Aquatic Botany, 26 (1986) 271—283
Elsevier Science Publishers B.V., Amsterdam — Printed in The Netherlands

OXYGEN RELEASE FROM ROOTS OF THE SUBMERSED MACROPHYTE *POTAMOGETON PERFOLIATUS* L.: REGULATING FACTORS AND ECOLOGICAL IMPLICATIONS[1]

W. MICHAEL KEMP[2] and LAURA MURRAY[2,3]

[2]*University of Maryland, CEES, Horn Point Laboratories, P.O. Box 775, Cambridge, MD 21613 (U.S.A.)*
[3]*Salisbury State College, Department of Biology, Salisbury, MD 21801 (U.S.A.)*

(Accepted for publication 18 July 1986)

ABSTRACT

Kemp, W.M. and Murray, L., 1986. Oxygen release from roots of the submersed macrophyte *Potamogeton perfoliatus* L.: regulating factors and ecological implications. *Aquat. Bot.*, 26: 271—283.

Rates of photosynthetic production, respiratory consumption and root release of dissolved oxygen (O_2) were measured for *Potamogeton perfoliatus* L. from an estuarine population. Incubations were conducted in split-compartment chambers, with shoots (leaves and stems) separated from roots (plus rhizomes). Time-course observations of O_2 exchanges between plants and filtered estuarine water were made at ambient temperatures in natural daylight and in darkness. Release of oxygen from roots (L_r) to surrounding water was directly proportional to photosynthetic production of oxygen in the shoot compartment (P_a). L_r for plants with medium (20—35-cm) stem lengths ranged from less than zero to 0.28 mg O_2 (g dry plant)$^{-1}$ h^{-1}. The fraction of P_a released from roots was inversely proportional to overall stem length, with L_r approaching 18% of P_a for short plants (10—15 cm). Mass-specific respiration rates of shorter, more actively growing plants were also 1.5—2.5 times greater than those for longer plants (50—55 cm). In addition, relative L_r (% P_a) was inversely related to mass/length, possibly reflecting a higher fraction of stem cross-section as gas space in plants with low mass/length. For natural populations of *P. perfoliatus* in Chesapeake Bay, L_r was calculated to be 17—22 mg O_2 m^{-2} h^{-1}, representing a relatively small fraction of P_a (3—7%). Potential effects of L_r on bacterial metabolism in sediments were also estimated. For example, oxygen release from roots would be sufficient to support 4—6 times ambient nitrification rates or to oxidize all of the sulfide produced from sulfate reduction in unvegetated sediments.

INTRODUCTION

Many submersed vascular plants possess well-developed lacunal systems which facilitate internal storage and transport of oxygen (O_2) and other met-

[1]University of Maryland Center for Environmental and Estuarine Studies (CEES) Contribution No. 1713, U.S.A.

0304-3770/86/$03.50

abolic gases (Sculthorpe, 1967). A portion of the O_2 which is transported downward through the lacunae to allow aerobic root respiration, may be released from roots to external sediment environments (Sand-Jensen et al., 1982). The resulting aeration of the rhizosphere can markedly influence sediment chemistry, enhancing such processes as nitrification (Iizumi et al., 1980) and sulfide oxidation (Joshi and Hollis, 1977). This aeration mechanism may benefit the vascular plant directly by stimulating oxidation of reduced metabolites, e.g. S^{2-}, Fe^{2+}, Mn^{2+}) which are otherwise phytotoxic (Tessenow and Baines, 1978; Penhale and Wetzel, 1983). It has also been suggested that root release of photosynthetically produced O_2 leads to underestimates of macrophyte primary production measured as O_2 evolution to water surrounding plant shoots (Zieman and Wetzel, 1980).

Field and laboratory experiments have provided evidence of rhizosphere aeration associated with several submersed vascular plants. For example, elevated redox potentials have been observed in vegetated sediments compared to adjacent bare substrates (Wium-Andersen and Andersen, 1970; Carpenter et al., 1983). Using split-compartment chambers, root release of O_2 has been measured directly for several macrophytes (Iizumi et al., 1980; Sand-Jensen et al., 1982; Thursby, 1984; Kemp et al., 1986). For most species investigated, root release of O_2 represented a minor fraction of total photosynthetic production (Sand-Jensen et al., 1982).

In general, physiological and environmental factors regulating root release of O_2 by submersed plants are not well described. For emergent wetland plants it has been shown that rhizosphere oxidation is related directly to irradiance and photosynthesis, and inversely to shoot length (Vámos and Köves, 1972; Armstrong, 1978; Yamasaki, 1984). Similar data are lacking for submersed species, although several recent studies (Sand-Jensen et al., 1982; Carpenter et al., 1983; Smith et al., 1984; Thursby, 1984) have shown reduced root release of O_2 in the dark.

