THE LOWLAND MAYA AREA

THREE MILLENNIA AT THE HUMAN-WILDLAND INTERFACE

A. Gómez-Pompa
M. F. Allen
S. L. Fedick
J. J. Jiménez-Osornio
EDITORS

Chapter

The Role of Periphyton in the Regulation and Supply of Nutrients in a Wetland at El Edén, Quintana Roo

Eberto Novelo
Rosaluz Tavera

INTRODUCTION

Wetlands are unique ecosystems that are neither wholly terrestrial nor aquatic, but are characterized by the fact that they are inundated long enough to promote significant alterations in the soil properties due to chemical, physical, and biological changes (Vymazal 1995; Kadlec and Knight 1996). Wetlands are one of the most biologically active ecosystems; as a consequence, wetlands are ecosystems with very high net primary productivity. The algae in wetlands regulate the nutrient flow rate from sediment interstitial water, either through the algal assimilation of sediment nutrient, which prevents their release to the water column, or by forming an oxidized microzone produced by epipelic algal photosynthesis at the sediment-water interface (Carlton and Wetzel 1988).

Algal ensembles differ based on their capacity to remain in fluctuating conditions; the result is an association of species often growing in different life-forms. One such association—periphyton—corresponds to those algae growing firmly or loosely attached to emergent or submerged vegetation, or any other substrate (Sladecková 1962; Marvan et al. 1978; Hillebrand 1983;

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Roos 1983). This concept can include life-forms such as epipelon, plocon, and epiphyton, given that all are attached to some substrate; periphyton, then, represent a broad spectrum of communities distinguished by the way they grow as well as by their species assemblages.

Based on studies of wetlands (e.g., tundra, temperate, and subtropical) in North America, Europe, and Australia, Goldsborough and Robinson (1996) proposed a model explaining how the interaction between physical and chemical factors determines the type of periphyton and their spatial and temporary variation in wetland areas. Their model proposes four relatively stable stages: (1) lake, (2) open, (3) protected, and (4) dry. In each stage, the following life-forms predominate: phytoplankton, epiphyton, metaphyton, and epipelon, respectively. Wetland ontogeny does not assume cyclic passage of a wetland through all four stages; instead, the dominant algal assemblage is determined by several factors, including natural grazing pressure and water column stability (Goldsborough and Robinson 1996). Although several aspects of tropical wetlands have been intensively studied (Gopal, Junk, and Davis 2000), further studies on algal life-forms and communities are necessary.

The inundated savanna of the El Edén Ecological Reserve is one of the most interesting tropical zones for studying algae. In addition to differences in soil and vegetation types, duration of the period of inundation, radiation intensity, and wind exposure, the site is exceptional in its extensive algal growths, which cover the entire substrate. In this area, algal growths are different in texture, color, shape, and species composition. To explain relationships between the environment and differences in species composition, four representative sites within the El Edén wetland were chosen. Measurements of nutrients in the water, soil, and periphyton *(sensu lato)* revealed the common role of algae in controlling nutrient flux. Every hydrologic cycle, algae take nutrients from the water column and soil, thus impoverishing the water and preventing the establishment of a phytoplankton community; then, during the dry period, the periphyton supply nutrients, which enrich the soil. Given that the phytoplankton community is not firmly established during periods of flooding, the algal community model proposed for wetlands (Goldsborough and Robinson 1996) should be reanalyzed for El Edén.

STUDY AREA AND SAMPLING METHODS

The 1,492 hectare (ha) El Edén Ecological Reserve is located in the Yalahau Region of the northeast Yucatán peninsula, in the state of Quintana Roo, Mexico. El Edén is situated at 5 to 10 meters (m) above sea level, between lat 21°11'30"N and lat 21°14'N and long 87°10'30"W and long 87°12'30"W.

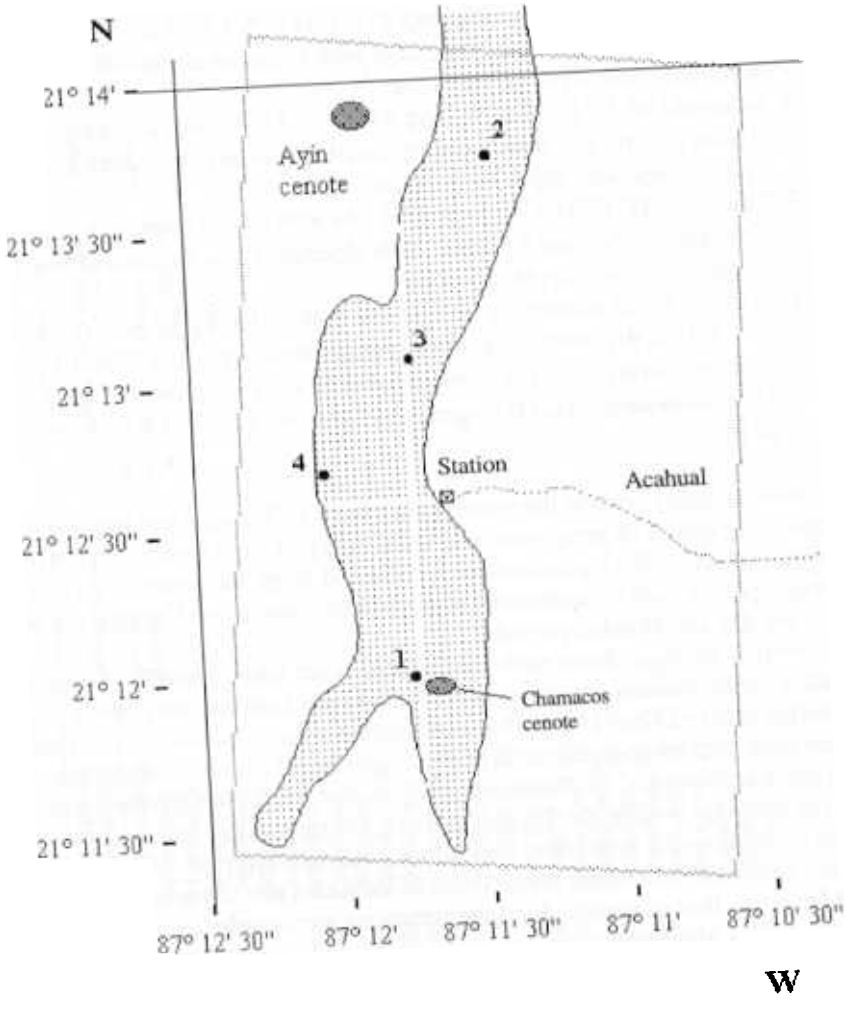

FIGURE 11.1. Sampling sites 1 through 4 within El Edén Ecological Reserve. The shaded area represents savanna that is flooded for three to four months each year.

