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Distribution and Structure
of Floodplain Plant Communities
in the Upper Basin of the
St. Johns River, Florida

by

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ABSTRACT

The floodplain marsh of Blue Cypress Lake, in southern Florida, was examined to determine the spatial pattern of vegetation and its relationship to hydrologic conditions. Visual observation and direct gradient analysis of shoreline vegetation indicated six floristic zones. Beginning at the water's edge, these zones were dominated (in terms of mean percentage of above-ground, dry biomass) by: 1) Panicum hemitomon (99 %); 2) P. hemitomon (36 %), Eupatorium capillifolium (30 %), and Amaranthus australis (13 %); 3) Ipomoea alba (32 %), Calystegia sepium (30 %) and Osmunda regalis (16 %); 4) Cladium jamaicense (52 %), Kostelevskya virginica (19 %) and O. regalis (11 %); 5) O. regalis (52 %), and C. jamaicense (40 %); and 6) C. jamaicense (91 %). Zones 1-3 occupied the moderate slope of the shore from the water's edge to the berm. Zone 4 occupied the area immediately behind the berm, where elevations were slightly lower than the berm. Zones 4-6 were less distinct than were zones 1-3 and together formed a coenocline along a gentle upward slope onto the marsh flat.

The sequence of biomass maxima and the distributional limits of species on the shore suggested that zonation was the result of a complex-gradient in long-term hydrologic factors (as indicated by frequency of inundation over the previous ten years) caused by topographic relief. Certain species, such as E. capillifolium, however, were present due to drought conditions during sampling. For these species hydrologic factors were probably less influential on spatial patterns of abundance than on temporal patterns and extreme hydrologic events of short duration were

probably more important than long-term hydrologic conditions.

Beyond the lake shore, on the marsh flat, the zoned pattern was replaced by a mozaic of communities similar to those of large areas of the Everglades. These were dominated (in terms of subjective estimates of cover) by P. hemitomon (9621 acres), C. jamaicense (5936 acres), Myrica cerifera and Salix caroliniana (3917 acres), C. jamaicense and S. caroliniana (3368 acres), or Nymphaea odorata and Utricularia spp. (1010 acres).

That portion of the mozaic accounted for by communities dominated by C. jamaicense and P. hemitomon apparently did not result from hydrologic factors. This was suggested by the sharp borders typically found between these two communities and by the low topographic relief, and consequent uniformity of hydrologic conditions, of the marsh flat. Fire was probably the major effector of pattern in these communities. P. hemitomon, and it's associated species, may rapidly colonize areas where dense stands of C. jamaicense were destroyed by intense fire and then inhibit establishment of C. jamaicense seedlings. C. jamaicense apparently reclaims these areas, through vegetative reproduction, as a slowly moving front which monopolizes space and light.

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INTRODUCTION

The upper St. Johns River, located in east-central Florida, consists of a chain of shallow lakes lying within a vegetated floodplain of low relief. In its pristine condition, the floodplain from the Florida Turnpike to S.R. 520 occupied approximately 340,594 acres (calculated from data in St. Johns River Water Management Disrict, 1980, excluding lake acreages reported in Florida Bd. Cons., 1969) and was densely vegetated with emergent species. This is evident from the topography, the distribution and nature of the vegetation in undisturbed areas, and the distribution of wetlands soils (St. Johns River Water Management District, 1980). The primary and secondary production, habitat, water quality enhancement, low-flow augmentation and storm-water management provided by the floodplain was probably the basis for the outstanding fishing once characteristic of upper basin lakes (Cox et. al, 1981).

Early in this century, alteration of the floodplain for agricultural development was initiated (Goolsby and McPherson, 1970). This entailed isolation and drainage of floodplain wetlands and diversion of water from the river basin to coastal drainage. As a result, the floodplain area now available to the river and it's lakes is approximately 118,108 acres, only 35 percent of the original floodplain acreage. Moreover, the remaining floodplain is not in a pristine state because the surface water hydrology has been altered, primarily through the reduction in natural storage caused by floodplain development (SJRWMD, 1980; Tai and Rao, 1983). The ecological responses to basin development have apparently included: 1) a shift in the balance between deposition and oxidation of

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peat soils with concomitant soil subsidence (SJRWMD, unpublished topographic data), 2) a change in the species composition of floodplain vegetation in favor of woody species (Hall, G. B., unpublished data), 3) a decline in populations of game fish (Cox, et. al., 1981), 4) a decline in waterfowl populations (Florida Game and Freshwater Fish Commission, 1981), and 5) an increase in lake sedimentation rates (Cox, et al., 1976). Unfortunately, the severity of these responses is difficult to demonstrate because insufficient ecologic and hydrologic data were collected prior to floodplain development. Because development of the basin, either for private agriculture or public water management, will continue, it is important that its present condition be well documented so that the effects of future modifications can be assessed. In addition, it is imperative that the extents and causes of the ecological impacts of floodplain development be determined as accurately as possible so that appropriate mitigative measures may be implemented.

This study was designed to provide quantitative information regarding the present condition of the floodplain vegetation adjacent to the southernmost lake of the upper basin, Blue Cypress Lake (27 43'36" N; 80 45'12" W; Figure 1). Additionally, the study was designed to elucidate the relationship between the spatial distribution of plant species and hydrology. The management objectives of the study were: 1) to provide an analytical basis for prediction of the effects of alteration of the hydrologic regime on the distribution of floodplain communities, 2) to provide baseline data which would allow detection of vegetational responses to hydrologic changes, and 3) to provide species-specific information on the distribution of wetland plants with respect

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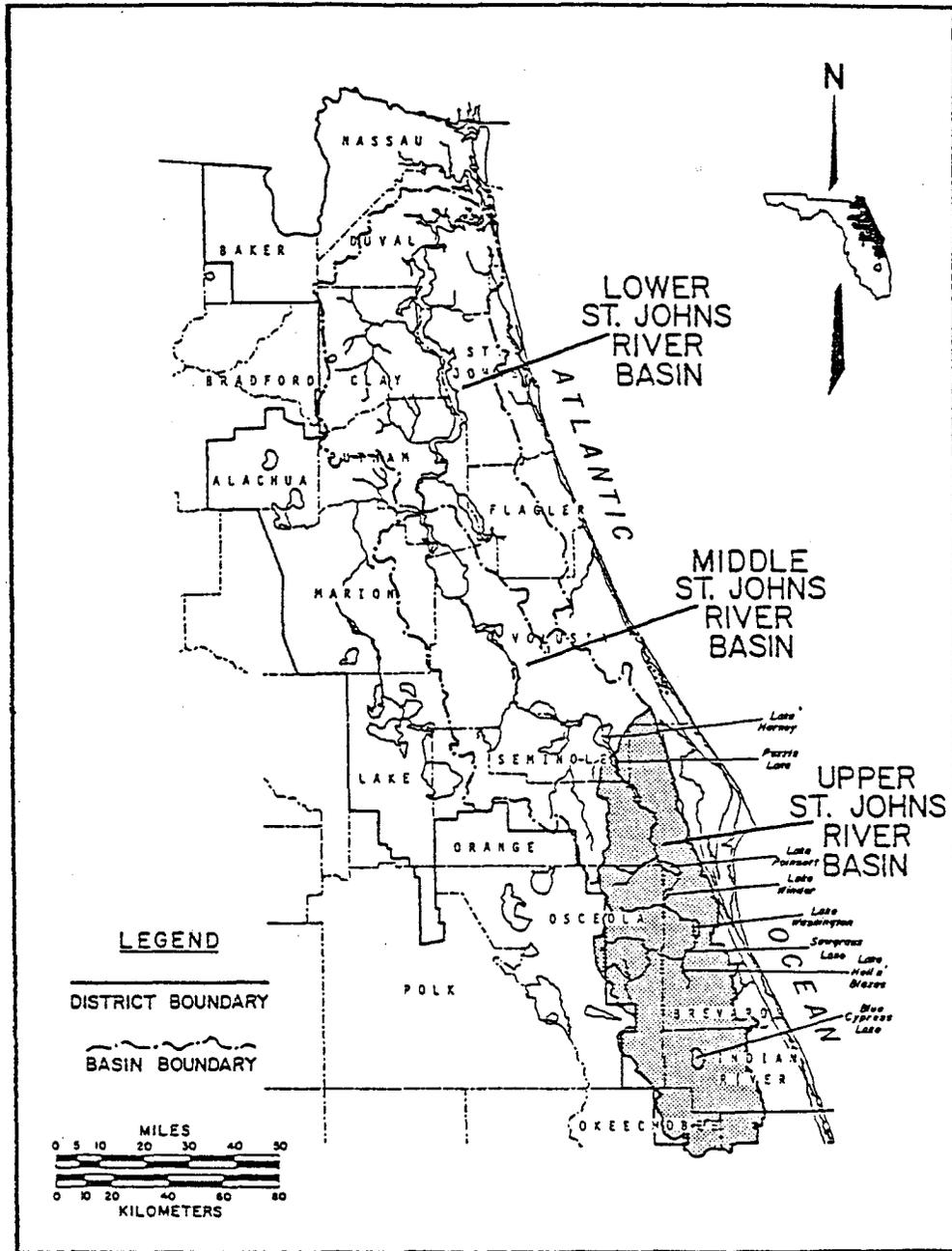
Figure 1. Map of the St. Johns River Water Management District
showing the location of the Upper Basin and of Blue Cypress Lake.

to hydrology in order to enhance the predictive capabilities of the
District for other areas.

METHODS

Characterization of the macrovegetation was accomplished through both extensive and intensive sampling. Extensive data were provided by color infra-red aerial photographs obtained by the remote sensing department of the Florida Department of Transportation (FDOT). Aerial transects of the marsh were flown at 6,000 feet elevation on March 20, 1981. Photographs were obtained with a Zeiss RMK camera (certified by the National Bureau of Standards) loaded with Kodak type 2443 color aerial infra-red film. Stereo pair transparencies at a scale of 1:12,000 were examined with a stereo viewer to delineate vegetation and land-use signatures. The interpreted photographs were then digitized and polyconic projections of the area surveyed were plotted through use of the Intergraph Interactive Computer Graphics System. The areal extent of each signature was also determined via Intergraph software. Finally, the signatures were color-coded to facilitate examination of vegetation patterns. The color-coded map is available for examination at the St. Johns River Water Management District headquarters in Palatka, Florida.

Ground-verification of vegetation signatures occurred on November 9-11, 1983. In this work, several examples of the most prevalent communities were visited. At each site the most common species were listed and dominance was assessed through subjective estimates of cover. In addition, five measurements of water depth were obtained. Depth was later converted to elevation by subtraction from the elevation of the lake's surface as indicated by a continuous recorder (described below).

Intensive data were obtained from a belt transect which extended

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approximately 270 m into the marsh from the southeastern shore of the lake. The transect consisted of five contiguous stations and a sixth station approximately 200 m into the marsh beyond the fifth station. All stations except station 2, which measured 20 m X 20 m, had dimensions of 10 m by 40 m and each station lay within or spanned a visually distinct zone of vegetation. Sampling locations within each station were determined by considering the two dimensions of each station to be x and y coordinates marked at meter intervals. Random number pairs indicating locations on the coordinate grid were generated by a computer program which utilized the random number generator of Prime (Prime Computer, Inc. 1977). These procedures yielded a stratified random sampling design; a design highly recommended for studies of aquatic plant biomass (Nichols, 1982).

Because of variation in size and density of vegetation among the stations, samples were obtained using quadrats of different size and shape. For station 1, a 0.25 m diameter circle was sampled; for station 2, a 0.50 m diameter circle was sampled; and for stations 3 - 6, a square measuring 0.50 m on each side was sampled. A square quadrat was used for stations 3 - 6 so that a three-sided sampler could be inserted into the dense vegetation at ground level and the fourth side be added after the sampler was in place. Within each quadrat all macrovegetation was removed to ground level and placed in plastic bags for transport to the laboratory. The elevation of the ground surface within each quadrat was determined by standard surveying techniques using the lake elevation indicated by a staff guage at Middleton's Fish Camp as the reference elevation. Depending on the variability and density of the vegetation,

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10 - 20 locations were sampled within each station. Samples were
collected between June 1981 and February 1982 a time of drought and low
surface water elevations (Figure 2). Although sampling spanned several
months, I do not believe seasonal variation materially affected the
conclusions of the study in that the dominant species, such as Cladium
jamaicense Crantz (hereafter Cladium) and Osmunda regalis (Willd) Gray,
exhibited no seasonal senescence. The demonstrated aseasonality of
above-ground biomass for Cladium in the Everglades (Steward, 1974) lends
support to this conclusion.

In the laboratory, samples were sorted by species and desiccated in
an oven at 100 C for 24 - 48 h to determine dry weight biomass. For
large samples, subsamples were desiccated to determine coefficients for
converting wet weight totals to dry weights. For appropriate species
stem or shoot numbers were counted prior to desiccation. When Cladium
occurred in a sample, the culms were counted and the length of the
longest blade of each culm was measured to the nearest millimeter.
Species identifications were according to Godfrey and Wooten (1979, 1981)
for monocots and dicots, Lakela and Long (1976) for ferns, and Radford et
al., (1968) for gymnosperms.