The actual mechanism by which O_2 is transported to the roots and released to the surrounding rhizosphere is uncertain for fully submersed plants. Several mechanisms for mass flow of O_2 to the roots have been demonstrated for specific emergent wetland plants (Dacey, 1981; Raskin and Kende, 1985). Mechanisms of mass flow have not been identified for submersed macrophytes, and for many emergent plants simple molecular diffusion models have been used successfully to describe the root aeration processes (Armstrong, 1978). In this case, O_2 flux can be represented by $\delta C/\delta t = \epsilon A\ \tau D(\delta C/\delta x)$, where D is molecular diffusivity, A is area of plant leaf or stem cross-section, ϵ is fractional porosity of the cross-section, τ is tortuosity of the diffusion path and $\delta C/\delta x$ is the gradient of O_2 concentration along the diffusion path.

Even if O_2 flux to the roots of submersed plants is driven by a mass flow mechanism, it is likely that several terms in the above equation (such as O_2 concentration gradient and cross-sectional area) would still influence O_2 flux.

The difference in O_2 concentration at opposite ends of the transport path (δC) should be a direct function of both photosynthetic O_2 production and root respiration for fully submersed macrophytes, and the average distance over which O_2 flux occurs (δx) is related to overall macrophyte shoot length (Armstrong, 1978). Furthermore, if the density (specific gravity) of the plant shoot does not vary, then the shoot's cross-sectional area (A) would be directly proportional to mass per unit length of shoot.

In the present paper, direct measurements of intravascular transport and root-release of O_2 are provided for the submersed macrophyte, *Potamogeton perfoliatus* L., a formerly abundant species in upper Chesapeake Bay (Kemp et al., 1983). Effects of selected physiological factors (photosynthetic production, root respiration, shoot length and length-specific mass) on root O_2 release are examined, and the potential ecological implications of rhizosphere oxidation are discussed for a natural macrophyte population.

MATERIAL AND METHODS

Experimental plants were obtained from a population of *P. perfoliatus* inhabiting an estuarine pond (Twilley et al., 1985) in the upper reaches of Chesapeake Bay, U.S.A. During this study period (1 July—15 August 1984), salinity and temperature ranges were ca. 10—14‰ and 24—30°C, respectively. Plants were collected approximately 36 h prior to experiments and held in aerated estuarine water under controlled temperature (24—27°C) and light (PAR = 150 μE m^{-2} s^{-1}, 14-h photoperiod) conditions. Plants were collected and handled with special care so as not to damage root systems. Plant shoots and roots were washed thoroughly free of attached material in a gentle stream of ambient water. Associated with each shoot was a 10—15-cm section of horizontal rhizome; broken ends of rhizomes were sealed with vacuum grease.

Each incubation was conducted in a two-chambered apparatus constructed from clear acrylic cylinders (i.d. = 20.2 cm), with an upper "shoot compartment" (volume 1.80 l) and a lower "root compartment" (volume 0.45 l) allowing separation of leaves and stems from roots and rhizomes. Three replicate two-chamber systems were constructed and used in parallel. Square acrylic flanges at the bottom and top of the shoot and root chambers, respectively, were separated by a matching intermediate plate (for mounting plants) which could be fixed and sealed to the flanges via two rubber gaskets. Three plants were mounted in separate split serum-stoppers which were inserted into three individual holes in the plate and sealed with vacuum grease. Both root and shoot chambers were fitted with Clark-type O_2 electrodes with built-in stirrers (Orbisphere Model 2603). The two chambers and intermediate plate (with plants) were attached together with screws inserted through matching holes in the flanges and tightened with wing-nuts. Both chambers were filled with

filtered (GF/F, 0.45 μ) ambient water, and bottom water was spiked with nutrients (100 μM NH_4^+, 10 μM PO_4^{3-}) and rhodamine dye (to test for exchange between chambers) and bubbled with N_2 gas to reduce O_2 content (to ca. 10—15% saturation) prior to incubations.

During incubations the chambers were placed in a 50-l glass aquarium with a continuous exchange of tap water which maintained temperature control ($26 \pm 2°C$). Incubations were conducted under ambient daylight conditions between 1000 and 1400 h with irradiance controlled using neutral density screening; mean PAR during incubations ranged from 80 to 400 $\mu E\ m^{-2}\ s^{-1}$. The root compartments were made opaque using black tape. Temperature, O_2 and PAR were measured at 30—90-min intervals over an incubation period of 2—5 h. Water in shoot compartments was mixed continuously using the stirrer attached to the electrode, while water in root chambers was left unstirred except for brief periods (ca. 1 min) during O_2 measurements.

