5	4	52	47	4	7
Scleria triglomerata	0	0	0	0	0	4	0	2	0	1	0	r	15	3	3	3
Xyridaceae																
Xyris elliottii	5	43	2	3	12	18	r	4	11	14	1	2	2	7	r	2
Xyris fimbriata	45	28	4	3	0	4	0	2	17	0	1	0	40	17	4	3
Eriocaulaceae																
Eriocaulon decangulare	25	15	1	3	0	4	0	3	0	7	0	3	8	22	2	2
Syngonanthus flavidulus	35	15	7	5	29	0	5	0	5	14	r	5	2	2	1	r
Pontederiaceae																
Pontederia cordata	0	0	0	0	0	0	0	0	0	0	0	0	35	40	6	7
Juncaceae																
Juncus repens	60	28	5	7	2	8	6	2	52	48	9	10	35	25	7	7
Hypericaceae																
Hypericum fasciculatum	0	53	0	2	17	33	r	2	16	12	r	2	0	15	0	2
Hypericum myrtifolia	35	35	3	1	44	29	3	2	46	15	3	1	8	13	3	2
Melastomataceae																
Rhexia mariana	0	17	0	1	0	55	0	5	5	5	r	r	0	0	0	0
Onagraceae																
Ludwigia linearis	50	15	3	2	44	8	3	2	0	0	0	0	13	20	3	4
Haloragaceae																
Proserpinaca pectinata	30	45	3	4	27	45	3	3	35	8	3	1	25	17	4	3
Loganiaceae																
Polypremum procumbens	23	15	1	2	7	0	2	0	16	12	1	3	7	10	1	3
Apiaceae																
Centella asiatica	20	20	2	2	0	1	0	r	28	16	2	3	7	2	3	2
Asteraceae																
Eupatorium leptophyllum	3	0	r	0	0	0	0	0	0	0	0	0	30	0	3	0
Eupatorium capillifolium	5	3	r	r	0	0	0	0	0	0	0	0	25	0	3	0

species of Xyris, Xyris fimbriata and Xyris elliottii, were present in all marshes. Xyris fimbriata was more prevalent in the wetter areas of shallow marshes and declined in frequency from June to December, while Xyris elliottii was more evenly distributed and increased in frequency during the same interval. Hypericum myrtifolium was widespread with low cover values during both seasons, while Hypericum fasciculatum was far more common in December. Proserpinaca pectinata was an inconspicuous but common species in all marshes, while Ludwigia suffruticosa was common in all marshes except in Marsh 2. The grasses Paspalum setaceum, Panicum sp. 1, Andropogon virginicus, Axonopus furcatus, and Eragrostis elliottii were present in all marshes. Aristida stricta was present in all marshes except Marsh 4, but was confined to the borders of the marshes where it was frequently found in association with Syngonanthus flavidulus. Polypremum procumbens and Centella asiatica were common in Marshes 1,3, and 4 but were rare in Marsh 2. Rhynchospora fasicularis was present in June in all marshes but was heavily grazed at that time; it was absent in December.

The species present in Marsh 1 were essentially similar to those in Marsh 2 and the shallow areas of Marsh 3, although frequencies varied considerably. Marsh 1 also shared two species of Eupatorium with Marsh 4. In addition, there was a small stand of Rhynchospora microcarpa near the clump of trees.

Marsh 2 had higher frequencies of grasses than the other marshes. Panicum sp. 1, Andropogon virginicus, Axonopus furcatus, and Eragrostis elliottii were all more abundant and had higher cover values in this marsh than in all other marshes. Aristida stricta was present in 20% of the quadrats sampled in this marsh.

Rhexia mariana was present in 55% of the Marsh 2 quadrats in December. Rhexia mariana, Aristida stricta, and Syngonanthus flavidulus all were found commonly in the surrounding pine flatwood community. In contrast to the presence of these typical dry habitat species, there also was a small but dense population of Juncus effusus in the wettest area (frequency 16%, cover 30%). This rush did not occur in other marshes.

Species distributions in Marsh 3 were similar to those in Marshes 1 and 2 in the shallow areas except that Eleocharis baldwinii and Centella asiatica were more abundant in Marsh 3. The deep areas of this marsh, however, were very different from the shallow areas. The deep areas had a dense, carpet-like stand of Juncus repens. Cover values for this species were >75% in June when Paspalum notatum, Eleocharis baldwinii, and Polypremum procumbens also were present. In December, cover values increased to 100%, and Panicum hemitomon was the only other species present; it had low cover and was in poor condition. Small amounts of Sagittaria graminea appeared in December at the edge of the waterline.

Marsh 4 had a community composition that differed from all other marshes. Pontederia cordata formed a dense stand (cover 30%-50%) in the center of the marsh. In addition, Panicum hemitomon, Juncus repens, Sagittaria graminea, and Utricularia inflata were present. Juncus repens formed a dense mat under the Pontederia cordata and Panicum hemitomon in June, but was less common in December. Sagittaria graminea increased from a frequency of 17% to 63% in the same interval and had a cover value of 33% in December. Panicum hemitomon also increased in December. A large amount of decaying organic matter and epiphytic algae that reduced water clarity was associated with the Pontederia cordata stems. The shallower areas of this marsh had a high frequency of Eupatorium spp. seedlings in both seasons but mature plants only in December. Scleria triglomerata, Carex verrucosa, and Fuirena sp. were other species present only in the shallow area of this marsh.

