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Temporal Variation in the Biomass of Submersed Macrophytes in Lake Okeechobee, Florida

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ABSTRACT

Random aboveground biomass samples of submersed vascular macrophytes were collected to document the relative effects of selected biotic and abiotic factors on temporal variation in abundance and community composition in three macrophyte communities in Lake Okeechobee, Florida. Submersed taxa included southern naiad (*Najas guadelupensis* (Spreng.) Magnus), Illinois pondweed (*Potamogeton illinoensis* Merong), vallisneria (*Vallisneria americana* Michx.), and hydrilla (*Hydrilla verticillata* (L.f.) Royle). Summer rainfall increased mean water column station depth by *ca.* 1.5 m. Biomass was negatively correlated to Secchi depth ($r = 0.74, p < 0.05$). Naiad was most negatively affected by changes in water transparency. Secchi depth, water depth, and subsurface light penetration (PAR) were the most consistent factors in the regression models, although macrophyte response to environmental factors is species specific.

Key words: algal epiphytes, depth, vallisneria, hydrilla, naiad, pondweed.

INTRODUCTION

Submersed vascular macrophytes are important ecological components of aquatic systems (Wetzel 1985). These primary producers provide habitat for invertebrates (Soszka 1975), epiphytes (Cattaneo and Kalff 1980), fish (Wiley *et al.* 1984) and a variety of other aquatic organisms (van der Velde 1987). Aquatic macrophytes can play a critical role in the nutrient dynamics of aquatic systems (Carpenter and Lodge 1986). Macrophyte distribution and biomass are influenced by a variety of environmental factors including water transparency and depth, light, and nutrient availability (Spence 1967, Canfield *et al.* 1983, Chambers and Kalff 1987), as well as biotic factors such as the degree of colonization by epiphytes

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(Sand-Jensen and Borum 1984, Stevenson 1988, Sand-Jensen 1990).

A review of the literature indicates that little research has been done on macrophyte dynamics in shallow tropical systems. In addition, much of the work that has been done on lakes occurring in tropical latitudes has been in deepwater oligotrophic systems located at high elevations (Denny 1972, Denny 1973, Harper 1992). Shallow lakes often possess extensive littoral zones relative to deeper water systems. Additionally, sampling regimes in previous investigations of submersed macrophytes in lacustrine systems typically consist of one or two samplings during the months of peak biomass (Langeland 1982, Duarte *et al.* 1986, Canfield and Duarte 1988, Chambers and Prepas 1990). Few studies have addressed temporal variation in the species composition of submersed aquatic macrophyte communities throughout the entire growing season. The purpose of this research was to observe changes in plant community composition and abundance within individual beds of submersed macrophytes in Lake Okeechobee, a subtropical-tropical lake located in south central Florida. Repeated point sampling during a 13 month period facilitated examination of the effects of temporal variation in water quality, lake stage, and epiphyte abundance on macrophyte biomass and species composition.

MATERIALS AND METHODS

Study site. Lake Okeechobee (26°56.00'N, 80°55.00'W) is a large, shallow subtropical-tropical lake (surface area *ca.* 1805 km^2, mean depth of *ca.* 2.7 m) with a littoral zone that occupies *ca.* 21% of the total surface area (Schelske 1989). The lake is a highly managed system serving as a reservoir, fishery, recreation site, and floodwater control. Lake Okeechobee is eutrophic to hypereutrophic (Canfield and Hoyer 1988).

Sample collection. Three stations were established in December 1990 in selected macrophyte beds (all greater than 275 m on the shortest axis). Stations were located by triangulation with fixed landmarks and Loran coordinates. All sites were protected from wind and wave action by nearby emergent vegetation and dense surrounding submersed vegetation.

Random aboveground biomass samples (0.25 m^2) were collected monthly in triplicate and transported to the laboratory for processing. Individual plants were also collected in triplicate to measure epiphytic chlorophyll. Samples were hand-collected (by snorkeling) in order to avoid the sampling error associated with mechanical collection methods which can either overestimate or underestimate plant biomass (Downing and Anderson 1985).

Coincident water column measurements were made at each station. A Hydrolab unit, model Surveyor II was used to measure water temperature, pH, conductivity, and dissolved oxygen concentration. Light penetration was measured as water transparency using a Secchi disk and as photosynthetically active radiation (PAR) using a LiCor data logger model LI-1000 equipped with a LI 193 SA spherical light probe. A depth pole marked at 0.1-m intervals was used to measure station depth. Surface water grab samples were collected to determine water column chlorophyll *a*, alkalinity, and total nitrogen, phosphorus, and silica. Samples were analyzed for chlorophyll *a* and nutrient concentrations according to APHA (1989) standard procedures. Water samples were stored on ice in the dark until processed.