Possible diffusion of O_2 through the acrylic walls of the root chamber was shown to be insignificant by conducting control experiments without plants. Similarly, effects of plankton metabolism on O_2 changes in chamber waters were found to be negligible based on incubations of the same filtered water in clear and opaque BOD bottles. Dark respiration measurements were made for roots and shoots of intact plants mounted in chambers by reoxygenating water in both chambers and observing decreases in O_2 during dark incubations in the afternoon/evening following selected daylight measurements. Oxygen consumption rates by excised root and shoot systems of plants were also measured within 30 min after collection. Here, incubations were conducted in opaque BOD bottles for triplicate plants in each size group (Sand-Jensen et al., 1982). Polarographic O_2 electrodes were calibrated in water-saturated air before each experiment. At the end of each incubation, shoot length (distance along vertical stem from intersection with rhizome to tip of apical bud) and number of leaves were recorded, and plants were separated into "shoot" and "root" parts, rinsed with fresh water and dried at 70°C to constant biomass (dry mass = d.m.).

RESULTS AND DISCUSSION

Regulating factors

Time-course changes of O_2 concentrations in root and shoot compartments were generally linear over the first 2—4 h of incubation (Fig. 1). Oxygen concentrations in the shoot compartment occasionally exhibited a reduced rate of increase after 3—4 h, possibly due to O_2 inhibition (Lloyd et al., 1977) or carbon limitation (Sand-Jensen, 1983). Only the linear parts of these curves were used to calculate rates of O_2 exchange. In the root compartments we variously observed O_2 increases or decreases depending on conditions (Fig. 1). This is consistent with the variable patterns reported by Smith et al. (1984) for *Zos-*

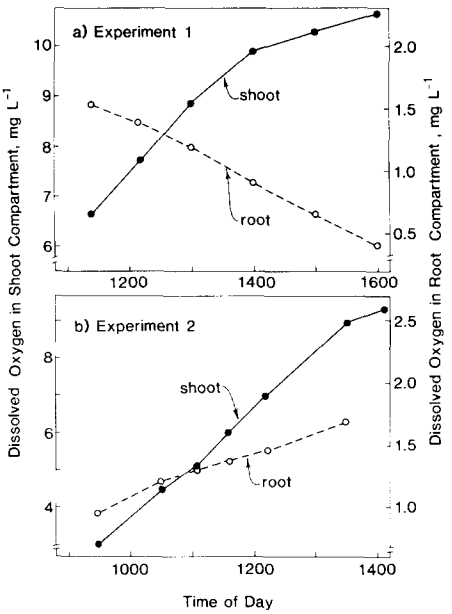

Fig. 1. Typical time-course changes in O_2 for water in "shoot compartments" (containing leaves and stems) and in separated "root compartments" (containing roots and rhizomes) for daylight incubations of the submersed macrophyte, *Potamogeton perfoliatus*. Panels (a) and (b) represent examples of experiments in which there was net consumption and net release, respectively, in the root compartments.

tera marina L. As evident in the two examples presented in Fig. 1, O_2 changes in the root compartment were not, per se, directly related to O_2 concentrations in the shoot compartment.

Using only *P. perfoliatus* plants with similar shoot length (20—35 cm) and manipulating PAR conditions, a significant relation between O_2 exchange in the root compartment (L_r) and apparent photosynthesis (P_a, O_2 production in shoot compartment) was observed (Fig. 2a). Net release of O_2 from roots (positive L_r) occurred only at rates of P_a exceeding ca. 4 mg O_2 g d.m.$^{-1}$ h^{-1}. Several recent studies have reported increased rates of O_2 release from roots under light compared to dark conditions for various submersed macrophytes (Sand-Jensen et al., 1982; Carpenter et al., 1983; Thursby, 1984; Smith et al., 1984). However, no previous studies have demonstrated how L_r varies in relation to changes in P_a. Smith et al. (1984) correlated L_r to shoot biomass for *Z. marina*, and they suggested (but provided no data) that differences in photosynthesis were involved.