Community Similarity

Little difference between the communities in shallow and deep areas of Marsh 1 was detected (Areas 1A and 1B of Fig. 2). Similarity between the two areas was 81% in June and 75% in December (Fig. 9). When this marsh flooded, the differences in water levels across the marsh were small, due to its shallow nature and gradual change in elevation (Fig. 2).

In contrast, Marsh 2 had a more distinct depression in the southeast end, although the remainder of the marsh was gently graded (Fig. 3). This marsh showed similarities of 67% and 59% (areas 2A and 2B) in June and December, respectively (Fig. 9). The deep area of this marsh had a stand of Juncus effusus as well as Juncus repens. Only a small portion of the deep area was subject to innundation, but the marked differences in the vegetation in this portion contributed to the overall difference between the two areas of the marsh.

The shallow areas (3A and 3B) of Marsh 3 were 72% similar in June, but only 60% similar in December (Fig. 9). Together with Marshes 1 and 2, these shallow areas formed a cluster with an overall similarity of 52% in June. Areas 1A, 1B, 2A, 2B, 3A, and 3B were subject to temporary flooding, but standing water rarely covered the entire surface. In December, when Marsh 1 and the outer areas of Marsh 3 (3A and 3B) had

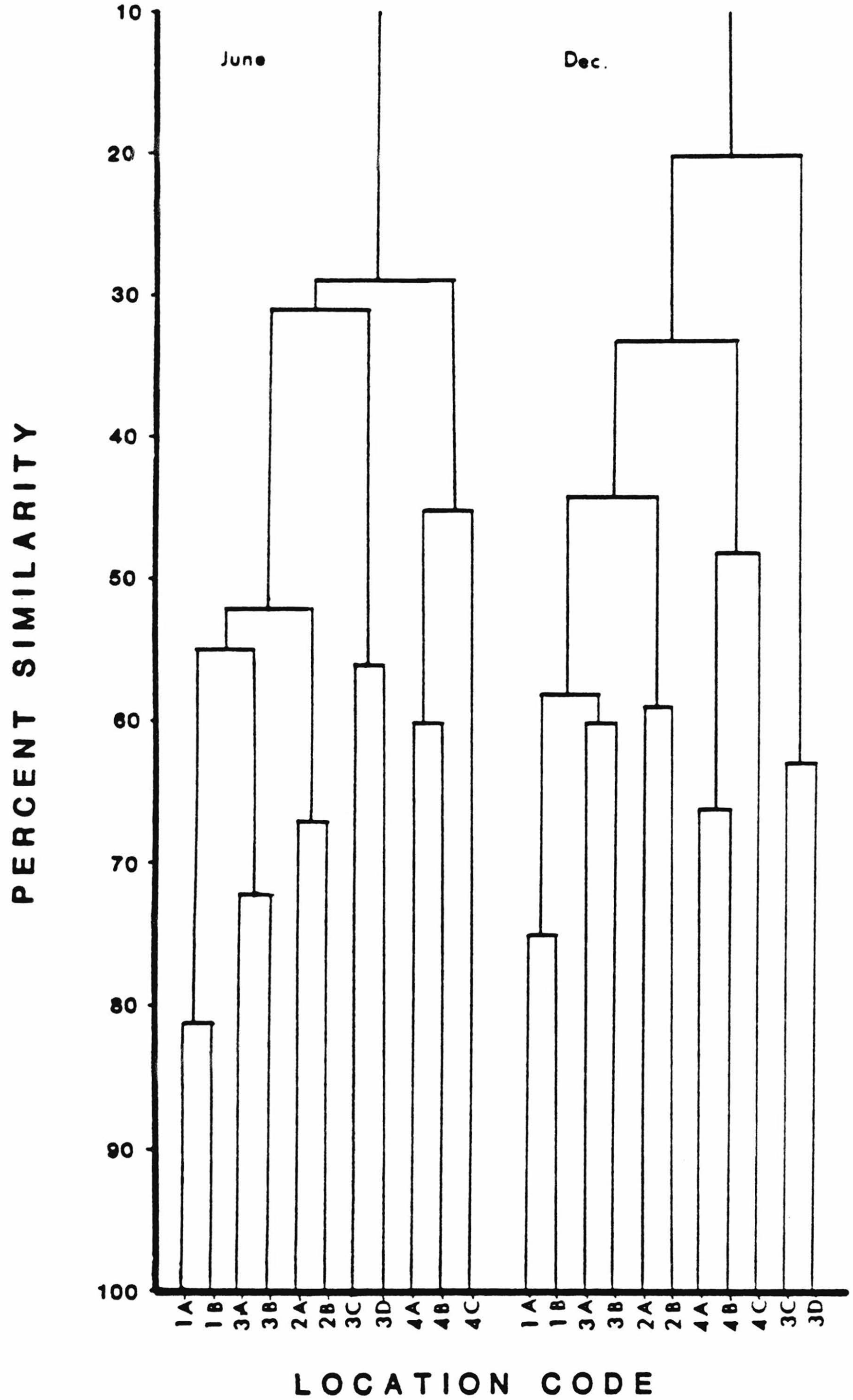


Figure 9. Dendrogram of cluster analyses performed in June 1986 and December 1986. The number in each location code represents the marsh identification. The letter represents the depth of the contour: A=<32 cm, B=36-64 cm, C=68-96 cm, D=>96 cm.

been dry for shorter amounts of time than Marsh 2, cluster similarity decreased to 44%.

