

Environmental Factors and Their Consideration in the Management of Submersed Aquatic Vegetation: A Review

J. W. BARKO, M. S. ADAMS AND N. L. CLESCERI¹

ABSTRACT

A variety of environmental factors interact in affecting the productivity, distribution, and species composition of submersed macrophyte communities. Foremost among these are light, water temperature, sediment composition, and inorganic carbon availability. Light and temperature are important in determining morphology and distribution (with latitude, season, and depth), thereby influencing productivity and species composition as well. Sediments provide an important source of nutrients, principally N, P, and micronutrients, which are relatively less available in the surface waters of most aquatic systems. Sediment composition (i.e., texture and organic matter content) markedly affects macrophyte growth rates, due to its influence on nutrition, but possibly due also to the inhibitory effects of reduced chemical constituents formed under anaerobic conditions. Due to slow CO₂ diffusion rates in water and to boundary layer resistance to carbon uptake at leaf surfaces, the availability of inorganic carbon can be an exceptionally important factor limiting the productivity of submersed macrophytes in freshwater systems. Prior to the implementation of management procedures designed to modify aquatic macrophyte production or community composition, it is necessary to consider both aquatic system use and the localized role of these important growth regulating factors.

Key words: ecology, light, temperature, nutrients, water chemistry, sediment chemistry, inorganic carbon.

INTRODUCTION

A concerted effort has been undertaken by various agencies within many of the industrialized countries of the world to manage aquatic macrophytes. Most of these efforts have been directed toward the control of adventive species in situations where they grow to nuisance proportions (cf. van Zon 1982). A variety of control techniques is available, and these include: herbicide treatment, biomass harvesting, nutrient diversion and chemical precipitation, dredging, drawdown, bottom sealing, use of biological control agents, and physical and chemical reductions in underwater irradiance (refer to the reviews of Dunst et al. 1974; Cooke 1980; van Zon 1982; Nichols and Shaw 1983). Another, yet less emphasized, aspect of aquatic plant man-

agement is that of habitat enhancement. Aquatic macrophytes play a key role in maintaining fish productivity, both by stimulating invertebrate production and by providing habitat diversity (Pennak 1971; Wiley et al. 1984). Cognizance of the overall ecological importance of submersed macrophytes in aquatic systems (cf. Wetzel and Hough 1973; Wetzel 1979; Carpenter 1981) has underscored major concern for the recent widespread demise of vegetation in the Chesapeake Bay, one of the world's largest estuaries (Orth and Moore 1983; Kemp et al. 1983). Similar declines in submersed aquatic vegetation have been reported worldwide (cf. Sculthorpe 1967; Carpenter 1980a), but as in the Chesapeake have not been adequately explained.

Our present inability to effectively anticipate changes in the productivity and distribution of submersed macrophytes, due either to natural causes or to human activities, directed (e.g., weed control) or otherwise, makes it difficult to redirect undesirable trends. This problem has been largely a consequence of our inadequate understanding of the role of environment in affecting submersed aquatic vegetation. Recently, however, a great deal of information related to the physiology and ecology of submersed macrophytes has been generated. Our purpose in this article is to synthesize important aspects of this information for consideration in the management of submersed macrophytes in lakes and in streams.

Views expressed herein are those of the authors, but were developed in part during the conduct of an international workshop, convened recently in Lake George, New York (refer to Acknowledgements for list of participants). This article is intended to disseminate findings and recommendations of that workshop, and is dedicated in memory of the late D. H. N. Spence (St. Andrews, Scotland), a participant in the workshop and a major contributor to the discipline of aquatic plant ecology.

Only abiotic environmental factors: light, temperature, nutrients, inorganic carbon, and sediment composition affecting submersed aquatic vegetation are considered here. The important influence under some circumstances of biotic factors (grazers, pathogens etc.; see Nichols and Shaw 1983) on submersed macrophytes is not denied, but at present there is too little information available for intended synthesis.

LIGHT

The importance of light availability in relation to the productivity and distribution of aquatic macrophytes (reviewed by Westlake 1981) was emphasized by a majority of

¹Environmental Laboratory, Waterways Experiment Station, Vicksburg, MS 39180; Department of Botany, University of Wisconsin, Madison, WI 53706; Department of Chemical Engineering and Environmental Engineering, Rensselaer Polytechnic Institute, Troy, NY 12180-3590

participants at the workshop. Westlake (1971) suggested that light is limiting in dense stands of aquatic plants even at midday in many situations, and can be particularly limiting with increasing depth and turbidity. Westlake (op. cit.) further stressed that need for space during plant growth is related to need for light, and that given space, many aquatic plants can develop an efficient arrangement of leaves for optimal light capture.

From an extensive survey of Scottish lochs, Spence (1967) proposed that the zonation of a variety of macrophyte species along a depth gradient was determined primarily by light regime. In related investigations, Spence and Chrystal (1970a, b) demonstrated greater photosynthetic capacity in deep-water compared to shallow-water pondweed (*Potamogeton*) species, and suggested that shade tolerance was directly linked with the natural depth distribution of these species. Ikusima (1965, 1966) incubated submersed macrophytes at depths of natural occurrence, and demonstrated large differences in photosynthetic rate at different light levels (depths). Adams et al. (1974) clearly demonstrated light limitation of photosynthesis within the canopy of Eurasian watermilfoil (*Myriophyllum spicatum* L.) growing in a dense stand in Lake Wingra. Further evidence for the importance of light as a rate-limiting factor, based on profile measurements of photosynthesis in the canopy of this species, is provided in Titus et al. (1975).

Robel (1961) demonstrated that increased turbidity resulted in decreased macrophyte biomass. Similarly, Peltier and Welch (1970) showed that, while the growth of rooted submersed macrophytes in an Alabama reservoir was unrelated to ambient nutrient concentrations, two years of severe infestation were directly correlated with the increased availability of light. Spence (1976) indicated that the depth of macrophyte colonization, related to the availability of light, was controlled to a great extent by phytoplankton density. Increased phytoplankton density resulting from nutrient enrichment can be an important factor in the decline of macrophyte populations (Jupp and Spence 1977). The near-collapse of the Eurasian watermilfoil community of Lake Wingra, Wisconsin during the 1970's presents an example of a macrophyte decline associated with planktonically-generated turbidity (Jones, et al. 1983), possibly reinforced also by a pathogen (John Andrews, personal communication). In other cases submersed macrophyte populations have been shown to decline due to light limitations caused by epiphytes and filamentous algal growth on leaf surfaces (Sand-Jensen 1977; Phillips et al. 1978; Sand-Jensen and Søndergaard 1981).

Light plays an important role in seasonal changes in macrophyte dominance and in interspecific competition. Westlake (1981) provides evidence that great reductions in irradiance may result in changes in species composition. In Europe, the total irradiance for a given month may vary by 50% from year to year, and among years can vary by 30%. In the well-studied chalk streams of southern Britain, tree-shaded reaches may be dominated by *Berula erecta* (Hudson) Colville or water starwort (*Callitriche*) species, while water buttercup (*Ranunculus*) species are excluded; in dense shade (light reduced 85%) aquatic mosses dominate (Westlake op. cit.). McCreary et al. (1983) provide

evidence that the slender spikerush (*Eleocharis acicularis* (L.) R&S) and the common rush (*Juncus pelocarpus submersus* L.) coexist in spite of differing light adaptations. However, greater shade tolerance in slender spikerush accounts for its wider distribution in Wisconsin, including lakes more turbid than those that support both species (Swindale and Curtis, 1957).

Westlake (1981) stresses that some plants can adapt within weeks to lowered light by reducing non-photosynthetic tissue and adjusting respiration rates. Another way in which submersed macrophytes can adapt to low irradiance is through adjustments in photosynthetic pigment composition. Total chlorophyll content of leaves generally increases with decreasing irradiance, (Bowes et al. 1977; McMillan and Phillips 1979; Wigington and McMillan 1979; Barko and Filbin 1983). Within individual plants, total chlorophyll content can vary significantly in response to irradiance, with the greatest chlorophyll concentration at the basal (darkest) portion of the plant (Ikusima 1965, 1966).

Morphological adaptations that optimize the capture of light are important in determining species success in low-light environments. Both whole-plant morphology (Spence and Dale 1978; Barko and Smart 1981a; Barko et al. 1982) and specific leaf morphology (Pearsall and Hanby 1925; Spence et al. 1973; Barko et al. 1982) in submersed macrophytes are responsive to light regime. In general, these plants tend to produce fewer but longer shoots, and longer leaves with a greater surface area under reduced irradiance conditions. Submersed macrophytes capable of elongating to the water surface and forming a foliar canopy, such as Eurasian watermilfoil and hydrilla (*Hydrilla verticillata* (L.F.) Royle), may grow to greater depths and have a competitive advantage in turbid situations over species possessing a prostrate growth form (Haller and Sutton 1975; Titus and Adams 1979; Barko and Smart 1981a). Past periods of dominance by Eurasian watermilfoil in the upper Chesapeake Bay (Bayley et al. 1978) may partially reflect the exceptional ability of this species to form a surface canopy under conditions of limited water transparency (Adams et al. 1974). Differences in the specific leaf area of certain pondweed species have been shown to be important in influencing their maximum depth of occurrence (Spence and Chrystal 1970b).