Sample processing. Each aboveground biomass sample was cleaned of contaminants and partitioned by species. Each sample was then dried at 60C for a minimum of 48 hr and weighed.

A modification of the mechanical removal method of Gough and Woelkerling (1976) was used to separate the epiphytic algae from the individual macrophytes (Zimba and Hopson in prep). Plants were placed in separate 1-L plastic bottles containing 100 mL of distilled water. Each bottle was then agitated by hand at approximately 180 revolutions per minute. A subsample of the resultant epiphyte suspension was filtered through glass fiber filters (0.7-µm porosity). Epiphyte chlorophyll samples were processed and chlorophyll concentrations calculated in accordance with APHA (1989) guidelines and equations. Epiphyte chlorophyll concentrations were normalized to dry weight of host plant. The monthly mean for epiphyte chlorophyll was then used to calculate algal biomass per square meter of macrophytes at each station per sample date.

Data analyses. The data were initially tested for normalcy by analysis of mean:standard deviation ratios. Log+1 transformations were used to reduce variance (Ricker 1973). Data were then analyzed using stepwise multiple regression analysis (SAS Institute, Inc. 1988). Macrophyte biomass was used as the dependent variable and epiphyte chlorophyll and field measurements were used as the independent variables in each of the macrophyte regression models. Forward independent variable selection was halted when the addition of new variables explained less than 10% more of the total variance. Use of regression analysis was deemed more appropriate to identify forcing variables than path analysis; regression techniques typically result in models containing more significant components than causal relationship models (Asher 1976, Zimba 1985).

RESULTS AND DISCUSSION

Total submersed plant biomass ranged from 27 to 1593 g/m^2 dry weight, with a mean value of 759 g/m^2 (Figure 1). This mean value is three times the maximum biomass reported by Langeland (1982) for several Florida lakes. Southern naiad was the dominant species, accounting for 70 to 99% of the total submersed plant dry weight at each station during at least 9 of the 13 months of the study (Figure 2). Community structure at the more northern stations (depicted in Figures 2a and 2b) had higher concentrations of hydrilla relative to the southern site, especially during the winter. The southern site was dominated by naiad throughout the study period.