The deep areas of Marsh 3 (3C and 3D) clustered together with 56% similarity in June; this increased to 63% in December (Fig. 9) when standing water had been present for 6 months (Fig. 6). The number of species coexisting with Juncus repens in the deeper areas decreased from 5 in June to 0 in December. As a result, the similarity between these areas and any other marsh, including the shallow areas of Marsh 3, decreased from 32% in June to 20% in December.

The internal similarities among areas of Marsh 4 remained consistent over time. The outer two areas (4A and 4B) were 59% and 62% similar in June and December, while the inner area (4C) was only 45% and 48% similar to these (Fig. 9). This marsh consisted of a narrow perimeter of relatively dry ground with species similar to shallow areas of other marshes, a transition zone characterized by both wet and dry species, and a wet central area characterized by Pontederia cordata, Panicum hemitomon, and Juncus repens. Water levels in this marsh were consistent from July to December (Fig. 6); the upper limit of the water covered the lower one-third of the transition zone. The outer two areas (4A and 4B) were more similar than the inner two areas (4B and 4C) (Fig. 9). Marsh 4, as a whole, was markedly different from the other areas in June, but clustered with the drier areas in December at 33%. The shift in clustering was due to the difference between the deep areas of Marsh 3 and the rest of the marshes.

Reciprocal Averaging

No floristic gradient was detected in Marsh 1 in June or December (r^2=0.07, p>0.05)(Fig. 10). The lack of a gradient agreed well with the results of the cluster analysis in which no differences were detected between inner and outer areas of the marsh (Fig. 9).

In Marsh 2, no gradient was detected in June (r^2=0.06, p>0.05), but one did exist in December (r^2 =0.22, p<0.0001) (Fig. 10). Differences along this gradient were reflected in the cluster analysis which showed a decrease in similarity between areas from June to December (Fig. 9).

June gradients in Marsh 3 were highly significant (r^2=0.29, p<0.0001); in December, however, a depth gradient explained 74% of the community variation (r^2=0.74, p<0.0001) (Fig. 10). Thus, December values indicate a much stronger relationship between depth and community variation. The water level in Marsh 3 increased from 0 cm in June to over 100 cm in December (Fig. 6). During the same interval, species coexisting with Juncus repens decreased markedly.

Marsh 4 showed strong gradients in both June (r^2=0.29, p<0.0001) and December (r^2=0.41, p<0.0001). The strength of these relationships showed relatively little variation with time (Fig. 10). Water levels in this marsh were relatively stable, and at no time did the soil dry out completely (Fig. 6). The lack of a seasonal gradient change was consistent with the results of the cluster analysis which showed little change in internal relationships. (Fig. 9)

Biotic Boundaries

Neither Marsh 1 or Marsh 2 showed strong departures from a random distribution of species, and no boundaries could be placed in these

