

## Daily Carbon Assimilation in Difference Four Growth

### Stage of Rice 'Phitsanulok 2'

## อัตราการดูดซับคาร์บอนในความแตกต่างที่สี่ระยะของการเจริญเติบโตรอบวัน ของข้าวพันธุ์พิษณุโลก 2

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### ABSTRACT

The canopy CO<sub>2</sub> exchange of the rice 'Phitsanulok 2' was measured in 4 different growth stages, 30, 60, 90 and 105 DAP (i.e. seedling, tillering, flowering and grain filling). They were planted individual clump in the cement pot. Canopy CO<sub>2</sub> exchange was measured with an open system. The chamber was made by transparent polyethylene bag to cover the whole rice canopy and light can pass. The CO<sub>2</sub> exchange was calculated from air flow rate, the different between CO<sub>2</sub> concentrations before and exit the chamber. Climatic data (PPFD, air temperature and humidity) and total leaf area were also recorded by data logger. The result found that all the different stages of growth has shown the diurnal pattern in CO<sub>2</sub> exchange which may be divided into 5 periods include morning, before noon, afternoon, evening and nighttime, according change in response. All growth stages show saturated response to PPFD but different in light compensation point and light saturated point. The difference in CO<sub>2</sub> assimilation was found between stages. The CO<sub>2</sub> assimilation was positive at daytime and negative at nighttime. The net daily CO<sub>2</sub> assimilation were 76.83, 495.97, 276.37 and 122.7  $\mu\text{mol clump}^{-1} \text{ day}^{-1}$  for 30, 60, 90 and 105 DAP, respectively which equivalent to carbon assimilation 0.92, 5.96, 3.32 and 1.35 g C  $\text{clump}^{-1} \text{ day}^{-1}$ . The relationship between total leaf area and the net C assimilation was found. The net C assimilation increased with increasing in total leaf area.

### บทคัดย่อ

การแลกเปลี่ยนก๊าซคาร์บอนไดออกไซด์ (CO<sub>2</sub>) ของเรือนพุ่มข้าวพันธุ์พิษณุโลก 2 วัดจากการเจริญเติบโตของข้าวใน 4 ระยะที่แตกต่างกัน คือ ที่ระยะ 30, 60, 90 และ 105 วันของภายหลังการปลูก (นั่นคือ ระยะต้นกล้า, ระยะแตกกอ, ระยะตั้งท้อง, ระยะสุกแก่) โดยจะนำข้าวมาปลูกเป็นกอในวงบ่อซีเมนต์ วัดการแลกเปลี่ยนก๊าซคาร์บอนไดออกไซด์ (CO<sub>2</sub>) ของเรือนพุ่มด้วยระบบเปิด โดยห่อคลุมอากาศ (chamber) สร้างด้วยถุงพลาสติกชนิดโปร่งใสเพื่อให้ครอบคลุมเรือนพุ่มของข้าวได้ทั้งหมดและแสงสามารถผ่านได้ การแลกเปลี่ยนก๊าซคาร์บอนไดออกไซด์ (CO<sub>2</sub>) สามารถ

