12 The Role of Algal Mats on Community Succession in Dunes and Dune Slacks

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12.1 Introduction

Different kinds of algal communities can live in dune slacks that may become temporarily flooded or remain moist throughout the year due to fluctuations in the proximity of the water table (Brown and McLachlan 1990). This chapter focuses on changes in the composition of algal communities during periods of flooding and drought, with special emphasis on the hydrological characteristics of slacks as well as on morphological and physiological factors that allow algae to survive in these stressful environments. Also discussed is the role of algae in the first stages of dune succession, when they form part of a soil community of so-called microbial mats (Belnap and Gillete 1998) as well as part of the aquatic community. In both circumstances, algae participate actively in sand stabilization and facilitate the development of several pioneer plants. Finally, changes in algal community composition are reported for the case where slacks became flooded in a tropical mobile dune system.

12.2 Hydrological Dynamics in Slacks Within Coastal Dune Systems

Dune slacks were defined by Tansley (1949, in Boorman et al.1997) as wet hollows left between dune ridges where groundwater reaches or approaches the surface of the sand. These systems are formed in different ways: (1) on coasts where the shoreline is advancing seawards, a new line of dunes can enclose an area of beach plain that, after desalinization, can become a dune slack or dune lake (Boorman et al. 1997), and (2) the action of the wind can form deep blowouts in already existing dune areas.

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Hydrologically, the height of the water table is decisive in whether a dune slack is dry, moist, wet, or permanently inundated. Although slacks appear to be simple in shape, their hydrology is not, being determined by dune geomorphology and local conditions of climate and topography. For instance, in temperate zones such as the Wadden Islands and the Frisian Island of Texel in The Netherlands, it has been noted that some slacks become flow-through lakes during the wet season, in which groundwater discharges into one part of the slack and surface water infiltrates on another side (Grootjans et al. 1998; Adema et al. 2002). This process occurs mainly during the rainy season, when the water table is so high that the slack is inundated. A similar hydrological mechanism was observed in the dune systems of Mont Saint Frieux in France, an area characterized by parabolic dunes with wet valleys and several dune streams. There, slacks are fed by subsurface flow from infiltration areas, infiltration of surface water from dune streams, and direct infiltration by rainfall (Bakker and Nienhuis 1990).

Similar to the effect of local weather, geographical position and local topographical conditions influence seasonal changes in the water table. In temperate zones, slacks can become flooded during winter and early spring and dry out in summer (Grootjans et al. 1997). In tropical zones, in contrast, the rainy season – with the resulting increase in the water table – occurs in the summer, while the dry season occurs during the winter (Moreno-Casasola and Vázquez 1999). Long-term research of a tropical dune system in La Mancha, Veracruz, Mexico (Moreno-Casasola and Vázquez 1999) showed that in the early rainy season (June), the water table started to rise and flooding depended on the amount of surplus rain that fell in June and July (Fig. 12.1). The study by Moreno-Casasola and Vázquez (1999) showed that the amount of precipitation necessary for flooding to occur in La Mancha slacks was 500 mm, thus, in very rainy years, the probability of flooding therefore increases. During autumn and early winter (October-December), the water level started to decrease and the water table remained below ground level until the following rainy season.

12.3 Algal Communities in Slacks and Other Coastal Zones

The hydrological characteristics of slacks, blowouts, and other coastal zones - such as coastal tidal sand flats and sand dunes- determine the composition and abundance of the algal communities found in these systems (Pluis and De Winder 1990; Stal 2000). In dry conditions, algae are sometimes found in macroscopic structures similar to microbial mats that are made up of cyanobacteria, diatoms, green algae, and eubacteria (Simons 1987; Lange et al. 1992; Norris et al. 1993; Grootjans et al. 1998; Vázquez et al. 1998; Stal 2000). Species such as *Crinalium epipsammum* (Pluis and De Winder 1990), which

