



CHARACTERIZATION OF PERIPHYTON RESPONSE TO HYDROPERIOD IN MARL PRAIRIE WETLANDS OF THE EVERGLADES

Final Comprehensive Report 2006

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**Evelyn E. Gaiser
Southeast Environmental Research Center and
Department of Biological Sciences
Florida International University
Miami, FL 33199**



**Southeast Environmental Research Center
11200 S.W. 8th Street, OE 148 • Miami, FL 33199 • Tel: (305) 348-3095 • Fax: (305) 348-4096 • www.fiu.edu**

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I. EXECUTIVE SUMMARY

A central goal of the Comprehensive Everglades Restoration Plan is to restore, to the extent possible, the natural volume and timing of water delivery to the Everglades (Everglades Consolidated Report 2004, CERP Report 2005). Several construction projects (CSOP and L-31N) are directed at restoring water flow the eastern portions of Everglades National Park that for decades have experienced unnaturally short-hydroperiods. Periphyton has been identified as a key performance measure for determining the success of these projects in restoring water flow to these areas. Reliance on periphyton to indicate environmental change has been well justified by scientific research conducted in the Everglades (McCormick & Stevenson 1998, Gaiser et al. 2006) which adds regional applicability to the existing body of literature in aquatic sciences that has supported the widespread employment of periphyton monitoring in aquatic ecosystem management (Hill et al. 2000, Stevenson 2001). The utility of periphyton to expose ecological ramifications to environmentally restorative or deconstructive change in the Everglades is due to its bearing several of the most desirable features of a reliable ecological indicator which include (1) being distributed throughout the system of study, (2) having rapid response to environmental change that is (3) readily quantifiable at several levels of biological organization (individual, species, population, community) with (4) consequences to levels above and below it's placement on the food web (Karr 1999).

Periphyton is abundant and ubiquitous in the short-hydroperiod Everglades, which is dominated by rocky glades and marl prairie habitat. The creation of periphyton-based habitat suitability indices facilitated the generation of hypotheses of the trajectories of ecosystem change that might be detected through monitoring (<http://www.evergladesplan.org/pm/recover/recover.cfm>). The ability to accurately predict ecological trajectories from periphyton will be improved through experimental work that mechanistically interprets periphyton response to key ecological drivers. Furthermore, understanding periphyton response to hydrologic change will improve food-web models that predict fish and bird abundance in the marsh. While periphyton-based water quantity and quality models are well supported in deeper, longer-hydroperiod areas of the Everglades, few studies have been conducted in the marl prairie and rocky glades where hydrologic restoration may have its largest impact.

The goals of this research were to:

- (1) Determine periphyton distribution and abundance in the Everglades marl prairie,**
- (2) Identify key drivers of that distribution through a large-scale, high-resolution survey,**
- (3) Conduct experimental work to quantify the effects of these drivers on periphyton abundance, composition and function.**

A central goal presented in the DOI Science Plan is to “assess the responses of ecological communities and species as a basis for adaptive management.” A key indicator throughout the Everglades ecosystem is periphyton, as it is ubiquitous and sensitive at appropriate time scales to environmental change, especially to alterations in water quantity and quality. Periphyton has been identified by the RECOVER Monitoring and Assessment Plan as a system-wide performance measure resulting in the construction of periphyton-based Habitat Suitability Indices based on available data on ecological responses to parameters expected to change in the

context of CERP (Davis et al., 2005). More recently, the RECOVER team has formulated hypotheses summarizing the expected trajectories of key hydrologic, biogeochemical and biological responses to CERP. The current hypothesis states that “periphyton structure composition integrates hydrology and water quality across the entire wetland system of the Everglades” and follows that “detection of periphyton response to changes in hydrology and water quality needs to be based on comparison to a habitat-specific baseline (i.e. ridge and slough, marl prairie, rocky glades, or oligohaline zone).”

While several studies have been conducted to determine periphyton response to changing hydrology and water quality in longer-hydroperiod ridge and slough habitats (Gaiser et al., 2006; Gottlieb et al., 2006; Iwaniec et al., 2006; Thomas et al., 2006), few studies have focused on the marl prairie and rocky glades, which comprise a large portion of the freshwater Everglades landscape. Hydrologic models predict significant lengthening of hydroperiod and increasing water depth in these habitats, particularly in the southeastern boundary of ENP where CERP is anticipated to have the greatest impact on water movement. Periphyton integrates temporal variability in water depth in shallow environments and can serve as an early warning indicator of impending ecosystem response to changes in water management. Such indicators are essential as they would provide the Park with very strong ecological metrics for region-specific assessments during CERP. They would improve understanding of habitat desirability for the endangered Cape Sable Seaside Sparrow, for which the DOI Science Plan calls for “monitoring of ecological communities including vegetation, periphyton and aquatic communities in the vicinity of the proposed C-111 buffers in Cape Sable Seaside Sparrow habitat.” (p. 74)

In this report we summarize research findings from survey work aimed at determining the abundance and distribution of periphyton throughout short-hydroperiod areas of the Everglades as well as experimental studies that identify the key drivers of these distribution patterns. In summary, we found that:

- (1) Periphyton biomass in the marl prairie is an order of magnitude higher than other wetlands and increases as water depth and phosphorus availability decreases.**
- (2) Periphyton biomass is higher in wet-prairie habitat than in the marsh or slough, particularly in assemblages dominated by vegetation associated with the preferred nesting habitat of the Cape Sable Seaside Sparrow.**
- (3) Periphyton is only temporarily inhibited by drying; fast recovery upon rehydration reduces leaching of nutrients to the water column and regulates water column nutrients to a low level.**
- (4) Periphyton production is unaffected by shading up to 98% reduction, likely due to very high irradiance in the marl prairie Everglades.**
- (5) Periphyton production is highest in the absence of plants while plant production increases in the presence of periphyton.**
- (6) Healthy periphyton mats regulate water P dynamics in marl prairie but P-buffering in burned areas is delayed in time and dependent on submersed patches that are less susceptible to fire.**

Findings are organized into 6 chapters that are in various stages of publication in the peer-reviewed scientific literature. An abstract of our findings from each of the studies is provided below.

(A) Periphyton distribution in CSSP habitat in the Everglades marl prairie

This study was designed to provide landscape-scale distribution maps of periphyton abundance across the Everglades marl prairie. The study was conducted in conjunction with survey by Ross et al. (2006) aimed at characterizing the habitat of the Cape Sable Seaside Sparrow (CSSP), providing the opportunity to link periphyton distribution patterns to other variables including vegetation abundance and composition, soils, hydrology and other habitat descriptors.

Periphyton was surveyed in the dry seasons of 2003-2005 in 612 sites across the marl prairie. A suite of periphyton attributes including cover, substrate characteristics, thickness and color were ranked visually at 5 plots at each site. Based on these rapid visual rankings, differences among the CSSP populations and plant community types could be discerned. A more detailed study was conducted in 2004, where periphyton was collected from a subset of 150 locations. Ash-free dry biomass averaged 350 g m^{-2} , exceeding by orders of magnitude those found in the literature from other wetlands. Biomass was highest in populations B and D and lowest in population A. These patterns were strongly negatively related to water depth, with highest biomass being found in sites <50 cm deep and lowest in deeper sites (characteristic of population A). Conversely, the height of the epiphyton (locally termed “sweaters”) was strongly positively correlated with water depth, and could serve as a reliable metric of maximum water depth, even after sites have dried (as dried epiphyton remains on standing plant stems). Finally, periphyton biomass declined precipitously with increasing phosphorus content, a pattern observed frequently in longer hydroperiod sloughs (i.e., Gaiser et al., 2005). Sites in population A and along the eastern boundary of Everglades National Park were most enriched with phosphorus. This study showed that periphyton can be used reliably to indicate water depth and phosphorus availability in the marl prairie, two key features in Everglades restoration.

(B) Periphyton distribution across hydrologic gradients in the marl prairie

The goals of this study were to (1) determine the distribution of periphyton along hydrologic gradients in the marl prairie and (2) determine linkages between periphyton distribution and plant community types. The study was also conducted in conjunction with a survey by Ross et al. (2006) that characterized plant community types and other key environmental features along hydroperiod gradients in the CSSP habitat. Transects were established along hydrologic gradients in 6 CSSP populations and 255 sites were sampled for periphyton in conjunction with other habitat variables. Hydroperiod, inferred from elevation data linked to nearby water level recorders, ranged from 63-305 days, and had a different effect on periphyton biomass in the different CSSP populations. Relationships to water level were much more predictable, and, as in the survey study, had a strongly inverse relationship to periphyton biomass. Wet prairie communities with shorter hydroperiod and shallower water supported a greater biomass of periphyton than marsh communities. Highest biomass was found in prairie sites dominated by *Schoenus nigricans*, *Cladium jamaicense*, *Muhlenbergia capillaris* var. *filipes* and *Schizachyrium rhizomatum*, vegetation assemblages associated with preferable nesting habitat for the CSSP.

(C) Effects of drying and rewetting on periphyton growth in the marl prairie

This study examined the effects of drying and rehydration on periphyton, addressing rates of recovery and the function of periphyton as a phosphorus (P) buffer and sink. Crusts subjected to 6 months of natural drying in the short-hydroperiod C-111 basin were sampled before flooding. Periphyton was artificially wetted for 20 days with a one-time addition of 20 L of artificial marsh water (AMW, no P added) in three 26 L microcosms placed in a green house. Auto-recovery of algae and bacteria were tracked through metabolic and compositional measurements and related to P dynamics. A separate pool of oven-dried, ground crust was also flooded with AWM in 7 repeated 24-h dilutions to determine rates of abiotic P-desorption. The crust was volumetrically dominated by cyanophytes (90%) containing taxa typical of xeric environments. TP-desorption from dried crust followed a Michaelis-Menten model. Only 0.82% of P contained in the crust was desorbed after 7 days and over half this amount was desorbed in the first 2 days. Total P (TP) desorption in the microcosms had same kinetics until days 2–3 when net P loss from the periphyton to the water dropped to close to zero. By day 5, cyanophytes and bacteria re-absorbed 90% of desorbed P and buffered water TP to a threshold level of 6.7 $\mu\text{g TP/L}$. Phosphomonoesterase (PMEase) activity was very high the first 24-h of wetting due to the release of a large pre-existing pool of extracellular PMEase during this period. Thereafter, PMEase activity dropped by 90% and increased gradually from this low level, indicating increasing P-starvation. We demonstrated that desiccated periphyton auto-recovers upon rehydration with no exogenous P addition and no long-term net P loss to the water. Periphyton buffers water column P dynamics in response to flooding, having implications for P budgets in algal-dominated temporary wetlands.

(D) Effects of shading on periphyton growth in the marl prairie

The effect of shade on periphyton production was examined in a short-hydroperiod marl prairie wetland. Eight 1-m² areas were isolated in a shade house, which did not spectrally change the incident irradiance but reduced it quantitatively by 0, 30, 50, 60, 70, 80, 90 and 98%. Periphyton mat was sampled monthly under each shade house for a 5 month period while the wetland was flooded. Periphyton was analyzed for thickness, DW, AFDW, chlorophyll *a* (chl *a*) and incubated in light and dark BOD bottles at 5 different irradiances to assess its photosynthesis-irradiance (PI) curve and respiration. The PI curves parameters P_{max} , I_k and eventually the photoinhibition slope (β) were determined following non-linear regression analyses. Taxonomic composition and total algal biovolume were determined at the end of the experiment. Periphyton composition did not change with shade because, unlike the effects of the natural plant canopy, the shade houses did not selectively filter the green component of the visible spectrum. The PI curves were significantly affected by shade. I_k increased linearly with increasing percent irradiance transmittance (%IT = 1 - % shade). P_{max} increased linearly with increasing %IT in the 90–98% shade range and leveled off at higher shade. Thus, the P_{max} -%IT curve could be fitted with a PI curve equation. For each shade level, the PI curve was used to integrate daily photosynthesis for a day of average irradiance. The daily photosynthesis followed a PI curve equation with the same characteristics as P_{max} -%IT. Thus, periphyton exhibited a high irradiance plasticity under 0–80% shade but was challenged photosynthetically at higher shade, causing a decrease in daily GPP 98% shade levels. The high irradiance plasticity was linked to an increase in the chl *a* content per cell in the 60–80% shade, while this increase was not required at lower

shade and was challenging energetically at higher shade. Thus, chl *a* is not a good metric for periphyton biomass assessment across variously shaded habitat. It is also hypothesized that irradiance plasticity is linked to photosynthetic coupling between differently comprised algal layers arranged vertically within periphyton mats that have different PI curves.

(E) Interactions between plants and periphyton in the marl prairie

Interactions between plants and periphyton were examined in a removal experiment in three areas of marl prairie with differing hydroperiod. Periphyton was removed on a regular basis for 3 years from 48, 0.25 m² plots at each site and plant biomass and productivity was monitored relative to paired control plots where periphyton was left alone. Similarly, plants were clipped to the sediment surface on a regular basis for 3 years from 48, 0.25 m² plots at each site and periphyton biomass and productivity was monitored relative to paired control plots where plants were left alone. We found that periphyton biomass and productivity increases in the absence of plants, possibly due to reduced shading as well as increased space available for colonization. Conversely, we found that plant biomass declines significantly in the presence of periphyton. Periphyton may enhance plant growth rates through enzymatic activity that increases the availability of nutrients. It also may act as a “sponge” during the dry season, increasing seed longevity and, possibly, seedling survivorship. It was clear from this study that periphyton and plants interact synergistically to create the mosaic of habitat types we observe in the Everglades marl prairie.

(F) Effects of fire on periphyton function in Everglades wetlands

Aside from hydrology that mainly drives this system, fire is also an important, yet episodic event. Although a fair number of studies have been conducted to examine vegetation recovery after fire, no studies have examined the effect of fire on periphyton and resultant biochemistry after re-flooding. We followed the 19-day revival of benthic periphyton from a newly burned freshwater oligotrophic marl prairie prior to the 2003 rainy season. Periphyton of varying degrees of wetness (dry crust on top of marl mounds, wet mat and submerged mat in small depressions) were sampled from adjacent burned and unburned areas. Similar amounts of each periphyton type were artificially rewetted with artificial marsh water containing no P in small enclosures in a green house. Periphyton revival (biomass, metabolism and algal taxonomic composition) as well as dynamics of P in the water were examined. P dynamics in periphyton treatments were compared to abiotic P-desorption from oven-dried ground subsample of each periphyton type. Burned periphyton from emerged surfaces did not recover and desorbed P at rates similar to dried material. Conversely, periphyton from submerged surfaces desorbed P rapidly in the first 10 days but increasingly re-absorbed P thereafter. Therefore, healthy periphyton mats regulate water P dynamics in marl prairie but P-buffering in burned areas is delayed in time and dependent on submersed patches that are less susceptible to fire.

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II. PARTICIPATING INDIVIDUALS

Principal Investigator:

Evelyn E. Gaiser, Ph.D., FIU*

Collaborating Scientists:

Serge Thomas, Ph.D., FIU**

Michael S. Ross, Ph.D., FIU

Jay Sah, Ph.D., FIU

Andrew Gottlieb, Ph.D., FIU, PBS&J/EPJV

Laboratory Managers:

Christine Taylor, FIU***

Pablo Ruiz, FIU

Research Technicians:

David Jones, FIU***

Raphael Travieso, FIU***

Franco Tobias, FIU***

Alejandro Leon, FIU

Graduate Students:

Anna Wachnicka, FIU

Elaine Fontes, FIU

Josette LaHee, FIU

Amanda Quillen, FIU

Undergraduate Students:

Angelikie Zafiris, FIU

Filipe Zuniga, FIU

Carlos Tudela, FIU

*Primary contributor to chapters IV.A, IV.B, IV.E

**Primary contributor to chapters IV.C, IV.D, IV.F

***Primary technical staff contributing to this report

III. PUBLICATIONS

Published and funded fully by this project:

- Thomas, S. E., E. E. Gaiser and F. A. C. Tobias. 2006. Effects of shading on calcareous benthic periphyton in a short-hydroperiod oligotrophic alkaline wetland (Everglades, FL, U.S.A.). *Hydrobiologia* 569: 209-221.
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In preparation and funded by this project:

- Gaiser, E. E. In Prep. Production and distribution of benthic algae along hydroperiod gradients in a short-hydroperiod, calcareous wetland.
- Gaiser, E. E., J. Sah and M. Ross. In Prep. Associations between benthic algal production and plant community composition in a short-hydroperiod, calcareous wetland.
- Gaiser, E. E. In Prep. Regulation of plant composition and turnover by benthic algae in a short-hydroperiod, calcareous wetland.
- Thomas, S. E. and E. Gaiser. In Prep. Effects of fire on benthic algal productivity and composition in a wetland subject to controlled burning.

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- Davis, S. M., E. E. Gaiser, W. F. Loftus and A. E. Huffman. 2005. Southern marl prairies conceptual ecological model. *Wetlands* 25: 821-831.
- Gottlieb, A. D., J. H. Richards and E. E. Gaiser. 2006. Comparative study of periphyton community structure in long and short hydroperiod Everglades marshes. *Hydrobiologia*. 569: 195-207.
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IV. FINDINGS

A. PERIPHYTON DISTRIBUTION IN CSSP HABITAT IN THE EVERGLADES MARL PRAIRIE

Introduction

Periphyton is widely distributed and abundant throughout the habitat of the Cape Sable Seaside Sparrow (CSSP) and its abundance has been thought to influence vegetation structure and, possibly, the quality of potential nesting and foraging habitat for the CSSP (Pimm et al., 2002). The habitat occupied or previously occupied by the 5 Everglades' populations of CSSP is characterized by short-hydroperiod marsh colonized by wet prairie vegetation (Ross et al., 2006). The landscape is a mosaic of sparse to dense emergent vegetation interspersed with tree islands, areas of bare or marl-coated limestone, small sinkholes and, in places infrequently exposed to fire, patches of low-stature woody vegetation. This patchiness, evident at small to large scales, results from natural topographic variation and water flow patterns and the local and recent history of flooding and drying events and fire (Lockwood et al., 2003). The extent to which this patchiness is exhibited or influenced by periphyton is unknown, although biomass estimates from several recent studies in marl prairie habitat ranging from 1517 to 2936 g m⁻² (Gottlieb et al. 2006, Iwaniec et al., 2006) suggest that periphyton may indeed be an important ecosystem engineer in this habitat. Although CSSP habitat monitoring projects have included rapid visual estimates of periphyton cover (Pimm et al., 2002), no study has examined periphyton biomass distribution at the landscape scale in the short-hydroperiod Everglades.

This goal of this study was to assess periphyton distribution throughout CSSP habitat in order to determine whether (1) biomass differs between habitats differentially utilized by CSSP, (2) distribution is correlated with vegetation community composition and (3) relationships exist between periphyton abundance and water depth and quality variables.

Methods

Periphyton was surveyed using both observational and destructive sampling approaches. Both types of data were collected in conjunction with vegetation monitoring reported by Ross et al. (2006).

Observational Census

The observational census of periphyton took place during vegetation sampling during the dry seasons of 2003-2005. Census coordinates were chosen at random in CSSP populations A-H (Table 1.1, Fig. 1.1).

At each coordinate, a 60-meter E-W transect was established and vegetation sampled according to Ross et al. (2006). Periphyton observations were made in 0.5 m² quadrats at 5 fixed locations along the transect (5, 17, 29, 41 and 53 m) that coincided with vegetation structure measurements. Data recorded included abundance and height of epiphytic periphyton, cover of floating periphyton cover, benthic periphyton cover, moisture, thickness and color, vegetation height, closure and cover, dominant plant species, soil depth and type and water depth. Data were ranked by ordinal or independent categories according to Table 1.2.

Table 1.1. Number of sites observed and sampled for periphyton in each CSSP population

Population	Observational Census (N)	Sampling Census (N)
A	275	56
B	153	40
C	37	9
D	30	10
E	59	20
F	35	10
G	6	5
H	17	0

Table 1.2. Criteria used to rank observational data for periphyton.

Parameter/Rank	0	1	2	3	4
Epiphytic Periphyton Cover	None	<50%	>50%		
Epiphytic Periphyton Height	None	<10 cm	<20 cm	>20 cm	
Floating Periphyton Cover	None	<50%	>50%		
Benthic Periphyton Cover	None	<50%	>50%		
Benthic Periphyton Moisture		Wet/Moist	Moist/Dry	Dry	
Benthic Periphyton Thickness	0 cm	<1 cm	>1 cm		
Benthic Periphyton Type	Organic	Calcareous			
Benthic Periphyton Color	None	White/Gray	Tan	Brown/red	Black
Green Algae Cover	None	Present			
Water Depth	None	<10 cm	<20 cm	<30 cm	>30 cm
Soil Type	Marl	Marl/Rock	Rock	Peat	Marl /Peat

Sampling Census

Periphyton was sampled at a subset of the census sites in the wet season (October) of 2003 (Table 1.1). Rebar markers were located and periphyton was sampled at 3 sites within 50 m of the marker. A 625 cm² open-ended bucket driven into the periphyton/soil was used to isolate the sampling area and all periphyton was removed. Periphyton was cleared of debris (dead vegetation, rocks, large snails) and placed in a Ziploc bag on ice. Observational data were also recorded using the same criteria as in the dry season survey (Table 1.2). In the laboratory, periphyton samples were split into 4 subsamples which were (1) dried to constant weight at 100 °C for dry weight biomass followed by ashing at 1000 °C for determination of ash-free dry biomass, (2) dried and then analyzed total phosphorus content by spectrometry after dry combustion, (3) extracted in acetone and analyzed for chlorophyll *a* by fluorometry and (4) frozen in a permanent archive.

Data Analysis

Ranks from the observational census were averaged within sampling location and the abundance of each rank expressed as a proportion for each population and vegetation community type category (assigned according to Ross et al., 2006). Hydroperiod was inferred from elevation data georeferenced to nearby water-level recorders (Ross et al., 2006). Average hydroperiod, soil depth and vegetation cover, closure and height were calculated for each periphyton category by rank. Parameters measured in the sampling census were averaged within locations and then by site and vegetation community type category. Relationships between periphyton biomass, water depth and phosphorus content were explored through linear regression.

Results

Observational Census

Rapid observational census information recorded for periphyton during the dry season vegetation survey was sufficient to attempt to distinguish differences among the 8 CSSP populations (Fig. 1.2). Most sites were dry, although some sites in populations C and H were flooded. Epiphytic periphyton was present at some sites in most populations except F, G and H where epiphytic periphyton was rare. Floating periphyton mat was present at about half of the locations in all populations except F, G and H, where the presence of floating mats was negligible. Soils were mostly calcareous marls, except in population F where many sites had abundant bare rock and populations G and H which both had significant organic/peat layers at the top of the soil. Benthic periphyton was found in moderate to high abundance throughout all populations and its moisture content reflected water depth and the length of exposure to desiccation. Green algal mats were present in only a small fraction of sites equally distributed among populations. Benthic periphyton otherwise appeared white to gray when dried (especially in populations A, F, G and H), tan at most sites with patches of black in populations C, E, F and G.

Observational data were also compared among plant community types (Fig. 1.3). Epiphytic periphyton was most abundant in *Cladium* sites or sites with a mix of *Cladium* and *Rhynchospora* or *Paspalum*. Floating mat was present occasionally in all community types except for the *Spartina* marsh. Benthic periphyton was also found in all community types but absent occasionally from *Eleocharis/Rhynchospora* and *Spartina* marsh.

Periphyton attributes were also associated with general site and vegetation cover characteristics (Fig. 1.4). Hydroperiod and soil depth increased with water depth across populations. Vegetation cover and height was highest at intermediate water depths. Epiphyte cover and thickness generally increased with water depth. Floating periphyton cover was highest at sites with lowest vegetation cover. Soil type was highly associated with hydroperiod, with dry sites having mostly calcareous soils and wetter sites having more organic soils. Benthic periphyton cover and thickness was highest at sites with little vegetation cover.

Sampling Census

Periphyton dry biomass ranged from 0-2800 g m⁻² with an average of 39% organic content; therefore ash-free dry (organic) biomass averaged 350 g m⁻² among sites (Table 1.3).

Table 1.3. Mean, minimum and maximum values for variables measured during the Fall 2004 sampling census.

	Water Depth (cm)	Periphyton Dry Mass (g m ⁻²)	Periphyton AFDM (g m ⁻²)	Organic Content (%)	Chlorophyll a (µg m ⁻²)	Total Phosphorus (µg g ⁻¹)
Mean	32	860	350	39	17900	98
Min	2	6	1	11	2700	53
Max	90	2800	1100	60	96900	237

Means of measured variables differed among populations (Fig. 1.5). Water depth was greatest in populations A and G and not different among populations B-F (Fig. 1.6). Epiphyton height

tracked water depth being highest in populations A and G (Fig. 1.7). Dry and AFD periphyton biomass were lowest in these same populations (Fig. 1.8, 1.9) and highest in populations B and D; organic content did not vary significantly among populations (Fig. 1.10). Chlorophyll *a* was highest in populations A and G and lowest in E and F (Fig. 1.11). Total phosphorus content was higher in sites in populations A and F and low in the remaining populations (Fig. 1.12).

Means of measured variables also differed among vegetation types (Fig. 1.13). Water depth was deepest in the *Cladium/Rhynchospora* marsh and shallowest in the *Muhlenbergia* Wet Prairie. Periphyton dry and AFD biomass followed the opposite trend, being highest in wet prairie sites and lowest in the *Cladium/Rhynchospora* marsh. Chlorophyll *a* was lowest in the wet prairie and phosphorus content did not differ among marsh types.

Total phosphorus (TP) and water depth explained significant variability in periphyton biomass across sites (Fig. 1.14). As TP and water depth increased among sites, AFD biomass decreased, although TP and water depth were not collinear. Chlorophyll *a* content also increased with phosphorus availability and water depth. Water depth also drove the maximum height of epiphytic periphyton.

Discussion and Conclusions

Periphyton biomass was very high throughout the CSSP habitat, with values averaging 350 g AFDM m⁻². These values exceed by orders of magnitude those found in other wetland literature (Davis et al., 2005), reiterating the probable importance of periphyton in structuring this habitat. Biomass is highly controlled by water depth and phosphorus availability, as has been shown in other studies in deeper water sloughs (Gottlieb et al., 2006; Gaiser et al., 2006). This is the first study to decisively conclude that shallow, benthic periphyton mats also decline with increased phosphorus availability. The relationship to water depth is also striking, as the negative correlation suggests adaptation to regularly desiccating conditions. The increase in chlorophyll *a* with phosphorus content suggests cellular response to increased availability that is not manifest in an increase in biomass. The high levels of total phosphorus in population F near the L-31 W canal and eastern boundary of Everglades National Park and in populations A south of the S-12 structures on the Tamiami Canal likely reflect long-term exposure to above-normal phosphorus loads from inlet points along these canals.

Populations B and D have the greatest abundance of periphyton, followed by C and E; with the exception of D, these sites also host the largest numbers of nesting CSSP, indicating the importance of periphyton to the CSSP habitat. Populations A and G had notably low biomass of periphyton. Periphyton is also thickest where vegetation cover is lowest, indicating a negative association that is either caused by correlated responses to hydrology or a direct effect of one on the other. The mixed *Cladium/Rhynchospora* marsh is least supportive of periphyton, among the marsh types, while wet prairie sites have dense periphyton mats throughout. These associations are likely important in controlling habitat suitability for the CSSP.

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Datasets

Census Periphyton Description.xls
Census 2003 Periphyton Data.xls

Figure 1.1. Location of census points sampled for periphyton in CSSP populations A-G in Everglades National Park.

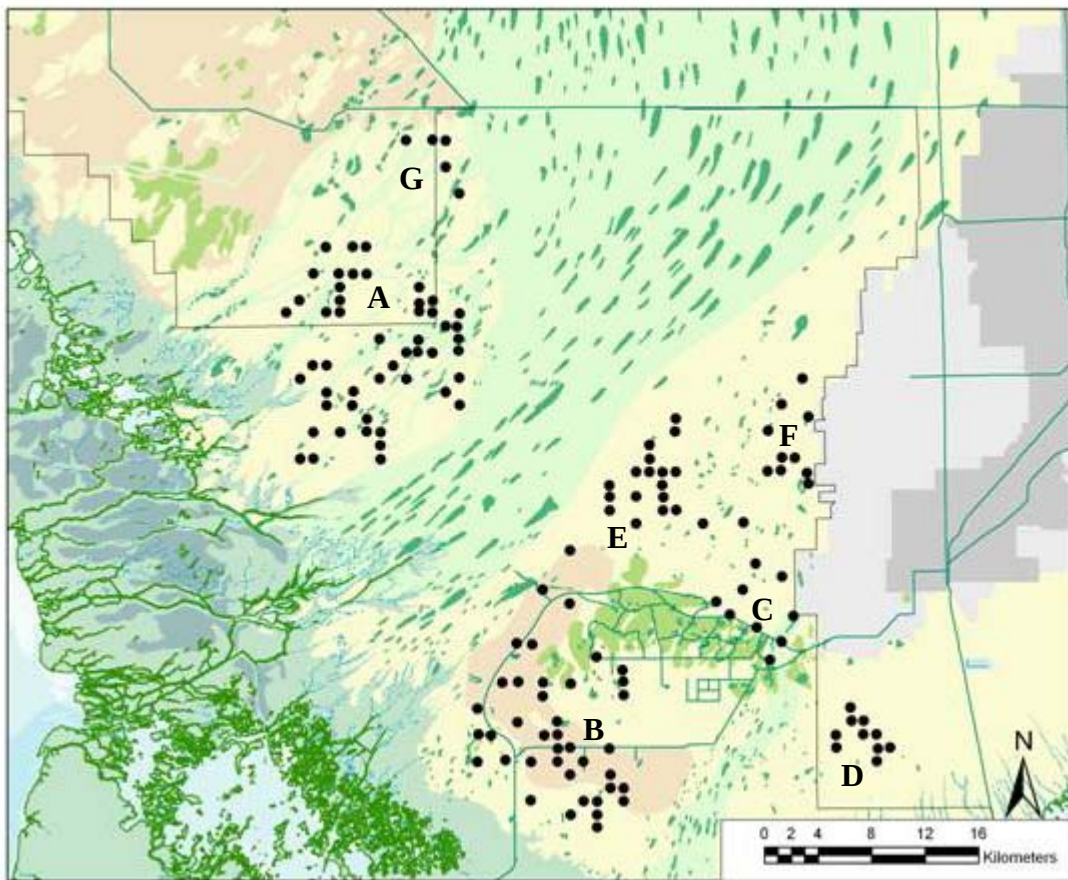


Figure 1.2. Percent of observations in rank categories 0 through 4 (see Table 2 for criteria) for periphyton attributes in CSSP populations A-H.

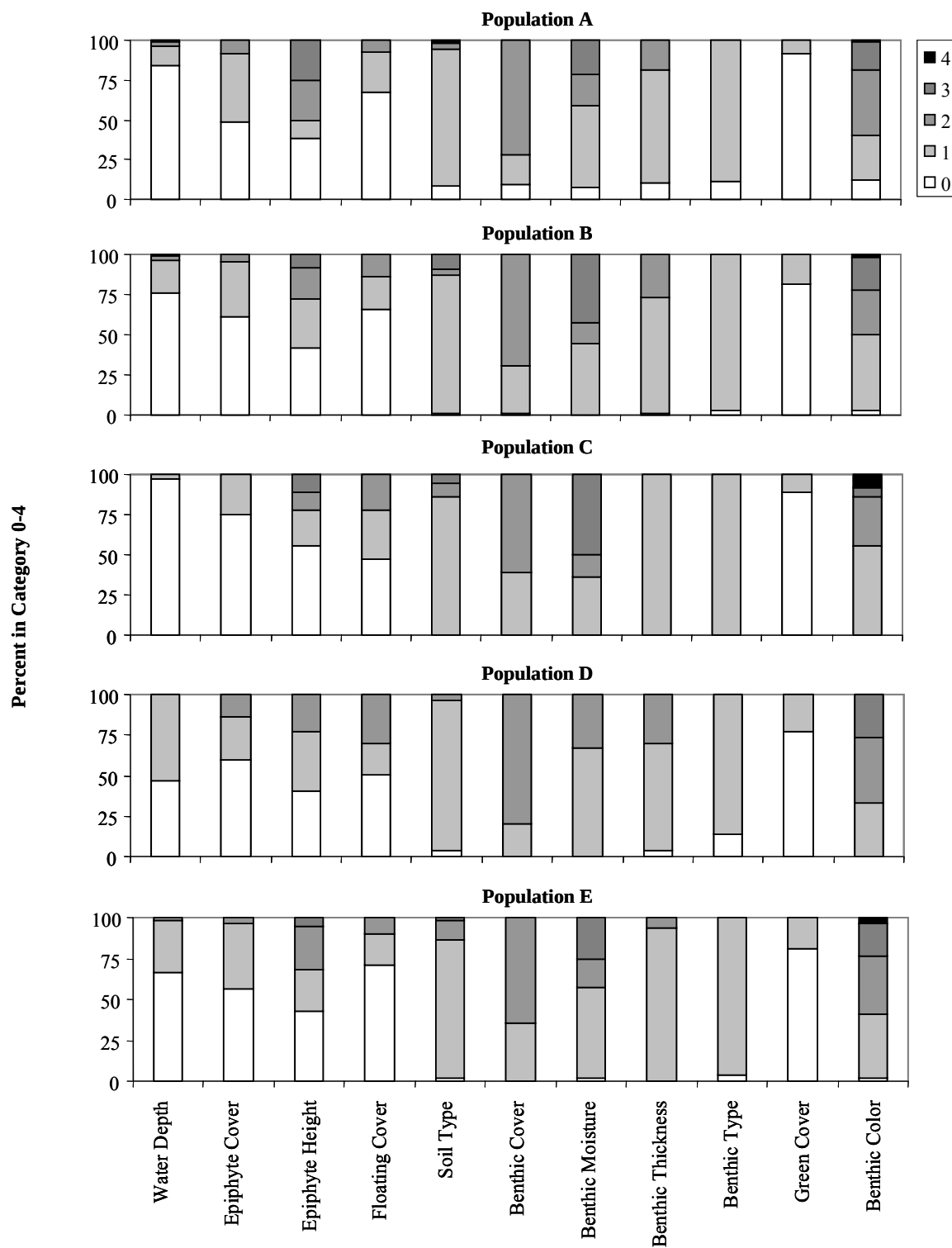


Figure 1.2. Continued...

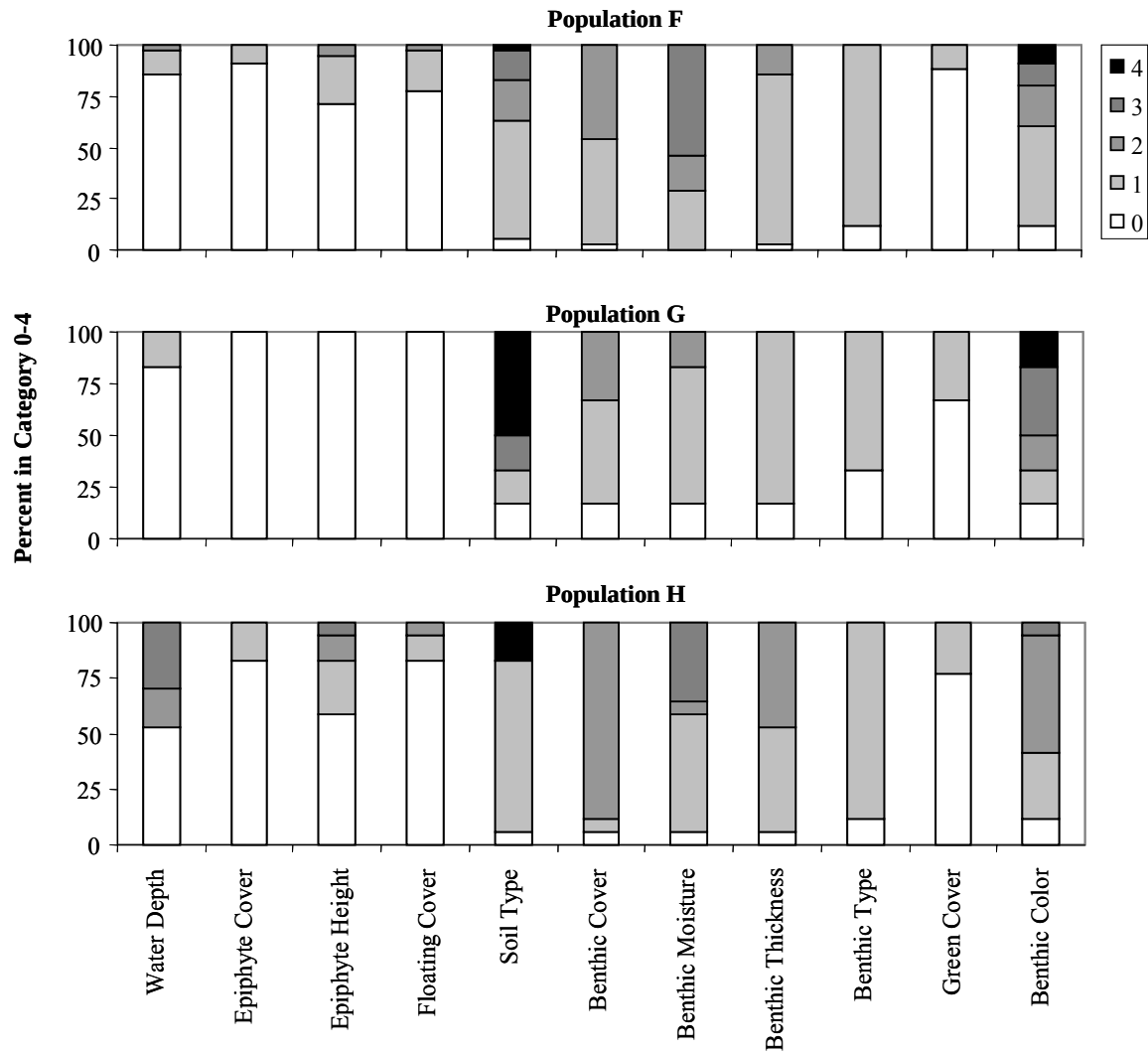


Figure 1.3. Percent of observations in rank categories 0 through 4 (see Table 2 for criteria) for periphyton attributes in different marsh types in the marl prairie.

