Assessing photosynthetic radiation-use efficiency of emergent aquatic vegetation from spectral reflectance

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Accepted 19 November 1996

Abstract

We studied the reflectance spectra of the emergent aquatic vegetation of Searsville Lake in coastal central California using a high spectral resolution hand-held spectroradiometer with the aim of assessing spectral indices as indicators of photosynthetic radiation-use efficiency. The photochemical reflectance index (PRI), defined as \((R_{531} - R_{570})/(R_{531} + R_{570})\), was strongly correlated with the ratio of secondary and protective pigments to chlorophyll \(a\) and with epoxidation state (EPS) of the xanthophyll cycle pigments (violaxanthin + 0.5 antheraxanthin)/(violaxanthin + antheraxanthin + zeaxanthin), and therefore, with photosynthetic radiation-use efficiency (PRUE) (measured as \(\text{mol CO}_2 \text{ mol}^{-1} \text{ photons}\)). This reflectance-based measure seems to be useful as a remote index of aquatic vegetation photosynthetic function and physiological status. These results extend and reinforce previous studies conducted in terrestrial vegetation that indicate a functional relationship between PRI, EPS, and PRUE at leaf and canopy scales. © 1997 Elsevier Science B.V.

Keywords: Emergent aquatic vegetation; Photosynthetic radiation-use efficiency (PRUE); Epoxidation state (EPS); Reflectance; Photochemical reflectance index (PRI)

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\textit{P}II S0304-3770(97)00042-9
1. Introduction

Remote sensing provides a growing set of tools for characterizing vegetation types and quantifying their processes (Peñuelas et al., 1993). Aerial photography has already been used to map aquatic vegetation (Orth and Moore, 1981, 1983; Dervieux and Tamisier, 1987; Nohara, 1991). Satellite images have also been used for detecting and mapping aquatic vegetation (Jensen et al., 1980; Ackleson and Klemas, 1987). Although the reflectance spectra of water masses are now understood quite well (Raitala and Lampinen, 1985), the reflectance of aquatic plants themselves has been less studied (Ackleson and Klemas, 1987; Peñuelas et al., 1993), mainly because of difficulties of interpretation resulting from water absorption in the infrared.

Our aim here was to assess the prospects for estimating pigment composition and photosynthetic behavior of aquatic emergent plants by using narrow reflectance spectral bands. The study focused on broad-leaved, emergent species for which photosynthesis can be measured more easily in the field and for which interference from water masses was minimal. We analyzed reflectance spectral signatures and spectral indices based on our previous work on pigment ratios between carotenoids and chlorophylls (Peñuelas, 1984a,b; Peñuelas et al., 1994) and on xanthophyll signals (Gamon et al., 1990, 1992; Peñuelas et al., 1995; Filella et al., 1996). The ratio of total pigments to chlorophyll a should rise in decaying plants and decrease in healthy plants (Peñuelas, 1984a,b). The Epoxidation state (EPS) of the xanthophyll cycle pigments should decrease when plants are under stress (Demmig-Adams et al., 1989). We focused on reflectance changes at 531 nm that are widespread among plant species upon changing illumination (Gamon et al., 1993). These reflectance changes are related to chloroplast conformational changes, thylakoid ΔpH, and related xanthophyll pigment interconversion, and therefore are closely related to PSII photochemical efficiency (Bilger and Lesch, 1995). When stress causes a decrease in photosynthesis rate, the ratio of photosynthetically active photon flux density (PPFD) to photosynthesis increases, even if the PPFD remains constant. This excess radiation induces photoprotective mechanisms such as dissipation as heat. There is strong evidence that zeaxanthin plays a role in this dissipation of excess energy (Demmig et al., 1988; Khamis et al., 1990; Maxwell et al., 1994). The photochemical reflectance index (PRI) based on reflectance changes at 531 nm linked to zeaxanthin formation (Peñuelas et al., 1995), was studied in a range of emergent aquatic species of Searsville Lake in California as a possible remote indicator of their photosynthetic function.

2. Material and methods

2.1. The study area

Searsville Lake is situated in Stanford University's Jasper Ridge Biological Preserve (37° 24' N, 122° 13' W) in coastal central California (San Mateo County, California, USA). It is a small lake (20 Ha) with luxurious aquatic vegetation. The
maximum depth is about 5 m in very limited areas, but most of the lake is very shallow, thus facilitating the growth of emergent macrophytes. The most abundant aquatic plants are the submerged Ceratophyllum demersum L., Myriophyllum aquaticum (Velloso) Verdc., M. verticillatum L., Chara sp., Potamogeton illinoensis Morong, P. pusillus L. and P. foliosus Raf.; the floating Lemna minor L., Azolla filiculoides Lam. and various Chlorophyceae algae; and the emergent Myriophyllum aquaticum, M. verticillatum, Ludwigia palustris (L.) Elliott and Polygonum lapathifolium L., P. coccineum Muhl., P. punctatum Ell. and Typha latifolia L. (Thomas, 1961).