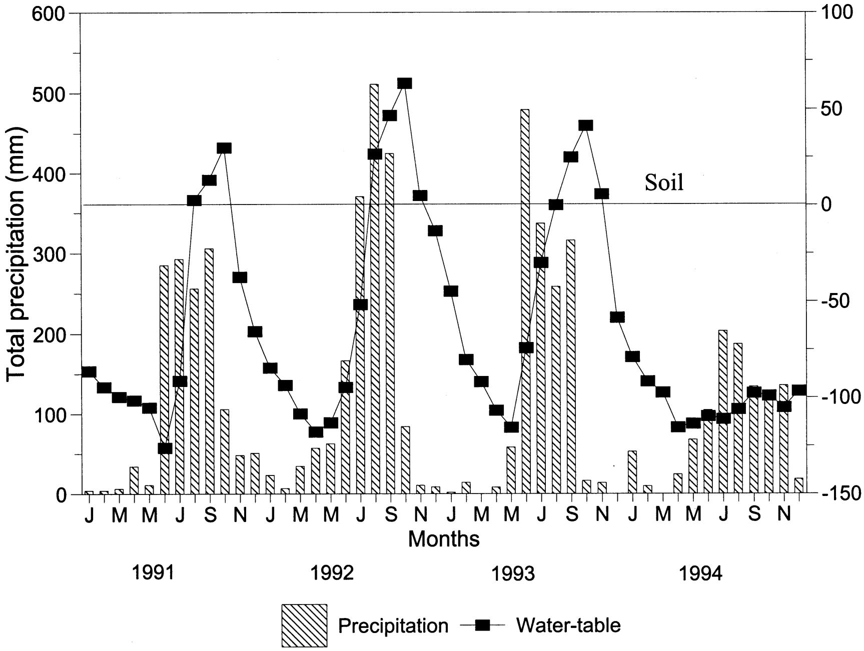

Fig. 12.1. Total monthly precipitation and fluctuation of water table from 1991 to 1994 in slacks from La Mancha, Ver. Depth of water table is established in relation to soil surface. Negative values denote depth beneath the sand surface

are unique band-shaped filamentous cyanobacteria, can also be found (Stal 2000). Another noteworthy species is the filamentous non-heterocystous *Microcoleus chthonoplastes,* which is observed in some desert crusts and intertidal marine zones (Brock 1975, Stal 2000). *Cylindrospermum, Oscillatoria, Lyngbya, Spirulina, Anabaena, Scytonema,* and *Nostoc,* along with unicellular species such as *Chroococcus, Chroococcidiopsis, Merismopedia,* and *Synechococcus,* also form mucilaginous colonies.

Microbial mats possess several characteristics that enable them to be successful in coastal environments. For instance, cyanobacteria form an extracellular polysaccharide sheath (EPS) that protects them against desiccation and grazing (Brock 1975 in Stal 2000). The EPS may retain large amounts of water, and organisms that produce it may thus tolerate long periods of drought. Due to this mechanism, in fact, they have been shown to be more successful than green algae (Stal 2000). When the moisture level increases, the sheath absorbs water and the organism resumes activity immediately, then particles of sand are trapped, thus stabilizing the soil. Although the mats are no more than a few millimeters thick, they play a decisive role in dune mechanics, as they influence rain interception as well as water infiltration into the soil, evaporation, soil stabilization, and moisture maintenance.

They also play a role in nutrient recycling, especially N, and carbon capture (Lange et al. 1992).

Cyanobacteria are the main primary producers in most microbial mats. They can photosynthesize with little oxygen availability and low light intensity, permitting them to make efficient use of light as an energy source, water as an electron donor, and CO_2 as a carbon source. This is very important because light is strongly attenuated in microbial mats, due both to sediment and absorption by the dense phototrophic community (Stal 2000). The dense biomass of cyanobacteria in the upper photic zones of microbial mats produces high rates of photosynthesis comparable to the productivity of rain forests, which are usually considered the most productive ecosystems on Earth (Guerrero and Mass 1989 in Stal 2000). Although their nutrient requirements are low, cyanobacteria can use dinitrogen as a nitrogen source, making it possible for them to grow regardless of whether or not there is nitrogen in the environment.

During the rainy season, slacks become small seasonal freshwater systems that are poor in nutrients and characterized by large fluctuations in volume due to the high evaporation rate. For this reason, the algal community changes dramatically. In dune pools and slacks from temperate zones such as The Netherlands (Simons 1987; 1994) and in tropical zones such as those discussed here, a diverse algal community can be found: filamentous green algae such as Zygnematales (*Spirogyra, Mougeotia, Zygnema, Zygogonium*), Oedogoniales (*Oedogonium*), and Klebsormidiales (*Klebsormidium*) as well as Desmidiales (*Cosmarium, Closterium, Staurastrum, Euastrum*) (Bowling et al. 1993), Charales (*Chara, Nitella*) (Simons 1987; Simons and Nat 1996), and diatoms (*Navicula, Cocconeis, Pinnularia, Melosira*) (Kling 1986).

