J. Phycol. **35,** 1100–1105 (1999)

藻類要聞 ✻ 繁楷體 – **Algues** ✻ **Avancées récentes**
– *Algas* ✻ *Alto interés* – Algae ✻ Highlights –
ВОДОРОСЛИ ✻ ВАЖНЕЙШИЕ МОМЕНТЫ – أخبار ✻ الطحالب

FIELD TESTING OF SEAWEED-POM RELATIONS: ALGAE GET A DUSTING

Improvements of sampling methods and microanalysis techniques over the last 20 years are allowing new insights on the various roles that particulate organic matter (POM) plays in marine systems. Previous models have consistently overlooked the contributions of POM to primary production, nutrient cycling and energy flows (Kies 1995).

Particulate organic matter includes live or dead organic residues larger than 0.45 μm in size (Valiela 1984). Smaller-sized particles are considered part of what is called dissolved organic matter (DOM). Depending on the system, POM may originate from planktonic organisms, resuspended remains of benthic fauna and flora, terrestrial organisms, and even from human activities. The particles undergo a continuous process of aggregation and break-up (van Leussen 1988), especially when shear forces in turbulent waters are above a certain level. The size range distribution of particles is often continuous, reaching up to 10^3 μm and constituting a large pool of organic carbon and organic nitrogen, amounting, in some places, to 10% of the total organic carbon in the water (Wetzel 1983).

Seaweed–POM interactions seem to be complex and multifaceted; they also seem to depend on other environmental factors and are likely to exhibit frequent sign reversals. Until recently, experimental field studies examining the ecological importance of particulate organic matter to seaweeds were missing. Although available information suggests some rather general effects, we have ignored whether they are valid for all kinds of seaweeds. Thus, it is generally suggested that abundant POM increases turbidity in the water column to reduce light penetration (Jerlov 1970) and limit algal growth (e.g. Hay and Norris 1984), but the effects of POM-induced turbidity on light sensitive species has never been tested. Overcoating of algal thallus surfaces with debris and particles may interfere with diffusion and nutrient uptake, somewhat similar to the diffusion impairment resulting from epiphyte overgrowth (Enright 1979, Buschmann and Gomez 1993, Fletcher 1995). However, particles and debris may also protect the thallus against micro and mesograzing, an aspect not yet experimentally tested. POM may also act as a chelator of some metallic elements, some of which may be metabolically important for the seaweeds, whereas others may be toxic. However, the relationship seems to be more complex than this (Kies 1995, Muller 1996). Due to anionic matrix polysaccharides, POM is negatively charged. Protons are exchanged against organic or inorganic cations such as heavy metals or iron. These can be accumulated on or within flocs of POM and transported, sedimented, or resuspended. Absorption and desorption processes may occur, depending on the redox potential and the salinity of the surrounding water. Therefore, flocs of organic matter may act as sources or sinks of these metallic elements. Even though there are many coastal systems where some of these toxic metallic elements have been found to reach high concentrations (see Gledhill et al. 1999 for examples), there seems to be a complete absence of field experimental evaluation of the effects of POM on the bioavailability of these elements and on the respective consequences on seaweed populations and communities.

From the above perspective, Schaffelke's study on the effects of POM on growth and nutrition of seaweeds (pp. 1150–57, this issue) stands out as an elegant combination of field and laboratory experiments evaluating an ecologically important function of POM. By studying seaweed communities on nearshore reefs of the Great Barrier Reef, Australia, Schaffelke and Klumpp (1997) first noticed high biomass abundance and high biomass turn-over rates of some large-sized brown algal species such as *Sargassum.* Using a combination of continuous flow culture and starvation experiments, complemented with tissue nutrient analyses and field measurements of nutrient availability and seaweed growth rates, Schaffelke and Klumpp (1998) then found the growth rates of some of the ecologically important seaweed species (*Sargassum baccularia*) to be both N and P limited by the respective nutrient availability in seawater, particularly during austral summer, the season of maximal

