



Estimation of respiratory parameters for rice based on long-term and intermittent measurement of canopy CO₂ exchange rates in the field.

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ABSTRACT

Estimation of respiratory parameters, such as maintenance coefficient and growth conversion efficiency, is important for simulating crop growth. The objective of this study was to estimate respiratory parameters for rice (*Oryza sativa* L.) by model analysis based on long-term and intermittent measurement of canopy CO₂ exchange rate (CER) in the field conditions. Canopy CER was intermittently measured in the field conditions for three rice varieties every 30 min from around the panicle initiation stage to maturity in 2004. Based on this measurement, rice respiration model was established and respiratory parameters were estimated by Simplex method. There was a big difference in respiration rate among rice varieties and large seasonal changes as evidenced by the long-term and intermittent measurement of canopy CER. The model explained the varietal difference and seasonal changes in respiration rate without any bias despite that all respiratory parameters, maintenance coefficient and growth conversion efficiency, were fixed for the three varieties. The results indicated that genotypic differences and seasonal changes in respiration rate result not from differences in respiratory parameters, but from differences in dry matter production, its allocation, and the N concentration of each tissue. Estimated respiratory parameters explained well the large variations in the directly measured canopy respiration rate of field grown rice. The model analysis suggested that the varietal differences and seasonal changes in canopy respiration rate were caused by differences in the dynamics of dry matter and nitrogen accumulation in plants.

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1. Introduction

To keep pace with the increasing Asian population and the demand for their staple food rice, further increases in rice production per unit land area will be required because of limited arable land. These increases in rice yield must be brought on by increasing biomass production, because it is thought that the harvest index is already close to its maximum value of around 0.5 (Mann, 1999). Since respiration loss can reach about half of total gross photosynthesis (Yamagishi et al., 1980; Saitoh et al., 1998; Thornley and Cannell, 2000; Sakai et al., 2001), respiration rate is important factor to determine the biomass production and it should be cleared the dominant factors of respiration rate.

Respiration (R) can be divided into growth and maintenance respiration, R_g and R_m , respectively (McCree, 1974).

$$R = R_g + R_m$$

This equation can be converted using existing biomass (W), growth conversion efficiency of growth from P_g to biomass (Y_G), and the coefficient of maintenance respiration (m) into the following equation (Thornley, 1971).

$$R = \frac{1 - Y_G}{Y_G} \frac{dW}{dt} + mW$$

Because this concept is very useful for understanding respiration functionally, a number of researchers measured the respiration rate and calculated the Y_G and m (Amthor, 1989, 2000). However, different values have been reported for both Y_G and m in rice (Tanaka and Yamaguchi, 1968; Cock and Yoshida, 1973; Hirota and Takeda, 1978; Osaki and Tanaka, 1982; Hirai et al., 1997). The value of Y_G ranged from 0.46 to 0.88 g g⁻¹ and m ranged from 7.5 to 40.7 mg CH₂O g⁻¹ d⁻¹ in these reports. This is mainly because respiration rate is affected by environmental factors, mainly air temperature (McCree, 1974; McCree and Silsbury, 1978; Saito et al., 2005), and by the physiological characteristics of the plant, such as N concentration (Hole and Barnes, 1980; Hirai et al., 1997; Cannell and Thornley, 2000; Sakai et al., 2001; Xu et al., 2006). Therefore, to explain the variation in the measured respiratory

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parameters and to achieve a comprehensive understanding of these effects on respiration rate, further study is necessary. Respiration rate is also strongly affected by the daytime photosynthetic rate (Amthor, 1989; Gifford, 1995), and differs among plant tissues, such as the leaf, stem and panicle (Saitoh et al., 1998), and consequently changes with growth stages (Sakai et al., 2001; Saito et al., 2005). This means a long-term measurement of whole plant CER throughout the entire growth stage is necessary to analyze factors that affect respiration dynamics. However, very few studies have examined the canopy CER intermittently throughout the growth stage in the field because of technical difficulties.

On the other hand, various systems have been developed and utilized for the measurement of crop canopy CER. The closed chamber system (Takeda, 1961; Musgrave and Moss, 1961) yields accurate canopy CER data, but it creates largely different environment in the chamber from the field and is difficult to make a long-term measurement. The open-top chamber system (Collins et al., 1995) is a useful system for long-term and continuous measurement of canopy CER, but the possibility of mixing of inside and outside air limits the accuracy of CER measurements. The aerodynamic system (Inoue et al., 1958; Toda et al., 2000) allows measurement of canopy CER under non-disturbed natural conditions, but it requires a sufficiently large fetch, which limits its applicability for genotype-comparison for CER. Katsura et al. (2006) developed a periodically closing chamber system, which is frequently utilized for measurements of methane emission rates from soil-plant systems (Shütz et al., 1989; Wassman et al., 2000; Nishimura et al., 2004) and soil CO₂ flux (Liang et al., 2003), for the long-term and intermittent measurement of rice canopy CER. Before now, there were few reports that linked the long-term and intermittent measurement of canopy CER of field grown plants to model analysis to estimate respiratory parameters.