Most of the dominant species are filamentous and macroscopic green algae in flooding conditions and can form large macroscopic clouds or are, like the filamentous periphyton, found on and around larger aquatic plants. When the slack border dries, these filamentous matrices stay on the border and maintain a relatively high humidity in the substrate, favoring germination of phanerogam species (Vázquez et al. 1998).

Some of the species found in such unstable environments have characteristics that allow them to survive drought conditions when the water table decreases and the slack dries out. For example, the thick walls of *Spirogyra* and *Oedogonium* zygospores contain sporopollenin, an inert material that protects the cell from drought (Simons 1987; Van den Hoeck et al. 1998). Thus, cells adopt a latent state that permits survival until the following rainy season (Simons 1987). Another adaptation to stressful environments is zygote dormancy and survival. Van den Hoeck et al. (1998) have shown that the length of the dormant period depends on temperature. At 4 °C, *Spirogyra maxima* zygotes remain dormant for 14 months, while at 18–20 °C they are dormant for only 3.5 months.

Also common in slacks during the rainy period are desmids such as *Cosmarium, Staurastrum*, and *Closterium*. Diverse desmid floras are characteristic of freshwater systems that are shallow, transparent, and stagnant, with low conductivity and little nutrients, as is the case in ponds lying in leached dunes. They also flourish in high sodium:potassium and calcium:magnesium ratios of less than 2. In this type of environment, they may live as phytoplankton, on the bottom as benthic dwellers, or on the submerged parts of plants. Coesel (1981, in Van den Hoek et al. 1998) found that a diverse desmid flora is favored by small-scale patchiness in nutrient concentration within natural habitats such as small ponds where mixing between ground water and rain water occurs. In desmids, sexual reproduction has been observed only sporadically in nature. Most desmids survive adverse conditions such as low temperature, low light intensities, or partial desiccation as vegetative cells rather than hypnozygotes.

12.4 The Role of Algae During Primary Succession in Coastal Dunes

Primary succession in dune slacks is considered to occur during four phases (Grootjans et al. 1997), and algae play a fundamental role during the first two. Algal and microbial mats are predominant during the first phase, when there is little organic matter in the soil. During the second, algae facilitate the colonization of phanerogams that can tolerate limited nutrient availability. Later, in the third phase, a layer of mosses and bryophytes develops and tall grasses and shrubs establish, increasing vegetation structure and composition. Finally, once there is more organic material, species replacement occurs, allowing trees to establish (Pluis and De Winder 1990; Grootjans et al. 1998; Vázquez et al. 1998).

One of the mechanisms for dune slack stabilization is the fixation of sand by algal crusts or mats. This diminishes the wind's impact by increasing the resistance surface: mucilage produced by algae remains adhered to grains of sand and acts as a fixing agent (Pluis 1994). In sandy soil, colonization starts just under the surface with the arrival of cyanobacteria such as *Microcoleus, Oscillatoria*, and *Tychonema*, which are considered primary colonizers and are sometimes followed by the green algae *Klebsormidium flaccidum*. It has been observed that cyanobacteria adapt rapidly to variations in water availability, while *K. flaccidum* appears to be associated with conditions of water retention caused previously by cyanobacteria. If unremoved by subsequent storms, algae can be followed by annual phanerogam communities. Slack size influences stabilization efficiency, as very large areas of small slacks are covered with algal crusts and these contribute to the establishment of colonizing species, especially in the rainy season, when moisture conditions favor both (Pluis and De Winder 1990).

During flooding, algal mats may also participate in succession by facilitating the germination of phanerogams. Water volume in slacks fluctuates considerably, decreasing due to high temperatures and evaporation and increasing after precipitation. When slack borders dry somewhat but remain moist, algal mats may stay on the soil, forming a crust that maintains moisture and thus facilitates the germination of the seeds found there. The mechanism that has been suggested under these conditions is that algae maintain the moisture necessary for germination even in dry conditions. This was demonstrated experimentally on three substrates (sand, algae, and cotton) with two irrigation treatments: the first one consisted of continuous watering to keep sand permanently moist (wet treatment) and the second involved watering once a week (dry treatment). Vázquez et al. (1998) found that tropical Cyperaceae (*Fuirena simplex, Fimbristilys cymosa*, and *Rhyncosphora colorata*) germinated successfully (>50 %) on moist algal mats of *Spirogyra, Mougeotia, Oedogonium*, and *Microspora*, which form dense clouds that can act as seed traps. In the wet treatment, the highest final humidity was maintained in the algal and cotton substrate, while in the dry treatment the algal substrate maintained more humidity than the sand and cotton substrate. *Cyperus articulatus* responded differently, as it showed a high germination percentage in every type of experimental substrate (algae, sand, and cotton), suggesting that humidity was not a determinant factor for the germinability of this species. The first three species are found principally on slack borders, so that algae appears to play a very important role in maintaining the moisture necessary for germination. *C. articulatus*, in contrast, can be found both in dry and wet parts of tropical dunes, indicating humidity requirements that are probably broader than those of the other three species (Fig. 12.2).