Mixed assemblage of Phaeophyceae at Great Palm Island, central Great Barrier Reef, Australia. Foreground, *Padina* sp.; center, *Turbinaria ornata* (Turner) J. Agardh; on both sides, several *Sargassum* species. The suspended particle load is high in waters of the nearshore regions of the GBR, and the particles are deposited as a layer of grayish material on the algal thalli. Note particles that emphasize the concentric rows of phaeophycean hairs in *Padina* (foreground). *Sargassum* species supplement their nutrient supply with dissolved nutrients derived from the particle layer on their thalli. (Photograph courtesy of Britta Shaffelke)

growth for *S. baccularia.* These field observations led Schaffelke (1999) to suggest that these brown algae may be supplementing their nutritive supply from the layer of particulate matter deposited on their thalli. The concentration of POM in the shallow water of the coastal zone was found to be high (0.6 to 0.9 $gC{\cdot}org\ gDW\ alga^{-1}$) and well retained because of the presence of hyline hairs in the fronds of *S. baccularia.* Experimental additions or removals of POM in the field resulted in significant changes in seaweed growth rates. Thalli with undisturbed POM cover exhibited 120 to 170% higher growth rates than thalli that had the adhering particulate matter repeatedly removed. Tissue nitrogen and phosphorus levels of thalli with a surface POM layer were 10 to 30% higher than those of thalli without POM. Schaffelke (1999) suggested that a nutrient rich layer on the algal surface may be formed by an association of deposited POM, algal mucus, and bacteria, which remineralize the organic matter.

Schaffelke's (1999) findings are important at various levels. At the individual level, they demonstrate the field existence of an alternative and generally overlooked nutrient source for the seaweeds. The use of remineralized nutrients from decaying tissues by seaweeds has previously been suggested (e.g. Newell and Field 1982) but not experimentally tested. The use of POM through *in situ* remineralization of nutrients also differs from the uptake of nutrient-rich, interstitial water in sedimentary patches exhibited by green algal species in the orders Caulerpales (Williams 1984) and Siphonocladales (Larned and Stimson 1996).

The widespread occurrence of habitats where the above process might be ecologically important underlines its significance at community and ecosystem levels. Coral reefs, estuaries, shallow bays, bottom areas of kelp beds, and intertidal and subtidal pools are all examples of habitats where POM may accumulate either as fragments and particles suspended in the water or as remains lying loose on macroalgal assemblages. In these systems, the use of particle-derived nutrients by macroalgae emphasizes a new and different pathway in the alternative uses of POM. Traditional models on nutrient cycling and energy flows in marine systems have assumed two main fates for POM. They are remineralized through microbial loops in the sediments or they are incorporated and integrated into higher trophic levels through consumption. Integration through consumption could be through grazing of rather larger algal remains (e.g. Castilla and Moreno 1982, Bustamante and Branch 1996) or through the detrital pathway, typically consumed by amphipods and filter feeders (Duggins and Eckmann 1997). Schaffelke's (1999) findings emphasize POM remineralization, but not through the rather diffuse pathway that occurs in the sediments. Rather, the remineralization occurs directly on the thallus surface and directly benefits the seaweed covered by the particulate matter.

Bernabé Santelices
Departamento de Ecología
P. Universidad Católica de Chile
P.O. Box 114-D
Santiago, Chile
e-mail: bsanteli@genes.bio.puc.cl

Buschmann, A. H. & Gomez, P. 1993. Interaction mechanism between *Gracilaria chilensis* (Rhodophyta) and epiphytes. *Hydrobiologia* 260/261:345–51.

Bustamante, R. H. & Branch, G. M. 1996. The dependence of intertidal consumers on kelp-derived organic matter on the west coast of South Africa. *J. Exp. Mar. Biol. Ecol.* 196:1–28.

Castilla, J. C. & Moreno, C. 1982. Sea urchins and *Macrocystis pyrifera*. Experimental test of their ecological relations in southern Chile. *In* Lawrence, J. M. [Ed.] *International Echinoderm Conference*. Balkema, Rotterdam, pp. 257–63.