All conspicuous and distinct algal growths (periphyton assemblages) were collected during July and October 1999 and in April, August, and November 2000. Collections were made at four established sites (4×8 m^2) within the flood zone of El Edén (Figure 11.1):

1. Savanna (lat 21°12'06.3"N; long 87°11'44.6"W), with a vascular vegetation canopy less than 30 percent with *Solanum donianum* Walp. as dominant; soil depth 10 to 15 cm
2. Savanna (lat 21°13'42.2"N; long 87°11'26.3"W), with a vascular vegetation canopy less than 40 percent with *Cladium jamaicensis* Crantz. as dominant; soil depth 10 to 30 cm
3. Tintal (lat 21°13'01.1"N; long 87°11'44.8"W), with a vascular vegetation canopy less than 5 percent with *Haematoxylon campechianum* L. as dominant; soil depth 3 to 5 cm
4. Ecotone tintal-subdeciduous tropical forest (lat 21°12'44.1"N; long 87°12'01.6"W), with a vascular vegetation canopy less than 10 percent with a mixture of *H. campechianum, Erythroxylon confusum* L., *Manilkara sapota* (L.) P. Rogen, and *Crescentia cujete* L.; soil depth 5 to 15 cm

Other samples outside the studied sites were collected when the macroscopic appearance of periphyton was quite different from those found in the permanent sites. Phytoplankton was collected from the water during the flooded period, and in permanent water bodies (cenotes and ponds) during both the dry and flooded periods.

Samples of algae from each assemblage were taken directly in plastic bottles for herbarium documentation. Periphyton samples were made on a constant area (~25 cm^2) for herbarium documentation; subsamples of 1 cm^2 were separated for quantification of chlorophyll *a* for biomass estimation. A periphyton sample of ~100 cm^2 was collected at the same time for nutrient quantification. During the flooded period, phytoplankton and water samples were taken for herbarium specimens with a 10 μm pore net; also, two water samples were taken for analysis of nutrients and chlorophyll *a* (200 ml from one liter of water). All determinations were made in the laboratory immediately after collection.

Formaldehyde (3 percent)-preserved algal samples have been deposited in the Herbarium of the Faculty of Sciences at the Universidad Nacional Autónoma de México in the Edén–FCME collection. Species description will be prepared for a later publication; a list of genera is included here (Table 11.1).

Soil samples were taken using a PVC coring device (5 cm diameter, 35 cm length). Nutrient determinations of algae and soils were made on dried samples; algal growths (periphyton) were treated as plant tissue for nutrient analysis. Quantification of chlorophyll *a* was based on the 1 cm^2 samples of periphyton collected, and is expressed in volume units following the extraction method. For more accurate results, detritus was previously removed; algal mucilage does not interfere with the extraction method used.

TABLE 11.1. Algae of El Edén Ecological Reserve, Quintana Roo, Mexico

Cyanoprokaryota	Chlorophyta	Heterokontophyta Bacillariophyceae		Chrysophyceae	Euglenophyta	Dinophyta	Glaucophyta
Anabaena sp.	*Ankistrodesmus* spp. (3)	*Achnanthes* spp. (3)	*Ophiocytium* sp.	*Dinobryon* sp.	*Euglena* spp. (2)	*Peridinium* spp. (2)	*Glaucocystis* sp.
Aphanocapsa spp. (5)	*Aphanochaete* sp.	*Amphipleura* sp.	*Vaucheria* sp.	*Mallomonas* sp.	*Peranema* sp.		
Aphanothece spp. (5)	*Botryococcus* sp.	*Amphora* spp. (2)			*Phacus* spp. (2)		
Bacularia sp.	*Bulbochaete* sp.	*Asterionella* sp.			Trachelomonas spp. (3)		
Calothrix sp.	*Carteria* sp.	*Caloneis* sp. (2)					
Camptylonemopsis sp.	*Chara* sp.	*Campylodiscus* sp.					
Chlorogloea sp.	*Chlamydocapsa* sp.	*Cocconeis* spp. (2)					
Chroococcus spp. (6)	*Chlamydomonas* sp.	*Cyclotella* sp. (2)					
Coelomoron sp.	*Cladophora* sp.	*Cymbella* spp. (6)					
Cyanokybus sp.	*Closterium* spp. (2)	*Denticula* sp.					
Entophysalis spp. (2)	*Coelastrum* spp. (2)	*Diploneis* spp. (3)					
Eucapsis spp. (2)	*Coelosphaerium* sp.	*Epithemia* sp.					
Gloeocapsa spp. (5)	*Coenocystis* sp.	*Eunotia* spp. (4)					
Gloeocapsopsis sp.	*Cosmarium* spp. (4)	*Fragilaria* spp. (4)					
Gloeothece spp. (8)	*Crucigeniella* sp.	*Gomphonema* spp. (3)					
Gloeotrichia sp.	*Desmidium* sp.	*Gyrosigma* spp. (3)					
Gomphosphaeria sp.	*Dictyosphaerium* sp.	*Hantzschia* sp.					
Heteroleiblenia sp.	*Dimorphococcus* sp.	*Mastogloia* sp.					
Hydrocoleus sp.	*Euastrum* spp. (2)	*Melosira* sp.					
Jaaginema sp.	*Gloeocystis* spp. (2)	*Navicula* spp. (6)					
Komvophoron sp.	*Gloeotaenium* sp.	*Neidium* sp.					
Leiblenia sp.	*Kirchneriella* sp.	*Nitzschia* spp. (6)					
Leptolyngbya sp.	*Micractinium* sp.	*Pinnularia* spp. (4)					
Limnothrix sp.	*Micrasterias* sp.	*Rhoicosphenia* sp.					
Lyngbya spp. (2)	*Monoraphidium* spp. (3)	*Rhopalodia* sp.					
Merismopedia spp. (2)	*Mougeotia* sp.	*Stauroneis* sp.					
Microcoleus sp.	*Nephrochlamys* sp.	*Synedra* sp.					
	Nephrocytium spp. (2)						

