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A biophotonic sensing method for plant drought stress

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ABSTRACT

Physiologically-based drought stress evaluation is very desirable for sustainable plant production, but effective measures and technologies are lacking. Drought stress limits photons utilized for photosynthetic reactions and delayed fluorescence (DF) generated by photosystem II (PSII). In this research, DF is measured as an output variable of the PSII phototransduction system and its dependence on photon utilization rate as affected by water status is modeled and analyzed. This yields an effective way to define and measure plant water status or deficiency (drought stress) according to PSII photon utilization rate. Water deficiency is determined by the deficit from the maximum photon utilization rate achievable through rehydration. The method was validated experimentally with drought-stressed plant samples. Analysis and experiments show that this drought-dependent deficit in photon utilization rate can be effectively evaluated from measured DF emissions and it varies with drought severity.

1. Introduction

Measurement technologies are important to site-specific management and sustainable plant production [1]. Many sensors have been reported for monitoring plant health conditions, evaluating photosynthetic activities, and quantifying nutrient needs. An FPGA-based fused smart sensor was developed for real-time plant-transpiration dynamic estimation by Millan-Almaraz et al. [2], which permitted users to observe measured and computed variables at the same time. Smart cameras are essential for precision agriculture but high cost often limits their applications. In Dworak et al. [3], a smart one-chip camera with NDVI (normalized difference vegetation index) capability was demonstrated in terms of low cost and simplified design. Contreras-Medina et al. [4] reported an FPGA-based smart sensor that can indicate plant health and nutrition conditions. Barócsi [5] developed a complete sensor that is capable of online extraction of features with phenotypically-relevant information from fluorescence data. Kissinger and Wilson [6] designed a portable fluorescence-lifetime-detection system for chlorophyll analysis in marine environments with reduced power consumption.

Water is essential for plant growth and modern agriculture relies on irrigation. Only one sixth of the agricultural land in the world is irrigated but it produces more than one third of the total food [7,8]. Water resource, however, has become limited. For example, California alone is short of 2.46-billion cubic meters of water annually for an average-rainfall year and the shortage is much greater for drought years [9]. Restrictive laws have been erected in many European countries to limit water wastage [10]. As the world turns to biomass as a significant source of energy and other renewable products, the need for water will further increase in great quantities. Efficient use of water has become extremely critical for the environmental and economical sustainability of the world.

Optimized irrigation should regulate the timing and quantity of applied water to satisfy the continuously changing crop requirements without wastage [11]. Traditional irrigation scheduling methods mainly rely on soil moisture measurements or soil water balance calculations [12–14]. In Charoenhirunyingyos et al. [15], soil hydraulic parameters were estimated from a leaf area index and actual evapotranspiration based on satellite observations. Champagne et al. [16] investigated the possibility of quantifying surface soil moisture conditions through passive microwave remote sensing. Soil water is often maintained close to its capacity, but plants respond directly to water in plant tissues rather than that in soil [17]. Simply maintaining high soil moisture thus results in wastage of water, energy and labor. Excessive irrigation may also cause fertilizer runoff and over-seepage, leading to fertilizer waste and water pollution.

It has been long proposed to use plant-based methods to assess crop conditions [18]. Thermal sensing of stomatal closure [19] and trunk diameter variations [9,20,21] have been used as plant-based methods to indicate drought stress in previous research. By comparing with water potential and stomatal conductance measurements, Ballester et al. [22] concluded that canopy temperature obtained from thermal imaging is a good tool to predict drought stress effects on fresh fruit weight. Zhao et al. [23] developed a 3D-image method to estimate morphological wilting of plants for drought stress assessment. In Fensholt et al. [24], shortwave

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infrared reflectance data from polar orbiting and geostationary platforms were used to detect canopy water status. Jones [17] reviewed existing work and pointed out the need for effective plant-based drought stress sensors.

A major physiological function of water in plants is to serve as the electron donor. When plant chlorophylls capture photons, the light energy is passed to electrons that must be continuously replenished with electrons originating from water molecules. The energy carried by electrons is transported forward for subsequent photochemical reactions, and part of the energy may revert to photo-energy in the form of delayed fluorescence (DF) off the antenna complexes of photosystem II (PSII) [25,26]. Drought stress limits photons used for photosynthetic reactions and CO_2 assimilation [27] and reduces DF generation by PSII [28]. If water availability is limited, therefore, photon utilization efficiency is hampered. Different from prompt fluorescence, which results from the action of a single molecule, DF generation depends on the inner workings of a functional PSII and thus on the water-dependent photon utilization process. This makes DF a potentially useful indicator of photosynthesis efficiency and plant stresses [29–31].

In this research, the influence of water on photon utilization rate is exploited for a physiologically-based measure and a measurement method of plant drought stress. Phototransduction in PSII was modeled with DF as a measurable output previously [28,35]. Based on the model, DF emission is analyzed and modeled as a function of the water-dependent photon utilization rate. Coupled with rehydration, the analysis provides both a measure and a measurement technique of water deficiency in photosynthetic plants.