Data were analyzed on two levels. First, the data were segregated
by station and statistically analyzed to provide baseline descriptions
for detection of changes in vegetation biomass and community structure.
In this analysis, means and variances for dry weight biomass and percent
of total dry weight biomass were calculated for each species for each
station (Appendix A). For each station, the total number of species and
means and variances for species density (the total number of species per
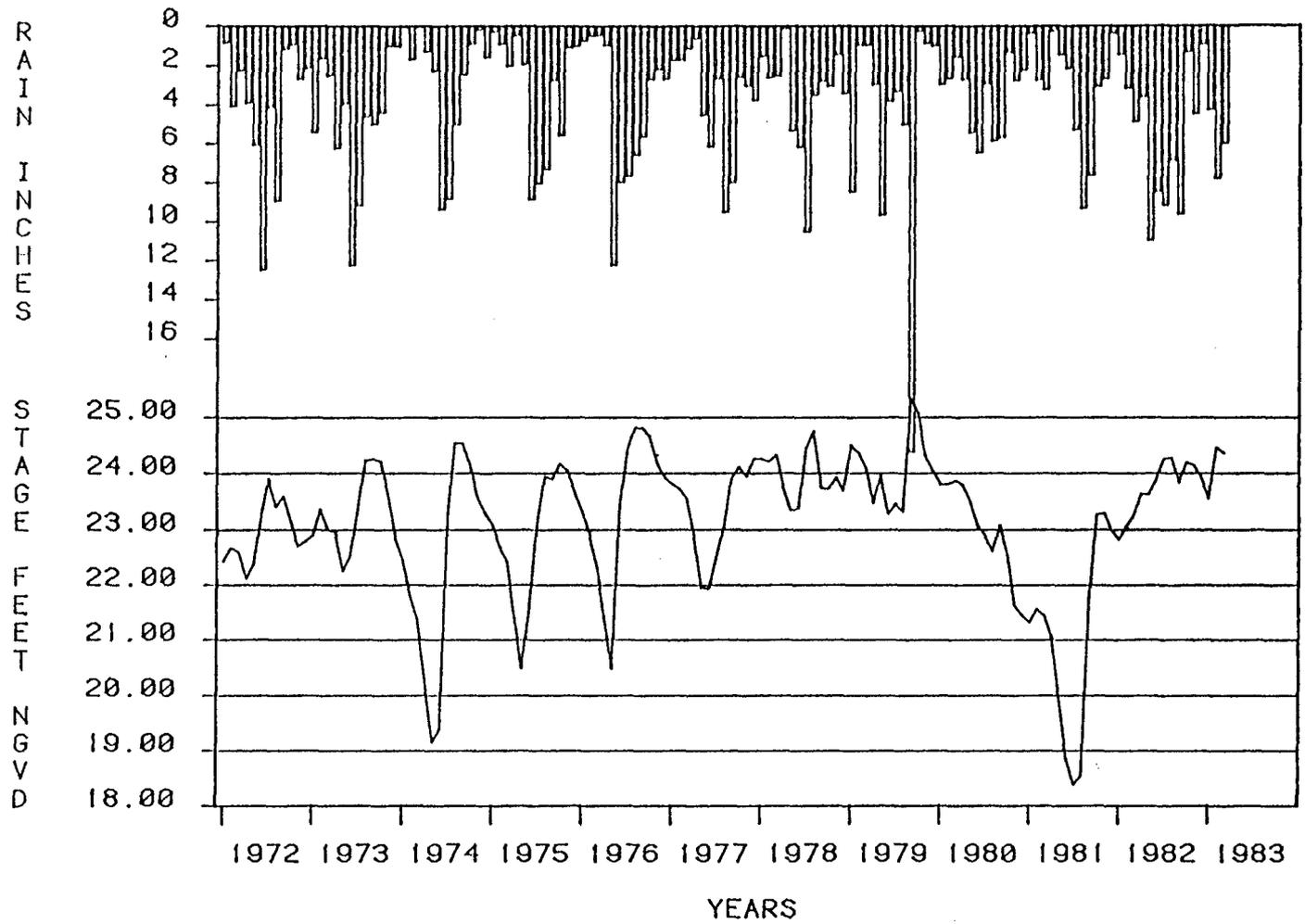
Figure 2. Variation in lake elevation and rainfall from 1972 - 1982.
Blue Cypress Lake, Florida.

sample) were also determined. Second, the entire data set was used to perform a gradient analysis using frequency of inundation (percent of time an elevation was equaled or exceeded by the lake elevation) as the environmental gradient. The progression of plant associations along the environmental gradient (the coenocline) was examined through construction of an association table in which samples were sorted by elevation and species by their median elevation of occurrence. The distributions of species along the coenocline were examined more closely by a graphical examination of the relationship between frequency of inundation and dry weight biomass. In this portion of the gradient analysis, the median biomass of a selected species, determined for data grouped over one percent intervals of frequency of inundation, was plotted against frequency of inundation. Before plotting, each series of medians was smoothed using running medians (4253H, Twice, Velleman and Hoaglin, 1981) and values between the smoothed points were interpolated by a local procedure (Akima, 1970). Lake elevation data utilized for gradient analyses were those obtained by a continuous recorder located at the lakeward end of the canal extending from Middleton's Fish Camp (USGS #02231400). Only those data for the previous ten years (October 1971 - September 1981) were used so that the time-scale of the hydrologic data would be pertinent to existing spatial patterns in the vegetation.

RESULTS

Transect

Forty-six macrophytic species were identified from the area within and adjacent to the belt transect (Table 1). A total of ninety-one samples, spanning an elevational range of 18.3 - 23.4 feet NGVD (Figure 3) and a range of frequency of inundation of 46 - 100 percent (Figure 4), were taken, yeilding quantitative data for 28 species. The other species were not represented in the quantitative samples either due to seasonal absence, low frequency of occurrence or intentional exclusion (eg. floating-leaved species, trees).

The six stations were distinct in several respects. The species list for each was unique (Table 1) as was the apportionment of the total living biomass among the species (Table 2). Station 1 was strongly dominated by Panicum hemitomon Schultes (hereafter Panicum) which exhibited a mean percentage of total biomass of 99, a high frequency of occurrence (85 %; Table 3) and a high mean biomass (284 g dry wt./m2; Table 4). Station 2 was also dominated by Panicum but its dominance as indicated by mean biomass (179 g dry wt./m2)), mean percentage of total biomass (36 %), and frequency of occurrence (65 %) was lower than for station 1. In addition to Panicum, station 2 contained substantial amounts of the opportunistic species Eupatorium capillifolium (Lam.) and Amaranthus australis (Gray) Sauer., and the perennial species Polygonum punctatum Ell. The opportunistic species were present because water levels were low due to the intense drought (Figure 2). Once water levels returned to normal these species, and the vines which dominated

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Table 1. List of species which occurred within or near the transect boundaries and the number of quantitative samples obtained for each species in each station. Species identifications were according to Godfrey and Wooten (1979, 1981), Lakela and Long (1976), or Radford et al. (1968). "-" indicates intentional exclusion of a species from the samples. St. Johns Marsh, southeast shore of Blue Cypress Lake, Florida, June 1981 - February 1982.

| TAXON | STATION | | | | | | TOTAL |
	1	2	3	4	5	6	
Osmundaceae							
Osmunda regalis (Willd.) Gray	0	0	9	18	8	5	40
Blechnaceae							
Woodwardia virginica (L.) Smith	0	0	0	0	0	0	0
Blechnum serratulatum L. C. Rich	0	0	0	0	4	1	5
Parkeriaceae							
Ceratopteris pteroides (Hook.) Heiron	-	-	-	-	-	-	-
Salviniaceae							
Salvinea rotundifolia Willd.	-	-	-	-	-	-	-
Taxodiaceae							
Taxodium distichum (L.) Richard	-	-	-	-	-	-	-
Typhaceae							
Typha sp.	0	1	0	0	0	0	1
Alismataceae							
Sagittaria lancifolia L.	0	2	0	1	0	0	3
Hydrocharitaceae							
Limnobium spongia (Bosc.) Steud.	-	-	-	-	-	-	-
Poaceae							
Sacciolepis striata (L.) Nash	0	0	0	0	0	0	0
Panicum hemitomon Schult.	17	13	0	5	0	0	35
unidentified grass	0	2	0	1	0	0	3
Cyperaceae							
Cyperus oderatus L.	0	4	0	0	0	0	4
Eleocharis sp.	0	8	0	0	0	0	8
Rhynchospora corniculata (Lam.) Gray	0	0	0	0	0	0	0
Rhynchospora inundata (Oakes) Fern.	0	0	0	0	0	0	0
Rhynchospora sp.	1	0	0	0	0	0	1
Cladium jamaicense Crantz	0	1	10	18	8	11	48
unidentified sedge	0	1	0	0	0	0	1
Araceae							
Peltandra virginica (L.) Schott and Endl.	0	0	1	4	0	1	6
Pistia stratiotes L.	0	1	0	0	0	0	1
Lemnaceae							
Lemna trisulca L.	-	-	-	-	-	-	-
Lemna minor L.	-	-	-	-	-	-	-

Table 1 (cont.). List of species which occurred within or near the transect boundaries and the number of quantitative samples obtained for each species in each station.

	STATION						
TAXON	1	2	3	4	5	6	TOTAL
Pontederiaceae							
Pontederia cordata L.	0	0	1	0	0	0	1
Eichhorinia crassipes (Mart.) Solms	0	0	0	0	0	0	0
Juncaceae							
Juncus sp.	0	1	0	0	0	0	1
Amaryllidaceae							
Crinum americanum L.	0	0	0	0	0	1	1
Haemodoraceae							
Lachnanthes caroliniana (Lam.)	0	5	0	0	0	0	5
Salicaceae							
Salix caroliniana Michx.	0	0	0	0	2	0	2
Urticaceae							
Boehmeria cylindrica (L.) Sw.	0	0	0	6	0	0	6
Polygonaceae							
Rumex verticillatus L.	0	0	0	0	0	0	0
Polygonum punctatum Ell.	0	11	1	5	1	0	18
Amaranthaceae							
Amaranthus australis (Gray) Sauer	0	14	0	0	0	0	14
Nymphaceae							
Nuphar luteum (L.) Sibth. and Sm.	0	0	0	0	0	0	0
Annonaceae							
Annona glabra L.	-	-	-	-	-	-	-
Aceraceae							
Acer rubrum L.	1	0	0	0	0	0	1
Malvaceae							
Kosteletskya virginica (L.) Presl.	0	0	4	12	5	1	22
Onagraceae							
Ludwigea alata Ell.	0	6	0	0	1	0	7
Apiaceae							
Hydrocotyl umbellata L.	0	0	0	1	0	0	1
Cicuta mexicana Coult. and Rose	0	0	0	0	0	0	0
Convulvulaceae							
Calystegia sepium (L.) R. Br.	0	0	7	0	0	0	7
Ipomoea alba L.	0	6	9	3	0	0	18
Rubiaceae							
Cephalanthus occidentalis L.	0	0	3	2	3	4	12
Asteraceae							
Eupatorium capillifolium (Lam.) Small	2	11	2	2	0	0	17
Pluchea purpurascens (Sw.) DC.	0	0	0	0	0	0	0
Baccharis halimifolia L.	0	0	0	1	0	0	1
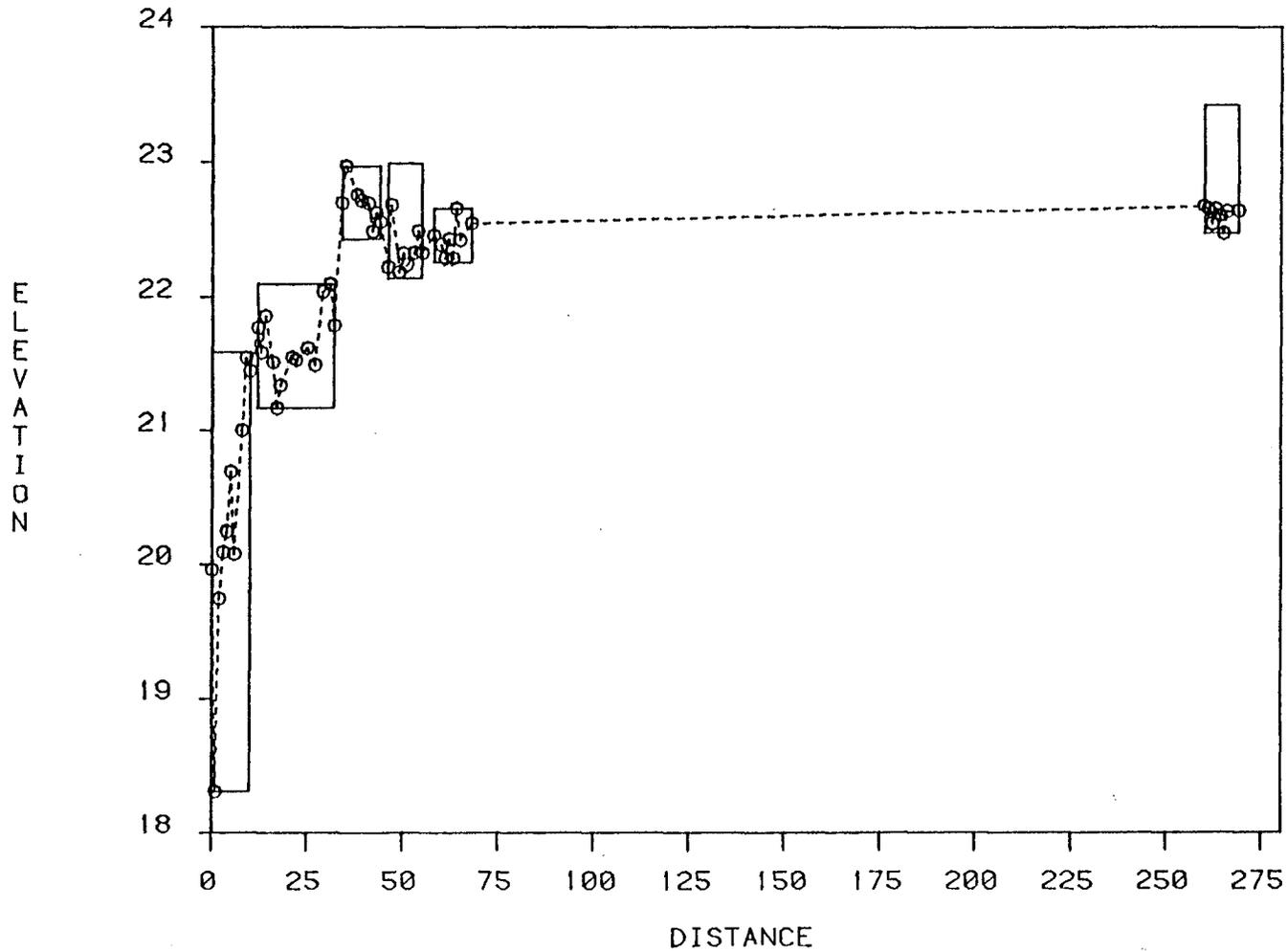
Figure 3. Variation in median elevation with respect to distance
from the water's edge along the belt transect. Boxes indicate the ranges
of distance and elevation for each station. St. Johns Marsh, southeast
shore of Blue Cypress Lake, Florida, June 1981 - February 1982.
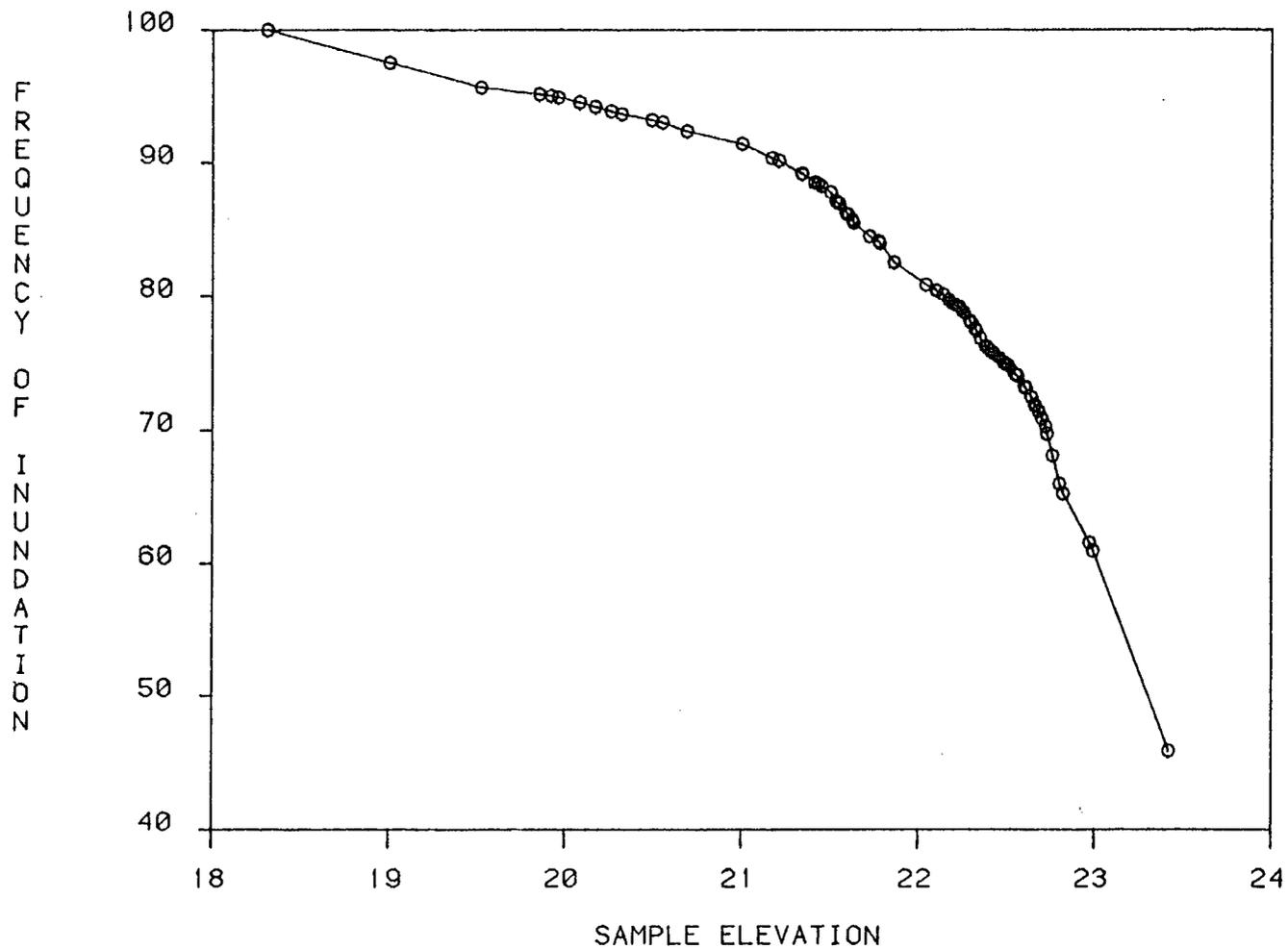
Figure 4. Percent time elevations sampled were equaled or exceeded
by lake elevations (frequency of inundation) from October 1, 1971 -
September 30, 1981. Sample elevations indicated by open circles. St.
Johns Marsh, southeast shore of Blue Cypress Lake, Florida.

