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Original research article

Photosynthesis and Transpiration Rates of Rice Cultivated Under the System of Rice Intensification and the Effects on Growth and Yield





Nurul Hidayati,¹ Triadiati,^{2*} Iswandi Anas³

¹ Department of Biology, Plant Biology Study Program, Graduate School, Bogor Agricultural University, Bogor, Indonesia.

² Department of Biology, Faculty of Mathematics and Natural Sciences, Bogor Agricultural University, Bogor, Indonesia.

³ Department of Soil Science and Land Resources, Soil Biotechnology Division, Faculty of Agriculture, Bogor Agricultural University, Bogor, Indonesia.

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ABSTRACT

The system of rice intensification (SRI) crop management method has been reported by many authors to significantly increase rice yield with lower inputs, but physiological bases of yielding improvement has not been studied. In this research we assessed some physiological parameters and the mechanism of rice yield improvement of rice plants under SRI cultivation method during both vegetative and generative phases compared to conventional rice cultivation methods. We measured photosynthetic rate, transpiration rate, leaf temperature, chlorophyll content, N and P uptake, plant growth parameters and yield for those comparison. SRI methods significantly increased both vegetative and reproductive (generative) parameters of rice plants compared to conventional cultivation methods. Photosynthetic rate, chlorophyll content, N and P uptake under SRI cultivation were significantly higher compared to those of the conventional rice cultivation, but no differences were found in transpiration rate and leaf temperature. With SRI method, plants in their generative phase (especially in the grain-filling phase) had the highest photosynthetic and the lowest transpiration rates. Grain yield under SRI method was significantly higher (ca. 24%) than that of conventional method.

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1. Introduction

The methodology of rice cultivation practice known as the system of rice intensification (SRI) is an innovation in agriculture that is still assessed continually, but its concepts and practices have been shown to increase rice productivity and farmers' incomes while reducing their need for water and other inputs. SRI method is focus on improving the growing environment of rice plants, above and below ground, by improving the management of plants, soil, water and nutrients, to stimulate the growth of bigger and better root systems and the number and activity of beneficial soil organisms. The effectiveness of SRI cultivation practices has been shown in over 50 countries, including the major rice producers in the world such as India, China, Vietnam, Cambodia and Philippines (Katambara *et al.* 2013) as well as in Indonesia.

Certain basic principles of SRI method can be identified, including, planting of young seedlings (8–12 days), planting of

Corresponding author.
 E-mail address: adiatiipb@gmail.com (Triadiati).
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single seedlings (just one seedling per hill), wider spacing (usually 25 cm \times 25 cm), maintaining moist soil condition (without flooding), and control of weeds by mechanical weeding, which improves soil aeration while eliminates the weeds. It is also recommended to use organic fertilizers (Barison & Uphoff 2011). However, SRI method can be applied using inorganic fertilizer or combination of organic and inorganic fertilizers that aims for increasing of nutrient amounts and type (Lin *et al.* 2011). SRI practices contrast with conventional method which generally involves considerably older seedlings (25 days old or more), planting of 3–5 seedlings per hill, closer spacing (20 cm \times 20 cm, or less), maintaining soil condition mostly flooded, and fertilization mostly using inorganic fertilizers (Kediyal & Dimri 2009).

The advantages of application of SRI method compared to the conventional method are less seed requirement, water savings up to 50%, reduction in the use of inorganic fertilizers by 50% if coupled with 50% organic fertilizer, or some combination of organic fertilizer and biological fertilizer, production costs reduced by 20%, and increasing yield (Hutabarat 2011).

Physiology of rice under conventional cultivation method has been widely reported, however, the physiology of rice plants under SRI cultivation method which supports high yield has received only

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limited study (e.g. Thakur *et al.* 2011; Mishra & Salokhe 2010), even SRI methods have been used in some number of countries. For example, SRI method applied in Afghanistan increased rice production by 66% compared to the conventional method (Thomas & Ramzi 2010). Similar results were reported from Iraq, where rice production increased by 42% with SRI method (Hameed *et al.* 2011). SRI method applied in eastern Indonesia (Nusa Tenggara) with a large number of comparison trials (>11,000) over nine seasons was able to increase rice production by 78% (Sato *et al.* 2011), whereas in Situ Gede, West Java, it was increase by 33% (Bakrie *et al.* 2010). As shown, the increase in rice yield of SRI method has a wide range. It is influenced primarily by soil microbes, which can vary widely under soil and climatic conditions in different places. Microbial closely related to soil health. The good aeration soil could maximize aerobic microbial activity (Araújo *et al.* 2009).