In two successive experiments, three distinct size-groups of plants were established (shoot length: 10—15 cm; 25—30 cm; and 50—55 cm) and incubated in separate chambers. Since L_r was directly related to P_a (Fig. 2a), data are presented here in terms of relative root release of O_2 (100 L_r/P_a). Using

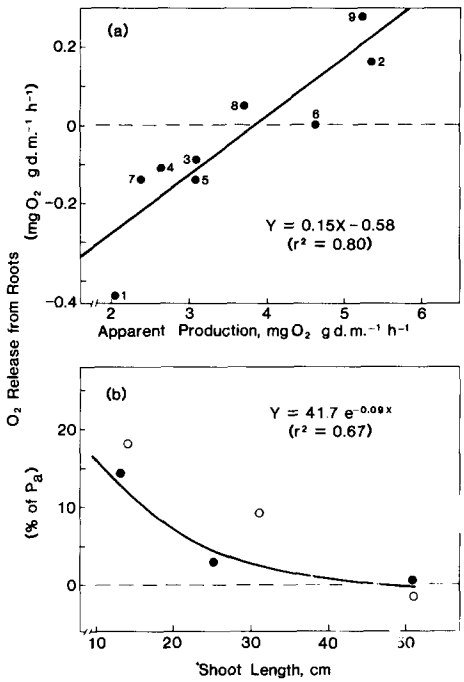

Fig. 2. Rates of O_2 exchange from roots of *Potamogeton perfoliatus* incubated in split-compartment chambers under daylight conditions: (a) compared to apparent O_2 production (P_a) from leaves for plants of similar stem length (20—35 cm), where both rates are specific to total plant biomass, and numbers adjacent to points identify different experiments; (b) net O_2 release as a percent of P_a compared to stem (shoot) length, where open and closed circles identify two separate experiments, both involving plants from three different size groups.

this relative measure of L_r allows the influence of shoot length to be considered directly without the confounding effects of variations in P_a. For both experiments, a significant inverse correlation was observed using an exponential model (Fig. 2b). The general shape of this relation is consistent with the hyperbolic form predicted from theory (Armstrong, 1978). Even considering absolute rates of L_r, the inverse relation to shoot length holds: mean rates for short shoots ($+0.09$ mg $O_2\,h^{-1}$) were substantially greater than those for long shoots (-0.02 mg $O_2\,h^{-1}$), indicating that shoot length exerts a more pronounced effect on L_r than does P_a.

Other factors associated with plant age may also contribute to the interaction between shoot length and root aeration indicated in Fig. 2b. It is well established that the epidermal layers of young, vigorously growing plant roots are more permeable to gas transport, and that these younger roots are metabolically more active (e.g. Armstrong, 1978). Both roots and shoots excised from shorter *P. perfoliatus* plants exhibited higher mass-specific rates of O_2 consumption compared to older plants; however, P_a values were not different

TABLE I

Metabolic O_2 balances for three size classes of *Potamogeton perfoliatus* shoots and roots (plus rhizomes)

Size class (cm)	Plant part	Biomass[1] (mg d.m.)	Production[2]		Respiration[2]	
			mg O_2 g d.m.$^{-1}$ h^{-1}	mg O_2 plant^{-1} h^{-1}	mg O_2 g d.m.$^{-1}$ h^{-1}	mg O_2 plant^{-1} h^{-1}
0—20	Shoot	31±5	6.1[3]	0.19	3.7±0.7	0.11
	Root	12±2	—[4]	—	6.9±0.2	0.08
21—40	Shoot	85±8	5.5±1.3	0.47	1.6±0.2	0.14
	Root	22±4	—	—	3.0±0.0	0.07
41—60	Shoot	228±10	5.2±0.9	1.19	1.2±0.1	0.27
	Root	22±2	—	—	2.6±0.3	0.06

[1]Biomass of plant parts from a sample of six plants (3 plants in each of 2 chambers) in each size-class ($\bar{x}\pm$S.E.).
[2]Apparent production values ($\bar{x}\pm$ range, $n=2$) for intact plants, and respiration rates ($\bar{x}\pm$S.E., $n=3$) for excised plant parts incubated in dark BOD bottles, with rates specific to the dry weight of the given plant part.
[3]Single experiment.
[4]Root release of O_2 not measured in these experiments.

among the three size groups (Table I). The rate of decrease in respiration with increasing shoot length was greater for roots compared to shoots such that the fraction of total plant respiration comprised by root metabolism decreased from 44 to 33 to 17% for the 10—15-, 25—30- and 50—55-cm size classes, respectively. Thus, it is clear that roots of younger *P. perfoliatus* plants are metabolically more active in both absolute (mass-specific) and relative terms. If, indeed, gas permeability is directly related to growth and metabolic rates (Armstrong, 1978), then this may partially explain the trend observed in Fig. 2b.