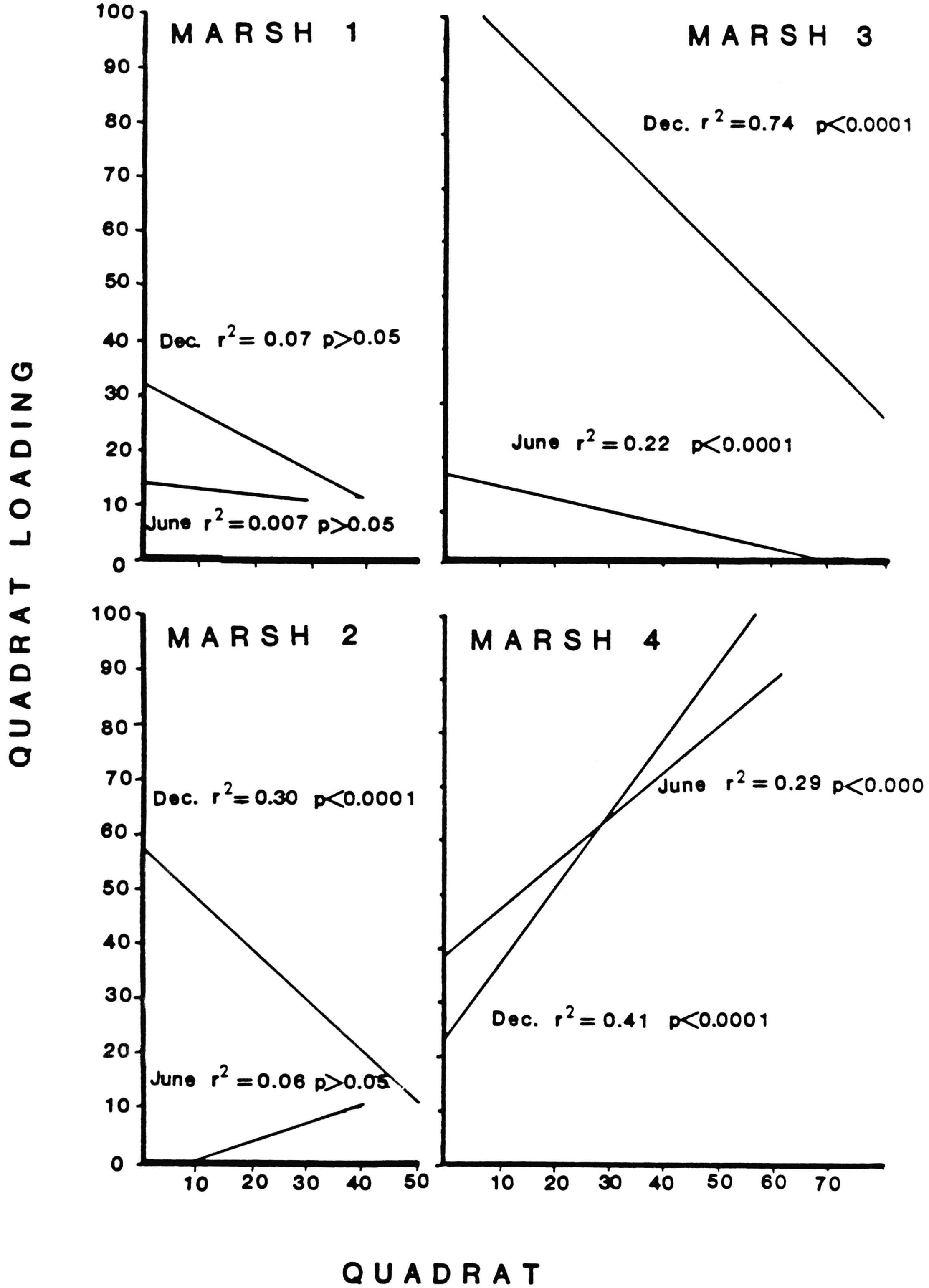


Figure 10. Graph of quadrat loading from the reciprocal averaging analysis plotted against quadrat number. Quadrats are arranged in order of depth from shallow to deep. The regression was calculated by regressing the quadrat loading against order.

marshes. The cluster analysis and reciprocal averaging results supported this outcome (Figs. 9 and 10). The lack of boundaries in Marsh 2 in December may reflect insufficient sampling of the small area in the deepest part of the marsh (n=2).

In Marsh 3 in June, a boundary could be placed that roughly corresponded to the 60 cm depth contour, although both shallower and deeper areas were included (see Fig. 11 for transect and boundary placements). This area corresponded well with the two deeper marsh areas used in the cluster analyses. It also was the area in which Juncus repens formed a dense mat on the bottom. In December, the boundaries were expanded considerably and fell around 40 cm depth. This coincided well with the area of standing water in the marsh. In December, an additional boundary could be established near the southern tip of the marsh where a second, more shallow depression existed. Juncus repens also was present in this location but did not form a monospecific stand.

The northern end of Marsh 3 also had some boundaries. In June, they were located near the edges of the marsh and on a rise near the center of the area. The extreme edge of this marsh was characterized by the presence of Aristida stricta tussocks and Syngonanthus flavidulus. The edge boundaries may reflect the presence of these species. In December, the boundary had shifted but was still in the same general vicinity.

Marsh 4 boundaries corresponded well with the 40 cm depth contour (see Fig. 12 for transect and boundary placement). Areas inside the boundary were characterzied by the presence of Pontederia cordata, Panicum hemitomon, Sagittaria graminea, and Juncus repens. The lack of change in the boundary over time reflects the lack of change in water