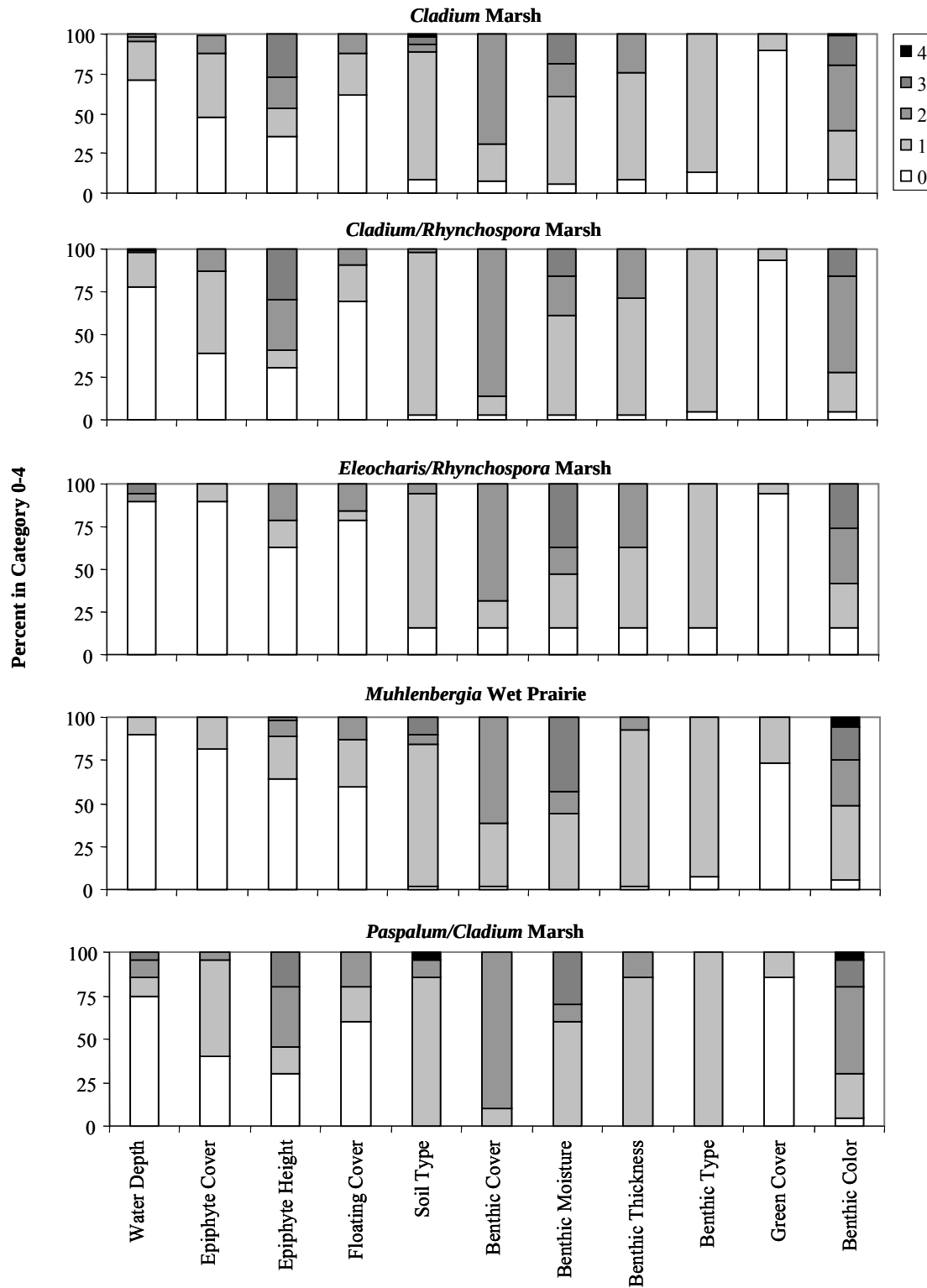


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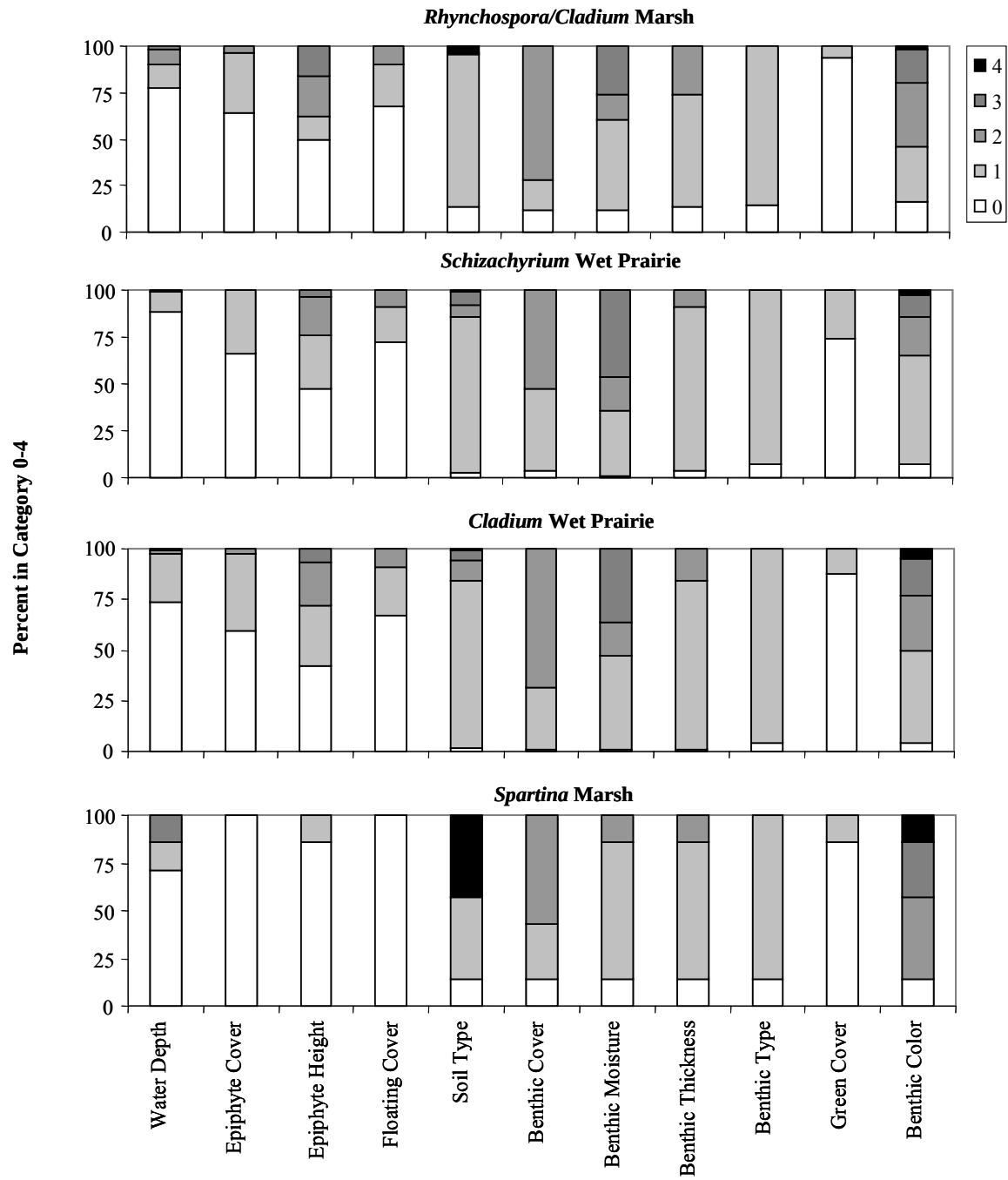


Figure 1.4. Mean and standard deviation of hydroperiod, soil depth and vegetation cover, closure and height for rank categories 0 through 4 for periphyton attributes in the marl prairie.

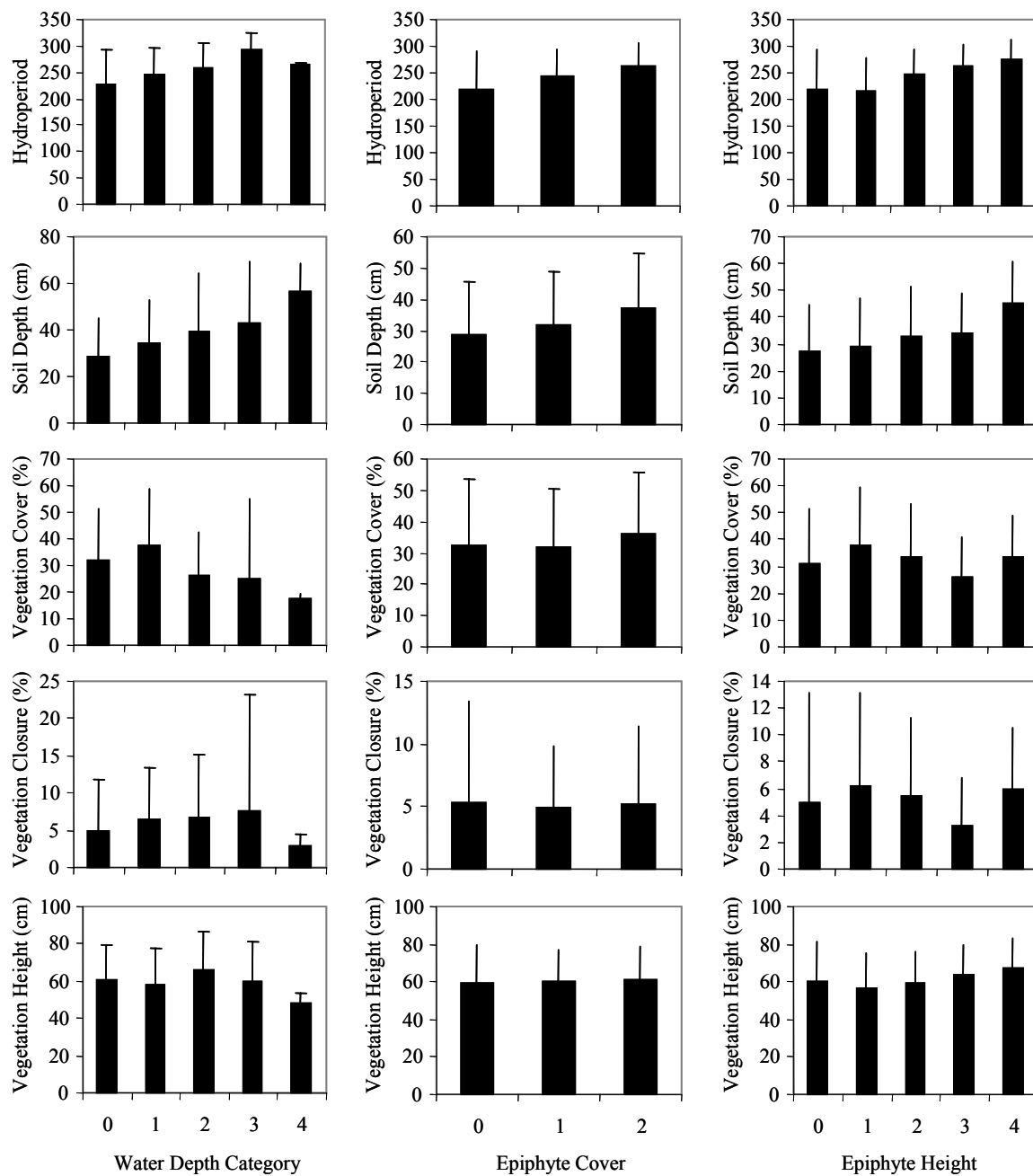


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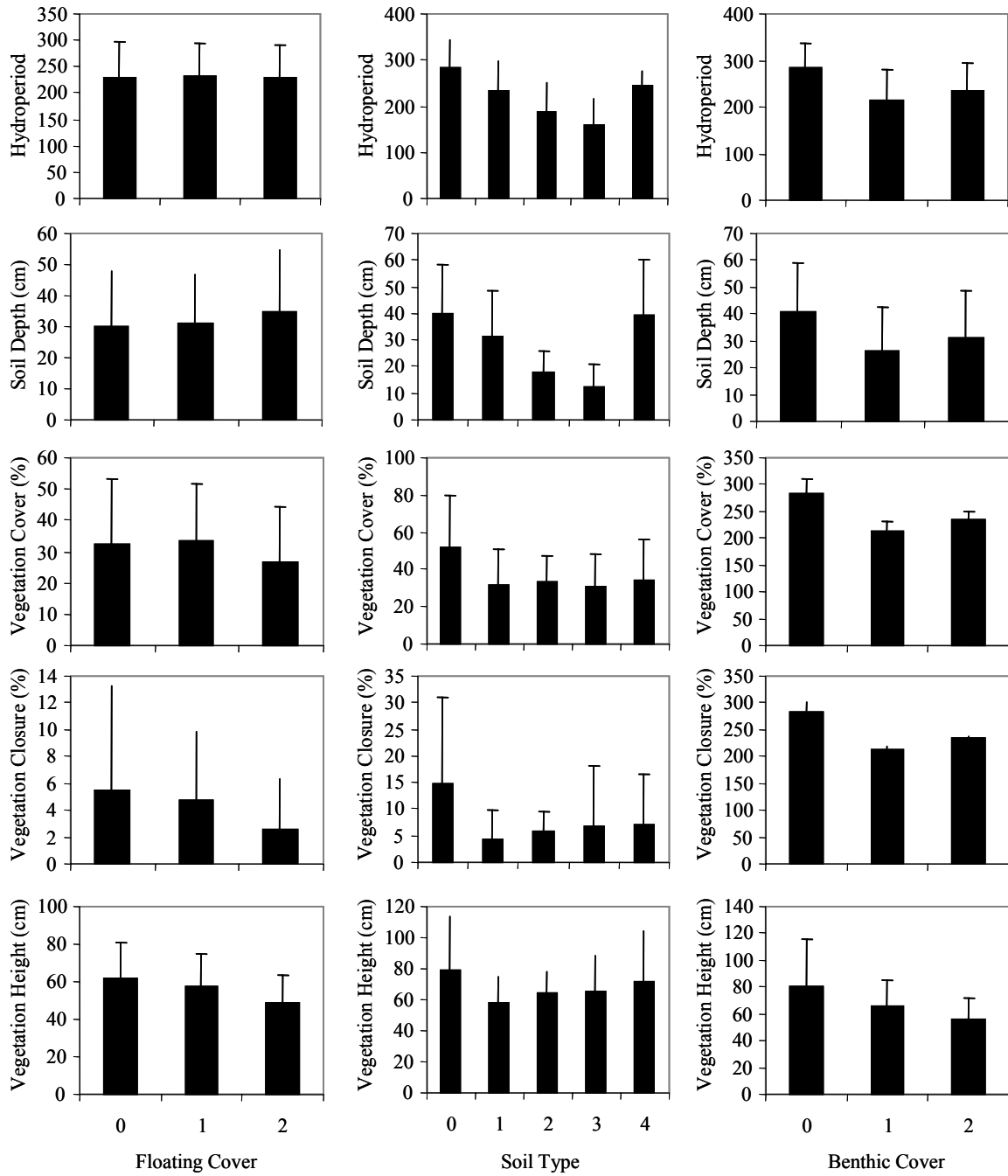


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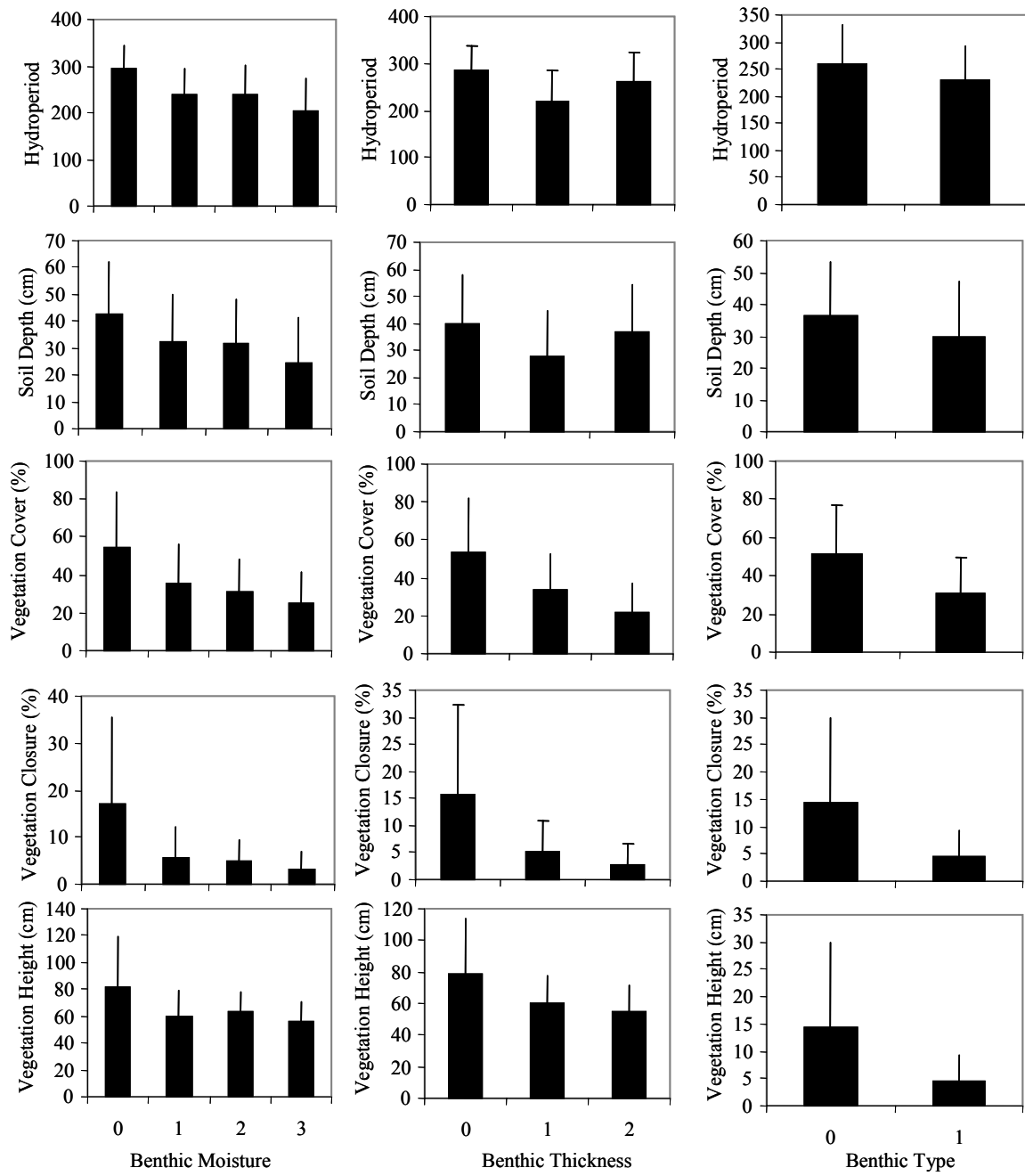


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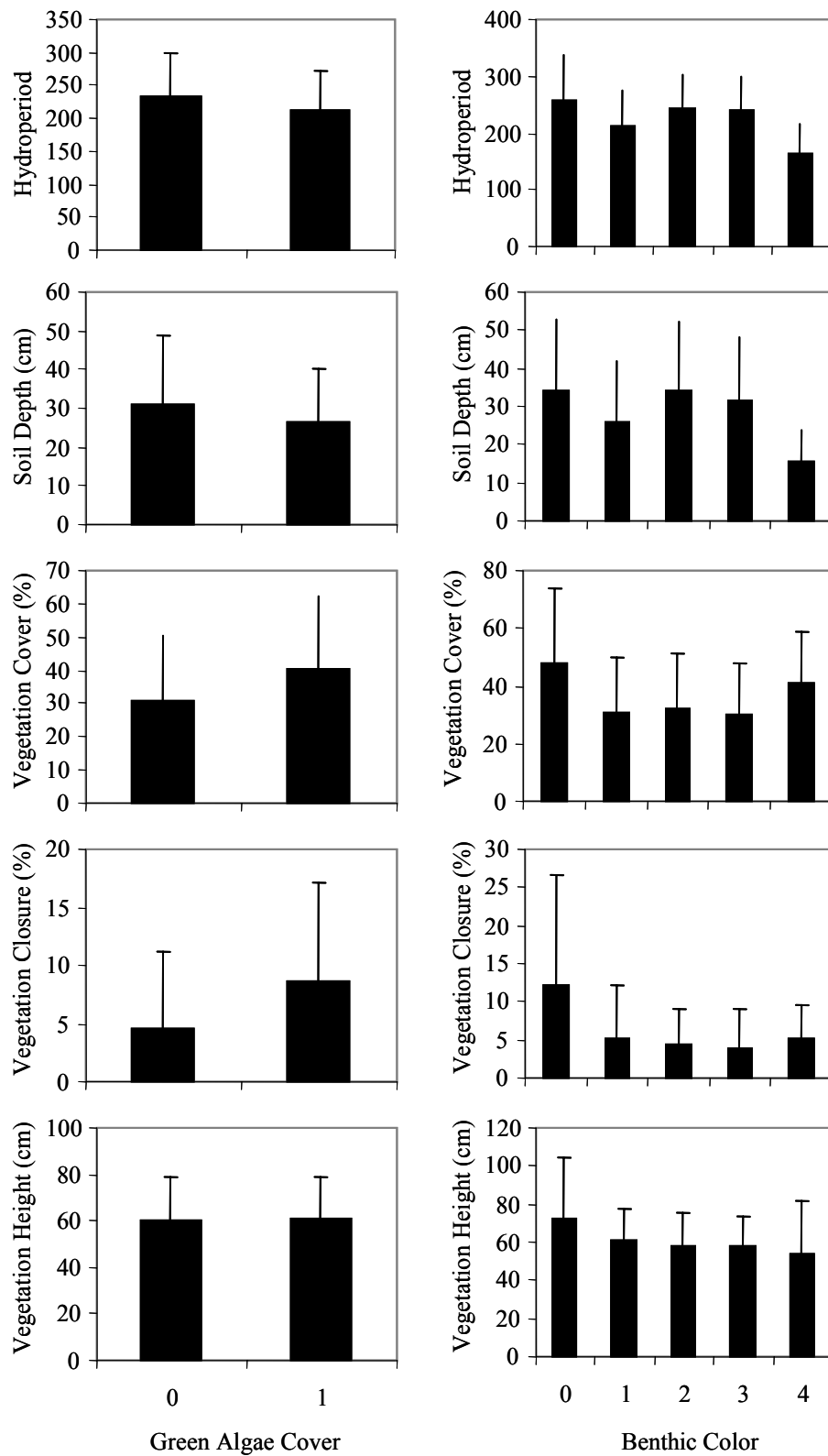


Figure 1.5. Means and standard deviation of water depth, periphyton dry mass and ash-free dry mass (AFDM), chlorophyll *a* and total phosphorus content among the 8 CSSP populations.

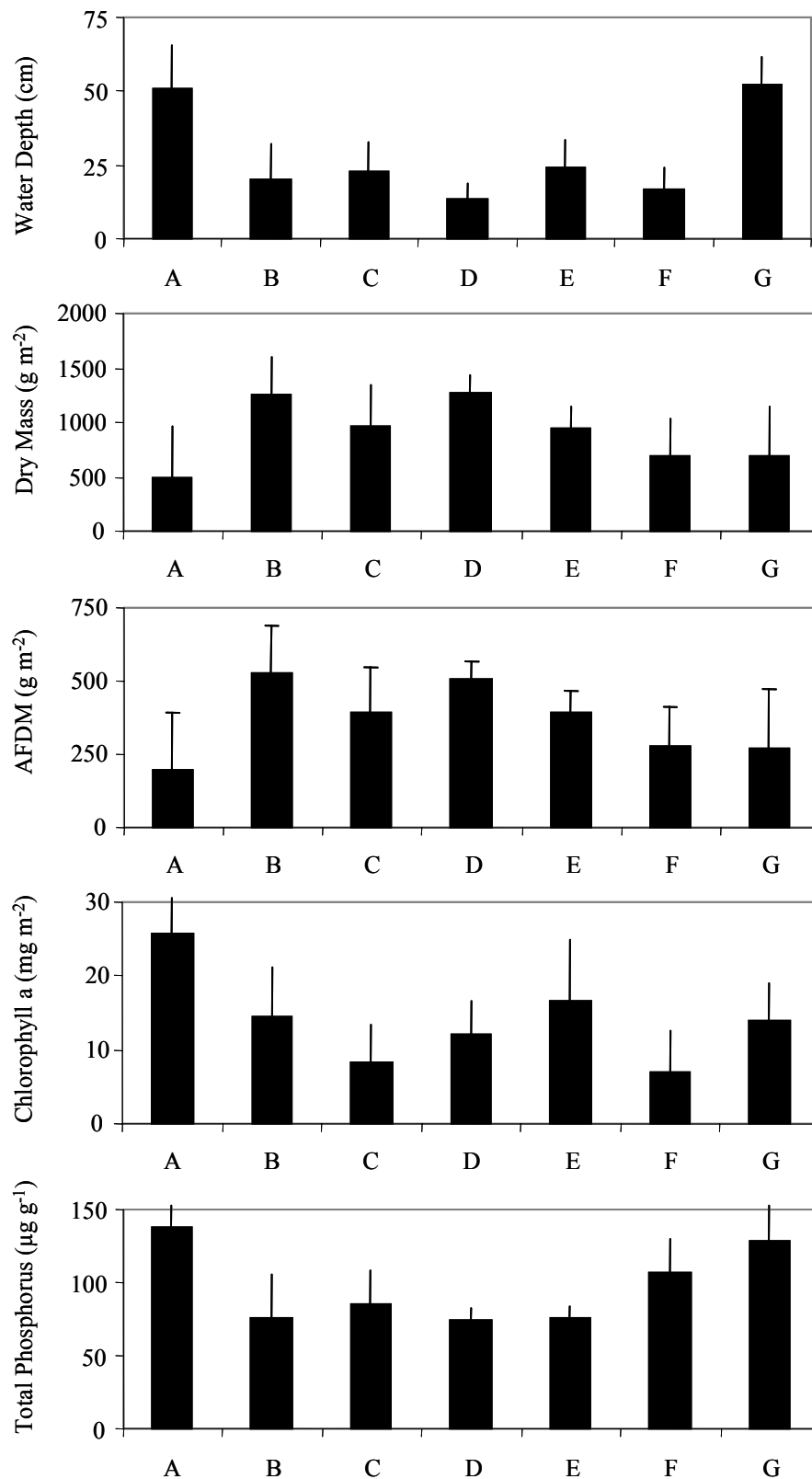


Figure 1.6. Mean water depth during the October 2003 periphyton census at locations in CSSP populations A-G.

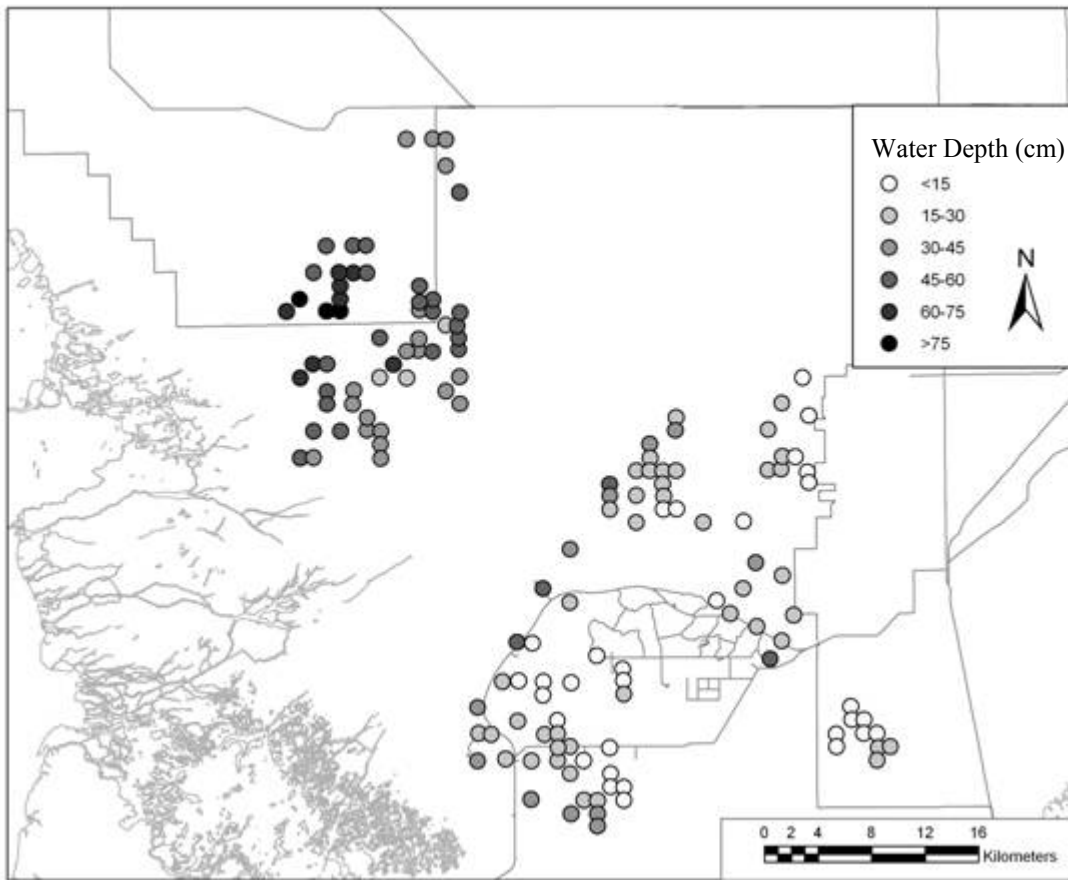


Figure 1.7. Mean epiphyton height during the October 2003 periphyton census at locations in CSSP populations A-G.

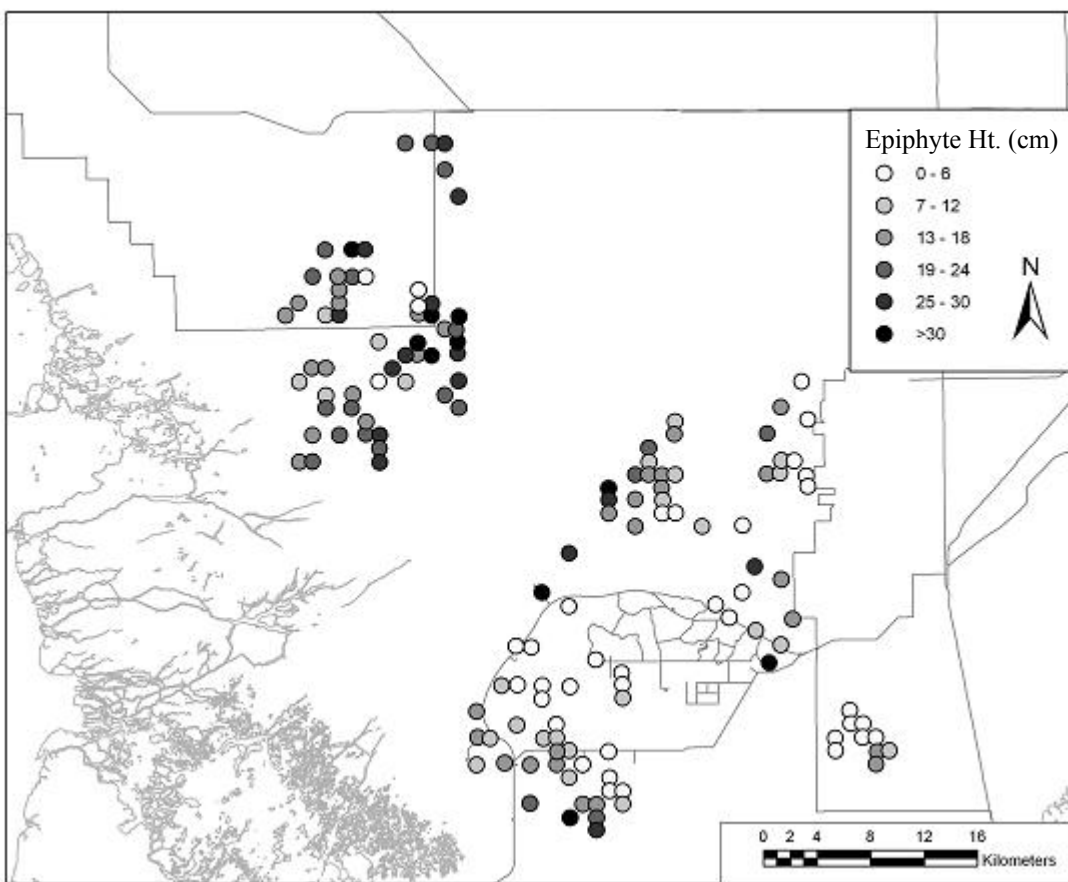


Figure 1.8. Mean periphyton dry biomass during the October 2003 periphyton census at locations in CSSP populations A-G.

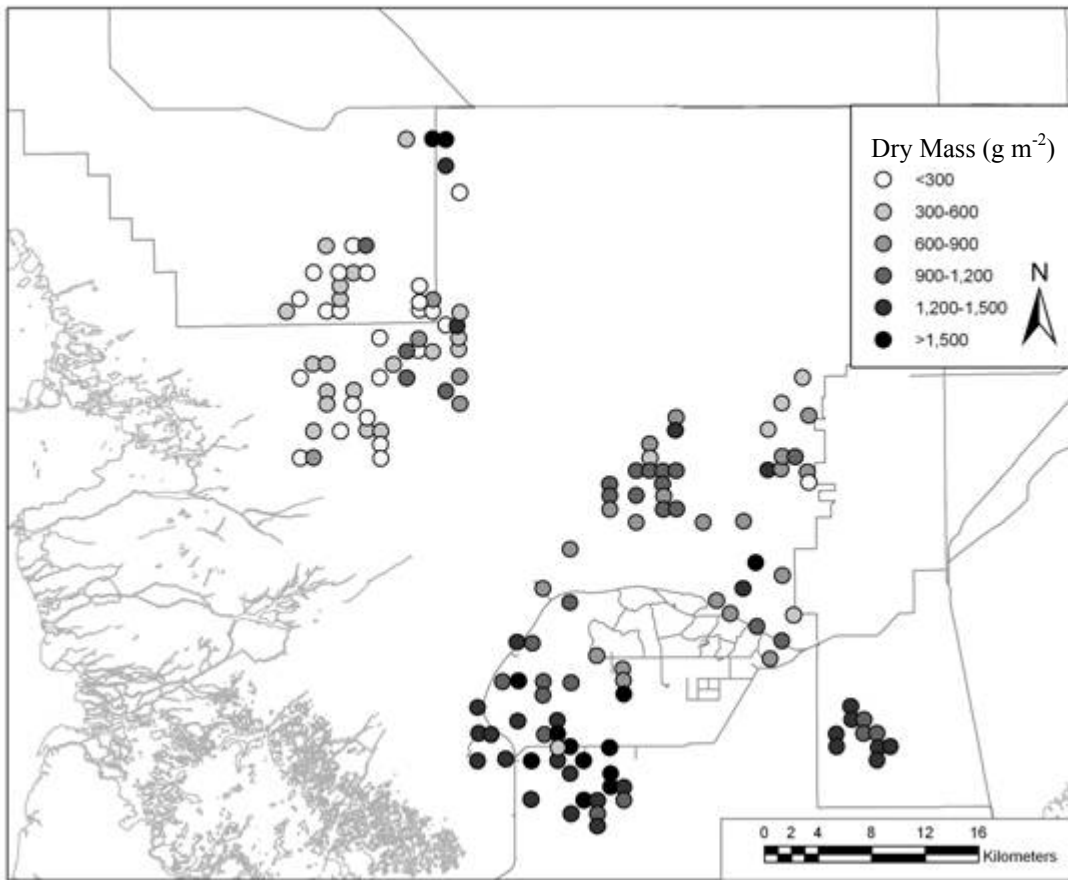


Figure 1.9. Mean periphyton ash-free dry biomass (AFDM) during the October 2003 periphyton census at locations in CSSP populations A-G.

