Short Communication

Role of Seagrass Photosynthesis in Root Aerobic Processes

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ABSTRACT

The role of shoot photosynthesis as a means of supporting aerobic respiration in the roots of the seagrass Zostera marina was examined. O2 was transported rapidly (10–15 minutes) from the shoots to the root-rhizome tissues upon shoot illumination. The highest rates of transport were in shoots possessing the greatest biomass and leaf area. The rates of O2 transport do not support a simple gas phase diffusion mechanism. O2 transport to the root-rhizome system supported aerobic root respiration and in many cases exceeded respiratory requirements leading to O2 release from the subterranean tissue. Release of O2 can support aerobic processes in reducing sediments typical of Z. marina habitats. Since the root-rhizome respiration is supported primarily under shoot photosynthetic conditions, then the daily period of photosynthesis determines the diurnal period of root aerobiosis.

The inundation of soils or sediment with water can lead to O2 deficiency due to the low solubility of O2 in water and its low rate of diffusion in the aqueous phase compared to that in the gas phase (12). Under such conditions, whether caused by episodic, periodic, prolonged, or indefinite flooding as in natural wetland conditions, lake bottoms, or coastal marine areas, soil anoxia can develop and persist (2, 3). As a consequence, the portions of vascular plants growing in such soils can become anaerobic resulting in fermentative metabolism in these tissues (1, 5). The predominance of glycolysis over mitochondrial activities of the Krebs cycle and electron transport can lead to dramatic reductions in ATP levels, reduced protein synthesis and plant growth, inhibition of ion uptake, and the accumulation of toxic metabolic end products (1–3, 5, 12). If such conditions persist, tissue death usually occurs; a response characteristic of flood-intolerant species (2, 3).

Many species, however, have evolved physiological or morphological means by which tissue anoxia is avoided or minimized. These species, termed flood-tolerant species (2, 3), often possess aerial roots (3), have extensive aerogenous tissue (8, 12, 16, 20), show pressurized ventilation (4), have O2 transport from aerated tissue to anoxic tissues (10, 11, 15, 16, 19), or have metabolic means to minimize the harmful consequences of anoxia (1–3, 5). In the latter situation, carbon skeletons from glycolysis are most often shunted away from ethanol to less toxic compounds, such as organic or amino acids, which may be oxidized subsequently for energy or used for other metabolic activities (see Refs. 1, 5).

Though there have been numerous investigations of flood tolerance in terrestrial species (2, 3), there have been few studies examining this phenomena in submerged angiosperms which grow in anoxic and/or reducing sediments. In the present study, we sought to examine the flood tolerance of the submerged marine angiosperm Zostera marina (eelgrass). This temperate seagrass inhabits coastal areas of the Northern Hemisphere which are characterized, for the most part, by the presence of reducing sediments (9) and light limitation for growth (7). Despite this apparently inhospitable environment, Z. marina is one of the most productive marine primary producers known (14). Previous investigations have shown that seagrass plants can release O2 into the sediments under photosynthetic conditions (14, 15) and in doing so support the activity of oxygenic nitrifying bacteria (10, 16). Therefore, we examined the extent of photosynthesis-dependent O2 transport from shoots to roots-rhizomes and considered the importance of growth light environment and shoot biomass on these processes.

MATERIALS AND METHODS

Plant Materials. Zostera marina plants were collected at 1 to 2 m depth at Great Harbor, Woods Hole, MA (40° 31.5'; 70° 40.5'). Cores, 10 to 12 cm in depth and 20 cm diameter, containing 8 to 15 shoots were extracted from the sediment with plexiglass corers. The cores were transferred promptly to the laboratory and placed in running seawater aquaria.

Root, rhizome, and shoot (aerial stem and leaves) biomass were determined from dry weight measurements of tissues washed thoroughly in distilled H2O prior to drying. Leaf areas per shoot were determined from conversion factors of dry weight to leaf area derived from Dennison and Alberte (7) on plants collected at the same time.

O2 Exchange Measurements. The O2 exchange from the root-rhizome systems of intact Z. marina plants was measured polarographically in a two-chambered apparatus (Fig. 1) fitted to a Clark-type O2 electrode (Rank Bros, England) following the procedures of Delieu and Walker (6). This apparatus allowed for the separation of the root-rhizome system (lower chamber) from the shoot (upper chamber), and prevented shoot to root gas exchange except through living tissue. A syringe needle was inserted through the chamber separation stopper to maintain a continuous pressure gradient between both chambers. The temperature of both the shoot and root chambers were maintained at ambient seawater levels (20 ± 1°C). Mixing in the electrode chamber was rapid and uniform as determined from dye studies.