Oxygen budgets were also developed for groups of *P. perfoliatus* plants having different values of length-specific shoot biomass. The results of two incubation series are summarized in Fig. 3, where metabolic rates are normalized to biomass of the whole plant. The mean values for length-specific mass in the first experiment (3.4—4.6, Fig. 3a) were significantly higher (ANOVA, $P<0.05$) than those in the second (2.5—3.3, Fig. 3b). Number of leaves per unit length of stem was relatively constant for these plants (0.7—0.8 cm^{-1}) regardless of the total shoot length. Overall, metabolic rates (including P_a) in the second group of plants (Fig. 3b) were lower than for the first group. Although rates of O_2 release from roots were similar for the two experiments, relative L_r (% of P_a) was greater in the plants with lower mass per length.

If specific gravity of shoot material was constant for all plants, the cross-sectional area of stem would be proportional to length-specific mass. This would result in higher relative L_r for plants with greater length-specific mass, which is just the opposite of what was observed. If, on the other hand, the lower length-specific mass was attributable to greater porosity, this would account for the pattern observed in Fig. 3. In this case, increased porosity would mean that lacunae constituted a greater fraction of the stem or leaf cross-section, thus facilitating gas diffusion. Recently, Penhale and Wetzel (1983) reported

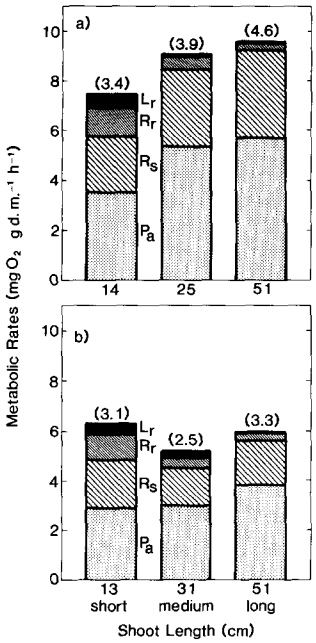

Fig. 3. Rates of O_2 exchange (specific to total plant biomass) associated with metabolism of intact *Potamogeton perfoliatus* plants for three size-groups of shoots (stems plus leaves). Total O_2 production (histogram) is defined as the sum of: apparent production (P_a, net O_2 evolution from shoots); shoot respiration in dark (R_s); root respiration in dark (R_r); and loss from roots to surrounding medium (L_r). Experiments conducted with two plant groups of relatively different length-specific mass (mass/length): (a) high; (b) low. Values in parentheses above each histogram are means of length-specific mass (g d.m. cm^{-1}) for plants in each chamber.

that lacunal cross-sectional areas in *Zostera marina* were larger for plants taken from more reduced sediments, possibly indicating an adaptation for enhanced O_2 transport to roots in anaerobic conditions.

Ecological implications

A traditional technique used to measure photosynthetic production of submersed macrophytes involves monitoring changes in O_2 concentration in waters surrounding a plant population (e.g. Odum, 1957; Nixon and Oviatt, 1972). Based on observations of O_2 storage in macrophyte lacunae (Hartman and Brown, 1967) and, more important, O_2 release from roots to the external rhizosphere (Oremland and Taylor, 1977), various investigators concluded that O_2 techniques were generally unsuitable for estimating macrophyte production (e.g. Zieman and Wetzel, 1980). Quantitative evidence to address this question was lacking until Sand-Jensen et al. (1982) showed that rates of root release of O_2 for eight macrophyte species ranged from <0.1 to ca. 100% of total O_2 production. However, interpreting the significance of these kind of data for a

TABLE II

Calculated release of oxygen from roots for *Potamogeton perfoliatus* population as a percentage of apparent oxygen production (P_a)

Month	Population size-structure[1]		Plant biomass[2]		O_2 Release from roots[3]	
	Interval (cm)	Number (% total)	(g d.m. shoot^{-1})	(% Total)	(mg O_2 g d.m.$^{-1}$)	(% P_a)
June	0—20	65	0.03	30	18.0	5.4
	21—40	30	0.11	52	3.0	1.6
	41—60	5	0.23	18	0.3	0.1
	Total					7.1
August	0—20	35	0.03	10	18.0	1.8
	21—40	50	0.11	55	3.0	1.6
	41—60	15	0.23	35	0.3	0.1
	Total					3.5

[1]Observations for *P. perfoliatus* population growing in upper Chesapeake Bay (salinity $\approx$ 10‰) where %'s are rounded to nearest 5 (Kemp et al., unpublished data, 1983).
[2]Biomass data (g d.m. shoot^{-1}) are means for plants used in this experiment; % of total biomass calculated for each size-class in field population.
[3]Estimated from regressions in Fig. 2b (per g d.m.); total O_2 release for each size-class is based on % of total biomass for given size-group.

given macrophyte population in nature requires an understanding of factors regulating O_2 release from roots.