Duggins, D. O. & Eckman, J. E. 1997. Is kelp detritus a good food for suspension feeders? Effects of kelp species, age and secondary metabolites. *Mar Biol.* 128:489–95.

Enright, C. T. 1979. Competitive interaction between *Chondrus crispus* (Florideophyceae) and *Ulva lactuca* (Chlorophyceae) in *Chondrus* aquaculture. *Proc. Int. Seaweed Symp.* 9:209–18.

Fletcher, R. L. 1995. Epiphytism and fouling in *Gracilaria* cultivation: an overview. *J. Appl. Phycol.* 7:325–33.

Gledhill, M., Nimmo, M., Hill, S. & Brown, M. T. 1999. The release of copper-complexing ligands by the brown alga *Fucus vesiculosus* (Phaeophyceae) in response to increasing total copper levels. *J. Phycol.* 35:501–9.

Hay, M. E. & Norris, J. N. 1984. Seasonal reproduction and abundance of six sympatric species of *Gracilaria* Grev. (Gracilariaceae; Rhodophyta) on a Caribbean subtidal sand plain. *Hydrobiologia* 116/117:63–94.

Jerlov, N. G. 1970. Light: general introduction. *In* Kinne, O. [Ed.] *Marine Ecology*, vol. 1, part 1, J. Wiley & Sons, New York, pp. 95–102.

Kies, L. 1995. Algal snow and the contribution of algae to suspended particulate matter in the Elbe estuary. *In* Wiessner, W., Schnepl, E. & Starr, R. C. [Eds.] *Algae, Environment and Human Affairs*. Biopress Ltd., Bristol, U.K., pp. 93–121.

Larned, S. T. & Stimson, J. 1996. Nitrogen-limited growth in the coral reef chlorophyte *Dictyosphaeria cavernosa*, and the effect of exposure to sediment-derived nitrogen on growth. *Mar. Ecol. Prog. Ser.* 145:95–108.

Muller, F. L. L. 1996. Interaction of copper, lead and cadmium, with the dissolved, colloidal and particulate components of estuarine and coastal waters. *Mar. Chem.* 52:245–68.

Newell, R. C. & Field, J. G. 1982. The contribution of bacteria and detritus to carbon and nitrogen flow in a benthic community. *Mar. Biol. Lett.* 4:23–36.

Schaffelke, B. 1999. Particulate organic matter as an alternative nutrient source for tropical *Sargassum* species (Fucales, Phaeophyceae). *J. Phycol.* 35:XX–XX.

Schaffelke, B. & Klumpp, D. W. 1997. Biomass and productivity of tropical macroalgae on three nearshore fringing reefs in the Central Barrier Reef, Australia. *Bot. Mar.* 40:373–83.

Schaffelke, B. & Klumpp, D. W. 1998. Nutrient limited growth of the coral reef macroalga *Sargassum baccularia* and experimental growth enhancement by nutrient addition in continuous flow culture. *Mar. Ecol. Progr. Ser.* 164:199–211.

Valiela, I. 1984. *Marine Ecological Processes*. Springer-Verlag, New York, 546 pp.

van Leussen, W. 1988. Aggregation of particles, settling velocities of mud flocs. A review. *In* Dronkers, J. & van Leussen, W. [Eds.] *Physical Processes in Estuaries*. Springer, Berlin, pp. 347–403.

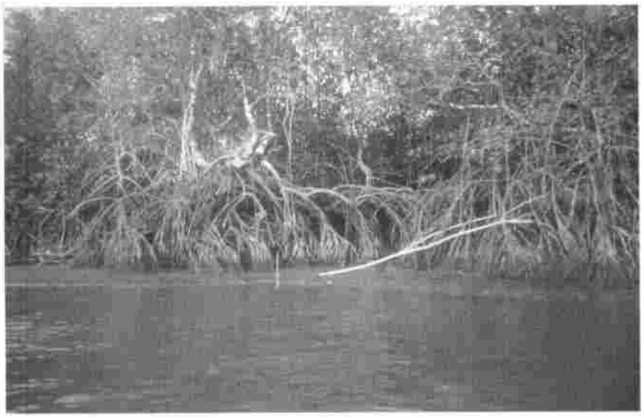
Williams, S. L. 1984. Uptake of sediment ammonium and translocation in a marine green macroalga *Caulerpa cupressoides*. *Limnol. Oceanog.* 29:374–9.