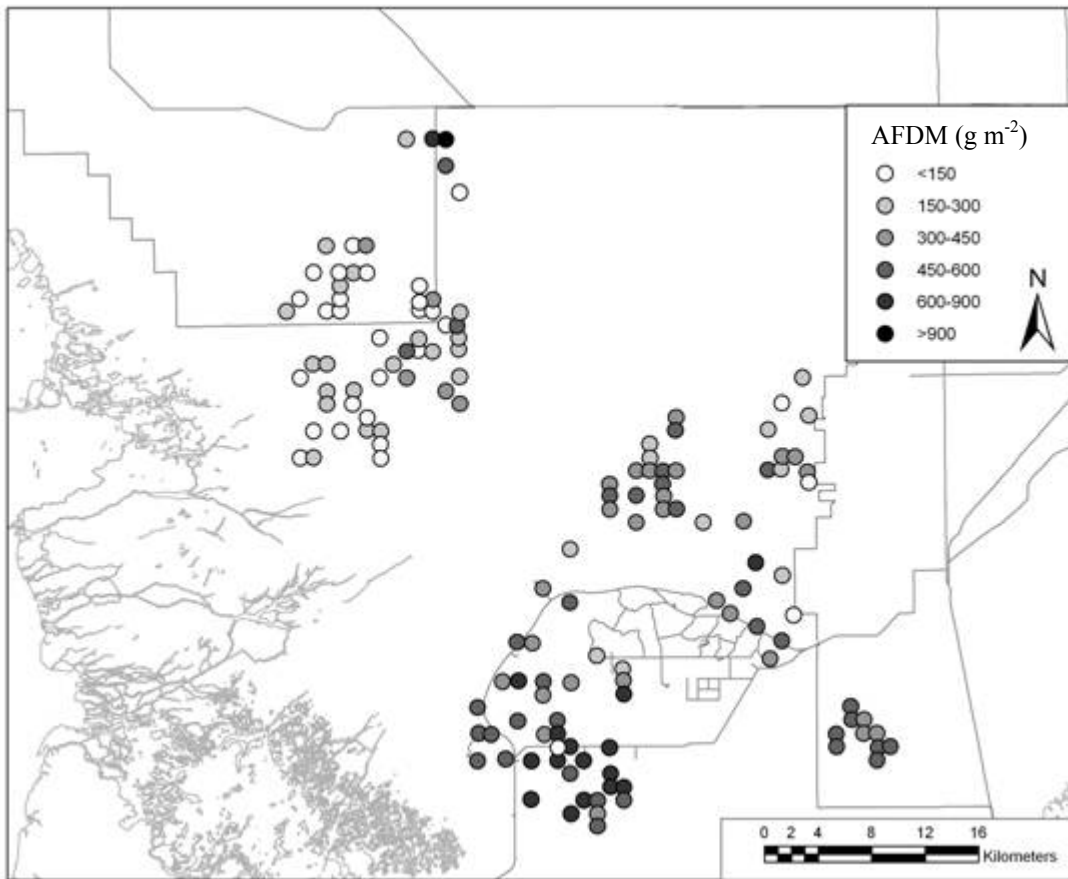


Figure 1.10. Mean periphyton organic matter content (%) during the October 2003 periphyton census at locations in CSSP populations A-G.

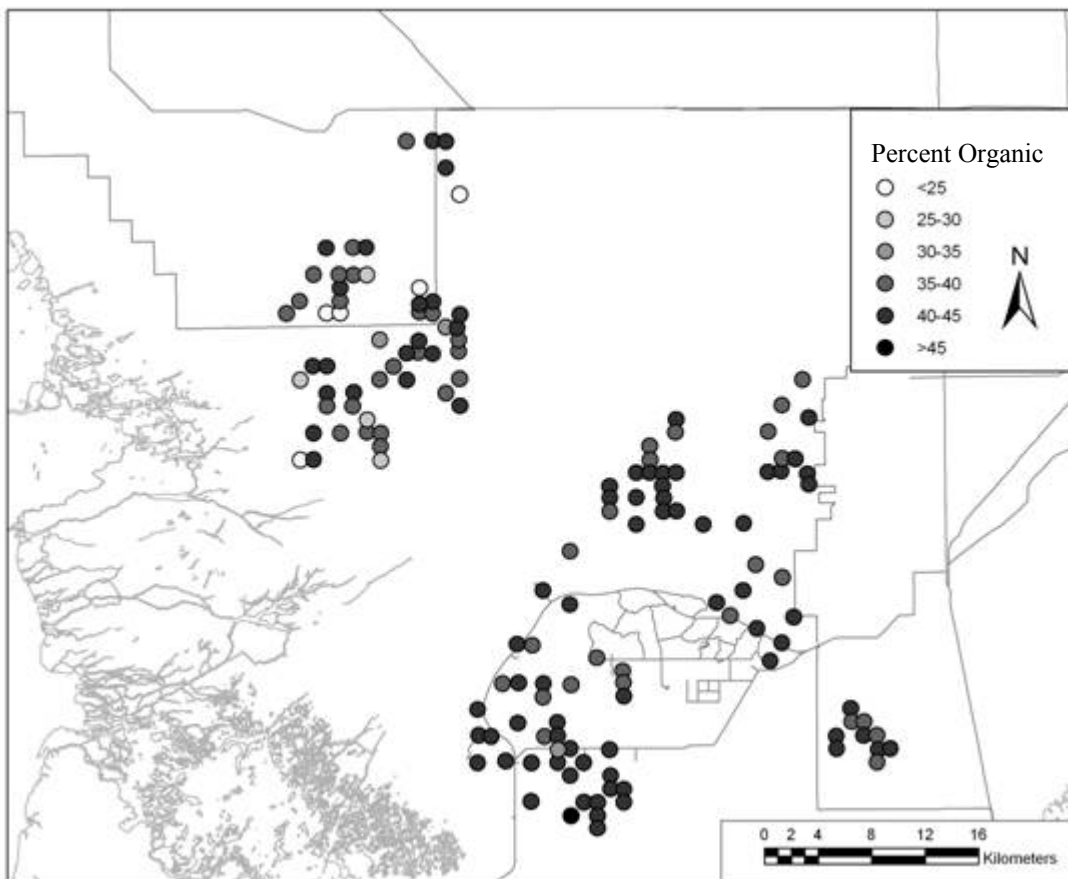


Figure 1.11. Mean periphyton chlorophyll *a* biomass during the October 2003 periphyton census at locations in CSSP populations A-G.

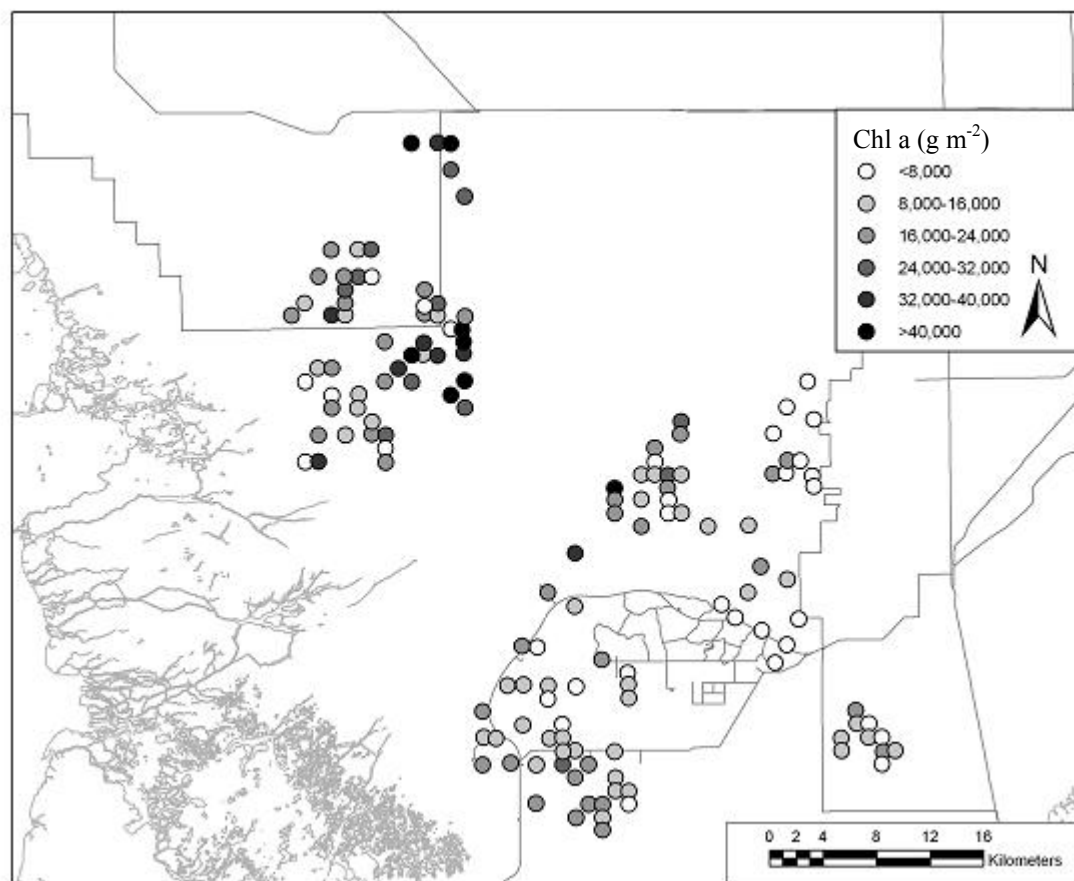


Figure 1.12. Mean periphyton total phosphorus (TP) content during the October 2003 periphyton census at locations in CSSP populations A-G.

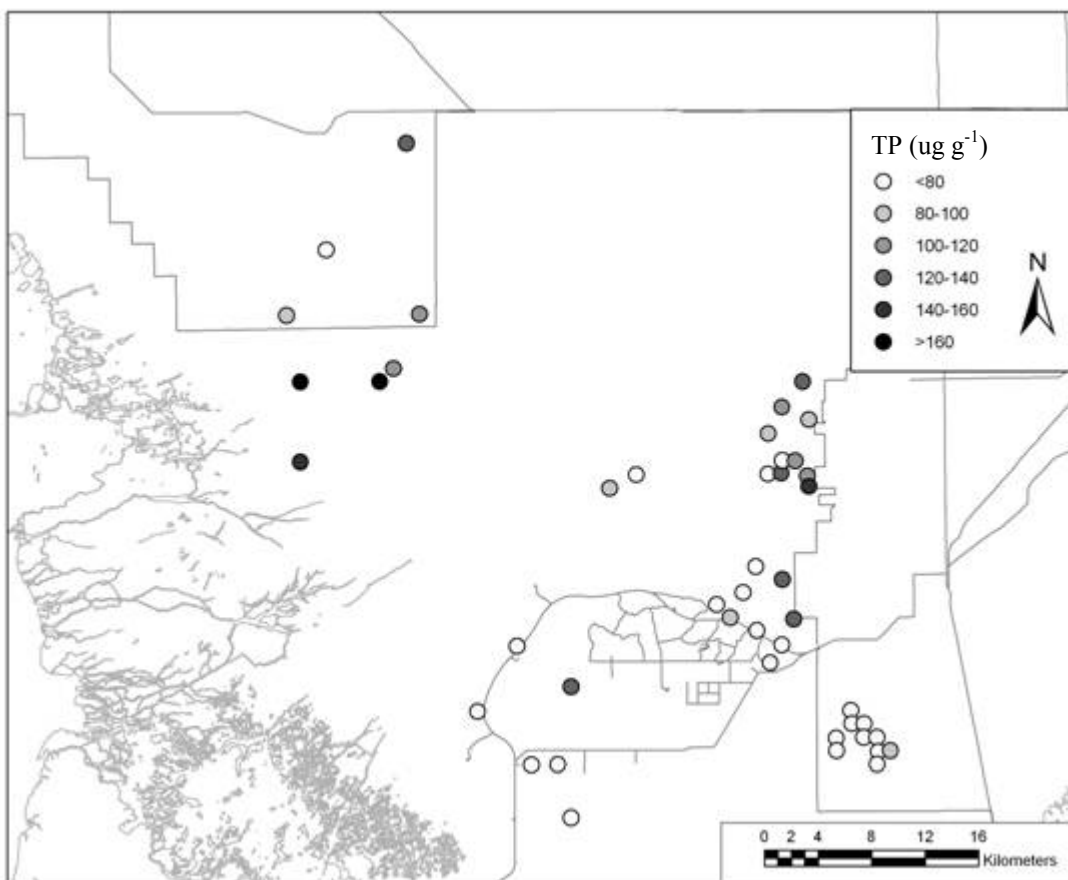


Figure 1.13. Means and standard deviation of water depth, periphyton dry and AFD biomass, chlorophyll a and total phosphorus content among the 6 marsh types. CM = *Cladium* Marsh, CRM = *Cladium/Rhynchospora* Marsh, CWP = *Cladium* Wet Prairie, MWP = *Muhlenbergia* Wet Prairie, RCM = *Rhynchospora/Cladium* Marsh, SWP = *Schizachyrium* Wet Prairie.

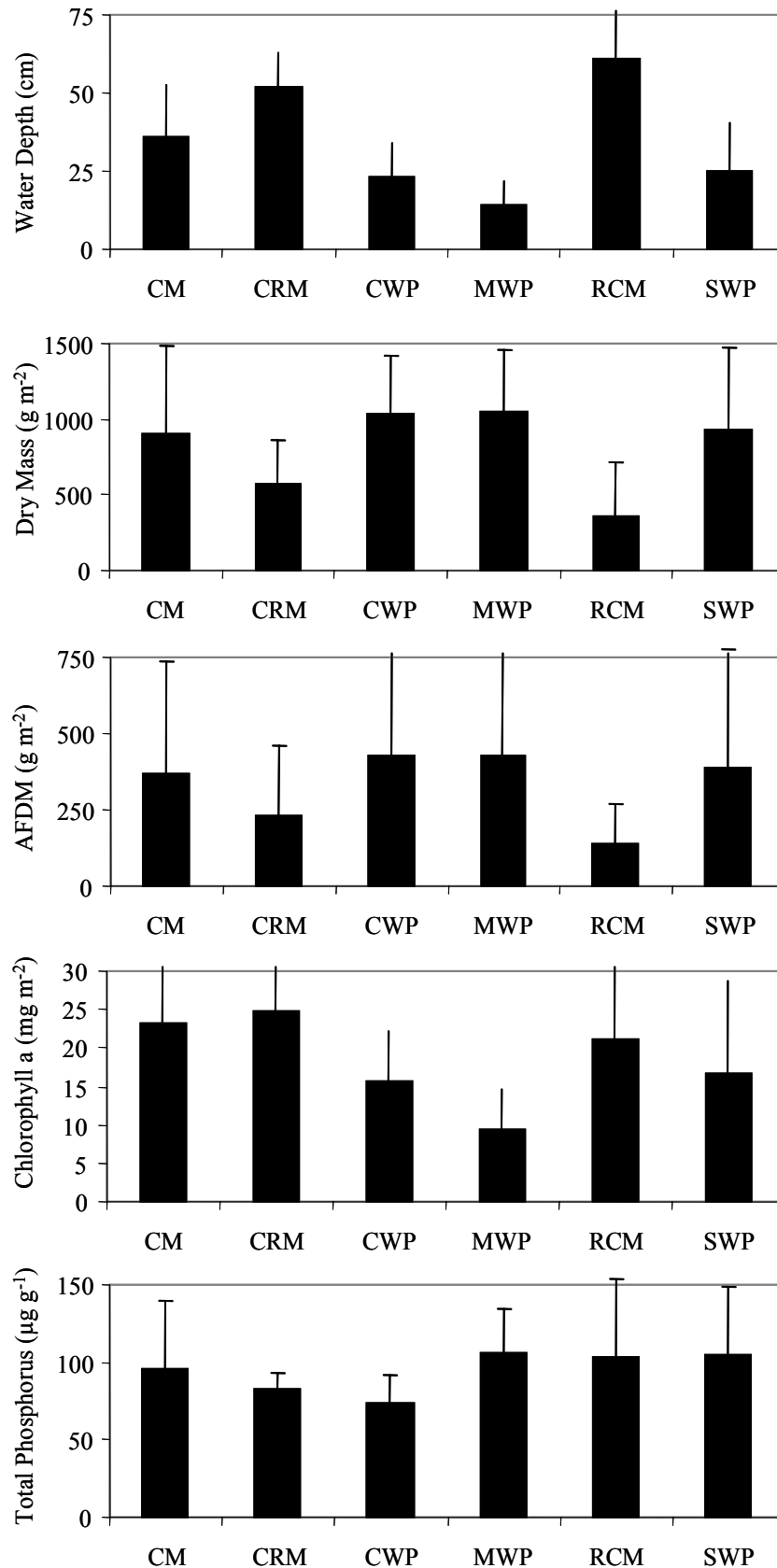
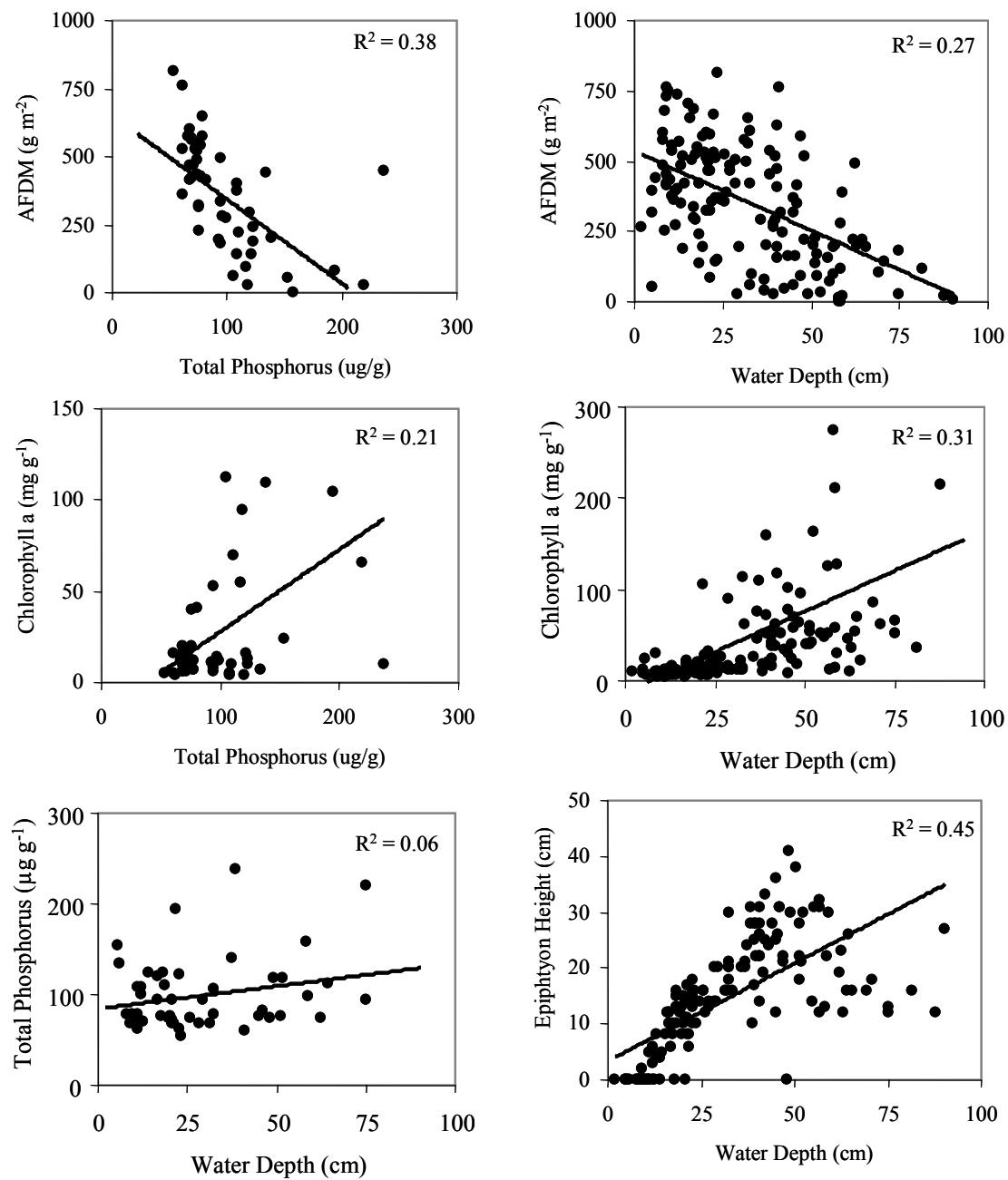


Figure 1.14. Relationships between periphyton total phosphorus content, ash-free dry (AFDM) biomass, chlorophyll *a* and water depth in the marl prairie.



B. PERIPHYTON DISTRIBUTION ACROSS HYDROLOGIC GRADIENTS IN THE EVERGLADES MARL PRAIRIE

Introduction

Large-scale surveys throughout the greater Everglades landscape have shown that periphyton distribution is largely controlled by water depth and nutrient availability (Gaiser et al., 2006, Gottlieb et al., 2006, Thomas et al., 2006). Because the Everglades landscape expresses very long gradients of both hydroperiod (from always dry to permanently flooded) and water depth (from zero to >2 meters), the overriding effect of water availability and depth on periphyton distribution at this scale is not surprising. However, although the shallow, short-hydroperiod marl prairie encompasses a large area of the Everglades and is likely the habitat type that will be most effected by changes in water management, no study has yet examined periphyton distribution across the relatively short hydrologic gradients expressed in this ecotype.

The Everglades marl prairie contains a mosaic of plant community types that have been also shown to exhibit strong relationships to hydrology. Wet prairie communities containing a mix of *Cladium*, *Muhlenbergia* and *Schoenus* are highly productive in the shallow regions prone to drying and frequent fire while marsh communities containing sedges such as *Rhynchospora* and *Eleocharis* are more prolific in wetter sites of longer hydroperiod (Ross et al., 2006). Both wet prairie and marsh communities have been shown to support highly productive periphyton communities that often exceed the biomass of associated plant communities (up to 2936 g m⁻² recorded with productivities exceeding 10,000 g C m⁻² yr⁻¹; Iwaniec et al., 2006; Ewe et al., 2006). However, whether hydrologic gradients have a similar effect on periphyton communities, either directly or indirectly through their associations with these plant community types, has not been explored.

The goal of this study was to (1) determine the distribution of periphyton along hydrologic gradients in the marl prairie and (2) determine linkages between periphyton distribution and plant community types.

Methods

Six transects were established in the marl prairie, purposefully positioned perpendicular to elevation gradients present in CCSP populations A-F (Fig. 2.1). The length of the transects varied depending on the size of the area and the length of the hydrologic gradient present; plots were positioned along sub-transects located every 100 m along the main transect except for the long transect in population B where plots were 200 m apart (Table 2.1).

Periphyton was surveyed along the transects using both observational and destructive sampling approaches. Both types of data were collected in conjunction with vegetation monitoring reported by Ross et al. (2006).

Table 2.1. Length of transects in CSSP populations A-F and the number of plots positioned along each transect.

Population	Transect Length (m)	Number of sub-transects
A	5000	51
B	11000	56
C	4000	39
D	2500	26
E	5000	51
F	3100	32

Observational Census

The observational census of periphyton took place during vegetation sampling during the dry seasons of 2003-2005. At each transect point, a 60-meter sub-transect was established perpendicular to the main transect and vegetation assessed and sampled according to Ross et al. (2006). Periphyton observations were made in 0.5 m² quadrats at 5 fixed locations along the sub-transect (5, 17, 29, 41 and 53 m) that coincided with vegetation structure measurements. Data recorded included abundance and height of epiphytic periphyton, cover of floating periphyton cover, benthic periphyton cover, moisture, thickness and color, vegetation height, closure and cover, dominant plant species, soil depth and type and water depth. Data were ranked by ordinal or independent categories according to Table 1.2.

Sampling Census

Periphyton was sampled at the transect sites in the wet season (October) of 2004 (Table 1.1). Rebar markers were located and periphyton was sampled at 3 sites within 50 m of the marker. A 625 cm² open-ended bucket driven into the periphyton/soil was used to isolate the sampling area and all periphyton was removed. Periphyton was cleared of debris (dead vegetation, rocks, large snails) and placed in a Ziploc bag on ice. Observational data were also recorded using the same criteria as in the dry season survey (Table 1.2). In the laboratory, periphyton samples were split into 4 subsamples which were (1) dried to constant weight at 100 °C for dry weight biomass followed by ashing at 1000 °C for determination of ash-free dry biomass, (2) extracted in acetone and analyzed for chlorophyll *a* by fluorometry and (3) frozen in a permanent archive.

Data Analysis

Hydroperiod for each point along the main transect was inferred from elevation data georeferenced to nearby water-level recorders (Ross et al. 2006). Parameters were averaged at each transect point and means were plotted by distance along the transect. Periphyton parameters were averaged within locations and then by population and vegetation community type category. Relationships between periphyton biomass, water depth and hydroperiod were explored through linear regression.

Results

Inferred hydroperiod along the transects varied from population to population from a low of 63 days at a point along transect F to a high of 308 days at a point along transect D (Fig. 2.2). Transects A and B represented a gradient from short to longer hydroperiods, while values along

the remaining transects varied from site to site in no particular direction. Hydroperiod was only weakly but significantly correlated to October 2004 water depth ($R^2=0.14$).

Observational Census

Two observational parameters from the periphyton census were weakly driven by water level and/or hydroperiod (Fig. 2.2). These included epiphyte height and floating mat cover. Epiphyte height was weakly but significantly related to hydroperiod ($R^2=0.16$) and water depth ($R^2=0.14$). Floating mat was only present in sites with deeper water ($R^2=0.14$). Benthic mat cover and thickness were unrelated to water depth or hydroperiod among transects.

Sampling Census

Much stronger hydrologic relationships were found in the quantitative periphyton data collected during the sampling census. Transect A showed a strong trend of decreasing periphyton biomass toward the center of the transect (Fig. 2.3) where hydroperiod was longest and water deepest. Population B also had peak values at the east end of the transect where values exceeding 3000 g AFDM m^{-2} were found. Relationships to soil depth and vegetation height and cover were weak (Fig. 2.4). While hydroperiod did not explain a significant proportion of variation in periphyton biomass across transects, water depth was significantly and negatively correlated with periphyton ash-free dry mass (Figs. 2.5, 2.6). Across transects, periphyton biomass was highest in wet prairie habitat where water was shallowest and lowest in marsh communities where water was deepest, while vegetation height, closure and cover were unrelated to marsh community type (Fig. 2.7).

At a larger scale, periphyton attributes differed among marsh and wet prairie communities (Table 2.2). Periphyton ash-free dry mass and chlorophyll *a* were highest in the wet prairie where water was shallower and hydroperiod shorter and lowest in the marsh where water was deeper and hydroperiod longer. Epiphyte height was greater in the deeper water marsh habitat, where soils were also deeper and vegetation cover slightly higher.

Table 2.2. Means and standard deviation () of parameters that differed significantly ($P<0.001$) between marsh and wet prairie sites.

Parameter	Marsh	Wet Prairie
N	67	187
Dry Season Water Depth (cm)	7 (5)	1 (2)
Wet Season Water Depth (cm)	16 (12)	9 (10)
Hydroperiod (days)	250 (25)	190 (50)
Vegetation Cover	35 (11)	30 (13)
Soil Type	1.5 (0.5)	1.1 (0.3)
Wet Season Ash-Free Dry Mass (g m^{-2})	320 (170)	520 (310)
Wet Season Chlorophyll <i>a</i> (mg m^{-2})	40 (25)	60 (30)
Wet Season Epiphyte Height (cm)	7 (7)	5 (7)
Dry Season Epiphyton Height (cm)	15 (8)	5 (6)
Dry Season Floating Cover	0.3 (0.4)	0.05 (0.18)

Discussion

One of the more striking findings in this study was the absence of a strong relationship within or among transects of periphyton attributes to hydroperiod. While other studies have shown very strong effects of hydroperiod on periphyton production, composition and structural attributes, these studies have been conducted along very long gradients from sites that are rarely wet to those that are flooded continuously (Gottlieb et al., 2006). The present study focused on short-hydroperiod sites, all with measurable but shorter than 1-year hydroperiods. In a related study (section 7.3 in this report) we found that periphyton recovers remarkably fast (within ~ 5 days) following re-hydration after flooding. It is this response that allows periphyton to be highly productive throughout the range of short-hydroperiod habitats present in the marl prairie.

Although strong relationships to hydroperiod were not detected in this study, we did find a strong response of periphyton biomass to water depth. Across the shallow range studied here (0-50 cm), this relationship is negative: periphyton biomass declines as water deepens. The true form of this relationship is probably unimodal, with the driest of sites having very little periphyton, but such extremely dry sites were omitted from this study. The decrease in periphyton biomass as water deepens is counter-intuitive yet has been shown elsewhere in the Everglades system (Gaiser et al., 2005; Gottlieb et al., 2006; Iwaniec et al., 2006). Indeed, periphyton seems to be most productive in water ranging from about 10-30 cm, where consolidated sediments or limestone bedrock provides a solid surface for dense benthic mat formation and plant density is low enough to prevent heavy shading.

Biomass estimates across the hydrologic and water depth gradients studied exceed those measured for other parts of the Everglades (Gaiser et al., 2006) and, by orders of magnitude, those reported in other wetlands globally (Hall et al., In Press). While calcite comprises about 70% of the dry biomass of these mats, this does not explain the high estimates, as these are expressed in ash-free (organic) units (mean = 450 g AFDM m⁻²). This study confirms that shallow marl prairie wetlands are among the most productive habitats in the world, even though they are subject to the extreme stresses of limited nutrient availability and variable moisture.

Among the rapid measurements taken during the observational census, the most reliable estimate for tracking water depth was epiphyton height. When present, periphyton covered most surfaces, including the stems of emergent grasses. The height of periphyton colonization reflects the depth of submersion of the host plant stem in the water. This can be a useful metric of water depth, particularly after sites have dried, as dried epiphyton remains on the plant stems and the height can still be measured. This explains the significant correlation between dry season epiphyton height and water depth of the previous wet season.

Although periphyton differences among the 9 plant community types were somewhat ambiguous, strong patterns were detected when communities were grouped as “marsh” or “wet prairie”. Periphyton biomass was highest in wet prairie sites where water depth was shallower and plant cover lowest. However, epiphyton height and floating periphyton cover were highest in the marsh sites where deeper water allowed for higher epiphyton colonization while also encouraging growth of floating periphyton mats on submersed plants such as *Utricularia purpurea*.

Overall, this study points to some predictions about periphyton response to changing hydrology within the Everglades marl prairie. While alterations in hydroperiod within a 3-9 month window may not directly instigate major changes in periphyton production, if such a manipulation resulted in a change in wet season water depths within a narrow 10-50 cm window, significant alterations to the periphyton community would be expected. While increased water levels in the marl prairie would mean a drop in periphyton production, a change in this direction is not necessarily a negative result for the ecosystem. Periphyton in marl prairie habitats prone to a deeper flooding regime would become more like those in adjacent marshes and sloughs. Slough periphyton is characterized as having a greater organic content than prairie periphyton (70 vs. 30 %; Gaiser et al., 2006), and is, therefore, more edible to grazers even though it may not be as productive. Slough periphyton is also more 3-dimensional; rather than a carpet of benthic mat, sloughs contain periphyton that is suspended in the water column, and therefore accessible to a wider diversity of aquatic and terrestrial grazers. In summary, this study shows the importance of scaling in interpreting responses of various indicators to environmental gradients. At the landscape scale, hydrology remains one of the primary controlling variables of periphyton biomass; however, within the marl prairie, water depth, rather than duration, has an overriding influence on periphyton attributes.

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Datasets

Transect Periphyton Description.xls

Transect 2004 Periphyton Data.xls

Figure 2.1. Location of transects sampled for periphyton in October 2004 in CSSP populations A-F superimposed on locations sampled for vegetation.

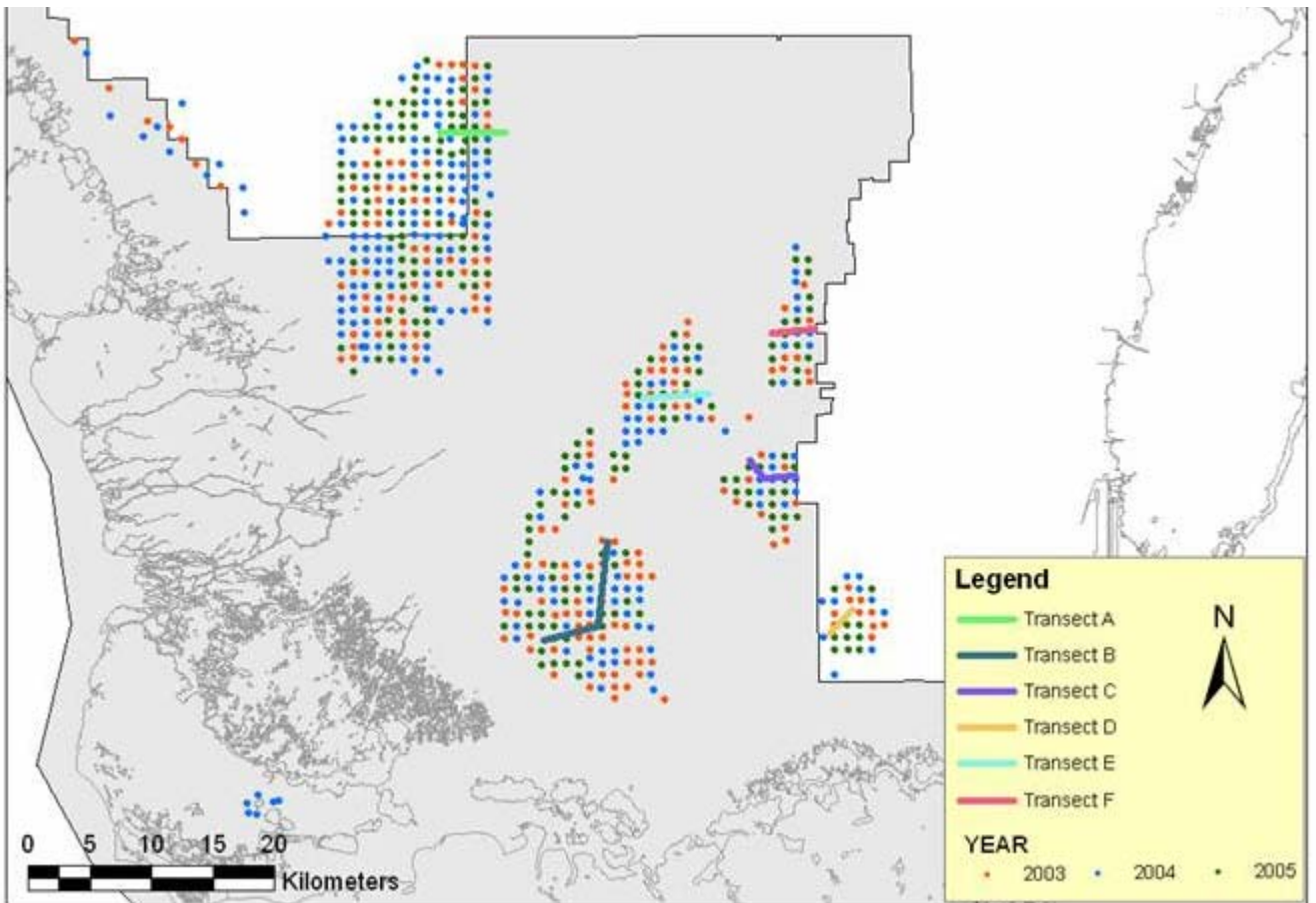


Figure 2.2. Mean hydroperiod, water depth, epiphyte height and floating and benthic periphyton cover along transects in populations A-F during wet (2004) and dry (2003-2005) seasons.