TABLE 11.1 *(continued)*

Cyanoprokaryota	Chlorophyta	Heterokontophyta Bacillariophyceae	Xanthophyceae	Chrysophyceae	Euglenophyta	Dinophyta	Glaucophyta
Microcystis spp. (2)	*Nitella* sp.						
Nostoc spp. (2)	*Oedogonium* spp. (3)						
Onkonema sp.	*Oocystis* sp.						
Oscillatoria spp. (2)	*Pediastrum* spp. (2)						
Phormidium spp. (5)	*Planktosphaeria* sp.						
Planktolyngbya sp.	*Pleudorina* sp.						
Pseudanabaena spp. (2)	*Pleurotaenium* sp.						
	Rahpidocelis spp. (2)						
Rhabdogloea sp.	*Rhizoclonium* sp.						
Rivularia sp.	*Scenedesmus* spp. (9)						
Schizothrix sp.	*Selenastrum* sp.						
Scytonema spp. (4)	*Sphaerozosma* sp.						
Stigonema sp.	*Spinocosmarium* sp.						
Synechococcus sp.	*Spirogyra* spp. (2)						
Tychonema sp.	*Staurastrum* sp.						
	Stigeoclonium sp.						
	Tetraedron sp.						
	Ulothrix sp.						
	Willea sp.						
	Zygnema sp.						

LABORATORY METHODS AND MATERIALS

- Phytoplankton and periphyton growths: Chlorophyll *a* was determined by modified fluorimetric method 445.0 without acidification, using a Turner AU10 fluorometer (USEPA 1997).
- After aqueous extraction, all periphyton growths were examined for dissolved inorganic nitrogen (NO_3^- by cadmium reduction and NH_3 with salicylate), and phosphorus, including particulate phosphate determined as orthophosphate (molybdate digestion with ascorbic acid as a reducing agent and molybdovanadate). All determinations were made with a DR/2010 spectrophotometer and based on accepted USEPA methods according to Hach (1997).
- Water samples: Analyzed for nutrients using the methods mentioned previously.
- Soil samples: Dissolved inorganic nitrogen was determined by the previous methods after extraction by shaking 3 g of air-dried soil in 30 ml of 0.01 M $CaSO_4$ for 15 minutes, and then filtration with a Whatman No. 2 filter. Soluble reactive phosphorus determination followed the same methods, after extraction by shaking 1 g of air-dried soil in 20 ml of 0.5 M $NaHCO_3$, pH 8.5, for 30 minutes, and then filtration with a Whatman No. 2 filter.

RESULTS

Species Composition of Periphyton

In the flooded period, the open wetland environment contains both periphyton and rhizobenthos communities, but phytoplankton communities are very scarce. In the dry period, the dominant communities are all periphyton ("plocon" *sensu* Goldsborough and Robinson 1996).

Periphyton structure consists of a dense weft of entangled cyanophycean filaments as well as empty sheaths accumulated from several seasons of growth. In some cases, sheaths of at least two years of age are visible. Among the wefts are mucilaginous algal colonies to which detritus adheres. Periphyton in the flooded period looks like a brownish sponge, but does not disaggregatè when touched.

An epiphytic algal assemblage of a few filamentous species grows upon the vascular vegetation. Most of these leaves and stems fall down at the end of the flooded period, and the epiphytic algae join the wefts of periphyton on the substrate. As the wetland dries, this "dry" periphyton acquires a crusty appearance, eventually forming the gray crusts so evident in the dry period.

To date, 230 species of algae have been recognized in El Edén. These species belong to the following divisions: Cyanoprokaryota, Chlorophyta, Heterokontophyta, Euglenophyta, Dinophyta, and Glaucophyta. Their distribution in the permanent water bodies and study sites is shown in Tables 11.2 and 11.3. In spite of this apparent diversity, a high proportion of algal component comes from species of Cyanoprokaryota.

Structure, Types, and Distribution of Periphyton in El Edén

The species composition shows a very rich flora with aquatic, subaerial, and edaphic components. A clear distinction exists when comparing typically aquatic algae in the permanent bodies of water (e.g., ponds and cenotes) with those algae from sites in which a flora with a high capacity for desiccation resistance predominates. Only 30 species are present in periphyton in the dry period, and they survive such conditions successfully; by comparison, there are more than 70 species present in the permanent bodies of water, and only some of these are found in the study sites during flooded periods. In the subdeciduous tropical forest and "acahual" (secondary

TABLE 11.2. Compared species richness of algae between permanent water bodies and sites 1 through 4. Species of other environments within El Edén are not included.

	Sites	Ponds	Cenotes	Total species
Cyanoprokaryota				
Chlorophyta				
Heterokontophyta				
Euglenophyta				
Dinophyta				
Glaucophyta				

TABLE .3. Species richness in each group (division) of algae in sites 1 through 4

	Site 1	Site 2	Site 3	Site 4	Total species
Cyanoprokaryota					
Chlorophyta					
Heterokontophyta				4	
Dinophyta					
Euglenophyta	2				

successional forest), the only massive growths of algae found are of *Nostoc* spp., even though these areas are partially flooded once a year.