In general, but dependent upon the amounts and composition of dissolved materials and suspended particulate materials in water, the penetration of different light spectra in aquatic systems varies with wavelength (Ruttner 1963). Selective attenuation of far red (FR, ≥ 700 nm) light increases the red (R, 660 nm) to FR ratio steeply with increasing depth. It has been suggested that variations in some aspects of submersed macrophyte morphology, such as leaf form (Bodkin et al. 1980) and shoot internode spacing (Spence 1976; Spence and Dale 1978), are mediated by the pigment phytochrome and affected by the ratio of R to FR light. Moreover, diurnal underwater variations in R:FR, as perceived by phytochrome, may be a mechanism whereby submersed macrophytes detect the length of photoperiod (Chambers and Spence 1984). Chambers (1982) demonstrated that long-day induction of winter bud production in curly leaf pondweed (*Potamogeton crispus* L.)

is under phytochrome control. Tuber formation in hydrilla, induced under short-day conditions (Haller et al. 1976; Van et al. 1978; Bowes et al. 1979; Klaine and Ward 1984), is also mediated by phytochrome (Klaine and Ward op cit.). Thus the quality as well as the quantity of light in aquatic systems has an important influence on the growth and development of submersed macrophytes.

TEMPERATURE

Seasonal changes in photoperiod and incident solar radiation promote corresponding changes in water temperature in most aquatic systems. Thus the influence of light on submersed macrophytes cannot be properly evaluated without also considering the influence of temperature. In controlled laboratory experiments, water temperature has been shown to interact with light in affecting submersed macrophyte growth and morphology (Barko and Smart 1981a; Barko et al. 1982), photosynthesis (Barko and Smart 1981a), chlorophyll composition (Barko and Filbin 1983), and reproduction (Sastroutomo 1980, 1981; Chambers 1982). Higher temperatures within ranges of thermal tolerance generally promote greater chlorophyll concentration and productivity, with concomitant increases in both shoot length and shoot number; increasing temperature and increasing light appear to elicit opposing responses in shoot length.

In thermally stratified systems, decreasing water temperature with depth may promote depth-related reductions in the seasonal growth of macrophytes. For example, it has been reported that the dynamics of thermal stratification in a dimictic north-temperate lake limit the growing season of purple bladderwort (*Utricularia purpurea* Walt) to 8 weeks at a depth of 6 m compared to 17 weeks at a depth of 2 m (Moeller 1980). By reducing the length of the growing season, low temperatures can diminish the capacity of submersed macrophytes to colonize depths consistent with their maximum photosynthetic potential.

The thermal optimum for many submersed freshwater macrophytes appears to be rather high, in the range of 28 to 32 C (Barko and Smart 1981a; Barko et al. 1982; however cf. Tobiessen and Snow 1985). Consequently, adaptability of submersed macrophytes to lower temperature regimes may confer a competitive advantage in northern localities. For example, the lack of dormancy in elodea (*Elodea canadensis* Rich. in Michx.) in combination with its high overwintering standing crop under ice free conditions apparently contributed to the success of this species in Lake Wabamun, Alberta, during a period of temperature elevation (Haag and Gorham 1977). Changes in the species composition of submersed freshwater macrophyte communities due to thermal alterations (Anderson 1969; Allen and Gorham 1973) suggest that temperature may be as important as light in influencing competitive relations among coexisting species.

NUTRITION

In view of the large volume of information available related to the nutrition in nature of submersed macrophytes, it is significant that there have been few substantiated reports of nutrient-related growth limitation. Nu-

trients supplied from sediments in combination with those in solution have been considered adequate to meet macrophyte nutritional demands even in oligotrophic systems (Patterson and Brown 1979). An additional advantage in such nutrient-poor systems on the part of some species (e.g., *Littorella* spp. and *Lobelia* spp.) is their ability to conserve seasonally both biomass and nutrients (Moeller 1978a, Sand-Jensen and Søndergaard 1979). However, macrophyte production under these conditions is often limited.

It is now generally accepted that rooted macrophytes can fulfill their P requirements by direct uptake from sediments (Bristow and Whitcombe 1971; DeMarte and Hartman 1974; Best and Mantai 1978; Bole and Allan 1978; Carignan and Kalff 1979, 1980; Welsh and Denny 1979; Barko and Smart 1980, 1981b; Huebert and Gorham 1983). Recent studies have likewise demonstrated significant mobilization of N from sediments (Toetz 1974; Nichols and Keeney 1976a, b; Best and Mantai 1978; Barko and Smart 1981b; Barko 1982; Huebert and Gorham 1983). The role of sediment as a direct source of P and N for submersed macrophytes is ecologically quite significant, since these elements are normally very low in concentration in available forms in the open water of aquatic systems.

The availability to submersed macrophytes of micronutrients in the open water of most aquatic systems is usually very low due to removal from solution by microorganisms and by precipitation and complexation (Wetzel 1983). In contrast, micronutrients are relatively abundant in available (i.e., chemically reduced) forms within most sediments. Submersed macrophytes can satisfy their requirements for micronutrients in addition to P and N by direct uptake from sediments (Huebert and Gorham 1983; Smart and Barko 1985).

Although some sediments may provide sufficient potassium (K) via root uptake for moderate growth of submersed macrophytes, experimental additions of K to solutions lacking in this element have been demonstrated to stimulate macrophyte growth on a variety of sediments (Barko 1982). Since ammonium and potassium ions have the same charge and nearly identical ionic radii, they may compete for cation exchange sites in sediments and on root surfaces. In this connection, the more effective uptake of N (as ammonium) than K from sediments (Barko and Smart 1981b; Barko 1982) suggests some degree of ion selectivity associated with nutrient uptake systems operating in roots. The open water rather than sediment appears to be the primary source of K supply to submersed macrophytes in most aquatic systems.

Calcium (Ca) can be mobilized from sediments by submersed macrophytes (DeMarte and Hartman 1974). However, in the investigation of Huebert and Gorham (1983) sago pondweed (*Potamogeton pectinatus* L.) failed to grow in the absence of Ca in solution, and in Barko (1983) the growth of Eurasian watermilfoil was markedly reduced in solutions low in Ca. For many species, Ca may be required in the open water due to its apparent involvement in bicarbonate utilization during photosynthesis (Lowenhaupt 1956; Lucas and Dainty 1977). Reduced growth of sago

pondweed in Mg-free solutions (Huebert and Gorham 1983) suggests that Mg may also be required in the open water by some submersed macrophyte species.

Both shoot and root uptake of SO_4 , Na, and Cl have been demonstrated for submersed macrophytes (cf. Smart and Barko 1985). Considering the normal abundance and conservative nature of these elements (S, Na, and Cl) in the open water of many aquatic systems, it is unlikely that low concentrations directly limit the growth of submersed macrophytes. High concentrations of these and other elements, however, in saline environments can directly limit the growth and distribution of submersed macrophytes, dependent upon specific differences in salinity tolerance (Haller et al. 1974; Howard-Williams and Liptrot 1980).

It is clear that submersed macrophytes make use of both aqueous and sedimentary nutrient sources, and that sites (roots vs. shoots) of uptake are related at least in part to nutrient-specific differences in sediment vs. overlying water nutrient availability (Denny 1980). Nutrient transport in these plants is clearly multidirectional, but specific biochemical mechanisms involved in transport, particularly at the membrane level, are essentially unknown. A variety of biochemically complex nutrient uptake systems have been postulated for terrestrial plants (reviewed by Hewitt and Smith 1975). Several of these systems rely metabolically on the establishment of redox gradients, which in rooted macrophytes may be facilitated, with perhaps lesser energy expenditure, by the contrasting redox environments of roots (reducing conditions) and shoots (oxidizing conditions). This contrast represents a fundamental distinction between the environments of terrestrial and aquatic plants, and should be considered in any biochemical studies of submersed macrophyte nutrition.

Losses of nutrients from submersed macrophytes can occur through excretion, senescence (leaching), and microbial decomposition (decay). Substantial losses of P to the water due to excretion have been reported for the seagrass, *Zostera marina* L., (McRoy et al. 1972). However, considerable experimental evidence obtained since then, based on studies involving freshwater macrophytes, has indicated only minor losses of P due to physiological excretion from healthy plants (Pevery and Brittain 1978; Welsh and Denny 1979; Barko and Smart 1980, 1981b; Gabrielson et al. 1984). Nutrient losses from macrophytes appear to be predominantly connected with senescence and decay (Carpenter 1980b), and can be quite large, particularly in eutrophic systems due to excessive biomass turnover (Westlake 1982; Wetzel 1983). Fundamental variations in the abilities of different submersed macrophyte species to retain nutrients (i.e., different degrees of "evergreenness") may bear on floristic differences between oligotrophic and eutrophic aquatic systems.

