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Research Paper

Quantification of CO_2 fluxes in paddy rice based on the characterization and simulation of CO_2 assimilation approaches

Jinsil Choi[a], Jonghan Ko[a,*], Chi Tim Ng[b], Seungtaek Jeong[a], John Tenhunen[c], Wei Xue[a], Jaeil Cho[a]

[a] Applied Plant Science, Chonnam National University, 77 Youngbong-ro, Buk-gu, Gwangju 61186, Republic of Korea
[b] Statistics, Chonnam National University, 77 Youngbong-ro, Buk-gu, Gwangju 61186, Republic of Korea
[c] Plant Ecology, BayCEER, University of Bayreuth, 95440 Bayreuth, Germany

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ABSTRACT

Quantification of the canopy photosynthesis of crops is essential for elucidation of the effects of environmental changes on CO_2 fluxes in agricultural ecosystems and crop productivity. This study was conducted to characterize the CO_2 fluxes of paddy rice (*Oryza sativa*), simulate CO_2 assimilation based on the development of a photosynthesis model, and project spatiotemporal variations in CO_2 assimilation using a crop model based on remotely sensed data in an effort to identify a link between photosynthetic productivity and accumulation of plant biomass. To perform the research practically under actual farming conditions, we investigated the effects of nitrogen (N) fertilization on canopy photosynthesis of rice grown under two levels of N application. Gross primary productivity (GPP) was calculated using net ecosystem exchange and ecosystem respiration measured in a closed-system canopy chamber. GPP was the highest in the maximum tillering stage and its minimum in the heading stage. The initial slope of the light response curve was similar during the four growth stages observed. The sensitivity of GPP to the amount of chlorophyll in the lower N treatment was higher than that in the optimum N treatment, whereas the GPP and yield in plants in the lower N treatment were lower. The photosynthesis model that was developed simulated CO_2 assimilation that had statistically acceptable agreement with the corresponding experimental measurements. In addition, projections of spatiotemporal variations in CO_2 assimilation were established using the GRAMI-rice model using remotely sensed data. These results indicated that CO_2 fluxes in paddy rice could be well quantified based on measurement and simulation projecting spatiotemporal CO_2 assimilation. As most of the information was derived from fields, it is not well organized to form one acceptable scientific streamline, efforts should be made to seek ecological implications through a fusion between at-ground measurements and remote sensing observations via model development.

1. Introduction

Exchange of CO_2 within the crop-atmosphere continuum plays an important role not only in the carbon cycle in agricultural ecosystems but also in the water and nitrogen cycles, and is closely related to the energy budget (Gilmanov et al., 2003; Saito et al., 2005). Crop plants absorb CO_2 through their leaf stomata, and its absorption through CO_2 flux between the atmosphere and the plant ecosystem is represented by gross primary productivity (GPP) (Nishimura et al., 2005; Muhr et al., 2011). GPP is "an integration of apparent photosynthesis, i.e., true photosynthesis minus photorespiration" (Wohlfahrt and Gu, 2015). The amount of CO_2 fixed from radiant energy absorbed by the crop canopy is significantly related to the physiological and phenological activities of crop plants (Hanan et al., 2002; Müller et al., 2009). CO_2 is released into the atmosphere through ecosystem respiration (R_{eco}), which includes dark respiration (R_{dark}) and photorespiration, by the crop canopy and respiration from all other plant organs (e.g., stems and roots) and soil organisms (Wohlfahrt and Gu, 2015). Thus, the investigation of CO_2 fluxes in an agricultural ecosystem is critically important for elucidating the physiological responses of crops to environmental conditions. Furthermore, understanding this process will be useful for projection of food production in climate change models and carbon sequestration into the soil by fixation of atmospheric CO_2 (Nishimura et al., 2005).

Although radiant energy absorbed by the crop canopy is the strongest driving factor in the carbon cycle, the level of N fertilization in an agricultural ecosystem must also be understood because of its significant physiological and phenological effects on the crop canopy.

* Corresponding author.
E-mail address: Jonghan.ko@jnu.ac.kr (J. Ko).

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Previous studies have reported an increase in crop yield in response to higher soil inorganic N (NH_4^+ and NO_3^-) concentrations [e.g., for rice (Liu et al., 2014), corn (Di Paolo and Rinaldi, 2008; Cela et al., 2011), wheat (Abad et al., 2004), and barley (Cantero-Martınez et al., 2003)]. The yield of crops limited by N supply can be considered to be the product of three factors: total N uptake/amount of N applied (Q), total plant dry matter produced per unit of N uptake (ε), and the fraction of total dry matter harvested (H) (Hay and Porter, 2006). Q is determined from the interaction between the N supply of the soil and N demand by the crops (Gastal and Lemaire, 2002). H is related to crop types or genetic characteristics, whereas ε can be represented by overall photosynthetic efficiency. Lafitte and Edmeades (1994) reported that the increase in yield resulting from high levels of N fertilization is attributed more to ε than to Q or H. In addition, changes in photosynthetic efficiency per unit of N uptake can occur in two ways. Canopy N content per unit ground area increases in N-abundant soil, and this can give rise to a higher leaf area index (LAI) (Scott et al., 1994). A greater amount of intercepted radiant energy results in greater biomass. Stroppiana et al. (2009) reported that an increase in chlorophyll compounds in rice was associated with an increase in N content in leaves with higher N fertilization. Generally, the maximum assimilation rate is positively related to chlorophyll concentration in the leaves (Lawlor et al., 2001). This facilitates higher radiation use efficiency by the crop plants. However, these processes need to be better understood in order to advance sustainable agriculture management and assist in the development of crop growth models (Suyker et al., 2005). For example, it has been demonstrated that changes in CO_2 assimilation and crop phenology under different levels of N fertilization are not evident at each crop growth stage, even though the rate of N uptake is governed by crop growth rate and soil N concentration and not by N deficiency in plants (Devienne-Barret et al., 2000). Therefore, an understanding of the photosynthetic responses of crop plants to solar radiation is necessary in the investigation of canopy CO_2 fixation (Hoffmann et al., 2015).

