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Diurnal response of effective quantum yield of PSII photochemistry to irradiance as an indicator of photosynthetic acclimation to stressed environments revealed in a xerophytic species

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A B S T R A C T

Monitoring responses of plants to stresses *in situ* using the chlorophyll-fluorescence (ChlF) technique has been of growing interest, but challenged by lack of stable daytime indicators, limiting the method's application. Seasonal changes in diurnal responses of effective quantum yield of photosystem II (PSII) photochemistry (Φ_{PSII}) to photosynthetically active radiation (PAR) have been assumed to reflect changes in physiological status of plants in changing environments. We examined the responses of diurnal Φ_{PSII} to PAR in relation to environmental factors through continuous season-long monitoring of ChlF of PSII in a desert shrub species, *Artemisia ordosica*. Response data were analysed with a modification of the diurnal regression method by Durako (2012). Diurnal variation in Φ_{PSII} for *A. ordosica* was largely controlled by PAR, decreasing with increasing PAR. The rates of the response of diurnal Φ_{PSII} to PAR (slopes) were down-regulated by seasonal changes in environmental factors, in particular, high values for daily mean air temperature (T_a) and vapor pressure deficit (VPD), and up-regulated with increases in soil water content (SWC). The y-intercepts of diurnal Φ_{PSII}-PAR regressions were linearly related to maximal quantum yield of PSII photochemistry (F_v/F_m) during the growing season, increasing with increasing SWC. Our results confirm the suggestion by Durako (2012) that the y-intercept of diurnal Φ_{PSII}-PAR relationship serves as a good proxy for F_v/F_m in non-invasive monitoring of the physiological status of plants with the ChlF technique.

1. Introduction

Semi-arid and arid areas (drylands) cover about 40% of the Earth's terrestrial surface and contribute to approximately 40% of terrestrial net primary production (Wang et al., 2012). Dryland plants are beginning to exhibit significant stress as low precipitation and drought events become more prevalent under a changing climatic regime (Li et al., 2013).

Multiple stresses of varying severity and duration can reduce photosynthetic assimilation (Vitolo et al., 2012; Bertolli and Souza, 2013). During photosynthesis, ~5% of absorbed light energy by photosystem II (PSII) is re-emitted as chlorophyll-fluorescence (ChlF). Changes in ChlF induced by illumination of dark-acclimated leaves can be qualitatively correlated with changes in photosynthetic CO_2 assimilation. Fluorescence emissions in photosynthetic organisms can be correlated to their photosynthetic rates (Logan et al., 2007; Durako, 2012). As a result, there is growing interest in monitoring responses of vegetation to stresses by observing ChlF, which can be applied rapidly and in a non-destructive manner, giving insight as to the ability of plants to tolerate environmental stresses and extent

Abbreviations: ChlF, chlorophyll-fluorescence; PSII, photosystem II; Φ_{PSII}, effective quantum yield of PSII photochemistry; F', steady-state fluorescence yield of the light acclimated state; F_m, maximal fluorescence yield of the dark-acclimated state; F_m', maximal fluorescence yield of the light-acclimated state; F_o, minimal fluorescence yield of the dark-acclimated state; F_o', minimal fluorescence from the light-acclimated state; F_v, variable fluorescence; F_v/F_m, maximal quantum yield of PSII photochemistry; PAR, photosynthetically active radiation; PPT, precipitation; RH, relative humidity; SWC, soil water content; T_a, air temperature; VPD, vapor pressure deficit.

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these stresses may have inhibited or damaged the photosynthetic apparatus *in vivo* (Logan et al., 2007; Baker, 2008).

PSII photochemistry is considered to be the most sensitive part of the photosynthetic pathway to stress (Becker et al., 1990). Pulse-amplitude modulated (PAM) fluorescence measurements have been used to identify changes in physiological status in response to varying environmental conditions before morphological changes are evident (Ralph et al., 2007; Durako, 2012; Murchie and Lawson, 2013). PAM-fluorometry has become a powerful tool in the study of plant photosynthesis and is increasingly being used for ecological monitoring *in situ* (Campbell et al., 2003; Adams and Demmig-Adams, 2004; Durako, 2012). Maximal quantum yield of PSII photochemistry (F_v/F_m), a parameter derived by PAM-fluorometric measurements, reflects the potential quantum efficiency of PSII, which is used as an indicator of plant photosynthetic performance and health status (Zunzunegui et al., 2011; Wong et al., 2012). However, measurements of F_v/F_m need to ensure that all PSII-reaction centres open rapidly at the end of an illumination event, prior to full darkness. This requirement of darkness makes it particularly difficult to obtain daytime indicators in the field with *in-situ* monitoring.