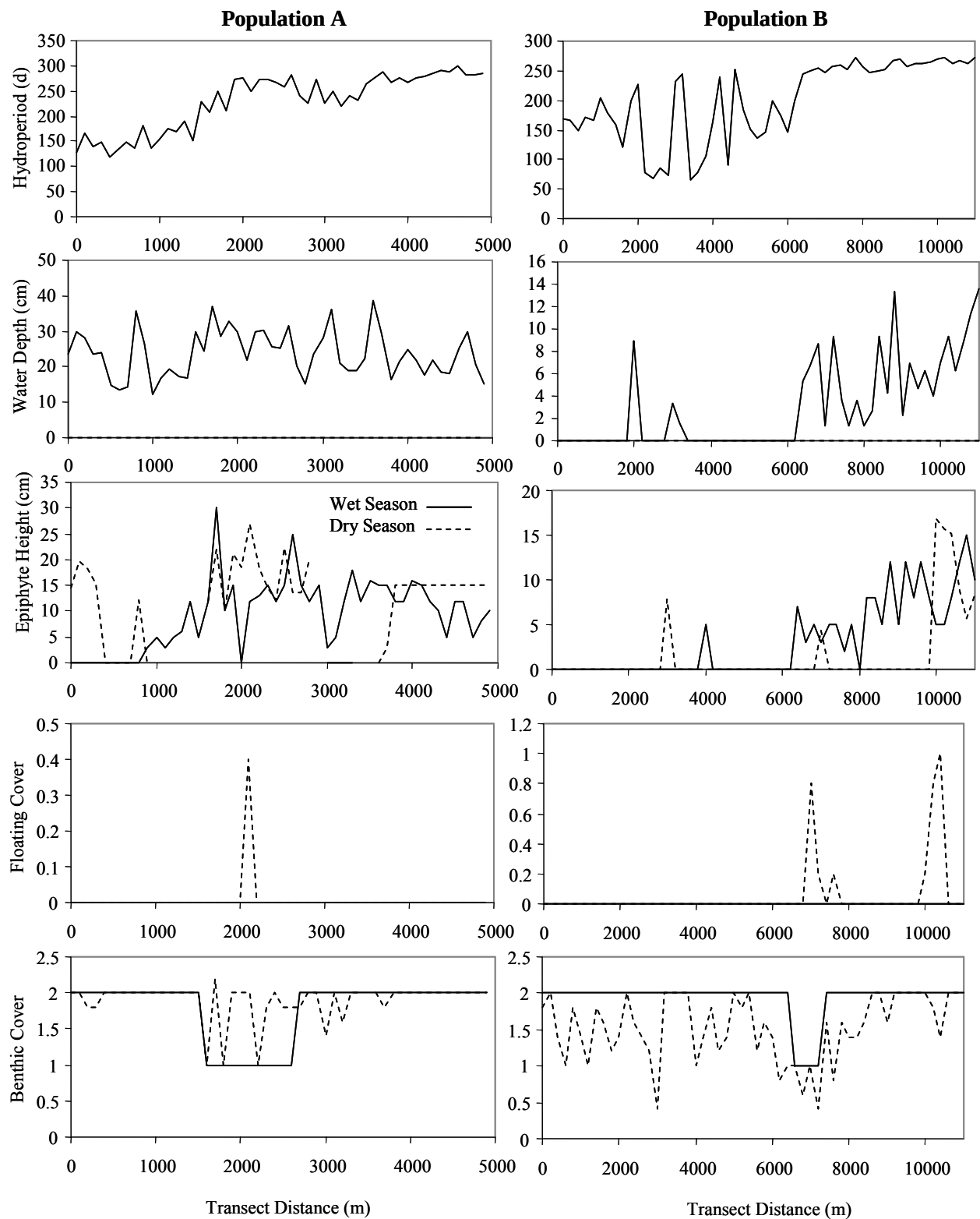


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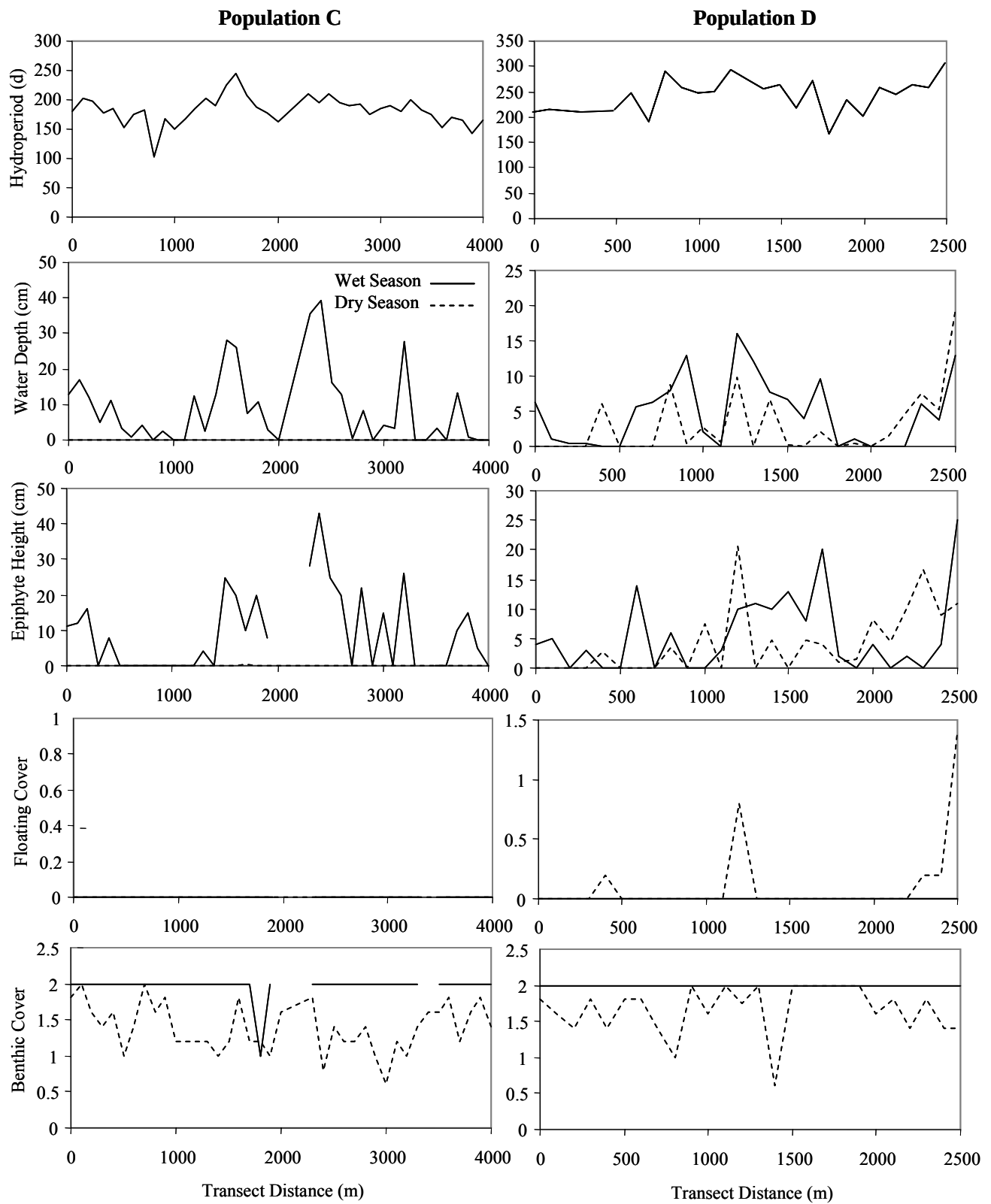


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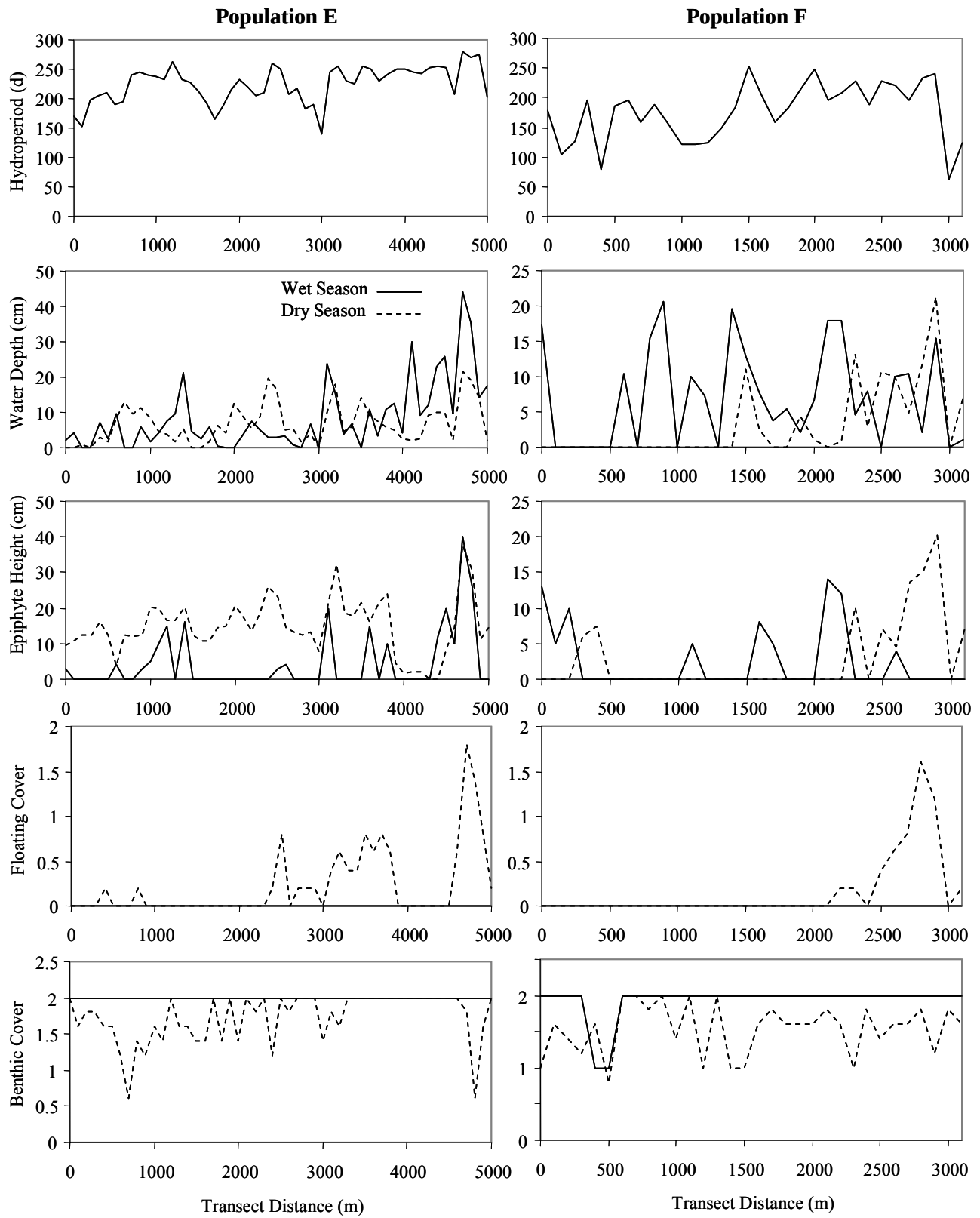


Figure 2.3. Periphyton dry mass, ash-free dry mass and chlorophyll *a* across transects in populations A-F.

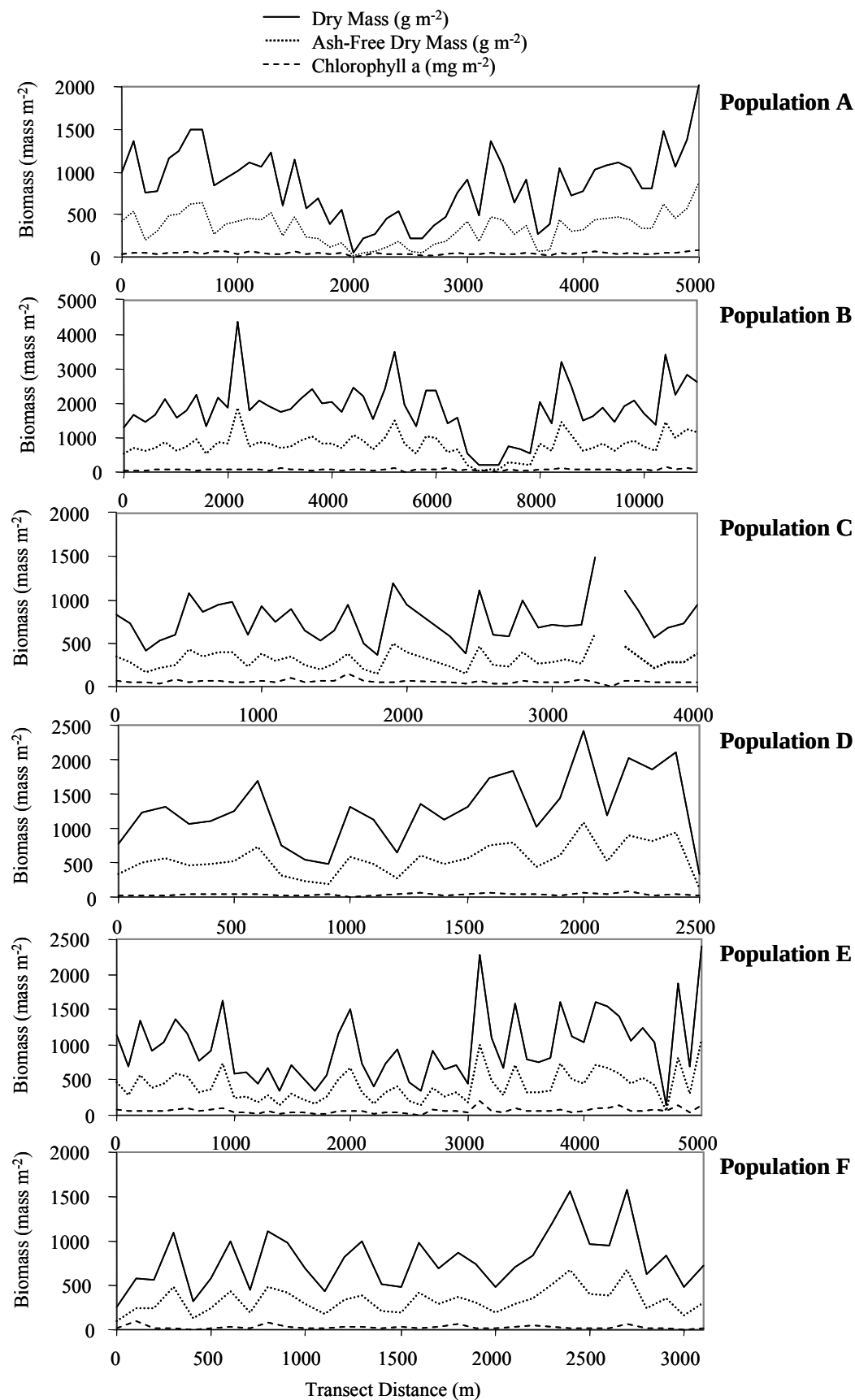


Figure 2.4. Vegetation height and cover and soil depth across transects in populations A-F.

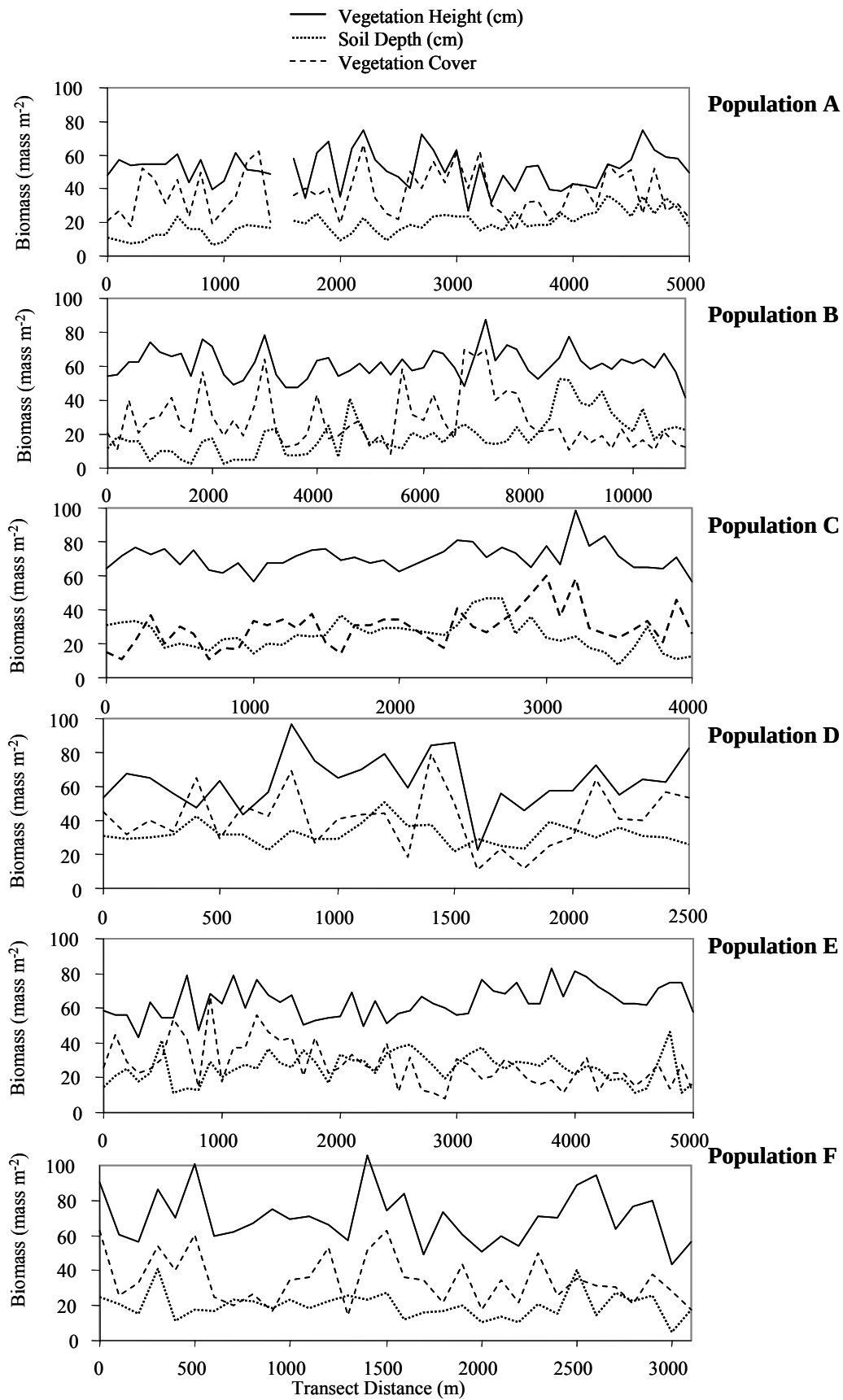


Figure 2.5. Relationships between periphyton ash-free dry biomass and hydroperiod and water depth across transaction points, coded by population.

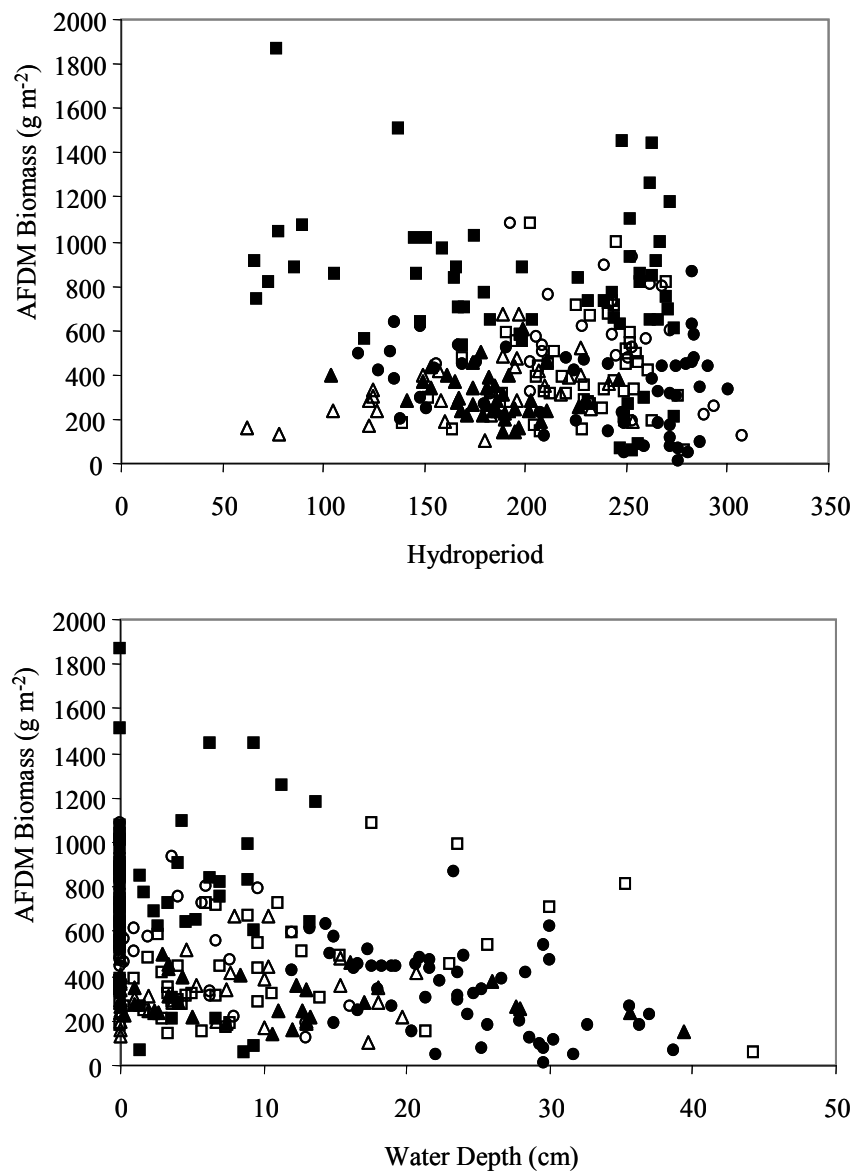


Figure 2.6. Relationships between periphyton ash-free dry biomass and hydroperiod and water depth across transaction points, coded by plant community type. CM = *Cladium* Marsh, CRM = *Cladium/Rhynchospora* Marsh, CWP = *Cladium* Wet Prairie, MWP = *Muhlenbergia* Wet Prairie, PCM = *Paspalum/Cladium* Marsh, SCWP = *Schizachyrium* Wet Prairie, SOWP = *Schoenus* Wet Prairie.

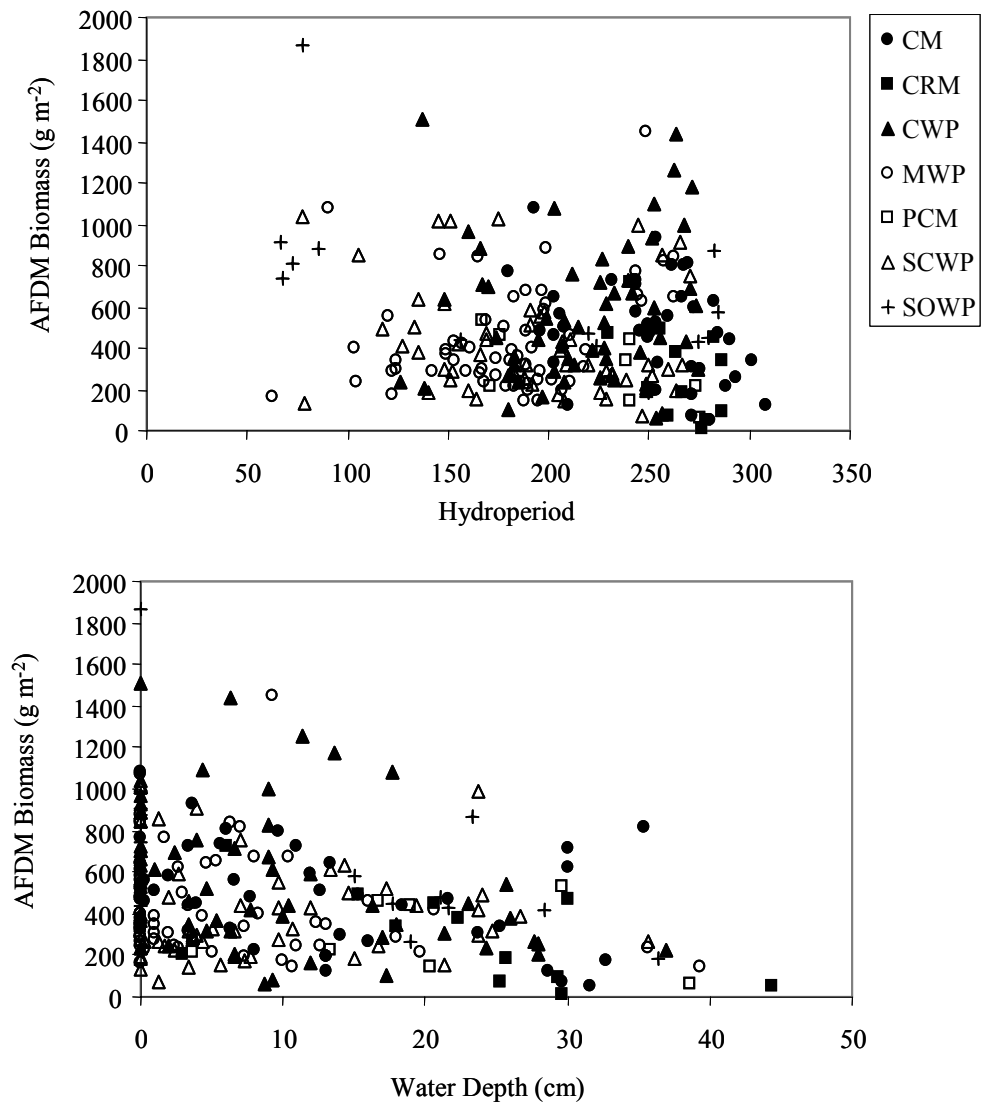
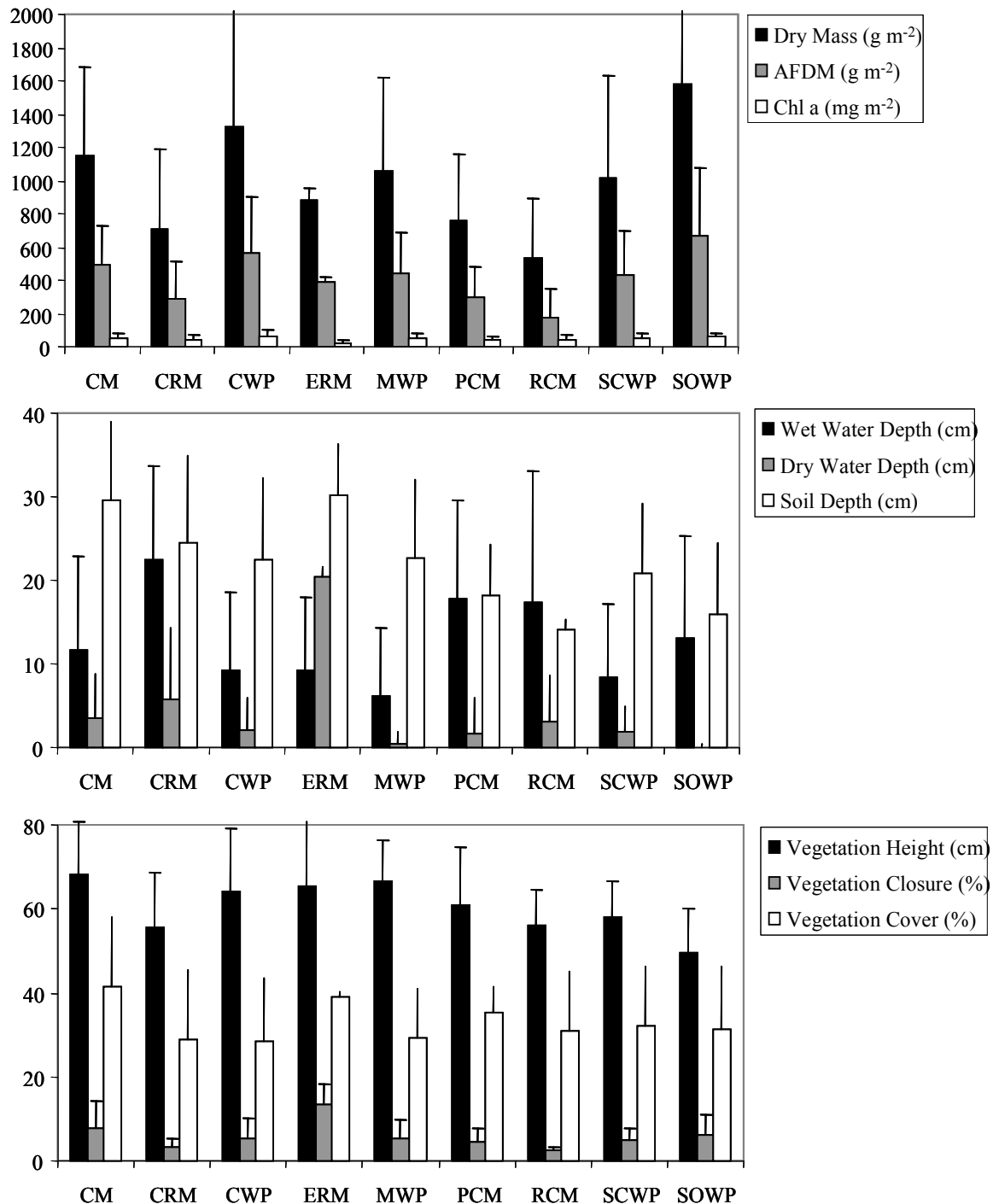


Figure 2.7. Mean and standard deviation of periphyton dry mass, ash-free dry mass and chlorophyll a, wet and dry season water and soil depth, and vegetation height, closure and cover across the 9 vegetation types in the 6 CSSP populations. CM = *Cladium* Marsh, CRM = *Cladium/Rhynchospora* Marsh, CWP = *Cladium* Wet Prairie, MWP = *Muhlenbergia* Wet Prairie, PCM = *Paspalum/Cladium* Marsh, SCWP = *Schizachyrium* Wet Prairie, SOWP = *Schoenus* Wet Prairie.



C. EFFECTS OF DRYING AND REWETTING ON PERIPHYTON GROWTH IN THE EVERGLADES MARL PRAIRIE

Introduction

The Everglades is a subtropical, oligotrophic, alkaline wetland strongly depleted in phosphorus (P), where the distribution of vascular vegetation, microbial communities and consumers across wetland landscape is primarily controlled by hydroperiod. When flooded, thick periphyton mats support the food web and control the concentration of dissolved substances (including nutrients and gasses) in the water column (e.g. reviewed in Noe et al., 2001; Dodds, 2003). During the dry state, periphyton turns into an apparently dormant crust, the ecological importance of which has yet to be examined.

The ability of many prokaryotic and eukaryotic algae to withstand severe and prolonged drying has been widely documented (e.g. Bristol, 1920, Evans, 1958, 1959, Hostetter and Hoshaw, 1970) even in deserts (e.g. Wynn-Williams, 2000). Most studies have focused on drought-tolerant cyanobacteria (e.g. Whitton and Potts, 2000), the effect of desiccation duration on algal survival (e.g. Morison and Sheath, 1985, Peterson, 1987, Caiola et al., 1996, Shaver et al., 1997, Mosisch, 2001), algal recovery upon rehydration (e.g. Evans, 1958, 1959, Mosisch, 2001), and specific mechanisms of recovery (e.g. Garcia-Pichel and Pringault, 2001). Yet, the mechanism of desiccation tolerance, particularly at the community level, is not well understood. However, Gottlieb et al. (2005) recently manipulated drought duration for periphyton from short- and long-hydroperiod Everglades wetlands and found that desiccation resistant algae were encouraged in long-hydroperiod communities exposed to uncharacteristically long (1-month) drought. Short hydroperiod periphyton communities already containing these taxa recovered more quickly after reflooding than long-hydroperiod communities. While this study contributed to our understanding of community response to drying, it did not examine the short-term changes in nutrient efflux and periphyton metabolism in the dynamic period following rehydration. Moreover, because natural marsh water containing live organisms was used for rewetting the periphyton, it is unclear whether periphyton could have recovered on its own, as it is the case prior to establish flooding conditions in the Everglades wet prairies. Inundation is characterized by high rates of biogeochemical reactions compared to that of the established flooded and dry states and thus a decisive episode for the ecosystem which deserves to be examined (qualified as "hot moment"; McClain et al., 2003).

Thus, we conducted a study to determine the short-term temporal dynamics of dried periphyton communities immediately following rehydration, in settings similar to that of Gottlieb et al. (2005) but with the addition of a fixed volume of water containing no P and no exogenous algae. In this way, we mimic natural hydrologic conditions at the onset of the wet season when heavy downpours inundate dry parts of the pristine Everglades wet prairie. Rainwater in this region is typically low in TP ($<7.9 \mu\text{g TP}\cdot\text{L}^{-1}$; Ahn, 1999) and contributes very little to P inputs compared to P atmospheric deposition (e.g. Noe et al., 2001).

In addition to following periphyton metabolism (photosynthesis, respiration), taxonomic and bacterial composition after rehydration, we also link water TP dynamics to periphyton desorption and/or uptake upon recovery. Everglades periphyton has been shown to be very efficient in

scavenging P from the water column and storing it more or less permanently in continuously flooded habitats (e.g. Noe et al., 2001). Moreover, measurements of TP concentration subsequent to evaporation will illustrate the capability of recovered periphyton to regulate water P concentrations (Jones and Amador, 1992, Gaiser et al., 2004). Finally, parallel to the microcosm experiment, we also assess how much P can potentially be released from ground crusts prior to biological revival to evaluate to what extent periphyton sequesters permanently P after drying.

Materials and methods

Periphyton collection

Periphyton crusts were collected one week before flooding from the marl prairie Everglades wetlands area in Everglades National Park (N25° 17.553' W80° 27.492'). Periphyton had colonized for 3 years following scraping to the bedrock substrate and was distinctly layered into a compact top 1–2 mm grey/brown layer and a loose ~13 mm tan bottom layer.

Periphyton characterization

Crusts were dried to determine water content. Once ground, four subsamples of dried ground crust (DGC) were analyzed for TP (EPA, 1983) and TN (Nelson and Sommers, 1996). Six 100–g DGC portions were also decalcified overnight in an HCl solution (2 L of 1 N HCl; pH ~ 4), then condensed to pellets by centrifugation. Pellets were dried, weighed, then pooled and mixed with 1% EDTA for 48 hours. The mixture was centrifuged to separate the cellular material in the pellet from the polysaccharides in the supernatant. The supernatant was mixed with ethanol (1:1) in a freezer to condense the polysaccharides, which were centrifuged, dried, and weighed.

Maximized TP desorption from the crusts

Four 2–g DGC portions were mixed in centrifuge tubes containing 25 ml of artificial marsh water for 24 hours. One liter of AMW contains 23 mg NaHCO₃, 1 mg KCl, 1 mg MgSO₄×7H₂O, 11 mg MgCl₂×6H₂O, and 46 mg CaCl₂×2H₂O (Jones and Amador, 1992). After centrifuging, the supernatant was analyzed for TP (APHA, 1999) and the pellet was reused for 6 subsequent TP extractions. The cumulative TP release normalized to the TP concentration in the initial crust was fitted with an exponential equation used to simulate pollutant accumulation in water runoff (Hubert and Dickinson, 1988): $\alpha(1-\text{EXP}(-\beta t))$, α and β are constants.

Periphyton crust rehydration

Three microcosms (51×37×14 cm, L×W×H) containing 841, 805 and 617 g fresh weight of periphyton crusts were placed in a greenhouse. The experiment began after each tray was filled with 20 L of AMW (10 cm water depth), which was not compensated for evaporative losses.