Intact shoots were carefully removed from the cores prior to experimentation and the root-rhizome system washed thoroughly with seawater. The older portions of the rhizome were excised and the cut ends sealed with silicone grease. Seedlings were also used in which rhizomes and roots were kept fully
The rhizome system of Zostera marina L. (eelgrass) is depicted in Fig. 1. The system is composed of the leaf chamber, root chamber, gas inlet, and water bath. The root-rhizome system was placed in the electrode chamber containing ultrafiltered (0.22 μm) seawater (33% salinity) under reduced O2 tension (10-15% of air saturation). The leaf chamber was kept in total darkness during measurement, while the root chamber was illuminated with photosynthetically saturating light (150 μE m⁻² s⁻¹ PAR; see Ref. 7) or kept in darkness. The O2 exchange rates (uptake and release) were recorded continuously for up to 8 h during shoot illumination and darkness. The O2 transport rates were calculated by subtracting root-rhizome respiration from O2 release rates (10).

**RESULTS AND DISCUSSION**

When *Z. marina* plants were maintained in total darkness, root-rhizome O2 uptake from the electrode chamber seawater occurs (21 ± 7.1 nmol O2 h⁻¹ mg⁻¹ dry weight of root-rhizome) (Fig. 2). Upon illumination of only the shoots, photosynthetically produced O2 was transported rapidly from shoots to the root-rhizome system as seen in a typical trace of the O2 exchange rates of the root-rhizome system in Fig. 2. The use of the term transport does not imply an active process, but merely a directional movement of O2 (see further discussion below).

In every case (n = 9), the highest rates of O2 uptake from the electrode chamber seawater were observed when the shoots were kept in darkness. Upon illumination of the shoots with photosynthetically saturating light, however, O2 uptake by the root-rhizome system begins to decrease within 15 to 30 min and, in many cases, results in the release of O2 from the roots (positive slope, Fig. 2) presumably from O2 availability in excess of respiratory demand. The reduced root-rhizome demand for external O2 (electrode chamber seawater) reflects the increasing availability of an internal source of O2 resulting from transport of O2 from net shoot photosynthesis. The O2 exchange rates during shoot illumination ranged from −6.2 (uptake) to +7.4 (release) nmol O2 h⁻¹ mg⁻¹ dry weight of root-rhizome or −1.92 to +0.46 nmol O2 h⁻¹ mg⁻¹ dry weight (shoot).

The transport of O2 from shoot to roots can be demonstrated simply by separating the base of the meristem from the rhizome, which results in an increased O2 uptake from the rhizosphere (electrode chamber seawater) (data not shown). Previous studies have demonstrated that *Z. marina* possesses a system of air-filled lacunae (16, 20) which are continuous from shoots through the meristem region to the root tips (16; see also Ref. 11; Smith, unpublished). These channels provide a system for gas phase movement of O2.

The precise mechanism of O2 transport in *Z. marina* is unknown. However, based on the rates of transport, the diameters of typical lacunae and the distances over which transport must occur (approximately 20 cm), rates of gas phase diffusion are simply too slow (approximately 10⁻³ times slower than the transport rates measured here assuming that 50% of the root-shoot volume is lacunal volume and the distance for transport is 20 cm) to account for the observed transport rates. Therefore, it seems unlikely that only a gas phase diffusion mechanism functions in the movement of O2 from shoots to roots in eelgrass.

The amount of O2 transported and the potential for O2 release to the sediment is determined in part by the total amount of active photosynthetic tissue in *Z. marina*. Plants with greater shoot biomass transport proportionately more O2 to the root-rhizome system than plants with low shoot biomass (Fig. 3). Since *Z. marina* leaf biomass is directly proportional to leaf area (7), a minimum leaf area (based on the O2 exchange data) of about 4 × 10⁻³ m²/shoot is required for O2 release. A typical mature eelgrass shoot has a leaf area of about 5 × 10⁻³ m² when the canopy is at its seasonal maximum (7).

Larger, fully developed shoots with greater biomass (Fig. 4) and leaf areas are capable of transporting O2 in excess of respiratory demand to their roots which can be released into the sediments or support oxygenic activities in older portions of the

**FIG. 2.** The effects of illumination of Zostera shoots on O2 exchange rate in the root-rhizome tissue. Plants were maintained in either total darkness or the shoots were illuminated with photosynthetically saturating light (150 μE m⁻² s⁻¹). The O2 exchange was monitored continuously between the root tissue and the O2 electrode solution. A negative slope indicates O2 uptake by the root-rhizome system (respiration during dark periods) while a positive slope indicates O2 release. The time period between a change in illumination state and a significant change in slope is indicated as the lag period.