The types of periphyton are distinguished by their species composition. The main recognized types are as follows:

1. Type *a:* Compact wefts, mainly subaerial
2. Type *b:* Loose epiphytic wefts, mainly aquatic
3. Type *c:* Compact edaphic wefts forming crusts
4. Type *d:* Subaerial flakes, mainly edaphic and covered by type *c* crusts
5. Other forms with limited distribution

The first two types cover the most area in El Edén and dominate the landscape. When wet, these growths can reach a thickness of up to 10 cm.

The periphyton types are quite variable in time and space (Figure 11.2); there are, however, some recurrent species:

1. Type *a:* Compact wefts, mainly subaerial (Figure 11.3). The upper part of the periphyton is formed by at least three species of *Scytonema* and one species of *Camptylonemopsis*. The lower part is formed by a complex weft of Oscillatoriales, composed mainly of several species of *Phormidium*. Colonial species of Cyanoprokaryota such as *Chroococcus, Gloeocapsa, Gloeothece, Aphanothece,* or *Aphanocapsa* are intermingled. The main weft is formed by the former filamentous, heterocytic nitrogen-fixing species. The presence of *Chara,* a chlorophyte, is noteworthy, as it behaves as an annual herb with massive and rapid growth during the flooded period, but whose thalli disintegrate in the dry period. These growths were evident during the flooded period in sites 1 and 2.
2. Type *b:* Loose epiphytic wefts, mainly aquatic (Figure 11.4). These are composed of filamentous species of Cyanoprokaryota and Chlorophyta. The abundance of colonial species is less than in the previous type. Species of *Phormidium, Leptolyngbya, Oedogonium, Bulbochaete,* and *Ulothrix* are the most frequent. The former two genera form the wefts, which are responsible for the majority of the periphyton's structural composition. These wefts were found in sites 1 and 2 during the dry period.
3. Type *c:* Compact edaphic wefts forming crusts (Figure 11.5). Wefts are similar in appearance to type *a* periphyton, but species composition does not include as many colonial species; filaments are found exclusively from species of *Stigonema,* which is another Cyanoprokaryota. Type *c* periphyton were present in all sites during the dry period.

4. Type *d:* Subaerial flakes, mainly edaphic, and covered by type *c* crusts (Figure 11.5). These growths are formed by one or two species only, and are found in zones that remain wet during a prolonged period, but never fully inundated. These flakes reach a thickness of 2 cm between the soil and the compact edaphic wefts. *Gloeocapsa, Gloeothece, Aphanocapsa,* and *Aphanothece* species are present in these flakes, but the main component is a *Cyanokybus* species, which is a monotypic genus known in Cuba and Venezuela from marine environments. These flakes were present in sites 3 and 4 during the end of flooded and dry periods.
5. Other forms with limited distribution (Figure 11.6): Other visible periphyton growths in El Edén are found only sporadically, or in restricted areas. The most conspicuous are growths of *Nostoc* spp., which can sparsely cover several square meters in the more poorly illuminated zones with rich humus soil. Another algal growth consists of loose mats of green filaments (*Mougeotia, Spirogyra,* etc.) with many companion species. None of these growths were present in the study sites, but were found only along the edges of subdeciduous tropical forest and "acahual" communities, or in some places with very open canopies inside these communities.

Periphyton and Phytoplankton Biomass

When evaluated in terms of chlorophyll *a,* periphyton showed a differential growth rate in each period (Figure 11.7); this may be interpreted as a biomass increase from dry to flooded periods.

The four studied periphyton types had similar growth rates. Although in the first two types (subaerial and aquatic wefts in sites 1 and 2), the chlorophyll *a* values showed a trend of being conserved or slightly decreasing

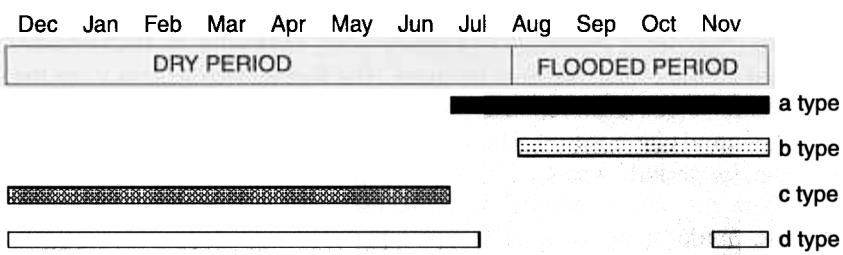

FIGURE .2. Temporal distribution of periphyton types in El Edén Ecological Reserve.

FIGURE 11.3. Compact wefts of periphyton (type *a*) during the flooded period. Note the continuous weft on the substrate.

FIGURE 11.4. Loose epiphytic wefts of periphyton (type *b*), on *Cladium jamaicensis* leaves, during the flooded period.

FIGURE 11.5. Compact edaphic wefts (type *c*) and subaerial flakes (type *d;* see arrow) during the dry period.

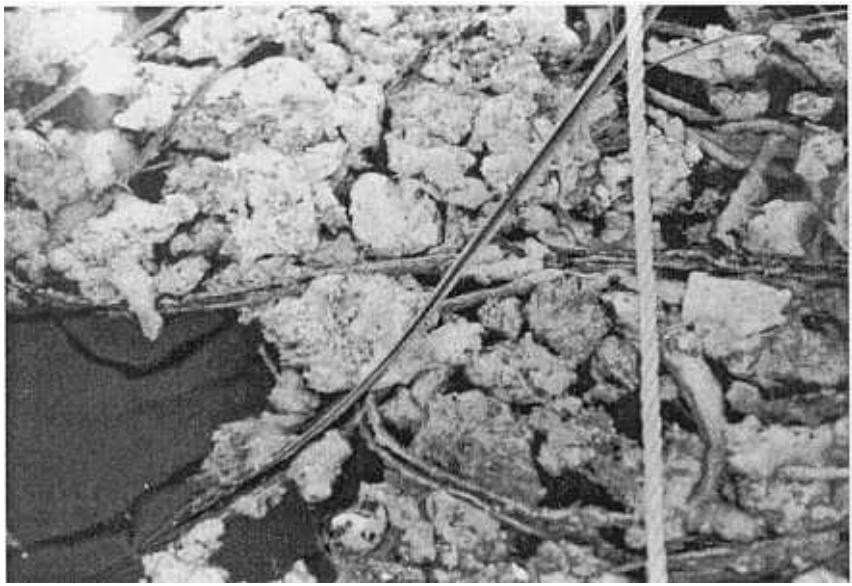

FIGURE 11.6. Loose mats of filamentous algae—floating unattached to any substrate.