In a preliminary experimental study designed to determine the importance of algae for the growth of several Cyperaceae, Vázquez, Moreno-Casasola and Barrera (unpublished data) compared the growth of seedlings of *Fimbristylis cymosa* and *Cyperus articulatus* under different nutrient treatments: (1) wet sand with nutrients provided by filamentous algae decomposition lasting 3 months, (2) sand to which a diluted solution was added (1:10) that consisted of fertilizer with N-P-K (low nutrient values), (3) sand to which a concentrated fertilizer with N-P-K high-nutrient solution was added (1:1), and (4) sand with no nutrients added (control). The dry biomass that accumulated was measured every 5 to 6 weeks for each treatment. *Fimbristylis cymosa* showed the greatest biomass increment in both the algal and high-nutrient concentration treatments (Fig. 12.3a). Growth in sand and with low nutrient concentrations was, in contrast, significantly lower. *Cyperus articulatus* only underwent a significant biomass increment in the high nutrient concentration treatment, but no difference was noted between sand, algae, and low nutrient concentrations (Fig. 12.3b). These results suggest that algae maintain favorable growing conditions for *F. cymosa* seedlings, possibly supplying necessary nutrients, while the growth of *C. articulatus* does not seem to be affected by the presence of algae. This corroborates previous findings regard-

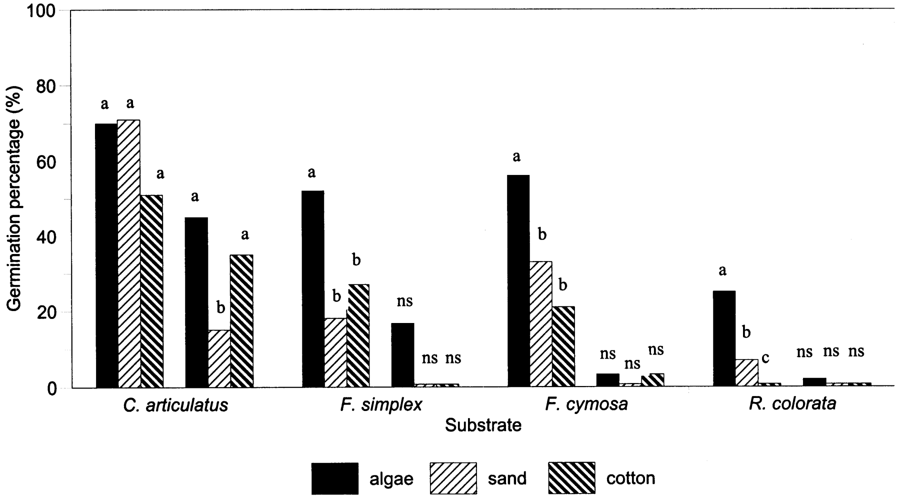

Fig. 12.2. Mean final germination percentages (%) of Cyperaceae species on different substrates in the wet and dry treatment for each species. Different letters indicate significant differences between treatments for each species. *ns* Non-significant differences between treatments

ing germination for the same species (Vázquez et al. 1998). Thus, algae facilitate the germination and growth of *F. cymosa*.

In temperate calcareous slacks in The Netherlands, Adema et al. (2002) found evidence of alternative stable states in the pattern of pioneer vegetation and in later successional stages, suggesting that positive-feedback mechanisms are responsible of these states, one of which relates to microbial mats. The combined metabolic activities of microbial mats (with cyanobacteria, colorless sulfur bacteria, purple sulfur bacteria, and sulfate-reducing bacteria) result in microgradients of oxygen and sulfide which are toxic for most higher plants as their growth is stunted. However, dune slack pioneer species can protect themselves against the toxic sulfide, as they release oxygen from their root system and favor colorless sulfur bacteria that detoxify free sulfide. This results in stable, open pioneer vegetation with a microbial mat that cannot be invaded by later species that have not adapted to anoxic soils containing free sulfide. Grootjans et al. (1997) also found that microbial mats prolonged the life of pioneer stage species such as *Samolus valerandi*, and inhibited the growth of later successional stage species (*Calamagrostis epigejos* and *Juncus alpinoarticulatus*). This is apparently due to the fact that the roots of the latter species cannot penetrate microbial mats and also to the limited accumulation of organic matter, a condition that favors pioneer species.