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คำนวณได้จากอัตราการไหลของอากาศที่แตกต่างกันระหว่างความเข้มข้นของก๊าซคาร์บอนไดออกไซด์ ( $\text{CO}_2$ ) เข้าและออกจากเรือนพุ่มของข้าวได้ทั้งหมดและแสงสามารถผ่านได้ การแลกเปลี่ยนก๊าซคาร์บอนไดออกไซด์ ( $\text{CO}_2$ ) สามารถคำนวณได้จากอัตราการไหลของอากาศที่แตกต่างกันระหว่างความเข้มข้นของก๊าซคาร์บอนไดออกไซด์ ( $\text{CO}_2$ ) เข้าและออกจากห้องควบคุมอากาศ (chamber) ข้อมูลภูมิอากาศ (ความหนาแน่นของของเหลวโปรตอนสังเคราะห์ (PPFD.) อุณหภูมิอากาศและความชื้น) และพื้นที่ใบรวมถูกบันทึกไว้โดยเครื่องบันทึกข้อมูล ผลการศึกษาพบว่า ทุกระยะของการเจริญเติบโต ได้แสดงให้เห็นรูปแบบของเวลารายวันในการแลกเปลี่ยนก๊าซคาร์บอนไดออกไซด์ ( $\text{CO}_2$ ) ซึ่งอาจจะแบ่งออกเป็น 5 เวลา ได้แก่ เช้า ก่อนเที่ยง บ่าย เย็นและกลางคืน) ตามการเปลี่ยนแปลงในการตอบสนอง ทุกระยะการเจริญเติบโตแสดงการตอบสนองที่สัมพันธ์กับความหนาแน่นของของเหลวโปรตอนสังเคราะห์ (PPFD.) แต่ความแตกต่างกันในประเด็นจุดชดเชยแสงและจุดอิ่มตัวของแสง ความแตกต่างในการดูดซับก๊าซคาร์บอนไดออกไซด์ ( $\text{CO}_2$ ) ถูกพบระหว่างระยะ ดูดซับก๊าซคาร์บอนไดออกไซด์ ( $\text{CO}_2$ ) เป็นบวกในเวลากลางวันและลบในเวลากลางคืน การดูดซับก๊าซคาร์บอนไดออกไซด์ ( $\text{CO}_2$ ) สุทธิในแต่ละวันคือ 76.83, 495.97, 276.37 และ 122.7  $\mu\text{mol clump}^{-1} \text{ day}^{-1}$  สำหรับ 30, 60, 90 และ 105 วันของการปลูกตามลำดับ ซึ่งเท่ากับข้าวสามารถดูดซับคาร์บอนได้ 0.92, 5.96, 3.32 และ 1.35 g C  $\text{clump}^{-1} \text{ day}^{-1}$ . ความสัมพันธ์ระหว่างพื้นที่ใบรวมและการดูดซับคาร์บอนสุทธิพบว่า การดูดซับคาร์บอนสุทธิเพิ่มขึ้นด้วยการเพิ่มขึ้นของพื้นที่ใบรวม

**Keywords:** Rice, Carbon assimilation,  $\text{CO}_2$  exchange

**คำสำคัญ:** ข้าว การดูดซับคาร์บอน การแลกเปลี่ยนคาร์บอนไดออกไซด์

## Introduction

Rice is an important crop of the world because it is a food or an energy source of about more than two billion people. Thailand is one of the leading countries in the world that produces rice. The rice farming area in Thailand estimated to cover 10.1 million hectares [1]. Thailand is one of the Asian countries whose people chiefly consume rice. The Thais have been closely bound to rice since the ancient times. They have several beliefs, customs and ceremonies that show how important rice is to them [2].

Global warming is global climate change is now effect worldwide countries. Recent investigations have shown that inconceivable catastrophic changes in the environment will take place if the global temperatures increase by more than 2 °C. A warming of 2 °C corresponds to a carbon dioxide ( $\text{CO}_2$ ) concentration of about 450 ppm in the atmosphere [3]. Simulation model has shown decrease in rice production affected by global warming [4]. The impact of climate change on rice production in Thailand may decrease the production up to 12.04 % [5]. The Intergovernmental Panel on Climate Change report that  $\text{CO}_2$  and  $\text{CH}_4$  are the most effective greenhouse gases [6]. Rice plantation fixed  $\text{CO}_2$  through the photosynthesis while it released  $\text{CH}_4$  especially in lowland rice [7]. The tropical rice acts as net C sink both seasonally and annually. Although  $\text{CH}_4$  is a source of C loss from lowland flooded rice ecosystem, considering all the components of carbon balance on system basis, this ecology has a good potential to store considerable amount of carbon [7]. It was because the rice uses  $\text{CO}_2$  by photosynthesis. This is important part of the carbon balance but the lack of basic information about the  $\text{CO}_2$  exchange of rice canopy.

As the climate and environment change, to predict or estimate change in carbon balance and rice production need modeling [4-5]. Modeling carbon balance response to environment may need to know the response to CO<sub>2</sub> exchange of canopy, but this type of data is scarce. In this experiment, we measured the canopy CO<sub>2</sub> exchange of rice with an open system. The objective is to get basic information about the CO<sub>2</sub> exchange of the rice canopy i.e. diurnal CO<sub>2</sub> exchange, response to light environment and daily carbon assimilation. The rice 'Phitsanulok 2' was chosen. This cultivar was grown in the lower northern region due to its suitability for most areas. It is a photoperiod insensitive variety which high yield [8]. The canopy CO<sub>2</sub> was measured in 4 different stages. The result of diurnal CO<sub>2</sub> exchange, response to light environment and daily carbon assimilation were presented. This result should be useful to modeler or researcher who interesting in carbon balance or CO<sub>2</sub> exchange of rice at canopy level.