Water sampling and characterization

Water depth, conductivity, temperature and pH were measured daily in the microcosms. After gently mixing the water in the microcosm, a water sample (20 mL) was taken for TP analysis (APHA, 1999) at $\frac{1}{12}$, 0.5, 1, 4, 8 and 12 hours the first day, once a day for the next 7 days and then once every 3–4 days.

Periphyton metabolism

Photosynthesis and respiration in each chamber were measured with the oxygen method by incubating one periphyton core (1.9 cm²) in a light/dark BOD bottle filled with AMW.

Incubations were performed daily during the first week, then every 3–4 days. On day 20, in addition to regular incubations, the top and bottom layers were incubated separately. PPFD was recorded at the level of the bottles with an underwater LI–COR flat sensor.

Changes in dissolved oxygen (DO) were measured with a self–stirring YSI BOD DO probe and a YSI 52 DO meter. DO changes were converted into carbon units as described for periphyton in McCormick et al. (1998). GPP was PPFD–corrected and normalized to the surface area of the cores (GPP–area) and per unit of algal biovolume (GPP–biov).

Biomass, TP, TN and PMEase activity of periphyton

Following incubations, each periphyton core was homogenized in the BOD bottle. The suspension was then treated as a lake water sample (APHA, 1999) and was subsampled to determine DW, AFDW, chlorophyll *a* (Chl *a*), TP, TN and PMEase activity. Chl *a* was determined after acetonic extraction with a Gilford FLUORO IV spectrofluorometer (excitation 435 nm, emission 667 nm). PMEase activity was measured by mixing 200 µL of sample with 50 µL of 50 µM 4–methylumbelliferyl phosphate (MUFP). Upon 2–hours of incubation in the dark, fluorescent MUF was determined with a Cytofluor 4000 fluorometer (excitation 360 nm, emission 460 nm).

Algal enumeration

For each microcosm, three standard cores were sampled after flooding, then every 6–7 days. The cores were homogenized in 100 mL of deionized water and a 0.2 mL subsample was used for algal enumeration at 1000× magnification. Morphotypes were identified using Prescott (1962), Komárek and Anagnostidis (1986, 1989, 1999) and Komárek and Hindak (1975).

Enumeration of total bacteria and cyanobacteria under epifluorescence

One standard core was collected from each microcosm after 0, 3, 6, 13 and 20 days of flooding. Each core was mixed to a paste and 2 subsamples were homogenized with 2.5% (v/v) glutaraldehyde. Bacteria were stained with the DNA stain SYBR green. After filtration (Poretics 0.2 µm pore size), bacteria were enumerated under blue excitation (Weinbauer et al., 1998). Cyanobacteria were quantified under green excitation (546 nm).

Data analysis

For a given variable, data were pooled over the microcosms and tested for normality and variance homoscedasticity. Then, a one-way ANOVA was conducted to test for significant temporal differences. Differences between the top and bottom layers on day 20 were compared with Student's T-tests. Algal composition was compared among sample intervals using a one–way Analysis of Similarity (ANOSIM, using PRIMER 5.2.9[®] software) employing the Bray–Curtis similarity metric on relativized, fourth–root transformed species abundance and biovolume data. The global *r* statistic was used to define the similarity among samples with bootstrapped significance level of *P*<0.05 (Clarke and Warwick, 1994).

Results

Environmental variables

PPFD was 11 mol photons $\text{m}^{-2} \text{d}^{-1}$ and water temperature 28–33°C during the first 5 days, increasing thereafter to 20 mol photons $\text{m}^{-2} \text{d}^{-1}$ and 38.5°C. The pH increased steadily from 8.1 to 9.5. During the first four hours of flooding, conductivity rose from 142 $\mu\text{S}/\text{cm}$ to 945 $\mu\text{S}/\text{cm}$ in microcosms A and B and 650 $\mu\text{S}/\text{cm}$ in C. Then, it increased gradually to 1134, 1283 and 803 $\mu\text{S}/\text{cm}$ for microcosms A, B and C, respectively. The evaporation rate in the trays averaged 4 mm/d (13.5 L lost).

Crust characteristics

Before rehydration, the crust contained 15% of water, 119 μg TP/g and 7.6 mg TN/g DW, AFDW and Chl *a* did not change significantly over time and averaged 356 mg/cm^2 , 62 mg/cm^2 and 79.9 μg Chl *a*/ cm^2 , respectively (Table 3.1). The organic fraction contained 10.7% cells and 3.8% polysaccharide.

No significant differences in TN, N:P ratio and Chl *a* were found between the top and bottom layers after 20 days of wetting, but stratigraphic differences in DW, AFDW, organic content and TP were significant (Table 3.1). The top layer accounted for 23% of the total crust DW, 34% of the total AFDW, and 40% of the TP.

Table 3.1: Characteristics of the periphyton mat ($\pm$ S.D.) during the whole study († , $n=72$), in the dry ground crust ($^\#$, $n=6$), and for 20-day old mat (‡ , $n=6$). Significant differences between top and bottom layers are shown by * ($P<0.05$) and *** ($P<0.001$).

	All layers	Top layer	Bottom layer	T test
Dry weight (mg cm^{-2})	356 $\pm$ 69 †	87 $\pm$ 13 ‡	313 $\pm$ 89 ‡	***
AFDW (mg cm^{-2})	62 $\pm$ 10 †	23 $\pm$ 2 ‡	45 $\pm$ 10 ‡	***
Organic content (%)	17.1 $\pm$ 1.7 †	26.5 $\pm$ 2.2 ‡	14.6 $\pm$ 1.4 ‡	***
Chl <i>a</i> ($\mu\text{g cm}^{-2}$)	79.9 $\pm$ 16.5 †	55.4 $\pm$ 9.5 ‡	67.3 $\pm$ 20.9 ‡	
TN (mg g DW $^{-1}$)	7.6 $\pm$ 3.0 $^\#$	5.9 $\pm$ 2.1 ‡	3.0 $\pm$ 0.7 ‡	
TP ($\mu\text{g g DW}^{-1}$)	118.6 $\pm$ 1.9 $^\#$	196.6 $\pm$ 12.4 ‡	91.5 $\pm$ 31.1 ‡	*
Molar N:P ratio	64 $\pm$ 31 $^\#$	51 $\pm$ 14 ‡	83 $\pm$ 42 ‡	
GPP ($\mu\text{g C cm}^{-2} (\text{mol photon m}^{-2})^{-1}$)	1.8 $\pm$ 0.5 ‡	1.9 $\pm$ 0.1 ‡	0.2 $\pm$ 0.0 ‡	***
Respiration ($\mu\text{g C cm}^{-2} \text{h}^{-1}$)	7.5 $\pm$ 0.8 ‡	3.9 $\pm$ 0.4 ‡	8.0 $\pm$ 2.1 ‡	*

Algal composition

Thirty-nine different morphotypes were identified (Table 3.2) but no patterns based on taxonomy or algal group (filamentous/coccoid cyanobacteria, green or diatoms) using relative abundance or biovolume could be identified over time. The crust was dominated volumetrically by filamentous cyanobacteria (72.1% of the total biovolume; 3.4% of the cells). This group was mainly represented by the large *Scytonema hoffmanii* (64.3% of the total biovolume), while small coccoid cyanobacteria dominated numerically (95.6% of the cells; 17.7% of the total biovolume). The latter consisted of 1–3 μm long solitary or aggregated undetermined algae, *Chroococcidiopsis* sp., *Aphanothece* sp. and *Gloeothece* sp.. Green algae and diatoms accounted for 7.9% and 2.2% of the total biovolume. When pooled together they represented 1.0% of all

algal cells. Dominant green algae included *Pediastrum obtusum* and *Scenedesmus* sp. and the diatom flora was dominated by *Encyonema* spp. and *Nitzschia* spp..

Table 3.2. List of the 39 taxa observed in the mat during the whole study and their associated individual biovolume.

Taxa	Individual biovolume (μm^3)	Taxa	Individual biovolume (μm^3)
<u>Cyanobacteria</u>		<u>Green algae (Chlorophyta)</u>	
<i>Filamentous</i>		Undetermined coccoid 1	61
Undetermined 1 (sheath, 0.8-1 μm width)	79	Undetermined coccoid 2	228
Undetermined 2 (sheath 1.5 μm width)	138	<i>Characium</i> spp.	301
Undetermined 3 (sheath 1.5-2 μm width)	214	<i>Pediastrum obtusum</i>	400
Undetermined 4 (no sheath, 1.5-2 μm width)	255	<i>Scenedesmus</i> sp.1	159
<i>Scytonema</i> cf. <i>hoffmanii</i>	8694	<i>Tetraedron minimum</i>	400
<i>Coccoid</i>		<i>Oedogonium</i> sp.1	7854
Undetermined coccoid 1	4	<i>Oedogonium</i> sp.2	2238
Undetermined coccoid 2	34	<i>Mougeotia</i> sp.	70686
Undetermined coccoid 3	19	<i>Cosmarium</i> spp.	200
Cf. <i>Chroococcidiopsis</i> sp. 1 (1-3 μm)	4	<i>Euastrum</i> spp.	200
Cf. <i>Chroococcidiopsis</i> sp. 2 (~ 4 μm)	34	<i>Staurastrum</i> spp.	409
<i>Aphanothece</i> sp.1	1		
<i>Aphanothece</i> sp.2	1	<u>Diatoms (Bacillariophyta)</u>	
<i>Aphanothece</i> sp.3	35	<i>Brachysira</i> spp.	240
<i>Chroococcus</i> cf. <i>minutus</i>	10	<i>Diploneis</i> spp.	500
<i>Chroococcus</i> cf. <i>turgidus</i>	382	<i>Encyonema</i> spp.	120
<i>Coelosphaerium</i> sp.	17	<i>Fragilaria</i> spp.	400
<i>Gloeocapsa</i> sp.	10	<i>Mastogloia</i> spp.	560
<i>Gloeotheca</i> sp.1	39	<i>Navicula</i> spp.	300
<i>Gloeotheca</i> sp.2	13	<i>Nitzschia</i> spp.	140
<i>Rhabdoderma linearis</i>	8		

Cyanobacterial and total bacterial changes

Total bacterial abundance rose rapidly from $1.3 \times 10^9/\text{cm}^2$ after flooding to $8.1 \times 10^9/\text{cm}^2$ on day 13 and then dropped to $3.8 \times 10^9/\text{cm}^2$ on day 20 (Fig. 3.1). Cyanobacterial abundance increased steadily from $1.9 \times 10^7/\text{cm}^2$ after flooding to $8.6 \times 10^7/\text{cm}^2$ on day 13 and dropped to $4.5 \times 10^7/\text{cm}^2$ on day 20.

Mat PMEase activity

PMEase activity remained high the first 24 hours after wetting ($0.24 \mu\text{mol cm}^{-2} \text{h}^{-1}$, Fig. 3.2). It abruptly dropped and leveled on days 2-7 ($0.03 \mu\text{mol cm}^{-2} \text{h}^{-1}$) and increased linearly thereafter to reach $0.08 \mu\text{mol cm}^{-2} \text{h}^{-1}$ by day 20.

Phosphorus dynamics

The exponential equation accurately fitted the cumulative rate of TP release (R) from dry ground crusts: $\alpha = 0.0066$, $\beta = 0.52$; $r^2 = 0.97$. In the microcosms, water TP increased rapidly during the first 24 hours and reached a maximum of $17 \mu\text{g TP/L}$ in A, B and $14 \mu\text{g TP/L}$ in C after 48–72 hours (Fig. 3). Then, water TP decreased until day 6, after which it maintained a constant level of $6.6 \mu\text{g/L}$.

Mat photosynthesis and respiration

Photosynthesis on day 5 was not considered as cloud cover reduced light to unusual levels during the incubation. GPP-area increased from $1.0 \mu\text{g C cm}^{-2} \text{ h}^{-1}$ ($\text{mol photons m}^{-2}$) $^{-1}$ after flooding to $3.0 \mu\text{g C cm}^{-2}$ ($\text{mol photons m}^{-2}$) $^{-1}$ from day 1 to 3 (Fig. 3.4A). Thereafter, GPP-area decreased to $1.58 \mu\text{g C cm}^{-2} \text{ h}^{-1}$ ($\text{mol photons m}^{-2}$) $^{-1}$ on day 7. GPP-biov followed the same pattern (Fig. 3.4A) and was linearly correlated with water TP concentration ($r^2 = 0.65$, $P < 0.01$).

Respiration increased from $5.9 \mu\text{g C cm}^{-2} \text{ h}^{-1}$ after flooding to $8.8 \mu\text{g C cm}^{-2} \text{ h}^{-1}$ on day 13. Thereafter respiration decreased to reach $7.5 \mu\text{g C cm}^{-2} \text{ h}^{-1}$ on day 20 (Fig. 3.4B). Respiration was positively correlated with the number of total bacteria ($r^2 = 0.40$, $P = 0.02$) but not with the number of cyanobacteria counted under epifluorescence ($r^2 = 0.05$, $P = 0.46$). On day 20, GPP-area was significantly higher in the top layer than in the bottom layer while respiration showed the converse (Table 3.1).

Discussion

Crust recovery after flooding was rapid, evidenced not only through visual observation of greening on top of the crust that grew thicker with time, but also through metabolic measures and, after two days, the net re-absorption of most of TP that had been initially released. Our experiment showed that the crusts were able to fully recover using their own algal and P resources.

The fast recovery was linked to the large biovolume of cyanobacteria inhabiting the top layer, while the contribution of diatoms and green algae in this layer was small. Gottlieb et al. (2005) found a similar cyanobacterially-dominated community residing in short-hydroperiod mats that had been dry for 8 months. Cyanobacteria have been described elsewhere as desiccation resistant, including *Scytonema* (found at the very surface of the crust, Wynn-Williams, 2000, Garcia-Pichel and Pringault, 2001), *Chroococcidiopsis* (e.g. Potts and Fridmann, 1981, Caiola et al., 1993, 1996, Billi et al., 2001), *Chroococcus* (Potts, 1999, Garcia-Pichel and Pringault, 2001), *Gloeotheca* and *Gloeocapsa* (Pentecost and Whitton, 2000, Wynn-Williams, 2000). Moderate amounts of polysaccharide measured in the crusts secreted by cyano- and eu-bacteria likely limits water loss during dry-down (Mazor et al., 1996), not only for the originating cells but also for taxa living nearby such as the green algae and diatoms that themselves produce less polysaccharide (Douglas, 1958, Shephard, 1987, Mosich, 2001). Eubacteria exhibited similar recovery patterns upon flooding, also showing resistance to desiccation. Eubacteria were responsible for the high respiration rates localized in the heterotrophic bottom layer but they were also present in the top layer (as suggested by the low photosynthesis/respiration ratio) where photosynthetic exudates are available to fuel bacterial metabolism. However, our data do not address whether this coupling drove the change in bacterial abundance over time because we did not examine the bacterial population separately in each layer at all times.

The rapid photosynthetic recovery in the hours following rehydration was also shown for short-hydroperiod crusts of the Everglades (Gottlieb, 2003) and for desert crusts inhabited by some of the same cyanobacteria (Garcia-Pichel and Pringault, 2001). However, whether photosynthetic capabilities are lost during desiccation is debatable, as some studies show they

can be sustained at low levels with minimal hydration (Lange et al., 1992, Dodds et al., 1996, Garcia-Pichel and Belnap, 1996, Mazor et al., 1996) while some species are photosynthetically inactive in these moments (e.g. *Chroococcidiopsis*, Potts and Friedman, 1981).

GPP-biov was driven by water TP concentration mainly because we normalized GPP by the algal biovolume and light (cf. the limitations of such procedure in Dodds et al., 1999), leaving the water TP as the main controlling factor. Temperature plays a lesser role in controlling daily variation in photosynthesis subtropical than temperate environments (Payne, 1986). The strong relationship suggests limitation by P, as has been shown elsewhere (McCormick et al., 1998). As suggested by the asymptote of the equation predicting the cumulative rate of mass TP release from DGC (0.66%), the theoretical pool of released TP was very limited. After an extended period of drying, the periphyton crust was thus a good sink for P. Such a low pool of TP available for desorption explains why we could not track any change in TP content in the crust. The rapid increase in water TP concentration during the first 48 hours suggested low P uptake rates that were unable to compensate for TP release (over 60% of P was in the water). Thereafter, TP uptake, enhanced by P co-precipitation with calcite (reviewed in Dodds, 2003), was stronger than TP release. In the experiment of Gottlieb et al. (2005), net TP effluxes were measured after 2 days and thus, likely reflected positive effluxes. Our TP efflux after two days was similar to those Gottlieb et al. (2005) measured for short-hydroperiod mats that had been rehydrated after 8 month of desiccation ($0.49 \mu\text{g TP g DW}^{-1} 48\text{h}^{-1}$). After 6 days, the crust could not decrease water TP concentration below $6.6 \mu\text{g/L}$ through uptake but was able to maintain this concentration level despite water TP concentration through evaporation. This illustrates the periphyton control on water P concentration in the Everglades (e.g. Jones and Almador, 1992, Gaiser et al., 2004) with typical concentrations below $10 \mu\text{g/L}$ (Flora and Rosendahl, 1982, McCormick and O'Dell, 1996).

High PMEase activity the first 24 hours after wetting likely enhanced TP release (orthophosphates) from organic P in the crust. Four hours after wetting, water column TP concentration was below $6.6 \mu\text{g/L}$ and the high PMEase activity at that time suggested P-limitation. Recently rehydrated cells can rapidly excrete enzymes (Potts, 1985) but it was doubtful that the small microbial community at the time of wetting could account for such a high PMEase activity as, 13 days after flooding, the larger cyanobacterial community exhibited a 5 times smaller PMEase activity (while water TP concentration was similar). Therefore it was unlikely that the high PMEase activity observed just after flooding was biologically driven but rather liberated from a pre-existing pool. Extracellular PMEases secreted during the last drawdown may have been stored in the copious polysaccharide matrix (= immobilization matrix, Caiola et al., 1996, Potts, 1999, Billi et al., 2001). PMEase can also be stored and remain active in non-viable cells (e.g. Potts, 1999) to be released rapidly upon rewetting (Caiola et al., 1996). After the pool of free PMEase was used, PMAse activity was a good indicator of increasing P-starvation.

Finally, although the crust was visually changing, biomass or taxonomic changes remained undetected over time. This was likely due to dilution of the active thin layer at the top of the crust with the much thicker (13-15 times), less active bottom layer. In particular, the Chl *a* pool from photosynthetically active cells found in the first few illuminated millimeters of the crust (e.g. Dodds et al., 1999) was diluted into the pool of Chl *a* found in buried live algae below.

Extracellular Chl a should otherwise have degraded to pheophytine a when the crusts were air exposed in humid, oxic and hot conditions of the dry season. The lack of algal density patterns over time may also have been due to complications in separating live from dead cells, and small cyanobacteria from bacteria under light microscopy (Peterson, 1987, Wetzel, 1993), though this was not the case for the cells counts made under epifluorescence. Subsequent studies on laminated mats should examine the bottom and the top layers separately.

In conclusion, our study showed that the top layer of periphyton crust contained the main constituents facilitating rapid recovery in our experimental settings: desiccation-resistant cyanobacteria, P and likely free enzymes such as PMEase that effectuate early P release. During the first two days after flooding, periphyton had not yet fully recovered and P uptake did not counterbalance P release to water column, indicating crusts are an efficient P sink when dry. After two days of flooding, however, rapid recovery incurred the re-absorption of 90% of released TP. Thereafter, periphyton regulated TP at a threshold concentration of 6–7 µg/L in stagnating water, despite concentration through evaporation.

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Datasets

Rehydration Experiment.xls

Figure 3.1. Mean change in total bacteria ($\times 10^9/\text{cm}^2$, left axis) and cyanobacteria ($\times 10^7/\text{cm}^2$, right axis) in incubated periphyton (mean $\pm$ S.D., $n=3$ with the exception of days 3 and 6, $n=2$ for the total bacteria and $n=2$ on day 3 for the cyanobacteria).

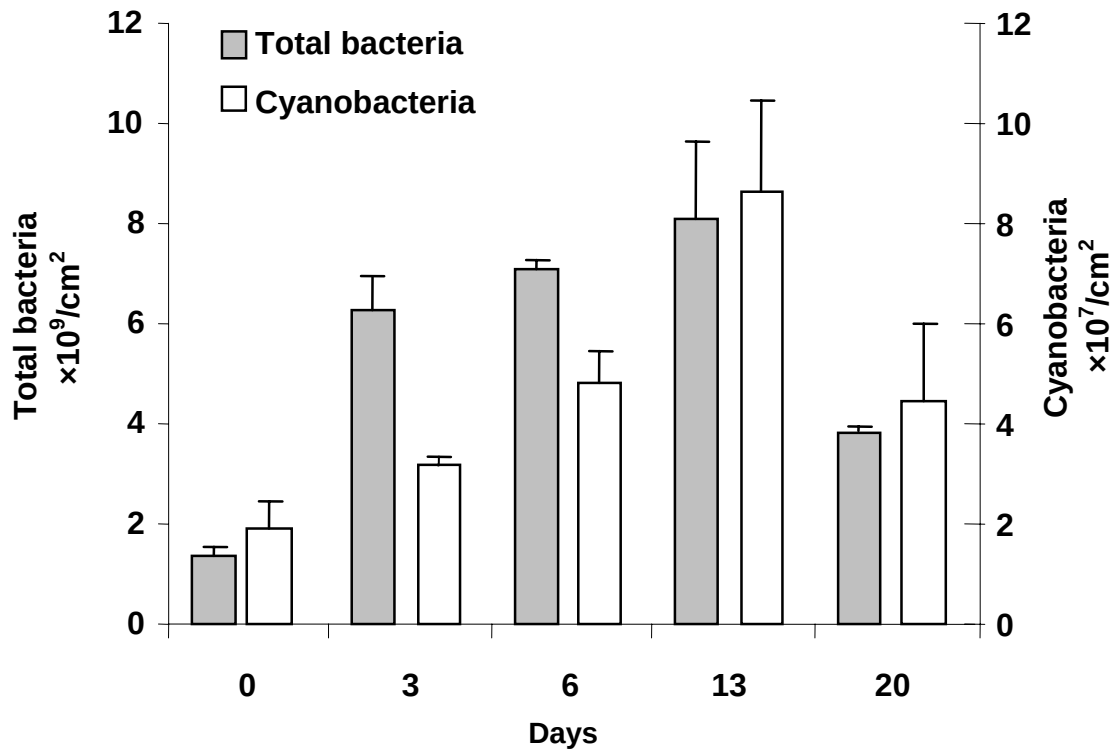


Figure 3.2. Phosphomonoesterase activity as measured by the mass of 4-methylumbelliferone liberated from 4-methylumbelliferyl-phosphate (MUF-P) substrate in periphyton mat homogenates (mean±S.D., n= 6).

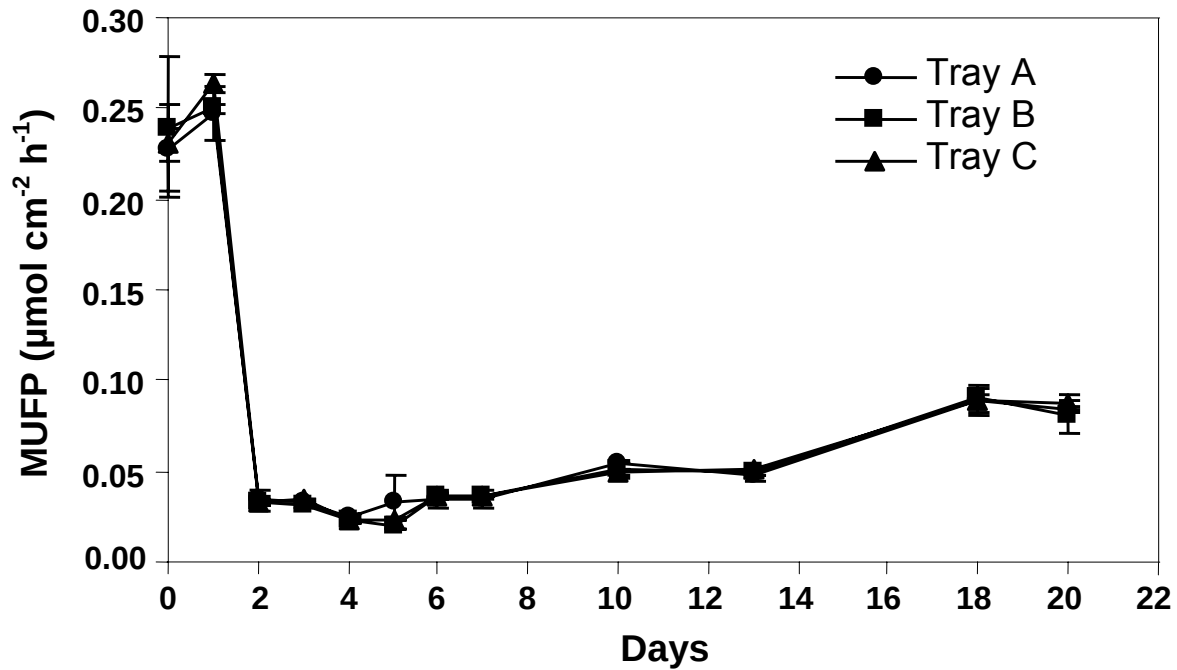


Figure 3.3. Change in water TP concentration in trays A, B, C.

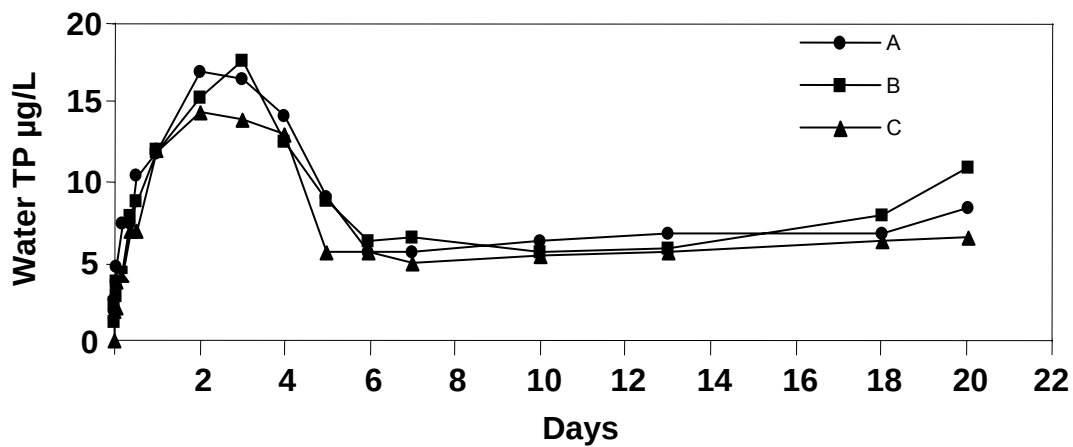
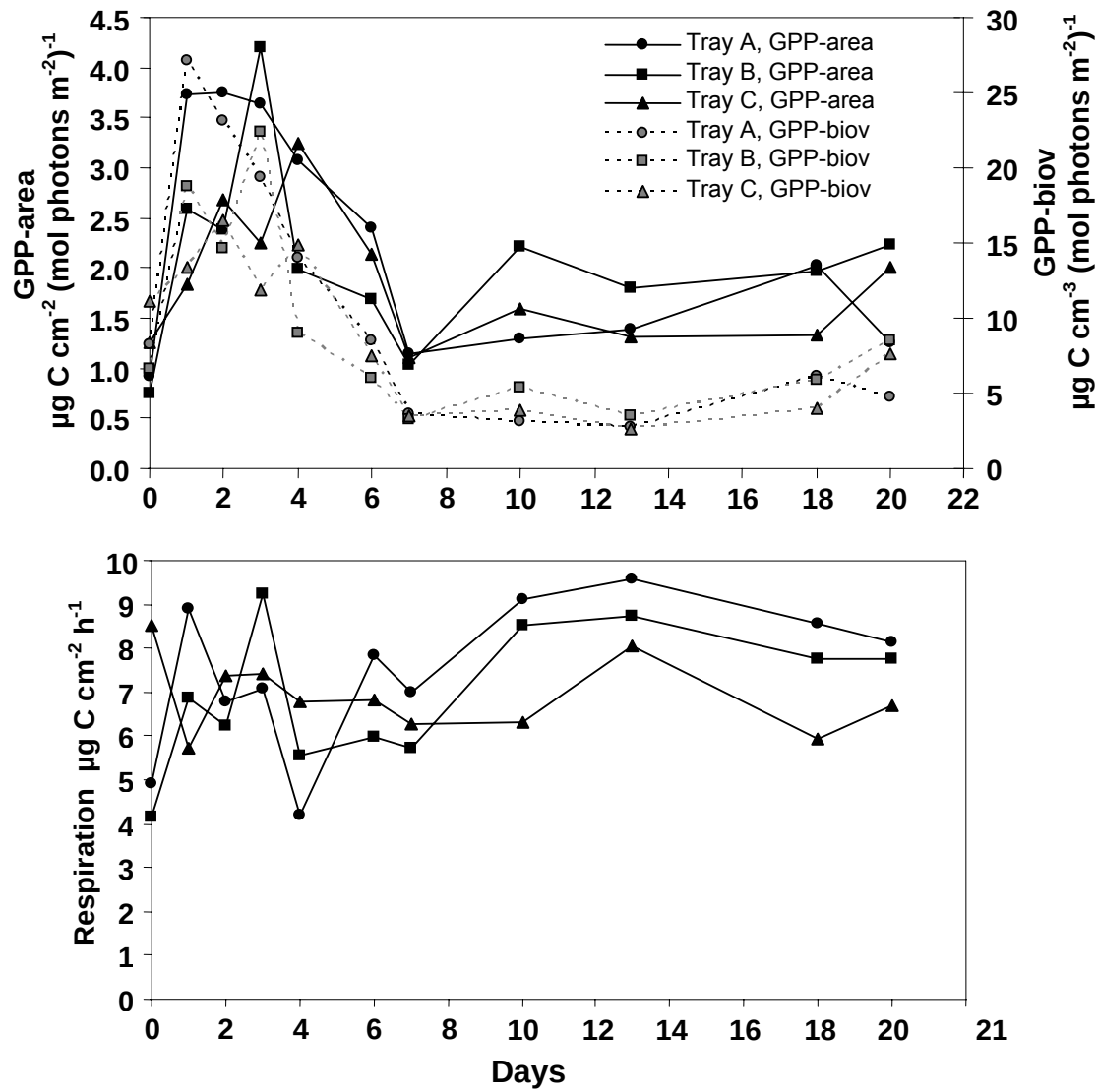


Figure 3.4. A. Change in PPFD-corrected GPP per surface area (closed dots, left axis, mean $\pm$ S.D., n= 3) and per algal biovolume (opened dots, right axis, mean $\pm$ S.D., n= 3). B. Change in respiration per surface area (mean $\pm$ S.D., n= 3).



D. EFFECTS OF SHADING ON PERIPHYTON GROWTH IN THE EVERGLADES MARL PRAIRIE

Introduction

In clear, shallow hydrosystems, irradiance reaches a great surface area of benthic substrata, which promotes the development of a mixed attached community of micro- and macrophytes (e.g. Sand-Jensen & Borum, 1991). The Everglades is an example of such a system where periphyton, a group of attached algae, fungi and bacteria, plays a major role supporting the food web and oxygenating the water column (e.g. McCormick et al., 1997; Geddes & Trexler, 2003). Although the freshwater Everglades is highly depleted in phosphorus (P), periphyton thrives because it is positioned where the nutrients are released (e.g. Hansson, 1988, 1989, 1990; Wetzel, 1996). Periphyton also maintains low phosphorus levels in the water column because it acts as a barrier to nutrient release from the bottom and also uptakes P as soon as it is found in the water so that soluble reactive phosphorus (SRP) is very low ($0 \mu\text{g.L}^{-1}$ SRP; $<10 \mu\text{g TP.L}^{-1}$, e.g. Noe et al., 2001). Thus, periphyton is very efficient in using the resources of the system, so that despite oligotrophic waters, it has a high biomass per surface area (e.g. 3-4 kg DW.m⁻² in the short-hydroperiod Everglades, Thomas et al., 2002). Being P depleted, the water column in much of the Everglades is clear and devoid of seston (phytoplankton, zooplankton and inert particles), reducing irradiance scattering in the water column. Other than natural fluctuations in incident irradiance (seasonality, cloud coverage etc.), irradiance attenuation is linked to direct shading from (sloughing mats), rooted or floating macrophytes colonized by epiphytes (Grimshaw et al., 1997). This “overstory” vegetation alters both the quantity and spectral character of irradiance reaching the “understory” benthos (Hill, 1996). Though of major importance, studies on the effect of the quantity and the quality of irradiance in benthic systems are scarce compared to planktonic counterparts (Hill, 1996), partly due to complexities in measuring periphyton biomass and production. Vertical compression, spatial and substrate heterogeneity and variability in structural integrity complicate sampling methodologies (e.g. review in Aloï, 1990).

The majority of studies on the effects of shading on periphyton have been confined to lotic systems (e.g. Lowe et al., 1986; Hill & Knight, 1988; Mosisch et al., 2001) where riparian vegetation can block or spectrally alter >95% incident irradiance to the stream (Hill, 1966). In deep to moderately deep lakes, riparian shading is limited to the littoral zone where effects of vertical irradiance extinction on periphyton attached to vertical and bottom substrata have been investigated (e.g. Lang & Austin, 1984; Hansson, 1992; Müller, 1995; Thomas, 2000). In shallow, lentic hydrosystems and wetlands, even though the rooted macrophyte canopy can be substantial, the effect of shading on periphyton has been largely overlooked. In the Everglades, Armentano et al. (submitted), showed that the macrophyte *Cladium jamaicense* has median aeral coverage of 35% (minimum 10% and maximum 65%). Grimshaw et al. (1997) found 3% shade (1- [ratio of below to above canopy irradiance]) for an oligotrophic open marsh, 36% for a *C. jamaicense* canopy and 85% for a *Typha domingensis* dominated canopy in an enriched marsh. As in lotic systems, senescent leaves and stems also contribute to the vertical canopy. Grimshaw et al. (1997) showed a strong decreasing gradient of relative net primary productivity of epiphyton and periphyton with increasing shading by macrophytes. However, neither the taxonomic composition of the periphyton nor the photosynthesis-irradiance (PI) curves for these different periphyton communities was examined. In contrast, PI curves developed from streams

with different natural or artificial canopies have shown a decrease in $P_{\max}$ (light-saturated maximum photosynthesis) and I_k (light level at which photosynthesis saturates) with increasing shade (e.g. Towns, 1981; Quinn et al., 1997; Mosisch 2001; Franken et al., 2005). These stream studies have also documented effects of shading on both taxonomic and pigment composition.

In this study, we determine how benthic periphyton PI curves, respiration, biomass and taxonomic composition are altered when subjected to 5 months of shading at 8 levels ranging from 0% to 98%. Thus, we can examine the mathematical relationship of PI curve parameters (I_k and $P_{\max}$) to % of irradiance transmittance (%IT = 1 - %shade). To our knowledge, no such mathematical relationships have heretofore been developed.

Methods

Shade experiment

The study site is located in the southern Everglades marl prairie, a habitat dominated by sparse mixed graminoid vegetation and periphyton. The area is representative of 190,000 ha of higher-elevation marl prairies that flank either side of Shark River Slough in the southern Everglades and have a relatively short hydroperiod of 2-6 months with water depth averaging 10-cm (Davis et al., 2005). The experiment took place on the southern bank of a canal, the C-111, that extends along the eastern boundary of Everglades National Park (ENP). The bank resulted from the 1997 removal of the southern levee of the P-depleted C-111 canal to increase freshwater flow into ENP (Thomas et al., 2002). The remaining bare and flat limestone bedrock was colonized by periphyton, which builds prolific mats during the approximately 6-month annual flooding period (typically June to December). These periphyton mats are highly laminated due to compaction during the dry season (cf. Thomas et al., in press), which increases the ease of sampling. Rooted macrophytes also colonized the bank over the years subsequent to levee removal (cf. Thomas et al., 2002 for more details about the study area).

Two years prior to the experiment, 3 sites positioned 1 km apart on the bank were selected for study and periphyton was removed, exposing bedrock. During the two subsequent wet seasons, the experimental sites were colonized by a uniform laminated mat, 0.75 ± 0.26 -cm (standard deviation) thick, with rare occurrences of rooted macrophytes. All rooted macrophytes were removed before the experiment started.