Wetzel, R. G. 1983. *Limnology*, 2nd ed. CBS Publishing, Philadelphia, 767 pp.

PHOTOSYNTHESIS IN THE INTERTIDAL ZONE: ALGAE GET AN AIRING

The cyanobacteria and eukaryotic algae evolved in aqueous (mainly marine) environments. However, a significant number of algal species spend some or all of their time in subaerial environments. By convention, phycologists are barred from considering the embryophyte members of the monophyletic Streptophyta (charophycean green algae and their embryophyte descendants), which are the predominant photosynthetic organisms on land in terms of species number, biomass, productivity, and impact on other biota, with only a small minority of secondarily aquatic embryophytes. Peña, Zingmark and Nietch (pp. 1206–1214, this issue) provide new data on how two intertidal red algae perform during the time they spend exposed to air in the "higher plant environment."

Algae that spend some or all of their life out of water include intertidal and supralittoral marine algae (e.g. Peña, Zingmark and Nietch 2000), terrestrial freeliving algae, algae living in external freshwater bodies, and algae in terrestrial and intertidal lichens. None of these organisms can control its wa-



The red mangrove *Rhizophora mangle*, dominates the shore near low tide in Buenaventura Estuary, southern Pacific Coast of Colombia, South America. Prop roots support a dense, productive, epiphytic community dominated by the red algae *Bostrychia calliptera*, *Caloglossa leprieurii* and *Catanella impudica*, and the green alga *Boodleopsis verticillata*. Each of these algae occupies a distinct vertical range within the approximately 3 meter intertidal zone, which correlates with its ability to overcome desiccation stress during low tide. (Photograph by Richard Zingmark).

ter content in a desiccating atmosphere (i.e. they are poikilohydric); those that spend a significant fraction of their time out of water are tolerant of desiccation. This means that the organisms can become metabolically inactive after equilibration with an atmosphere of low relative humidity and can be restored to full function upon exposure to liquid water with not too negative a water (as osmotic) potential. In some free-living green algae and green algal lichens, this occurs by equilibration with an atmosphere with a relative humidity above a critical level; such a humidity is not linearly related to water potential (see Raven 1999).

These algal characteristics are shared by some embryophytes: the sporophytes and gametophytes of mosses, liverworts, and hornworts, the free-living photosynthetic gametophytes of ferns and horsetails, and some secondarily aquatic vascular plant sporophytes. However, the terrestrial sporophytes of vascular plants are homoiohydric (i.e. can, to differing extents, maintain their hydration status despite variations in external conditions). Furthermore, they are generally desiccation intolerant in the vegetative phase, although they frequently have desiccation-tolerant propagules. In any event, all vascular land plants that grow to more than a meter in height, and the great majority of those that do not grow taller than 1 m are desiccation-tolerant homoiohydric plants (see Raven 1999).

Homoiohydric higher plants dominate many terrestrial habitats, but there are constraints on their activities. Three such constraints, which provide niches for other phototrophs, are the minimum size of functionally homoiohydric organisms, the need for a small-grained sediment as a rooting medium, and the poor photosynthetic performance of homoiohydric organisms when they are submerged (Sand-Jensen et al. 1992, Raven 1999, Vervuren et al. 1999). Thus, there are ample niches for poikilohydric organisms in habitats with variable supplies of surface water.