## Materials and Method

This research was conducted in order to study daily carbon assimilation of the rice 'Phitsanulok 2'. Four developmental stages were used in this study, 30 DAP (tillering), 60 DAP (panicle initiation), 90 DAP (flowering) and 105 DAP (grain filling).

### Rice planting

The experiment was setup at the paddy field of the farmer in Muang district, Phitsanulok province, Thailand. It was done between August to December 2011. Four replications were used for each stage. The rice was grown in the cement pot with 1 m in diameter and 80 cm in height. Each pot was set to have one clump. Each clump came from direct seeding 3 seed per clump. The rice was seeded in August. The water level in the pot was controlled at 10 – 15 cm throughout the experiment. air temperature and relative humidity were also recorded every minute throughout the experiment. The photosynthetic photon flux density (PPFD) was measured by light sensor LI-189 (LI-COR, Inc.). Air temperature and humidity were measured by the Humiter 50Y (Vaisala, Inc.).

### CO<sub>2</sub> Exchange measurement

Canopy CO<sub>2</sub> exchange was measured with an open system. The chamber was made by transparent polyethylene bag to cover the whole rice canopy. An adjustable speed fan was used to blow the air through 1.5 inch PVC pipe into the chamber. The speed of the air was measured by air velocity transducer (TSI, Inc; model 8455-03). The air flow rate was calculated using the air flow and the pipe diameter as following [9].

$$U_e = \frac{V \times \frac{22}{7} \times r^2 \times 10^9}{22.4} \quad (1)$$

When  $U_e$  = Air flow rate to the chamber ( $\mu\text{mol s}^{-1}$ )

$V$  = Air velocity ( $\text{m s}^{-1}$ )

$r$  = Air pipe radius (m)



The air before enter and after exit the chamber was sampling then analyzed with LI-840 CO<sub>2</sub>/H<sub>2</sub>O analyzer (LI-COR, Inc.). The CO<sub>2</sub> exchange rate was calculated using the value of flow rate and the difference of CO<sub>2</sub> concentration before and after exit the chamber as following (modified from (9)).

$$P_{canopy} = U_e \times (C_c - C_e) \quad (2)$$

When  $P_{canopy}$  = Canopy CO<sub>2</sub> exchange rate (μmol CO<sub>2</sub> s<sup>-1</sup>)

$U_e$  = Air flow rate to the chamber (μmol s<sup>-1</sup>)

$C_c$  = CO<sub>2</sub> concentration in the air before enter the chamber (μmol CO<sub>2</sub> per mole air)

$C_e$  = CO<sub>2</sub> concentration in the air exit from the chamber (μmol CO<sub>2</sub> per mole air)

#### Daily Carbon Assimilation

The canopy CO<sub>2</sub> exchange rate was calculated for every minute throughout 24 hours for each canopy. The daily CO<sub>2</sub> assimilation was obtained by sum of net CO<sub>2</sub> exchange in each minute for 24 hours. Daily carbon assimilation ( $D_c$ ) was calculated from fraction of C in daily CO<sub>2</sub> assimilation as following.

$$D_c = \frac{12}{44} \cdot \sum_{i=1}^{1440} (P_{canopy} \cdot 60 \cdot 10^{-6}) \quad (3)$$

#### Total Leaf Area

Thirty leaves which different sizes were sampled from rice canopies (the reserved canopies that were not used for the CO<sub>2</sub> exchange measurement) at 60 DAP (i.e. the stage that has wide range of leaf size). The leaf length and width were measured with a ruler then leaf area was measured with LI-3000c Portable Leaf Area Meter (LI-COR, Inc.). The allometric relationship between was found ( $R^2=0.9972$ ) as following equation.

$$A = 0.778 * W * L \quad (4)$$

Where  $A$  = Leaf area (cm<sup>2</sup>)

$W$  = Leaf width (cm)

$L$  = Leaf length (cm)

The leaf width and length of every leaf on the canopy were measured after CO<sub>2</sub> exchange measurement. The area of each leaf was calculated from the allometric equation as mention above. Then total leaf area of each canopy was calculated from summation of all leaf area on the canopy.