Table 2. Mean percentage of the total living, above-ground dry biomass for the fifteen species most common on the transect. The standard deviation and other statistics are given in Appendix A. St. Johns Marsh southeast shore of Blue Cypress Lake, Florida, June 1981 - February 1982.

SPECIES	STATION					
	1	2	3	4	5	6
C. jamaicense	0.00	5.00	6.64	51.57	40.00	90.87
O. regalis	0.00	0.00	16.42	11.08	51.76	3.48
P. hemitomon	99.17	36.37	0.00	0.07	0.00	0.00
K. virginica	0.00	0.00	0.36	18.54	0.20	0.00
P. punctatum	0.00	9.22	0.73	0.54	0.08	0.00
I. alba	0.00	1.30	32.40	0.39	0.00	0.00
E. capillifolium	0.53	29.51	0.00	1.57	0.00	0.00
A. australis	0.00	12.92	0.00	0.00	0.00	0.00
C. occidentalis	0.00	0.00	7.68	0.10	0.00	4.86
C. sepium	0.00	0.00	29.83	0.00	0.00	0.00
L. alata	0.00	1.29	0.00	0.00	0.62	0.00
P. virginica	0.00	0.00	4.20	0.25	0.00	0.11
B. cylindrica	0.00	0.00	0.00	7.48	0.00	0.00
B. serratulatum	0.00	0.00	0.00	3.40	7.33	0.00
L. caroliniana	0.00	0.36	0.00	0.00	0.00	0.00

Table 3. Frequency of occurrence (percent) for the fifteen species most common on the transect. St. Johns Marsh southeast shore of Blue Cypress Lake, Florida, June 1981 - February 1982.

	STATION					
SPECIES	1	2	3	4	5	6
C. jamaicense	0	5	100	90	80	100
O. regalis	0	0	90	90	80	45
P. hemitomon	85	65	0	25	0	0
K. virginica	0	0	40	60	50	9
P. punctatum	0	55	10	25	10	0
I. alba	0	30	90	15	0	0
E. capillifolium	10	55	20	10	0	0
A. australis	0	70	0	0	0	0
C. occidentalis	0	0	30	10	30	36
C. sepium	0	0	70	0	0	0
L. alata	0	30	0	0	10	0
P. virginica	0	0	10	20	0	9
B. cylindrica	0	0	0	30	0	0
B. serratulatum	0	0	0	20	10	0
L. caroliniana	0	25	0	0	0	0

Table 4. Mean living, above-ground, dry biomass for the fifteen species most common on the transect. The standard deviation and other statistics are given in Appendix B. St. Johns Marsh southeast shore of Blue Cypress Lake, Florida, June 1981 - February 1982.

			STATION			
SPECIES	1	2	3	4	5	6
C. jamaicense	0.00	20.93	24.28	797.92	182.40	492.20
O. regalis	0.00	0.00	42.15	48.82	104.24	11.31
P. hemitomon	284.24	178.84	0.00	0.44	0.00	0.00
K. virginica	0.00	0.00	2.24	138.21	0.08	0.00
P. punctatum	0.00	39.72	1.44	4.60	0.24	0.00
I. alba	0.00	2.16	59.85	1.33	0.00	0.00
E. capillifolium	2.65	196.21	0.00	11.37	0.00	0.00
A. australis	0.00	37.20	0.00	0.00	0.00	0.00
C. occidentalis	0.00	0.00	56.00	2.02	0.00	29.20
C. sepium	0.00	0.00	56.88	0.00	0.00	0.00
L. alata	0.00	6.93	0.00	0.00	1.96	0.00
P. virginica	0.00	0.00	9.52	1.23	0.00	0.47
B. cylindrica	0.00	0.00	0.00	53.94	0.00	0.00
B. serratulatum	0.00	0.00	0.00	33.08	10.56	0.00
L. caroliniana	0.00	1.04	0.00	0.00	0.00	0.00

station 3, were eliminated. In station 3 the herbaceous vines Ipomoea alba L. and Calystegia sepium (L.) R. Brown accounted for the greatest portion of the biomass (117 g dry wt./m2, 62 %) and, probably through the exclusion of light, were killing the understory of wetland species such as Cladium. During the study, the height of Cladium in station 3 visably declined as it died and collapsed under the weight of the vines. By the time normal water levels eliminated the vines, most culms of Cladium in station 3 appeared to be dead. Cladium accounted for 52 percent of the biomass of station 4 (798 g dry wt./m2) and probably also dominated (in sensu Hurlbert, 1971) station 5 although the largest mean percentage of the total biomass (52 %,104 g dry wt./m2) was accounted for by Osmunda regalis (Willd.) Gray. Station 6 was a nearly monospecific stand of Cladium with a relatively high mean biomass (492 g dry wt./m2) and high mean percentage of the total biomass (91 %) and frequency of occurrence (100 %).

Biomass and frequency data allow identification of a species which was most characteristic of the lake shore zone represented by each station. Beginning with the zone closest to the lake's edge these species were Panicum, E. capillifolium, I. alba, Kosteletskya virginica (L.) Presl., O. regalis and Cladium. The floristic distinctions among zones were emphasized by the drought. During normal years, when species such as E. capillifolium and I. alba would be absent as adults, delineation of zones 1-3 might depend upon more subtle differences, such as species density, the density of dominant species or the presence of less obvious wetland perennials (eg. P. punctatum in station 2).

There were distinctions among stations even if compositional

differences are ignored. Because the sample area was the same for stations 3 - 6, comparisons of species density (number of species/sample) can be made (Table 5). There was a statistically significant (t-test, Ho:u_1.NE.u_2, t=5.248, 13 degrees freedom, p<0.001) decline in mean species density for these stations from a maximum of 5 (station 3) to a minimum of 2 (station 6). A similar trend existed for species richness (total number of species/station) for those stations in which the total area sampled was roughly equivalent (stations 3, 5 and 6). Despite the fact that the sample area and the total area sampled were both minimal for station 1, the low species richness, low mean species density, and high dominance of <u>Panicum</u> in terms of biomass (see above) indicate that its comparatively low variety of species was not a sampling artifact. These same statistics indicate that the species variety of station 2 was at least as great as that of stations 3 and 4. Taken as a whole these data support the subjective assessment I made in the field, that the variety of species decreased near the ends of the transect.

A single distinction among stations can be made in terms of total biomass (Table 6). The highest mean biomass (1103 g dry wt./m2) occurred in station 4 and was significantly greater (t test, Ho: u_1.ne.u_2, t=3.342, 28 degrees freedom, p<0.005) than the minimum biomass (288 g dry wt/ m2) which occurred in station 1.

The distribution of species with respect to elevation and frequency of inundation (Table 7) indicates that station differences were correlated with an inundation gradient caused by topographic relief. The minimum elevation supporting <u>Panicum</u> (19.5 ft. NGVD) marked the lakeward border of emergent vegetation and corresponded to an inundation frequency

Table 5. Total number of species and descriptive statistics for species density for each station. St. Johns Marsh, southeast shore of Blue Cypress Lake, Florida, June 1981 - February 1982.

STATION	N	TOTAL	MEAN	STD	MAX	MIN	AREA PER SAMPLE	TOTAL AREA SAMPLED
1	20	5	1.10	0.72	3	0	0.0491	0.9817
2	20	16	4.35	2.39	9	1	0.1963	3.9270
3	10	11	5.00	1.56	8	2	0.2500	2.5000
4	20	15	4.15	1.98	8	1	0.2500	5.0000
5	10	8	2.90	1.52	5	1	0.2500	2.5000
6	11	6	2.09	0.83	3	1	0.2500	2.7500

Table 6. Descriptive statistics for total living, above-ground, dry biomass for each station. St. Johns Marsh, southeast shore of Blue Cypress Lake, Florida, June 1981 - February 1982.

STATION	N	MEAN	STD	MAX	MIN
1	19	287.57	295.63	823.03	0.00
2	20	498.80	367.03	1375.09	9.17
3	10	347.68	251.74	882.40	78.40
4	20	1103.10	1125.50	3923.84	15.60
5	10	330.02	330.58	1044.80	39.20
6	11	487.89	391.43	1236.00	23.20

of 96 percent. From the lakeward border of emergent vegetation to approximately 21 ft. NGVD (91 % inundation) only Panicum was represented in the samples, this corresponds to the nearly monotypic stand of station 1. Proceeding up the elevation gradient, the species density increased markedly so that from 21-22 ft. NGVD (91 - 81 % inundation; station 2) an additional 18 species occurred. The addition of species caused median species density to increase over the same range of elevation from 1 to >4 (Figure 5). Some of this increase was undoubtedly due to increases in sample area (see Table 5) but the use of a larger quadrat within the Panicum zone (Station 1) would have yielded very few additional species due to the extremely monotypic nature of the stand. Cladium was distributed from approximately 22 ft. NGVD (80 % inundation) to the maximum elevation sampled (23.4 ft. NGVD, 46 % inundation). Coincident with the appearance of Cladium the species assemblage changed rather abruptly. Of the 20 species recorded from 19.5 - 22.0 ft. NGVD, only 7 remained at 22.5 ft. NGVD (75 % inundation) and the distributions of none extended to 23.0 ft. NGVD (61 % inundation). The disappearance of these species from higher elevations was probably due to monopolization of space and light by Cladium. Species which occurred with Cladium were either able to grow above it (eg. Salix caroliniana Michaux) or tolerate shading (eg. O. regalis). They were most prevalent where Cladium grew as large, widely spaced tussocks. This growth form was characteristic of stations 4 and 5 which had lower mean elevations than did station 6 where Cladium density was so great that space for other species was virtually non-existant. The strong dominance of Cladium probably accounted for the decline in maximum species density from approximately 22.5 ft. NGVD

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Table 7. Species association table sorted by median elevation of occurrence for species and by elevation for samples. Species names truncated at ten characters. "x" indicates presence, "." indicates absence within the elevational range over which the species occurred, " " indicates absence outside the elevational range over which the species occurred. St. Johns Marsh, southeast shore of Blue Cypress Lake, Florida, June 1981-February 1982.

