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SCIENCE DIRECT

Remote Sensing of Environment 97 (2005) 403 – 414

Remote Sensing of Environment

www.elsevier.com/locate/rse

Simple reflectance indices track heat and water stress-induced changes in steady-state chlorophyll fluorescence at the canopy scale

S.Z. Dobrowski [a,*], J.C. Pushnik [b], P.J. Zarco-Tejada [c], S.L. Ustin [a]

[a] *Center for Spatial Technologies and Remote Sensing, University of California, Davis, Davis, CA, USA*
[b] *Department of Biological Sciences, California State University, Chico, Chico, CA, USA*
[c] *Instituto de Agricultura Sostenible (IAS), Consejo Superior de Investigaciones Científicas (CSIC), Córdoba, Spain*

Received 2 March 2005; received in revised form 28 April 2005; accepted 22 May 2005

Abstract

Non-invasive remote sensing techniques for monitoring plant stress and photosynthetic status have received much attention. The majority of published vegetation indices are not sensitive to rapid changes in plant photosynthetic status brought on by common environmental stressors such as diurnal fluxes in irradiance and heat. This is due to the fact that most vegetation indices have no direct link to photosynthetic functioning beyond their sensitivity to canopy structure and pigment concentration changes. In contrast, this study makes progress on a more direct link between passive reflectance measurements and plant physiological status through an understanding of photochemical quenching (qP) and non-photochemical quenching processes. This is accomplished through the characterization of steady-state fluorescence (Fs) and its influence on apparent reflectance in the red-edge spectral region. A series of experiments were conducted under controlled environmental conditions, linking passive reflectance measurements of a grapevine canopy (*Vitis vinifera* L. cv. Cabernet Sauvignon) to leaf level estimates of CO_2 assimilation (A), stomatal conductance (g), qP, and Fs. Plant stress was induced by imposing a diurnal heat stress and recovery event and by withholding water from the plant canopy over the course of the experiment. We outlined evidence for a link between Fs and photosynthetic status, identified the Fs signal in passive remote sensing reflectance data, and related reflectance-derived estimates of Fs to plant photosynthetic status. These results provide evidence that simple reflectance indices calculated in the red-edge spectral region can track temperature and water-induced changes in Fs and, consequently, provide a rapid assessment of plant stress that is directly linked to plant physiological processes.

Keywords: Plant stress monitoring; Chlorophyll fluorescence; Remote sensing; Photochemical quenching; Non-photochemical quenching; Grapevines

1. Introduction

Much effort has been devoted to developing non-invasive remote sensing techniques for monitoring plant stress and photosynthetic status. Most remotely sensed vegetation indices are used for characterizing the amount and spatial distribution of vegetation (Baret & Guyot, 1991; Price, 1992). Vegetation indices have also been used to estimate potential levels of canopy photosynthesis and net primary productivity with mixed success (Choudhury, 2001; Gamon et al., 1995; Verma et al., 1993). Nevertheless, the majority of published vegetation indices are not sensitive to rapid changes in plant photosynthetic status brought on by common environmental stressors such as diurnal fluxes in irradiance and heat. This is due to the fact that most vegetation indices have no direct link to photosynthetic functioning beyond their sensitivity to canopy structure (e.g., leaf angle) and pigment concentrations. Consequently, measurements of canopy reflectance have proven less useful for real-time monitoring of plant photosynthesis and/or water status at the whole plant level (Gamon et al., 1990; Peñuelas et al., 1995).

One exception to this involves remote estimates of the xanthophyll cycle captured by the photochemical reflec-

* Corresponding author. Tel.: +1 530 752 5092.
E-mail address: szdobrowski@ucdavis.edu (S.Z. Dobrowski).

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doi:10.1016/j.rse.2005.05.006

tance index (PRI) (Gamon et al., 1990, 1992, 1995, 1997). The PRI has been linked to the status of the epoxidation state of xanthophyll pigments, one of the components of the non-photochemical de-excitation pathway (Demmig-Adams & Adams, 1992). The PRI is intended for estimating changes in xanthophyll cycle pigments as they vary due to changes in photosynthetic light use efficiency (Gamon et al., 1992, 1997; Peñuelas et al., 1995, 1997). The PRI is one of the few spectral indices which has been shown to be sensitive to rapid changes in plant photosynthetic status (Gamon et al., 1990, 1992, 1997; Peñuelas et al., 1997).