One of the ecophysiologically important features of these poikilohydric plants is their ability to use inorganic carbon from the aqueous phase when the plants are covered by water and from the atmosphere when there is minimal or no liquid water on the surface. Diffusion boundary layers can restrict photosynthesis using inorganic carbon from a continuous aqueous phase, whereas acquisition of CO_2 from air is less constrained by diffusion boundary layers. This is because although these diffusion boundary layers are usually thicker in air than water, this constraint on inorganic carbon supply is more than offset by the 10,000-fold higher diffusion coefficient for CO_2 in air than in water (Cowan et al. 1992, Madsen and Maberly 1990, Raven 1994). These constraints on inorganic carbon acquisition from water can be offset by the presence of inorganic carbon at high pH (e.g. in seawater at pH 8) with bicarbonate in great excess of CO_2, provided that the organisms can directly or indirectly catalyze bicarbonate use (Raven 1996). Furthermore, any advantage in inorganic carbon acquisition by use of atmospheric CO_2 rather than aqueous CO_2 is offset as water evaporates and the water content—and water potential—of the organism decreases (Cowan et al. 1992, Madsen and Maberly 1990, Peña et al. 2000). This problem is especially severe for marine algae where salt is concentrated extracellularly as water evaporates.

A number of researchers have investigated the rate of photosynthesis by intertidal (and supratidal) marine algae under submerged (that is, immersed) and emersed conditions (reviewed by Peña et al. 2000). One problem with such comparisons is that different methods are used for photosynthetic measurements in the two media. Typically, as in the work of Peña et al. (2000), photosynthesis in seawater is measured by aqueous phase O_2 electrode methodology, whereas it is estimated in air by infrared gas analysis measurements of CO_2. However, Madsen and Maberly (1990) measured uptake of inorganic carbon from each medium in their work on the brown alga *Fucus spiralis*. By contrast, Britting (1992) measured O_2 evolution from both submerged and emersed specimens of the red alga *Endocladia muricata*. These experiments used a technique for gas-phase O_2 measurements that was sensitive enough to determine the small changes in O_2 in the gas phase relative to the large background O_2 under conditions that do not cause large changes in the CO_2 concentration in the experimental chamber. Of course, submerged O_2 and emersed CO_2 measurements can be compared using assumptions as to the photosynthetic quotient.

The ecological relevance of these laboratory measurements requires consideration of the length of time that the organism spends in air and in water in the light, the extent of water loss during emersion and its influence on integrated photosynthesis during emersion, and the extent of light saturation and the temperature during the periods of emersed and submersed photosynthesis, among other factors. Maberly and Madsen (1990) and Britting (1992) worked on single intertidal species at different rocky intertidal sites; Peña et al. (2000) have investigated two red algal species growing in different intertidal zones on roots of the red mangrove *Rhizophora mangle* on the Pacific coast of Colombia, following the work of Mann and Steinke (1988) on the same two red algal genera.

Mangrove ecosystems ("mangals") occupy coastal marine habitats and are dominated by salt-tolerant woody phanerophytic flowering plants; they occur in appropriate (fine-grained sediments) habitats from 31° N to 37° S (Tomlinson 1986). These diverse ecosystems are under threat from humankind's activities worldwide (Tomlinson 1986). Table 5.5 of Bolin et al. (1979) estimates that mangals occupy 0.3×10^{12} m^2 of the total 149.3×10^{12} m^2 of land area on earth, and that their yearly net primary terrestrial productivity is 0.14×10^{15} g carbon out of the total terrestrial productivity of 60×10^{15} carbon. Thus, mangals may be slightly more productive than the "average" terrestrial ecosystem. Even with the most optimistic assumptions about the performance of the red algae associated with the illuminated intertidal parts of the mangroves, it is not likely that these algae contribute more than 1% of the woody plant productivity of mangals (i.e. not more than 1.4×10^{12} g carbon globally each year or 4.7 $g \cdot C \cdot m^{-2}$ of mangal habitat per year). This estimate is based on less than 10% of the photosynthetically active radiation incident on the tree canopy reaching the intertidal part of the understory and not more than 10% of this radiation absorbed by red algae on mangrove stems, prop roots and pneumatophores and is of a similar magnitude to productivity estimates per square meter of mangrove tissue occupied by red algae (Clark 1987). This 1.4×10^{12} g carbon each year is very small compared with up to 50×10^{15} g carbon fixed by primary producers in the ocean per year, admittedly over an area twice that of the total land surface (Falkowski & Raven 1997). This brief discussion shows that these mangrove red algae face a unique combination of environmental factors: shade by trees and the intertidal habitat.