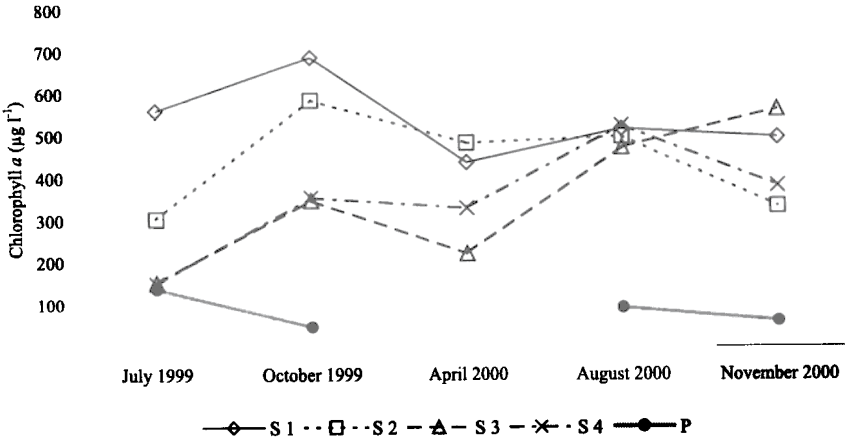

FIGURE 11.7. Periphyton and phytoplankton biomass: S1-S4 = periphyton; P = phytoplankton (average values from sites 1 and 2 when flooded).

through the hydrologic cycle, biomass of the two other types (compact edaphic weft and subaerial flake types in sites 3 and 4) increased in the flooded period and was maintained for a longer time.

The biomass of phytoplankton in water was high in sites 1 and 2 at the beginning of the rainy season (Figure 11.7). By the end of the flooded period, phytoplankton biomass decreased. The average values from sites 1 and 2 in 1999 were 135 at the beginning and 45.5 $\mu g \cdot l^{-1}$ at the end. In 2000, the average values from these sites were 90.5 at the beginning and 57.5 $\mu g \cdot l^{-1}$ at the end. In sites 3 and 4, which were prone to rapid and intermittent flooding, phytoplankton biomass was much lower in the flooded period, but the area did not remain inundated for sufficient time to evaluate fluctuations.

Nutrients in Soil, Water, and Periphyton

In the flooded period, inorganic nitrogen compounds in the soil were higher than in periphyton and water (Table 11.4, Figure 11.8). In sites 1, 2, and 3, for example, nitrate (NO_3^-) was 2 to 17 times higher in the soil than in water, and in site 4 about 40 times higher. Nitrate in soil was 8 to 16 times higher than in periphyton. Nitrate in periphyton was higher than in water in sites 1 and 4 (1.8 to 2.5 times); in sites 2 and 3, nitrate was 2 to 4 times less. Ammonia (NH_3) was always higher in periphyton than in soil or water, except in site 2.

With the exception of site 3, phosphorus (expressed in terms of orthophosphates, PO_4^{3-}) was also higher in the soil than in periphyton. Phospho-

TABLE 11.4. Values obtained for dissolved inorganic nitrogen compounds and phosphorus expressed as orthophosphate for each site in a hydrologic cycle

	Dry Period			Flooded Period		
Sites	NO_3^- ($mg \cdot l^{-1}$)	NH_3 ($mg \cdot l^{-1}$)	PO_4^{3-} ($mg \cdot l^{-1}$)	NO_3^- ($mg \cdot l^{-1}$)	NH_3 ($mg \cdot l^{-1}$)	PO_4^{3-} ($mg \cdot l^{-1}$)
Soil	6.3	6.9	464.0	15.8	3.7	272.0
	3.4	12.9	344.0	3.1	20.8	312.0
	7.8	2.0	64.0	6.3	1.5	8.8
	7.0	2.6	200.0	16.0	3.1	120.0
Water				0.9	0.4	0.3
				1.4	0.4	0.05
				0.9	0.2	0.1
				0.4	0.0	0.02
Periphyton	0.9	0.2	65.2	1.7	4.0	46.3
	3.9	0.5	77.0	0.38	3.5	48.5
	0.26	0.3	78.0	0.38	3.9	45.9
	0.4	0.6	70.8	1.0	4.1	58.0

rus tended to be hundreds of times less concentrated in water than in the soil. Probably more important than concentration values was the fact that the ratio of nitrogen and phosphorus did not follow the optimal 16:1 ratio for algae (Hillebrand and Sommer 1999).

In the dry period, inorganic nitrogen concentration was again higher in the soil than in periphyton (Figure 11.9). Nitrate (NO_3^-) was 7 to 30 times higher in soil than in periphyton in sites 1, 3, and 4; in site 2, however, nitrate concentration remained almost the same. Ammonia (NH_3) was 4 to 34 times higher in soil than in periphyton.

Phosphorus (again expressed in terms of orthophosphates, PO_4^{3-}) was three to seven times higher in soil than in periphyton, except in site 3. Compared to the flooded period, nitrogen concentration decreased in periphyton, with the exception of site 2. Nitrate in soil was reduced by 50 percent in sites 1 and 4, while remaining almost the same in the other sites. Ammonia (NH_3) also was reduced in sites 2 and 4, but increased in sites 1 and 3 (Table 11.4).

Phosphorus concentration in the soil increased twofold in this period in sites 1 and 4, and in site 3 increased almost eightfold. The increase in site 2 was only 10 percent.