In the present study, we adopted this long-term and intermittent canopy CER measurement system (Katsura et al., 2006) and estimate respiratory parameters, such as maintenance coefficient and growth conversion efficiency, of rice. The objectives of this study are (1) to evaluate the respiration rate of field grown rice varieties with different yield potential by long-term and intermittent measurement of canopy CER and (2) to estimate respiratory parameters which explain well the variations in the directly measured canopy respiration rate of field grown rice by linking the long-term measurement of rice canopy CER.

2. Materials and methods

An experiment was carried out at Kyoto University Farm, Kyoto, Japan (35°02'N and 135°47'E, 60 m above sea level) in 2004. The rice varieties Liangyoupeijiu (indica F1 hybrid rice), Takanari (indica) and Nipponbare (japonica) were sown to the nursery boxes for raising seedlings on 3 May and transplanted to the paddy field on 26 May. For measuring the canopy CER, plot sizes of 10.56 m² were arranged for each variety with one replication. The experiments for measuring dry matter accumulation pattern were arranged in a completely randomized block design with three replications each with a plot size of 32.0 m². Planting density was 22.2 plants m⁻² (0.3 m × 0.15 m) with two seedlings per hill (rice stubble). Chemical fertilizers were applied at the rate of 14 g m⁻² P₂O₅ and 7 g m⁻² K₂O as a basal dressing, and 3 g m⁻² N at 1 week after transplanting, 7 g m⁻² K₂O and 4 g m⁻² N at panicle initiation, 4 g m⁻² N at 2-week preceding heading and 3 g m⁻² N at heading as the topdressing. Water, weeds, insects and disease were controlled as required to avoid yield loss.

For measurement of the dry matter accumulation pattern, plant materials were periodically sampled with three replications. Eight

plants outside the chamber were sampled from each replicate at panicle initiation, 3-weeks preceding heading, 2-weeks preceding heading, 1-week preceding heading, heading, 1-week following heading, 2-weeks following heading, 3-weeks following heading and at maturity. Dry weight was determined for leaf, stem (culm and leaf sheath), panicle and the dead plant portion. The N concentration of each tissue was determined by Kjeldahl method.

Canopy CER was measured by the multichannel automated chamber system (Katsura et al., 2006) equipped with an infrared gas analyzer (ASSA-1100, HORIBA, Japan). One chamber was set in the middle of a standing rice canopy under flooded condition with four hills inside the chamber for each variety, and one chamber set in a paddy field with no plants as a blank under flooded condition in order to avoid the effect of soil/water CO₂ flux. Each chamber was closed for 3 min every 30 min. During the closure of the chamber, inside air was pumped to the infrared gas analyzer and the change in CO₂ concentration ([CO₂]; ppm) inside the chamber was measured. The average [CO₂] in the chambers was 379 ppm during the closure of the chambers. The measurements were continued from 13 July (around panicle initiation stage of Liangyoupeijiu) to the time of harvest for each variety. The measurements were continued for 10–14 days for the same rice plant, after which rice plants in the chamber were harvested and the dry weight and N concentration was determined. Then, the measurements of CER were resumed for the new rice plants. The temperature inside every chamber was measured with a radiation shielded waterproof data logger (TR-52, T and D, Japan). Canopy CER (mg CO₂ m⁻² s⁻¹) is given by,

$$\text{CER} = -44 \times 10^3 \times \frac{d[\text{CO}_2]}{dt} \frac{1.013 \times 10^5}{8.31 \times (273 + T)} \frac{V}{S}$$

where V and S are the volume and floor area of the chamber, and are 0.216 m³ and 0.18 m², respectively. T is the temperature inside chamber (°C), and t the elapsed time (s). CER was further converted to the daily increase of plant biomass by multiplying 30/44 for CH₂O/CO₂. There might be some chamber effects, such as water vapor, CO₂ concentration, wind and so on in the present measurement system. However, the chamber effect on canopy CER was negligible small, because the dry matter accumulation inside the chamber calculated from the above equation was approximately equal to the dry matter accumulation outside the chamber (Katsura et al., 2006).

2.1. Model description

In rice, there might be significant differences between the composition of the two tissues, vegetative tissue and grain, enough to give rise to different growth conversion efficiencies and maintenance coefficients as other crops (Amthor, 1989). Also, stored carbohydrates in the vegetative tissue translocate to the panicle during the ripening stage in addition to newly assimilated photosynthate. On this case, stored carbohydrate, such as starch or sugars, in vegetative tissue must be mobilized into a mobile form, such as sucrose. This means that the respiration accompanied by synthesis of grain could be divided into three components: growth respiration in grain (R_{gp}), respiration accompanied by translocation of newly assimilated photosynthate from photosynthetic tissue to panicle (R_{tr}), and respiration accompanied by mobilization and translocation of stored carbohydrates in vegetative tissue to panicle (R_{mt}). Consequently, rice respiration rate (R , g g⁻¹ d⁻¹) could be divided into six components as follows:

$$R = R_{gv} + R_{gp} + R_{tr} + R_{mt} + R_{mv} + R_{mp} \quad (1)$$

where R_{gv} is growth respiration in vegetative tissue, R_{mv} is maintenance respiration in vegetative tissue, and R_{mp} is maintenance respiration in grain. Maintenance respiration in grain is

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