To further our understanding of the ecophysiology of these red algae, Peña et al. (2000) examined *Caloglossa leprieurii* growing low on the prop roots and *Bostrychia calliptera* growing higher up the prop roots. *Bostrychia* was found to tolerate prolonged periods of emersion and recovered its capacity for photosynthesis after partial desiccation more rapidly than did *C. leprieurii* (Peña et al. 2000). Furthermore, emersed photosynthesis contributed 17% of the daily carbon gain for *B. calliptera* for 17 June 1996 and 12% for *C. leprieurii*, with the time of emersion contributing 29% and 21% of the photoperiod, respectively, so that the fractional contribution of emersed photosynthesis to daily carbon gain per hour of emersion is similar for the two algae (Peña et al. 2000). Thus, although the alga (*B. calliptera*) found higher up the prop root is exposed to air for 40% more time each tidal cycle than is *C. leprieurii*, with a correspondingly greater possibility for desiccation, the alga from the higher intertidal zone is clearly capable of contributing more to the daily carbon gain per unit time of emersion.

We have many other things to learn about the ecophysiology of these red algal epiphytes on prop roots (and pneumatophores) of mangroves. Although carbon and energy gain by these red algae can occur during emersion in the light, uptake of nutrients other than carbon is much less likely during emersion. Acquisition of nutrients such as ammonium, nitrate, and phosphate is presumably, as in other algae, possible during submersion in the dark in these intertidal algae. However, these algae still have a smaller time available for nutrient uptake relative to that available for photosynthesis than do algae that are continuously submersed. Do submersed mangrove red algae have higher ratios of nutrient uptake rate to photosynthetic rate than do continually submersed red algae with similar elemental ratios? Evidence from other intertidal marine algae is somewhat inconclusive (see chapter 5 of Lobban and Harrison 1994).

A further question concerns the mechanism of inorganic carbon acquisition by these mangrove algae. There are theoretical grounds for believing that algae with inorganic carbon concentrating mechanisms can, other things being equal, increase the amount of inorganic carbon fixed per unit water lost in evaporation in emersed, poikilohydric, photosynthetic organisms, such as some intertidal and supratidal marine algae and some terrestrial lichens as well as the high intertidal lichen *Lichina* (Raven 1994). Mercado and Niell (1999) have shown that *Bostrychia scorpioides* depends on CO_2 diffusion to supply CO_2 to RUBISCO. Furthermore, Raven et al. (1995) report natural abundance $^{13}C/^{12}C$ data consistent with diffusive CO_2 supply to RUBISCO in intertidal *Bostrychia flagellifera, Caloglossa leprieurii* var. *leprieuriim*, and *Catanella nipae* from pneumatophores of *Avicennia marina*. var. *australasica*. These two data sets suggest that mangrove red algae do not have CO_2 concentrating mechanisms. Raven et al. (1995) also comment on the possible contribution of CO_2 respired by the mangroves to photosynthesis by mangrove algae, especially for algae growing on pneumatophores. However, we clearly need more investigation of the inorganic carbon acquisition mechanisms of the mangrove red algae, and of its implication for the quantity of carbon assimilated per unit water lost.

John A. Raven
Department of Biological Sciences
University of Dundee
Dundee DD1 4HN
United Kingdom
email: j.a.raven@dundee.ac.uk

Bolin, B., Degens, E. T., Kempe, S. & Ketner, P. [Eds.] 1979. *The Global Carbon Cycle. Scope 13.* John Wiley & Sons, Chichester, U.K.

Britting, S. A. 1992. Effect of emergence on the physiology and biochemistry of a high intertidal alga, *Endocladia muricata* (Post & Rupt.) J. Ag. (Cryptonemiales, Rhodophyta). Ph.D. dissertation, University of California, Los Angeles.