## Results

### Climatic data during CO<sub>2</sub> exchange measurement

The climatic data (i.e. air temperature, relative humidity, photosynthetic photon flux density (PPFD) and solar radiation) in 24 hours of the canopy CO<sub>2</sub> exchange measurement was shown in table 1.

The average air temperature was found close together in all 4 growth stages which ranged between 27.23 - 28.83 °C. The maximum and minimum air temperature was found close together in 3 growth stages (30, 60 and 90 DAP). While 105 DAP shown higher value maximum air temperature but lower value in minimum temperature.

The average relative and maximum humidity was found close together (ranged between 64.74-66.88 and 84.70-86.6) in 3 growth stages (30, 60 and 90 DAP) but lower in 105 DAP. The minimum relative humidity was found higher (40.5%) in 60 DAP.

The daily PPFD was found varies in different growth stage. The highest PPFD was found in 90 DAP (31.9, 32.4 and 31.27 mol day<sup>-1</sup> for average, maximum and minimum, respectively). The lowest PPFD was found in 30 DAP (21.27, 21.96 and 20.83 for average, maximum and minimum, respectively).

The daily solar radiation was also found varies in different growth stage. The highest solar radiation was found in 30 DAP (17.04, 17.74 and 16.29 MJ day<sup>-1</sup> for average, maximum and minimum, respectively). The lowest PPFD was found in 60 DAP (14.86, 17.97 and 8.83 for average, maximum and minimum, respectively). Table 1

### Diurnal CO<sub>2</sub> Exchange

The canopy CO<sub>2</sub> exchange rate has change in during the day as changing in PPFD. Different stage of growth has shown the diurnal pattern as was found in rice 'IR64' [10]. It rose up in the morning and down the evening. At night, the rate of CO<sub>2</sub> exchange of canopy is negative due to emitting of gas carbon dioxide from the canopy by respiration [11]. It may be divided into five time periods, 1) in the morning, 6:00 to 09:00, the CO<sub>2</sub> exchange rate of the rice canopy rose sharply, 2) before noon between 09:00 to 12:00, the CO<sub>2</sub> exchange rate increased gradually to highest at about noon, 3) in the afternoon between 12:00 to 16:00, CO<sub>2</sub> exchange decreased gradually, 4) in the evening between 16:00 to 19:00 CO<sub>2</sub> exchange decreased sharply to negative value, 5) at night between 19:00 to 6:00, CO<sub>2</sub> exchange was negative which showed respiration of the rice canopy (Figure 1). At daytime, the CO<sub>2</sub> exchange rate has changed due to change in PPFD. The CO<sub>2</sub> exchange of rice 'Pisanulok 2' was found highest 33.46 μmol clum<sup>-1</sup> s<sup>-1</sup> at 60 DAP. The same age that was found in rice 'IR64' [10]. The canopy CO<sub>2</sub> exchange rate may change in different water condition [10] or different variety [12].

### Response of CO<sub>2</sub> exchange to PPFD

The Figure 2 showed the response of the CO<sub>2</sub> exchange to PPFD. All growth stages shown saturated response curve. The difference between growth stages was found for light saturated point and light compensation point. At 30 DAP, the light compensation point was found between 90-200 μmol m<sup>-2</sup> s<sup>-1</sup> while it was saturated between PPF 400-600 μmol m<sup>-2</sup> s<sup>-1</sup>. At 60 and 90 DAP, the light compensation point was found between 50-100 μmol m<sup>-2</sup> s<sup>-1</sup> while they were not saturated at 1600 μmol m<sup>-2</sup> s<sup>-1</sup> (i.e. maximum PPF was found in this experiment). At 105



DAP, the light compensation point was found between 70-150  $\mu\text{mol m}^{-2} \text{s}^{-1}$  while the  $\text{CO}_2$  exchange was found to be saturated between PPFD 800-1000  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Figure 1, Figure 2