A first-order approximation of the error associated with ignoring rhizosphere oxygenation in estimating total O_2 production for *P. perfoliatus* is presented in Table II. Here, data from Fig. 2 are combined with information on size-structure and biomass of a macrophyte population in Chesapeake Bay in early June and mid-August (Kemp et al., 1984). Early in the macrophyte growing season, many of the shoots are less than 20 cm long, while in mid-summer the larger size-classes dominate. Because smaller shoots release from their roots a larger percentage of the O_2 produced photosynthetically (Fig. 2b), the effect of this process on underestimating total production as O_2 evolved from shoots is greater in the earlier period. However, even in this case the error would be ca. 7%, a relatively small discrepancy compared with other factors such as spatial variability of plant biomass. Later in the season the error is only about half this value. Hence, if one can independently account for O_2 metabolism of water, sediments and epiphytes, then measurements of O_2 evolution in the water surrounding a *P. perfoliatus* population should provide a reasonable estimate ($\pm$ 10%) of net daytime O_2 production.

Although release of O_2 by *P. perfoliatus* roots may be relatively inconsequential in the macrophyte's O_2 balance, its influence on oxidation—reduction chemistry and microbiology of associated sediments needs to be considered separately. A number of important microbially-mediated processes in aquatic sediments are limited by availability of O_2. One such process, nitrification, is a critical link between ammonium regeneration and denitrification in aquatic nitrogen-cycles. Several studies have reported relatively high nitrification rates

TABLE III

Estimated potential chemo-autotrophic nitrification or sulfide oxidation supported by release of O_2 from *Potamogeton perfoliatus* roots

Time period	Shoot biomass[1] ($g\ d.m.\ m^{-2}$)	Apparent O_2 production (P_a)[1]		Release of O_2 from roots[2]		Chemo-autotrophic potential[3] ($\mu mol\ m^{-2}\ h^{-1}$)
		$mg\ g^{-1}\ h^{-1}$	$mg\ m^{-2}\ h^{-1}$	% P_a	$mmol\ O_2\ m^{-2}\ h^{-1}$	
June	53	4.4	235	7.1	0.52	260
August	74	8.4	620	3.5	0.68	340

[1]Data for *P. perfoliatus* population in upper Chesapeake Bay for summer 1981 (Kemp et al., 1984). All biomass values are given as dry mass (d.m.).
[2]Based on data presented in Table II.
[3]Potential nitrification or sulfide oxidation which could be supported by root release of O_2 based on stoichiometric relations suggested by Keeney (1973) and Howarth and Teal (1980), respectively. Rates are given as μmol (N or S) $m^{-2} h^{-1}$.

in macrophyte inhabited sediments (Koike and Hattori, 1978; Chan and Knowles, 1978; Iizumi et al., 1980). However, none of these experiments directly considered the influence of plant metablism on this nitrogen-transformation process. Recent work (Christiansen and Sørensen, 1986) has demonstrated that sediment denitrification and nitrate concentrations were strongly associated with growth of the perennial macrophyte, *Littorella uniflora* (L.) Aschers. This isoetid macrophyte has been shown to release most of its photosynthetic O_2 production to the rhizosphere (Sand-Jensen et al., 1982).

Direct quantification of nitrification enhancement associated with macrophyte metabolism is complicated by limitations of currently-available methods (Henriksen and Kemp, 1986). Potential effects, however, can be estimated from data such as those developed in the present study. Again, combining root release rates (Table II) with field data on *P. perfoliatus* biomass and O_2 production (Kemp et al., 1984), and applying simple stoichiometric relations (Keeney, 1973), the potential nitrification rates supported via macrophyte rhizosphere oxidation were calculated (Table III). If availabilities of NH_4^+ and CO_2 did not limit nitrification, then O_2 supplied by rhizosphere oxidation could support rates of 260—340 $\mu mol\ N\ m^{-2}\ h^{-1}$. Even though relative rates of O_2 release from roots would be higher in spring (Table II), absolute rates per m^2 are estimated to be higher in summer due to greater macrophyte biomass and O_2 production (Table III).

These nitrification potentials are 4—6 times higher than typical mean ambient rates reported for unvegetated coastal sediments (Henriksen and Kemp, 1986). Thus, even if only 10% of this O_2 released from macrophyte roots was used by nitrifier bacteria, it would result in about a 50% increase compared to rates in unvegetated sediments. Macrophyte ventilation of sediments is analogous to animal irrigation of tubes and burrows which can markedly alter sediment nitrogen cycling (Henriksen et al., 1980; Chartapaul et al., 1980; Kristensen et al., 1985).

