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Supplement understanding of the relative importance of biophysical factors in determination of photosynthetic capacity and photosynthetic productivity in rice ecosystems

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Extensive variation in gross primary production (GPP) among growing seasons in rice ecosystems, which has previously been reported, may be caused by a number of biophysical factors. Two field-based studies, one on *Oryza sativa* L. cv. Odae in the Haean Basin and the other on *O. sativa* L. cv. Unkwang in Gwangju, South Korea, were conducted to evaluate physiological regulators of the ecosystem. A literature survey across climatic zones was additionally undertaken to unravel the roles of relevant climatic factors. The results from the two field studies showed that the correlation between the fraction of canopy light interception (fPAR) and leaf area index (LAI) across all data sets exhibited a common trajectory. Analogous values of canopy light use efficiency (LUE_c) at similar growth stages of the two rice crops, but, clearly varietal and nutritional differences in LAI development were present, which implies that temporal differences in carbon gain capacity are related to modifications in LAI, thereby influencing fPAR. The literature survey revealed that most variations in growing season GPP can be explained by changes in daily solar radiation (SR) which is negatively correlated to the proportion of rainy days; this is supported by the two field studies. In the context of temperature warming, a reduction in SR noticeably exacerbated impacts on photosynthetic productivity. Moreover, global values of maximum carbon gain capacity over the growing season ($GPP_{day\text{-}max}$) in field-cultivated rice were significantly affected by SR. We suggest that: 1) temporal differences in carbon gain capacity and variations in $GPP_{day\text{-}max}$ are jointly driven by LAI development, which varies according to nutrient availability and rice genotypes, and SR, especially at the reproductive stage; 2) although photosynthetic productivity of rice ecosystems is vulnerable to temperature increasing and prolonged growth duration contributes to larger photosynthetic productivity, its fluctuations across growing seasons are profoundly mediated by SR, which statistically correlates with the amount of precipitation; and 3) the important regulating implication of SR changes is attributed to the structure rather than physiology dependent light sensitivity of canopy photosynthesis at the reproductive stage. Further researches regarding interactions among climate change, phenology and canopy carbon dynamics are discussed.

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1. Introduction

Globally, there are more than 100 million ha of land under rice cultivation, with 89% of that land found in Asia. More than 60% of rice fields are flooded (Hijmans and Serraj, 2008). Completion of the life cycle is rapid, commonly accounting in ca. 120 days (Yoshida, 1981; Tuong and Bouman, 2003; Köhl, 2015), and its rapidity exerts significant growth transformation from one stage to the next with large fluctuations of CO_2 fluxes and biomass accumulation, which is a detrimental factor in regional controls of carbon balance and biogeochemical processes in intensive agricultural zones (Kwon et al., 2010; Bhattacharyya et al., 2013; Lee, 2014; Lindner et al., 2015).

Regulations of CO_2 exchange between a managed ecosystem and the atmosphere is a core component of ecological processes as related to ecosystem regulating and provisioning services (Bouman, 2001; Alberto et al., 2012; Maharjan et al., 2016). Biomass

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production is a direct result of canopy photosynthesis. An increasing number of studies have added to our understanding of the hourly and daily rates of carbon uptake by rice (Miyata et al., 2000; Campbell et al., 2001a; Inoue et al., 2008; Nishimura et al., 2008; Hossen et al., 2011; Hatala et al., 2012; Alberto et al., 2013; Bhattacharyya et al., 2013, 2014; Lee, 2014; Lindner et al., 2015; Vote et al., 2015), and a large range in total growing season GPP (growing season photosynthetic productivity), from approx. 470 to approx. 1500 g C m^{-2}, and in maximum daily GPP_{day} over the growing season ($GPP_{day\text{-}max}$, maximum carbon gain capacity throughout the growing season), from approx. 8 to approx. 18 g C m^{-2} d^{-1}, have been reported. Between research sites and climate regimes large fluctuations in photosynthetic production occurred, while, interannual fluctuations of growing season GPP in rice under similar field management practices may not be as large as those differences (Lee, 2014; Knox et al., 2016), indicating that research into field crops across geographic sites and into specific crop genotypes should be implemented to gain new insights into how seasonal changes in plant growth and climate factors affect photosynthetic processes.