#### Daily $\text{CO}_2$ and Carbon Assimilation of Rice Canopy

The Daytime  $\text{CO}_2$  assimilation, Nighttime shoot respiration, Net  $\text{CO}_2$  assimilation, Daytime carbon assimilation, Nighttime carbon loss by shoot respiration, Net carbon assimilation at different growth stage of rice 'Phitsanulok 2' were shown in Table 2. The difference was found between stages. The daytime assimilation increased from 158.7  $\mu\text{mol CO}_2 \text{ clump}^{-1} \text{ day}^{-1}$  (equivalent to 1.91 g C  $\text{clump}^{-1} \text{ day}^{-1}$ ) at 30 DAP to the highest value 591.00  $\mu\text{mol CO}_2 \text{ clump}^{-1} \text{ day}^{-1}$  at 60 DAP (equivalent to 7.1 g C  $\text{clump}^{-1} \text{ day}^{-1}$ ). Then it has decreased to 166.73  $\mu\text{mol CO}_2 \text{ clump}^{-1} \text{ day}^{-1}$  (equivalent to 2.00 g C  $\text{clump}^{-1} \text{ day}^{-1}$ ) at 105 DAP. The nighttime assimilation was negative for all growth stages which showed the release of  $\text{CO}_2$  during nighttime. The nighttime assimilation decrease from -81.87  $\mu\text{mol CO}_2 \text{ clump}^{-1} \text{ day}^{-1}$  (equivalent to 0.98 g C  $\text{clump}^{-1} \text{ day}^{-1}$ ) at 30 DAP to lowest value -95.03  $\mu\text{mol CO}_2 \text{ clump}^{-1} \text{ day}^{-1}$  (equivalent to 1.14 g C  $\text{clump}^{-1} \text{ day}^{-1}$ ) at 60 DAP. Then it increased to -54.03  $\mu\text{mol CO}_2 \text{ clump}^{-1} \text{ day}^{-1}$  (equivalent to 0.65 g C  $\text{clump}^{-1} \text{ day}^{-1}$ ). The net daily assimilation at 30 DAP was the lowest 76.83  $\mu\text{mol CO}_2 \text{ clump}^{-1} \text{ day}^{-1}$  which equivalent to 0.92 g C  $\text{clump}^{-1} \text{ day}^{-1}$ . The highest net daily assimilation was found at 60 DAP which was 495.97  $\mu\text{mol CO}_2 \text{ clump}^{-1} \text{ day}^{-1}$ , equivalent to 5.96 g C  $\text{clump}^{-1} \text{ day}^{-1}$ . The net daily assimilation then decreased from 90 to 105 DAP which were 276.37  $\mu\text{mol CO}_2 \text{ clump}^{-1} \text{ day}^{-1}$  (equivalent to 3.32 g C  $\text{clump}^{-1} \text{ day}^{-1}$ ) and 122.7  $\mu\text{mol CO}_2 \text{ clump}^{-1} \text{ day}^{-1}$  (equivalent to 1.35 g C  $\text{clump}^{-1} \text{ day}^{-1}$ ) respectively. Table 2, Figure 3

### Conclusion

The  $\text{CO}_2$  exchange of the rice canopy 'Phitsanulok 2' was measured in 4 different growth stages, 30, 60, 90 and 105 DAP (i.e. Seedling, tillering, flowering and grain filling). They were planted individual clump in the cement pot. Canopy  $\text{CO}_2$  exchange was measured with an open system. The difference in  $\text{CO}_2$  assimilation was found between stages. The  $\text{CO}_2$  assimilation was positive at daytime and negative at nighttime. The net daily  $\text{CO}_2$  assimilation were 76.83, 495.97, 276.37 and 122.7  $\mu\text{mol CO}_2 \text{ clump}^{-1} \text{ day}^{-1}$  for 30, 60, 90 and 105 DAP, respectively which equivalent to carbon assimilation 0.92, 5.96, 3.32 and 1.35 g C  $\text{clump}^{-1} \text{ day}^{-1}$ . The relationship between total leaf area and the net C assimilation was found. The net C assimilation increased with increasing in total leaf area.