A similar avenue of research gaining both past and recent attention is the study of chlorophyll fluorescence (CF) as a means for the remote estimation of plant physiological status. CF is a protective process by which plants dissipate energy that is in excess of photosynthetic demands. CF is emitted primarily from chlorophyll *a* of the antennae system of photosystem 2 (PS II). Any physiological process that influences the function of photosystem II and other photosystem de-excitation pathways will have an effect on CF. There are two main controls on the relaxation pathways: (i) the redox state of plastoquinone, the primary stable electron acceptor of PSII, which determines the level of quenching by photochemistry (qP); and (ii) the changes in non-photochemical quenching processes, which are light-induced protective processes that result in the de-excitation of the chlorophyll singlet to the ground state with the production of heat (Johnson et al., 1994; Müller et al., 2001; Pospisil, 1997). CF, qP, and non-photochemical quenching all have rate constants associated with them and any process that increases the rate constants of the other de-excitation pathways will decrease CF intensity (Bjorkman & Demmig-Adams, 1994; Demmig-Adams & Adams, 1992).

CF intensity can vary over time as a function of the photosynthetic activity of the plant tissue being measured. This relationship was initially described by Kautzky (Kautzky & Hirsch, 1931) and has garnered much attention from plant physiologists who have used leaf level CF measurements as a non-invasive plant monitoring tool for many years. More specifically, leaf level CF measurements utilizing a class of instruments known as pulse amplitude modulating fluorometers have been used with varying degrees of success to estimate plant stress, quantum yield, PS II efficiency, and electron transport rates. CF measurement, interpretation, and relation to photosynthesis and plant physiological status have been the subject of several detailed reviews (Larcher, 1994; Lazar, 1999; Lichtenthaler, 1992).

In addition to leaf level measurements, CF can be measured for entire leaves and plants. Fluorescence imaging, as it is commonly referred to, is conducted using laser or flash lamps to induce CF. Concurrently, spectral or imaging sensors are used to measure the CF signal for entire leaves, groups of leaves, or entire plants depending on the sensor type and configuration. These types of measurement systems have been shown to be effective for non-destructive monitoring of plant stress and functioning at near distances and far distances (for reviews, see Buschmann et al., 2000; Lang et al., 1996). Unfortunately, the application of these techniques to larger spatial scales is limited primarily by the small spatial extent of the laser induction pulse as well as incomplete coverage in the spatial domain.

An area of active CF research is exploring the link between steady-state fluorescence (Fs) and plant photosynthetic status. Fs is the fluorescence emitted under constant illumination without saturating flashes. Flexas et al. (1999, 2000, 2002a) showed that Fs exhibits a strong positive correlation with diurnal variations in H_2O stomatal conductance (g), and to a lesser extent, CO_2 assimilation (A) influenced by variable irradiance conditions and water stress. Their findings are promising in that Fs can be monitored directly without the use of laser induction pulses or saturation flashes. This provides an avenue for long-term plant stress monitoring using passive remote sensing strategies. Concurrent to these findings, a small but growing body of research has found support for the potential of identifying the Fs signal in reflectance data from passive platforms at near and far distances. This is further expanded below.

1.1. CF emission spectra

Understanding the spectral characteristics of Fs is critical if remote estimates of its properties are attempted. The emission spectra of chlorophyll fluorescence is characterized by two bands spanning the range between 600 nm and 800 nm but with maxima at 690 nm (F_{690}) and 740 nm (F_{740}) (Buschmann et al., 2000). The intensity, shape, and position of these emission bands are affected by a number of factors. Gitelson et al. (1998) showed that a significant portion of the shape of the CF emission spectra of PS II can be explained by re-absorption processes due to chlorophyll pigments. The re-absorption of fluorescence emission is greatest at F_{690} because this emission peak overlaps the in vivo chlorophyll *a*, and to a lesser extent, chlorophyll *b* absorption maxima located in this region of the spectrum. This suggests that the F_{690} intensity is sensitive to chlorophyll concentration of the leaf tissue as was demonstrated by a number of investigators (Gitelson et al., 1998, 1999). In contrast, F_{740} is minimally affected by chlorophyll concentration, and thus, the ratio F_{690}/F_{740} has been shown to be inversely related to chlorophyll content (Gitelson et al., 1998; Lichtenthaler et al., 1998).

1.2. Fs and remote sensing

The remote detection of Fs in vegetation using passive remote sensing techniques is in a nascent state. Early on, investigators showed that Fs was related to water stress and photosynthetic function using a Fraunhofer line discrim-