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Conditional variations in temperature response of photosynthesis, mesophyll and stomatal control of water use in rice and winter wheat

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ABSTRACT

Environmental responses of photosynthesis and CO_2 diffusive conductance as fundamental information for photosynthesis-transpiration coupled model have been increasingly concerned while are still research areas with unanswered questions in cereal crops. Photosynthesis (A), light utilization efficiency (α), mesophyll conductance (g_m) and stomatal coefficient (g_{fac}) in temperate rice and winter wheat were investigated. There were no seasonal trend, no inter- and intra-species differences in relative temperature responses (activation energy ΔH_a) of V_{cmax} or J_{max}. A phenomenon that grain-filling plants generally decreased g_m and had a lower Q_{10} as compared to that at early growth stage existed, particularly in rice. Analyses of environmental influences indicated that optimal temperatures (T_{opt}) in V_{cmax}/J_{max} depended on the prevailing temperature environment. Although prevailing temperature dependence in T_{opt} of g_m was not as profound as that of V_{cmax} or J_{max}, T_{opt} of g_m in winter wheat was significantly lower than rice. Temperature response of R_{dark} in all sampled leaves shared a common trajectory. α were almost invariant, while, high sensitivity to soil desiccation was observed. g_{fac} in sunlit leaves was conservative during wet soil conditions. Shaded leaves with lower N_a had higher g_{fac}, resulting in a negative correlation between N_a and g_{fac} in canopy profiles. g_{fac} was susceptible to fluctuations in soil water potential (ψ_s), rapidly declined at a threshold of top-layer ψ_s approx. −0.1 MPa. Numerical analyses regarding $g_m/V_{cmax}/J_{max}$ effects on photosynthetic performance in rice and between rice and winter wheat documented that in context of climate change, consider growth environment-induced differences in temperature responses of photosynthetic parameters among cereal crops is indispensable to better predict interactions among soil-plant-atmosphere consortium.

1. Introduction

Understanding of leaf assimilatory processes and the mechanisms involved in the phenotypic plasticity of plants in response to their environment is an essential part for the application of photosynthesis-transpiration coupled model (PTC) to estimate the photosynthetic productivity (Lee et al., 2008; Bernacchi et al., 2013; Lombardozzi et al., 2015). Photosynthetic rates of individual leaves under given leaf nitrogen content (N_a) are determined by the light energy conversion efficiency (α), the maximum electron transport rate (J_{max}), the maximum carboxylation rate (V_{cmax}), CO_2 diffusive conductance across the stomata and mesophyll tissues, dark respiration (R_{dark}), light respiration and the characteristics of their environmental responses (Farquhar et al., 1980; Harley et al., 1986; Harley and Tenhunen, 1991). Of these key parameters, V_{cmax} and J_{max} and their linkages to N_a, leaf morphology, meteorological factors, and/or spectrum index have been widely investigated in C_3 species, rice included (Wullschleger, 1993; Niinemets and Tenhunen, 1997; Wohlfahrt et al., 1998; Xu and Baldocchi, 2003; Wang et al., 2008; Jin et al., 2012; Noda et al., 2015; Xue et al., 2016a,b).

Previous studies have shown the dependence of V_{cmax} and J_{max} on leaf temperature (Farquhar et al., 1980; Harley and Tenhunen, 1991), increasing to maximum rates at the optimal leaf temperature and then declining again. Review by Medlyn et al. (2002a) reported a relatively consensus in shape of temperature response among tree species. Similar findings were reported by Lin et al. (2012, 2013), suggesting that shifts in the relative temperature response of photosynthesis among species are driven by

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prevailing climate environment and water vapor pressure deficit (VPD) and/or plant type. The shapes of temperature response of V_{cmax} and J_{max} are commonly treated to be less variant as compared to absolute values during life cycles, and semi-empirically adjust the relative temperature curves based on absolute values at given leaf temperature was usually seen (Wang et al., 2003; Tenhunen et al., 2009; Ruidisch et al., 2014). Nevertheless, comparisons of the seasonal temperature responses amongst grass species showed significant differences (Wohlfahrt et al., 1998). Seasonal fluctuations in Populus trees were evident as well (Zhu et al., 2011). Temporal uncertainties in temperature response properties to be involved in PTC model may lead to an over- or under-estimation of photosynthesis at given temperature therefore biased understanding in satisfaction of PTC model application in cereal crop species under varying climate conditions. Potential risks imposed by the speculation of parameter estimation on evaluation of daily gross primary production in trees species and across different climate zones have been reported (Owen et al., 2007; Lombardozzi et al., 2015). Whereas, field reports to evaluate temperature response of photosynthesis and assess the extent to which the uncertainties influence temporal courses of photosynthetic capacity in response to varying temperatures in cereal crops especially rice and winter wheat are scarce.

Stomatal coefficient (g_{fac}) links stomatal conductance to water vapor (g_{sw}), leaf transpiration and carbon dioxide assimilation in PTC model (Ball et al., 1987; Harley and Tenhunen, 1991). Relatively constant g_{fac} over growing season were reported for populous (Zhu et al., 2011), mature maritime pine (Medlyn et al., 2002b), blue oak (Xu and Baldocchi, 2003), and alpine grasses (Wohlfahrt et al., 1998). Sala and Tenhunen (1994) suggested that large seasonal fluctuations in g_{fac} may occur in leaves of plants that are exposed to drying soils. g_{fac} as a measure of balance CO_2 uptake and water use reflects long-term stomatal adaptation and its short-term variation in leaves grown under varying ecological conditions (Leuning, 1995). Variations of stomatal conductance to biotic and abiotic environment in rice and winter wheat have been widely reported, however, field evaluations of their gas-exchange performance and their comparisons remain sparse (Xu et al., 2014). Large shifts in g_{fac} between paddy rice and winter wheat, among rice genotypes under different ecological conditions, and in canopy profiles may occur.