Another mechanism by which microbial mats may favor the growth of pioneer species is through precipitation of calcium carbonate, which prevents the

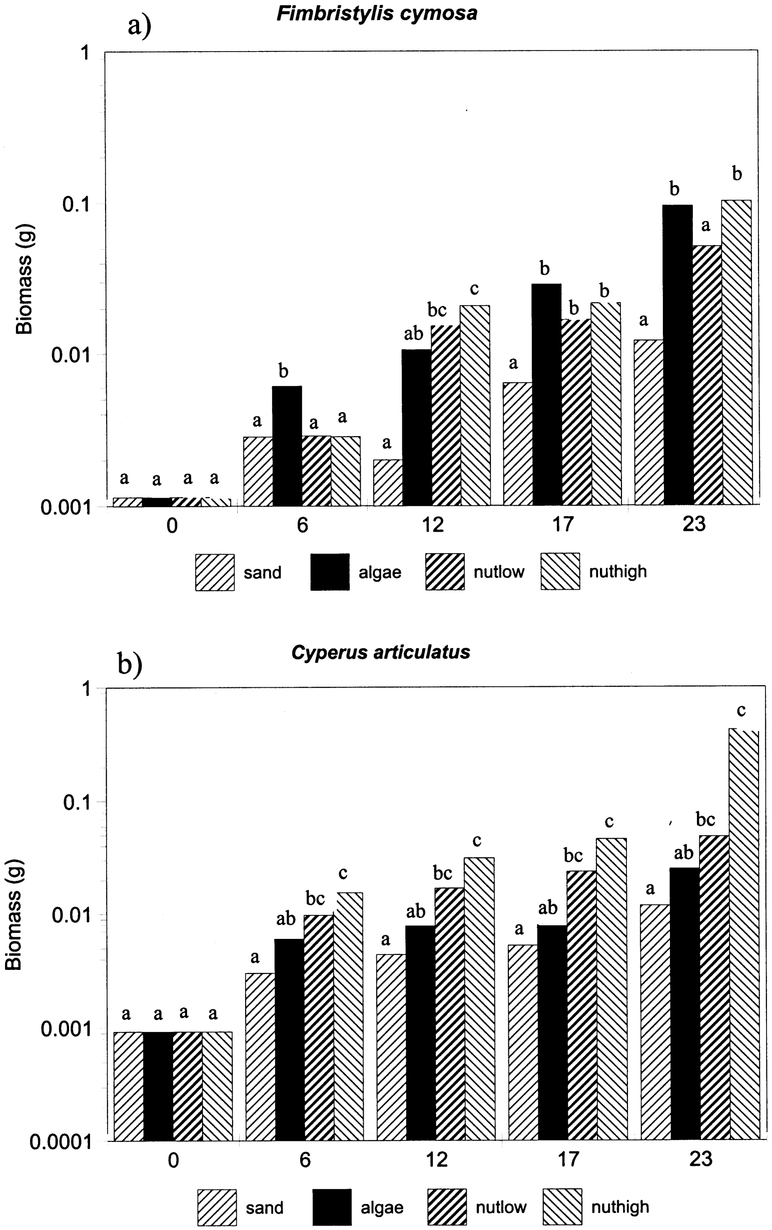

Fig. 12.3. Mean final biomass (g) of *Fimbristylis cymosa* (**a**) and *Cyperus articulatus* (**b**) over 23 weeks for different treatments with nutrient concentrations. Biomass was measured each 5 to 6 weeks. *Different letters* indicate significant differences between nutrient treatments

soil from acidifying rapidly. This generally occurs in infiltration areas characterized by surplus precipitation (Grootjans et al. 1996, 1997).