Given that submersed macrophytes are capable of "mining" some sediment nutrients (primarily N, P, and micronutrients) and that nutrient losses from macrophyte beds to either outflow or profundal sedimentation do occur, then it is important to better understand the extent to which, and by what mechanisms, these losses are balanced. In addition to nutrient replacement by inputs from the watershed, nutrients are potentially redistributed within sediments by simple chemical diffusion, mass flow,

and by the burrowing activities of benthic invertebrates. Moreover, the microbial community of sediments, particularly in the root zone, is likely to play an important role in nutrient replenishment (cf. seagrass literature, e.g., Capone 1982; Smith and Hayasaka 1982, a, b; Craven and Hayasaka 1982; Smith et al. 1984). There is some evidence that N fixation by bacteria can occur in the rhizosphere of watermilfoil (*Myriophyllum heterophyllum* Michx.) (Blotnick et al. 1980). Importantly, vesicular-arbuscular mycorrhizae, which effectively facilitate increased efficiency of nutrient uptake by roots, have been identified in association with several macrophyte species growing in sandy oligotrophic systems (Søndergaard and Laegaard 1977), and more recently with a wider variety of species growing in lakes of varied trophic status (Clayton and Bagyaraj 1984).

SEDIMENT COMPOSITION

Recent concern for sediment as a source of nutrients for submersed macrophytes has been encouraged to some degree by earlier experimental accounts and observations of sediment-related variations in macrophyte growth and distribution (Pond 1905; Pearsall 1920; Misra 1938; Moyle 1945). However, given that these variations in some cases do involve nutrition, such has not yet been adequately demonstrated. It has been suggested that the influence of sediments on the growth of submersed macrophytes may be due to physical properties (Sculthorpe 1967). Texture, for example, can be important in relation to the rooting depth of species with different abilities to physically penetrate sediments (Denny 1980), and may influence rooting success in particular conditions of water flow (Haslam 1978). Extremely sandy or otherwise coarse-textured sediments can be considered as nutritionally poor substrata for macrophyte growth. Low level accumulations of organic matter in such sediments can apparently stimulate growth due presumably to improved ionic exchange properties and increased sediment nutrient content (Sand-Jensen and Søndergaard 1979; Kiørboe 1980).

Among numerous properties of sediments potentially affecting the growth of aquatic macrophytes, inorganic constituents formed under anaerobic conditions have received greatest attention. High concentrations of soluble reduced iron and manganese in sediments are normally considered toxic to plants (Ponnamperuma 1972; Sanderson and Armstrong 1980). High soluble iron concentrations can inhibit the growth of vegetation by interfering with sulfur metabolism or by limiting the availability of phosphorus (Jones 1975). Soluble sulfides including S^- , HS^- , and H_2S are also considered highly toxic to plants (Sanderson and Armstrong 1980). High concentrations of soluble sulfides in sediments require a sustained sulfur source, inputs of organic matter providing reducing potential, and low concentrations of precipitants and/or oxidants (Ponnamperuma 1972). These conditions are frequently encountered in anaerobic sediments of eutrophic lakes (Mortimer 1971; Wetzel 1983). However, some degree of protection from sulfides and other potential toxins on the part of submersed macrophytes may be provided by oxygen release from roots (Tessenow and Baines 1978; Carpenter et al. 1983; Penhale and Wetzel 1983).

Sediments containing excessive organic matter often contain high concentrations of organic acids, which can be toxic to vegetation (Ponnamperuma 1972). Other important organic constituents of anaerobic sediments potentially affecting macrophyte growth include methane, ethylene, phenols, and alcohols (Yoshida 1975; Drew and Lynch 1980). Organic compounds in both sediment and water have been demonstrated to reduce the growth of submersed aquatic vegetation in the laboratory (Dooris and Martin 1981; Barko and Smart 1983) and in the field (Kullberg 1974; Ozimek 1978). Allelopathic substances, presumably organic in nature, produced in the rhizosphere of dwarf spikerush (*Elodea coloradoensis* (Britt.) Gilly) have been shown to differentially inhibit growth and reproduction in a variety of submersed macrophytes (Frank and Dechoretz 1980; Yeo and Thurston 1984). In addition to possible direct inhibitory effects of organic compounds, high concentrations of sediment organic matter appear to decrease the growth rate of submersed macrophytes indirectly by decreasing mineral nutrient densities (Barko and Smart submitted). It has been suggested that increasing concentrations of organic matter in sediments may contribute to the general decline of submersed macrophytes (Barko and Smart 1983).

Submersed macrophytes are capable of effecting pronounced changes in sediment composition. For example, reductions in extractable sediment phosphorus in the root zone of Eurasian watermilfoil in Lake Wingra have been described (Prentki 1979). Barko and Smart (1980) reported a turnover greater than 1000 times the interstitial water $PO_4\text{-P}$ concentration due to root uptake from some sediments by both Eurasian watermilfoil and Brazilian elodea (*Egeria densa* Planch.) during a three month period of laboratory experimentation. Quillwort (*Isoetes lacustris* L.), a more robustly rooted species than the former, has been shown to alter profiles of dissolved iron and manganese in sediment (Tessenow and Baines 1978). Submersed macrophyte beds tend to accelerate sedimentation rates in lacustrine systems (Sculthorpe 1967; Gregg and Rose 1982; Carpenter 1983), which while possibly providing nutritional benefits in oligotrophic systems (Patterson and Brown 1979), can lead to changes in macrophyte community composition, and ultimately to lake aging due to sediment accumulation in eutrophic systems (Wetzel 1979; Carpenter 1981).

INORGANIC CARBON

Only in recent years has adequate attention been directed toward the importance of inorganic carbon as a nutrient limiting photosynthesis and growth of submersed macrophytes. The photosynthetic potential of a variety of submersed freshwater macrophytes appears to far exceed photosynthesis determined at ambient levels of available carbon in water (Browse et al. 1979; Beer and Wetzel 1981). This suggests that submersed macrophytes in many freshwater environments may be limited by inorganic carbon supply (Wetzel and Grace 1983). Adams et al. (1978) and Titus and Stone (1982) have demonstrated inorganic carbon limitation of photosynthesis in Eurasian watermilfoil and water celery (*Vallisneria americana* Michx.).

Whereas, the above articles describe photosynthesis (not growth) in relation to dissolved inorganic carbon, the recent work of Smart and Barko (submitted) couples increased growth with photosynthesis in Eurasian watermilfoil, under conditions of experimentally increased inorganic carbon supply.

Boundary layer resistance to CO_2 transport is known to be an important factor limiting photosynthesis in terrestrial plants, and is even more critical in submersed macrophytes since the diffusion of CO_2 in water is much slower than in air (Smith and Walker 1980). Rates of photosynthesis in submersed macrophytes have been shown experimentally to increase with moderate increase in water flow (Westlake 1967; Madsen and Søndergaard 1983). Flow velocity is one of the most important factors affecting submersed macrophytes in streams. Conditions of acute inorganic carbon depletion associated with photosynthesis in dense macrophyte beds (Van et al. 1976; Bowes et al. 1979) are probably less common in free-flowing or well mixed aquatic systems. In streams and rivers, the evolution of leaf shape, which may decrease resistance to physical disturbance, can also reduce boundary layer resistance.

Free carbon dioxide (CO_2) is generally considered to be the carbon form preferred in photosynthesis by submersed freshwater macrophytes (Steeman-Nielsen 1947; Van et al. 1976). However, in the majority of freshwater systems the largest fraction of inorganic carbon exists in the form of bicarbonate (HCO_3) ions (Hutchinson 1975; Wetzel 1983). Although the exact mechanism of bicarbonate utilization is not thoroughly understood at this time, the ecophysiological significance and taxonomic extent of bicarbonate use in photosynthesis by submersed macrophytes is well documented (Steeman-Nielsen 1947; Ruttner 1947; Sculthorpe 1967; Hutchinson 1975; Kadono 1980; Gessner 1959; Spence 1972; Moeller 1978b; Sand-Jensen and Gordon 1984).

The subject of bicarbonate use is discussed extensively in the Proceedings of the International Workshop on Bicarbonate Utilization by Photosynthetic Organisms (Berry and Williams (Eds.) 1985). Different submersed freshwater macrophyte species vary in their abilities to utilize HCO_3 in photosynthesis (Raven 1970; Kadono 1980; Allen and Spence 1981). This ability is likely to be of adaptive significance, and undoubtedly influences macrophyte species distribution (Hutchinson 1970; Hutchinson 1975; Wiegleb 1978; Pip 1979; Hellquist 1980). Various pondweed species are well-known bicarbonate users, and are common in alkaline systems. In contrast, isoetids (e.g., *Lobelia dortmanna* L.) cannot effectively use bicarbonate, and therefore occur in low alkalinity systems. Allen and Spence (1981) and Maberly and Spence (1983) have published extensive data detailing the apparent gradient among macrophytes (and algae as well) with respect to bicarbonate use.