Eight shade treatments were constructed at each site. Each treatment consisted of a shade house ($1 \times 1 \times 0.5$ m³, L $\times$ W $\times$ H) attenuating photosynthetic photon flux density (PPFD) from all sides except near the bottom where a 10-cm high clearance allowed free water movement. The shade houses attenuating more than 70% PPFD were wider ($3 \times 3 \times 0.5$ m³) to limit light intrusion through the clearance at the bottom. We used spectrally neutral horticultural black knitted cloth (Shade Rite, Green Tek Inc., WY, USA) that uniformly covered a measured surface of marsh. The shade cloths attenuated incident irradiance by 0%, 30%, 50%, 60%, 70%, 80%, 90% and 98% for treatments A, B, C, D, E, F, G and H respectively.

Sampling

The experiment began on 6/19/03, about a week after the annual flooding of the bank with sampling occurring at day 0, then every month starting 7/09/03 for 5 months. Sampling started

around 9am and ended around 11am. Prior to sampling, temperature and pH were recorded under each shade house, while water depth was measured at the gauge at each site. Sampling was performed within a $0.5 \times 0.5 \text{ m}^2$ area in the center of each shade house by randomly harvesting a $15 \times 15 \text{ cm}^2$ periphyton mat, which was carved with a knife. The sampled mat was kept in a clear plastic box filled with marsh water and stored in the dark until it could be processed the same day in the laboratory. Sampled areas were marked to prevent repeated sampling of the same locations.

Periphyton processing

In the laboratory, the average thickness of the sampled mat ($n = 10$) was measured with a caliper and recorded. Then, a first set of 15 cores (1.94 cm diam.), followed by a second set of 5 smaller cores (1.55 cm diam.) were randomly taken through the mat. The mats had 2 layers, a top and a bottom separated by a black/red conspicuous separation. From a previous study, the tan compact bottom layer was photosynthetically inactive but contained enough organic matter and chlorophyll *a* (chl *a*) to prevent tracking any changes in these metrics when mixed with the loose, green top layer (cf. Thomas et al., in press). The mats were thus sliced horizontally with a razor blade to separate both layers and only the top layer was retained for analysis.

The upper parts of the first set of 15 cores were pooled together, homogenized with a biohomogenizer™ (Biospec Products Inc., OK, USA), and the volume of the homogenate recorded (40-75mL). One subsample (1-mL) was filtered onto Whatman 25-mm GFF glass filter and the chl *a* on filter was determined with a Gilford FLUORO IV spectrofluorometer (Gilford Instrument, Oberlin, OH; excitation 435 nm, emission 667 nm) after 48-hr 90% cold acetone extraction at -20°C . The spectrofluorometer was calibrated with a chl *a* standard (Sigma), which concentration was checked spectrophotometrically using the trichromatic equations of Jeffrey & Humphrey (1975). Chl *a* was expressed per unit surface area of mat ($\mu\text{g chl } a \text{ cm}^{-2}$). A second subsample (1 mL) was taken, kept in a freezer in a microcentrifuge vial until taxonomic determination. The remaining homogenate was placed into a pre-weighed aluminum pan to determine gravimetrically DW and AFDW (APHA, 1999). DW and AFDW were expressed per unit surface area of mat (mg.cm^{-2}).

Periphyton taxonomic composition

Taxonomic composition was analyzed at the beginning and at the end (month 5) of the experiment. Slide preparations for compositional analysis were made by drying a measured volume of sample onto a coverslip, which was then inverted onto a glass microslide. At least 500 algal units were counted on random transects at $1000\times$ magnification. Units were defined as cells or 100- μm measured segments of filaments. Morphotypes were identified using Prescott (1962), Komárek and Anagnostidis (1986, 1989, 1999) and Komárek and Hindak (1975). Cell biovolume was estimated for each morphotype using length, width and depth measurements and applying appropriate geometric models. Algal units and biovolume (mm^3) were expressed per unit surface area of mat (cm^2).

Periphyton metabolism

The top layers of the second set of cores were used to assess the gross photosynthesis (GPP)-irradiance (PI) curve and respiration by tracking dissolved oxygen (DO) changes in 300-mL biological oxygen demand (BOD) clear glass bottles (e.g. McCormick et al., 1998). One core per

incubation was used and discarded thereafter. A warm (30-33°C) solution made of distilled water with dissolved salts that mimics the matrix of Everglades water was used to fill the bottles. One liter of this solution contained 23 mg NaHCO₃, 1 mg KCl, 1 mg MgSO₄×7H₂O, 11 mg MgCl₂×6H₂O, and 46 mg CaCl₂×2H₂O (Jones & Amador, 1992). Once the BOD filled, the initial DO was measured and, immediately after, one core was inserted in the bottle making sure it sat intact, in the upright position on the bottom. Four irradiance incubations at, roughly, 1000, 500, 300 and 100 $\mu\text{mol photons.m}^{-2}.\text{s}^{-1}$, plus one dark incubation, were performed. A metal halide 1000-W bulb (Venture MS BT37, Venture Lighting International, OH, USA) with reflector (Hydrofarm Inc., CA, USA) provided the irradiance. The lamp was steadily positioned at 0.5-m above a clear tub (1×1×0.2 m³, L×W×H) filled with water, which, despite the tremendous heating generated by the bulb, remained in the 29-33°C range (a typical summer water temperature in the Everglades; e.g. Al-Rabai'ah et al., 2002) because of the low air temperature in the laboratory. In these settings, the lamp provided 1100-700 $\mu\text{mol photons.m}^{-2}.\text{s}^{-1}$ from the center to the edges of the tub. Spatial PPFD variability was accounted for by mapping its distribution under the tub. The PPFD was measured, with a LI-COR quantum flat sensor coupled with a LI-COR 1400 meter, at the nodes of 1×1 m² with 5-cm square cells grid. The interpolation map was generated with Surfer 8.0 (Golden Software Inc., CO, USA, kriging interpolation and linear variogram). The incident PPFD was attenuated using 50%, 70% and 90% shade cloths. The dark incubation took place in a cooler filled with water maintained at 30-33°C with an aquarium heater. Changes in DO were measured after 3–4 hours with a self-stirring YSI BOD DO probe and a YSI 52 DO meter (Yellow Springs Inc, OH, USA). Gross photosynthesis and respiration were expressed in $\mu\text{g O}_2.\text{cm}^{-2}.\text{h}^{-1}$.

When no decrease in GPP occurred at high irradiance, PI curve parameters (P_{max} , I_k) were determined by fitting the Web et al. (1974) equation. When photoinhibition was conspicuous, the Platt et al. (1980) equation was used instead to determine the rate of photoinhibition (β). Once the PI curve parameters determined, the daily gross photosynthesis was computed assuming a sinusoidal daily PPFD variation, a 12-hr photoperiod, a maximal incident PPFD of 2000 $\mu\text{mol photons.m}^{-2}.\text{s}^{-1}$ and no photosynthesis saturation in the afternoon (McBride, 1992).

Statistical analysis

Measurements were analyzed from month 1 to 5 using a two-way split plot ANOVA with treatment structure: treatment×month, blocks= sites, whole plot= treatments and subplots= months. When needed, data were log transformed to achieve normality and homogeneity of variance of the residuals. In the case of significant differences, a small number of planned contrasts were performed to test differences between group means. A test for linear and quadratic trends in the group means was also performed by calculating the right coefficient contrasts for unequal spacing between factor levels (Kirk, 1995). Additionally, sites and treatment plots were compared at the beginning of the experiment using a one-way ANOVA, and pairwise comparisons were performed using the Ryan, Einot–Gabriel and Welsch (REGW) procedure (Welsch, 1977). All tests were performed at $\alpha= 0.05$ using GENSTAT 8.1 (www.vsn-intl.com, UK). The determinations of the PI curve parameters and other non-linear regressions were analyzed with SPSS v.12 using Levenberg–Marquardt algorithm. Species composition (relative abundance and biovolume) was compared among treatments using analysis of similarity (ANOSIM) employing the Bray-Curtis similarity metric PRIMER_E/ANOSIM[®] software.

Results

Sites and treatments variability at day 0: justification of the use of the split plot ANOVA

Sites and shade treatments at day 0 did not differ significantly for any of the biological variables measured. Thus, data could have been pooled over sites to conduct a two way ANOVA. However, in the various split plot ANOVAs, blocks had a variance ratio as high as 22% suggesting that treatments at each site behave quite differently over time (data not shown).

Environmental parameters

Site 2 was the deepest, followed by sites 1 (2.2 cm shallower) and 3 (3 cm shallower) and water depth increased steadily over time from 8.1 cm to 22 cm (site 2). Water temperature remained steady over time ($28.1 \pm 1.6^\circ\text{C}$) and the various shade cloths reduced water temperature slightly, but equally, compared to the control (0% shade) being on average 0.4°C higher. The pH remained within circumneutral range (6.9 ± 0.7) and was not significantly affected by shading at that time of the day.

Periphyton biomass

Periphyton thickness changed significantly with shading ($P = 0.03$); treatment H was lower than all other treatments ($P < 0.001$, Figure 1.a). Thickness remained constant during the first 3 months of the experiment (A-G 1.0 ± 0.2 cm; H 0.8 ± 0.3 cm) then increased significantly to a plateau the last two months (A-G 2.0 ± 0.5 cm; H 1.2 ± 0.2 cm).

No changes over time and among treatments could be found using DW (82 ± 19 mg.cm⁻²) and AFDW (16 ± 5 mg.cm⁻²) metrics. However, the AFDW/DW ratio (relative organic matter content) decreased linearly over time ($P < 0.001$) from $19.9 \pm 2.3\%$ to $18.7 \pm 7.8\%$ for treatments A–G on month 5 (Figure 1.b). The organic matter content in treatments A–G was increasingly higher over time than in treatment H, in which organic matter accounted for $13.6 \pm 0.2\%$ of the biomass by month 5 ($P < 0.01$).

Chl *a* increased linearly over time from 1.9 ± 0.5 µg chl *a*.cm⁻² to 3.5 ± 0.9 µg chl *a*.cm⁻² for all treatments except for H which remained constant (1.4 ± 0.4 µg chl *a*.cm⁻²; Figure 1.c). Chl *a* in treatment A was higher than in treatment H ($P = 0.002$) and both were lower than in treatments B–G ($P < 0.001$). The differences between chl *a* in treatment H and either chl *a* in treatments A ($P = 0.004$) or B–G ($P < 0.001$) increased over time.

In month 5, the biovolume plotted against percent shade followed roughly a cubic polynomial regression ($R^2 = 0.50$, $P < 0.001$; Figure 2.a): maximum at 30% (= treatment B, 0.08 mm³.cm⁻²), minimum at 86% shade (0.04 mm³.cm⁻²) with 0.03 mm³.cm⁻² for the constant. The chl *a* to biovolume ratio (chl *a*/BV) followed also roughly a polynomial regression ($R^2 = 0.37$, $P < 0.02$; Figure 2.b): minimum at 21% (27.0 µg chl *a*.mm⁻³), maximum at 70% shade (= treatment E; 85.3 µg chl *a*.mm⁻³) with 68.4 mm³.cm⁻² for the constant.

Periphyton metabolism

$P_{\max}$ changed over time ($P < 0.001$) but without any linear or quadratic trend (Figure 1.d). For each month considered, decreasing levels of shade (= increasing PPFD transmittance) had a positive linear effect on $P_{\max}$ ($P < 0.001$). The $P_{\max}$ in G (19.2 ± 6.0 µg O₂.cm⁻².h⁻¹) was significantly higher than the $P_{\max}$ in H (7.3 ± 5.6 µg O₂.cm⁻².h⁻¹, $P < 0.001$) and both treatments had a lower $P_{\max}$ than for treatments A–F (29.0 ± 7.8 µg O₂.cm⁻².h⁻¹, $P < 0.001$, Figure 1.d & 3.a).

For each month, the $P_{\max}$ plotted against PPFD transmittance could be fitted with the Webb et al. (1974) PI curve equation ($R^2 = 0.38\text{--}0.83$, Figure 3.a)

I_k changed over time ($P < 0.001$) but without any linear or quadratic trend (Figure 1.e). For each month considered, I_k increased linearly with decreasing levels of shade ($P < 0.001$, Figure 3.b), with lower I_k ($35 \pm 32 \mu\text{mol photons.m}^{-2}.\text{s}^{-1}$) for treatment H and higher I_k for treatment A ($135 \pm 46 \mu\text{mol photons.m}^{-2}.\text{s}^{-1}$).

Because photoinhibition was rare, the split-plot ANOVA could not be run (Figure 1.f). Photoinhibition never occurred for treatments A, B, C and G but occurred for the first time for the treatments D, E, F on month 5. On month 5, the photoinhibition was the strongest recorded ($0.02\text{--}0.15 \mu\text{g O}_2.\text{cm}^{-2}.\text{h}^{-1}/\mu\text{mol photons.m}^{-2}.\text{s}^{-1}$). Nearly all treatment H exhibited photoinhibition over time with the exception of month 2 with no photoinhibition observed. Photoinhibition occurred at irradiances I_p around $200 \mu\text{mol photons.m}^{-2}.\text{s}^{-1}$ for months 2, 3 and 5 and at $15\text{--}40 \mu\text{mol photons.m}^{-2}.\text{s}^{-1}$ for months 1 and 4.

Daily GPP changed over time ($P < 0.001$) without any linear or quadratic trend (Figure 1.g). Daily GPP was significantly lower in treatments H ($0.3 \pm 0.4 \text{ g O}_2.\text{m}^{-2}.\text{d}^{-1}$) than in treatments G ($2.2 \pm 0.7 \text{ g O}_2.\text{m}^{-2}.\text{d}^{-1}$) and both were significantly lower than in treatments A–F ($3.1 \pm 1.0 \text{ g O}_2.\text{m}^{-2}.\text{d}^{-1}$). For each month, the daily GPP plotted against PPFD transmittance could be fitted with the Webb et al. (1974) PI curve equation ($R^2 = 0.50\text{--}0.87$, Figure 3.c).

Respiration changed over time with lower values at months 1 and 5 ($7.9 \pm 2.1 \mu\text{g O}_2.\text{cm}^{-2}.\text{h}^{-1}$) and higher values at month 3 ($10.8 \pm 3.6 \mu\text{g O}_2.\text{cm}^{-2}.\text{h}^{-1}$; quadratic contrast, $P < 0.001$; Figure 1.h). Treatment H ($6.8 \pm 2.7 \mu\text{g O}_2.\text{cm}^{-2}.\text{h}^{-1}$) had lower respiration than all the other treatments ($9.5 \pm 2.8 \mu\text{g O}_2.\text{cm}^{-2}.\text{h}^{-1}$, $P < 0.001$).

Taxonomic composition

Taxonomic richness ($n = 21 \pm 3$), diversity and taxonomic composition did not differ among treatments ($H = 2.3 \pm 0.2$; $P = 0.1$). Coccoid and filamentous cyanophytes accounted for 38% and 33% of the total algal abundance, respectively. *Chroococcus* sp. (14%), *Aphanothece* sp. (9%), *Gloeotheca* sp. (5%), *Rhabdoderma linearis* (3%), *Rhabdoderma sigmoidea* (3%), *Chroococcidiopsis* sp. (1%) and *Microcystis* sp. (1%) were the most frequent of the 19 coccoid taxa. The most important filamentous cyanophytes among the 14 identified were 4 undetermined thin filaments (28%) and *Scytonema hoffmanii* (4%). *S. hoffmanii* was split into three subtaxa based on the color of the sheath, which ranged from dark brown, lighter brown to blue-green. No patterns were found when the proportion of each color group was compared across the different shade treatments. Various green algae (35) and diatoms (mostly *Encyonema evergladianum*, 25 diatom taxa in total) were comparatively less abundant (3% and 10% respectively).

Cyanophytes largely dominated algal biovolume estimates; cyanophyte coccoids (*Aphanocapsa* sp., *Gomphosphaeria* sp., *Chroococcus* sp., *Chroococcidiopsis* sp.) comprised 22% of the biovolume while filamentous cyanophytes comprised 73% (4 undetermined thin filaments 35%, *Scytonema hoffmanii* 28%, then *Fischerella* sp. 7% and *Johannesbaptista* sp. 3%).

Discussion

We found little effect of shading on periphyton community composition and overall daily GPP. This is linked to the compensatory effect of the PI curve, which makes the community photosynthetically efficient within its acclimated irradiance regime. However, before we describe how periphyton compensates for low irradiance levels, it is important to examine how well our shading treatments mimicked the natural shade environment.

How artificial was our artificial shading?

Plant canopy (or metaphyton) attenuates irradiance so that when it encompasses a large area, the temperature under it can be reduced which can alter the enzymatic reactions involved in photosynthesis (e.g. Davison, 1991). Commonly, an increase of 10°C results in an increase of photosynthesis reaction kinetics by 2 ($Q_{10}=2$; e.g. Davison, 1991; Ferris & Christian, 1991). However, with water temperature around 28-30°C and above commonly found in the Everglades, Q_{10} is much lower than 2 (Jacques Lemoalle, pers. com.). Thus, though the size of our shade houses precluded temperature effects, it is not likely that a temperature drop driven by canopy would have an important impact on photosynthesis.

Plant canopy also spectrally alters downward irradiance by selecting green wavelengths, which highly suppress growth of understory plants possessing chl *a* and *b*. However, algae have other pigments besides chlorophyll and thus are spectrally selected by the plant canopy (e.g. Falkowski & LaRoche, 1991). Since we used spectrally neutral shade cloths, we did not mimic plant canopy, and thus, algae were only subjected to a reduction in light quantity.

Taxonomic composition

Irradiance declines rapidly within the uppermost millimeters of periphyton (e.g. Losee & Wetzel, 1983; Meulemans, 1987; Hawes, 1993) which supplements effects of overstory shading. Numerous studies show that algae position themselves within the mat according to their irradiance requirements (e.g. Goldsborough, 1994; Johnson et al., 1997; Donar et al., 2004). As a general rule and unless algae are able to synthesize photoprotecting pigments, diatoms and cyanophytes are expected to dominate spectrally altered, generally low, irradiance settings where yellow-green wavelengths dominate while green algae are better suited to direct, un-altered irradiance typical of open sites (e.g. Langdon, 1988; Steinman et al., 1989; Hill, 1996; Quinn et al., 1997; Mosisch, 2001; Franken et al., 2005).

In this experiment, the photosynthetically active layer of the mat was studied as a whole and thus, the vertical taxonomic arrangement was not addressed. Yet, we expected to find more taxa in treatments with reduced shade and less taxa, mostly shade-adapted taxa, in the higher shade treatments. Due to a narrower range of irradiance environments available within the mat thickness with increased shading, we also anticipated a decrease in the taxonomic diversity with decreased irradiance (= loss of taxa with high irradiance requirement; e.g. Quinn et al., 1997). However, none of the patterns described above were found and this was especially surprising because our periphyton was laminated, cohesive, and probably had a very vertically organized structure. There are two possible explanations for the lack of taxonomic response to shading.

The first is that most of the taxa exhibited high irradiance plasticity. According to a recent study focusing on the vertical taxonomic arrangements in Everglades periphyton mat, Donar et al. (2004) showed that *S. hoffmanii* and coccoid cyanophytes are found throughout the mat thickness. Coccoid cyanophytes are mostly found on top and in the center of the mat, while *S. hoffmanii* is mostly found in the bottom of it (where it receives scattered irradiance). Arguably, *S. hoffmanii* is also described as being mostly found on the top of the mat in other areas, as this alga possesses UV-protecting compounds in its sheath (scytonemin, e.g. Garcia-Pichel & Pringault, 2001). Similarly, β -carotene in diatoms also has a photo-protectant role in dissipating excess excitation energy to protect both photosystems (Ferris & Christian, 1991; Mosisch et al., 1997). Thus, high irradiance plasticity has been reported for some cyanophytes and diatoms, but, we cannot transfer this assertion to the green algae.

The second possible explanation is that periphytic algae in high-irradiance environments may respond more strongly to changes in spectral quality than quantity. Since the shade cloths were spectrally neutral, spectral alterations created within the mat were likely too weak to have taxonomic influence (Meulemans, 1987).

Periphyton metabolism

PI curves are very useful in assessing photosynthetic capabilities of algae (e.g. Kirk, 1983; Hall et al., in press) as long as curve parameters are accurately measured. PI curves are non-linear and, therefore, the confidence interval of the fitted parameters following a non-linear regression is not readily available (Zimmerman et al., 1987). Furthermore, comparisons of PI curves theoretically require at least 12 to 25 photosynthesis measurements at different irradiances (Zimmerman et al., 1987). This requirement is rarely met because it is laborious and often impractical with classic incubation methods (^{14}C , ^{13}C , oxygen incubations; Ferris & Christian, 1991). In our case, periphyton material and incubation space were limited and prevented us from performing more than 4 incubations at different irradiance for all the treatments. The precision of the oxygen method and the incubation duration required by that method have been questioned, particularly because short-term photoadaptation can occur within the bottles (reviewed in Hall et al., in press). Finally, because we deal with periphyton grown under different shade treatments, PPFD during incubations should have been adapted according to the irradiance regime commonly encountered. This would have allowed better I_k determinations of periphyton grown under high shade settings. At last, the irradiance recorded outside the BOD to draw the irradiance map under the grow lamp is not really the same than in the BOD bottle. Irradiance distribution on the bottom of a BOD bottle indeed varies slightly ($\pm 10\text{--}20 \mu\text{mol photons.m}^{-2}.\text{s}^{-1}$) when a point source of artificial light is used (Thomas, unpublished data).

For the PI curves with high I_k (around $100 \mu\text{mol photons.m}^{-2}.\text{s}^{-1}$ or above) and no photoinhibition, the P_{max} assessment is likely accurate as the plateau is defined by 2 points of similar value. For the PI curves with low I_k and when photoinhibition was present, there are however some uncertainties about the determination of both I_k and P_{max} . Finally, photoinhibition actually rarely or never occurred *in situ*. Even on a very bright day ($2000\text{--}2800 \mu\text{mol photons.m}^{-2}.\text{s}^{-1}$), the maximum PPFD reaching the bottom under 98% shade cloth ($40\text{--}56 \mu\text{mol photons.m}^{-2}.\text{s}^{-1}$) is below or in the same order of magnitude as I_β (= irradiance for which photoinhibition occurs). Photoinhibition is then not taken into account in the calculation of the integrated daily GPP. Despite these uncertainties, contrasts between treatments for either P_{max} , I_k and daily GPP are quite clear and are mostly in agreement with the findings of other studies.

It has been reported for various environments that $P_{\max}$ and I_k generally decrease with increasing shade but these relationships still have not been expressed quantitatively (e.g. Ferris & Christian, 1991; Hill, 1996; Quinn et al., 1997). Our data show that the relationship between I_k and %IT (= decreasing shade) is linear, while the $P_{\max}$ –%IT relation is non-linear, and can actually be fitted with a PI curve equation. At this point, it is not known whether a PI curve model is biologically suitable, but neither are most of the PI curve equations which were developed empirically to mathematically fit the data (e.g. Han et al., 2000). The combination of the two relationships found is that shade-adapted periphyton is more efficient photosynthetically at low irradiance than the periphyton grown with more irradiance. For example, the periphyton grown at 90-98% shade is twice as efficient photosynthetically when the irradiance received equals I_k than the periphyton grown without canopy for the same irradiance. For comparison, the ratio is 4 in the study of Quinn et al. (1997) for lotic periphyton.

The daily GPP–%IT fitted with a PI curve equation shows that periphyton grown under various artificial canopies is equally productive when shading is below 90%. With 90% shade, periphyton is not able to compensate photosynthetically the lack of irradiance but still sustains a positive net production. This does not seem to be the case with 98% shade, though we do have conflicting results: on one hand, the thickness increases over time and, on the other hand, its daily GPP and organic matter content decreases over time (probably as a result of heterotrophic organic degradation). Our findings are in agreement with those of Quinn et al. (1997) with lotic periphyton: daily GPP higher in the more open (0% and 60% shade) stream, lower at 90% shade and close to zero at 98% shade.

The fact that no photoinhibition was found even under supersaturating irradiance (relative to the maximum PPFD really occurring in the shade house) suggests that communities residing deep in the mat compensate photosynthetically for the overlying algal community which may itself be photoinhibited. This “compensatory effect” explains part of the high irradiance plasticity of the periphyton which can thrive under various irradiance regimes (e.g. Hill, 1996). The photosynthetic coupling between the different photosynthetic functional layers is also reinforced by the long survival of algae buried deep under the photosynthetically active layer which receives light only on rare occasions when irradiance is particularly high (e.g. MacIntyre & Cullen, 1995). Finally, some algae can migrate up and down within the mat to position themselves at a favorable irradiance (e.g. Dodds et al., 1999). This feature exists with Everglades periphyton mat (Scot Hagerthey, unpublished data).

Biovolume and chl a

The high irradiance plasticity of periphyton described above is also linked to either an increase in the pigments of antennae of photosystem I and II or an increase in the number of the assembly of two light harvesting complexes and the electron transport system (Zonneveld, 1998). Because the shade cloths were spectrally neutral, they should not alter the pigment ratio at the antennae but rather increase pigment density within the algal cell. Thus, it appears logical to have a chl a /BV increase for the shade-adapted periphyton ratio. However this increase occurred only for periphyton growing under 60-80% shade, while a lower chl a /BV ratio is found at higher shade. For shade above 90% (and especially at 98%), the production of more chl a is probably too energetically costly. When shading is lower than 60%, periphyton cells may not need to produce

additional chl *a* (low chl *a*/BV ratio) and can even increase their biomass (highest algal biovolume for the 30% shade).

Chl *a* per unit surface area remained unchanged over 30–90% shading because when the biovolume was high, the chl *a*/BV ratio was low (e.g. 30% shade) and inversely, when the biovolume was low, the chl *a*/BV ratio was high (e.g. 80% shade). Biovolume seems to be the best metric to track algal biomass. However, since dead algae are hard to separate from live algae, it is possible that the biovolume is overestimated, *a fortiori* for the 90 and 98% shade. On the other hand, chl *a* is not a good metric to assess periphyton biomass when working in various environments exhibiting different canopies.

The majority of shade studies on lotic periphyton communities includes a grazer component (e.g. Steinman, 1992; Wellnitz & Rader, 2003) and shows grazing to be higher in open streams (e.g. Quinn et al., 1997; Franken et al., 2005). Grazing in open areas can also influence irradiance to the periphyton community by removing the overstory and exposing the understory to high irradiance to which it is not adapted (c.f. Wellnitz & Rader, 2003). Though the number of invertebrates picked out of our periphyton was low (data not shown), fishes and snail consumers are visually dense on the C-111 bank. The reduction in biomass in the open marsh, which, based on the daily GPP data, ought to be higher, might thus be linked to higher grazing.

Our experiment demonstrates the high irradiance plasticity of Everglades periphyton which can thrive within 0-80% shade range and to a lower extent at 90% shade. This plasticity partly explains the dominance of periphyton throughout variably shaded environments in the Everglades. This is achieved mostly through physiological means by increasing photosynthetic efficiency (by increasing cellular pigment density and modifying PI curves) but also, probably, through photosynthetic coupling among various algal communities in the mat. It is unclear whether periphyton under 98% shade sustains a net increase in biomass as some of our data are conflicting. However, based on the findings of other studies, it is likely that highly shaded (>98%) periphyton declines because the energetic cost to counterbalance shade effects is physiologically too costly.

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Datasets

Shading Experiment.xls

Figure 4.1. Change in periphyton parameters over time for the 8 shade treatments: A, 0% shade (◆); B, 0% shade (○); C, 0% shade (△); D, 0% shade (×); E, 0% shade (×); F, 0% shade (●); G, 0% shade (+); H, 0% shade (□). The average curve (continuous line) for each treatment is shown. Treatments joined by underlining do not differ significantly ($P < 0.05$, two-way split plot ANOVA, contrast comparison).

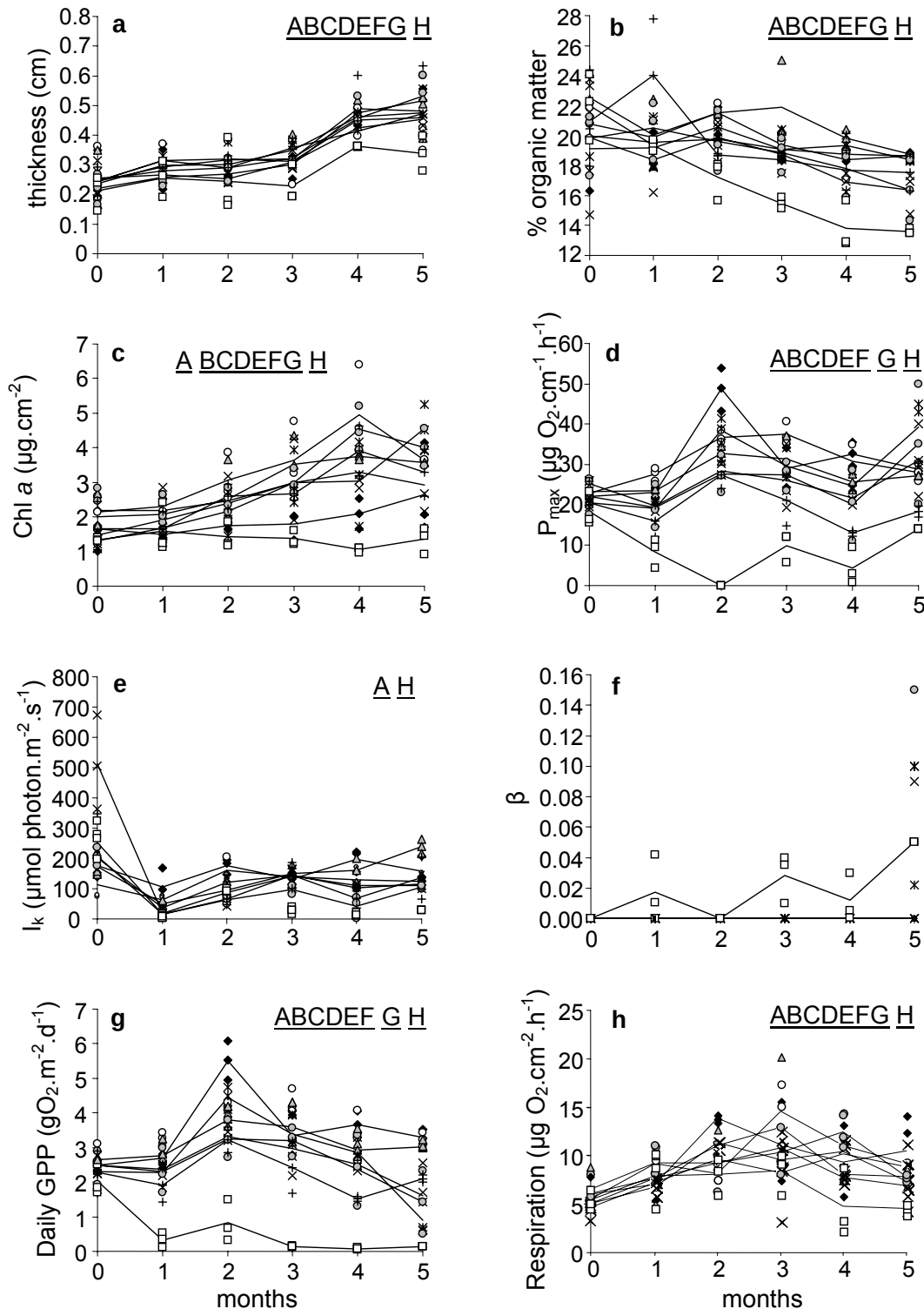


Figure 4.2. Relationship between (a) biovolume and (b) the chl *a*/BV ratio and percent shade. The cubic polynomial equation is displayed for each relationship.

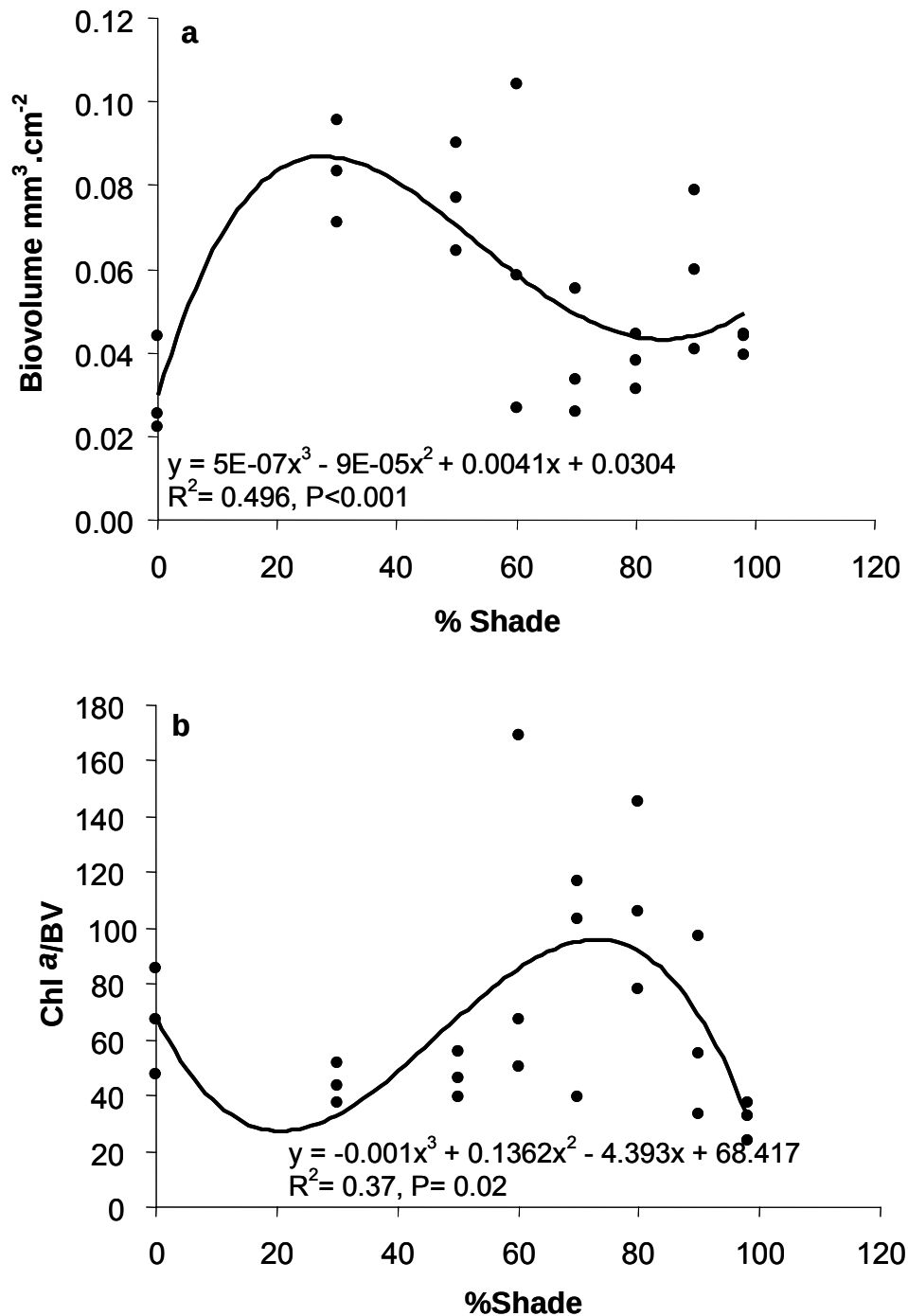
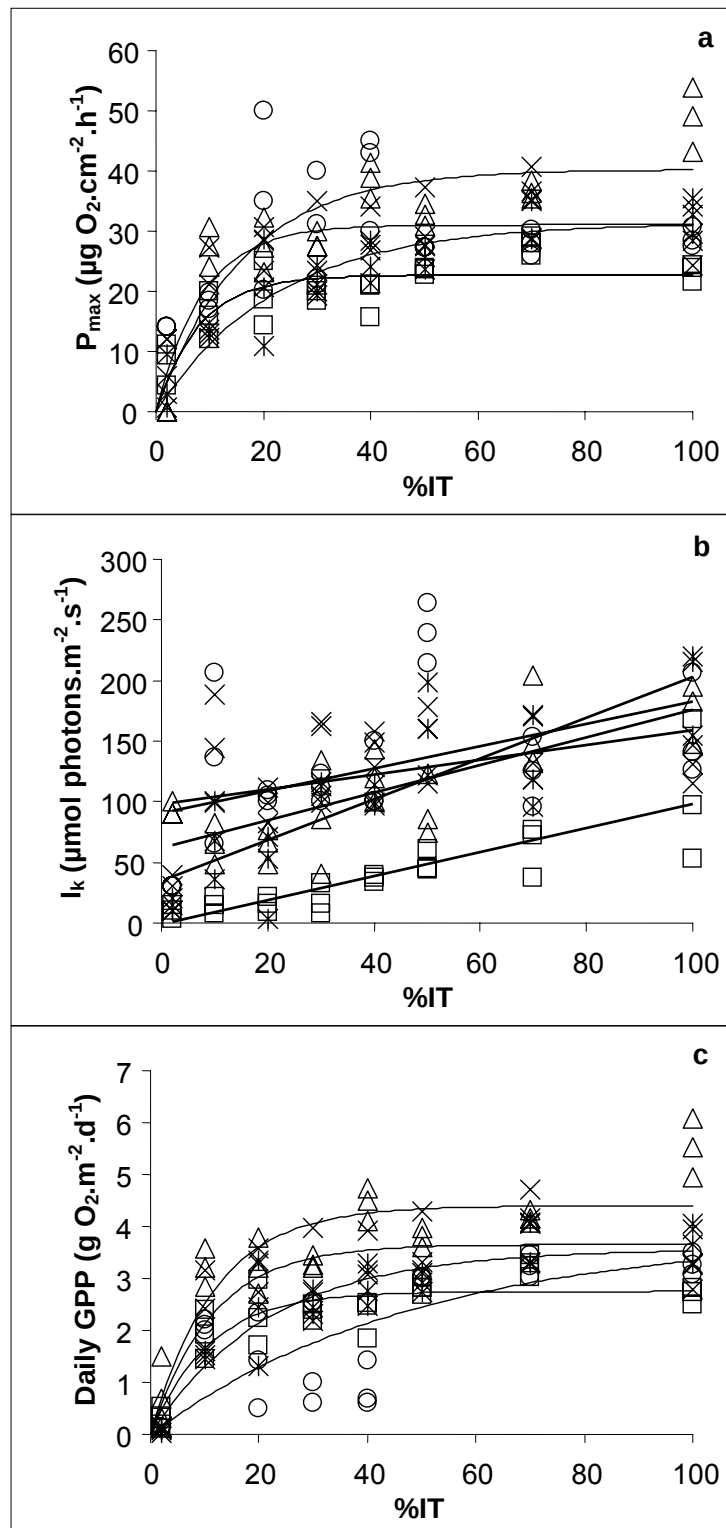


Figure 4.3. Relationships between $P_{\max}$ (a), I_k (b) and daily GPP (c) to % irradiance transmittance (%IT= 1-% shade) for months 1 through 5: month 1 ($\square$), month 2 (Δ), month 3 ($\times$), month 4 ($\ast$), month 5 ($\circ$). In graphics a and c, each relationship is fitted with a PI curve equation (Web et al., 1974): R^2 is 0.63, 0.79, 0.65, 0.83 and 0.38 for graphic a and 0.80, 0.73, 0.78, 0.87 and 0.50 for graphic c. See the text for more details about the fitting method used. Each relationship in graphic b is fitted with a linear equation which R^2 is 0.70, 0.60, 0.18, 0.70 and 0.21 for months 1 through 5 respectively.