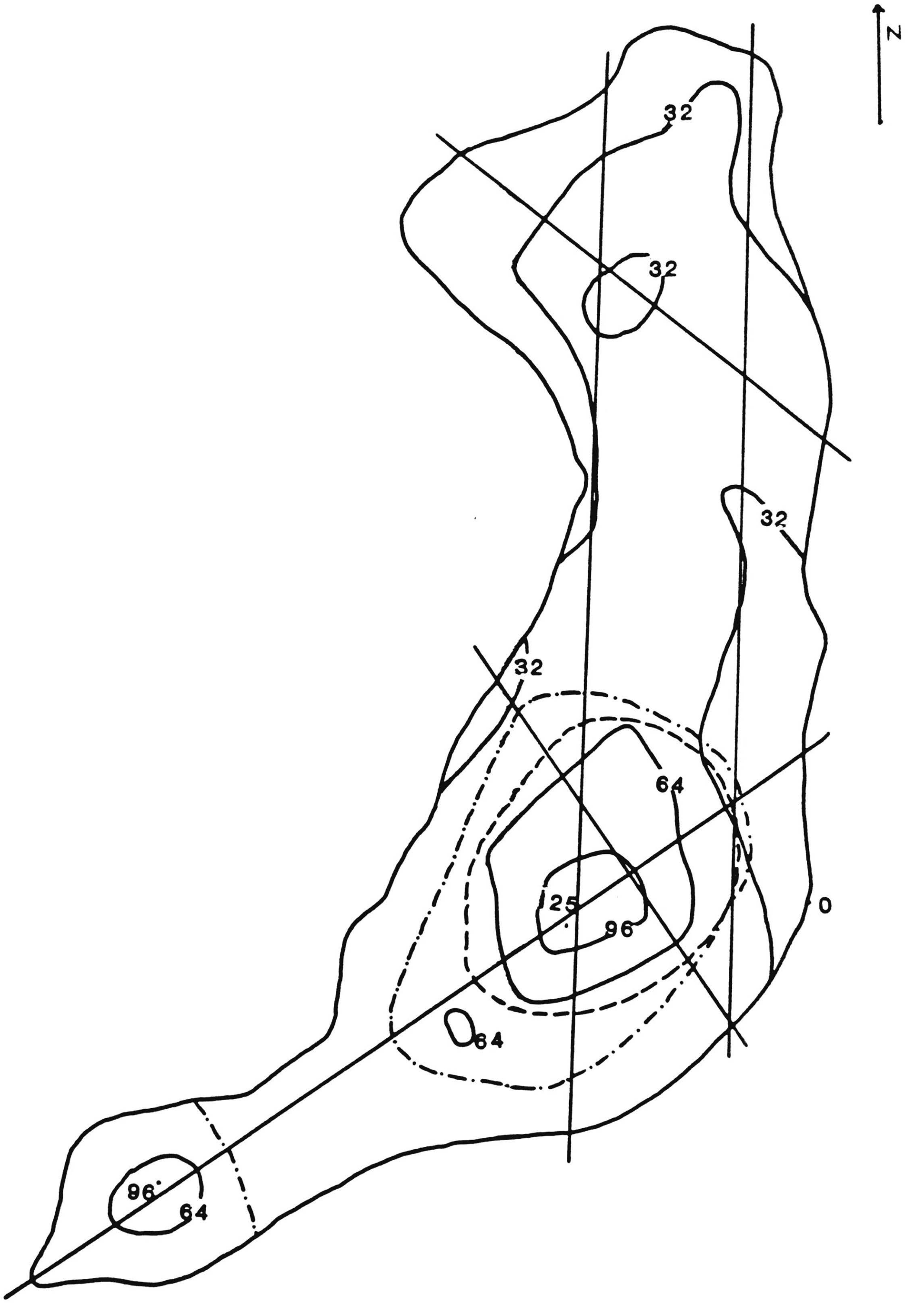


Figure 11. Transect locations in Marsh 3. (--)=boundaries placed in June, (-.-)=boundaries placed in December. Solid lines are contour lines or transect lines.