This research was conducted to assess the effects of cultivation methods on the rice plant's physiology. Thus, this research measured and evaluated differences in key physiological parameters, namely photosynthetic and transpiration rates of rice in response to SRI cultivation methods, comparing these with conventional rice cultivation methods, and to see their influence on growth and grain yield.

2. Materials and Methods

This research was conducted from October 2012 to September 2013 in Sindang Barang, Jero village, sub-district West Bogor, Bogor, West Java, Indonesia. The materials used were rice seed (Ciherang variety); chemical fertilizer including urea (45% N), SP-36 (39% P₂O₅), KCl (60% K₂O), and compost enriched with plant growth-promoting rhizobacteria (PGPR) (*Bacillus* sp., *Pseudomonas* sp., *Azospirillum* sp., and *Azotobacter* sp.) collected from the Laboratory of Microbiology in the Department of Biology, Faculty of Mathematics and Natural Sciences, Bogor Agricultural University. Measurements of photosynthesis, transpiration and leaf temperature were taken using the LI-COR Biosciences device (Nebraska, USA) at photosynthetically active radiation (PAR) 600–1200 nm and measured at 09:00–11:30, and chlorophyll content was determined according to the Arnon method (1949), which was measured by spectrophotometer type Spectro GenesysTM 20 (Massachusetts, USA).

The study was conducted using a randomized complete block design in which the methods of rice cultivation evaluated were the conventional method and the SRI. The size of the experimental plots was 4 m \times 5 m (20 m²), and each treatment was replicated five times.

Seedlings were prepared by soaking the seeds in warm water for 24 hours, then air-drained and incubated for 2 days until germination. In the SRI method, the seedlings were planted in a tray, with soil and organic fertilizers enriched by biofertilizers (1:1 v/v), and were grown for 10 days. For the conventional method, seeds that

Table 1. Comparison between conventional and system of rice intensification rice cultivation method

Planting	Conventional	System of rice intensification
a. Age of transplanted seedlings	25 d after sowing	10 d after sowing (60% less)
b. Spacing	$20\ cm \times 20\ cm$	25 cm $ imes$ 25 cm (25% wider)
c. Number of seedlings per hill	3 seedlings per hill	1 seedling per hill (33% fewer)
d. Number of seedlings per m ²	75 seedlings per m ²	16 seedlings per m ² (80% fewer)
e. Number of hills per m ²	25 hills per m ²	16 plants per m ² (36% fewer)
f. Irrigation	Flooding continuously	Soil was kept moist

had been incubated for 2 days and germinated were sown into a standard nursery for 25 days before transplanting using usual practices. The main differences between conventional and SRI rice cultivation methods are described in Table 1.

With respect to nutrient provision, both SRI and conventional treatments used the same type, dose, timing, and application of fertilizers, so soil nutrient amendments were not a variable in this trial. In here, we did not evaluate nutrient variations as a factor affecting production. In this experiment, the fertilizer application was 50% inorganic (125 kg urea/ha, 100 kg SP-36/ha, and 50 kg KCl/ha, which was equivalent to 250 g urea/plot, 200 g SP-36/plot, and 100 g KCl/plot) and 50% organic (2.5 t/ha, equivalent to 5 kg/plot). The organic fertilizers used in this research were compost enriched with biofertilizers, applied at transplanting together with SP-36 and KCl fertilizers, while urea was applied twice, half dosage was during transplanting and the remaining was 35 days after planting.

In the SRI method, to keep soil moist, a trench along the inner edge of the plot (size 20 cm \times 20 cm \times 30 cm) was flooded with water. Shortly before weeding, plots were flooded with a water level of about 2 cm. Weeding was carried out at 10, 20, and 30 days after planting using a conoweeder to ensure topsoil aeration. In the conventional method, flooded water was supplied continuously with water level of about 5 cm until 105 days after sowing (DAS). Weeding of the conventional method plots was performed at 10 and 20 days after planting manually by hand. For both cultivation methods, water was drained 5 days before harvest. Harvest of both SRI and conventional plots was carried out 110 DAS, when around 90%–95% of rice grains turned to yellow.