E. INTERACTIONS BETWEEN PLANTS AND PERIPHYTON IN THE EVERGLADES MARL PRAIRIE

Introduction

Chapter IV.A shows that periphyton biomass in the marl prairie averages about 860 dry g m⁻², about twice that of plant biomass reported for similar areas (Ewe et al., 2006). This large biomass of periphyton has the potential to influence plant community abundance and composition, possibly through decreasing light availability to seedlings or, conversely, by increasing soil moisture facilitating propagation from the seed bank. Additionally, it has been speculated that as shallow areas dry at the end of the wet season, floating periphyton may smother or break new plant stems as it drapes its heavy biomass onto the vegetation (Pimm et al. 2002). In chapter IV.B we establish relationships between periphyton biomass and plant community composition, yet the mechanism driving this relationship is not clear. Does periphyton play a controlling role in determining plant community composition and biomass in the marl prairie or are the roles reversed with plant communities determining the potential for periphyton growth and development?

We designed a 3-year manipulative experiment to determine: (1) the effect of periphyton on macrophyte biomass, composition and turn-over and (2) the effect of macrophytes on periphyton biomass, composition and turn-over.

Methods

The experiment consisted of replicate plots within which (1) periphyton was removed on a regular basis and plant growth, biomass and composition was monitored, (2) plants were clipped to bedrock and periphyton growth and biomass was monitored, and (3) control sites where periphyton and plants were left unchanged. Three sites were chosen for the experiment that spanned a range of hydroperiod so that plant-periphyton interactions can be documented along the hydroperiod gradient (Fig. 5.1).

Table 5.1. Location and description of sites for the plant and periphyton harvesting experiment.

Site	Description	Inferred Hydroperiod (days)	Latitude	Longitude
B	West CSSP Pop. B		25°19.17'	-80°47.68'
M	Mahogany Hammock		25°20.37'	-80°49.05'
S	Sisal Pond		25°23.50'	-80°47.70'

Within each community type, four permanent 50-m transects were established in May 2003. The ends were marked with rebar and connected with nylon rope. Twenty-four pairs of 0.5 m² plots were designated along each transect. Each pair consists of a treatment and control plot. Half of the pairs (12) contain periphyton-removal plots (with matched control) and the other half contains plant-removal plots (with matched control). Sparsely vegetated plots were chosen for the periphyton-removal treatment/control pairs and densely vegetated plots were selected for the plant-removal treatment/control pairs. Each pair of plots was carefully selected so that plant biomass and composition were as similar as possible between the treatment and control (which

were randomly designated). The pairs were numbered 1-12 for each treatment and assigned randomly to the marked plots along the transect. Plots were similarly designated along the other 3 transects to achieve four pairs of each numbered plot for each treatment.

Once the plots were established (late dry season 2003) all periphyton was removed from periphyton-removal treatment plots. Periphyton removal was done carefully by hand to minimize disruption to subsurface marl and growing plant stems. Periphyton removed from within the plot was placed in bags and returned to the laboratory. In the laboratory, the material was processed for dry mass, ash-free dry mass, chlorophyll *a* and living cell biovolume.

During the same visit, plants were removed from the plant-removal treatment plots. All plant stems and leaves were clipped at the sediment interface and plant material from within the plot was placed in a large bag. In the lab, the plant material was separated into living and dead fractions. Dead material was dried and weighed. Living material was sorted by species, the stems and leaves of each species were counted and then dried and weighed.

New periphyton and plants growing in and around the periphyton and plant removal plots, respectively, was then removed on a regular basis (monthly in wet season, bimonthly in dry season). Also at the outset of the experiment 8 pairs of additional plots were selected to estimate initial biomass at the sites. These plots were used to verify that visual assignment of control and treatment pairs adequately selects plots that are similar in composition and biomass (a large, but unavoidable assumption in our approach to this experiment). All above-ground plant biomass and periphyton was removed from 4 pairs of 0.5 m² plots resembling the periphyton-removal plots and 4 pairs of 0.5 m² plots resembling the plant-removal plots. In the lab, the plant material was separated into living and dead fractions. Dead material was dried and weighed. Living material was sorted by species, the stems and leaves of each species counted and then dried and weighed. Periphyton was processed for dry mass, ash-free dry mass, chlorophyll *a*, total P content and living cell biovolume.

After 1 year of plant and periphyton removal treatment, we began to harvest plots on a bimonthly basis for estimation of periphyton and plant biomass and production. The four plots labeled 1 were harvested after 1 year, the #2 plots after 1 year + 2 months, the # 3 plots after 1 year + 4 months, and so forth until all 12 plots were harvested (3 years). Plot # 12 for both treatments were used to track periphyton and plant production throughout the experiment, ending in a similar harvesting event at the end of the 3 year period.

At permanent periphyton-removal plots 1 through 11, we used a harvesting procedure similar to Wiegert & Evans (1964) to estimate effects on plant biomass and growth. Plants were clipped at the sediment surface and placed in a plastic bag. In the lab, the plant material was separated into living and dead fractions. Dead material was dried and weighed. Living material was sorted by species, the stems and leaves of each species counted and then dried and weighed. In the matched control plots, the same procedure was used to assess plant biomass. In addition, periphyton was removed from the entire plot, separated epipelic, epilithic, metaphytic and epiphytic portions, if necessary, and processed in the lab for dry mass, ash-free dry mass and chlorophyll *a*.

At the # 12 permanent periphyton-removal plots (4 plots at each site), we used the non-destructive method of Dai and Wiegert (1996) to estimate above-ground NAPP. At the outset, all live stems and leaves were counted, identified and measured (length and width). At two-month intervals thereafter, one newly mature leaf the dominant 3 taxa in each plot was tagged and followed until dead, and the new leaves originating since the last visit were counted. At the end of the experiment, plants were harvested as at plots 1-11 (above). At the matching control plot, plants were marked and followed in a similar manner and plants and periphyton harvested at the end of the experiment as above for sites 1-11.

At permanent plant-removal plots 1 through 11, the following procedure was used to estimate effects on periphyton biomass and growth. On the harvesting date, periphyton was removed by hand from treatment and control plots and processed for dry mass, ash-free dry mass and chlorophyll *a*. In addition, plants were clipped at the sediment surface and placed in a plastic bag. In the lab, the plant material was separated into living and dead fractions. Dead material was dried and weighed. Living material was sorted by species, the stems and leaves of each species counted and then dried and weighed.

At the # 12 permanent plant-removal plots (4 plots at each site), periphyton accumulation rates were measured over a 2-month incubation period using two small 135 cm² wire mesh screens as artificial growth substrates. The screens were placed within treatment and control plots during the growing season, for 195 days in 2004 (ending 12/1/2004) and 142 days in 2005 (ending 11/16/2005). Material was scraped from the mesh and processed for dry mass, ash-free dry mass and chlorophyll *a*. At the end of the experiment, plants and periphyton were harvested as at plots 1-11 (above).

Results

Initial Conditions: Analysis of biomass data show that, as planned, plant biomass was significantly higher in plots chosen for plant removal than periphyton removal plots and periphyton biomass was significantly higher in plots chosen for periphyton removal than plant removal plots (Fig. 5.2). In addition, we confirmed that there were no initial biomass differences between treatment-control pairs. Plant biomass was highest at Site M and lowest at Site S while periphyton biomass was similar among sites. In addition, we found that periphyton comprised >75% of total primary biomass in initial periphyton removal plots and that macrophytes comprised >50% of total above-ground biomass in initial plant removal plots (Fig. 5.3). We also found substantial differences among sites in initial vegetation species composition (Fig. 5.4). All sites were dominated by *Cladium jamaicense*, but had different sub-dominant species.

Effects of plant removal on periphyton: Pooling responses across sites and dates, macrophyte removal caused a significant increase in periphyton biomass. Maximum biomass with plants was 814 g m⁻² while plots without plants had 1085 g m⁻². This result was also significant for ash-free dry biomass (227 g m⁻² vs. 291 g m⁻²; with and without plants, respectively). Plots without plants had a lower organic content than plots with plants (0.30 vs. 0.32, respectively). Chlorophyll *a* biomass did not differ among treatments.

Macrophyte removal had a different effect on periphyton biomass among the 3 sites. Biomass effects were greatest at sites M and S, while the difference at site B was only significant when expressed in terms of ash-free dry mass (Figs. 5.5-5.7).

While plant removal caused no effect on periphyton production in the first year of treatment, by 2005 rates of production were significantly higher in treatment plots (Fig. 5.8, 5.9). In the second year of removal, dry periphyton production averaged 292 g m⁻² in control plants and 488 g m⁻² in plant-removal plots (86 vs. 150 g m⁻² ash-free dry mass, respectively). Chlorophyll *a* biomass was also higher in plant removal plots (16,000 vs. 14,000 µg m⁻² in treatment vs. control plots, respectively). The trend was similar among sites but differences were only significant for comparisons in sites M and S.

Effects of periphyton removal on plants: Pooling responses across sites and dates, periphyton removal caused a decrease in plant biomass. Plots with periphyton had a mean plant biomass of 185 g m⁻² while plots without periphyton had a mean plant biomass of 147 g m⁻². Biomass effects were greatest at sites M and S, while site B showed the same pattern but differences were not significant (Fig. 5.10, 5.11). Effects of periphyton removal on plant turnover rates are still being analyzed.

Discussion

Plants and periphyton interact in the short-hydroperiod Everglades to influence the distribution of biomass of both. When plants are removed, periphyton biomass increases. Where periphyton is removed, plant biomass declines significantly. Therefore, periphyton has a positive influence on plant growth while plants have a negative influence on periphyton. These patterns are strongest in the shortest-hydroperiod areas represented by sites M and S in this study, while effects in the longer hydroperiod site (B) were suggestive of the same pattern but not significant.

The mechanism for an increase in periphyton biomass in the absence of plants may be through increased light penetration when plant cover is low. This is certainly suggested by the production data, which shows an almost doubling of algal growth rates in the absence of plants. However, in our shading experiment (Chapter IV.G) we determined that periphyton growth is only diminished when light is reduced more than 95% from ambient, which is an unlikely level of reduction even at the highest macrophyte densities. It is possible that the biomass effect is driven by space competition, although this does not explain the increase in production rates (as the surface area of the artificial substrates was equal among treatments). When plants are absent, periphyton grows over the entirety of the plot whereas natural densities of large-culmed species such as *Cladium jamaicense* and *Muhlenbergia* displace a significant area that would otherwise be occupied by periphyton. It is interesting that this effect was minimized at site B which, at the beginning of the experiment had a plant biomass intermediate between sites M and S where the removal effect was greatest. It is, therefore, not a result of the magnitude of change that this relationship is mediated. Perhaps, instead, it is due to the difference in water depth at these sites. Deeper water at site B encouraged the development of floating mats and sweater (epiphytic) periphyton that would not be expected to respond in the same manner as benthic mats to plant removal.

The increase in plant biomass in the presence of periphyton was unexpected. We could find only one study that similarly manipulated periphyton mat biomass to determine effects on emergent plant growth – van Hulzen et al. (2006) removed mats monthly from plots in *Spartina* marsh in the Netherlands and found plant production in cleared plots to be nearly double that of plots covered by mats. We expected that periphyton cover would depress plant growth through light limitation and smothering. Instead, periphyton has a stimulatory effect on plants, perhaps by (1) increasing nutrient availability to roots through microbial enzymatic activity or (2) increasing the moisture content of soils favoring seed germination. The notion that periphyton may act as a “seed bank” for growing macrophytes is not new to the Everglades (Ronald Mossmann, Personal Communication) although no studies have looked directly at this effect. We acknowledge that in our periphyton removal we were also removing seeds and, possibly, seedlings (even though we avoided actively disturbing growing plants). This removal of seeds over the prolonged 3 year treatment may have had a significant negative effect on final plant biomass, verifying the presence of a repository in the periphyton layer. We have yet to analyze species-specific biomass and production responses to the periphyton removal and expect to find better explanation for this unexpected response. Compositional differences among sites at the outset of the experiment were significant, and we therefore expect that analyses at the species level will help ascertain mechanisms driving among-site differences in response to the removal treatments.

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Datasets

Harvest Experiment Initial Conditions.xls
 Harvest Experiment Production.xls
 Harvest Experiment Biomass.xls

Figure 5.1. Location of sites for the plant and periphyton harvesting experiment.

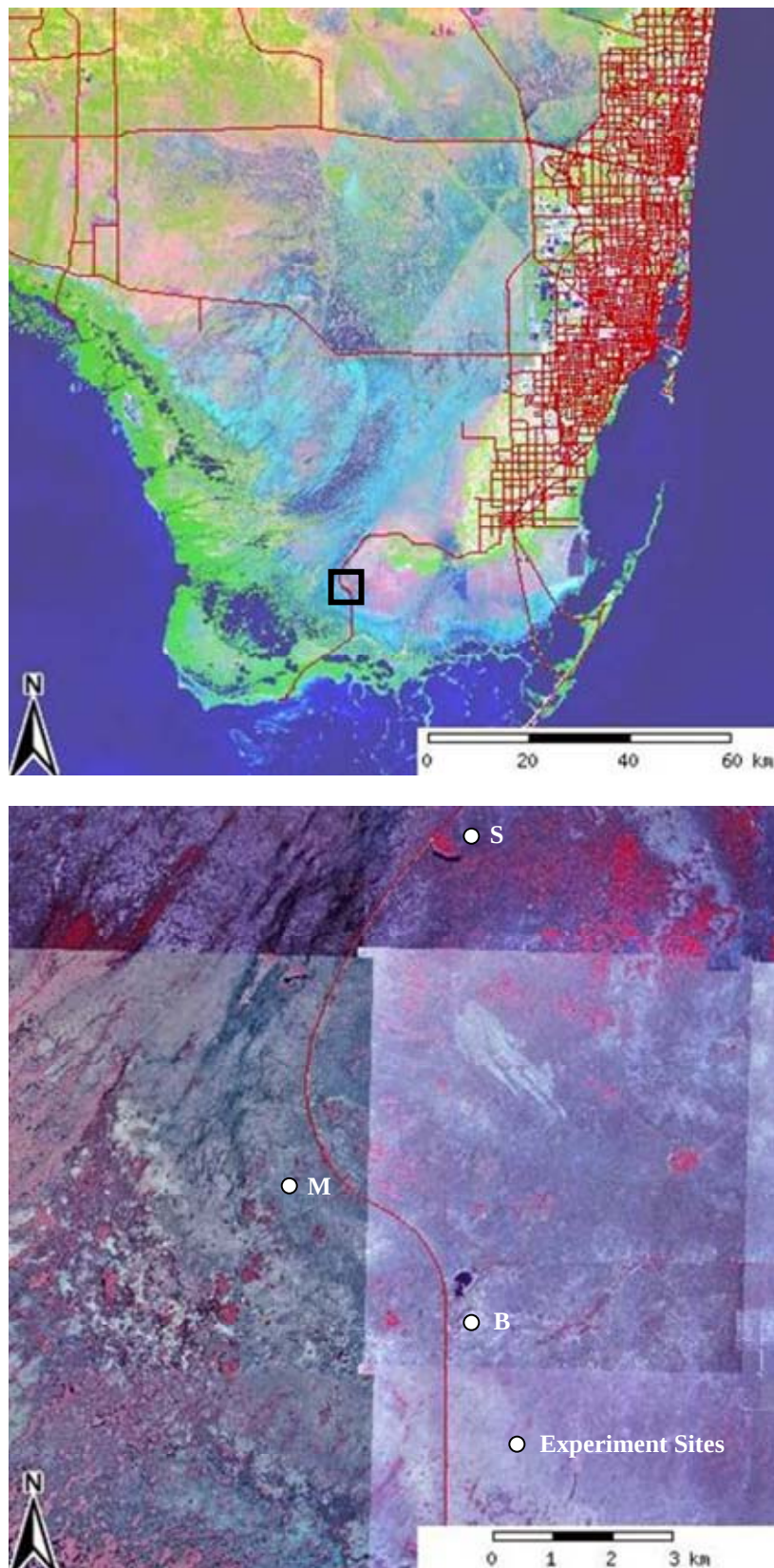


Figure 5.2. Initial biomass of plants and periphyton in treatment and control plots for the periphyton and plant removal experiments at sites B, M and S.

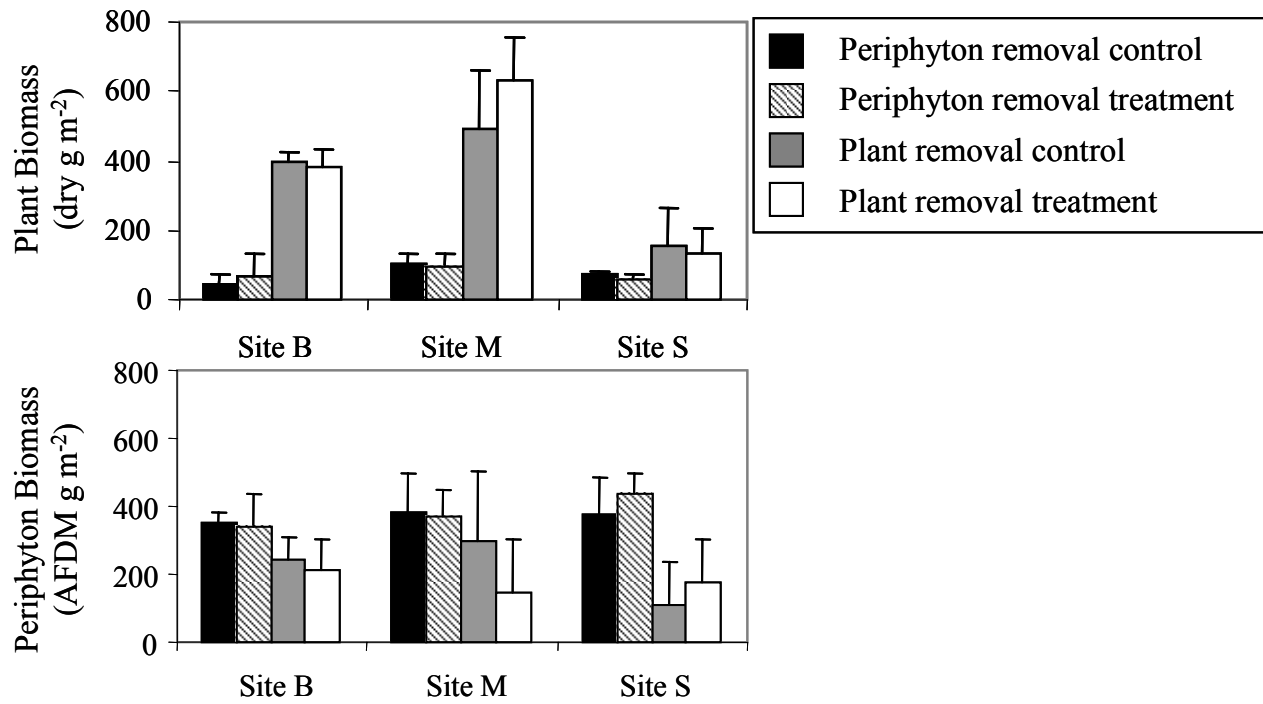


Figure 5.3. Ratio of plant to periphyton biomass in treatment and control plots for the periphyton and plant removal experiments at sites B, M and S.

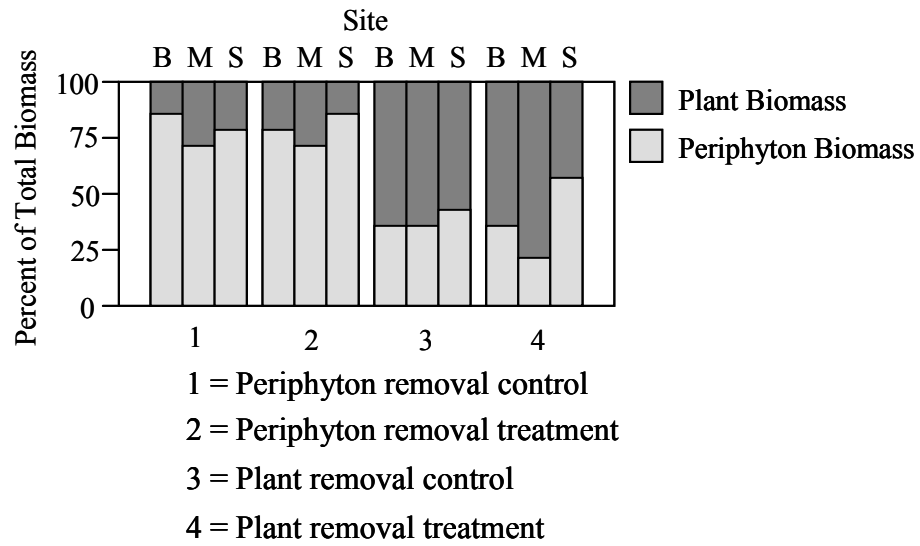


Figure 5.4. Initial plant composition (by relative biomass) at experimental sites B, M and S in the marl prairie.

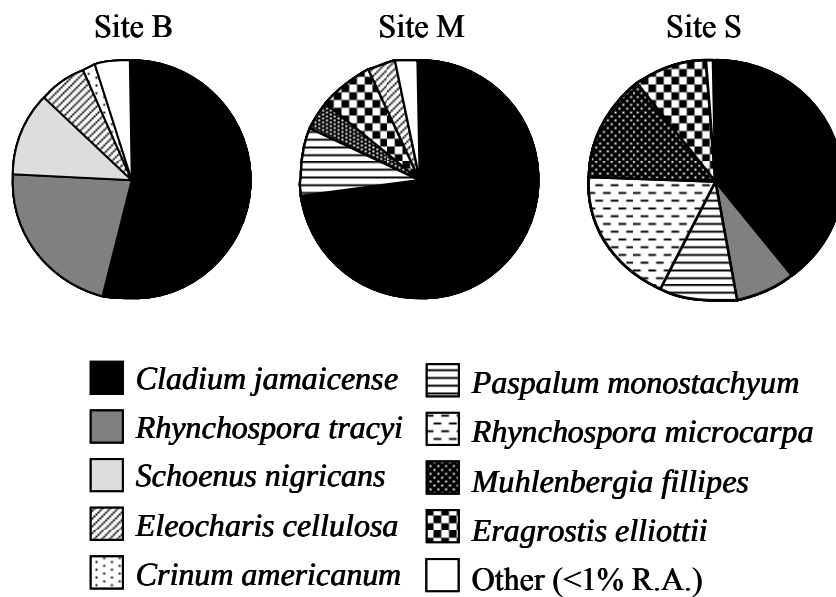


Figure 5.5. Mean and standard deviation of periphyton dry biomass, ash-free dry mass, organic content and chlorophyll *a* biomass in control and plant-removal treatment plots at sites B, M and S. Asterisk denotes significantly different means ($P < 0.001$).

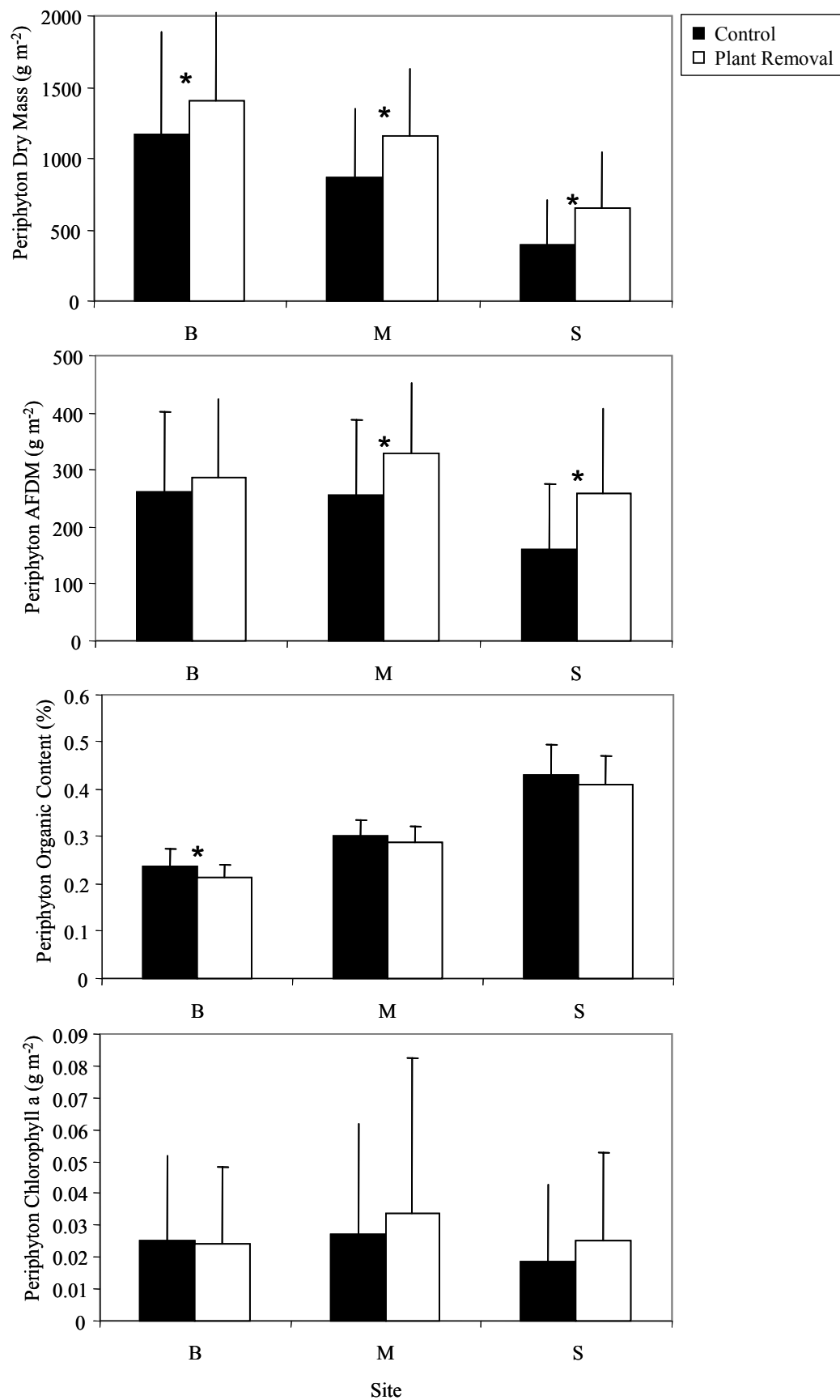


Figure 5.6. Mean periphyton dry and ash-free dry biomass over time in control and plant-removal treatment plots at sites B, M and S in the marl prairie.

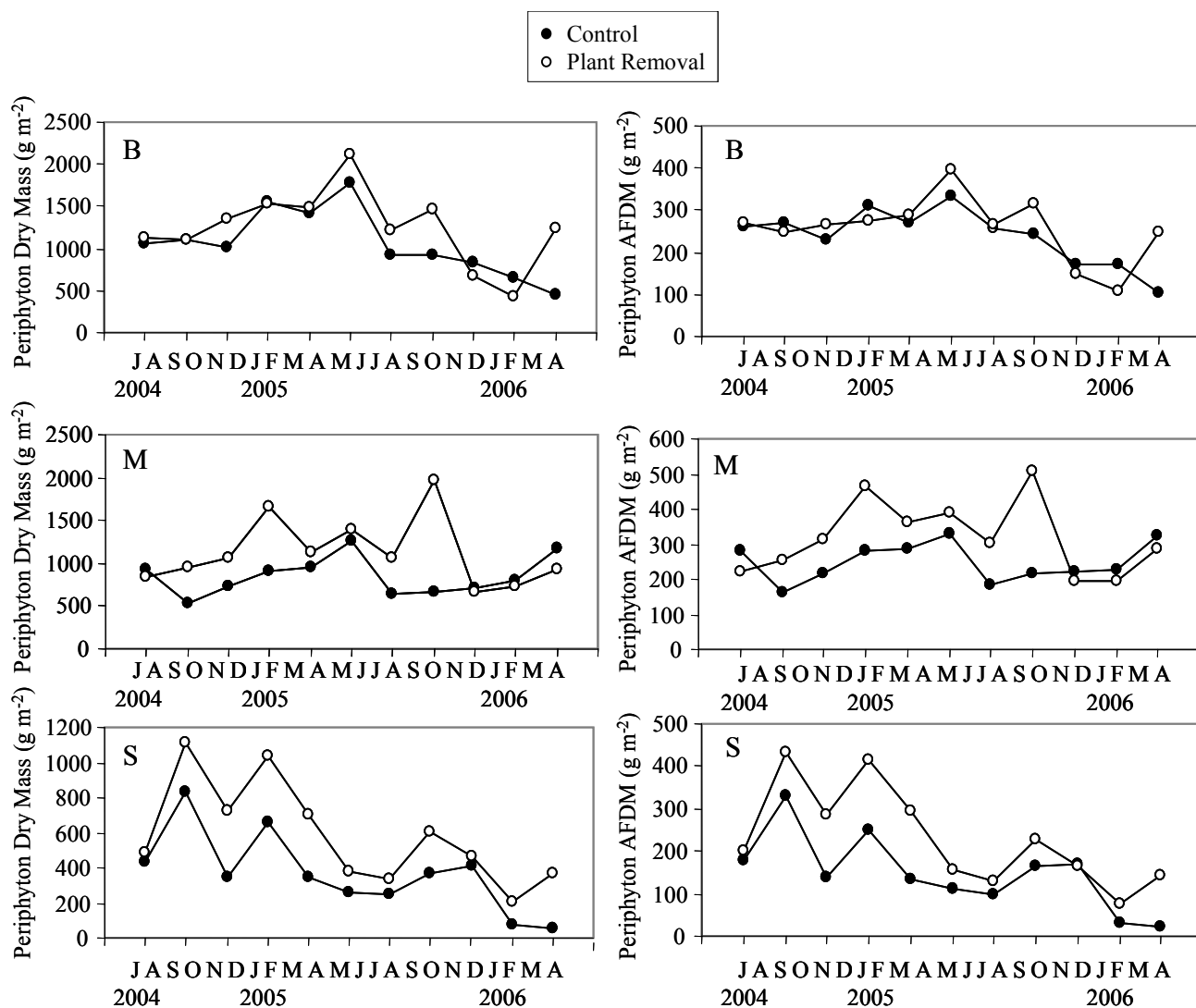


Figure 5.7. Mean periphyton organic content and chlorophyll *a* biomass over time in control and plant-removal treatment plots at sites B, M and S in the marl prairie.

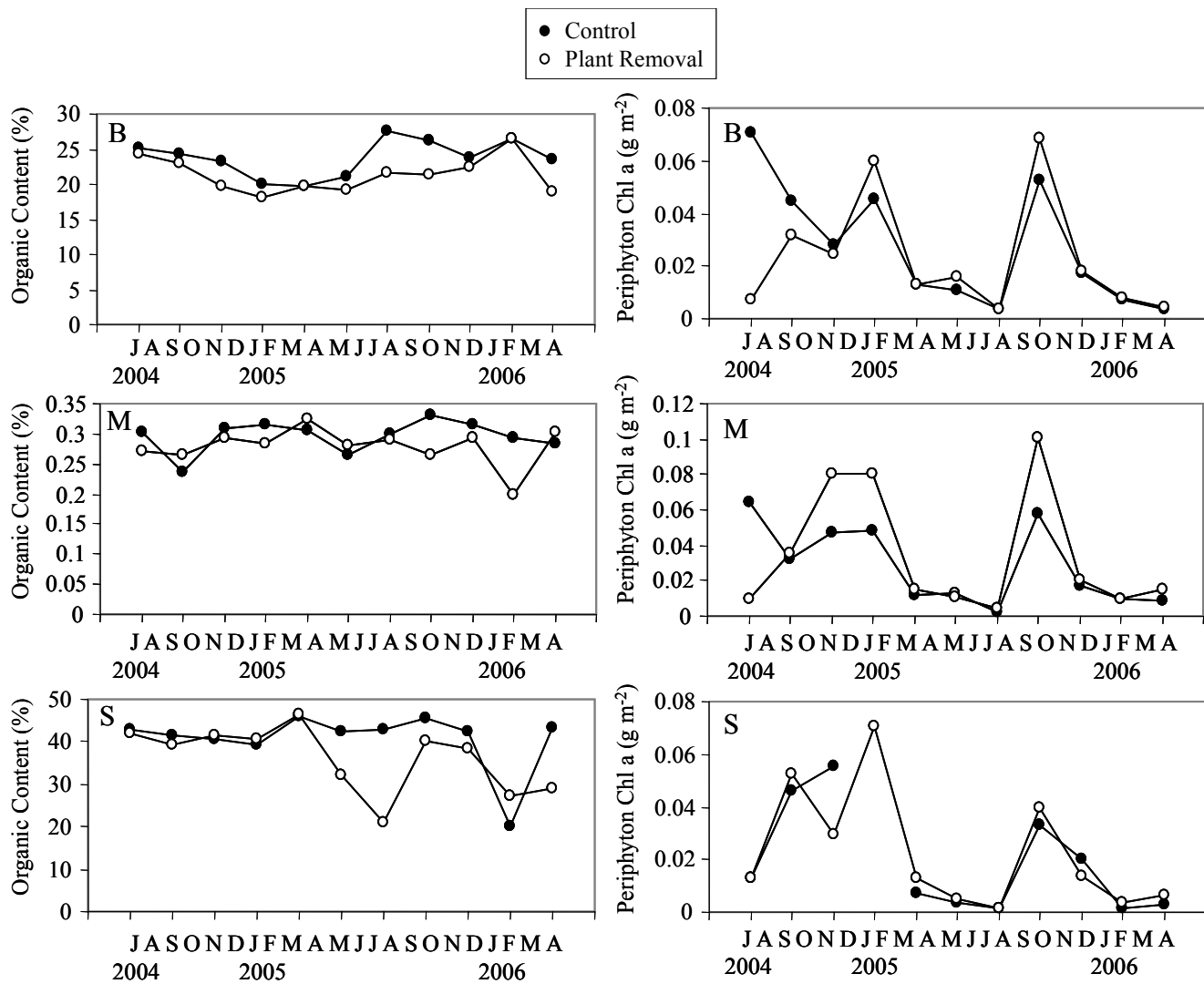


Figure 5.8. Periphyton production rates in units of dry, ash-free dry and chlorophyll a biomass accumulated per year on artificial substrates in control and plant-removal plots at sites B, M and S in the marl prairie in 2004. Asterisk denotes significantly different means ($P < 0.001$).