### Discussion

The response of the  $\text{CO}_2$  exchange to PPFD have shown saturated curve. This is the result from the response of single leaf photosynthesis which also was shown saturated photosynthetic response [12-14]. But the different in light compensation and saturation point were found for the different of plant age. The light compensation point is reached when photosynthetic  $\text{CO}_2$  assimilation equals the amount of  $\text{CO}_2$  evolved by respiration. Increasing light above the light compensation point proportionally increases photosynthesis. At higher photon fluxes, the photosynthetic response to light starts to level off and reaches saturation. Once the saturation point is reached, further increases in photon flux no longer affect photosynthetic rates, indicating that factors other than incident light, such as

electron transport rate, rubrics activity, or the metabolism of trios phosphates, have become limiting to photosynthesis. [11]. In this experiment, younger rice plant was found to have higher canopy light compensation. The higher light compensation was come from higher in growth respiration in younger plant [15]. On the other hand, the light saturation point was not reach for canopy CO<sub>2</sub> exchanges at 60 DAP. This showed that the PPFD 1600  $\mu\text{mol m}^{-2} \text{s}^{-1}$  still not reach the limit at the canopy level in this growth stage. Because this is stage highest canopy leaf area which can absorb more light.

The net carbon assimilation was found to have relationship with total leaf area. The net CO<sub>2</sub> assimilation increased with increasing in total leaf area (Figure 3). Highest CO<sub>2</sub> assimilation was found when 'Phitsanulok 2' has highest leaf area. The similar result was found in 'IR64' [10] or Japonica rice 'Nipponbare' [16]. 'Pisanulok 2' has highest CO<sub>2</sub> assimilation at 60 DAP, the same age as 'IR64', but different from 'Nipponbare' where the highest CO<sub>2</sub> assimilation was found at 80 DAP. Like 'Phitsanulok 2', 'IR64' is photoperiod insensitive which matures in 110 days and has a 45-day vegetative stage [17]. While 'Nipponbare' is photoperiod sensitive which have longer vegetative stage when growing in normal season.

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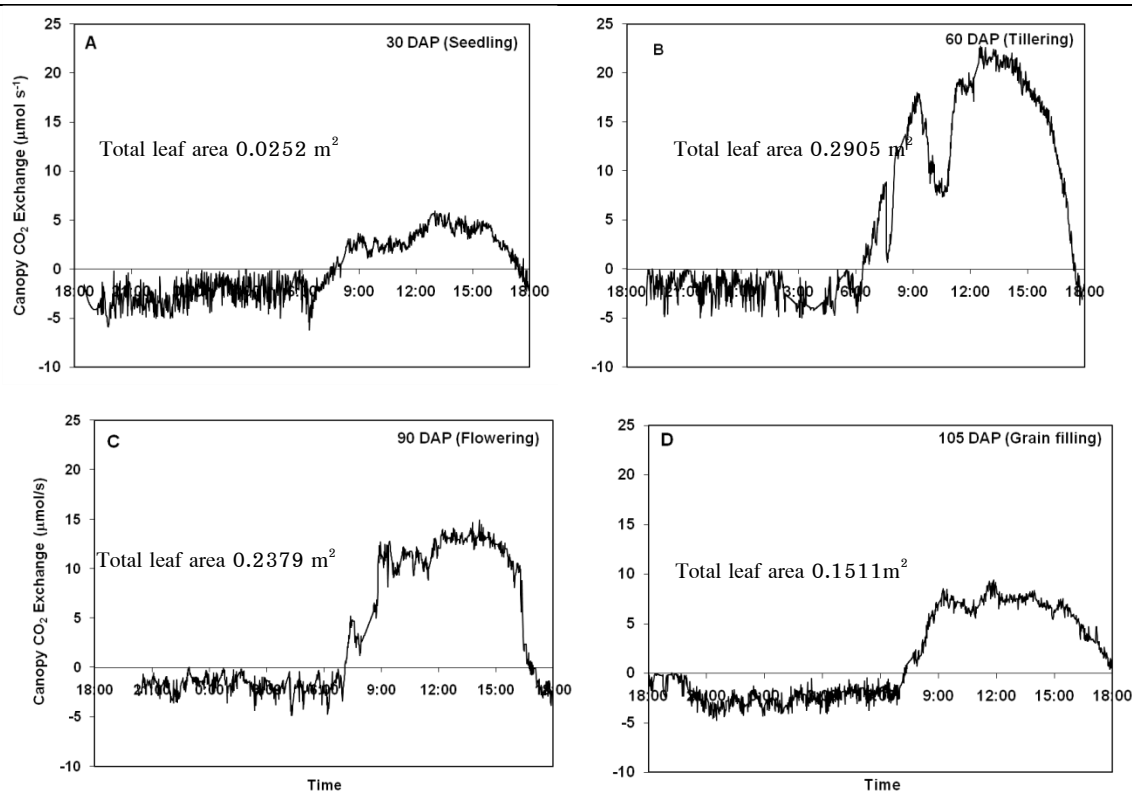
**Table 1** Air temperature, relative humidity, photosynthetic photon flux density (PPFD) and solar radiation during the canopy CO<sub>2</sub> exchange measurement of rice in 4 growth stages. The average values of each stage came from 4 replications.