In low alkalinity, low carbon environments the formation of four-carbon (C-4) acids during photosynthesis of some macrophyte species (e.g., hydrilla) appears to be adaptive, and is associated with a low level of photorespiration (Bowes et al. 1978; Holaday and Bowes 1980; Salvucci and Bowes 1981; Van, et al. 1976; Salvucci and Bowes 1983). In other species, e.g., Eurasian watermilfoil, a dif-

ferent mechanism (non C-4 acid dependent) involving carbonic anhydrase may be important in concentrating inorganic carbon (Salvucci and Bowes, 1983). In some rosette species (e.g., quillwort, *Littorella uniflora* L., *Crassula aquatica* (L.) Shonl., and *Isoetes* spp.), crassulacean acid metabolism (CAM) has been demonstrated to be a pathway important to the conservation of inorganic carbon (Holaday and Bowes 1980; Beer and Wetzel 1981; Keeley and Morton 1982; Boston and Adams 1983; Richardson et al. 1984).

Inorganic carbon supply to submersed macrophytes from sediment interstitial water in some cases may augment the supply of CO₂ from the overlying water. In isoetid species inorganic carbon enters the root, from which it is transported to leaf chloroplasts through an extensive network of continuous air spaces in the tissues (Wium-Anderson 1971; Sand-Jensen and Søndergaard 1978; Søndergaard and Wetzel 1980; Richardson et al. 1984). These large air spaces (gas lacunae) are also important in the recycling or "recapture" of carbon dioxide that would otherwise be lost from the plant due to respiratory or photorespiratory metabolism. The role of lacunae is critical in many circumstances, because of the limited availability of inorganic carbon in the water column (Søndergaard and Wetzel 1980; Wetzel et al. 1984). High sediment dissolved inorganic carbon, low shoot/root ratios, extensive aerenchyma, and the positioning of chloroplasts near inner surfaces of leaves all enhance the effectiveness of lacunal transport of carbon during photosynthesis. Sediment CO₂ supply via the lacunal system coupled with CAM activity provides an effective system for maximizing photosynthesis primarily by isoetids in oligotrophic systems, but may be less important in other environments or in other submersed macrophyte species (Loczy et al. 1983).

MANAGEMENT IMPLICATIONS

It was agreed at the workshop that high temperatures were conducive to the excessive growth and hastened phenological development of many species; however, thermal alterations for macrophyte management purposes are not considered economically and technologically feasible. In contrast, manipulation of light conditions can be a useful tool in the management of submersed aquatic macrophytes, since the availability of light appears to be one of the most important factors affecting macrophyte production. In British streams, for example, manipulated shade conditions obtained by varying the density of shoreline tree stands, seems to be a viable management approach (Dawson and Kern-Hansen 1977; Dawson 1978). The "half shade" concept (i.e. staggered shade conditions) was suggested at the workshop by Dawson as a means of maintaining macrophyte productivity, important to fisheries, while enhancing potential flow conditions to reduce flooding. Shade fabrics have been used in lakes to control the production of submersed macrophytes (e.g., Mayer 1978; Perkins 1980), but may be less useful in flowing water systems due to problems with anchorage. The photoreversible nature of tuber formation in hydrilla by white or red light (Van et al. 1978; Klaine and Ward 1984) suggests that manipulated photoperiod or R:FR may be

useful in reducing reproductive output and consequently seasonal regrowth in this species.

Considering the general abundance of nutrients (exclusive of inorganic carbon) in sediments and water combined, workshop participants reached general agreement that realistically attainable reductions in aqueous nutrients in most aquatic systems, although ecologically desirable, probably would not result in any significant decrease in macrophyte production. The only suggestions made to the contrary were related to observations that large quantities of macrophytes are associated in certain instances with sewage outfalls. An increase in nutrients in the open water under most circumstances would not be expected to increase macrophyte production, and in fact might depress macrophyte production due to shading by phytoplankton and epiphytes.

Attempts at controlling nutrients have been directed primarily at phosphorus, because of the widespread acceptance of the relationship between P loading and phytoplankton density (Vollenweider 1976; Schindler 1977). This relationship, however, does not apply to rooted macrophytes, because of their significant access to P in sediments. Since phytoplankton obtain their nutrients exclusively from the water column, the first response to P control in the water can be expected to be a reduction in phytoplankton, with a possibly concomitant increase in macrophytes due to improved water clarity. In any event, the regulation of aqueous nutrient levels in aquatic systems is not considered a useful management tool for controlling rooted submersed macrophytes.

Information related to the ecology of aquatic macrophytes, particularly with respect to nutrition, has accumulated to the extent that conclusions and recommendations from only a few years ago are undergoing rapid change. For example, at an earlier conference held in Madison, WI (cf. Proceedings edited by Breck et al. 1979), it was concluded that macrophyte harvesting would substantially reduce the phosphorus content of lakes. Participants at that conference foresaw an increased, widespread application of harvesting technology for mitigating lake eutrophication. Participants at the 1984 Lake George workshop concluded differently, however, expressing the opinion that although harvesting did improve recreational value, nutrients in aquatic systems could not be effectively managed through plant harvesting alone. Indeed, Carpenter and Adams (1977) earlier demonstrated that wholesale harvesting of the one-time extensive Eurasian watermilfoil community of eutrophic Lake Wingra could be expected to manipulate only a small fraction of the lake's metabolically active nutrient pool and remove only about a third of the annual input of phosphorus from the drainage basin.

Perhaps due to earlier controversy concerning the relative importance of carbon vs. phosphorus as factors limiting phytoplankton productivity (Likens 1972), carbon has been considered as something other than a nutrient. Inorganic carbon, however, is a nutrient, and in considering the frequently high availability of other nutrients to submersed macrophytes, workshop participants agreed that in many freshwater systems inorganic carbon potentially limits macrophyte growth. In support of this view, Wetzel

and Grace (1983) postulated a doubling of submersed macrophyte productivity in lakes, in response to a doubling in atmospheric CO₂ concentration anticipated during the next 100 years. Workshop participants also agreed that carbon limitation was primarily related to slow CO₂ diffusion rates in water and to boundary layer resistance at leaf surfaces. Accordingly, inorganic carbon may be less limiting to submersed macrophytes in flowing water systems than in most lakes, since relatively greater turbulence in the former can be expected to increase diffusion and decrease boundary layer resistance.

Management of macrophytes by the manipulation of inorganic carbon supply does not appear to be a feasible technique for present application. Rather, it is more appropriate to recognize that inorganic carbon supply in aquatic systems constitutes an intrinsic component of the regional environment, controlled by local geology, hydrology, and watershed use. It is most useful to consider the inorganic carbon level of a system as providing a limit on the range of macrophyte productivity and species composition that can be attained.

Sediment composition is also an intrinsic component of the regional environment, but in contrast with inorganic carbon, is more amenable to manipulation. Various sediment covers, including sand, gravel, and plastic liners have been used in attempts to control the production of submersed macrophytes by altering sediment texture and reducing sediment nutrient uptake (Engel and Nichols 1984). Alternatively, dredging has been employed to both remove nutrient-rich sediments (Peterson 1982; Nichols 1984) and to expose nutrient-poor underlying substrata, e.g. sand and gravel (Engel and Nichols op. cit.). Considered collectively, these efforts have indicated some reductions in macrophyte productivity, and in nearly all cases, dramatic shifts in the species composition of submersed macrophyte communities. These results underscore the important, but as yet incompletely understood, connection between submersed macrophyte production, species composition, and sediment properties.

MANAGEMENT PERSPECTIVES

Prior to the implementation of management procedures designed to modify aquatic macrophyte production or community composition, it is necessary to be fully cognizant of the localized role of growth-regulating factors. Generalizations may not apply in particular aquatic systems. Therefore, different management approaches may be required in different places. Another important consideration, which should influence the selection of management approaches, is system use. For example, management procedures designed to enhance flow (flooding avoidance, etc.) may not be compatible with fisheries goals; habitat manipulation for fish and wildlife purposes may not be in concert with those for hydraulic purposes. Management procedures directed toward aquatic plant eradication are generally ill-advised, not only on ecological grounds, but also because many aquatic systems serve multiple purposes, with consequently severe constraints on control options (I. M. Johnstone, personal communication). Recognition of the positive as well as the negative contributions of aquatic vegetation should underscore the development of rational

management approaches implemented on a regional basis.