12.5 A Case Study on the Gulf of Mexico

Various systems of tropical dunes, both stabilized and mobile, exist along the Gulf of Mexico coast. In mobile systems, there are numerous slacks that follow the hydrological behavior described herein: in summer they flood for 2 or 3 months and then dry out in winter. Thus, during rainy years as well as rainy periods, very shallow aquatic systems form; they are nutrient-poor and facilitate the development of algae; both macro -and microscopic, they are of little-known taxonomic composition and undetermined variation over time. Considering the importance of these communities as primary producers, and particularly due to their participation in dune succession, research was conducted over a 2-year period (1990–1991) during the flooding months. The objective was to identify community structure, taxonomic composition, and variation over time, in the dune slacks of Doña Juana, located in the state of Veracruz, Mexico (96°20′W, 19°28′N). Dunes in this system are parabolic and reach up to 20–30 m in height; each has a slack at its lowest point. The climate in the region is warm and sub-humid. The rainy season normally runs from June to September, when approximately 81 % of total precipitation (1230 mm) is registered. Mean annual temperature is 25 °C. During the short flooding period (3 or 4 months), algae samples were obtained from the slacks every 15–20 days. Sample analysis was qualitative, and quantification was performed using an arbitrary scale: 1- scarce, 2- abundant, and 3- very abundant.

Results showed that the macroscopic and microscopic algal community at Doña Juana is composed principally by cyanobacteria (Chroococcales, Oscillatoriales and Nostocales), diatoms (Pennales), and green algae (Chlorococcales, Desmidiales, and Zygnematales) (Table 12.1). For the most part, macroscopic algae were represented by *Mougeotia, Oedogonium, Spirogyra*, and *Zygnema* (Zygnematales), with *Spirogyra* and *Oedogonium* (also reported in temperate zones) as the most important components of dune pools. Other microscopic algal groups were found immersed in the filamentous masses. Among them, the most important were desmids such as *Cosmarium, Euastrum,* and *Staurastrum*, followed by the green algae Chlorococcales (*Oocystis, Sphaerocystis, Tetraedron*), cyanobacteria (*Anabaena, Chroococcus, Oscillatoria)* and diatoms (*Amphora, Cocconeis placentula, Rhopalodia, Mastogloia smithii*). The desmids *Cosmarium* and *Staurastrum* were observed in asexual reproduction.

The two sampling years were different in terms of the proportions of each group (Fig. 12.4). The dominant groups forming the floating masses were the

Zygnematales, Desmidiales and Chlorococcales. In 1990, the dominant species during the initial flooding were filamentous green algae (*Spirogyra*) and desmids (*Cosmarium* and *Staurastrum*), diatoms (*Rhopalodia* sp., *Mastogloia smithii, Nitzschia* sp. and *Cocconeis placentula*), and cyanobacteria (*Oscillatoria limosa*). In late August (1990), when filamentous green algae and desmids were dominant, unicellular green algae (Chlorococcales) and cyanobacteria disappeared. The diminution of algal mats and microscopic species in late autumn (26 November 1990) may be related to lower temperatures and the end of the rainy period. In 1991, during initial flooding (September), Chlorococcales (*Oocystis lacustris, Tetraedron minimum*), and desmids (*Cosmarium* sp. and *Staurastrum gracile*) were noted again; later, in October, a larger number of cyanobacteria such as *Chroococcus minor, Gloeotrichia, Merismopedia*, and *Anabaena* appeared.

Table 12.1. List of algal species found in dune slacks of the Doña Juana dune system in the state of Veracruz, Mexico. The classification system was proposed by Van Den Hoek et al. (1998)

CLASS CYANOPHYCEAE (cyanobacteria)
Order Chroococcales
Chroococcus limneticus Lemmermann
Chroococcus minor (Kützing) Nageli
Merismopedia sp.
Order Oscillatoriales
Lyngbya sp.
Oscillatoria limosa (Dillwyn) C. Agardh
Order Nostocales
Anabaena sp.
Gloeotrichia sp.

CLASS BACILLARIOPHYCEAE (diatoms)
Order Pennales
Amphora coffeaeformis Agardh
Amphora sp.
Cocconeis placentula Ehrenberg
Mastogloia smithii Thwaites
Navicula sp.
Nitzschia sp.
Pinnularia viridis (Nitzsch) Her.
Rhopalodia sp.

CLASS CHLOROPHYCEAE (green algae)
Order Chlorococcales
Gloeocystis ampla (Kützing) Rabenhorst
Oocystis lacustris Chodat
Oocystis solitaria Wittrock
Sphaerocystis schroeteri Chodat
Tetraedron minimum (A. Braun) Hangs
Order Oedogoniales
Oedogonium sp.