STA	XLOC	YLOC	ELEV	PERCENT
6	21	4	23.42	45.88
4	40	1	22.99	60.96
3	30	1	22.97	61.57
3	6	9	22.82	65.29
3	39	7	22.80	66.00
3	6	4	22.76	68.14
4	25	9	22.73	69.75
3	15	5	22.72	70.30
3	4	0	22.70	70.87
6	18	0	22.68	71.42
6	13	9	22.68	71.42
4	36	8	22.66	71.89
5	5	6	22.66	71.89
6	13	1	22.66	71.89
6	19	3	22.66	71.89
6	34	6	22.64	72.49
6	36	4	22.61	73.17
6	39	7	22.61	73.17
3	27	7	22.60	73.31
5	18	4	22.60	73.31
3	12	10	22.56	74.08
4	4	9	22.55	74.24
5	14	10	22.55	74.24
4	0	2	22.55	74.24
6	18	4	22.51	74.87
5	13	7	22.50	74.95
3	33	8	22.49	75.03
6	18	5	22.48	75.17
5	37	0	22.44	75.44
3	27	0	22.43	75.75
4	34	4	22.42	75.84
4	27	9	22.41	75.94
4	27	7	22.40	76.10
5	21	2	22.39	76.21
4	3	1	22.38	76.32
5	5	7	22.35	76.92
4	14	9	22.33	77.47
4	18	7	22.33	77.17
4	34	8	22.32	77.63
4	11	0	22.30	77.99
5	4	5	22.29	78.24
5	23	3	22.29	79.24
5	2	4	22.26	79.81
4	20	0	22.25	79.92
4	17	5	22.24	79.14
4	6	4	22.23	79.28
4	2	9	22.22	79.33
1	0	0	22.20	79.44
4	14	3	22.19	79.50
4	34	7	22.17	79.74
4	6	9	22.14	80.13
2	0	19	22.10	80.13
2	2	17	22.04	80.87
2	20	29	21.86	82.53
2	2	2	21.86	82.53
2	19	15	21.78	83.93
2	1	0	21.77	84.10
2	18	20	21.72	84.48
2	12	13	21.63	85.40
2	15	4	21.62	85.71
2	3	13	21.62	85.71
2	2	4	21.60	86.07
1	1	9	21.59	86.20
2	0	1	21.59	86.20
1	1	8	21.55	86.94
2	9	9	21.55	86.94
1	10	10	21.54	87.02
2	19	10	21.53	87.13
1	9	0	21.50	87.79
1	39	10	21.45	88.23
2	16	4	21.13	88.42
1	12	10	21.41	88.53
2	20	13	21.11	88.53
2	7	4	21.34	89.19
2	13	4	21.34	89.19
2	7	15	21.21	90.15
2	8	5	21.17	90.36
1	39	8	21.00	91.43
1	13	5	20.49	92.39
1	34	6	20.55	93.07
1	6	2	20.49	93.24
1	39	4	20.32	93.70
1	25	3	20.26	93.90
1	21	4	20.17	94.22
1	14	6	20.09	94.58
1	0	0	19.94	94.94
1	30	3	19.90	95.07
1	34	6	19.85	95.18
1	21	9	19.53	95.70
1	18	2	19.00	97.56
1	27	1	19.11	100.00

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Figure 5. Variation in median species density with respect to frequency of inundation (percent). St. Johns Marsh, southeast shore of Blue Cypress Lake, Florida, June 1981 - February 1982.

(75 % inundation) to 23.4 ft. NGVD (46 % inundation). Before the drought

C. jamaicense probably also dominated station 3, but the mortality which

resulted from the profuse growth of vines allowed by the drought may

result in its density in this zone being low for a considerable time.

The basis for vegetative patterns can be more clearly discerned

through examination of species distributions as indicated by a

quantitative, continuous variable, such as biomass, than by examination

of changes in the composition of species assemblages as indicated by

presence-absence data. This is because the distribution of a continuous

variable, such as biomass, indicates not only distributional limits but

also distributional optima, the optima being those points where maxima

are attained. For each species adequately sampled, the distribution of

biomass was roughly Gaussian and indicated a marked optimum with respect

to frequency of inundation (Figures 6 and 7). The species sequence

indicated by biomass optima closely parallels the sequence of the

association table (Table 7). Proceeding down the inundation gradient,

successive optima occurred for Ludwigea alata Ell. (88 %), Panicum

(87 %), P. punctatum (84 %), E. cappilifolium (84 %), O. regalis (77 %),

the vines I. alba and C. sepium (70 & 72 %, respectively), and Cladium

(<60 %). Total biomass reached a broad maximum from 80 - 85 % inundation

and showed a smaller peak at approximately 73 % inundation (Figure 8).

The overall maximum for total biomass indicated for less than 60 %

inundation was due to two large samples of Cladium and, due to the small

number of samples in this range, should be considered very tentative.

Sincock (1959) did find, however, that Cladium attained its highest

frequency of occurrence in the basin at elevations with a frequency of
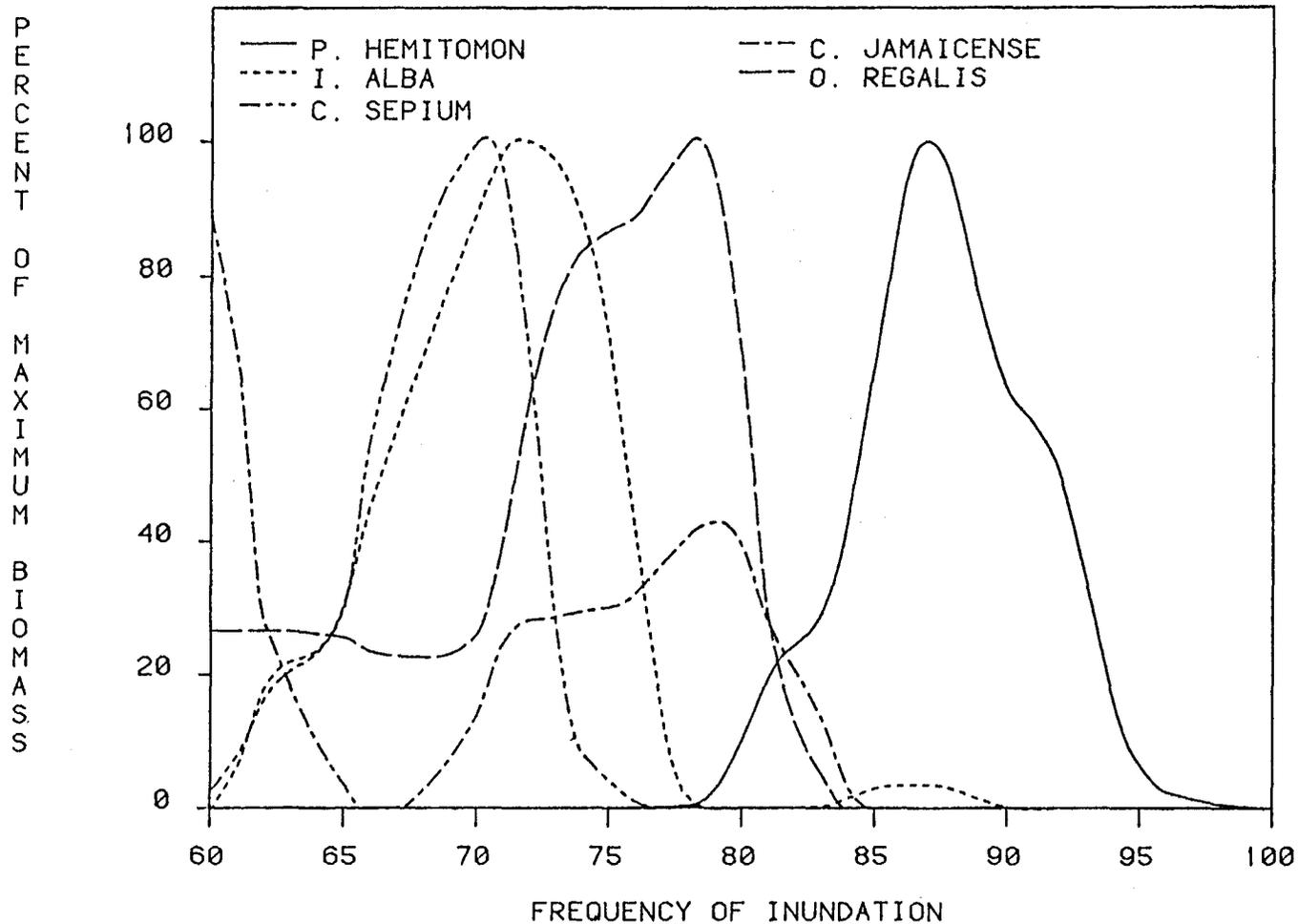
Figure 6. Variation in median living, above-ground, dry biomass of dominant species with respect to frequency of inundation (percent). Medians were smoothed by running medians (4253H, Twice, Velleman and Hoaglin, 1981). Intermediate values were interpolated using the local procedure of Akima (1970). St. Johns Marsh, southeast shore of Blue Cypress Lake, Florida, June 1981 - February 1982.

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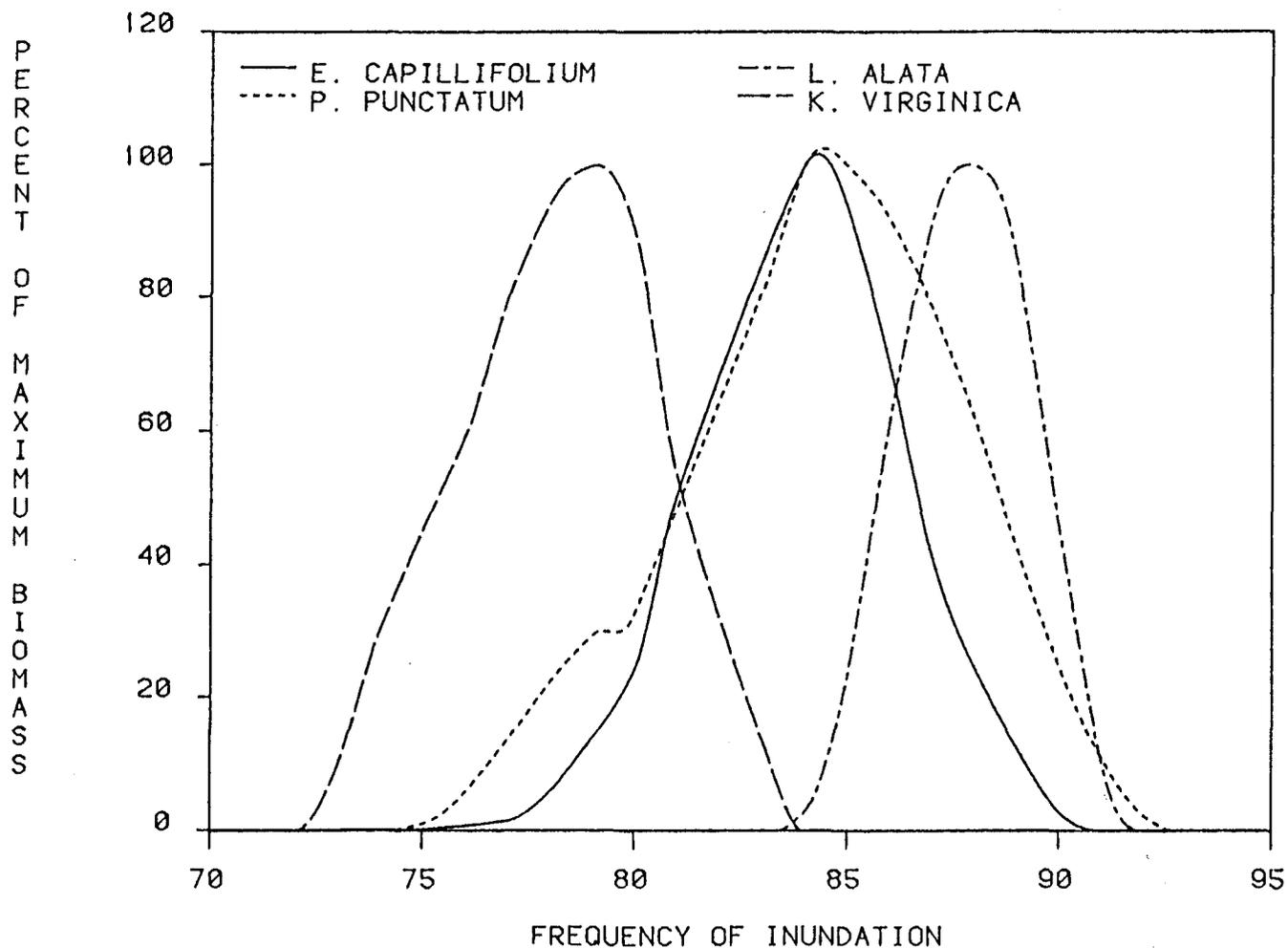
Figure 7. Variation in median living, above-ground, dry biomass of sub-dominant species with respect to frequency of inundation (percent). Medians were smoothed by running medians (4235H, Twice, Velleman and Hoaglin, 1981). Intermediate values were interpolated using the local procedure of Akima (1970). St. Johns Marsh, southeast shore of Blue Cypress Lake, Florida, June 1981 - February 1982.
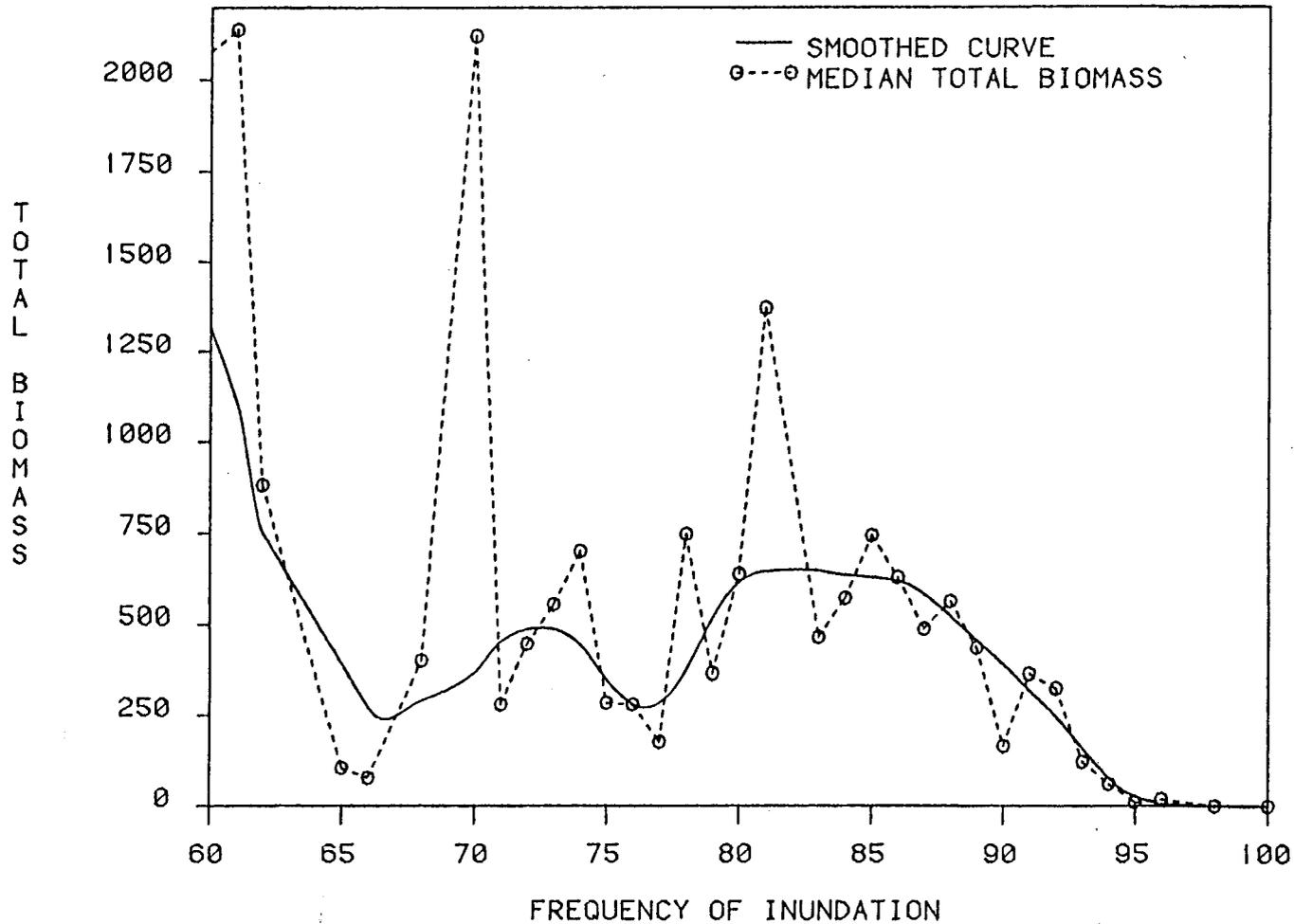
Figure 8. Variation in median total living, above-ground dry biomass with respect to frequency of inundation (percent). Medians were smoothed by running medians (4235H, Twice, Velleman and Hoaglin, 1981). Intermediate values were interpolated using the local procedure of Akima (1970). St. Johns Marsh, southeast shore of Blue Cypress Lake, Florida, June 1981 - February 1982.