The vegetative growth parameters measured were: plant height, leaf area, tiller number, leaf number, shoot dry weight at 70 and 110 DAS, width of the canopy at 20 cm above the soil's surface at 70 DAS, number of productive tillers per hill, and number of productive tillers per square-meter.

The generative growth parameters observed were: panicle length, number of filled grains per hill, number of total grains per hill, percentage of empty grains, grain dry weight per hill, weight of 1000 grains, grain dry weight at harvest per square-meter, and grain dry weight per square-meter (yield after drying under the sun).

Physiological parameters observed were the photosynthesis rate (A), transpiration rate (E), and leaf temperature (Tleaf) using a LI-COR Biosciences device (Nebraska, USA) at PAR 600-1200 nm and measured at 09:00-11:30; chlorophyll content was determined according to the Arnon method (1949), using spectrophotometer type Spectro GenesysTM 20 (Massachusetts, USA), with observations made at four phases of growth (vegetative, flowering, grain filling, mature grain); nitrogen content at 70 DAS was determined according to the Kjeldahl method (Jones 1991), nitrogen uptake was obtained by multiplying the nitrogen content with the leaves' dry weight of rice plants per hill, and phosphorus content at 70 DAS was determined according to the wet-ashing method using HNO3 and HClO4 and measured by ultraviolet-visible spectrophotometer, phosphorus uptake was obtained by multiplying the phosphorus content with the leaves' dry weight of rice plants per hill. All the data were analyzed statistically using the independent t test at 5% probability.

3. Results

3.1. Effects of cultivation methods on vegetative growth

Implementation of SRI method resulted in significantly different measurements (p < 0.05) in plant height, leaf area, tiller number per hill, and leaf number compared to the conventional method at 32–70 DAS (Figures 1A–C). Plant height using SRI method at 32, 46,

60, and 70 DAS was significantly higher compared to that of conventional method (Figure 1A). Leaf area under SRI method was significantly wider (p < 0.05) than that of conventional method at 46, 60, and 70 DAS. However, at 32 DAS, the leaf area of rice plants grown under both methods was not significantly different (p > 0.05; Figure 1B). Tiller number and total leaf number per hill when using SRI method at 32, 46, 60, and 70 DAS were significantly higher compared to that in conventional method (Figure 1C).

SRI method was able to increase significantly the shoot dry weight of rice at 70 and 100 DAS (p < 0.05) compared to that of conventional method (Table 2). These data were consistent with the development of the canopy, as indicated by canopy width of rice plant at 20 cm above the soil surface that was significantly different (p < 0.05) with relatively wider in SRI than that in conventional method (Table 2).

The number of productive tillers per hill under SRI method was also considerably and significantly higher compared to that under conventional method (p < 0.05) as by approximately 95% (Table 2). However, the difference was not as big as that if the calculation was carried out based on area, due to the lower plant population under SRI method. The number of productive tillers per square-meter with SRI method was increased by 22% (p < 0.05) compared to the conventional method (Table 2).

3.2. Effect of cultivation methods on physiological parameters

The rates of photosynthesis at the vegetative, flowering, grain filling, and mature grain phases in the SRI method were significantly different (p < 0.05) compared to that of the conventional method (Figure 2A). Meanwhile, plants' transpiration rates were not significantly different (p > 0.05) between SRI method and conventional method (Figure 2A). Similarly, there was also no significant difference (p > 0.05) in leaf temperature during the different developmental phases (Figure 2B).