Changes in nutrient concentration are reflected by changes in periphyton biomass (Figures 11.10, 11.11). Simultaneous changes in chlorophyll *a* and

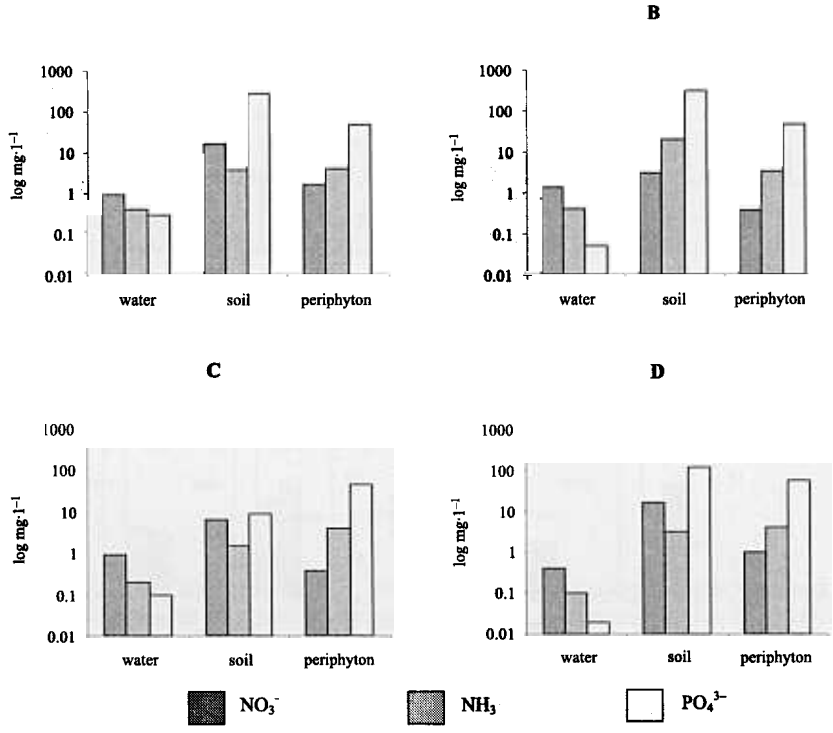

FIGURE 11.8. Flooded period nutrient concentrations in water, soil, and periphyton in sites 1 through 4 during October 1999; A = site 1; B = site 2; C = site 3; D = site 4.

ammonia could be explained by the metabolic utilization of nitrogen-reduced forms, while nitrate could be less important to the metabolic influence of nitrogen on biomass (Figure 11.10). Orthophosphate in periphyton seems to change inversely in relation to biomass, which suggests the direct utilization of the assimilable phosphorus (Figure 11.11). However, the biomass value in site 4 in November suggests that further study is necessary to explain its apparent decrease.

DISCUSSION

Periphyton Composition and Structure

Algal richness in El Edén is considerably high, even when compared to much larger geographical regions such as the Tehuacan–Cuicatlan Valley

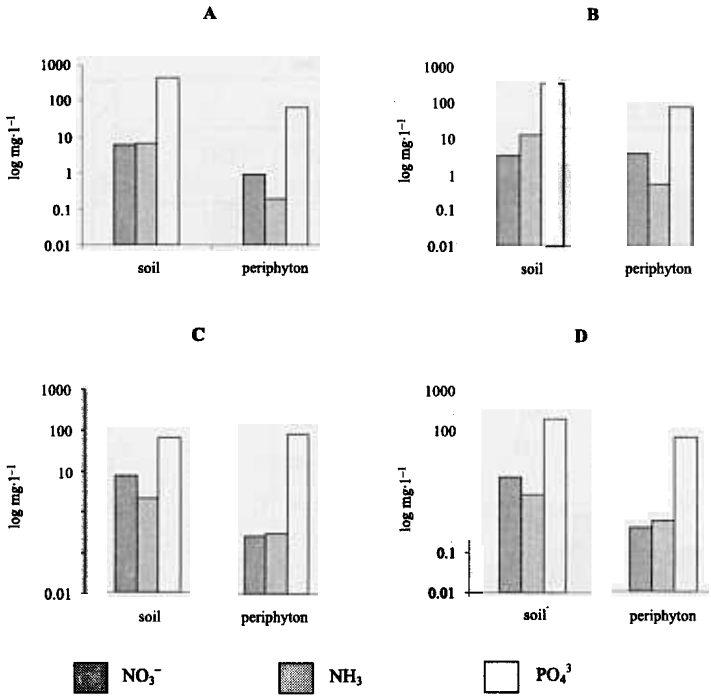

FIGURE 11.9. Dry period nutrient concentrations in water, soil, and periphyton in sites 1 through 4 during April 2000; A = site 1; B = site 2; C = site 3; D = site 4.

(Novelo 1998) or the Huasteca Potosina (Montejano, Carmona-Jiménez, and Cantoral-Uriza 2000). Importance of El Edén's algal flora is based, too, on the predominance of Cyanoprokaryota and the great number of rare or not well-known species. This richness is very important because of the abundance and cover of periphyton in the savanna. Species from other groups are present in the periphyton, but in much less abundance than the cyanophycean algae; still, their presence indicates microconditions whose effects should be evaluated. In the flooded period, water in the savanna is continuous with the ponds and cenotes and could suggest some kind of homogenized flora; the data in Tables 11.2 and 11.3, however, point to a more restricted distribution of species than might be suspected.