inundation of approximately 45 %.

The positive correlation between species sequences determined by biomass maxima and by median elevation of occurrence (the sorting criterion for the association table) suggests that the order of species along the hydrologic gradient can be assessed more easily, but adequately, by reliance on frequency, rather than biomass data. In this case the correlation of sequences by the two methods was, statistically, highly significant (Spearmans Rank Correlation Coefficient = 0.86; $p < 0.01$).

Aerial Survey

Of the total area surveyed, (66,352 acres), 34 percent (22,784 acres) was accounted for by various land uses (primarily agriculture), 59 percent (38,816 acres) by non-agricultural vegetative communities and 11 percent (7,614 acres) by water bodies lacking emergent vegetation (Table 8). Most of the non-agricultural vegetation was herbaceous marsh (25,883 acres, 67 %). Other non-agricultural vegetation was forest (10,071 acres, 26 %), thicket (shrubs and palmetto prairie; 2,862 acres, 4 %) or floating plants (68 acres,0.90 %). Forests were primarily associated with upland tributaries whereas marsh communities existed where the flat topography would yield little or no water flow.

For herbaceous marsh, the banded pattern of vegetation near the lake shore was replaced by a community mozaic on the marsh flat (Figure 9). The mozaic was primarily comprised of five communities: 1) Panicum prairie, 2) dense Cladium, 3) myrtle head, 4) Cladium/Salix association and 5) slough. These communities covered 23,852 acres (92 %) of the marsh.

Panicum prairie was the most abundant community of the marsh (9,621 acres, 37 % of marsh acreage). In most areas, Panicum was the dominant species in terms of relative cover. In some areas other common species, such as Sagittaria lancifolia L. and Cephalanthus occidentalis L., shared dominance with Panicum. Other species which were observed in Panicum prairie were Peltandra virginica (L.) Kunth, Crinum americanum L., Lachnanthes caroliniana (Lam.) Dandy, Erianthus strictus Baldwin., Pontederia cordata L., P. punctatum, Nymphaea ordorata Aiton, Bidens, mitis (Michaux) Sherff., Cyperus haspan L., and Pluchea longifolia Nash.

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Table 8. A classification of land-uses and natural vegetation of the St. Johns Marsh between the Florida Turnpike and Fellsmere Grade. Percentages for each category are hierarchical and relative to the total acreage of the next highest category. Classification and acreages were determined from color infra-red, aerial photographs obtained and entitated by the Florida Department of Transportation. Photographs were taken from an altitude of 6,000 ft. on March 20, 1981.

CATEGORY	ACREAGE	PERCENTAGE
I. Land uses	19922	30.02
A. Improved pasture	19393	97.34
B. Roads	225	1.13
C. Citrus	211	1.06
D. Land in transition	68	0.34
E. Residential	25	0.13
II. Vegetation	38816	58.50
A. Forest	10071	25.95
1. Hardwood Swamp	3516	34.91
2. Mixed hardwood	3091	30.69
3. Cypress	1580	15.69
4. Pine flatwood	856	8.50
5. Cabbage palm wood	642	6.37
6. Mixed hardwood-Panicum-Cephalanthus	185	1.84
7. Unidentified hardwood	185	1.84
8. Upland temperate hammock	16	0.16
B. Marsh	25883	66.67
1. Panicum prairie	9621	37.18
2. Dense Cladium	5936	22.94
3. Myrtle head	3917	15.14
4. Cladium/Salix association	3368	13.01
5. Slough	1010	3.90
6. Dense Typha	932	3.60
7. Panicum/Myrtle head association	796	3.08
8. Dense E. capillifolium	160	0.62
9. Undetermined	143	0.55
C. Other	2862	4.31
1. Shrub	2106	73.58
2. Palmetto prairie	756	26.42

Table 8 (cont.). A classification of land-uses and natural vegetation of the St. Johns Marsh between the Florida Turnpike and Fellsmere Grade.

CATEGORY	ACREAGE	PERCENTAGE
III. Water bodies and floating vegetation	7614	11.48
A. Lake	7025	92.26
B. Stream or waterway	521	6.84
C. Water hyacinth	66	0.87
D. Water lettuce	2	0.03
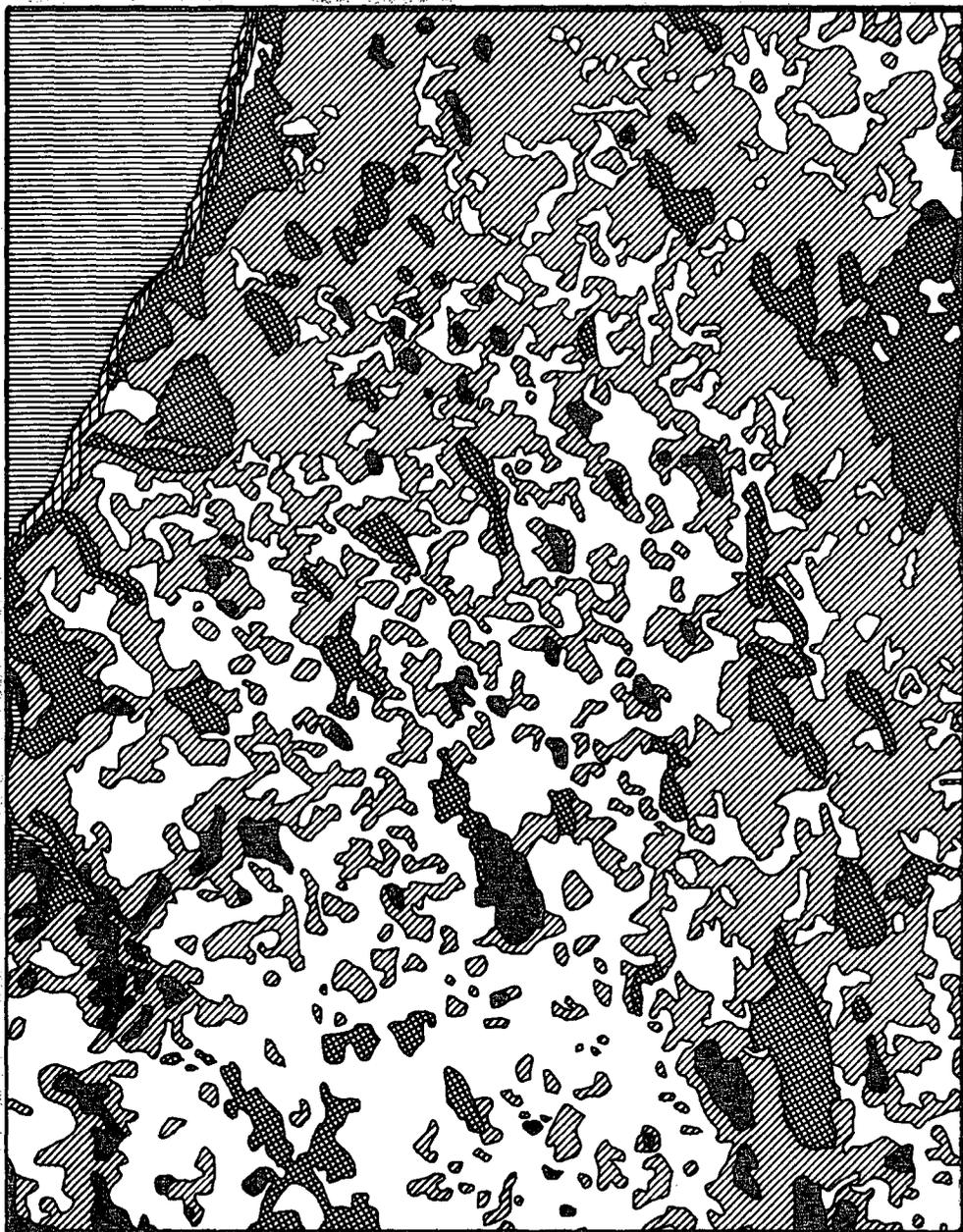
PANICUM PRARIE

PANICUM ZONE
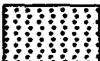
EUPATORIUM ZONE

WATER
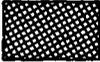
CLADIUM/SALIX

DENSE CLADIUM

IPOMOEA ZONE

MYRTLE HEAD

N

SCALE 1:24000

1/2 1/4 0   1/2 MILE

Figure 9. Distribution of floodplain plant communities of the St. Johns Marsh adjacent to the southeast shore of Blue Cypress Lake. Determined from infra-red, aerial photographs obtained and partly interpreted by the Florida Department of Transportation. Photographs taken from an altitude of 6,000 feet on March 20, 1981.

This community is apparently quite similar to the wet prairie community dominated by Panicum which occupies large areas in the northern Everglades (Loveless, 1959; Goodrick, 1974). As has been observed in the Everglades, the transition between prairies and the next community discussed, dense Cladium, was typically abrupt.

The dense Cladium community, which consisted of almost pure stands of Cladium, was second to Panicum prairie in its areal extent (5,936 acres, 23 % of the marsh). No emergent macrophyte other than Cladium was abundant but some species, such as S. lancifolia, P. virginica, O. regalis, S. caroliniana, and C. occidentalis, occurred with low densities. This community was examined in detail on the transect (station 6). It commonly exhibited a broad, graded transition to the Cladium/Salix association apparently correlated with increasing frequency and depth of inundation.

Cladium usually dominated the Cladium/Salix association which covered 13 % of the marsh (3,368 acres). In this community, Cladium was typically taller and more clumped in its distribution than in the dense Cladium community. The clumped distribution left open areas between the large tussocks which allowed a greater variety of species than in dense Cladium. Species which commonly occurred in addition to those found in dense Cladium stands included S. caroliniana, K. virginica, Boehmeria cylindrica (L.) Swartz, Blechnum serratulatum L. C. Rich, Ludwigia alata Ell., and Acer rubrum L. This community is represented by stations 4 and 5 of the transect. It exhibited a smooth transition to myrtle head which apparently corresponded to a gradient of decreasing depth and frequency of inundation.

Cladium was well represented in the myrtle head community but did not dominate due to the presence of larger, woody species. This community, typically dominated by some combination of Myrica cerifera L., S. caroliniana, C. occidentalis, and A. rubrum, accounted for 15 % of the marsh (3917 acres) and was associated with raised areas, transitional areas from marsh to forest, and disturbed areas such as the borders of canals.

There was a gentle decline in elevation of the marsh from west to east. As a result, mean depth and hydroperiod probably also increased in this direction. This was probably the basis for the replacement of typical marsh flat communities by the slough community on the east side of the marsh. The slough community, typically dominated by Nymphaea odorata Aiton and Utricularia spp., was distributed over 4 % of the marsh. Other species which commonly occurred in the slough community were S. lancifolia, Panicum and Limnobium spongia (Bosc.) Steudel.