Table 2. Effects of cultivation methods on vegetative growth of rice

Vegetative growth Rice cult		ltivation methods	
	Conventional	SRI	
Shoot dry weight 70 DAS 110 DAS Canopy width at 20 cm above soil surface Number of productive tillers/hill Number of productive tillers/m ²	$\begin{array}{c} 28.2 \pm 1.62^{b} \\ 22.3 \pm 1.26^{b} \\ 15.2 \pm 0.66^{b} \\ 12.9 \pm 0.57^{b} \\ 323.3 \pm 14.28^{b} \end{array}$	53.0 ± 4.82^{a} 48.4 ± 1.74^{a} 19.2 ± 0.52^{a} 24.7 ± 1.13^{a} 394.7 ± 18.06^{a}	

DAS = days after sowing; SRI = system of rice intensification.

 a,b The same letter in the same row was not significantly different with independent t test at $\alpha=0.05.$

The contents of chlorophyll a, chlorophyll b, and total chlorophyll in leaves during flowering, grain filling, and mature grain in the SRI method were significantly higher (p < 0.05) compared to the conventional method. On the other hand, in the vegetative phase, the contents of chlorophyll a, chlorophyll b, and total chlorophyll were not significantly different (p > 0.05; Figure 3) between the cultivation methods. Furthermore, nitrogen and phosphorus content and uptake in the leaves at 70 DAS with the SRI method were significantly higher (p < 0.05) compared to the conventional method (Table 3).

3.3. Effect of cultivation methods on the generative phase of rice performance

Panicle length of rice plant was significantly longer with SRI method (p < 0.05) compared to the conventional method. The number of filled grains per hill and number of total grains per hill in the SRI method were significantly higher (p < 0.05) compared to the conventional method. The SRI method showed the lower percentage of empty grains (p < 0.05; 14.7%) compared to the conventional method (21.2%; Table 4). The grain dry weight per hill in the SRI method was also significantly higher (p < 0.05) compared to

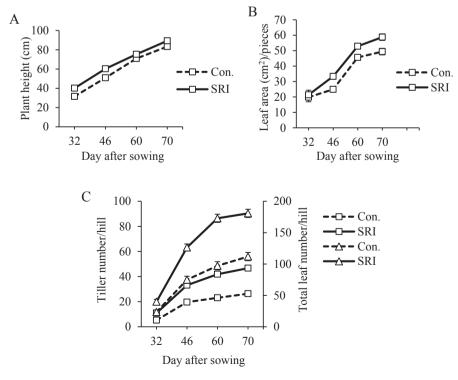
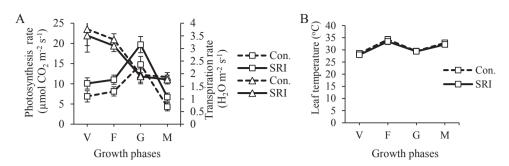


Figure 1. Effects of cultivation methods on vegetative growth of rice. (A) Plant height, (B) leaf area, (C) tiller and total leaf number. ----: Tiller number (conventional); ----: tiller number (SRI); ----: total leaf number (conventional); ----: total leaf number (SRI). Bar lines indicate standard error of independent t test at a = 0.05.



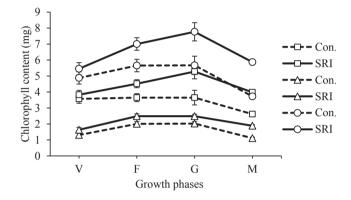


Figure 3. Effects of cultivation methods on chlorophyll content in four phases of growth (V: vegetative; F: flowering; G: grain filling; M: mature grain). -----: Chlorophyll a (conventional); ---------: chlorophyll b (conventional); --------: chlorophyll b (SRI); ------: total chlorophyll (conventional); ------: total chlorophyll (SRI). Bar lines indicate standard error of independent t test at $\alpha = 0.05$.

Table 3. Effects of cultivation methods on nitrogen and phosphorus uptake at 70 days after sowing

Nutrient uptake of rice	Rice cultivation method		
	Conventional	System of rice intensification	
Leaf N-content (%) Leaf N-uptake (g/hill) Leaf P-content (%) Leaf P-uptake (g/hill)	$\begin{array}{c} 0.41 \pm 0.02^b \\ 0.12 \pm 0.01^b \\ 0.29 \pm 0.00041^b \\ 0.08 \pm 0.006^b \end{array}$	$\begin{array}{c} 1.34 \pm 0.03^{a} \\ 0.71 \pm 0.09^{a} \\ 0.32 \pm 0.00087^{a} \\ 0.16 \pm 0.019^{a} \end{array}$	

 $^{a,b}\mbox{The same letter}$ in the same row was not significantly different with independent t test at $\alpha=0.05.$

the conventional method. Therefore, the use of the SRI method of rice cultivation can increase the grain dry weight per hill by 121.35%. However, the grain weight (measured as weight of 1000 grains) was not significantly different (p > 0.05) between SRI method and conventional method (Table 4).