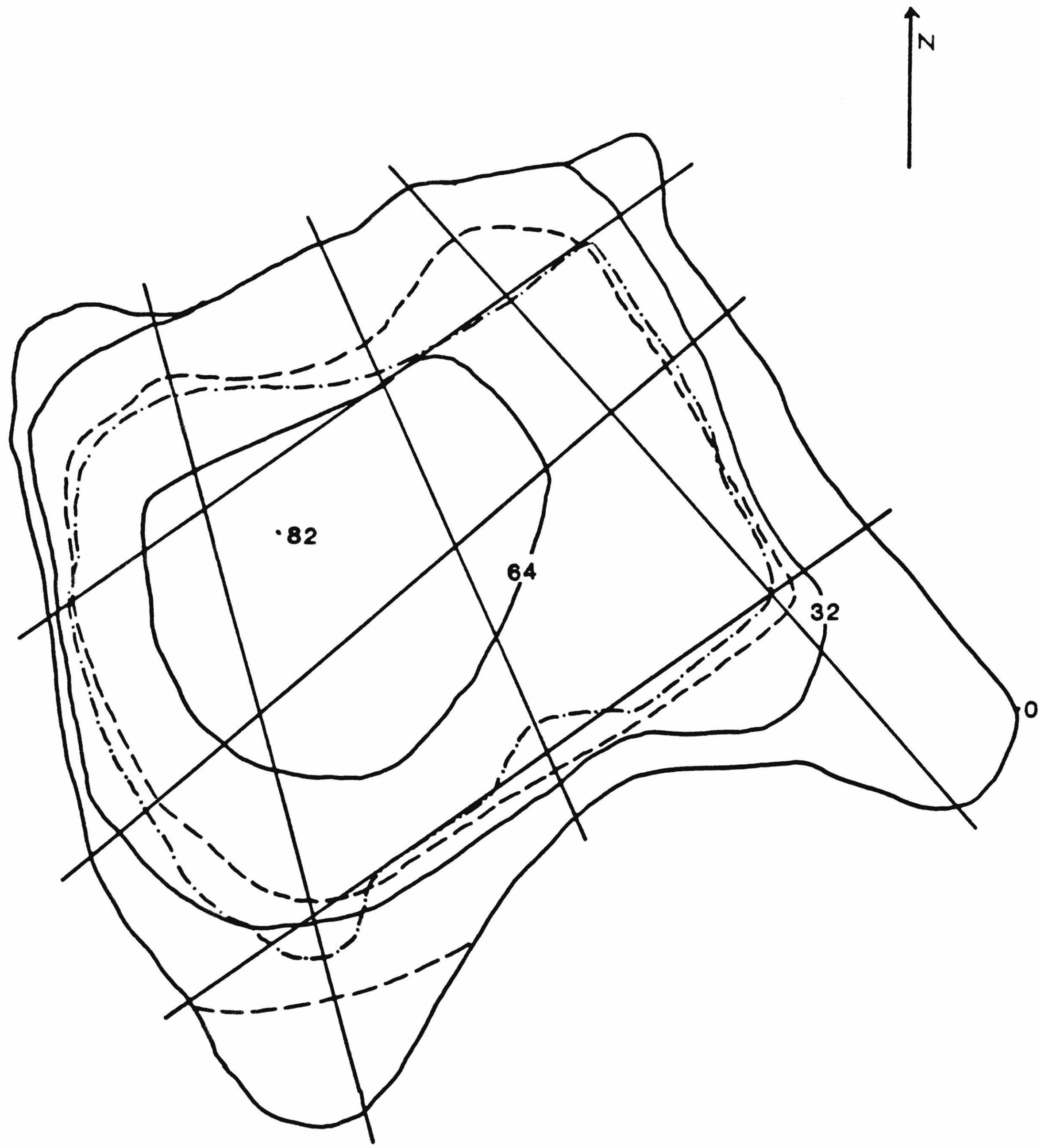


Figure 12. Transect locations in Marsh 4. Symbols are as in Fig. 11.

level (Fig. 6) and the results of the cluster analysis (Fig. 9). Furthermore, these results agree well with the consistent ordinations obtained in both June and December (Fig 10).

DISCUSSION

A number of investigators (Gauch *et al*. 1977, Gauch 1982, Pielou 1984) have recommended the use of several complementary techniques when describing plant communities, since the weaknesses of one technique may be corrected by the strengths of others. The community analyses in this investigation were performed on three levels. Since the principal factor of interest was the relationship between species distribution and depth, a similarity index and cluster analysis technique was used to establish whether differences between deep and shallow areas existed. The second step, accomplished with a reciprocal averaging technique, was to examine the data for a gradient relating quadrat depth to species composition. Finally, species distributions were analysed to determine locations of boundaries between communities and whether the boundaries were related to water levels.

Cluster Analyses

Cluster analysis provided an intuitively satisfying method for quantifying the degree to which species composition varied with depth. This technique also permitted quantitative comparisons to be made between different marshes. Although the 32 cm intervals were selected arbitrarily, two points were clear from the results. First, shallow areas tended to be similar to each other both within and between marshes. Shallow areas of Marsh 3 were more similar to Marshes 1 and 2 (both were shallow marshes) than to deep areas of Marsh 3. Second, deep parts of the marshes differed not only from shallow areas but also from each other. Thus, water depth does not appear to be the only regulatory factor in these marshes. Marsh 3 had a sandy, inorganic substrate that was dry following a period of no precipitation, while Marsh 4 was highly organic and remained moist at all times. The differences in substrate moisture and organic content suggest that drainage patterns may be another regulating factor in these marshes.

A relationship between drainage and community composition has been reported by other investigators. Similar results were found by Dix and Smeins (1968) in a prairie community where a vegetation continuum was found from well-drained upland areas to poorly-drained marsh areas. Large numbers of species reached their limits of occurrence in a transition zone between upland and lowland areas. In the lowland areas, a mosaic pattern of differing stand types was common, and individual depressions often differed markedly.

Because the areas compared with the clustering technique were selected on the basis of an arbitrary elevation interval, the results are regarded as preliminary. No sound biological reason existed for selecting an interval of 32 cm; however, with this division, gross comparisons between communities at different depths could be addressed. These differences were so great that any inconsistencies due to inappropriate boundary selection did not affect interpretation of general patterns. The community similarities found should be regarded as conservative estimates; that is, differences were probably greater than calculated between shallow and deep areas and smaller than calculated between shallow areas.

Reciprocal Averaging

Reciprocal averaging has been used by Gauch and Stone (1979) and Persson (1981) to elucidate floristic gradients. This ordination technique is highly objective and is free of investigator bias (Gauch et al. 1977); however, the floristic ordination generated may be difficult to interpret if no obvious environmental gradient correlates with it. For this reason, the technique is most useful when a single strong environmental gradient is present (Gauch et al. 1977).

When the Hunter's Green data were analyzed using reciprocal averaging, two important relationships were evident. First, species in the marshes responded to an environmental factor which correlated with depth within the marsh. Second, the importance of this factor was higher in marshes with standing water and in seasons when water was present. Marshes 1 and 2 showed no gradients in June when no standing water was present and no relationship could be found between soil moisture and depth. In December, when the marshes were wetter, a gradient was detected in Marsh 2. Marsh 3 showed marked differences in both water level and gradient importance between seasons. The numerically dominant species present in the wet area of the marsh was capable of living under a wide variety of hydrologic conditions including both dry and submerged states; however, dry species which were present throughout the marsh in June were confined to the shallow areas in December. Thus, when water levels were high, species ordination was highly correlated with contour. In contrast, Marsh 4, which remained wetter than all other marshes year round showed strong gradients in both seasons. It was the only marsh not dominated by grasses or sedges; instead, this marsh supported a community of emergent wetland species characteristic of systems with a stable water table. In this marsh, little seasonal change in the community and little change in the importance of the depth gradient with season was noted.