Most of the forested area surveyed (9,685 acres, 96 %) was accounted for by five communities: 1) hardwood swamp, 2) mixed hardwood, 3) cypress swamp, 4) pine flatwood and 5) cabbage palm wood.

The hardwood and cypress swamp communities apparently formed a continuum from areas of shorter to longer hydroperiod (duration of inundation), respectively. Thus, cypress swamp was largely confined to the border of the lake and deeper areas of tributaries. It accounted for 16 % (1,580 acres) of the forested area and was dominated by Taxodium distichum (L.) Richard with other tree species (eg. Fraxinus caroliniana Miller and Sabal palmetto Lodd. ex Schultes) being present at low densities. Hardwood swamp covered 35 % (3,516 acres) of the forested

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area and was dominated by _A. rubrum, _F. caroliniana and _T. distichum.

The mixed hardwood community was largely confined to artificially drained areas behind levees. In the single area examined, it was dominated by _A. rubrum and Ilex cassine L. Thirty-one percent (3,091 acres) of the forested area was mixed hardwood.

Pine flatwood and cabbage palms accounted for 856 (8.5 % of forested area) and 642 (6.4 %) acres, respectively. Cabbage palms occurred within the swamp communities of Fort Drum Creek and on agricultural lands. Pine flatwood occurred primarily on Hog and Sick Islands in Fort Drum Creek and on pastures. The species composition of these communities was not examined.

DISCUSSION

The St. Johns Marsh is botanically similar to the Everglades in several respects: 1) The dominant species over large areas is Cladium and species commonly associated with Cladium in the marsh are also associated with Cladium in the Everglades (eg. S. lancifolia, P. cordata, C. occidentalis, S. caroliniana, P. virginica and O. regalis, Davis, 1943, Loveless, 1959). 2) In both areas, sawgrass communities are interrupted by graminoid wet prairies. In areas of the Everglades these wet prairies are dominated by Panicum (Loveless, 1959; Goodrick 1974) and are floristically similar to the Panicum prairies here described. 3) Both areas are dotted by tree islands, which occur on high areas and sloughs, which occur on low areas. The sloughs have a similar flora but the tree islands are in many cases floristically distinct because tree islands in the Everglades are commonly dominated by subtropical species (Craighead 1971, 1974).

The floristic and physiognomic similarities of vegetation of the St. Johns Marsh and Everglades are not surprising given their geographic proximity and geologic similarity. The importance of recognizing their similarity is that observations on the ecological consequences of altered hydrology in the Everglades (Davis, 1949; Loveless, 1959; Dineen, 1972; Alexander and Crook, 1974) can facilitate management decisions regarding marshes of the upper St. Johns. This is not to say that site-specific studies within the upper basin are not required but rather that, in the absence of site-specific data, approximations can be drawn from appropriate studies in the Everglades.

The seminal premise of this work was that the spatial heterogeneity of vegetation in the upper St. Johns Marsh is largely determined by spatial variation in hydrologic conditions due to topographic relief. This supposition is supported by the relationships between frequency of inundation, elevation and vegetation observed on the transect. Numbers and kinds of species varied continuously with both elevation and frequency of inundation as did the above-ground biomass of individual species. This resulted in a zoned pattern in the vegetation correlated with recognizable features of the lake shore. The Panicum zone (station 1) included the lowest elevation sampled and was the zone most exposed to wave action. The Panicum, Eupatorium (station 2) and Ipomoea (station 3) zones together formed a coenocline along the moderate slope of the shore to the lake's berm. Behind the berm, Cladium was highly dominant and species variety was low. At higher frequencies of inundation, (lower elevations) the growth form of Cladium was markedly clumped and other species, such as O. regalis (station 5) and K. virginica (station 4), were common. At lower frequencies of inundation, Cladium grew so densely that other species were excluded (station 6). On a broader scale, the emergent marsh graded to floating-leaved marshed as elevations declined (this transition occurred across the marsh flat from west to east or towards the lake shore) or to tree island communities as elevations increased.

An implication of these relationships is that modification of the hydrological cycle of the marsh would alter the spatial pattern of the vegetation. This conclusion is supported by long-term observations of the effects of hydrologic changes in the Everglades (Craighead, 1971;

Alexander and Crook, 1974) and by quantitative sampling of a wetland coenocline in Iowa (van der Valk and Davis, 1976). The relationship between vegetation and hydrology is particularly important in an area such as the St. Johns Marsh where, because of its flat topography, most acreage lies within the narrow range of elevation of the marsh flat (22-24 feet NGVD in the area studied). The movement of species into or out of this elevational range, or a change in dominance within this range, would result in significant vegetational changes over thousands of acres. Considering the central role of vegetation in the implementation of wetland functions (Mitchell, D. S., 1974; Greeson et al., 1979), this would be expected to have profound ecological effects.

The relationship between the spatial distribution of a species and hydrology is complex and undoubtedly varies with the species. Although some distributional phenomena may primarily reflect physiological tolerances (eg. the lakeward distribution of P. punctatum), most probably result from variation in the competitive balance among species along the hydrologic gradient. For example, the dominance of Panicum over large areas of the marsh flat indicates that its physiological range is broader than was indicated by its distribution along the transect. Field observations and biomass distributions (Figure 5) suggest that Panicum was absent at lower frequencies of inundation due to competitive exclusion by Cladium. Panicum may exist on the marsh flat only where competition with Cladium can be avoided as, for instance, in areas where fire has eliminated Cladium. Because competition was a pervasive factor in this work, the distributional optima and limits must be considered ecological phenomena specific to the area studied rather than

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physiological phenomena of broader applicability.

Frequency of inundation is an indicator of a variety of hydrologic factors. A gradient in frequency of inundation is, thus, a complex gradient (sensu Whittaker, 1967), along which many factors vary together, as opposed to a factor-gradient, along which a single factor varies. The lakeward distribution of Panicum, for example, may be primarily determined by depth or wave action rather than frequency of inundation, per se. Moreover, although the distribution of vegetatively reproducing perennials, such as Panicum and Cladium, probably reflect long-term hydrologic parameters, such as frequency of inundation or mean depth, the distributions of other species may depend upon extreme events of relatively short duration. This is particularly true for species which cannot survive both soil exposure and inundation as adults. For these species, hydrologic conditions act as an environmental sieve (van der Valk, 1981). As fluctuation between the alternative states of exposure and inundation occurs, the nature of the sieve changes and species enter, or are eliminated from the wetland environment. Hydrologic conditions thus determine the suite of species present in a wetland at any given time. As emphasized by van der Valk (1981), species which can not survive both inundation and drawdown rely on seed banks or seed dispersal for maintenance of their populations. For many of these species (eg. E. capillifolium, A. australis) the influence of hydrology on temporal patterns of abundance is probably more important than its influence on spatial patterns. Long-term hydrology may, however, cause spatial gradients in seed bank density and viability which are later expressed in the spatial patterns of adult populations.

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In this work, several species were present during sampling (eg. $\underline{I}$. $\underline{alba}$, $\underline{C}$. $\underline{sepium}$, $\underline{E}$. $\underline{capillifolium}$, $\underline{A}$. $\underline{australis}$) which were eliminated when water levels rose. Because of the temporal instability of populations of these species, the relationships between their distributions and frequency of inundation may be misleading. For example, the distributions of $\underline{I}$. $\underline{alba}$ and $\underline{C}$. $\underline{sepium}$ probably reflected an age gradient from their centers of dispersal rather than a gradient of frequency of inundation. These species apparently became established along a seed line located on the berm of the lake. This was indicated by their absence elsewhere in the marsh and the centering of their distributions about the berm of the lake. Seeds floating in the lake were apparently deposited on the berm as water levels fell. The width of the zone they occupied at the time of sampling was thus determined by growth rates and the time available for growth. As would be expected, biomass was greatest in the center of the zone where there had been the longest time for growth.

Many environmental factors other than hydrology affect the temporal and spatial distribution of wetland plants. Notable among these are soils and fire. The relative importance of hydrology in determination of vegetational patterns would be expected to decline as the depth and duration of inundation decline and the physiological stresses caused by inundation become less severe. The low mean depth of most of the St. Johns Marsh thus diminishes the relative importance of hydrology in shaping vegetational patterns. More importantly, hydrology can not account for spatial patterns perpendicular to hydrologic gradients. Because topographic relief is very slight in the St. Johns Marsh, much of

the vegetational pattern on the marsh flat is nearly perpendicular to hydrologic gradients. Variation in hydrologic conditions would probably determine only broad, graded variation in the vegetation except where topographic relief is greater than that which is typical as, for example, near levees, the lake shore and tree islands. Thus, the vegetation mosaic formed by the dense Cladium and Panicum prairie communities is probably caused by non-hydrologic factors, especially when one considers the abrupt borders typically found between the two communities. Variation in soils apparently does not cause this pattern because all areas sampled had deep peat soils. A more likely cause is fire. Although there are no data on the frequency with which the St. Johns Marsh near Blue Cypress Lake has burned, it did burn as recently as 1959 (Herke, 1959). Given the strong similarity between the marsh and the Everglades, where fire is a frequent and ecologically potent event (Wade et al., 1980; Taylor, 1981), it is reasonable to assume that fire has been a significant factor in development of vegetative patterns in the marsh. Fire may be particularly important for Panicum and other species of the Panicum prairie which apparently exist in the marsh primarily where competition with Cladium can be avoided. On the lake shore, wave action may prevent colonization by Cladium whereas on the marsh flat severe fire may eliminate Cladium from an area and allow prairie species access to it. I suggest that prairie species can more rapidly colonize severely burned areas than can Cladium and then inhibit the establishment of Cladium seedlings. Cladium apparently reclaims these areas, through vegetative propagation, as a slowly moving front which monopolizes space and light. This explanation for development of the mosaic formed by

Cladium and prairie communities is suggested by several lines of evidence: 1) Although Cladium is morphologically adapted to withstand fire (Forthman, 1973), and in some areas, may require fire to maintain its dominance (Wade et al., 1980), severe burns can kill the meristems and thus eliminate it from an area. Fire has, in fact, been a major factor in reduction of Cladium populations in the Everglades (Craighead, 1971). 2) Panicum is well adapted to survive fire. In the Everglades, Loveless (1959) observed rapid resprouting of Panicum only 3 - 4 days after burning and Tilmant (1975, in Wade et al., 1980) found that six months after a fire the total cover in a Panicum marsh was 77 percent, compared to only 27 percent in an adjacent stand of Cladium. Perhaps more importantly, Panicum prairies are less likely to be severely burned than are Cladium communities. During the 1971 drought in the Everglades, wet prairies did not burn at the same time there were intense fires in stands of Cladium (Goodrick, 1974). Goodrick (1974) suggested this was due to the low fuel content of wet prairies and pointed out their importance as fire breaks and refugia. The prescribed fires studied by Forthman (1973) also "stopped (without suppression) when they reached areas without heavy sawgrass fuel". The juxtaposition of unburned prairies with severely burned areas would promote rapid colonization of the burned area by prairie species. 3) The very low densities of Cladium in prairies indicate that seed dispersal is a largely ineffective means for colonization of the prairie by Cladium. Studies in the Everglades have, in fact, directly demonstrated that Cladium does not typically rely on seed dispersal (Alexander, 1971). Moreover, when seedlings of Cladium do become established on newly burned areas, they

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frequently die during the next dry season (Craighead, 1971). 4) Field observations indicate that the elevations of Panicum prairies are often slightly lower (1 to several inches) than the elevations of adjacent sawgrass stands. This would be expected if Cladium was eliminated from the area by a fire sufficiently severe to burn the peat. The sharp borders between Cladium stands and wet prairie communities and the slight difference in elevation have also been observed in the Everglades (Wade et al., 1980; Olmstead et al., 1980).

If fire is, indeed, the primary effector of the distributional pattern formed by Panicum prairie and Cladium communities, it would account for a large portion of the spatial heterogeneity of the marsh flat. It would determine not only the mozaic formed by these communities, but also the generally decreasing percentage of area occupied by wet prairie from west to east across the marsh. As elevations decline in this direction, opportunities for Panicum establishment would occur less frequently due to declining frequency and intensity of fires.

Although fire may be the direct cause of much of the vegetational pattern of the marsh flat, it should be remembered that its frequency and intensity, and the suite of species upon which it acts, are largely determined by hydrologic conditions. It also can not be discounted that the small difference in hydroperiod implied by elevational differences between the two communities is the primary cause of the mozaic.

A secondary mechanism for replacement of sawgrass stands by prairie may be senescence. As Cladium stands age, the percentage of above-ground biomass represented by dead leaf material increases. This can inhibit

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growth and cause the stand to become decadent unless the quantity of accumulated dead biomass is periodically reduced by fire (Alexander, 1974). Elimination of living culms from the oldest parts of a stand through the shading effect of dead leaf biomass could open up a space for colonization by other species. This mechanism may explain the doughnut shape frequently exhibited by Cladium stands in aerial photographs (P. Kinser, personal communication).

The conclusions which can be drawn from this work regarding the roles of fire and hydrology in shaping vegetative patterns must be tentative. Because of the shallow elevational gradient in the marsh, the transect could not be extended so that it would exit the wetland environment. Consequently, the hydrologic relationships of most species could not be completely defined. Conclusions regarding fire were largely hypothetical. Unfortunately, the scientific literature provides little help in more rigorously defining the effects of fire or hydrology on spatial patterns. Of the few studies which have examined the effects of hydrology on the vegetational patterns of Florida wetlands (Sincock, 1958; Pesnell and Brown, 1977; Goodrick, 1974; Olmstead, 1981) only two directly addressed the problem via gradient analysis and those studies are of limited value in understanding spatial patterns of species in the St. Johns Marsh either due to methodology (Sincock, 1958) or location (Pesnell and Brown, 1977). Quantitative, synecological study of the effects of fire in Florida wetlands is equally rudimentary (Wright and Bailey, 1982; Hall, 1983). Because the ecological values of wetlands are largely based upon their vegetation it is extremely important that managers of wetlands understand the factors which regulate species

distributions.   Investigation of the ecological roles of hydrology and
fire thus remains an area of research vital to sound management of the
wetland resources of Florida.