Derivative and original light use efficiency models proposed by Monteith (LUE model, 1972; 1977) found that high biomass accumulation in such short life history requires relatively high photosynthetic activity, which not only relies on high soil water/nutrient availability and a constant climate (Alberto et al., 2012; Okami et al., 2013), but is also regulated by changes in canopy structure and physiology over the growing season (Sinclair and Horie, 1989; Sinclair, 1991; Tilman et al., 1997; Sheehy and Mitchell, 2013). Canopy light use efficiency (LUE_c calculated based on canopy light interception) varied by several folds among crop species (Chen et al., 2014), and was not constant during the life cycle (Cheng et al., 2014). However, prevailing arguments claim that leaf area development is the primary factor responsible for fluctuations in seasonal GPP_{day} within and among rice cultivars and in other crops (Setter et al., 1995; Li et al., 2009; Zhao and Lüers, 2012; Alberto et al., 2012; Okami et al., 2013; Lindner et al., 2015; Xue et al., 2016a; Alton, 2016). Plants grown in heterogeneous climate environments have similar canopy structures, i.e. LAI, and may exhibit large differences in LUE_c due to differences in leaf structural and functional properties (Sinclair and Horie, 1989; Niinemets and Valladares, 2004). On the other hand, analogous structural and functional traits in leaves may not necessarily produce similar degrees of light interception and LUE_c when taking canopy radiation transfer and canopy geometry into account (Sheehy and Mitchell, 2013; Gao et al., 2014; Lee, 2014). Temporal development of LUE_c in rice ecosystems exhibits large fluctuations that may be related to canopy structure and leaf photosynthetic physiology over the growing season. Fluctuations in temporal courses of carbon gain capacity (capacity of CO_2 uptake per day that healthy canopies possess without suffering abiotic stressors, such as drought, shading, extreme storm conditions, cold, and heat) in agronomically prevailing genotypes under different ecological conditions could be interactively driven by LAI and LUE_c.

Although prior knowledge suggests large influences of climatic factors such as sunlight, precipitation and temperature in rice growth and yield (IRRI, 1976; Yoshida, 1981; Peng, 1995), field observations to underpin understanding of their conclusions regarding the influences in rice yield via their quantitative effects and relative importance of those effects on photosynthetic processes are still required. Recent studies using conceptual modelling method reported that gross primary productivity of temperate wetland ecosystems is vulnerable to climate change, especially temperature increases, more so than changes in precipitation (Wang et al., 2012). Temperature increasing projected for the years 2050–2100 in Asian monsoon regions is strongly emphasized as a primary climatic factor that will impact crop photosynthetic production (Review by Cho and Oki, 2012; Kim et al., 2013; Yu et al., 2014; Deb et al., 2015; Luo et al., 2015; Wang et al., 2015; Review by Tripathi et al., 2016). One study suggested that, in context of global warming, a reduction in solar radiation during the rice growing season may exacerbate the impact of climate change (Choi et al., 2013). Precipitation changes, which cause variations in incident solar radiation on land surface, may impact regional vegetation CO_2 sink capacity (Ciais et al., 2013; Nguy-Robertson et al., 2015). Global warming projections state that precipitation during the East Asian monsoon season is expected to intensify and the duration of the monsoon season is likely to be extended (Boo et al., 2004; Yun et al., 2008). The total amount of cloud cover over the rice growing season in those regions is therefore anticipated to increase. There are still considerable uncertainties regarding important factors, such as how and to what extent such climate factors will influence the magnitude of CO_2 uptake in rice ecosystems.

Experimental studies done at one geographic location are commonly limited in their ability to reveal information on the extent to which climatic drivers regulate daily carbon gain in crops. Because of the relatively small variations in seasonal climate at a single site over the course of a few years (IRRI, 1976; Yoshida, 1981; Welch et al., 2010). Cross-site evaluation can be more useful in uncovering how climatic factors affect rice ecosystem GPP, which is required information for validation of global biosphere models. Therefore, intensive measurements of seasonal photosynthetic traits at the leaf and canopy level in Odae (*Oryza sativa* L. cv. Odae) rice paddies under the normal fertilization in the Haean Basin (northern part of S. Korea) and in Unkwang (*Oryza sativa* L. cv. Unkwang) rice paddies subjected to three levels of nutrient addition in Gwangju (southern part of S. Korea) were conducted. Data from previous studies on rice paddies across the globe were analyzed and compared with the two extra sites in this study to evaluate the following inferences:

1) Fluctuations in temporal courses of carbon gain capacity in prevailing genotypes under different ecological conditions (i.e. nutrient management practices) could be concurrently determined by canopy structural development (i.e. LAI) and differences in canopy physiology (i.e. light use efficiency).
2) Rice ecosystem as agricultural landscape receives intensively anthropogenic interventions. Multiple biophysical factors may govern large fluctuations of growing season photosynthetic productivity observed before. Besides concurrent effects of LAI and LUE_c in carbon gain capacity, solar radiation (i.e. light intensity) as a unique environmental variable in the original and derivative LUE models plays an important role in mediating the strength of growing season photosynthetic productivity. Physiological activity of photosynthesis is known to be sensitive to temperature increasing. Hence, the fluctuations seem to be not only related to ecophysiological characteristics but also primarily to how climate environment changes that their growth senses.

2. Materials and methods

2.1. Study sites

The study was conducted in two regions. The first was in Haean catchment (128°73′E, 38°16′N, altitude from 340 m at the valley to 1320 m at the ridges), Yanggu county in Gangwon province, S. Korea. The climate of the "punch-bowl" shaped basin is temperate, with a mean annual air temperature of 10.5 °C in the valley and a mean annual precipitation of ~1614 mm over the past 12 years. More than half of the precipitation falls during the summer monsoon season between July and September. The texture of the top soil layer used to grow paddy rice has a pH of 6.2, a total organic carbon level of 17.2 g kg^{-1}, total nitrogen level of 0.81 g kg^{-1} (Table 1,

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