It is likely that much of the oxygen released from *P. perfoliatus* roots to the sediment rhizosphere is used in redox reactions other than nitrification. Var-

ious studies have shown that macrophyte metabolism results in elevated redox potential (Eh) in the rhizosphere (e.g. Carpenter et al., 1983). Since Eh is inversely related to sulfide concentration in coastal marine sediments (Fenchel, 1969), much of the macrophyte-induced increases in Eh probably arise from decreases in sulfide concentration. Sulfide, which appears to be generally phytotoxic (e.g.Vámos and Köves, 1972), is one of the most abundant reduced products of microbial metabolism in marine sediments (e.g. Jørgensen, 1983). Rates of bacterial sulfide production for shallow marine sediments are of the same order as the rhizosphere oxidation rates calculated for *P. perfoliatus* (Table III). While root release of O_2 would be sufficient, therefore, to oxidize all of the sulfide produced in most systems, only a small percentage of the total sulfide generated (i.e. that diffusing into the immediate root-zone) poses a toxic threat for the macrophyte (Joshi and Hollis, 1977). Penhale and Wetzel (1983) provide indirect evidence to suggest that rhizosphere ventilation rate for the seagrass, *Z. marina*, is directly proportional to sulfide concentration.

In conclusion, it appears that O_2 release by roots of *P. perfoliatus* to the surrounding rhizosphere is a direct function of photosynthetic production and root respiration, and inversely related to shoot length. Although rates of rhizosphere oxidation for an estuarine population of this species are relatively unimportant in the plant's O_2 economy, they appear to be sufficient to support markedly enhanced nitrification and to oxidize sulfide diffusing into the macrophyte root-zone.

REFERENCES

Armstrong, W., 1978. Root aeration in the wetland condition. In: D.D. Hook and R.M.M. Crawford (Editors), Plant Life in Anaerobic Environments. Ann Arbor Sci. Publ., Ann Arbor, MI, pp. 269—297.

Carpenter, S.R., Elser, J.J. and Olson, K.M., 1983. Effects of roots of *Myriophyllum verticillatum* L. on sediment redox conditions. Aquat. Bot., 17: 243—249.

Chan, Y.-K. and Knowles, R., 1978. Measurement of denitrification in two freshwater sediments by an in situ acetylene inhibition method. Appl. Environ. Microbiol., 37: 1067—1072.

Chartapaul, L., Robinson, J.B. and Kaushik, N.K., 1980. Effects of tubificid worms on denitrification and nitrification in stream sediment. Can. J. Fish. Aquat. Sci., 37: 656—663.

Christiansen, P.B. and Sørensen, J., 1986. Temporal variation of denitrification activity in plant covered, littoral sediment (Lake Hampen, Denmark). Appl. Environ. Microbiol., in press.

Dacey, J.W.H., 1981. Pressurized ventilation in the yellow waterlily. Ecology, 62: 1137—1147.

Fenchel, T., 1969. The ecology of marine microbenthos. 4. Structure and function of the benthic ecosystem, its chemical and physical factors and the microfauna communities with special reference to the ciliated protozoa. Ophelia, 6: 1—182.

Hartman, R.T. and Brown, D.L., 1967. Changes in internal atmosphere of submersed vascular hydrophytes in relation to photosynthesis. Ecology, 48: 252—258.

Henriksen, K. and Kemp, W.M., 1986. Nitrification in estuarine and coastal marine sediments: methods, patterns and regulating factors. In: T.H. Blackburn and J. Sørensen (Editors), Nitrogen Cycling in Coastal Marine Environments. John Wiley, in press.

Henriksen, K., Hansen, J.I. and Blackburn, T.H., 1980. Influence of benthic infauna on exchange rates of inorganic nitrogen between sediments and water. Ophelia (Suppl.), 1: 249—256.

Howarth, R.W. and Teal, J.M., 1980. Energy flow in a salt marsh ecosystem: the role of reduced inorganic sulfur compounds. Am. Nat., 116: 862—872.

Iizumi, H., Hattori, A. and McRoy, C.P., 1980. Nitrate and nitrite in interstitial waters of eelgrass beds in relation to the rhizosphere. J. Exp. Mar. Biol. Ecol., 47: 191—201.

Jørgensen, B B., 1983. Processes at the sediment water interface. In: B. Bolin and R.B. Cook (Editors), The Major Biogeochemical Cycles and Their Interactions. John Wiley (SCOPE), New York, pp. 477—509.

Joshi, M.M. and Hollis, J.P., 1977. Interaction of *Beggiatoa* and rice plant: detoxification of hydrogen sulfide in the rice rhizosphere. Science (Washington), 195: 179—180.

Keeney, D.R., 1973. The nitrogen cycle in sediment-water systems. J. Environ. Qual., 2: 15—29.