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Appendix A. Descriptive statistics for percentage of total living, above-ground, dry biomass for each species in each station. St. Johns Marsh, southeast shore of Blue Cypress Lake, June 1981 – February 1982.

Table A.1. Species codes.

SPECIES	CODE
PANICUM HEMITOMON SCHULTES	01
EUPATORIUM CAPILLIFOLIUM (LAM.)	02
AMARANTHUS AUSTRALIS (GRAY) SAUER.	03
IPOMOEA ALBA L.	04
ACER RUBRUM L.	05
RHYNCHOSPORA SP.	06
POLYGONUM PUNCTATUM ELL.	07
CYPERUS ODERATUS L.	09
CLADIUM JAMAICENSE CRANTZ	10
JUNCUS SP.	11
LUDWIDGEA ALATA ELL.	12
ELEOCHARIS SP.	13
SAGITTARIA LANCIFOLIA L.	14
LACHNANTHES CAROLINIANA (LAM.) DANDY	15
PISTIA STRATIOTES L.	16
TYPHA SP.	17
BACCHARIS HALIMIFOLIA L.	18
PLUCHEA PURPURASCENS (SWARTZ) DC.	19
OSMUNDA REGALIS (WILLD.) GRAY	20
KOSTELETSKYA VIRGINICA (L.) PRESL.	21
BOEHMERIA CYLINDRICA (L.) SWARTZ	22
BLECHNUM SERRATULATUM L. C. RICH	23
SALIX CAROLINIANA MICHAUX	24
TAXODIUM DISTICHUM (L.) RICHARD	25
ANNONA GLABRA L.	26
PONTEDERIA CORDATA VAR. LANCIFOLIA L.	27
SACCIOLEPIS STRIATA (L.) NASH	28
CALYSTEGIA SEPIUM (L.) R. BROWN	29
WOODWARDIA VIRGINICA (L.) SMITH	30
RHYNCHOSPORA CORNICULATA (LAM.) GRAY	31
SALVINEA ROTUNDIFOLIA WILLD.	32
AZOLLA CAROLINIANA WILLD.	33
HYDROCOTYL UMBELLATA L.	34
CICUTA MEXICANA C. & R.	35
PELTANDRA VIRGINICA (L.) KUNTH	36
LIMNOBIUM SPONGIA (BOSC) STEUDEL	37
CERATOPTERIS PTEROIDES (HOOK.) HIERON	38
RUMEX VERTICILLATUS L.	39
NUPHAR LUTEUM L. SIBTHORP & SMITH	40
CEPHALANTHUS OCCIDENTALIS L.	41
CRINUM AMERICANUM L.	42
RHYNCHOSPORA INUNDATA (OAKES) FERNALD.	43
UNIDENT. VINES	95
RESIDUAL	96
UNIDENT. SEDGE	97
UNIDENT. GRASS	98
UNIDENT. HERB	99

STATISTICS FOR PERCENTAGE OF TOTAL BIOMASS FOR STATION 1

SPECIES	N	MEAN	STD	MAX	MIN	NO. MISSING
1	19	83.51	37.20	100.00	0.00	1.00
2	19	0.44	1.85	8.06	0.00	1.00
3	19	0.00	0.00	0.00	0.00	1.00
4	19	0.00	0.00	0.00	0.00	1.00
5	19	0.02	0.08	0.35	0.00	1.00
6	19	0.18	0.79	3.45	0.00	1.00
7	19	0.00	0.00	0.00	0.00	1.00
9	19	0.00	0.00	0.00	0.00	1.00
10	19	0.00	0.00	0.00	0.00	1.00
11	19	0.00	0.00	0.00	0.00	1.00
12	19	0.00	0.00	0.00	0.00	1.00
13	19	0.00	0.00	0.00	0.00	1.00
14	19	0.00	0.00	0.00	0.00	1.00
15	19	0.00	0.00	0.00	0.00	1.00
16	19	0.00	0.00	0.00	0.00	1.00
17	19	0.00	0.00	0.00	0.00	1.00
18	19	0.00	0.00	0.00	0.00	1.00
20	19	0.00	0.00	0.00	0.00	1.00
21	19	0.00	0.00	0.00	0.00	1.00
22	19	0.00	0.00	0.00	0.00	1.00
23	19	0.00	0.00	0.00	0.00	1.00
24	19	0.00	0.00	0.00	0.00	1.00
27	19	0.00	0.00	0.00	0.00	1.00
29	19	0.00	0.00	0.00	0.00	1.00
34	19	0.00	0.00	0.00	0.00	1.00
36	19	0.00	0.00	0.00	0.00	1.00
41	19	0.00	0.00	0.00	0.00	1.00
42	19	0.00	0.00	0.00	0.00	1.00
95	19	0.00	0.00	0.00	0.00	1.00
96	19	0.00	0.00	0.00	0.00	1.00
97	19	0.00	0.00	0.00	0.00	1.00
98	19	0.00	0.00	0.00	0.00	1.00
99	19	0.06	0.25	1.08	0.00	1.00

STATISTICS FOR PERCENTAGE OF TOTAL BIOMASS FOR STATION 2

SPECIES	N	MEAN	STD	MAX	MIN	NO. MISSING
1	20	36.37	37.08	99.86	0.00	0.00
2	20	29.51	34.28	85.76	0.00	0.00
3	20	12.92	23.06	100.00	0.00	0.00
4	20	1.30	4.24	18.87	0.00	0.00
5	20	0.00	0.00	0.00	0.00	0.00
6	20	0.00	0.00	0.00	0.00	0.00
7	20	9.22	19.19	83.33	0.00	0.00
9	20	2.46	6.27	25.22	0.00	0.00
10	20	5.00	22.36	100.00	0.00	0.00
11	20	0.58	2.58	11.54	0.00	0.00
12	20	1.29	3.19	13.10	0.00	0.00
13	12	0.00	0.00	0.00	0.00	8.00
14	20	0.59	1.83	6.02	0.00	0.00
15	20	0.36	0.88	3.30	0.00	0.00
16	20	0.02	0.07	0.32	0.00	0.00
17	20	0.18	0.82	3.66	0.00	0.00
18	20	0.00	0.00	0.00	0.00	0.00
20	20	0.00	0.00	0.00	0.00	0.00
21	20	0.00	0.00	0.00	0.00	0.00
22	20	0.00	0.00	0.00	0.00	0.00
23	20	0.00	0.00	0.00	0.00	0.00
24	20	0.00	0.00	0.00	0.00	0.00
27	20	0.00	0.00	0.00	0.00	0.00
29	20	0.00	0.00	0.00	0.00	0.00
34	20	0.00	0.00	0.00	0.00	0.00
36	20	0.00	0.00	0.00	0.00	0.00
41	20	0.00	0.00	0.00	0.00	0.00
42	20	0.00	0.00	0.00	0.00	0.00
95	20	0.00	0.00	0.00	0.00	0.00
96	20	0.00	0.00	0.00	0.00	0.00
97	20	0.11	0.48	2.16	0.00	0.00
98	20	0.10	0.31	1.27	0.00	0.00
99	20	0.00	0.00	0.00	0.00	0.00

STATISTICS FOR PERCENTAGE OF TOTAL BIOMASS FOR STATION 3

SPECIES	N	MEAN	STD	MAX	MIN	NO. MISSING
1	10	0.00	0.00	0.00	0.00	0.00
2	10	0.00	0.00	0.00	0.00	0.00
3	10	0.00	0.00	0.00	0.00	0.00
4	10	22.88	22.20	62.24	0.00	0.00
5	10	0.00	0.00	0.00	0.00	0.00
6	10	0.00	0.00	0.00	0.00	0.00
7	10	0.43	1.37	4.32	0.00	0.00
9	10	0.00	0.00	0.00	0.00	0.00
10	10	5.90	12.56	33.07	0.00	0.00
11	10	0.00	0.00	0.00	0.00	0.00
12	10	0.00	0.00	0.00	0.00	0.00
13	10	0.00	0.00	0.00	0.00	0.00
14	10	0.00	0.00	0.00	0.00	0.00
15	10	0.00	0.00	0.00	0.00	0.00
16	10	0.00	0.00	0.00	0.00	0.00
17	10	0.00	0.00	0.00	0.00	0.00
18	10	0.00	0.00	0.00	0.00	0.00
20	10	11.82	13.77	36.66	0.00	0.00
21	10	0.36	1.14	3.60	0.00	0.00
22	10	0.00	0.00	0.00	0.00	0.00
23	10	0.00	0.00	0.00	0.00	0.00
24	10	0.00	0.00	0.00	0.00	0.00
27	10	0.01	0.02	0.06	0.00	0.00
29	10	22.69	31.50	91.95	0.00	0.00
34	10	0.00	0.00	0.00	0.00	0.00
36	10	2.99	9.46	29.90	0.00	0.00
41	10	6.35	20.07	63.46	0.00	0.00
42	10	0.00	0.00	0.00	0.00	0.00
95	10	0.00	0.00	0.00	0.00	0.00
96	10	25.16	21.79	74.85	0.00	0.00
97	10	0.00	0.00	0.00	0.00	0.00
98	10	0.00	0.00	0.00	0.00	0.00
99	10	1.41	4.25	13.51	0.00	0.00

STATISTICS FOR PERCENTAGE OF TOTAL BIOMASS FOR STATION   4

SPECIES	N	MEAN	STD	MAX	MIN	NO. MISSING
1	20	0.07	0.21	0.70	0.00	0.00
2	20	1.56	6.32	28.26	0.00	0.00
3	20	0.00	0.00	0.00	0.00	0.00
4	20	0.38	1.69	7.54	0.00	0.00
5	20	0.00	0.00	0.00	0.00	0.00
6	20	0.00	0.00	0.00	0.00	0.00
7	20	0.53	1.34	5.21	0.00	0.00
9	20	0.00	0.00	0.00	0.00	0.00
10	20	50.81	43.97	99.99	0.00	0.00
11	20	0.00	0.00	0.00	0.00	0.00
12	20	0.00	0.00	0.00	0.00	0.00
13	20	0.00	0.00	0.00	0.00	0.00
14	20	0.00	0.02	0.07	0.00	0.00
15	20	0.00	0.00	0.00	0.00	0.00
16	20	0.00	0.00	0.00	0.00	0.00
17	20	0.00	0.00	0.00	0.00	0.00
18	20	4.87	21.79	97.44	0.00	0.00
20	20	10.55	14.30	52.56	0.00	0.00
21	20	17.94	28.84	93.82	0.00	0.00
22	20	7.36	21.18	85.41	0.00	0.00
23	20	3.40	11.03	44.80	0.00	0.00
24	20	0.00	0.00	0.00	0.00	0.00
27	20	0.00	0.00	0.00	0.00	0.00
29	20	0.00	0.00	0.00	0.00	0.00
34	20	0.00	0.00	0.02	0.00	0.00
36	20	0.24	0.60	2.19	0.00	0.00
41	20	0.09	0.42	1.89	0.00	0.00
42	20	0.00	0.00	0.00	0.00	0.00
95	20	0.00	0.00	0.00	0.00	0.00
96	20	2.19	2.85	9.62	0.00	0.00
97	20	0.00	0.00	0.00	0.00	0.00
98	20	0.00	0.00	0.00	0.00	0.00
99	20	0.00	0.00	0.00	0.00	0.00

STATISTICS FOR PERCENTAGE OF TOTAL BIOMASS FOR STATION 5

SPECIES	N	MEAN	STD	MAX	MIN	NO. MISSING
1	10	0.00	0.00	0.00	0.00	0.00
2	10	0.00	0.00	0.00	0.00	0.00
3	10	0.00	0.00	0.00	0.00	0.00
4	10	0.00	0.00	0.00	0.00	0.00
5	10	0.00	0.00	0.00	0.00	0.00
6	10	0.00	0.00	0.00	0.00	0.00
7	10	0.06	0.20	0.63	0.00	0.00
9	10	0.00	0.00	0.00	0.00	0.00
10	10	36.47	47.64	100.00	0.00	0.00
11	10	0.00	0.00	0.00	0.00	0.00
12	10	0.52	1.64	5.18	0.00	0.00
13	10	0.00	0.00	0.00	0.00	0.00
14	10	0.00	0.00	0.00	0.00	0.00
15	10	0.00	0.00	0.00	0.00	0.00
16	10	0.00	0.00	0.00	0.00	0.00
17	10	0.00	0.00	0.00	0.00	0.00
18	10	0.00	0.00	0.00	0.00	0.00
20	10	43.40	41.76	97.96	0.00	0.00
21	10	0.20	0.65	2.04	0.00	0.00
22	10	0.00	0.00	0.00	0.00	0.00
23	10	7.33	23.19	73.33	0.00	0.00
24	10	0.00	0.00	0.00	0.00	0.00
27	10	0.00	0.00	0.00	0.00	0.00
29	10	0.00	0.00	0.00	0.00	0.00
34	10	0.00	0.00	0.00	0.00	0.00
36	10	0.00	0.00	0.00	0.00	0.00
41	10	0.00	0.00	0.00	0.00	0.00
42	10	0.00	0.00	0.00	0.00	0.00
95	10	0.00	0.00	0.00	0.00	0.00
96	10	12.00	12.72	31.43	0.00	0.00
97	10	0.00	0.00	0.00	0.00	0.00
98	10	0.00	0.00	0.00	0.00	0.00
99	10	0.00	0.00	0.00	0.00	0.00

STATISTICS FOR PERCENTAGE OF TOTAL BIOMASS FOR STATION 6

SPECIES	N	MEAN	STD	MAX	MIN	NO. MISSING
1	11	0.00	0.00	0.00	0.00	0.00
2	11	0.00	0.00	0.00	0.00	0.00
3	11	0.00	0.00	0.00	0.00	0.00
4	11	0.00	0.00	0.00	0.00	0.00
5	11	0.00	0.00	0.00	0.00	0.00
6	11	0.00	0.00	0.00	0.00	0.00
7	11	0.00	0.00	0.00	0.00	0.00
9	11	0.00	0.00	0.00	0.00	0.00
10	11	82.26	17.47	100.00	57.84	0.00
11	11	0.00	0.00	0.00	0.00	0.00
12	11	0.00	0.00	0.00	0.00	0.00
13	11	0.00	0.00	0.00	0.00	0.00
14	11	0.00	0.00	0.00	0.00	0.00
15	11	0.00	0.00	0.00	0.00	0.00
16	11	0.00	0.00	0.00	0.00	0.00
17	11	0.00	0.00	0.00	0.00	0.00
18	11	0.00	0.00	0.00	0.00	0.00
20	11	3.47	8.44	26.73	0.00	0.00
21	11	0.00	0.00	0.00	0.00	0.00
22	11	0.00	0.00	0.00	0.00	0.00
23	11	0.00	0.00	0.00	0.00	0.00
24	11	0.00	0.00	0.00	0.00	0.00
27	11	0.00	0.00	0.00	0.00	0.00
29	11	0.00	0.00	0.00	0.00	0.00
34	11	0.00	0.00	0.00	0.00	0.00
36	11	0.11	0.37	1.22	0.00	0.00
41	11	4.86	12.83	42.16	0.00	0.00
42	11	0.58	1.93	6.39	0.00	0.00
95	11	0.00	0.00	0.00	0.00	0.00
96	11	8.71	14.33	39.66	0.00	0.00
97	11	0.00	0.00	0.00	0.00	0.00
98	11	0.00	0.00	0.00	0.00	0.00
99	11	0.00	0.00	0.00	0.00	0.00

Appendix B. Descriptive statistics for total living, above-ground, dry biomass for each species in each station. Species codes are as in Table A.1. St. Johns Marsh, southeast shore of Blue Cypress Lake, June 1981 - February 1982.