CLASS ZYGNEMATOPHYCEAE (green algae)
Order Zygnematales
Mougeotia sp.
Spirogyra sp.
Zygnema sp.
Order Desmidiales
Cosmarium botrytis Meneghini
Cosmarium sp. 1
Cosmarium sp. 2
Cosmarium sp. 3
Cosmarium sp. 4
Cosmarium sp. 5
Cosmarium sp. 6
Euastrum sp. 1
Euastrum sp. 2
Staurastrum gracile Ralfs
Staurastrum sp.

Mat composition appeared to vary considerably during the two flooding periods (Fig. 12.5). In July and early August of 1990, *Spirogyra* dominated, although *Oedogonium*, *Zygnema*, and *Mougeotia* were also present in smaller quantities. In late August and October, the situation was reversed: *Oedogonium* and *Zygnema* increased considerably and the other species diminished, although they did not disappear. When slacks flooded the following year, in September of 1991, *Zygnema* dominated throughout and was always observed to be in a reproductive state. Large quantities of *Mougeotia* appeared only in mid-October, but without a decrease in the occurrence of *Zygnema*. *Spirogyra* and *Oedogonium* maintained a limited presence during this second cycle. During the study period, *Spirogyra, Oedogonium*, and *Zygnema*, had a high rate of sexual reproduction. *Spirogyra* is an especially common genus, with up to 70 species reported in The Netherlands (Simons 1987). Other studies have shown zygospores of *Spirogyra* and *Oedogonium* as decay-resistant resting spores, which are considered part of a life strategy that facilitates the tolerance of stressful conditions in ephemeral bodies of water (Simons 1987). As previously mentioned, these results are interpretable as a way that algae adapt to highly stressful slack conditions.

Although the two cycles studied represent a short period of time, the results indicate that important changes occur in the community from one

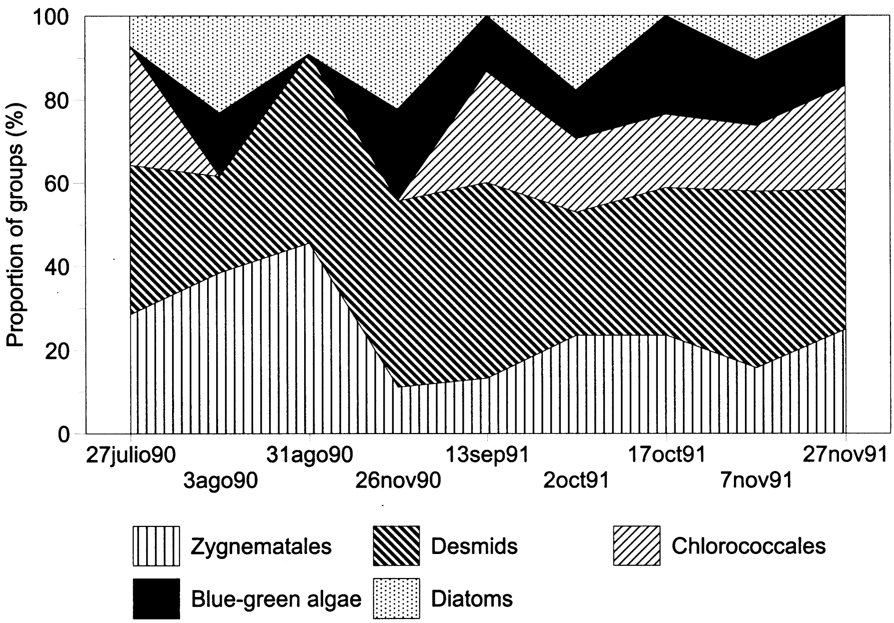

Fig. 12.4. Temporal variation in the number of species from the most important taxonomical groups of algae in slacks from a mobile dune system in Doña Juana, Ver.