There are no simple universal solutions to the problems of excessive macrophyte growth in aquatic systems; rather, specific needs have to be addressed. Participants at the workshop agreed that aquatic plant management in the past has been unwisely directed almost exclusively toward short-term solutions. Energies should be redirected toward the attainment of long-term solutions to aquatic plant problems, with attention given to adequate conservation of the diverse aquatic habitats containing submersed aquatic vegetation. Questions related to the response of fish and other wildlife to vegetative manipulations need to be more thoroughly addressed, with local needs considered in establishing management goals. An integrated approach to aquatic plant problems should be implemented at every step in the management process and in the development of related research goals. Particularly troublesome in the past has been the problem of public ignorance in relation to the role and importance of aquatic macrophytes and to the real difficulties encountered in implementing long term solutions to aquatic macrophyte problems. To counter this trend, appropriate information campaigns need to be developed and implemented. The level of communication among universities, government, industry, and the general public needs to be increased.

ACKNOWLEDGMENTS

We wish to acknowledge a grant to Rensselaer Polytechnic Institute from the Soap and Detergent Association for the conduct of an international "Submersed Macrophytes Workshop," October 18, 19 and 20, 1984 at the Canoe Island Lodge on Lake George (N.Y.). Invited participants were Michael Adams, John Barko, Charles Boylen, Nicholas Clesceri, George Bowes, F. Hugh Dawson, Patrick Denny, Sylvia Haslam, Jacob Kalff, Mahlon Kelly, Stanley Nichols, Kaj Sand-Jensen, Richard Sparks, David Spence, John Titus, Derek Westlake and Robert Wetzel. Invited observers were Larry Eichler, John Madsen, Gordon Robertson, Roy Stein, Laura Tangle, and Alan Wentz. Planning for the workshop was a joint endeavor of Michael Adams, John Barko and Nicholas Clesceri. Lars Anderson, Kurt Getsinger, Gordon Godshalk, Thomas Hart and R. Michael Smart reviewed an earlier draft of this article. Support for manuscript preparation and publication was provided by the U.S. Army Corps of Engineers' Aquatic Plant Control Research Program.

LITERATURE CITED

- Adams, M., S. Guilizzoni, and S. Adams. 1978. Relationship of dissolved inorganic carbon to macrophyte photosynthesis in some Italian lakes. *Limnol. Oceanogr.* 23:912-913.
- Adams, M. S., J. E. Titus, and M. D. McCracken. 1974. Depth distribution of photosynthetic activity in a *Myriophyllum spicatum* community in Lake Wingra. *Limnol. Oceanogr.* 19:377-389.
- Allen, E. D. and R. R. Gorham. 1973. Changes in the submerged macrophyte communities of Lake Wabamung as a result of thermal discharge. *Proc. Symp. Lks. W. Can., Univ. Alberta, Edmonton.* pp. 313-324.
- Allen, E. D. and D. H. N. Spence. 1981. The differential ability of aquatic plants to utilize the inorganic carbon supply in fresh waters. *New Phytol.* 87:269-283.

- Anderson, R. R. 1969. Temperature and rooted aquatic plants. *Chesapeake Sci.* 10:157-164.
- Barko, J. W. 1982. Influence of potassium source (sediment vs. open water) and sediment composition on the growth and nutrition of a submersed freshwater macrophyte [*Hydrilla verticillata* (L.f.) Royle]. *Aquat. Bot.* 12:157-172.
- Barko, J. W. 1983. The growth of *Myriophyllum spicatum* L. in relation to selected characteristics of sediment and solution. *Aquat. Bot.* 15:91-103.
- Barko, J. W. and G. J. Filbin. 1983. Influences of light and temperature on chlorophyll composition in submersed freshwater macrophytes. *Aquat. Bot.* 15:249-255.
- Barko, J. W., D. G. Hardin, and M. S. Matthews. 1982. Growth and morphology of submersed freshwater macrophytes in relation to light and temperature. *Can. J. Bot.* 60:877-887.
- Barko, J. W. and R. M. Smart. 1980. Mobilization of sediment phosphorus by submersed freshwater macrophytes. *Freshwat. Biol.* 10:229-238.
- Barko, J. W. and R. M. Smart. 1981a. Comparative influences of light and temperature on the growth and metabolism of selected submersed freshwater macrophytes. *Ecol. Monogr.* 51:219-235.
- Barko, J. W. and R. M. Smart. 1981b. Sediment-based nutrition of submersed macrophytes. *Aquat. Bot.* 10:339-352.
- Barko, J. W. and R. M. Smart. 1983. Effects of organic matter additions to sediment on the growth of aquatic plants. *J. Ecol.* 71:161-175.
- Bayley, S., V. D. Stotts, P. F. Springer, and J. Steenis. 1978. Changes in submersed aquatic macrophyte populations at the head of the Chesapeake Bay, 1958-1975. *Estuaries* 1:73-84.
- Beer, S. and R. G. Wetzel. 1981. Photosynthetic carbon metabolism in the submersed aquatic angiosperm *Scirpus subterminalis*. *Pl. Sci. Lett.* 21:199-207.
- Berry, J. and L. Williams (Eds.). 1985. Proceedings of the International Workshop on Bicarbonate Utilization by Photosynthetic Organisms (tentative title). *Am. Soc. of Plant Physiol.* Waverly Press, Baltimore (in press).
- Best, M. D. and K. E. Mantai. 1978. Growth of *Myriophyllum*: sediment or lake water as the source of nitrogen and phosphorus. *Ecology* 59:1075-1080.
- Blotnick, J. R., J. Rho, and H. B. Gunner. 1980. Ecological characteristics of rhizosphere microflora of *Myriophyllum heterophyllum*. *J. Environ. Qual.* 9:209-210.
- Bodkin, P. C., D. H. N. Spence, and D. C. Weeks. 1980. Photoreversible control of heterophylly in *Hippuris vulgaris* L. *New Phytol.* 84:533-542.
- Bole, J. B. and J. R. Allan. 1978. Uptake of phosphorus from sediment by aquatic plants, *Myriophyllum spicatum* and *Hydrilla verticillata*. *Wat. Res.* 12:353-358.
- Boston, H. L. and M. S. Adams. 1983. Evidence of crassulacean acid metabolism in two North American isoetids. *Aquat. Bot.* 15:381-386.
- Bowes, G., A. S. Holaday, and W. T. Haller. 1979. Seasonal variation in the biomass, tuber density, and photosynthetic metabolism of *Hydrilla* in three Florida lakes. *J. Aquat. Plant Manage.* 17:61-65.