Clark, H. 1987. The effects of environmental factors on photosynthesis and respiration of two species of *Bostrychia* (Ceramiales, Rhodophyta) from a mangrove algal community of Western Port Bay, Victoria. B.Sc. (Hons.) dissertation, La Trobe University, Victoria.

Cowan, I. R., Lange, O. L. & Green, T. G. A. 1992. Carbon dioxide exchange in lichens: determination of transport and carboxylation characteristics. *Planta* 187:282–94.

Falkowski, P. G. & Raven, J. A. 1997. *Aquatic Photosynthesis.* Blackwell Science, Malden, Massachusetts.

Lobban, C. S. & Harrison, P. J. 1994. *Seaweed Ecology and Physiology.* Cambridge University Press, Cambridge.

Maberly, S. C. & Madsen, T. V. 1990. The contribution of air and water to the carbon balance of *Fucus spiralis* L. *Mar. Ecol. Prog. Ser.* 62:175–83.

Madsen, T. V. & Maberly, S. C. 1990. A comparison of air and water as environment for photosynthesis by the intertidal alga *Fucus spiralis* (Phaeophyta). *J. Phycol.* 26:24–30.

Mann, F. D. & Steinke, T. D. 1988. Photosynthetic and respiratory responses of the mangrove associated red algae, *Bostrychia radicans* and *Caloglossa leprieurii. S. Afr. J. Bot.* 54:203–7.

Mercado, J. & Niell, F. X. 1999. Carbonic anhydrase activity and use of HCO_3^- in *Bostrychia scorpioides* (Ceramiales, Rhodophyceae). *Eur. J. Phycol.* 34:13–9.

Peña, E. J., Zingmark, R. & Nietch, C. 2000. Comparative photosynthesis of two species of intertidal macroalgae or mangrove roots during submersion and emersion. *J. Phycol.* 36: in press.

Raven, J. A. 1994. Photosynthesis in aquatic plants. In: Schultze, E. D. & Caldwell M. M. [Eds.] *Ecophysiology of Photosynthesis.* Springer-Verlag, Berlin, pp. 299–318.

Raven, J. A. 1999. The size of cells and organisms in relation to the evolution of embryophytes. *Plant Biol.* 1:2–12.

Raven, J. A., Walker, D. I., Johnston, A. M., Handley, L. L. & Kübler, J. E. 1995. Implications of ^{13}C natural abundance measurements for photosynthetic performance by marine macrophytes in their natural environment. *Mar. Ecol. Prog. Ser.* 123:193–205.

Sand-Jensen, K., Pedersen, M. F. & Nielsen, S. L. 1992. Photosynthetic use of inorganic carbon among primary and secondary water plants in streams. *Freshwater Biol.* 27:283–93.

Tomlinson, P. B. 1986. *The Botany of Mangroves.* Cambridge University Press, Cambridge.

Vervuren, P. J. A., Beurskens, S. M. J. H. & Blom, C. W. P. M. 1999. Light acclimation, CO_2 response and long-term capacity of underwater photosynthesis in three terrestrial plant species. *Plant Cell Environ.* 22:959–68.

Future Meetings of the Phycological Society of America

2000: The 54th annual meeting of the Phycological Society of America will be held 15 to 19 July, 2000 at the Town & Country Resort & Convention Center in San Diego, California, USA. The Phycological Society of America will meet with the American Society of Plant Physiologists in a 'side-by-side' meeting format. The Phycological Society of America portion of the meeting will consist of a Plenary Lecture, organized symposia, and contributed oral and poster papers.

For information regarding this meeting, please contact the Program Director, Dr. David F. Millie, Phycological Society of America, ℅ Mote Marine Laboratory, 1600 Thompson Parkway, Sarasota, Florida 34226 USA. Telephone: (941) 388-4441, E-mail: dmillie@mote.org.

This document is a scanned copy of a printed document. No warranty is given about the accuracy of the copy. Users should refer to the original published version of the material.