2.2. Spectral reflectance

The fieldwork was conducted during the summer of 1990. We measured spectral reflectance in late morning and early afternoon on cloudless days with similar daily courses of PPFD. For each site, most of which consisted of a single, predominant species, we made three to five replicate determinations of spectral reflectance with a spectroradiometer outfitted with 15° field-of-view optics (SE 590 Spectron Engineering, Inc., Denver, CO, USA). During each measurement, the instrument was held in a nadir orientation, approximately 1 m above the top surface of the vegetation. The instrument detects approximately 252 evenly spaced spectral bands between 390 and 1100 nm. Reflectance was calculated by dividing the radiance detected from the canopy by the radiance from a horizontal white halon panel used as the reflectance standard (Gamon et al., 1990).

The broadband Normalized Vegetation Reflectance Index (NDVI) was estimated as described in Peñuelas et al. (1993). We explored two additional narrow-band spectral indices with the potential to indicate physiological status, based on previous work using absorbance and reflectance ratios to evaluate the ratio of total pigments to chlorophyll a (Peñuelas, 1984a;b; Peñuelas et al., 1994; Filella et al., 1995) and using reflectance signatures to assess the EPS of the xanthophyll cycle (Gamon et al., 1990, 1992; Peñuelas et al., 1995; Filella et al., 1996). We tested the Normalized total Pigment–Chlorophyll a ratio Index (NPCI), defined as \(\frac{R_{430} - R_{680}}{R_{430} + R_{680}}\), to estimate the ratio of total pigments to chlorophyll a and the PRI, defined as \(\frac{R_{531} - R_{570}}{R_{531} + R_{570}}\), to estimate the EPS of the xanthophyll cycle pigments.

2.3. Physiological measurements

For each emergent macrophyte, we measured the net CO₂ uptake rate of three to five upper, mature leaves in the spectroradiometer field of view, near the canopy top. These leaves were typical of those that contributed most of the radiance detected by the spectroradiometer. Gas exchange rates were determined with a portable gas exchange system (LI-6200, LI-COR, Inc., Lincoln, NE, USA). PRUE was determined as the ratio of net CO₂ uptake to the incident PPFD measured at the leaf chamber, and corrected for the transmittance of the chamber lid.
Five leaves of similar size, orientation and canopy position to the gas exchange leaves were used for pigment analyses. Leaf discs were punched with a cork borer, rapidly frozen in liquid nitrogen, taken to the lab and stored in the dark at \(-60^\circ\text{C}\) for later analysis. Violaxanthin (V), antheraxanthin (A), zeaxanthin (Z), lutein, neoxanthin, \(\alpha\)-carotene, \(\beta\)-carotene, chlorophyll \(a\) and chlorophyll \(b\) extraction and analysis followed the HPLC procedure of Thayer and Björkman (1990). Each data point consisted of five samples extracted and assayed together and thus represents the mean of five top-canopy leaves.

To determine emergent biomass, we harvested all biomass within vertical cylinders 0.25 m in diameter. The material was transported to the lab in plastic bags on ice, and then oven-dried to a constant mass at 65\(^\circ\text{C}\).

3. Results and discussion

3.1. The photochemical reflectance index (PRI) and photosynthetic radiation-use efficiency (PRUE)

The reflectance spectra of emergent species had more distinct red/near-infrared boundaries than those of either submerged or floating species (Peñuelas et al., 1993). The high near-infrared reflectances and relatively low red reflectances of Myriophyllum, Ludwigia and Polygonum species were due to the luxuriant canopy development of these emergent species. Fig. 1a shows representative spectra for a typical emergent aquatic species, Ludwigia palustris, in a healthy stand compared with a chlorotic stand.