- Bowes, G. A., A. S. Holaday, T. K. Van, and W. T. Haller. 1978. Photosynthetic and photorespiratory carbon metabolism in aquatic plants. *Proc. 4th Internat. Congr. Photosyn., Biochem. Soc., London.* pp. 289-298.
- Bowes, G., T. K. Van, L. A. Garrard, and W. T. Haller. 1977. Adaptation to low light levels by *Hydrilla*. *J. Aquat. Plant Manage.* 15:32-35.
- Breck, J. E., R. T. Prentki, and O. L. Loucks (Eds.). 1979. *Aquatic Plants, Lake Management, and Ecosystem Consequences of Lake Harvesting.* Proc. Conf. Madison, WI, Feb. 1979. Institute for Environmental Studies, Univ. Wisconsin-Madison. 435 pp.
- Bristow, J. M. and M. Whitcombe. 1971. The role of roots in the nutrition of aquatic vascular plants. *Am. J. Bot.* 58:8-13.
- Browse, J. A., F. I. Dromgoole, and J. M. A. Brown. 1979. Photosynthesis in the aquatic macrophyte *Egeria densa*. III. Gas exchange studies. *Aust. J. Pl. Physiol.* 6:499-512.
- Capone, D. G. 1982. Nitrogen fixation (acetylene reduction) by rhizosphere sediments of the eelgrass *Zostera marina*. *Mar. Ecol. Prog. Ser.* 10:67-75.
- Carignan, R. and J. Kalf. 1979. Quantification of the sediment phosphorus available to aquatic macrophytes. *J. Fish. Res. Bd. Can.* 36:1002-1005.
- Carignan, R. and J. Kalf. 1980. Phosphorus sources for aquatic weeds: water or sediment? *Science* 207:987-989.
- Carpenter, S. R. 1980a. The decline of *Myriophyllum spicatum* in a eutrophic Wisconsin lake. *Can. J. Bot.* 58:527-535.
- Carpenter, S. R. 1980b. Enrichment of Lake Wingra, Wisconsin, by submersed macrophyte decay. *Ecology* 61:1145-1155.
- Carpenter, S. R. 1981. Submersed vegetation: an internal factor in lake ecosystems succession. *Am. Nat.* 118:372-383.
- Carpenter, S. R. 1983. Submersed macrophyte community structure and internal loading: relationship to lake ecosystem productivity and succession. *In: Taggart, J. (Ed.) Lake Restoration, Protection, and Management.* U.S. Environmental Protection Agency, Washington, DC. pp. 105-111.
- Carpenter, S. R. and M. S. Adams. 1977. The macrophyte tissue nutrient pool of a hardwater eutrophic lake: implications for macrophyte harvesting. *Aquat. Bot.* 3:239-255.
- Carpenter, S. R., J. J. Elser, and K. M. Olson. 1983. Effects of roots of *Myriophyllum verticillatum* L. on sediment redox conditions. *Aquat. Bot.* 17:243-249.
- Chambers, P. A. 1982. Light, temperature and the induction of dormancy in *Potamogeton crispus* and *Potamogeton obtusifolius*. Ph.D. thesis. University of St. Andrews.
- Chambers, P. A. and D. H. N. Spence. 1984. Diurnal changes in the ratio of underwater red to far red light in relation to aquatic plant photoperiodism. *J. Ecol.* 72:495-503.
- Clayton, J. S. and D. J. Bagyaraj. 1984. Vesicular-arbuscular mycorrhizas in submerged aquatic plants of New Zealand. *Aquat. Bot.* 19:251-262.
- Cooke, G. D. 1980. Lake level drawdown as a macrophyte control technique. *Wat. Res. Bull.* 16:317-322.
- Craven, P. A. and S. S. Hayasaka. 1982. Inorganic phosphate solubilization by rhizosphere bacteria in a *Zostera marina* community. *Can. J. Microbiol.* 28:605-610.
- Dawson, F. H. 1978. Aquatic plant management in semi-natural streams: the role of marginal vegetation. *J. Envir. Manage.* 6:213-221.
- Dawson, F. H. and U. Kern-Hansen. 1977. Aquatic weed management in natural streams; the effect of shade by marginal vegetation. *Proc. 10th Congr. Int. Ver. Theor. Angew. Limnol.* Copenhagen. pp. 1451-1456.
- DeMarte, J. A. and R. T. Hartman. 1974. Studies on absorption of ³²P, ⁵⁹Fe and ⁴⁵Ca by water milfoil (*Myriophyllum exalbescens*, Fernald). *Ecology* 55:188-194.
- Denny, P. 1980. Solute movement in submerged angiosperms. *Biol. Rev.* 55:65-92.
- Dooris, P. M. and D. F. Martin. 1981. Growth inhibition of *Hydrilla verticillata* by selected lake sediment extracts. *Wat. Res. Bull.* 16:112-117.
- Drew, M. C. and J. M. Lynch. 1980. Soil anaerobiosis, microorganisms, and root function. *Annu. Rev. Phytopathol.* 18:37-66.
- Dunst, R. C., S. M. Born, P. D. Uttormark, S. A. Smith, S. A. Nichols, J. O. Peterson, R. D. K. Knauer, S. L. Serns, D. R. Winter, and T. L. Wirth. 1974. *Survey of Lake Rehabilitation Techniques and Experiences.* Technical Bulletin No. 75. Wisconsin Department of Natural Resources, Madison. 179 pp.
- Engel, S. and S. Nichols. 1984. Lake sediment alteration for macrophyte control. *J. Aquat. Plant Manage.* 22:38-41.
- Frank, P. A. and N. Dechoretz. 1980. Allelopathy in Dwarf Spikerush (*Elodea coloradoensis*). *J. Weed Sci.* 28:499-505.
- Gabrielson, J. O., M. A. Perkins, and E. B. Welch. 1984. The uptake, translocation and release of phosphorus by *Elodea densa*. *Hydrobiologia* 111:43-48.
- Gessner, F. 1959. *Hydrobotanik 2. Stoffhaushalt.* VEB Deutscher Verlag der Wissenschaften, Berlin. 701 pp.
- Gregg, W. W. and F. L. Rose. 1982. The effects of aquatic macrophytes on the stream microenvironment. *Aquat. Bot.* 14:309-324.
- Haag, R. W. and P. R. Gorham. 1977. Effects of thermal effluent on standing crop and net production of *Elodea canadensis* and other submerged macrophytes in Lake Wabamung, Alberta. *J. Appl. Ecol.* 14:835-851.
- Haller, W. T. and D. L. Sutton. 1975. Community structure and competition between *Hydrilla* and *Vallisneria*. *Hyacinth Contr. J.* 13:48-50.
- Haller, W. T., D. L. Sutton, and W. C. Barlowe. 1974. Effects of salinity on growth of several aquatic macrophytes. *Ecology* 55:891-894.
- Haller, W. T., J. L. Miller, and L. A. Garrard. 1976. Seasonal production and germination of hydrilla vegetative propagules. *J. Aquat. Plant Manage.* 14:26-28.
- Haslam, S. M. 1978. *River Plants.* Cambridge Univ. Press, Cambridge. 396 pp.
- Hellquist, C. B. 1980. Correlation of alkalinity and the distribution of *Potamogeton* in New England. *Rhodora* 82:331-344.
- Hewitt, E. J. and T. A. Smith. 1975. *Plant Mineral Nutrition.* Halsted Press, Division of John Wiley and Sons, Inc., New York. 298 pp.