BIOMASS STATISTICS FOR STATION 1

SPECIES	N	MEAN	STD	MAX	MIN	NO. MISSING
1	19	284.24	292.10	823.03	0.00	1.00
2	20	2.65	11.37	50.93	0.00	0.00
3	20	0.00	0.00	0.00	0.00	0.00
4	20	0.00	0.00	0.00	0.00	0.00
5	20	0.10	0.46	2.04	0.00	0.00
6	20	0.10	0.46	2.04	0.00	0.00
7	20	0.00	0.00	0.00	0.00	0.00
9	20	0.00	0.00	0.00	0.00	0.00
10	20	0.00	0.00	0.00	0.00	0.00
11	20	0.00	0.00	0.00	0.00	0.00
12	20	0.00	0.00	0.00	0.00	0.00
13	20	0.00	0.00	0.00	0.00	0.00
14	20	0.00	0.00	0.00	0.00	0.00
15	20	0.00	0.00	0.00	0.00	0.00
16	20	0.00	0.00	0.00	0.00	0.00
17	20	0.00	0.00	0.00	0.00	0.00
18	20	0.00	0.00	0.00	0.00	0.00
20	20	0.00	0.00	0.00	0.00	0.00
21	20	0.00	0.00	0.00	0.00	0.00
22	20	0.00	0.00	0.00	0.00	0.00
23	20	0.00	0.00	0.00	0.00	0.00
24	20	0.00	0.00	0.00	0.00	0.00
27	20	0.00	0.00	0.00	0.00	0.00
29	20	0.00	0.00	0.00	0.00	0.00
34	20	0.00	0.00	0.00	0.00	0.00
36	20	0.00	0.00	0.00	0.00	0.00
41	20	0.00	0.00	0.00	0.00	0.00
42	20	0.00	0.00	0.00	0.00	0.00
95	20	0.00	0.00	0.00	0.00	0.00
96	20	0.00	0.00	0.00	0.00	0.00
97	20	0.00	0.00	0.00	0.00	0.00
98	20	0.00	0.00	0.00	0.00	0.00
99	20	0.31	1.37	6.11	0.00	0.00

BIOMASS STATISTICS FOR STATION 2

SPECIES	N	MEAN	STD	MAX	MIN	NO. MISSING
1	20	178.84	217.82	625.41	0.00	0.00
2	20	196.21	271.78	952.38	0.00	0.00
3	20	37.20	81.81	369.24	0.00	0.00
4	20	2.16	4.37	13.24	0.00	0.00
5	20	0.00	0.00	0.00	0.00	0.00
6	20	0.00	0.00	0.00	0.00	0.00
7	20	39.72	67.54	224.60	0.00	0.00
9	20	8.63	24.50	101.35	0.00	0.00
10	20	20.93	93.61	418.64	0.00	0.00
11	20	3.92	17.54	78.43	0.00	0.00
12	20	6.93	14.27	52.46	0.00	0.00
13	12	0.00	0.00	0.00	0.00	8.00
14	20	1.63	6.19	27.50	0.00	0.00
15	20	1.04	3.06	13.24	0.00	0.00
16	20	0.08	0.34	1.53	0.00	0.00
17	20	0.69	3.07	13.75	0.00	0.00
18	20	0.00	0.00	0.00	0.00	0.00
20	20	0.00	0.00	0.00	0.00	0.00
21	20	0.00	0.00	0.00	0.00	0.00
22	20	0.00	0.00	0.00	0.00	0.00
23	20	0.00	0.00	0.00	0.00	0.00
24	20	0.00	0.00	0.00	0.00	0.00
27	20	0.00	0.00	0.00	0.00	0.00
29	20	0.00	0.00	0.00	0.00	0.00
34	20	0.00	0.00	0.00	0.00	0.00
36	20	0.00	0.00	0.00	0.00	0.00
41	20	0.00	0.00	0.00	0.00	0.00
42	20	0.00	0.00	0.00	0.00	0.00
95	20	0.00	0.00	0.00	0.00	0.00
96	20	0.00	0.00	0.00	0.00	0.00
97	20	0.43	1.94	8.66	0.00	0.00
98	20	0.38	1.25	5.09	0.00	0.00
99	20	0.00	0.00	0.00	0.00	0.00

BIOMASS STATISTICS FOR STATION 3

SPECIES	N	MEAN	STD	MAX	MIN	NO. MISSING
1	10	0.00	0.00	0.00	0.00	0.00
2	10	0.00	0.00	0.00	0.00	0.00
3	10	0.00	0.00	0.00	0.00	0.00
4	10	59.85	56.41	161.44	0.00	0.00
5	10	0.00	0.00	0.00	0.00	0.00
6	10	0.00	0.00	0.00	0.00	0.00
7	10	1.44	4.55	14.40	0.00	0.00
9	10	0.00	0.00	0.00	0.00	0.00
10	10	24.28	64.77	205.60	0.00	0.00
11	10	0.00	0.00	0.00	0.00	0.00
12	10	0.00	0.00	0.00	0.00	0.00
13	10	0.00	0.00	0.00	0.00	0.00
14	10	0.00	0.00	0.00	0.00	0.00
15	10	0.00	0.00	0.00	0.00	0.00
16	10	0.00	0.00	0.00	0.00	0.00
17	10	0.00	0.00	0.00	0.00	0.00
18	10	0.00	0.00	0.00	0.00	0.00
20	10	42.15	68.53	227.92	0.00	0.00
21	10	2.24	7.08	22.40	0.00	0.00
22	10	0.00	0.00	0.00	0.00	0.00
23	10	0.00	0.00	0.00	0.00	0.00
24	10	0.00	0.00	0.00	0.00	0.00
27	10	0.04	0.13	0.40	0.00	0.00
29	10	56.88	74.61	216.80	0.00	0.00
34	10	0.00	0.00	0.00	0.00	0.00
36	10	9.52	30.10	95.20	0.00	0.00
41	10	56.00	177.09	560.00	0.00	0.00
42	10	0.00	0.00	0.00	0.00	0.00
95	10	0.00	0.00	0.00	0.00	0.00
96	10	83.28	93.66	301.20	0.00	0.00
97	10	0.00	0.00	0.00	0.00	0.00
98	10	0.00	0.00	0.00	0.00	0.00
99	10	12.00	37.67	119.20	0.00	0.00

BIOMASS STATISTICS FOR STATION 4

SPECIES	N	MEAN	STD	MAX	MIN	NO. MISSING
1	20	0.44	1.38	5.16	0.00	0.00
2	20	11.37	48.50	217.20	0.00	0.00
3	20	0.00	0.00	0.00	0.00	0.00
4	20	1.33	5.94	26.56	0.00	0.00
5	20	0.00	0.00	0.00	0.00	0.00
6	20	0.00	0.00	0.00	0.00	0.00
7	20	4.60	10.62	36.80	0.00	0.00
9	20	0.00	0.00	0.00	0.00	0.00
10	20	797.92	1137.97	3923.60	0.00	0.00
11	20	0.00	0.00	0.00	0.00	0.00
12	20	0.00	0.00	0.00	0.00	0.00
13	20	0.00	0.00	0.00	0.00	0.00
14	20	0.01	0.05	0.24	0.00	0.00
15	20	0.00	0.00	0.00	0.00	0.00
16	20	0.00	0.00	0.00	0.00	0.00
17	20	0.00	0.00	0.00	0.00	0.00
18	20	0.76	3.40	15.20	0.00	0.00
20	20	48.82	51.59	167.20	0.00	0.00
21	20	138.21	227.57	735.20	0.00	0.00
22	20	53.94	132.18	483.20	0.00	0.00
23	20	33.08	102.78	374.00	0.00	0.00
24	20	0.00	0.00	0.00	0.00	0.00
27	20	0.00	0.00	0.00	0.00	0.00
29	20	0.00	0.00	0.00	0.00	0.00
34	20	0.02	0.10	0.44	0.00	0.00
36	20	1.23	3.26	12.40	0.00	0.00
41	20	2.02	9.03	40.40	0.00	0.00
42	20	0.00	0.00	0.00	0.00	0.00
95	20	0.00	0.00	0.00	0.00	0.00
96	20	9.35	13.63	54.00	0.00	0.00
97	20	0.00	0.00	0.00	0.00	0.00
98	20	0.00	0.00	0.00	0.00	0.00
99	20	0.00	0.00	0.00	0.00	0.00

BIOMASS STATISTICS FOR STATION   5

SPECIES	N	MEAN	STD	MAX	MIN	NO. MISSING
1	10	0.00	0.00	0.00	0.00	0.00
2	10	0.00	0.00	0.00	0.00	0.00
3	10	0.00	0.00	0.00	0.00	0.00
4	10	0.00	0.00	0.00	0.00	0.00
5	10	0.00	0.00	0.00	0.00	0.00
6	10	0.00	0.00	0.00	0.00	0.00
7	10	0.24	0.76	2.40	0.00	0.00
9	10	0.00	0.00	0.00	0.00	0.00
10	10	182.40	362.11	1009.60	0.00	0.00
11	10	0.00	0.00	0.00	0.00	0.00
12	10	1.96	6.20	19.60	0.00	0.00
13	10	0.00	0.00	0.00	0.00	0.00
14	10	0.00	0.00	0.00	0.00	0.00
15	10	0.00	0.00	0.00	0.00	0.00
16	10	0.00	0.00	0.00	0.00	0.00
17	10	0.00	0.00	0.00	0.00	0.00
18	10	0.00	0.00	0.00	0.00	0.00
20	10	104.24	142.43	409.60	0.00	0.00
21	10	0.08	0.25	0.80	0.00	0.00
22	10	0.00	0.00	0.00	0.00	0.00
23	10	10.56	33.39	105.60	0.00	0.00
24	10	0.00	0.00	0.00	0.00	0.00
27	10	0.00	0.00	0.00	0.00	0.00
29	10	0.00	0.00	0.00	0.00	0.00
34	10	0.00	0.00	0.00	0.00	0.00
36	10	0.00	0.00	0.00	0.00	0.00
41	10	0.00	0.00	0.00	0.00	0.00
42	10	0.00	0.00	0.00	0.00	0.00
95	10	0.00	0.00	0.00	0.00	0.00
96	10	30.54	24.15	63.60	0.00	0.00
97	10	0.00	0.00	0.00	0.00	0.00
98	10	0.00	0.00	0.00	0.00	0.00
99	10	0.00	0.00	0.00	0.00	0.00

BIOMASS STATISTICS FOR STATION 6

SPECIES	N	MEAN	STD	MAX	MIN	NO. MISSING
1	11	0.00	0.00	0.00	0.00	0.00
2	11	0.00	0.00	0.00	0.00	0.00
3	11	0.00	0.00	0.00	0.00	0.00
4	11	0.00	0.00	0.00	0.00	0.00
5	11	0.00	0.00	0.00	0.00	0.00
6	11	0.00	0.00	0.00	0.00	0.00
7	11	0.00	0.00	0.00	0.00	0.00
9	11	0.00	0.00	0.00	0.00	0.00
10	11	429.20	397.37	1236.00	14.00	0.00
11	11	0.00	0.00	0.00	0.00	0.00
12	11	0.00	0.00	0.00	0.00	0.00
13	11	0.00	0.00	0.00	0.00	0.00
14	11	0.00	0.00	0.00	0.00	0.00
15	11	0.00	0.00	0.00	0.00	0.00
16	11	0.00	0.00	0.00	0.00	0.00
17	11	0.00	0.00	0.00	0.00	0.00
18	11	0.00	0.00	0.00	0.00	0.00
20	11	11.31	25.86	75.60	0.00	0.00
21	11	0.00	0.00	0.00	0.00	0.00
22	11	0.00	0.00	0.00	0.00	0.00
23	11	0.00	0.00	0.00	0.00	0.00
24	11	0.00	0.00	0.00	0.00	0.00
27	11	0.00	0.00	0.00	0.00	0.00
29	11	0.00	0.00	0.00	0.00	0.00
34	11	0.00	0.00	0.00	0.00	0.00
36	11	0.47	1.57	5.20	0.00	0.00
41	11	29.20	86.76	289.20	0.00	0.00
42	11	1.13	3.74	12.40	0.00	0.00
95	11	0.00	0.00	0.00	0.00	0.00
96	11	16.58	28.02	95.20	0.00	0.00
97	11	0.00	0.00	0.00	0.00	0.00
98	11	0.00	0.00	0.00	0.00	0.00
99	11	0.00	0.00	0.00	0.00	0.00