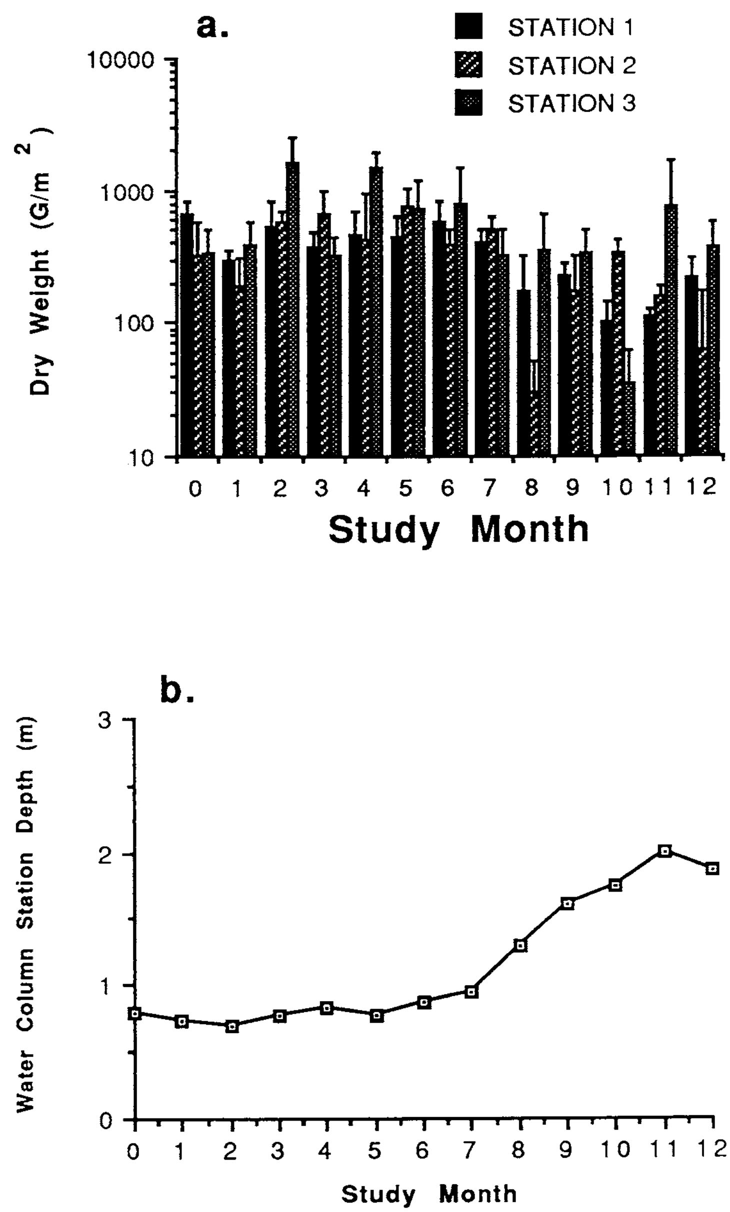

Figure 1. (a) Temporal variation in total mean biomass (g/m^2 dry weight) at three sites in Lake Okeechobee, Florida. Monthly mean values (n = 3) were determined for December 1990 through December 1991. (b) Mean water column depth at the three sampling sites.

Secchi depth was identified by multiple regression analysis as the factor explaining more than 54% of the variation in total submersed plant biomass (Table 1). Addition of subsurface light to the total biomass model explained an additional 10.15% of the variation. Water transparency (measured as Secchi depth) also accounted for the greatest amount of the variation in southern naiad biomass. The results indicate an inverse relationship between water transparency and macrophyte biomass whereas subsurface light and biomass were positively related. In each model where epiphyte chlorophyll was a significant factor, epiphyte chlorophyll and macrophyte biomass were directly related. This positive relationship contrasts with the conclusions of Sand-Jensen and Borum (1984), Stevensen (1988), and Sand-Jensen (1990) that increases in epiphyte biomass negatively influence macrophytes. It is possible that the enhanced productivity levels of macrophyte communities in tropical habitats (Stevenson 1988, Duarte 1989) allow macrophytes to "outcompete" epiphytic floras by rapid growth. Macrophyte success would be limited to environments where macrophyte:epiphyte competition for limiting resources such as light, nutrients, and gaseous exchange (*cf.* Allen 1971, Sand-Jensen and Borum 1984, Sand-Jensen 1990) does not significantly decrease maximal growth rates (μmax) of the macrophytes.

Our results may reflect fluctuation in water levels caused by heavy rainfall in the watershed during the summer months of the study. Higher water levels would result in increased total fetch and the increased water turbulence and mixing would increase the frequency of sediment resuspension and seiche events.

Such events result in an increase in the quantity of suspended solids in the water column and in turn a decrease in water transparency. As indicated by the results of the regression analyses, we would expect decreased light availability to have the greatest effect upon plants with a decumbent habit such as naiad. The results indicate that, ultimately, each of these interrelated factors, water transparency, water depth, and subsurface light penetration, represent factors which play a significant role in determining the growth of submersed macrophytes. However, the differential weights of the independent variables in each respective regression model indicate the species specific nature of macrophyte response to environmental conditions.

In summary, our results indicate that total biomass in submersed macrophyte communities in Lake Okeechobee is most influenced by fluctuations in water transparency and subsurface light penetration (PAR). The response of component taxa to environmental conditions is species specific.