When comparing reflectance of chlorotic and healthy Ludwigia palustris canopies with different PRUE values, a dip near 531 nm appears indicating lower reflectance in this area for the chlorotic canopy (arrow, Fig. 1b). We associated this reflectance trough with the signal at 531 nm linked to zeaxanthin, EPS and PRUE, as described by Gamon et al. (1990), Gamon et al., 1992, Peñuelas et al. (1994, 1995), and Filella et al. (1996). PRUE values of canopies decreased at midday (not shown) and was lower in the stressed chlorotic canopies. As expected, both PRI and EPS varied with PRUE, presumably because of the role of zeaxanthin in dissipating excess radiation (Fig. 2) (Björkman and Demmig-Adams, 1995). Lower values of EPS and PRI, associated with lowered PRUE values, indicate enhanced thermal dissipative processes. This dissipation allows PSII to remain relatively oxidized under conditions of limited carbon uptake, thus protecting the plant from photoinhibitory damage. There were larger amounts of xanthophylls relative to chlorophyll \(a\) in chlorotic than in healthy Ludwigia palustris indicating a higher investment in protective pigments (data not shown). PRI was also correlated with the carotenoid–chlorophyll \(a\) ratio (Fig. 3), which provides another measure of protective pigment content. In other studies with plants suffering high light and additional stresses (Demmig et al., 1988; Khamis et al., 1990; Maxwell et al., 1994), decreases in the efficiency of photosynthetic energy conversion were also associated with changes in zeaxanthin formation and thermal energy dissipation. At midday, in parallel to PRUE, PRI was significantly different \((P < 0.01)\) between
Fig. 1. (a) Spectral reflectance for characteristic healthy and chlorotic emergent *Ludwigia palustris* canopies of Searsville Lake (California), and (b) ratio of reflectance spectra (chlorotic/healthy). Arrow marks 531 nm.

the healthy and the chlorotic *Ludwigia palustris* canopies (Figs. 1 and 2), indicating that PRI was not an artifact of sun angle changes and, therefore, that this reflectance index is able to distinguish the PRUE values of these two emergent aquatic plant canopies exposed to identical illumination.

One potential limitation of this study was the small sample size (eight averages of three to five spectral replicates each, corresponding to eight stands dominated by either *Ludwigia palustris* or *Polygonum* spp.). Many of the relationships were strongly driven by a single mean representing five scans on a chlorotic *Ludwigia palustris* canopy that expanded the range of physiological status. Despite the limited sample size, the results are consistent with a growing body of similar studies on terrestrial plants.

PRI like NPCI was correlated to carotenoids/chlorophyll a (Fig. 3) in another indication of scaling between general physiological status (assessed by NPCI) and short-term PRUE (assessed by PRI). The widely used NDVI of the emergent aquatic plants apart from being correlated with plant chlorophyll concentration (Fig. 4), was also correlated with total carotenoids/chlorophyll a, neoxanthin, lutein, photosynthetic efficiency, and the EPS of the xanthophyll cycle pigments.
Fig. 2. Relationship of PRUE, photosynthetic radiation-use efficiency (mol CO₂ mol⁻¹ photons), with EPS (Epoxidation State of the xanthophyll cycle pigments) and PRI (Photochemical Reflectance Index) in *Ludwigia palustris* and *Polygonum* spp. canopy tops (*n* = 8 means of 3–5 measurements each).

Fig. 3. Relationship between PRI and carotenoids/chlorophyll a ratio in *Ludwigia palustris* and *Polygonum* spp. canopy tops (*n* = 8 means of 3–5 measurements each).

(Peñuelas et al., 1993). Therefore, it was difficult to distinguish photosynthetic function from canopy structure and biomass, probably as a consequence of the high proportion of green biomass of these aquatic emergent plants (NDVI was highly correlated with chlorophyll (Fig. 4)).

3.2. Photochemical reflective index (PRI) and remote sensing applications

This application of spectral reflectance to assess photosynthetic function through PRI opens additional opportunities in the field of remote sensing of aquatic plants, where even accepting that remote sensing can estimate canopy photosynthetic
capacity through vegetation indices such as NDVI, it is not clear how much of this capacity is realised in practice (Field et al., 1995; Gamon et al., 1995). By tracking short-term changes in photosynthetic light regulation at PSII, PRI provides a new way to assess the photosynthetic efficiency using spectral reflectance.

However, application of PRI at canopy scale requires attention to disturbing effects of canopy structure, sun angle, and leaf movement on this relatively small reflectance signal. Normalization of $R_{531}$ by reflectance at 570 nm partly corrects for these complicating effects. Applications at the landscape and larger scales would presumably be challenged by additional complications associated with aircraft and satellite remote sensing that include varying landscape composition, atmospheric and water interference and calibration errors (Guyot, 1990; Gamon et al., 1995). However, the generally consistent correlation between PRI and photosynthetic efficiency found here and also reported in terrestrial leaves and canopies (Gamon et al., 1992; Peñuelas et al., 1995; Filella et al., 1996) indicates that this index might be applied as a useful tool for non-destructive, non-contact optical study of emergent aquatic plant photosynthetic function at the leaf and canopy levels.

Future work must be done under conditions where canopy structure and biomass do not necessarily scale with physiological activity to further test the utility of these remote indices.

Acknowledgements

We thank the Jasper Ridge Biological Preserve for permission to study the lake and for the use of the spectroradiometer, and K. Griffin for field assistance. Grants from CICYT AMB94-0199 (Spain) to Josep Peñuelas are gratefully acknowledged.
References