- Holaday, A. S. and G. Bowes. 1980. C₄ acid metabolism and dark CO₂-fixation in a submersed macrophyte (*Hydrilla verticillata*). *Plant Physiol.* 65:331-335.
- Howard-Williams, C. and M. R. M. Liptrot. 1980. Submerged macrophyte communities in a brackish South African estuarine—lake system. *Aquat. Bot.* 9:101-116.
- Huebert, D. B. and P. R. Gorham. 1983. Biphasic mineral nutrition of the submersed aquatic macrophyte *Potamogeton pectinatus* L. *Aquat. Bot.* 16:269-284.
- Hutchinson, G. E. 1970. The chemical ecology of three species of *Myriophyllum* (Angiospermae, Haloragaceae). *Limnol. Oceanogr.* 15:1-5.
- Hutchinson, G. E. 1975. A Treatise on Limnology. III. Aquatic Macrophytes and Attached Algae. John Wiley and Sons, New York. 660 pp.
- Ikusima, I. 1965. Ecological studies on the productivity of aquatic plant communities 1. Measurement of photosynthetic activity. *Bot. Mag. Tokyo* 78:202-211.
- Ikusima, I. 1966. Ecological studies on the productivity of aquatic plant communities 2. Seasonal changes in standing crop and productivity of a natural submerged community of *Vallisneria spiralis*. *Bot. Mag. Tokyo* 79:7-19.
- Jones, R. 1975. Comparative studies of plant growth and distribution in relationship to waterlogging. VIII. The uptake of phosphorus by dune and dune slack plants. *J. Ecol.* 63:109-116.
- Jones, R. C., K. Walti, and M. S. Adams. 1983. Phytoplankton as a factor in decline of the submersed macrophyte *Myriophyllum spicatum* L. in Lake Wingra, Wisconsin. *Hydrobiologia* 107:213-219.
- Jupp, B. P. and D. H. N. Spence. 1977. Limitations on macrophytes in a eutrophic lake, Lock Leven. I. Effects of phytoplankton. *J. Ecol.* 65:175-186.
- Kadono, Y. 1980. Photosynthetic carbon sources in some *Potamogeton* species. *Bot. Mag. Tokyo* 93:185-194.
- Keeley, J. E. and B. A. Morton. 1982. Distribution of diurnal acid metabolism in submerged aquatic plants outside the genus *Isoetes*. *Photosynthetica* 16:546-553.
- Kemp, W. M., W. R. Boynton, R. R. Twilley, J. C. Stevenson, and J. Means. 1983. The decline of submerged vascular plants in upper Chesapeake Bay: summary of results concerning possible causes. *Mar. Sci. Tech.* 17:78-89.
- Kjørboe, T. 1980. Distribution and production of submerged macrophytes in Tipper Grund (Ringkøbing Fjord, Denmark), and the impact of waterfowl grazing. *J. Appl. Ecol.* 17:675-687.
- Klaine, S. J. and C. H. Ward. 1984. Environmental and chemical control of vegetative dormant bud production in *Hydrilla verticillata*. *Ann. Botany* 53:503-514.
- Kullberg, R. G. 1974. Distribution of aquatic macrophytes related to papermill effluents in a southern Michigan stream. *Am. Midl. Nat.* 91:271-281.
- Likens, G. E. (Ed.) 1972. Nutrients and Eutrophication: the Limiting-Nutrient Controversy. Special Symp., Amer. Soc. Limnol. Oceanogr. 1, 328 pp.
- Loczy, S., R. Carignan, and D. Planas. 1983. The role of roots in carbon uptake by the submersed macrophytes *Myriophyllum spicatum*, *Vallisneria spiralis*, and *Heteranthera dubia*. *Hydrobiologia* 98:3-7.
- Lowenhaupt, B. 1956. The transport of calcium and other cations in submerged aquatic plants. *Biol. Rev.* 31:371-395.
- Lucas, W. J. and J. Dainty. 1977. HCO₃ influx across the plasmalemma of *Chara corallina*: divalent cation requirement. *Plant Physiol.* 60:862-867.
- Maberly, S. C. and D. H. N. Spence. 1983. Photosynthetic inorganic carbon use by freshwater plants. *J. Ecol.* 71:705-724.
- Madsen, T. V. and M. Søndergaard. 1983. The effects of current velocity on the photosynthesis of *Callitriche stagnalis* Scop. *Aquat. Bot.* 15:187-193.
- Mayer, R. J. 1978. Aquatic weed management by benthic semi-barriers. *J. Aquat. Plant Manage.* 16:31-33.
- McCreary, N. J., S. R. Carpenter and J. E. Chaney. 1983. Coexistence and interference in two submersed freshwater perennial plants. *Oecologia* 59:393-396.
- McMillan, C. and R. C. Phillips. 1979. Differentiation in habitat response among populations of new world seagrasses. *Aquat. Bot.* 7:185-196.
- McRoy, C. P., R. J. Barsdate, and J. Nebert. 1972. Phosphorus cycling in an eelgrass (*Zostera marina* L.) ecosystem. *Limnol. Oceanogr.* 17:58-67.
- Mirsa, R. D. 1938. Edaphic factors in the distribution of aquatic plants in the English Lakes. *J. Ecol.* 26:411-451.
- Moeller, R. E. 1978a. Seasonal changes in biomass, tissue chemistry, and net production of the evergreen hydrophyte, *Lobelia dortmanna*. *Can. J. Bot.* 56:1425-1433.
- Moeller, R. E. 1978b. Carbon uptake by the submersed hydrophyte *Utricularia purpurea*. *Aquat. Bot.* 5:209-216.
- Moeller, R. E. 1980. The temperature-determined growing season of a submerged hydrophyte: tissue chemistry and biomass turnover of *Utricularia purpurea*. *Freshwat. Biol.* 10:391-400.
- Mortimer, C. H. 1971. Chemical exchanges between sediments and water in the Great Lakes—speculations on probable regulatory mechanisms. *Limnol. Oceanogr.* 16:387-404.
- Moyle, J. B. 1945. Some chemical factors influencing the distribution of aquatic plants in Minnesota. *Am. Midl. Nat.* 34:402-420.
- Nichols, D. J. and D. R. Keeney. 1976a. Nitrogen nutrition of *Myriophyllum spicatum*: variation of plant tissue nitrogen concentration with season and site in Lake Wingra. *Freshwat. Biol.* 6:137-144.
- Nichols, D. J. and D. R. Keeney. 1976b. Nitrogen nutrition of *Myriophyllum spicatum*: uptake and translocation of ¹⁵N by shoots and roots. *Freshwat. Biol.* 6:145-154.
- Nichols, S. A. 1984. Macrophyte community dynamics in a dredged Wisconsin Lake. *Wat. Res. Bull.* 20:573-576.
- Nichols, S. A. and B. H. Shaw. 1983. Physical, chemical, and biological control of aquatic macrophytes. Lake Restoration, Protection and Management. Proc. 2nd Ann. Conf. N. Amer. Lk. Manage. Soc., Oct. 1982, Vancouver, British Columbia. EPA 404/5-83-001. U.S. Environmental Protection Agency, Washington, DC. pp. 181-192.
- Orth, R. J. and K. A. Moore. 1983. Chesapeake Bay: an unprecedented decline in submerged vegetation. *Science* 222:51-53.
- Ozimek, T. 1978. Effect of municipal sewage on the submerged macrophytes of a lake littoral. *Ekol. Pol.* 26:3-39.
- Patterson, K. J. and J. M. A. Brown. 1979. Growth and elemental composition of the aquatic macrophyte *Lagarosiphon major*, in response to water and substrate nutrients. *Prog. Wat. Tech.* 2:231-246.
- Pearsall, W. H. 1920. The aquatic vegetation of the English Lakes. *J. Ecol.* 8:163-199.
- Pearsall, W. H. and A. M. Hanby. 1925. The variation of leaf form in *Potamogeton perfoliatus*. *New Phytol.* 24:112-120.
- Peltier, W. H. and E. B. Welch. 1970. Factors affecting growth of rooted aquatic plants in a reservoir. *Weed Sci.* 18:7-9.
- Penhale, P. A. and R. G. Wetzel. 1983. Structural and functional adaptations of eelgrass (*Zostera marina* L.) to the anaerobic sediment environment. *Can. J. Bot.* 61:1421-1428.
- Pennak, R. W. 1971. Toward a classification of lotic habitats. *Hydrobiologia* 38:321-334.
- Perkins, M. A. 1980. Managing aquatic plants with fiberglass screen. Proc. Int. Symp. Restoration of Lakes and Inland Waters. EPA 440/5-81-010. U.S. Environmental Protection Agency, Washington, DC. pp. 245-248.
- Peterson, S. A. 1982. Lake restoration by sediment removal. *Wat. Res. Bull.* 18:423-425.
- Pevery, J. H. and J. Brittain. 1978. Effect of Milfoil (*M. spicatum* L.) on phosphorus movement between sediment and water. *J. Great Lakes Res.* 4:62-68.
- Phillips, G. L., D. Eminson, and B. Moss. 1978. A mechanism to account for macrophyte decline in progressively eutrophicated freshwaters. *Aquat. Bot.* 4:103-126.
- Pip, E. 1979. Survey of the ecology of submerged aquatic macrophytes in central Canada. *Aquat. Bot.* 7:339-357.
- Pond, R. H. 1905. The relation of aquatic plants to the substratum. Rpt. U.S. Fish. Comm. 19:483-526.
- Ponnamperuma, F. N. 1972. The chemistry of submerged soils. *Adv. Agron.* 24:29-96.
- Prentki, R. T. 1979. Depletion of phosphorus from sediment colonized by *Myriophyllum spicatum* L. In: Breck, J. E., R. T. Prentki, and O. L. Loucks (Eds.). Aquatic Plants, Lake Management, and Ecosystem Consequences of Lake Harvesting. Proc. Conf. Madison, WI, Feb. 1979. Institute for Environmental Studies, Univ. Wisconsin-Madison. pp. 161-176.
- Raven, J. A. 1970. Exogenous inorganic carbon sources in plant photosynthesis. *Biol. Rev.* 45:167-221.
- Richardson, K., H. Griffiths, M. L. Reed, J. A. Raven, and N. M. Griffiths. 1984. Inorganic carbon assimilation in the isoetids, *Isoetes lacustris* L. and *Lobelia dortmanna* L. *Oecologia* 61:115-121.