Investigators in temperate marshes and sedge meadows have repeatedly demonstrated the importance of water regimen as a regulator of community structure (e.g., Dix and Smeins 1967, Auclair _et al_. 1973, 1976). Initial water level had a strong influence on vegetation in Saskatchewan sloughs (Walker and Coupland 1968), while rate of water loss and drainage patterns had an equally important effect in other marshes (Harris and Marshall 1963, Dix and Smeins 1967, Walker and Wehrhahn 1970). The importance of water regimen as a community regulator in subtropical marshes has not been as well documented, although Bayley _et al_. (1985) reported that water levels were more important than nutrient addition for marsh productivity in a central Florida wetland.

Biotic Boundaries

The use of null models in ecology has provided a rigorous means of determining whether data give an indication of the operation of processes which determine the organization of the community (Connor and Simberloff 1986). In Marshes 1 and 2, a weak or non-existant gradient was found, and the probabilistic similarity technique of Raup and Crick (1979) showed that the species distributions were not statistically different than that expected on the basis of a null model. Thus, at the level at which these communities were studied, no evidence of a controlling process was detected; however, examination of a micro-environmental factors might detect regulators of small-scale organization.

Raup and Crick (1979) originally used their technique as a measure of faunal similarity in which species assemblages were grouped based on their similarity to an arbitrary reference group. McCoy et al. (1986) used the technique to place boundaries along a one-dimensional gradient. Here, the technique was extended and used to place boundaries in two dimensions, thereby defining the spatial location of a particular species assemblage or community. The McCoy et al. (1986) technique was sensitive to the arrangement of quadrats within a contour interval; that is, boundaries were placed between quadrats widely separated in space, but similar in depth. To evaluate the effect of distance between quadrats, the quadrats were arranged in order along a number of intersecting transects. When boundaries were placed along the transects, it was found that they could be connected to define distinct floristic assemblages in space. Furthermore, in Marsh 3, where the importance of water level changed seasonally, the boundaries also fluctuated, following the waterline. In Marsh 4, where water levels were relatively stable, the boundaries were stable. The technique failed to yield boundaries in drier areas, suggesting that, at the level examined, no single controlling factor was operating. Beta diversity, species turnover along an environmental gradient, may have been so low in the shallow areas that no strong interspecific associations were apparent. Thus, the biotic boundary technique confirmed the reciprocal averaging results and further defined the controlling factors.

In the northern end of Marsh 3, the technique placed boundaries which had no obvious explanation based on casual inspection of the species distributions. Whether these particular boundaries reflected the effects of water level changes is difficult to determine. It is possible that another environmental gradient existed and was regulating the community composition in these areas. McCoy et al. (1986) remarked that during their analyses they found occasional spurious boundaries and suggested that such boundaries merit further attention.

Succession and Disturbance

Although the role of water regimen in controlling succession in the marshes was not directly investigated, it was noted that Marsh 2, the driest marsh, tended to have more species characteristic of the surrounding pine flatwood (personal observation). If this marsh is indeed subject to a drawdown effect from the Morris Bridge well field and is now drier than in the past, then loss of the influence of higher water levels may be permitting succession to proceed toward a pine flatwood community. When water levels were low in Marsh 3, dry species could be found throughout the Juncus repens bed, but subsequent flooding eliminated them. Similarly, species richness of dry species in the deep area of Marsh 4 was much lower than in the shallow areas.

Lieffers (1984) reported that frequent fluctuation of water levels in boreal marsh communities kept them in an early successional stage, while sites with stable water levels tended to have lower species richness. Auclair et al. (1976) also found evidence that species diversity was lowest in the deep areas of the marsh. Van der Valk and Bliss (1971) suggested that the height of the permanent water table in Alberta oxbow marshes controlled succession.

Species such as Polygonum hydropiperoides, which are capable of colonizing disturbed areas rapidly, were present in areas of Marshes 1 and 3 where the substrate had been disturbed by digging during a dry period. Heavy grazing by cattle markedly reduced the frequency of Rhynchospora fasicularis in all marshes. No attempt, however, was made to evaluate quantitatively the effects of these disturbances.

Disturbance, particularly by fire, drawdown, or grazing, has frequently been noted as an important factor in regulating the composition of marsh communities. Walker and Wehrhahn (1970) conservatively estimated that disturbance could explain 20% of the variation in vegetation gradients in Saskatchewan marshes. A study of Carex wetlands subjected to elevated water conditions and altered temperatures (Bedford and Loucks 1984) found differential sensitivity of the vegetation to disturbance.

Marked seasonal changes were noted in the species composition, distribution, and abundance in the Hunter's Green marshes. Changes in distribution apparently were due to seasonal changes in water level. Auclair et al. (1976) noted marked seasonal changes in species composition across growing seasons. They attributed these changes to differences in the timing of growth periods of different species throughout the year. Within species differences in growth patterns were attributed to changes in water depth. Similar results have been reported for New Jersey marshes (Jervis 1969) and Florida wetlands (Bayley et al. 1985). Other investigators have reported seasonal changes in biomass or standing crop for individual species such as Carex rostrata Stokes (Bernard 1974), Eleocharis quadrangulata (Michx.) Rand (Boyd and Vickers 1971), Nymphaea tuberosa Paine and Ceratophyllum demersum L. (Smart 1980), and Typha latifolia L. and Scirpus americanus Pers. (Boyd 1970).

