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Submerged versus air-exposed intertidal macrophyte productivity: from physiological to community-level assessments

João Silva[a,*], Rui Santos[a], Maria Ll. Calleja[b], Carlos M. Duarte[b]

[a]ALGAE-Marine Plant Ecology Research Group, Centre of Marine Sciences, Universidade do Algarve, Campus de Gambelas, 8005-139 Faro, Portugal

[b]IMEDEA (CSIC-UiB), Grupo de Oceanografia Interdisciplinar, Instituto Mediterráneo de Estudios Avanzados, C/Miquel Marqués 21, 07190 Esporles (Islas Baleares), Spain

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Abstract

The photosynthetic productivity of the intertidal communities dominated by the seagrass *Zostera noltii* and the cordgrass *Spartina maritima* was assessed in two contrasting situations during a tidal cycle, i.e., air exposure and water immersion. Two complementary methods were used: infra red gas analysis of CO_2 flux measurements in whole communities and chlorophyll *a* fluorescence measurements of individual plants photosynthetic activity. Higher photosynthetic rates of *Z. noltii* in air were observed both at the individual plants response level determined by chlorophyll fluorescence and at the community level measured as gas exchange (CO_2 uptake). *S. maritima* plants consistently showed low photosynthetic response when immersed. Gross community production (GCP) measured as carbon dioxide uptake was always higher in air than in water for both communities. When immersed, the GCP of both communities was similar. However, when exposed to the air, the GCP of the *S. maritima* community was higher than the one of *Z. noltii*'s. The key factor in CO_2 assimilation by air-exposed *Z. noltii* was the retention of water in sediment microdepressions. During low tide, depressions in the sediment retain a considerable amount of water, enough to maintain leaf hydration. In these conditions, rapid air–water CO_2 diffusion occurs, making it readily available to plants. The community gas exchange measurements compared well with the fluorescence indications. Both *Z. noltii* and *S. maritima* were shown to be responsible for the overall pattern of photosynthetic carbon fixation within their respective communities, both during submersion and emersion periods. The short-term incubations method described in this report proved to be a valuable tool for field measurements of intertidal lagoon productivity. It provides fast and precise values of carbon dioxide fixation, both in submerged and air-exposed communities.

Keywords: Methods; Community production; Photosynthesis; IRGA; Pulse amplitude-modulated (PAM) fluorescence; Seagrasses; *Zostera noltii*; *Spartina maritima*

* Corresponding author. Tel.: +351 966859276; fax: +351 289818353.
E-mail address: jmsilva@ualg.pt (J. Silva).

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1. Introduction

The productivity of macrophytes in intertidal lagoons and salt marshes is usually assessed from plant growth (Short and Duarte, 2001). More recently, estimates based on the activity of photosystem II, inferred from Chl *a* fluorescence, have been used to derive estimates of photosynthetic activities at the physiological, individual leaf level. However, the scaling of these estimates to community-level estimates of productivity is not straightforward and has not yet been attempted. Community-level productivity estimates of intertidal macrophytes has been assessed from gas exchange methods based on infrared gas analysis (IRGA) of carbon dioxide (CO_2) fluxes, using flow-through systems or closed chambers (Streever et al., 1998). Studies of community-level productivity involving CO_2 flux measurements are more common in salt marsh communities than in seagrass meadows. In the former systems, carbon fluxes have been measured either in individual leaves, incubated on special leaf chambers with temperature control and artificial light or in whole plants, using larger incubation chambers (Streever et al., 1998 and references therein), but not yet in intact communities. These chambers may be more or less complex, with or without temperature and/or humidity control and usually use natural light.

Carbon flux measurements using infrared gas analysis in seagrasses are scarce, particularly on *Zostera noltii*. Leuschner and Rees (1993), Pérez-Lloréns and Niell (1994) and Leuschner et al. (1998) measured apparent rates of *Z. noltii* CO_2 uptake in air in laboratorial experiments. These measurements were performed with minicuvette-type IRGA systems, with individual leaves being incubated in temperature-controlled leaf chambers.

In salt marsh plants and in seagrasses, all CO_2 uptake measurements reported so far were done in air-exposed plants. Considering the long submersion periods that both communities experience along the tidal cycle, it is necessary to also measure CO_2 fluxes underwater.

Streever et al. (1998) described an apparatus which included a closed transparent incubation chamber fitted to the sediment and an external CO_2 analyser. This system proved to be rather efficient in estimating salt marsh productivity in the air. One advantage of this kind of apparatus is that both the plants and the sediments beneath them are included in the incubations, which allows a more reliable measurement of productivity per ground area. We propose that the same concept can be used to examine CO_2 fluxes during submersed conditions by equilibrating CO_2 between water and a low-volume air circuit circulating through the IRGA. Efficient exchange columns are now available (e.g., minimodule, CELGARD) which allow the fast equilibration of the gas (i.e., CO_2) partial pressure between water and air and the subsequent analysis of the CO_2 partial pressure in air.

Here, we examine the consistency of physiological-level estimates of photosynthesis derived using Chl *a* fluorescence methods on individual leaves and community-level estimates of productivity from the gross CO_2 uptake of intertidal stands of the cordgrass *Spartina maritima* and the seagrass *Z. noltii*, both when exposed to the air and during submersion. Specific objectives were (i) to investigate the differences in the photosynthetic behaviour of *Z. noltii* and *S. maritima* communities in the two contrasting situations they experience during a tidal cycle, air exposure and submersion and (ii) to determine the contribution of these dominant species to the pattern of photosynthetic carbon fixation within their respective communities, establishing a relationship between individual plant chlorophyll *a* fluorescence measurements and community CO_2 fluxes.

2. Materials and methods

We followed the same basic approach of Streever et al. (1998), i.e., to use large incubation chambers fitted to the sediment and to route the air through an external gas analyser for continuous carbon dioxide flux measurements. When submersed, water from the incubation chamber was circulated through a closed circuit fitted with a gas exchange column connected to a short, low-volume closed air circuit circulating through an IRGA. The CO_2 fluxes derived from this system represent the net metabolism of the entire community dominated by the target plant species both in the water and in the air. The simultaneous measurement of the individual plants photosynthetic activity by chlorophyll fluorescence allowed us to assess how the community metabolism (CO_2 fluxes) compared with plant photosynthesis.