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**TABLE 1.** The effects of different conditions on O2 exchange rates of Zostera shoots. The data are presented as mean ± standard error. The samples were maintained in total darkness or illuminated with photosynthetically saturating light (150 μE m⁻² s⁻¹). The O2 exchange was monitored continuously between the root tissue and the O2 electrode solution.

<table>
<thead>
<tr>
<th>Condition</th>
<th>Uptake (nmol O2 h⁻¹ mg⁻¹ dry weight)</th>
<th>Release (nmol O2 h⁻¹ mg⁻¹ dry weight)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dark</td>
<td>0.2 ± 0.1</td>
<td>0.4 ± 0.2</td>
</tr>
<tr>
<td>Light</td>
<td>1.5 ± 0.3</td>
<td>0.9 ± 0.1</td>
</tr>
</tbody>
</table>

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**FIGURE 1.** Two chambered apparatus for measurement of O2 evolution and uptake in the root-rhizome system of Zostera marina L. (eelgrass). A, Shoot chamber; B, 25-gauge syringe needle maintains pressure gradient with minimal O2 exchange between chambers; C, magnetic stirring bar allows rapid and uniform mixing throughout the electrode chamber; D, water bath (20°C); E, silicone grease; F, electrode; G, lead to recorder.
rhizome. It is also likely that this excess O$_2$ is utilized by roots of small developing shoots branching off the main rhizome which probably do not carry out net photosynthesis as light levels are well below photosynthetic saturation (approximately 20–30 μE m$^{-2}$ s$^{-1}$) at the bottom of dense eelgrass canopies (7, 13).

Lacunal diameter may also influence the O$_2$ transport in Z. marina plants. Increased root lacunal size in response to lower sediment redox potential has been observed (16). Reduced lacunal diameter may mechanically restrict exchange of gases within the root-rhizome system. We have observed that the lacunal system in shoots, basal meristems, and root-rhizome tissues are well developed in older plants from strongly reducing sediments which have high O$_2$ transport rates (R. D. Smith, unpublished observations). However, young plants and seedlings, characterized by low shoot dry weights and leaf areas and poorly developed lacunae, have reduced O$_2$ transport and generally do not release O$_2$ during shoot illumination (Fig. 4). These findings suggest that a combination of low leaf biomass and area, and small and few lacunae can account for reduced O$_2$ transport in eelgrass.

O$_2$ transport to the root-rhizome system is rapid upon shoot illumination with lag times of only 15 to 30 min. In a similar manner, the cessation of O$_2$ transport brought about by darkening the shoot chamber leads to an equally rapid cessation in O$_2$ transport from the shoot to the roots (see Fig. 2). Such rapid responses to illumination would ensure a maximum daily period of O$_2$ transport to underground tissues, thereby maximizing the daily period of root aerobic respiration. Furthermore, it would also ensure maximum oxygenation of the typically highly reducing sediments and consequently support the metabolic activities of the many facultative aerobic bacteria present in the sediments (see Ref. 17).

Since most Z. marina communities are distributed along a depth gradient, the portions of the population at depth are subject to greatly reduced light intensities due to the attenuation of light by the water column. Accompanying the reduced light intensities are reductions in the daily period of saturating photosynthesis (7), termed H$_{sat}$. Plants growing at depth can experience H$_{sat}$ periods 3 h shorter than plants growing in shallow water (7). Since aerobic respiration in the underground tissues is supported primarily during shoot photosynthetic periods, then H$_{sat}$ period will determine the daily period of aerobic respiration in the root-rhizome. Consequently, the roots of plants growing at depth in reducing sediment must endure longer periods of anoxia or hypoxia. Prolonged root-rhizome anoxia or hypoxia due to short H$_{sat}$ regimes should reduce growth and biomass production. Preliminary results (W. C. Dennison, unpublished data) show that plants subjected to in situ shortened H$_{sat}$ regimes (<5 h) have about a 4% reduction in root and shoot production compared with control plants (H$_{sat}$ = 8 h).

The results of this study have important implications with respect to the adaptive physiology and distribution of Z. marina. Since this species inhabits coastal marine waters along a significant depth gradient of a few meters to 30 m or more, then plants growing at depth experience lower light intensities, shorter periods of photosynthetic saturation (H$_{sat}$) (7), and consequently, longer periods of O$_2$ limitation for root-rhizome growth and metabolism. Therefore, it appears that the period of root anoxia, which is directly related to the daily period of saturating photosynthesis (H$_{sat}$), could dramatically influence the depth distribution of this ecologically important species.

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LITERATURE CITED

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\(^2\) Abbreviation: H$_{sat}$, daily period of light saturated photosynthesis.