Conclusions

The sensitivity of marshes in general, and of these marshes specifically, to water regimen changes makes the currently fashionable practice of using marshes as stormwater runoff retention ponds questionable since the resulting changes in water levels and drainage patterns may markedly affect the plant communities in the marshes. Elevated water levels may discourage sexual reproduction in species such as Juncus repens which flower only under dry conditions (Godfrey and Wooten 1981). An expansion of those species tolerant of wet conditions and a decline of those intolerant species might occur under more stable water conditions. Stabilization of the water levels may result in successional changes toward a community dominated by emergent genera such as Pontederia, Sagittaria, Typha, or Scirpus or to bare mud substrate (Bedford and Loucks 1984) rather than the present grass-sedge community. On the other hand, an alteration of drainage patterns that resulted in diversion of water away from the marshes possibly could lead to succession toward a pine flatwood community. Finally, the effect of nutrient addition to the grass-sedge marsh community is virtually unstudied. Specific hypotheses regarding the roles of water level, disturbance, and nutrient addition need to be tested experimentally before implementing changes in the existing conditions in these marshes.

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APPENDIX 1

Table 3. Temperature and precipitation data for 1986-87 as recorded at St. Leo, Florida (N.O.A.A. 1986, 1987).

	Temperature (°C)		Rainfall (cm)	
Month	Average	Departure from monthly mean	Total	Departure from mean monthly total
January	15.94	0.44	14.88	8.28
February	19.17	2.95	6.71	-2.59
March	19.17	-0.05	13.16	2.51
April	21.00	-1.11	3.63	-3.35
May	25.28	0.28	4.95	-7.19
June	27.33	0.39	13.28	-4.22
July	27.72	0.11	22.40	1.96
August	27.78	0.06	25.43	6.07
September	27.38	0.49	8.99	-6.83
October	24.50	1.17	4.85	-2.31
November	23.94	4.66	2.51	-3.10
December	18.33	2.00	6.83	0.64
January	Not available		14.78	8.18
February	Not available		11.33	2.03

APPENDIX 2

Table 4. Herbaceous angiosperms encountered in the Hunter's Green marshes. Species (n=9) encountered only as seedlings are not included.

Monocotyledonae
- Alismataceae
  - Sagittaria graminea Michx.
- Poaceae
  - Andropogon virginicus L.
  - Aristida stricta Michx.
  - Axonopus furcatus (Fluegge) Hitchc.
  - Dichanthelium sabulorum (Lam.) Gould and Clark
  - Dichanthelium strigosum (Muhl.) Freckmann
  - Eragrostis elliottii S. Wats.
  - Panicum sp.1 L.
  - Panicum hemitomon Schult.
  - Paspalum notatum Fluegge
  - Paspalum setaceum Michx.
- Cyperaceae
  - Bulbostylis barbata (Rottb.) Clarke
  - Carex verrucosa Muhl.
  - Cyperus retrorsus Chapm.
  - Eleocharis baldwinii (Torr.) Chapm.
  - Fuirena sp. Rottb.
  - Rhynchospora cephalantha A. Gray
  - Rhynchospora fasicularis (Michx.) Vahl
  - Rhynchospora filifolia A. Gray
  - Rhynchospora microcarpa Baldw. ex A. Gray
  - Rhynchospora rariflora (Michx.) Ell.
  - Scleria triglomerata Michx.
- Xyridaceae
  - Xyris elliottii Chapm.
  - Xyris fimbriata Ell.
  - Xyris jupicai L. Rich.
- Eriocaulaceae
  - Eriocaulon decangulare L.
  - Lachnocaulon anceps (Walt.) Morong
  - Syngonanthus flavidulus (Michx.) Ruhl.
- Pontederiacee
  - Pontederia cordata L.
- Juncaceae
  - Juncus effusus L.
  - Juncus marginatus Rostk.
  - Juncus repens Michx.

Table 4 continued

Dicotyledonae
  Polygonaceae
    Polygonum hydropiperoides Michx.
  Droseraceae
    Drosera capillaris Poir.
  Polygalaceae
    Polygala rugelii Shuttlew.
  Hypericaceae
    Hypericum fasciculatum Lam.
    Hypericum myrtifolium Lam.
  Violaceae
    Viola lanceolata L.
  Melastomataceae
    Rhexia mariana L.
    Rhexia nuttallii James
  Onagraceae
    Ludwigia linearis Walt.
    Ludwigia suffruticosa Walt.
  Haloragaceae
    Proserpinaca pectinata Lam.
  Apiaceae
    Centella asiatica (L.) Urban
    Hydrocotyle umbellata L.
  Ericaceae
    Lyonia lucida (Lam.) D. Don.
  Loganiaceae
    Polypremum procumbens L.
  Gentianaceae
    Sabatia grandiflora (A. Gray) Small
  Apocynaceae
    Amsonia ciliata (Walt.)
  Scrophulariaceae
    Agalinis linifolia (Nutt.) Britt.
  Lentibulariaceae
    Utricularia inflata Walt.
  Rubiaceae
    Hedyotis uniflora (L.) Lam.
  Campanulaceae
    Lobelia glandulosa A. Gray
  Asteraceae
    Ageratina jucunda (Greene) Clewell and Wooten
    Eupatorium capillifolium (Lam.) Small
    Eupatorium leptophyllum DC