	Growth Stage			
	30 DAP	60 DAP	90 DAP	105 DAP
	(Seedling)	(Tillering)	(Flowering)	(Grain Filling)
Air Temperature (°C)				
Maximum	40.88	40.27	40.53	44.06
Minimum	22.20	21.06	20.23	18.71
Average	28.35	28.83	27.23	27.87
Relative Humidity (%)				
Maximum	86.60	84.70	85.00	82.80
Minimum	22.10	40.50	28.07	17.84
Average	66.88	66.47	64.74	54.43
PPFD (mol day <sup>-1</sup> )				
Maximum	21.96	27.67	32.24	29.74
Minimum	20.83	16.77	31.27	28.49
Average	21.27	24.03	31.90	29.17
Solar Radiation (MJ day <sup>-1</sup> )				
Maximum	17.74	17.97	16.86	15.80
Minimum	16.29	8.83	16.47	15.14
Average	17.04	14.86	16.72	15.47

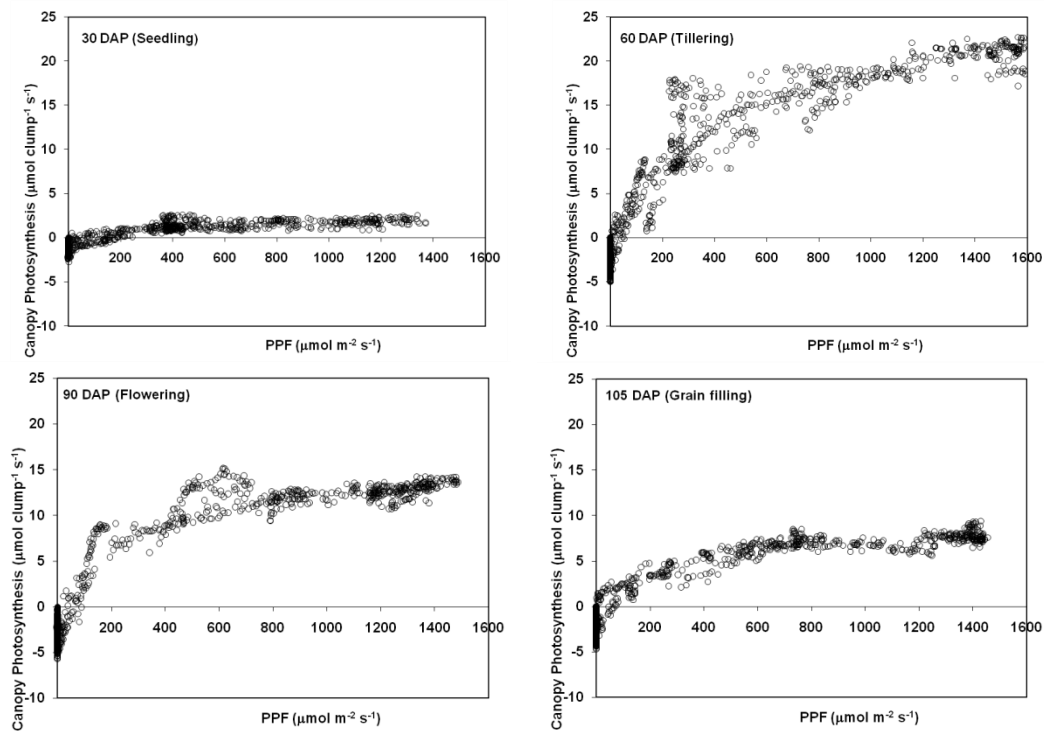


**Table 2** Daytime, Nighttime shoot respiration, Net CO<sub>2</sub> assimilation, Day time carbon assimilation, Nighttime carbon loss by shoot respiration, Net carbon assimilation at different growth stage of rice 'Phitsanulok 2'