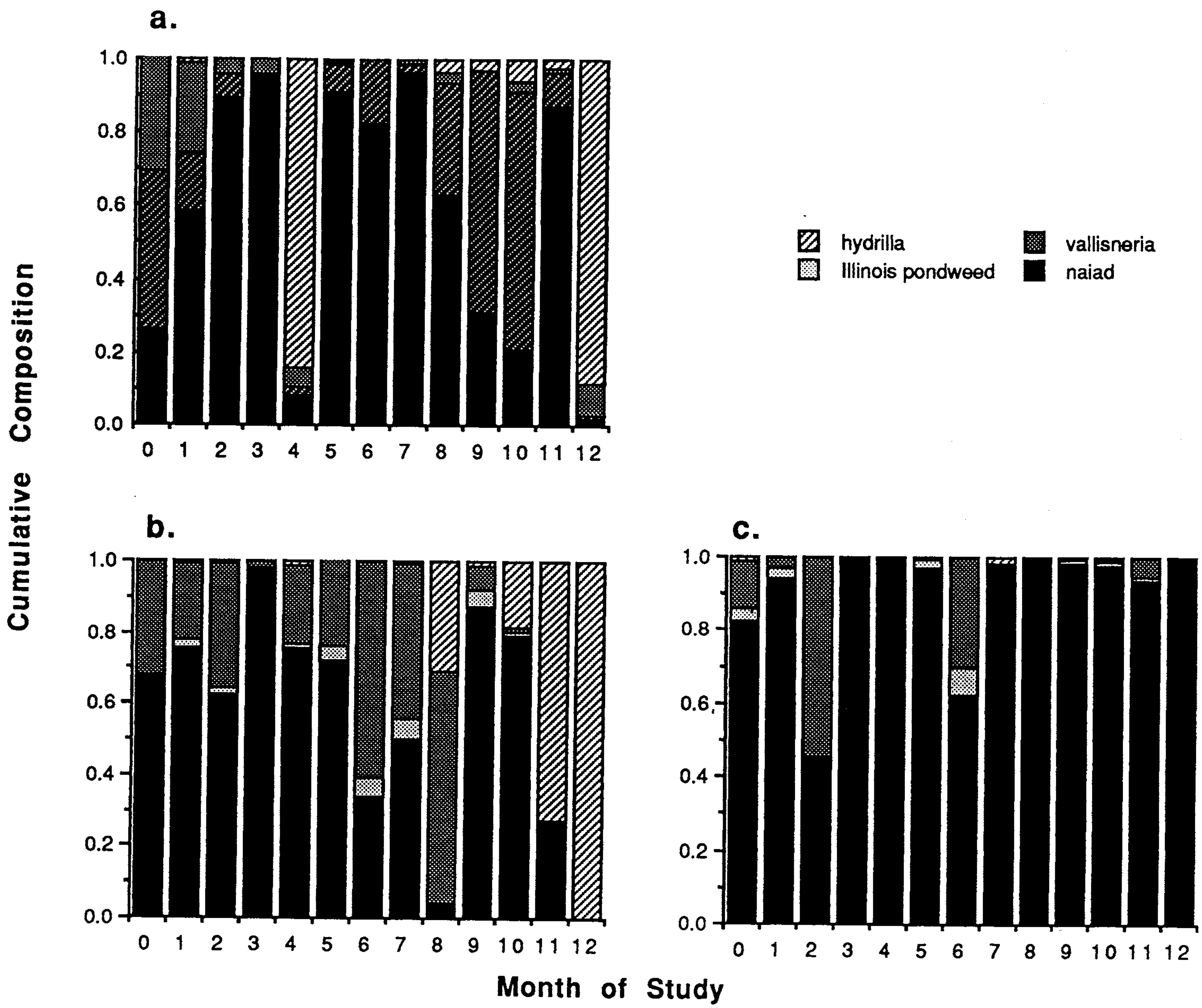

Figure 2. Community structure of macrophytes at stations 1 (a), 2 (b) and 3 (c) in Lake Okeechobee, Florida. Monthly mean values (n = 3) were determined for December 1990 through December 1991.

This conclusion agrees with findings reported by Scheffer *et al.* (1992) in which two species of pondweed exhibited differential responses to changes in water depth. Chambers (1987) concluded that the composition and relative abundance of macrophyte species are determined by differential physiological responses of plant species to environmental factors. We also agree with Canfield and Duarte's (1988) conclusion that generalizations about the response of macrophytes to different environmental conditions should be made with extreme caution. Species specific response to environmental conditions is of special importance in the management of lacustrine systems because fish appear to be differentially attracted to individual species of SAM (D. Fox, Florida Game and Freshwater Fish Commission pers comm., Chick 1992). Our predictive models may be useful in the development of strategies for lake management in tropical systems which promote more "desirable" species of macrophytes. Additional study in this field is required, however, before any predictive models such as the ones developed by Duarte *et al.* (1986) can be designed to facilitate management of other systems with similar limnological features.

TABLE 1. MULTIPLE REGRESSION ANALYSIS RESULTS USING PLANT BIOMASS AS THE DEPENDENT VARIABLE AND PHYSICAL/CHEMICAL STATION MEASURES AND EPIPHYTE CHLOROPHYLL AS THE INDEPENDENT VARIABLES. MACROPHYTE BIOMASS, SUBSURFACE LIGHT, EPIPHYTE CHLOROPHYLL, AND CONDUCTIVITY VALUES WERE LOG TRANSFORMED PRIOR TO ANALYSIS.

Dependent variables	Independent variables	Cumulative R^2	F value	Prob. > F
Total biomass	-0.898*Secchi	54.66	33.77	0.0001
	0.252*log (sub I_o)[a]	64.81	5.48	0.0303
Naiad biomass	-1.134*Secchi	47.66	18.21	0.0004
Pondweed biomass	-0.013*alkalinity	17.82	8.95	0.0086
	-1.080*depth	30.62	12.33	0.0029
	0.141*bottemp[b]	49.32	11.06	0.0043
Vallisneria biomass	-1.303*depth	32.22	17.92	0.0004
	-0.503*pH	53.20	8.52	0.0088
Hydrilla biomass	5.737*TP[c]	19.31	5.15	0.0352

[a]Submersed light insolation values (as PAR).
[b]Temperature measured at the bottom of the water column (C).
[c]Total water column phosphorus (ppm).

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