The grain dry weight per square-meter at harvest in the SRI method was significantly higher (p < 0.05) compared to that of the conventional method. The SRI method increased the grain dry weight at harvest about 23.88%. Similarly, the grain dry weight per square-meter (yield) in the SRI method was also significantly higher (p < 0.05) compared to the conventional method. The SRI method increased the yield about 24% (Table 4).

4. Discussion

System of rice intensification (SRI) methods were able to improve rice growth and performance at both the vegetative and generative stages. The plant height, tiller number, leaf number, and leaf area of rice were higher with SRI compared to the conventional methods (Figure 1). It was expected by the earlier transplanting of young seedlings, which was 10 DAS compared to 25 DAS for the conventional method. The 10 DAS of seedlings has advantage for early plant growth and minimized the effect of transplanting shock (Stoop *et al.* 2002). Those younger seedlings had a longer time to adapt to field condition, therefore the plant height and tiller number produced were higher in the SRI method. In addition, the SRI method of transplanting one seedling per hill, as well as the wider spacing between hills than with conventional method played a role in reducing competition between the plants for uptake of nutrients, water, light, and air, which can significantly increase the growth of individual rice plant under the SRI method (Thakur *et al.* 2010).

Maintaining the soil in moist but not flooded conditions provided good aeration for the plant roots (Figure 1). These favorable conditions for growth with SRI methods allowed to complete more phyllochrons of growth, producing more tillers and roots, before the flowering phase. It was easy to determine that rice plants under SRI management produced more tillers and their root systems were more extensive than with conventional methods. The leaf number of rice increases with increasing number of tillers (Figure 1C). Likewise, the leaf area increased due to a greater leaf elongation rate (Figure 1B), which may contribute to making the leaves wider (Thakur *et al.* 2011). Leaf elongation has been reported to increase significantly in conventionally cultivated rice plants when their soil was kept water saturated compared with flooded (Nguyen *et al.* 2009).

Shoot dry weight was higher in the SRI method compared to the conventional method (Table 2). Shoot dry weight at 70 DAS (transition from vegetative to generative phase) was higher than at 110 DAS (at harvest) because when flowering, the photosynthate was allocated for seed formation (the panicles become a strong sink) (Fukai et al. 1991). The increase in shoot dry weight in the SRI method was due to the increasing of rice plant growth. The rice plants in the SRI method showed wider canopy than those in conventional method, may be caused by better environmental conditions due to wider spacing between hills and the application of one seedling per hill which led to optimum shoot growth (Table 2). Consequently, the structure of canopy which influences the amount of light absorbed by the leaf was more favorable in SRI than in conventional system. Because the capacity of photosynthesis at canopy level depends not only on the factors that affect the rate of photosynthesis in leaf level but also the profile of light distribution on leaves (Weiss et al. 2004), SRI method may cause the increase in the total canopy photosynthesis, which resulted in improved growth substantially. In addition, under SRI, rice hills had greater canopy angle than that of conventional ones (Thakur et al.

Table 4. Effects of cultivation methods on generative phases of rice

Generative phases of rice	Rice cultivation method		
	Conventional	System of rice intensification	
Panicle length (cm) Number of filled grains/hill Number of total grains/hill Percentage of empty grains (%) Grain dry weight/hill (g) Weight of 1000 grains (g) Grain dry weight at harvest (g/m ²) Grain dry weight (yield) (g/m ²)	$\begin{array}{c} 21.7 \pm 0.18^{b} \\ 1023.0 \pm 74.56^{b} \\ 1385.1 \pm 59.17^{b} \\ 21.2 \pm 1.81^{b} \\ 25.2 \pm 1.40^{b} \\ 24.2 \pm 0.05^{a} \\ 716.2 \pm 6.15^{b} \\ 618.4 \pm 3.96^{b} \end{array}$	$\begin{array}{c} 22.5 \pm 0.12^{a} \\ 2491.3 \pm 154.99^{a} \\ 2928.1 \pm 199.46^{a} \\ 14.7 \pm 1.26^{a} \\ 55.8 \pm 3.03^{a} \\ 24.6 \pm 0.27^{a} \\ 887.3 \pm 24.73^{a} \\ 769.8 + 21.36^{a} \end{array}$	

 a,b The same letter in the same row was not significantly different with independent t test at $\alpha=0.05.$

2011). The wide canopy can increase the penetration of light to reach the lower leaves of the plant in a high light environment, thus maximizing opportunity for all of the leaves to perform photosynthesis optimally (Terashima & Hikosaka 1995).