Remarkably, nearly 60 percent of the total species that comprise the periphyton belong to Cyanoprokaryota and Chlorophyta. The principal structure of all types of periphyton, however, consists only of filamentous Cyanoprokaryota. The compact subaerial and edaphic wefts are formed by members of the family Scytonemataceae, which are responsible for the con-

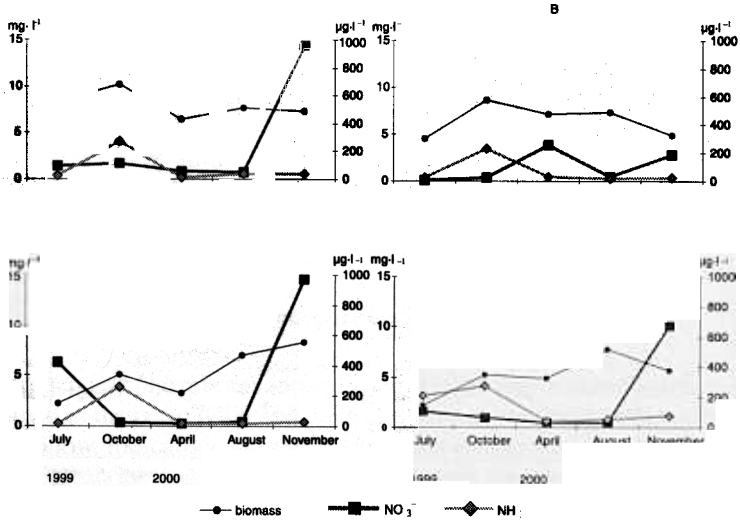

FIGURE 11.10. Changes in NO_3^-, NH_3, and biomass during the study period. Axis Y_1 = inorganic compounds in $mg \cdot l^{-1}$; axis Y_2 = biomass (chlorophyll *a* in $\mu g \cdot l^{-1}$); A = site 1; B = site 2; C = site 3; D = site 4.

sistency and the weave of the mucilaginous sheaths; meanwhile, colonial Chroococcales are intermingled with the filamentous wefts. The organization of species inside the weft is probably linked to a higher production of mucilage by colonial species. Dominance of scytonematalean species at the surface of wefts may be explained by the production of scytonemine pigments that filter the solar radiation (Garcia-Pichel and Castenholz 1991).

Massive periphyton growths are possible in El Edén because of at least two environmental conditions: (1) complete inundation for an extended period of time (three months or more), and (2) a lack of vascular plant canopy. In zones with a thicker canopy, such as median forest or acahual, periphyton is not present at all. Similarly, in areas with dense stands of *Typha* in the savanna, periphyton is not encountered, and even the *Nostoc*-type periphyton grows only along the edges of such stands.

The model proposed by Goldsborough and Robinson (1996) is inadequate to explain the hydrologic cycle at El Edén for two reasons. First, algal crusts are maintained all year long. Second, the periphytic growths block nutrient flux; thus, there is no planktonic community—the lake phase of the model does not exist, and the protected phase is rare. The periphyton structure is built over several years and does not disappear in dry periods. This means that the algal community participates permanently in the ecosystem,

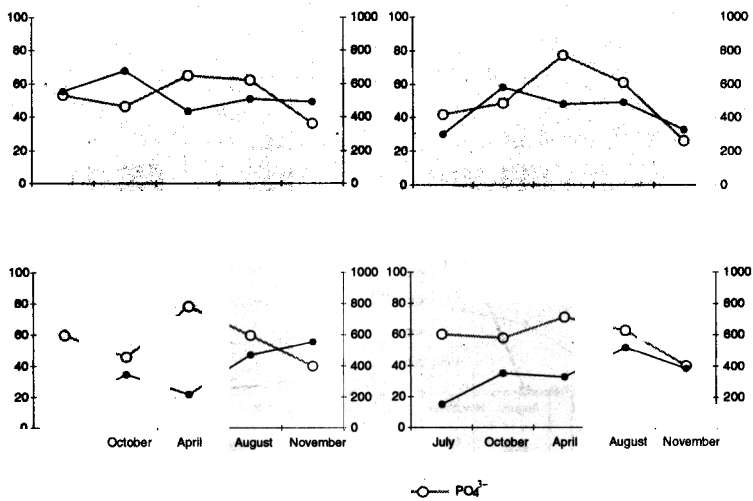

FIGURE 11.11. Changes in PO_4^{3-} and biomass during the study period. Axis Y_1 = orthophosphate in mg·1^{-1}; axis Y_2 = biomass (chlorophyll *a*) in µg·1^{-1}; A = site 1; B = site 2; C = site 3; D = site 4.

and loss of part of this community would require more than a year to recover.

Algal Biomass in the Hydrologic Cycle

Periphyton biomass (chlorophyll *a*) increased through the flooding of the wetland up to a maximum in October, then decreased through desiccation down to a probable minimum (see Figure 11.7). Biomass recovery in the following period of flooding reached more or less the same level as the previous flooded period, which probably means that biomass fluctuation is constant and likely regulated (perhaps even self-regulated) by the mobilization of nutrients in the ecosystem. This has been observed in constructed freshwater wetlands in the Midwestern United States, when periphyton productivity was measured (Cronk and Mitchs 1994), and high-flow wetland periphyton samples had significantly greater average amounts of chlorophyll *a* per unit area than low, flow wetlands.

Phytoplankton biomass decreased through the hydrologic cycle. Initial values of chlorophyll *a* in water (see Figure 11.7) revealed a high biomass that could be interpreted as typical for any eutrophic body of water (Tavera and Castillo 2000). This could be due to the liberation of inorganic dis-

solved nutrients from litter in response to rain and preliminary flooding. These nutrients then cause the phytoplankton communities to flourish. Later, rapid growth of periphyton removes nutrients from the water and forces the consequent decline of the phytoplankton. As observed in Lake Okeechobee in southeastern Florida, periphyton and plankton coexisting in shallow lakes have similar resource requirements with regard to nutrients and light, and periphyton growing on the sediment surface can affect nutrient dynamics in the overlying water column by direct uptake (Hwang, Havens, and Steinman 1998).

Nutrient Flux and Algal Communities in the Wetland

Nitrogen and phosphorus in water were rather low in comparison to those contained in the periphyton and the soil; the nitrogen-phosphorus ratio (N:P) was also low, indicating a possible limitation of nitrogen for phytoplankton. From microscope observations it was clear that the phytoplankton community was indeed very poor in the water column of each studied site when the wetland was flooded. Mesocosm studies (Hwang, Havens, and Steinman 1998) have reported that periphyton rapidly sequester large amounts of phosphorus and reduce soluble phosphorus concentrations, resulting in reduced phytoplankton biomass. Hansson (1990) demonstrated that periphytic algae growing on the sediment reduced total phosphorus concentration by 44 percent in the overlying water, and concluded that periphyton could competitively reduce phytoplankton growth in shallow water. In El Edén, phosphorus in the water column seemed to decrease over the duration of the flooded period—a 2- to 210-fold decrease from August to November, with values of 0.04 to 0.02 and 2.1 to 0.01 mg l^{-1}.