The other factor that directly influences CO_2 concentration inside chloroplasts is mesophyll conductance (g_m) which represents overall CO_2 diffusion from intercellular air spaces to CO_2 fixation sites. Ethier and Livingston (2004) and Niinemets et al. (2009a) reported that the shape of traditional A/C_i curves is largely influenced by variations of g_m. Those studies have added to our understanding of g_m and its possible determinants, as well as in shifts in g_m that occur in response to the prevailing environment. Leaf anatomy and growth environment such as light intensity inside canopies are identified as important determinants of maximum g_m across broad functional groups (Niinemets et al., 2009b; Flexas et al., 2012; Cano et al., 2013). Momentary g_m may change largely within minutes that depends on fluctuations of temperature and CO_2 concentration (Bernacchi and Long, 2002; Flexas et al., 2008, 2012; Xiong et al., 2015). Environmental response of g_m and the extent to which temporal temperature responses of g_m influence performance of PTC model and qualitative predictability in fluctuations of photosynthesis under varying climate among cereal crops are still insufficient but controversial (Bernacchi and Long, 2002; Niinemets et al., 2009a), but come into spotlight due to its important ecological implications such as water use strategies (Flexas et al., 2013; Cano et al., 2014). On the other hand, Werner and Beyschlag (2002) suggested to consider site/species specific light conversion efficiency, which is meaningful in evaluation of extent of interaction and adaption of plant photosynthetic physiology to varying environments.

Lowland rice grown under rainfed conditions has been proposed to be a promising way to significantly improve agronomic water use efficiency while maintaining relatively high yield in the East Asia monsoon regions (Katsura et al., 2010; Nie et al., 2011; Okami et al., 2013; Xue et al., 2016a). Variations in plant photosynthesis productivity in response to growth environment may relate to ecological conditions where rice are planted such as field management practice, nutrient application rates (Martindale and Leegood, 1997), and endogenous differences among species/genotypes (Berry and Bjorkman, 2003). Intensive researches in trees (Medlyn et al., 2002a; Kattge and Knorr, 2007; Zhu et al., 2011; Lin et al., 2013; Jensen et al., 2015; Slot et al., 2016) but only few in crops excluding wheat and rice (Harley et al., 1985, 1992a,b) regards temperature response of photosynthesis have been reported. Therefore, intensive measurements in temperature responses of photosynthesis, α, and mesophyll and stomatal control for water use in tropical rice (*Oryza sativa* L. cv. IR-2793) and temperate rice (*Oryza sativa* L. cv. Unkwang), and in winter wheat at grain-filling stage were conducted, to test the following hypotheses:

1. As commonly suggested before, temperature response characteristics of photosynthesis and dark respiration vary depending on surrounding climate environment.
2. Variations in light energy conversion efficiency and g_{fac} in rice and winter wheat canopies or over growing season are minimal.
3. Uniform temperature response function of photosynthesis, similar light energy conversion efficiency and g_{fac} can be applied in cereal crops based on classification of ecological conditions, simplifying parameter selection of PTC model.

2. Materials and methods

2.1. Study site

Field experiments were applied at the agricultural fields of Chonnam National University, Gwangju, South Korea (126°53′ E, 35°10′ N, altitude 33 m). More than 60% of annual precipitation here falls between June and September, during the East Asia monsoon season. Mean annual precipitation and mean annual air temperature during the past two decades are ca. 1400 mm and 13.8 °C, respectively. The top soil layer (0–30 cm) is categorized as loam with sand of 388 g kg^{-1}, silt of 378 g kg^{-1}, clay of 234 g kg^{-1}, pH 5.5, organic C 12.3 g C kg^{-1}, available P 13.1 mg P_2O_5 kg^{-1}, and total N before fertilization 1.0 g N kg^{-1} (Table 1). 30-day-old seedlings of Unkwang (*Oryza sativa* L. cv. Unkwang, Kim et al. (2006)) in 10 cm height were transplanted into flooded fields using an automatic rice planting machine on May 20, 2013 (DOY 140), with a row-line spacing of 12 × 30 cm. In average, 5 seedlings were planted in each hill. Fertilizer with a mass ratio of N–P–K of 11:5:6 was used to achieve fertilizer additions of 0 kg N ha^{-1} (no supplementary fertilization named as low nutrition group), 115 kg N ha^{-1} (normal nutrition group) and 180 kg N ha^{-1} (high nutrition group). 80% of N fertilizer was applied two days before transplanting (May 18, DOY 138), and the rest at the tillering stage 19 days after the transplanting (DOY 159). P fertilizer was applied as a 100% basal dosage, and 65% of K fertilizer as basal dosage and the rest during tillering were scheduled. Nutrient exchange between adjacent fields was minimized by establishment of cement walls 35 cm wide, inserted into a depth of one meter in the soil. Seeds of the same rice genotype were directly sown into the soil on April 22 (112 DOY) in a neighboring upland field, receiving fertilizer at the same level of 115 kg N ha^{-1} two times: 80% of total N before seeding and the rest on 160 DOY (tillering stage). No artificial water supply throughout growing seasons