Recently, Durako (2012) suggested that regression slopes and y-intercepts of diurnal relations between photochemical efficiency of PSII (Φ_{PSII}) and photosynthetic active radiation (PAR) can assist with assessing the physiological status of marine seagrass. This is possible because diurnally-based regression coefficients are less sensitive to changing irradiance than are individual values of Φ_{PSII}. Regression slopes in this context reflect the amount of absorbed light energy used for photosynthesis as PAR changes, with excess energy dissipated as heat (Howarth and Durako, 2013). Increasing magnitude of negative slopes represent plants' increasing inability to dissipate excess energy, thus slopes can be used as a measure of photochemistry sensitivity to stressed conditions. The y-intercepts (photochemical efficiency, modeled value when PAR = 0) during daytime hours provide estimates of F_v/F_m at night, with high values reflecting high F_v/F_m. Therefore, variations in the relationship between diurnal Φ_{PSII} and PAR reflect changes in the efficiency of the dissipation of excess energy and physiological and photo-acclimation state of the vegetation during any given time period (Wong et al., 2012; Tubuxin et al., 2015). Here, we investigated whether the slope and y-intercept could effectively reveal the photosynthetic performance of xerophytic plants to environmental stress in drylands.

Drylands offer contrasting challenges for plant growth that fluctuate between high-to-low solar radiation and temperatures and short-to-long term droughts (Reynolds et al., 2007). Plants growing in such environments should, in principle, provide a good examination of the ecological utility of field measurements of ChlF. The ecological and physiological responses of these plants to various environmental stresses have been a growing concern for scientists, particularly under global climate change. *Artemisia ordosica* is a widely distributed xerophyte in deserts. Some studies in understanding photo-acclimation in *A. ordosica* to stresses have been carried out at fix times using the ChlF technique (Xiao et al., 2003; Wu et al., 2015). Mechanisms of long-term acclimation in stressed environments through photochemical and non-photochemical protective mechanisms in plants are largely unknown. Long-term monitoring of ChlF provides an opportunity to fill this knowledge gap.

In this study, photosynthetic response in *A. ordosica* was continuously monitored with the ChlF technique during the growing season of 2013. Specific objectives of our study were to: (1) examine diurnal and seasonal processes of photosynthetic performance in response to varying environmental conditions, and (2) examine the role of the y-intercept in diurnal Φ_{PSII}-PAR relationships as a suitable eco-indicator of F_v/F_m in this xerophytic plant.

2. Materials and methods

2.1. Study site

The study was conducted at the Yanchi Research Station (37.73° N, 107.26° E, 1 550 m a.s.l.) of Beijing Forest University, Ningxia, northwest China. The site is located at the southern edge of the Mu Us desert and is characterized by a semi-arid continental monsoon climate. Mean annual temperature (1954–2004) is 8.1 °C (Wang et al., 2014). Mean annual rainfall is about 292 mm, most of it falling during the period from July through September (Wang et al., 2014). Mean annual total potential evapotranspiration is 2024 mm. Dominant shrub species of the area include *Artemisia ordosica*, *Salix psammophila*, *Hedysarum scoparium*, *Hedysarum mongolicum*, and *Caragana korshinskii*.

2.2. Chl fluorescence measurements

Continuous half-hourly measurements of ChlF were made *in situ* from 1 June to 30 September, 2013, with a MONITORING-PAM Multi-Channel Chlorophyll Fluorometer (Walz, Effeltrich, Germany). Attached branches were tied to aluminum supports, on which a MONI-head/485 fluorometer was fixed so that both the MONI-head and branches move together in the wind. The intensity of the measuring light and the saturating pulses were 0.9 μmol m^{-2} s^{-1} and 3500 μmol m^{-2} s^{-1}, respectively. A cluster of healthy leaves was clamped and the location of the head was adjusted to prevent shading. Photochemical efficiency of PSII (Φ_{PSII}) and maximal quantum yield of PSII photochemistry (F_v/F_m) were determined as:

$$\Phi_{PSII} = (F'_m - F')/F'_m, \quad (1)$$

$$F_v/F_m = (F_m - F_o)/F_m, \quad (2)$$

where, F' is the steady-state chlorophyll fluorescence in ambient light and F_m' is the maximum fluorescence in ambient light following a saturating light pulse. Daytime F' and F'_m become nighttime F_o and F_m, respectively (Porcar-Castell et al., 2008).

2.3. Meteorological measurements

Environmental factors were measured simultaneously. Incident photosynthetically active radiation (PAR) was measured using a quantum sensor (PAR-LITE, Kipp and Zonen, the Netherlands). Air temperature (T_a) and relative humidity (RH) were measured with a thermohygrometer (HMP155A, Vaisala, Finland). Vapor pressure deficit (VPD) was calculated from T_a and RH (VPD = 0.611e$^{17.27T/(T+237.3)}$(1-RH/100)). Soil water content (SWC) at 0.1 m depth were monitored using ECH$_2$O-5TE sensors (Decagon Devices, USA). Precipitation (PPT) was measured with a tipping bucket raingage (TE525WS, Campbell Scientific Inc., USA). All meteorological variables were measured every 10 s, which were then averaged or summed to generate 30-min values before being stored in dataloggers (CR200X for PPT, CR3000 for all others, Campbell Scientific Inc., USA).

2.4. Data processing and analysis

Raw data were processed using the batch file feature of the WinControl-3 software (pre-installed on datalogger). ChlF-values were screened using limit checking. Half-hourly values of F' under 100 (non-dimensional) were considered abnormal and were removed from the dataset. Data during rainy days with daily total