- Robert, R. J. 1961. Water depth and turbidity in relation to growth of sago pond weed. *J. Wildl. Mgmt.* 25:436-438.
- Ruttner, F. 1947. Zur Frage der Karbonat-Assimilation der Wasserpflanzen I. Die beide Haupttypen der Kohlenstoffaufnahme. *Oester. Bot. Z.* 94:265-294.
- Ruttner, F. 1963. *Fundamentals of Limnology.* (Translat. D. G. Frey and R. E. J. Fry). Toronto, Univ. Toronto Press. 295 pp.
- Salvucci, M. E. and G. Bowes. 1981. Induction of reduced photorespiratory activity in submersed and amphibious aquatic macrophytes. *Plant Physiol.* 67:335-340.
- Salvucci, M. E. and G. Bowes. 1983. Two photosynthetic mechanisms mediating the low photorespiratory state in submersed aquatic angiosperms. *Plant Physiol.* 73:488-496.
- Sanderson, P. L. and W. Armstrong. 1980. Phytotoxins in periodically waterlogged forest soil. *J. Soil Sci.* 31:643-653.
- Sand-Jensen, K. 1977. Effect of epiphytes on eelgrass photosynthesis. *Aquat. Bot.* 3:55-63.
- Sand-Jensen K. and D. M. Gordon. 1984. Differential ability of marine and freshwater macrophytes to utilize HCO_3^- and CO_2 . *Mar. Biol.* 80:247-253.
- Sand-Jensen, K. and M. Søndergaard. 1978. Growth and production of isoetids in oligotrophic Lake Kalgaard, Denmark. *Verh. Internat. Verein. Limnol.* 20:659-666.
- Sand-Jensen, K. and M. Søndergaard. 1979. Distribution and quantitative development of aquatic macrophytes in relation to sediment characteristics in oligotrophic Lake Kalgaard, Denmark. *Freshwat. Biol.* 9:1-11.
- Sand-Jensen, K. and M. Søndergaard. 1981. Phytoplankton and epiphyte development and their shading effect on submerged macrophytes in lakes of different nutrient status. *Int. Revue Ges. Hydrobiol.* 66:529-552.
- Sastroutomo, S. S. 1980. Environmental control of turion formation in curly pondweed (*Potamogeton crispus*). *Physiol. Plant.* 49:261-264.
- Sastroutomo, S. S. 1981. Turion formation, dormancy, and germination of curly pondweed (*Potamogeton crispus* L.). *Aquat. Bot.* 10:161-173.
- Schindler, D. W. 1977. Evolution of phosphorus limitation in lakes: natural mechanisms compensate for deficiencies of nitrogen and carbon in eutrophied lakes. *Science* 195:260-262.
- Sculthorpe, C. D. 1967. *The Biology of Aquatic Vascular Plants.* Arnold, London. 610 pp.
- Smart, R. M. and J. W. Barko. 1985. Laboratory culture of submersed freshwater macrophytes on natural sediments. *Aquat. Bot.* 21:251-263.
- Smith, F. A. and N. A. Walker. 1980. Photosynthesis by aquatic plants: effects of unstirred layers in relation to assimilation of CO_2 and HCO_3^- and to carbon isotopic discrimination. *New Phytol.* 86:245-259.
- Smith, G. W. and S. S. Hayasaka. 1982a. Nitrogenase activity associated with *Halodule wrightii* roots. *Appl. Environ. Microbiol.* 43:1244-1248.
- Smith, G. W. and S. S. Hayasaka. 1982b. Nitrogenase activity associated with *Zostera marina* from a North Carolina estuary. *Can. J. Microbiol.* 28:448-451.
- Smith, G. W., S. S. Hayasaka, and G. W. Thayer. 1984. Ammonification of amino acids by the rhizoplane microflora of *Zostera marina* L. and *Halodule wrightii* Aschers. *Bot. Mar.* 27:23-27.
- Søndergaard, M. and S. Laegaard. 1977. Vesicular-arbuscular mycorrhiza in some aquatic vascular plants. *Nature* 268:232-233.
- Søndergaard, M. and R. G. Wetzel. 1980. Photorespiration and internal recycling of CO_2 in the submersed angiosperm *Scirpus subterminalis* Torr. *Can. J. Bot.* 58:591-598.
- Spence, D. H. N. 1967. Factors controlling the distribution of freshwater macrophytes, with particular reference to Scottish lochs. *J. Ecol.* 55:147-170.
- Spence, D. H. N. 1972. Light on freshwater macrophytes. *Bot. Soc. Edinb. Trans.* 41:491-505.
- Spence, D. H. N. 1976. Light and plant response in freshwater. *In:* Evans, R. B. and O. Rockham (Eds.). *Light as an Ecological Factor: II.* 16th Symp. Brit. Ecol. Soc., Mar. 1974. Blackwell Scientific Publications, Oxford. pp. 93-133.
- Spence, D. H. N., R. M. Campbell, and J. Chrystal. 1973. Specific leaf areas and zonation of freshwater macrophytes. *J. Ecol.* 61:317-328.
- Spence, D. H. N. and J. Chrystal. 1970a. Photosynthesis and zonation of freshwater macrophytes. I. Depth distribution and shade tolerance. *New Phytol.* 69:205-215.
- Spence, D. H. N. and J. Chrystal. 1970b. Photosynthesis and zonation of freshwater macrophytes. II. Adaptability of species of deep and shallow water. *New Phytol.* 69:217-227.
- Spence, D. H. N. and H. M. Dale. 1978. Variations in the shallow water form of *Potamogeton richardsonii* induced by some environmental factors. *Freshwat. Biol.* 8:251-268.
- Steemann-Nielsen, E. 1947. Photosynthesis of aquatic plants with special reference to the carbon sources. *Dansk Bot. Ark.* 12:5-71.
- Swindale, D. N. and J. T. Curtis. 1957. Phyto-sociology of the larger submerged plants in Wisconsin lakes. *Ecology* 38:397-407.
- Tessenow, V. and Y. Baines. 1978. Experimental effects of *Isoetes lacustris* L. on the distribution of E_h , pH, Fe, and Mn in lake sediment. *Int. Ver. Theor. Angew. Limnol. Verh.* 20:2358-2362.
- Titus, J. E. and M. S. Adams. 1979. Coexistence and the comparative light relations of the submersed macrophytes *Myriophyllum spicatum* L. and *Vallisneria americana* Michx. *Oecologia* 40:273-286.
- Titus, J., R. A. Goldstein, M. S. Adams, J. B. Mankin, R. V. O'Neill, P. R. Weiler, Jr., H. H. Shugart, and R. S. Booth. 1975. A production model for *Myriophyllum spicatum* L. *Ecology* 56:1129-1138.
- Titus, J. E. and W. H. Stone. 1982. Photosynthetic response of two submersed macrophytes to dissolved inorganic carbon concentration and pH. *Limnol. Oceanogr.* 27:151-160.
- Tobiessen, P. and P. Snow. 1985. Temperature, light, and substrate effects on the growth of *Potamogeton crispus* L. in Collins Lake. *Can. J. Bot.* (in press).
- Toetz, D. W. 1974. Uptake and translocation of ammonia by freshwater hydrophytes. *Ecology* 55:199-201.
- Van, T. K., W. T. Haller, and G. Bowes. 1976. Comparison of the photosynthetic characteristics of three submersed aquatic plants. *Plant Physiol.* 58:761-768.
- Van, T. K., W. T. Haller, and L. A. Garrard. 1978. The effect of day-length and temperature on hydrilla growth and tuber production. *J. Aquat. Plant Manage.* 16:57-59.
- Vollenweider, R. A. 1976. Advances in defining critical loading levels for phosphorus in lake eutrophication. *Mem. Ist. Ital. Idrobiol.* 33:53-83.
- Welsh, R. P. H. and P. Denny. 1979. The translocation of ^{32}P in two submerged aquatic angiosperm species. *New Phytol.* 82:645-656.
- Westlake, D. F. 1967. Some effects of low velocity current on the metabolism of aquatic macrophytes. *J. Exp. Bot.* 18:187-205.
- Westlake, D. F. 1971. Water plants and the aqueous environment. *Biol. Human Affairs* 36:10.
- Westlake, D. F. 1981. Temporal changes in aquatic macrophytes and their environment. *Dynamique de Populations et Qualite' de L'Eau.* pp. 110-138.
- Westlake, D. F. 1982. Ecology-community metabolism and production: the primary productivity of water plants. *In:* Symoens, J. J., S. S. Hooper, and P. Compère (Eds.). *Studies on Aquatic Vascular Plants.* Royal Botanical Society of Belgium, Brussels. pp. 165-180.
- Wetzel, R. G. 1979. The role of the littoral zone and detritus in lake metabolism. *Arch. Hydrobiol.* 13:145-161.
- Wetzel, R. G. 1983. *Limnology.* W. B. Saunders, Philadelphia. 767 pp.
- Wetzel, R. G., E. S. Brammer, and C. Forsberg. 1984. Photosynthesis of submersed macrophytes in acidified lakes. I. Carbon fluxes and recycling of CO_2 in *Juncus bulbosus* L. *Aquat. Bot.* 19:329-342.
- Wetzel, R. G. and J. B. Grace. 1983. Aquatic plant communities. *In:* Lemon, E. R. (Ed.). *CO_2 and Plants.* AAAS Selected Symp. Series. Westview Press, Inc. Boulder. pp. 223-280.
- Wetzel, R. G. and R. A. Hough. 1973. Productivity and role of aquatic macrophytes in lakes. An assessment. *Pol. Arch. Hydrobiol.* 20:9-19.
- Wiegand Von, G. 1978. Untersuchungen über den Zusammenhang zwischen hydrochemischen Umweltfaktoren und Makrophytenvegetation in stehenden Gewässern. *Arch. Hydrobiol.* 83:443-484.
- Wiginton, J. R. and C. McMillan. 1979. Chlorophyll composition under controlled light conditions as related to the distribution of seagrasses in Texas and the U.S. Virgin Islands. *Aquat. Bot.* 6:171-184.
- Wiley, M. J., R. W. Gorden, S. W. Waite, and T. Powless. 1984. The relationship between aquatic macrophytes and sport fish production in Illinois ponds: a sample model. *N. Am. J. Fish. Mgmt.* 4:111-119.
- Wium-Anderson, S. 1971. Photosynthetic uptake of free CO_2 by the roots of *Lobelia dortmanna*. *Physiol. Pl.* 25:245-248.
- Yeo, R. R. and J. R. Thurston. 1984. The effect of Dwarf Spikerush (*Eleocharis coloradoensis*) on several submersed aquatic weeds. 22:52-56.
- Yoshida, T. 1975. Microbial metabolism of flooded soils. *In:* Paul, E. A. and A. D. McLaren (Eds.). *Soil Biochemistry.* Marcel Dekker, Inc. New York. pp. 83-122.
- Zon, J. C. J. van. 1982. Aquatic weeds. *In:* Holzner, W. and N. Numata (Eds.). *Biology and Ecology of Weeds.* Dr W. Junk Publishers. The Hague. pp. 449-456.