Kemp, W.M., Boynton, W.R., Stevenson, J.C., Twilley, R.R. and Means, J.C., 1983. The decline of submerged vascular plants in upper Chesapeake Bay: summary of results concerning possible causes. Mar. Tech. Soc. J., 17(2): 78—89.

Kemp, W.M., Boynton, W.R., Twilley, R.R., Stevenson, J.C. and Ward, L.G., 1984. Influences of submersed vascular plants on ecological processes in upper Chesapeake Bay. In: V.S. Kennedy (Editor), Estuaries as Filters. Academic Press, New York, pp. 367—394.

Kemp, W.M., Lewis, M.R. and Jones, T.W., 1986. Comparison of methods for measuring production by the submersed macrophyte, *Potamogeton perfoliatus* L., Limnol. Oceanogr., in press.

Koike, I. and Hattori, A., 1978. Simultaneous determinations of nitrification and nitrate reduction in coastal sediments by a ^{15}N dilution technique. Apl. Environ. Microbiol., 35: 893—957.

Kristensen, E., Jensen, M.H. and Andersen, T.K., 1985. The impact of polychaete (*Nereis virens* sars) burrows on nitrification and nitrate reduction in estuarine sediments. J. Exp. Mar. Biol. Ecol., 85: 75—91.

Lloyd, N.D.H., Canvin, D.T. and Bristow, J.M., 1977. Photosynthesis and photorespiration in submerged aquatic vascular plants. Can. J. Bot., 55: 3001—3005.

Nixon, S.W. and Oviatt, C.A., 1972. Preliminary measurements of midsummer metabolism in beds of eelgrass, *Zostera marina*. Ecology, 53: 150—153.

Odum, H.T., 1957. Primary production measurements in eleven Florida springs and a marine turtle-grass community. Limnol. Oceanogr., 2: 85—97.

Oremland, R.S. and Taylor, B.F., 1977. Diurnal fluctuations of O_2, N_2 and CH_4 in the rhizosphere of *Thalassia testudinum*. Limnol. Oceanogr., 22: 566—570.

Penhale, P.A. and Wetzel, R.G., 1983. Structural and functional adaptations of eelgrass (*Zostera marina* L.) to the anaerobic sediment environment. Can. J. Bot., 61: 1421—1428.

Raskin, I. and Kende, H., 1985. Mechanism of aeration in rice. Science, 228: 327—329.

Sand-Jensen, K., 1983. Photosynthetic carbon sources of stream macrophytes. J. Exp. Bot., 34: 198—210.

Sand-Jensen, K., Prahl, C. and Stokholm, H., 1982. Oxygen release from roots of submerged aquatic macrophytes. Oikos, 38: 349—354.

Sculthorpe, C.D., 1967. The Biology of Aquatic Vascular Plants. Edward Arnold, London, 610 pp.

Smith, R.D., Dennison, W.C. and Alberte, R.S., 1984. Role of seagrass photosynthesis in root aerobic processes. Plant Physiol., 74: 1055—1058.

Tessenow, U. and Baines, Y., 1978. Experimental effects of *Isoetes lacustris* L. on the distribution of Eh, pH, Fe and Mn in lake sediments. Verh. Int. Ver. Theor. Angew. Limnol., 20: 2358—2362.

Thursby, G.B., 1984. Root-exuded oxygen in the aquatic angiosperm *Ruppia maritima*. Mar. Ecol. Prog. Ser., 16: 303—305.

Twilley, R.R., Kemp, W.M., Staver, K.W., Stevenson, J.C. and Boynton, W.R., 1985. Nutrient enrichment of estuarine submersed vascular plant communities. I. Algal growth and effects on production of plants and associated communities. Mar. Ecol. Progr. Ser., 23: 179—191.

Vámos, R. and Köves, E., 1972. Role of the light in the prevention of the poisoning action of hydrogen sulphide in the rice plant. J. Appl. Ecol., 9: 519—525.

Wium-Andersen, S. and Andersen, J.M., 1970. The influence of vegetation on the redox profile of the sediment of Grane Langso, a Danish *Lobelia* lake. Limnol. Oceanogr., 17: 948—952.

Yamasaki, S., 1984. Role of plant aeration in zonation of *Zizania latifolia* and *Phragmites australis*. Aquat. Bot., 18: 287—297.

Zieman, J.C. and Wetzel, R.G., 1980. Productivity in seagrasses: methods and rates. In: R.C. Phillips and C.P. McRoy (Editors), Handbook of Seagrass Biology: An Ecosystem Perspective. Garland STPM Press, New York, pp. 87—118.