CO_2 assimilation of a crop canopy can be estimated using several methods, e.g., eddy covariance and gradient techniques, as well as in a steady-state open-chamber system or a non-steady state closed-chamber system (Nishimura et al., 2005; Burkart et al., 2007; Kutzbach et al., 2007). Closed-chamber systems are used to accurately measure direct CO_2 flux between the atmosphere and low canopies (Kutzbach et al., 2007; Müller et al., 2009; Hoffmann et al., 2015). The closed-chamber system is an alternative to plot-sized experimental agricultural studies (Steduto et al., 2002; Müller et al., 2009). The advantages of closed-chamber systems are that they are comparatively inexpensive, require low power consumption, provide easily measurable output, and can be managed by a single person (Drösler, 2005; Kutzbach et al., 2007; Hoffmann et al., 2015). Furthermore, many scientists have proposed photosynthesis models as a method for quantifying CO_2 assimilation (Kim and Lieth, 2003). Through earlier efforts by de Wit (1965) and Goudriaan and Van Laar (1978), photosynthesis models have been developed with consideration of the various mechanisms of plants. Farquhar et al. (1980) developed a model of CO_2 assimilation at the leaf level for C_3 plants, which has been frequently used in ecological and physiological modeling studies (Sellers et al., 1992; Kim and Lieth, 2003). More recently, Norman (1992) proposed a canopy photosynthesis model to formulate the amount of canopy photosynthesis, which has been adopted by other scientists (Hanan et al., 2002; Teh, 2006). The model equation estimates canopy photosynthesis by separating sunlit leaves receiving direct solar radiation and shaded leaves receiving no solar radiation (Teh, 2006). Although this model can simulate canopy photosynthesis, there is still a gap in the link between photosynthetic performance and the accumulation of plant biomass.

Crop growth models have been used in various aspects of agronomic research. These models can be useful tools for estimating the growth, development, and yield of a crop in accordance with various environmental changes, including climate change (Monteith, 1996; Guérif and Duke, 2000; Makowski et al., 2006; Steduto et al., 2009). Crop models are also capable of simulating chemical, physical, and biological processes in agricultural systems (Ma et al., 2005). A crop growth model generally reproduces the mechanisms of photosynthesis and respiration, and the production process in biological systems by simplifying the formulae based on scientific theory and hypotheses (Steduto et al., 2009; Sehgal, 2014).

Paddy rice fields are among the major agricultural ecosystems in Asia, contributing approximately 87% of the world's total rice production (Tseng et al., 2010; Bhattacharyya et al., 2013). Rice production depends on biomass accumulation derived from photosynthetic CO_2 assimilation. Thus, it is important to characterize and quantify the CO_2 assimilation of paddy rice to understand the changes in productivity according to environmental conditions. Development of a photosynthesis model is also necessary to facilitate estimates of the photosynthesis of crops under various environmental conditions, including the effects of climate change (Beyschlag and Ryel, 2007). The present study was performed to (1) estimate the photosynthetic characteristics of paddy rice via measurement of canopy CO_2 flux in a closed-chamber system, and (2) simulate CO_2 assimilation based on formulation of a photosynthesis model and project spatiotemporal variations of CO_2 assimilation using the GRAMI-rice model that incorporates remote sensing data. One of our fundamental research objectives was to also identify a method to link photosynthetic performance and accumulation of plant biomass based on the two different photosynthesis and crop growth modeling approaches. We investigated the effects of N fertilization on the canopy photosynthesis of rice grown with two levels of N application to fulfil the objectives under realistic farming conditions.

2. Materials and methods

2.1. Experimental site

This study was conducted in a paddy field at Chonnam National University (CNU), Gwangju, Korea (35°10′N, 126°53′E; alt. 33 m). During the 30-year period from 1981 to 2010, the annual mean temperature and mean precipitation at this site were 13.8 °C and ~1391 mm, respectively. Two different varieties of rice (*Oryza sativa* L.) were cultivated over a period of 2 years (Unkwang in 2013 and Chonnam-1-ho in 2014). Both varieties are early-maturing cultivars. These varieties were cultured in nursery beds in a temperature-controlled plastic house prior to transplanting 30-day-old seedlings (~10 cm in height). Unkwang was transplanted on May 20, 2013 and harvested on September 4, 2013. Chonnam-1-ho was transplanted on May 21, 2014 and harvested on August 30, 2014. Crop growth duration was 108 days in 2013 and 102 days in 2014. The soil texture of the experimental field is classified as a loam, based on the USDA classification method (for detailed soil properties, refer to Yun et al., 2012). In both years, the fields were treated with two levels of N as an organic compound of urea ($CO(NH_2)_2$): optimum fertilization with 110 kg ha^{-1} (~1387 m^2) in 2013 and 90 kg ha^{-1} (~511 m^2) in 2014, and minimum fertilization with 50 kg ha^{-1} (~511 m^2) in 2013 and 42 kg ha^{-1} (~511 m^2) in 2014. For each N treatment group, four experimental plots were arranged in the center of the paddy field to monitor diurnal canopy CO_2 flux based on the chamber measurement in 2013, as described in the following section. In 2014, three experimental plots for each nutrient treatment group were established to monitor spatiotemporal variation in crop growth according to different N application. The application regimes of N were achieved using fertilizer with a mass ratio of N-P-K of 11:5:6. N fertilizer was applied at a rate of