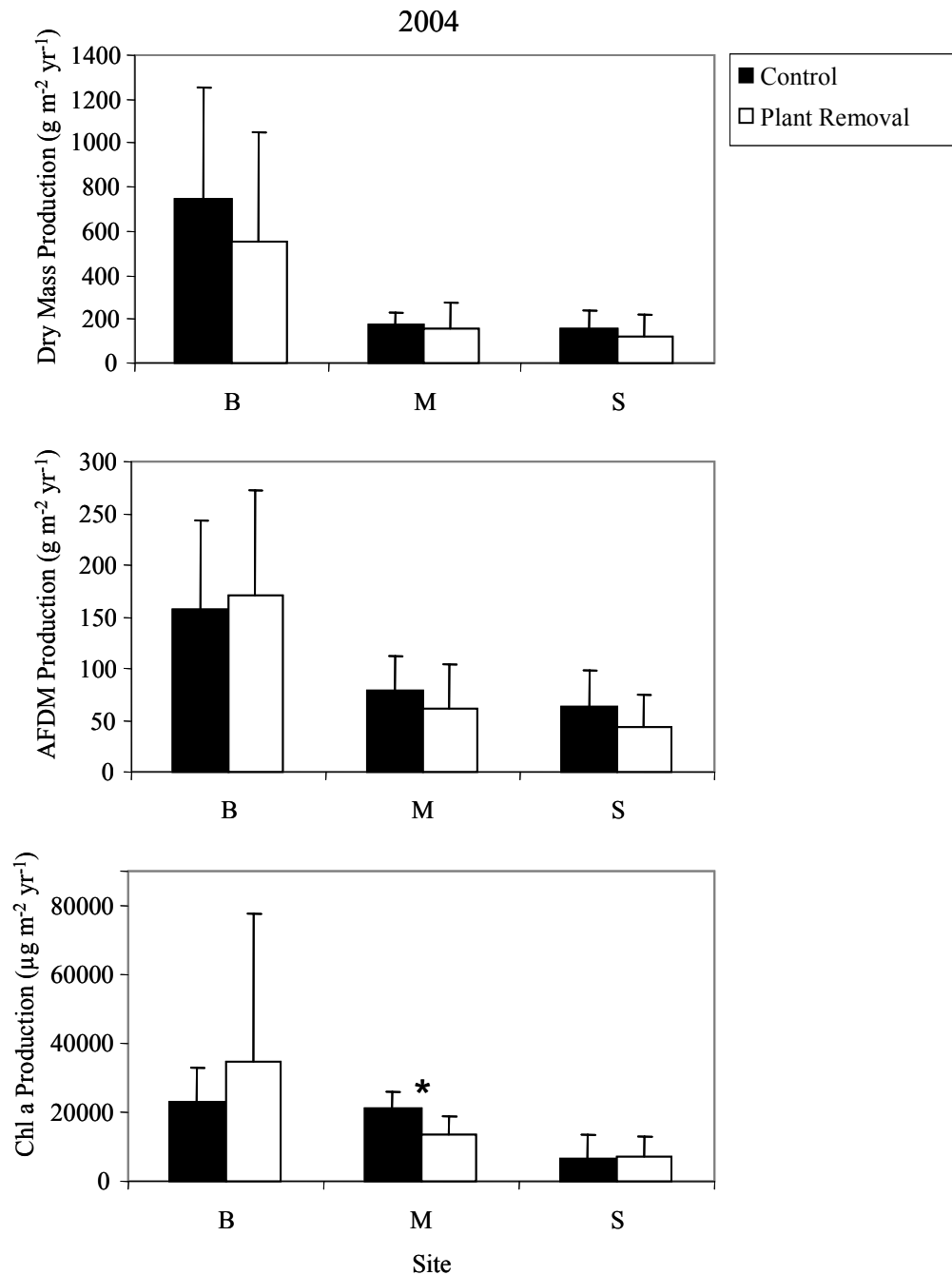


Figure 5.9. Periphyton production rates in units of dry, ash-free dry and chlorophyll a biomass accumulated per year on artificial substrates in control and plant-removal plots at sites B, M and S in the marl prairie in 2005. Asterisk denotes significantly different means ($P < 0.001$).

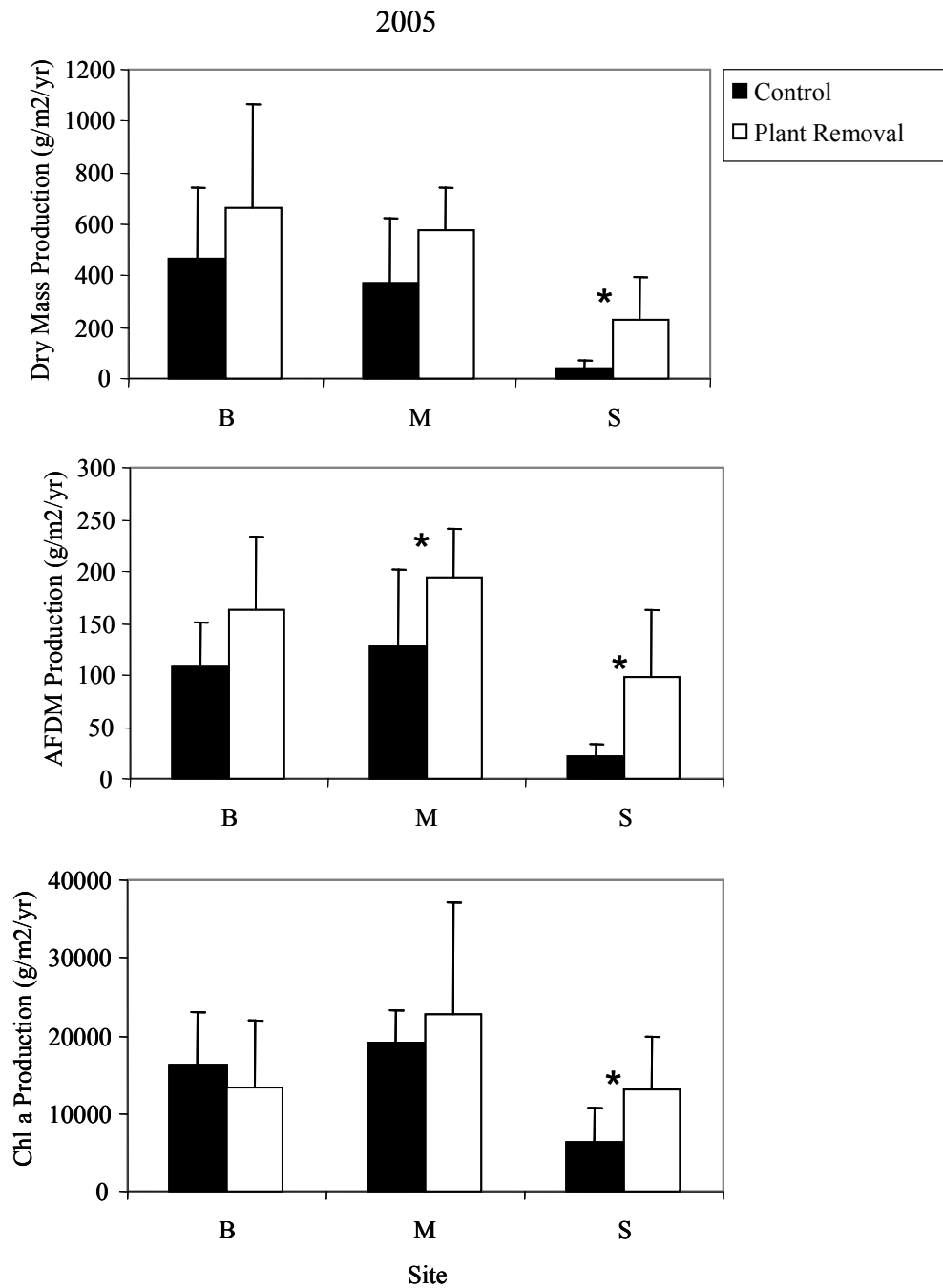


Figure 5.10. Mean and standard deviation of plant biomass in control and periphyton removal plots at sites B, M and S in the marl prairie. Asterisk denotes significantly different means ($P < 0.001$).

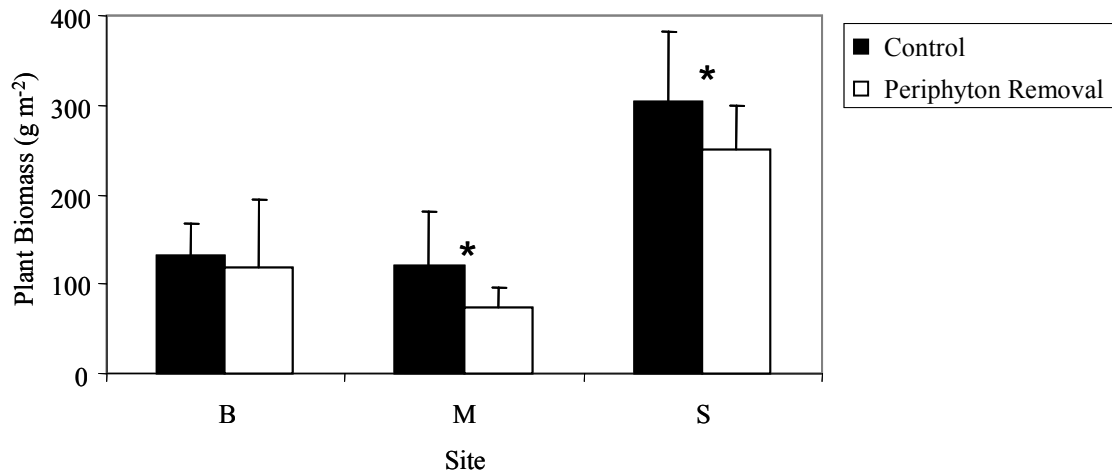
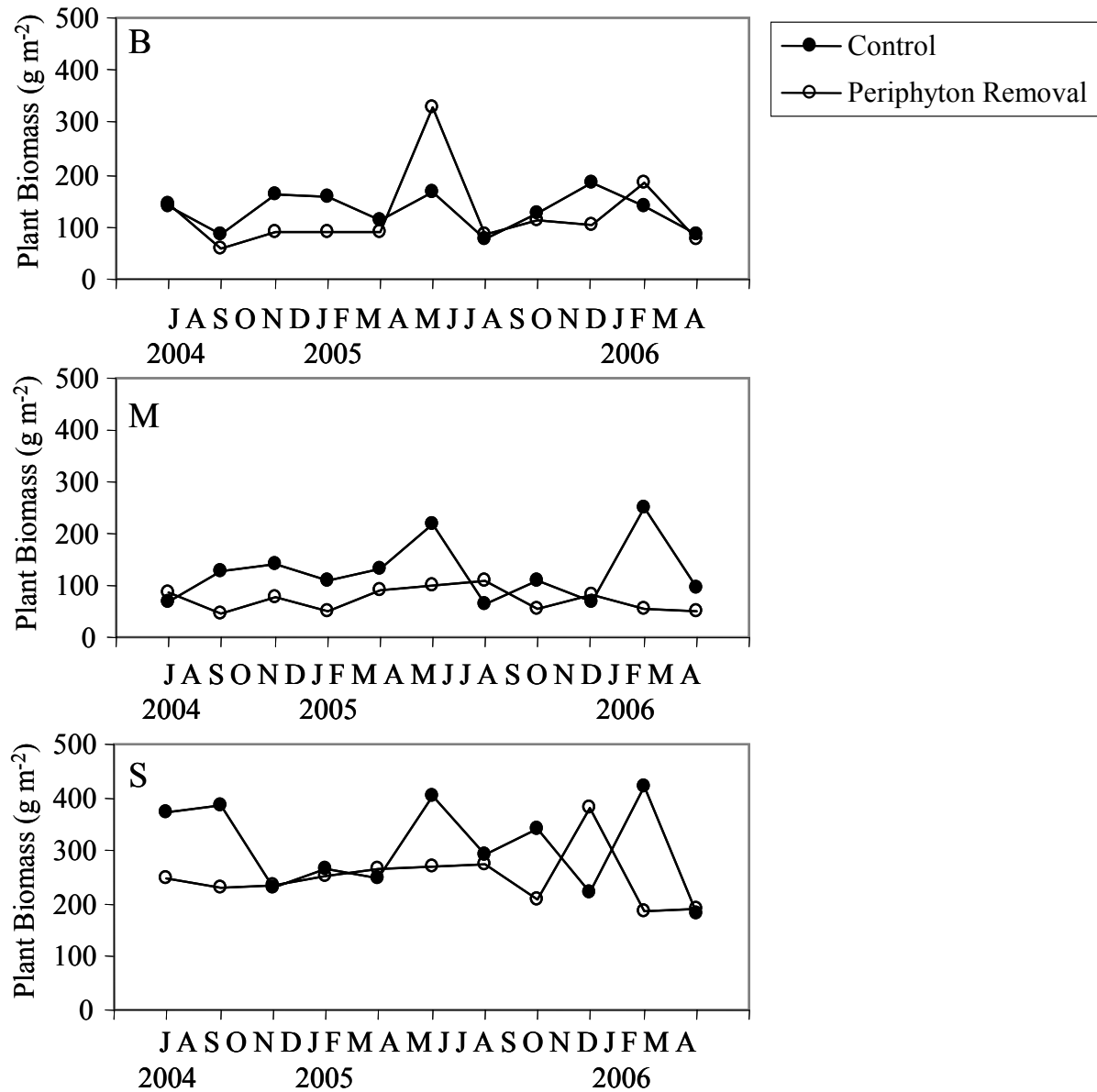


Figure 5.11. Mean plant biomass (dry mass) over time in control and periphyton-removal treatment plots at sites B, M and S in the marl prairie.



F. EFFECTS OF FIRE ON PERIPHYTON FUNCTION IN EVERGLADES WETLANDS

Introduction

The mosaic of wetlands comprising the Everglades includes freshwater marl prairies, which are situated on relatively elevated limestone and are, therefore, prone to prolonged episodes of drying. Flooded between 3 and 7 months a year during the subtropical rainy season, the marl prairie is colonized by a sparse yet diverse plant community which is tolerant of periodic and/or sustained drying. Lighted surfaces between plants and exposed stems and leaves are colonized during the flooding season by periphyton, a group of algae, bacteria and fungi, which grows when water is present but is mostly dormant the remainder of time. As the dominant primary producer in the system, periphyton forms the base of the food web, provides oxygen to the shallow water and produces marl soils. Aside from hydrology that mainly drives this system, fire is also an important, yet episodic event. Natural fires resulting from lightening strikes in the early rainy season (May-June) can enhance nutrient release and clear dead vegetation promoting new re-growth. In recent years, water management has decreased freshwater input into the marl prairie and altered the natural fire pattern in the Everglades. As a result, fire planning is now an important component of Everglades management, and timing and periodicity of controlled burns are scheduled to maximize the benefits of fire while minimizing its impacts on the system.

A fair number of studies have been conducted to examine the vegetation recovery after fire. Yet, to our knowledge, none has addressed periphyton recovery and its effect on phosphorus (P) biochemistry after fire and re-flooding. Thus, we followed the 19-day revival of benthic periphyton from a newly burned freshwater oligotrophic marl prairie of Everglades National Park prior to the 2003 rainy season. Periphyton of varying degrees of wetness (dry crust on top of marl mounds, wet mat and submerged mat in small depressions) were sampled from adjacent burned and unburned areas. Similar amounts of each periphyton type were artificially rewetted with artificial marsh water containing no P in small enclosures in a green house. Periphyton revival (biomass, metabolism and algal taxonomic composition) as well as dynamics of P in the water were examined. P dynamics in periphyton treatments were compared to (abiotic) P-desorption from oven-dried ground subsample of each periphyton type.

Methods

Biological material

On the morning of 05/22/2003, the periphyton was collected within a 100 square meter area (25°20'13"N; 80°49'26"W), the day after a prescribed fire (southwest1, fire #03036) which was set northeast of a visitor place in Everglades National Park called "Mahogany hammock". At the time of collection, general flooding still had not occurred, but numerous rain-fed pools were presents. The wet prairie vegetation in this location was mostly composed of *Cladium jamaicense*, *Muhlenbergia capillaris* var. *filipes*, *Rhynchospora microcarpa* and *Rhynchospora tracyi*, typical of the marl prairie Everglades (Ross et al. 2006). After fire, the marsh was deprived of any vegetation and burned bases of *Cladium jamaicense* were prevalent. This situation allowed us to visually assess the marsh micro-topography and to sample pieces of periphyton mats (roughly 25cm² each) at different elevations in the burned marsh: Type A, top of the mounds periphyton; type B, ground zero marsh periphyton and type C, periphyton in pools.

Unburned periphyton mats were also sampled as a control of the burned mats within an area that did not burn. It is supposed that this intact area of marsh was similar to the burned marsh in all points because it was within this burned area. Since the microtopography was hardly noticeable in the unburned marsh because of the dense vegetation cover, control of type A and B periphyton (= type D periphyton) was collected. Type E periphyton was also collected in pools within the unburned area as a control of type C periphyton. Each periphyton type collected was kept, unstacked, in plastic trays and stored uncovered in the FIU green house for 24-h. Special care was taken to keep the type C and E periphyton flooded with rain pool water until the experiment began.

Experimental setting

In a green house, the experiment lasted 19 days and started on 05/24/2003. For each periphyton type, pieces of periphyton were placed, fairly contiguous, and in the upright position on the bottom of three plastic trays ($30 \times 20 \times 20$ cm³; L×W×H). The total fresh weight of periphyton was 263-267 g, 367-380 g, 398-401 g, 301-313 g and 423-545 g in trays containing periphyton types A, B, C, D and E respectively. Between 18:00-18:30, the 15 trays were filled with 3 L of artificial marsh water (AMW, Jones and Amador, 1992) to achieve, depending on the volume of periphyton mat, ± 6 cm of water above the bottom of each tray. The initial water depth in each tray was recorded and water loss through sampling and evaporation was replaced with distilled water daily.

Physicochemical monitoring

Sampling events took place in late afternoon, 1 hour and 4 hours after flooding the first day; daily during a week past the first day, then every three days. After gently mixing the water in the tray, a water sample (50 mL) was taken for total phosphorus (TP) and total nitrogen (TN) analyses (APHA, 1999). Water temperature, pH and conductivity were recorded in each tray with an Orion 6175 phuture Pentrode probe and an Orion meter 635. Water dissolved oxygen (DO) was monitored in one of each triplicate tray every 15 minutes with an Orion polarographic probe connected to an Orion 835. Photosynthetic photon flux density (PPFD) was recorded in the green house with a LICOR QUANTUM sensor and a LICOR 1400 meter.

Periphyton monitoring

Two periphyton cores were randomly selected from each tray (1.9 cm²). Each freshly sampled core was incubated in light /dark BOD bottles filled with AMW and the changes in DO were recorded after 3-4 hours with a self stirring YSI BOD probe and a YSI 52 DO meter. All incubations took place under a 1000-W metal halide light (cf. Thomas et al. 2006 for setup detail). Upon incubation, the BOD bottles were stored overnight in the upright position in an icebox packed with ice to allow periphyton to settle down in the bottle. Water supernatant in each bottle was then vacuumed out, the periphyton removed, homogenized and mixed with deionized water to reach a final volume of 50 ml. The homogenate was finally treated as a lake water sample (APHA, 1999) to determine DW, AFDW and chlorophyll *a* (Chl *a*). On the last day of the experiment, one homogenate subsample was additionally taken (1 mL) for algal enumeration (cf. Thomas et al. 2006 for more details).

Statistics

Data in text, figures or tables are presented as means $\pm$ S.D. Conductivity in trays was compared by fitting a modified model of Hubert and Dickinson (1988) used to simulate pollutant accumulation in water runoff: $a(1-\text{EXP}(-bt)) \text{EXP}(-ct/a)$, where a , b and c ($c \geq 0$) are constants. The expression $\text{EXP}(-ct/a)$ takes into account of a decrease in conductivity after it has reached its maximum. For each variable and periphyton type, the triplicates water data were fitted using a non-linear regression (sequential quadratic programming, SPSS 14). The conductivity curves in the trays containing the various periphyton types were compared using the residuals of the fitted model of each curve (F test).

Results

Physical parameters

PPF was 18.0 ± 5.5 mol photons $\text{m}^{-2} \text{d}^{-1}$ and water temperature was $29.2 \pm 3.6^\circ\text{C}$. Water pH of AMW was 7.5. It dropped after 24-h to a steady value of 7.1 ± 0.3 in trays containing periphyton types A through C and rose to 8.3 ± 0.4 in trays with periphyton types D and E. Conductivity of AMW was $71 \mu\text{S cm}^{-1}$ and rose rapidly in all trays. Conductivity rise in trays with periphyton types A through C was the highest. Conductivity in trays with types A and B periphyton was similar ($P > 0.05$) with a maximum conductivity of $213 \mu\text{S cm}^{-1}$ reached within a week. No decrease in conductivity occurred thereafter (parameter of the model $c = 0$). Conductivity in trays with periphyton type C changed in a similar manner but conductivity decreased after a week to reach $138.7 \pm 12.5 \mu\text{S cm}^{-1}$ at the end of the experiment ($c = 5$). Conductivity in trays with periphyton types C and D were similar ($P > 0.05$) and leveled off after 24-h at $116 \pm 8 \mu\text{S cm}^{-1}$. DO in trays containing periphyton types A through C did not show any immediate diurnal patterns as it was the case in trays containing periphyton types D and E (Fig. 6.1). Small diurnal fluctuations in DO appeared after 7-d in the tray with periphyton type C, and 18-d in trays with periphyton types A and B. Average daily DO was $4.7 \pm 2.0 \text{ mg L}^{-1}$ and $4.0 \pm 1.5 \text{ mg L}^{-1}$ in trays containing periphyton D and E respectively. Average daily DO in trays containing periphyton type A, B and C decreased rapidly from 3.5 mg L^{-1} after flooding to $0.4 \pm 0.4 \text{ mg L}^{-1}$ after 3 days in tray containing periphyton C, $0.1 \pm 0.1 \text{ mg L}^{-1}$ after 11-d in tray with periphyton type A and $0.5 \pm 0.2 \text{ mg L}^{-1}$ after 8-d in tray with periphyton type B (Fig. 6.1). Daily DO increased thereafter in all trays with burned periphyton to reach at the end of the experiment $0.7 \pm 0.4 \text{ mg L}^{-1}$, $1.8 \pm 0.2 \text{ mg L}^{-1}$ and $1.9 \pm 1.0 \text{ mg L}^{-1}$ in trays with periphyton types A, B, and C respectively.

Nutrients

Nutrient concentrations in trays containing periphyton types D and E were similar and remained steadily low throughout the experiment with $2.7 \pm 1.0 \mu\text{g L}^{-1}$ and $0.014 \pm 0.014 \text{ mg L}^{-1}$ for TP and TN respectively (Fig. 6.2 and 6.3). TP increased rapidly after flooding reaching $59.0 \pm 17.3 \mu\text{g L}^{-1}$ after 5 days, $38.8 \pm 14.7 \mu\text{g L}^{-1}$ after 3-5 days in trays with periphyton types A and B respectively. TP in trays with periphyton type C leveled off within 24-h after flooding at $12.4 \pm 3.3 \mu\text{g L}^{-1}$. TN rose quickly after flooding, reaching after three days $6.2 \pm 1.1 \text{ mg L}^{-1}$, $4.6 \pm 1.0 \text{ mg L}^{-1}$ and $2.4 \pm 0.1 \text{ mg L}^{-1}$ in trays containing periphyton types A, B and C respectively. TN decreased steadily thereafter to reach at days 9-12 TN concentrations similar to the ones in trays containing periphyton types D and E.

Periphyton metabolism

GPP in trays with periphyton types A through C was low ($0.8 \pm 4.0 \mu\text{gO}_2 \text{ cm}^{-2} \text{ h}^{-1}$). GPP was much higher in the other trays and averaged $20.9 \pm 5.4 \mu\text{gO}_2 \text{ cm}^{-2} \text{ h}^{-1}$ and $19.3 \pm 5.0 \mu\text{gO}_2 \text{ cm}^{-2} \text{ h}^{-1}$ in trays with periphyton types D and E (Fig. 6.4). Respiration in all the trays followed a similar pattern with higher respiration the first two days after flooding ($12.3 \pm 3.4 \mu\text{gO}_2 \text{ cm}^{-2} \text{ h}^{-1}$), and much lower respiration thereafter ($5.9 \pm 2.0 \mu\text{gO}_2 \text{ cm}^{-2} \text{ h}^{-1}$; Fig. 6.5).

Discussion

We found similar rates of abiotic P-desorption from the different types of dried ground mats and less than 1% of the mat P-content desorbed to the water. Burned periphyton from emerged surfaces did not recover photosynthetically and desorbed P to the water column at rates similar to dried material. Burned periphyton from submerged substrates desorbed P rapidly in the first 10 days but increasingly reabsorbed P thereafter subsequent to patchy algal recovery. Unburned mats did not desorb P because of high photosynthetic rates and P uptake subsequent to flooding. Therefore, healthy periphyton mats regulate water P dynamics in the marl prairie but P-buffering in burned areas is delayed in time and dependent on submersed patches that are less susceptible to fire.

References

- Ross, M. S., J. P. Sah, P. L. Ruiz, D. T. Jones, H. C. Cooley, R. Travieso, J. R. Snyder and D. Hagyari. 2006. Effect of hydrology restoration on the habitat of the Cape Sable Seaside Sparrow. Third Annual Report to Everglades National Park.
- Thomas, S., E. E. Gaiser, M. Gantar and L. J. Scinto. 2006. Quantifying the responses of calcareous periphyton crusts to rehydration: A microcosm study (Florida Everglades). *Aquatic Botany* 84: 317-323.

Datasets

Fire Experiment.xls

Figure 6.1. Diurnal change in dissolved oxygen in mesocosms with periphyton from different burn treatments. A = dry burned periphyton, B = moist burned periphyton, C = submersed burned periphyton, D = dry/moist unburned periphyton, E = submersed unburned periphyton.

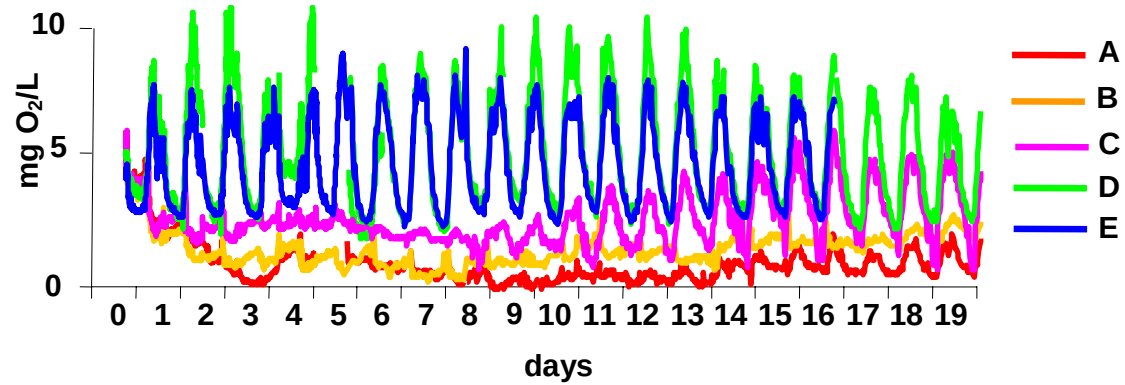


Figure 6.2. Total phosphorus (TP) concentration in water over time in mesocosms incubated with mats from different burn treatments. A = dry burned periphyton, B = moist burned periphyton, C = submersed burned periphyton, D = dry/moist unburned periphyton, E = submersed unburned periphyton.

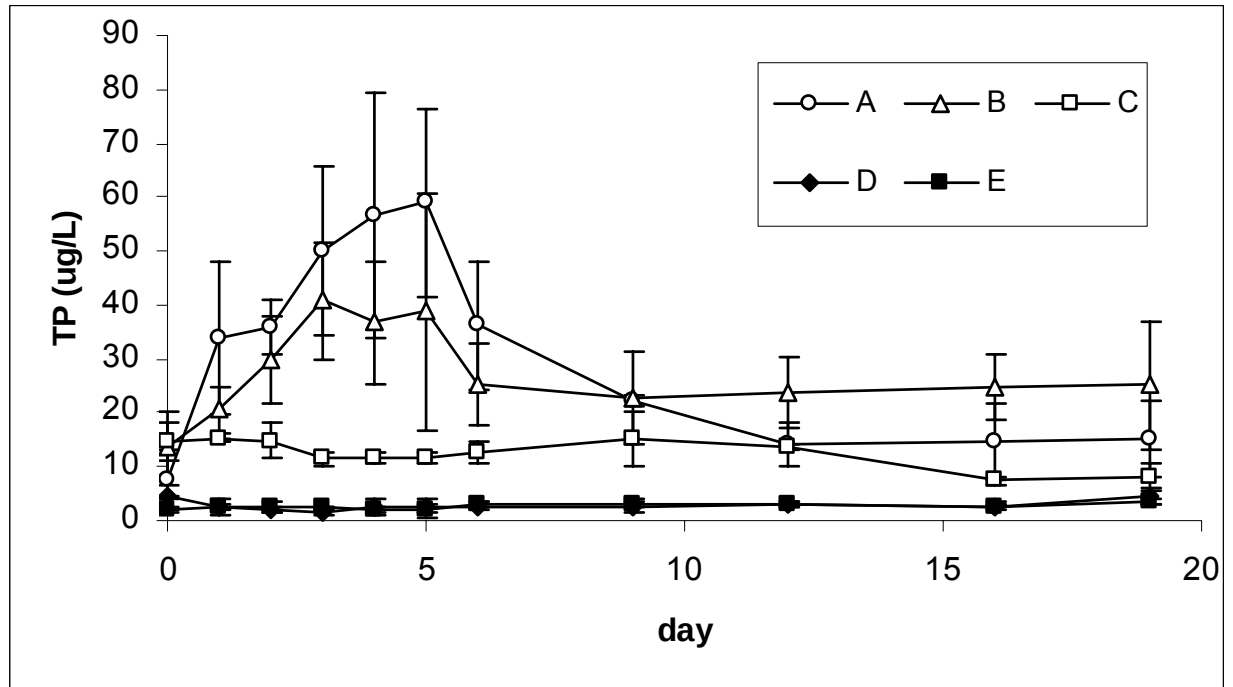


Figure 6.3. Total Nitrogen (TN) concentration in water over time in mesocosms incubated with mats from different burn treatments. A = dry burned periphyton, B = moist burned periphyton, C = submersed burned periphyton, D = dry/moist unburned periphyton, E = submersed unburned periphyton.

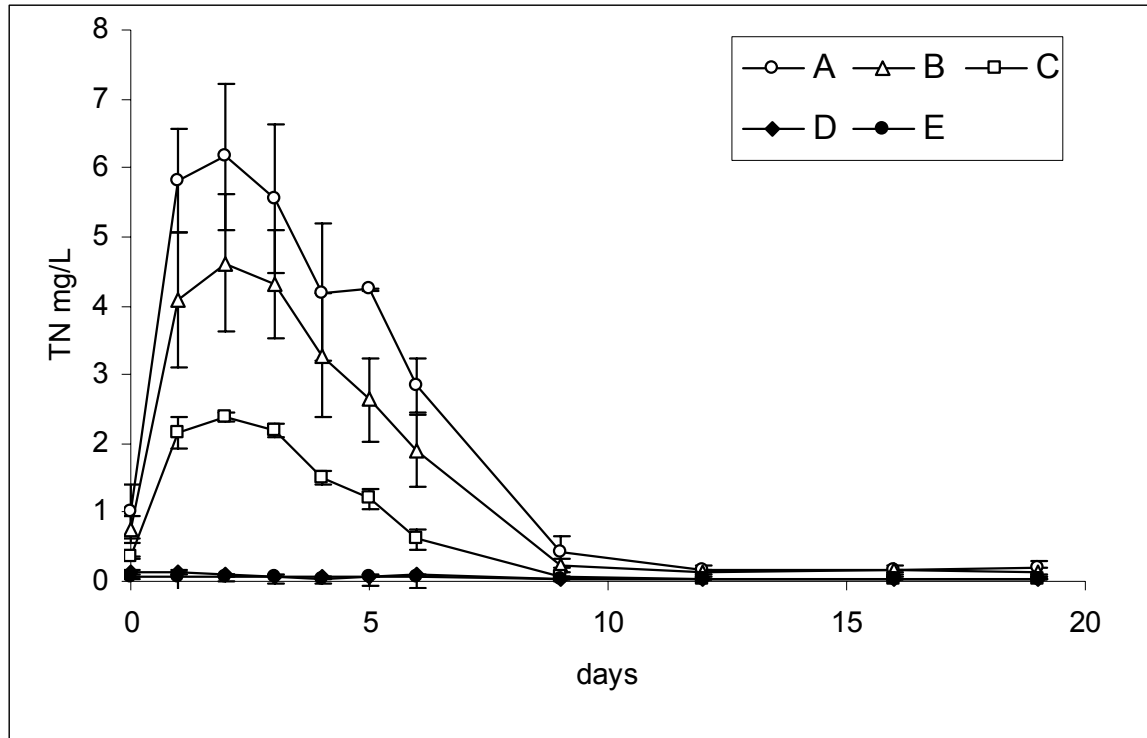


Figure 6.4. Changes in gross primary production over time in mesocosms incubated with mats from different burn treatments. A = dry burned periphyton, B = moist burned periphyton, C = submersed burned periphyton, D = dry/moist unburned periphyton, E = submersed unburned periphyton.

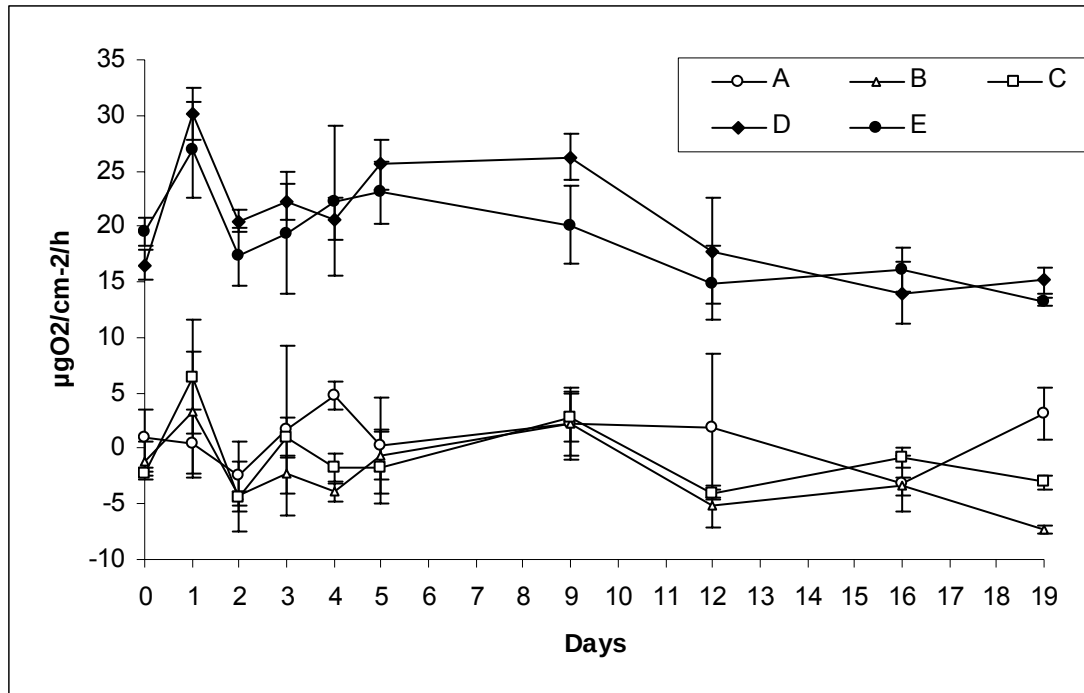


Figure 6.5. Changes in respiration in mesocosms incubated with mats from different burn treatments. A = dry burned periphyton, B = moist burned periphyton, C = submersed burned periphyton, D = dry/moist unburned periphyton, E = submersed unburned periphyton.