2. Dependence of DF emission on plant water status

After absorbing a photon, a chlorophyll molecule becomes excited and is commonly denoted as P680*. P680* may quickly pass the excited electron to the PSII electron transport chain and become oxidized ($P680^+$). $P680^+$ returns to the original state and is ready to accept another photon by acquiring an electron that originates from H_2O.

The water molecule is very stable. The OEC (oxygen-evolving complex) is the only known biological system in nature that can oxidize water [32]. The chemistry details of water oxidization by the OEC are not fully known; but Kok's clock hypothesis (or the S-State model) has been widely accepted and substantially proven, which states that Mn ions undergo cyclic oxidization states labeled as S_0, S_1, S_2, S_3, and S_4 [32]. When a Mn ion loses four electrons to $P680^+$ and reaches the quadruple-oxidized S_4 state, it quickly takes electrons from water molecules and returns to the S_0 state. This leads to the following changes to the water molecules:

$$2H_2O \rightarrow O_2 + 4e^- + 4H^+ \tag{1}$$

Regardless of the exact mechanism and process, it is known that water serves as the source of electrons for the photosynthetic process. Drought stress limits photons taken for photosynthetic reactions and CO_2 assimilation [27] and thus reduces the photon utilization efficiency.

There is not a generally accepted definition for drought or drought stress. Over one hundred definitions of drought can be found in the literature [33,34]. Since a major function of water in plants is photosynthetic electron donation, one meaningful measure of water deficiency or drought would be the degree to which water limits photon utilization rate r_e; in other words, a photosynthesis-based measure of drought can be defined as

$$D = \frac{r_{e_s} - r_{e_w}}{r_{e_s}} \tag{2}$$

where D is drought or water deficiency, r_{e_w} is photon utilization rate of a plant leaf sample with water concentration w, and r_{e_s} is the saturation or maximum r_e value achievable by varying the water concentration in the sample.

Eq. (2) defines drought as a percent deficit in photon utilization rate because of water deficiency. It measures drought by a primary function of water rather than the actual water concentration. This makes sense because water concentration itself may not be as useful an indicator of water deficiency [17]. Furthermore, because photon utilization directly depends on water, D is an indicator of present water availability rather than the long-term effects.

Measures may be defined from different perspectives, but a measure is not useful if it cannot be practically evaluated. Measurement of D defined in Eq. (2) is achieved by measuring DF emissions as discussed below.

In previous work, the transport kinetics of photoelectrons in the early stages of PSII was modeled as state space equations with DF as a measurable output. Experimental validation showed that DF emission could be effectively predicted with a five-state [35] or a three-state model [28]. In this research, measurement of D defined in Eq. (2) is achieved by analyzing the system kinetics based on the five-state model although similar results can also be obtained from the three-state model. The structure of the five-state model is:

$$\begin{Bmatrix} \dot{x}_1 \\ \dot{x}_2 \\ \dot{x}_3 \\ \dot{x}_4 \\ \dot{x}_5 \end{Bmatrix} = A \begin{Bmatrix} x_1 \\ x_2 \\ x_3 \\ x_4 \\ x_5 \end{Bmatrix} + \begin{Bmatrix} k_1 \\ 0 \\ 0 \\ 0 \\ 0 \end{Bmatrix} u \tag{3}$$

$$y = Kk_2(x_1 + x_3 + x_5) \tag{4}$$

where x_1, x_2, x_3, x_4, and x_5 are the probabilities of a reaction center being in plastoquinone states $[Q_A^- Q_B]$, $[Q_A Q_B^-]$, $[Q_A^- Q_B^-]$, $[Q_A Q_B^{2-}]$ or $[Q_A^- Q_B^{2-}]$, respectively; y is the DF emission intensity, u is the intensity of excitation light; K is a gain factor accounting for the instrumentation gain and sample size; and system matrix A is,

$$A = \begin{bmatrix} -k_1u - k_2 - k_3 & k_4 - k_1u & -k_1u & -k_1u & -k_1u + k_5u \\ k_3 & -k_1u - k_4 & k_2 & 0 & 0 \\ 0 & k_1u & -k_2 - k_3 & k_4 & 0 \\ 0 & 0 & k_3 & -k_4 - k_1u - k_5u & k_2 \\ 0 & 0 & 0 & k_1u & -k_2 - k_5u \end{bmatrix} \tag{5}$$

where k_1 through k_5 are reaction rates. The relationship between D defined in Eq. (2) and DF is analyzed as follows.

In the model, k_1 represents the quantum efficiency of photon utilization, which is the percentage of incident excitation photons that generate energized electrons carried forward by the electron transport chain [35]. As discussed earlier, this efficiency is affected by water availability. For a sample of unit area, k_1 and photon utilization rate r_e are related by

$$r_e = k_1 u \tag{6}$$

Furthermore, as demonstrated below, k_1 (or r_e) has a simple direct relationship with DF emission under dark-adapted and short-excitation-pulse conditions.