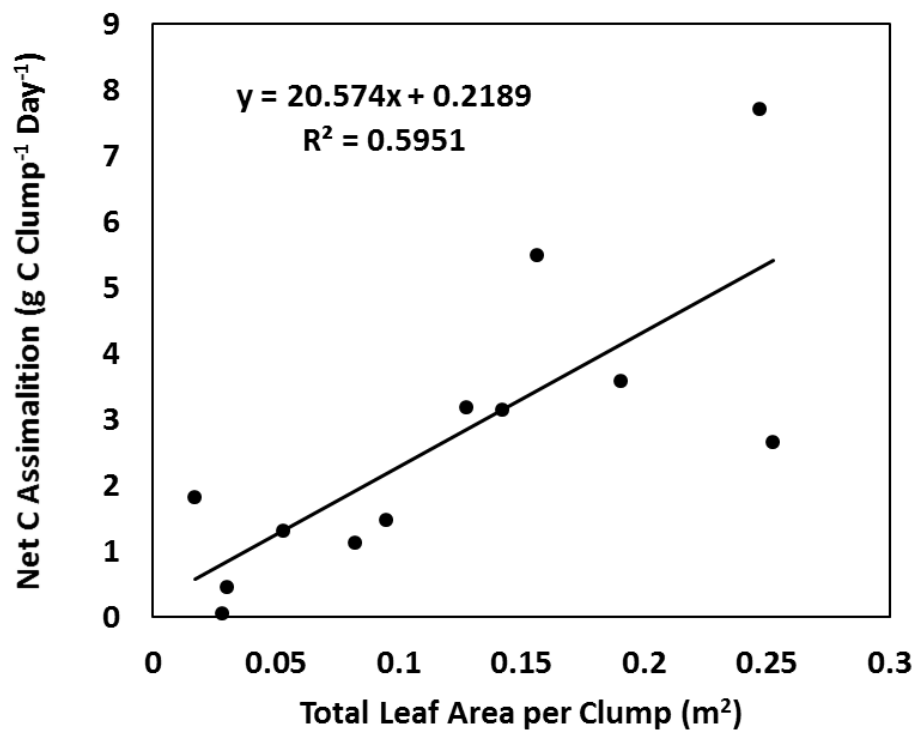
	Growth Stage			
	30 DAP (Seedling)	60 DAP (Tillering)	90 DAP (Flowering)	105 DAP (Grain Filling)
Daytime CO <sub>2</sub> assimilation ( $\mu\text{mol clump}^{-1} \text{ day}^{-1}$ )	158.70 $\pm$ 35.60	591.00 $\pm$ 97.49	366.33 $\pm$ 17.65	166.73 $\pm$ 27.92
Nighttime CO <sub>2</sub> assimilation ( $\mu\text{mol CO}_2 \text{ clump}^{-1} \text{ day}^{-1}$ )	81.87 $\pm$ 5.47	95.03 $\pm$ 6.06	89.97 $\pm$ 9.65	54.03 $\pm$ 24.49
Net CO <sub>2</sub> assimilation ( $\mu\text{mol clump}^{-1} \text{ day}^{-1}$ )	76.83 $\pm$ 37.55	495.97 $\pm$ 91.59	276.37 $\pm$ 12.54	122.70 $\pm$ 11.82
Daytime Carbon assimilation (g C clump <sup>-1</sup> day <sup>-1</sup> )	1.91 $\pm$ 0.42	7.10 $\pm$ 1.17	4.40 $\pm$ 0.21	2.00 $\pm$ 0.33
Nighttime carbon loss by shoot respiration (g C clump <sup>-1</sup> day <sup>-1</sup> )	0.98 $\pm$ 0.07	1.14 $\pm$ 0.07	1.08 $\pm$ 0.12	0.65 $\pm$ 0.29
Net Carbon assimilation (g C clump <sup>-1</sup> day <sup>-1</sup> )	0.92 $\pm$ 0.45	5.96 $\pm$ 1.10	3.32 $\pm$ 0.15	1.35 $\pm$ 0.14



**Figure 1** Diurnal CO<sub>2</sub> Exchange at different growth stage of rice 'Phitsanulok 2'



**Figure 2** Response of canopy CO<sub>2</sub> exchange to photosynthetically active photon flux (PPFD) of rice 'Phitsanulok 2'



**Figure 3** Relationship between net carbon assimilation and total leaf area per clump of rice 'Phitsanulok 2'