Concentration of phosphorus was generally higher in the soil than in the periphyton. Results indicate that the period of phosphorus increase in the periphyton, between the end of the flooded period and the desiccation of the wetland, could be due to the growth of charophycean species, which reaches its maximum at the same time. Once the water disappears and periphyton and charophytes begin to decline, phosphorus is transferred to the soil, producing the increase registered in the dry period. During April in sites 1 and 2, large quantities of white (calcified) fragments of charophytes were observed lying over the soil. It is thought that these thalli are an important source of phosphorus—one not observed in the other two study sites. This could well explain the higher levels of soil phosphorus in sites 1 and 2.

The low levels of phosphorus observed in the water is surprising. With a soil so rich in phosphorus in the dry period, this nutrient would be expected to enrich the water column through simple dissolution following every flooding of the wetland. Such was not the case in El Edén, and it is suspected that the periphyton, which completely covers the soil, prevent mobi-

lization of oxygen in the water-sediment interface by producing a thin oxidized layer at the soil surface. This has been demonstrated in Lake Windermere, located in Cumbria, United Kingdom (Carlton and Wetzel 1988). According to investigations there, this oxidized layer need only be between 3 to 5 mm thick to prevent the liberation of phosphorus. Another possible important factor in the binding of phosphorus to the soil may be the presence of carbonates, common in the limestone substrate of the Yucatán Peninsula.

Thus, trapped phosphorus in the soil is inaccessible even to algae until sporadic episodes of periphyton removal allow the sediments access to oxygen. Once the released phosphorus is transformed into reactive phosphorus, it could be utilized by mycorrhizae, algae, and other soil organisms. It may be assumed that the ecological role of periphyton in El Edén is the enrichment of phosphorus in the soils through the processes of the hydrologic cycle.

Experimental studies in periphyton mats have shown that periphyton can sequester large amounts of nitrogen (not only phosphorus) from the water column (Havens et al. 1999). Concentrations of ammonia in the soil were almost the same throughout the flooded period. This form of nitrogen increased in sites 1, 3, and 4 while nitrate diminished; the converse occurred in site 2 for unknown reasons. When the wetland is dry, loss of nitrogen is evident, with ammonia decreasing to a greater extent than nitrate. This difference may be due to the microbial and algal preference for reduced nitrogen compounds instead of nitrate (Norton 1981; Vymazal 1995).

Periphyton nitrate levels were maintained throughout the flooded period in site 2. In sites 1, 3, and 4, nitrate showed a 10- to 15-fold increase. As the dry period proceeded, nitrogen levels in the periphyton diminished, most notably due to a decrease in ammonia (four- to sixfold decrease). Nitrate decreased 30 to 50 percent in sites 1, 3, and 4; in site 2, however, nitrate levels showed a tenfold increase.

Other unpublished experimental data (not discussed in this chapter) have demonstrated the decrease in nitrogen fixation throughout the flooded period, which reaches its lowest values during the dry period. This may be consistent with the previous results on levels of nitrogen and ammonia.

CONCLUSION

Periphyton in El Edén are a rich and complex community, indispensable in the preservation of the wetland as a differentiated ecosystem. In these algal growths, wefts remain throughout the year to provide support and rapid hydration for the new growths when the rainy season begins. They contribute to the maintenance of humidity for the lower strata, and serve to protect these strata from heat and desiccation in the dry period by capturing water

during the night. In addition to this function, the accumulated wefts protect vegetative and resistant cells that will serve as propagules in the next phase of vegetative growth. This is important for organisms such as *Chara* and *Nitella,* whose thalli disaggregate during drought, but do form resistant oospores at the end of the rainy season.

In general, when periphyton dehydrate, they lose nitrogen—mainly as NH_3—and the phosphorus concentration is remarkably increased in the soil, probably because some algal material (mainly charophytes) is directly incorporated into the soil through desiccation and pulverization. This process is quite evident in sites 1 and 2. The phosphorus in periphyton decreases at the end of the flooded period; but, given the higher levels of phosphorus during the dry period, it is possible that loss and recovery take place in each hydrologic cycle. Indeed, chlorophyll *a* values seem to point to a rapid metabolic uptake of phosphorus. The lower quantities of reduced forms of nitrogen found in the periphyton at the end of the flooded period can be attributed to the lower rates of nitrogen fixation as the wetland dries out.

Periphyton biomass was constant, although deviations were noted in all four study sites during the study period. Chlorophyll *a* quantities in the dry period were sufficiently high to account for the persistence of vegetative structures inside the dry periphyton crust. On the other hand, growths in the flooded period did not multiply as they did in other environments. In this case, the sequence of sustained exponential growth followed by a stationary phase is not clear. Modifications in species composition surely play an important role in this conservative tendency. However, it could possibly be due to the regulation of nutrient flux by algal growths.

Such structured behavior within the ecosystem obliges a reanalysis of the use of periphyton as an exploitable resource. Crusts sampled from the study sites did not fully recover over the course of the study period. Although the recovery process was not followed systematically, the absence of periphyton in previously collected zones, microscopic observations of mucilaginous wefts of several ages throughout the hydrologic cycle, the conservative trend of biomass, the nitrogen flux from periphyton to soil, and the phosphorus flux from soil to periphyton all serve as evidence that recovery is distinctly retarded. Systematic removal of periphyton could possibly break the nutrient cycles completely, thereby impoverishing the soil and having drastic consequences for the rest of the ecosystem.

If periphyton are to be used as a biofertilizer for agricultural soils because of their high nutrient content, the effects of such extraction upon the ecosystem, as well as the slow recovery of the periphyton, must be taken into account. As is true of any other component of a complex, diverse ecosystem, periphyton cannot be indiscriminately exploited without a better knowledge of their role and importance in the ecosystem.

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