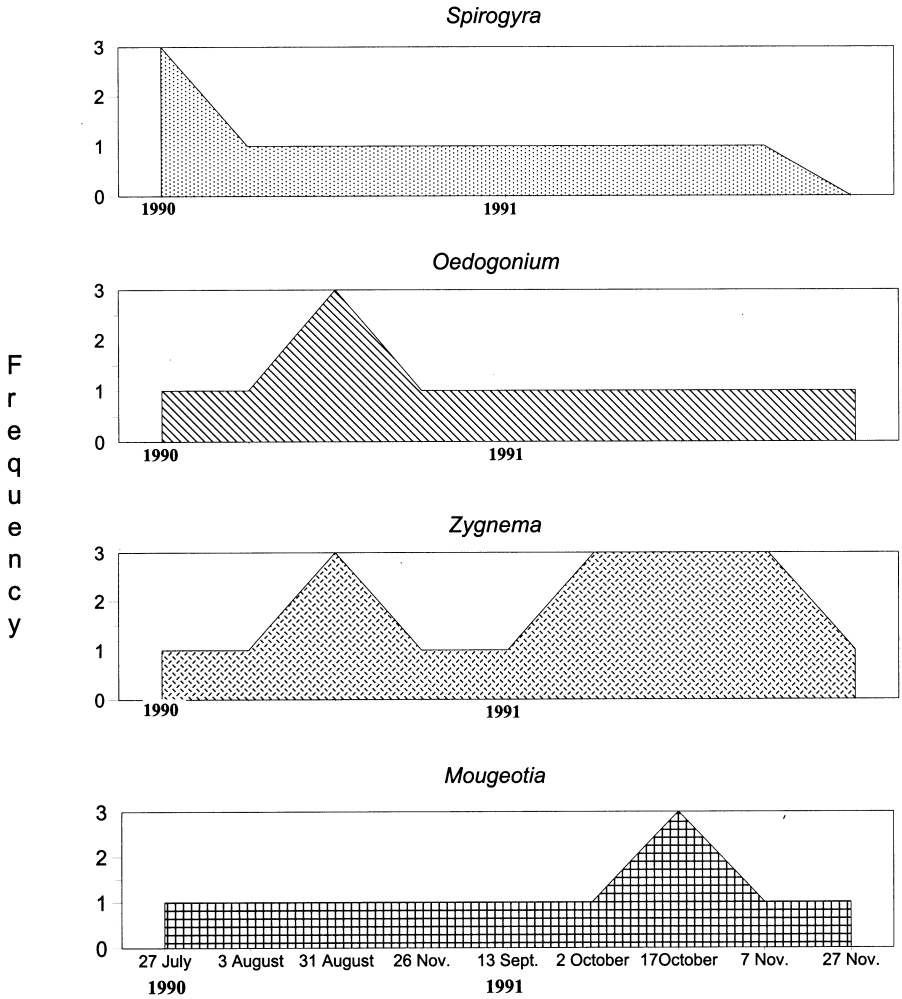

Fig. 12.5. Temporal variation in the abundance of the most important macroscopic green algae in a mobile dune system in Doña Juana, Ver.

year to the next. This can be considered a common phenomenon in tropical slacks due to the drastic environmental fluctuations that characterize them.

12.6 Importance of Algae for Slack Conservation

Dune slacks, which represent pioneer successional stages on mobile dunes, have great ecological importance due to their diversity in plants and animals (rare, endemic, and protected), which is the result of environmental conditions that are unique to slacks (Grootjans et al. 1998). Interannual variation of the water table and sand movement favor an internal cyclical succession in which algal mats plays different roles. As analyzed in this chapter, these roles in both temperate and tropical zones have been studied by different authors (Van den Ancker et al. 1985; Pluis and De Winder 1990; Grootjans et al. 1997; Vázquez et al. 1998; Adema et al. 2002) who have proved experimentally the existence of different stabilization mechanisms within the slacks studied: sand stabilization, the establishment of phanerogams through facilitation mechanisms, and in particular, the inhibition of late-successional stage species so that the presence of pioneer stage species is favored. Thus, some of these systems' conservation measures have led to the use of algae to maintain pioneer-stage succession in dunes. This prevents the loss of diversity within these systems that would occur if succession occurred in only one direction, so that pioneer-stage species would be replaced by shrubs and trees, eventually becoming a forest.

12.7 Conclusions

Algal communities play a very important role in dune slack dynamics and other systems such as blowouts. The importance of algae lies in their participation on ecological processes that occur in highly stressful systems. Algae favor the establishment and colonization of sand during early succession; they facilitate or detain the germination and establishment of different phanerogam species during various successional stages. As primary producers, their taxonomic composition and abundance influence nutrient availability in an aquatic system.

The taxonomic composition of these communities depends on the hydrological characteristics of the system in which they are found. Due to morphological and physiological characteristics, cyanobacteria (Cyanophyceae) can survive despite the highly stressful condition of limited water present in soil during periods of drought. During flooding, moreover, succession occurs and filamentous species such as *Spirogyra, Zygnema, Oedogonium,* and *Microspora* (green algae) become quite common.

During this study it became clear that while vast information exists on algae, most of it is limited to a soil setting; little research has addressed the composition and function of algal communities in dune systems. Further long-term studies are needed in order to better understand algal dynamics in slacks and the role that they play during dune succession.

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