The rate of photosynthesis with SRI method was higher than in the conventional method at the vegetative, flowering, grain-filling phase, and in mature grain stage (Figure 2). The rate of photosynthesis in plants with SRI method increased from the vegetative to grain filling and was higher than in plants with conventional method. When leaves remain green during grain filling, this enables photosynthesis to remain high, which is favorable for high yield because this increases the supply of photosynthate to seeds (Fu & Lee 2009). The higher photosynthesis rates may be caused by having a higher chlorophyll content in the SRI rice leaves than in the plant with conventional method (Figure 3).

Chlorophyll levels are closely related to the photosynthesis rate because they provide the photosynthetic apparatus which allows plants to absorb energy from light and transfer it to the chlorophyll a (Porra et al. 1993). With a higher amount of chlorophyll in the leaves, a higher photosynthesis rate can be maintained (Kura-Hotta et al. 1987). Chlorophyll a and total chlorophyll content were the highest at the grain-filling stage, whereas on the other hand, chlorophyll b was higher from the flowering to the grain-filling states. Measurements of chlorophyll were derived from the same leaves which were used for the measurement of photosynthesis and were measured at the same phase. The rate of photosynthesis increases with increasing nitrogen content in the leaves. Nitrogen is an essential component of both chlorophyll and RuBisCo, the enzyme facilitating photosynthesis. A high nitrogen content in the leaf tissue allows the plant to have more chlorophyll and RuBisCo, triggering a higher rate of photosynthesis (Osaki et al. 1995). The uptake of nitrogen and phosphorous in the leaves of SRI plants was higher compared to the conventional method (Table 3). Phosphorus is an element that directly affects the process of photosynthesis (Warren 2011). Phosphorus has been reported to affect the dark reactions of photosynthesis, the apparent quantum efficiency, and starch accumulation, but the rate of electron transport and stomatal conductance is not affected by phosphorus (Brahim et al. 1996). Besides that, PAR also correlated with photosynthesis rate, but in these studies the measurement of photosynthesis in every growth phase was conducted at the same time and in the same range of PAR in both methods.

When photosynthesis was high, transpiration on both methods was low especially in the grain filling due to much of H_2O used for photosynthesis before the water vapor was released in the transpiration process (Figure 2A). In addition, during the grain filling, much water was used to translocate photosynthate from the source to the sink, in this case panicles (spikelet) became strong sink to fill the grain. The grain-filling rate (grain yield) depends on the source activity and sink capacity, the capability of carbohydrate accumulation and also the translocation of assimilates from source tissues to spikelets (Zhao *et al.* 2006; Shahruddin *et al.* 2014). Source to sink transport of sugar (photosynthate) is affected by environmental factors, one of them is the availability of water in the plant's tissue (Lemoine *et al.* 2013). On the other side, the photosynthetic rate of SRI method was significantly higher compared to the conventional method, but transpiration in both methods was no different. These might indicate that the rice tiller in SRI method used more water in the plant tissue for metabolism reactions before transpiration process. Therefore, the photosynthesis rate was not always correlated with the transpiration rate. Besides that, the photosynthetic rate is more influenced by energy from light which is absorbed by chlorophyll (Maxwell & Johnson 2000).

Transpiration in plants from both SRI and conventional methods was not significantly different because the potential gradient was the same for both (Figure 2A). Water absorbed by the plant roots from the soil is not entirely used to produce dry matter, because most of the total water absorbed by the roots (90%) is lost via transpiration (Sterling 2004). The main driving force of transpiration is the water potential gradient between the inner space of stomata and the atmospheric air (air water potential). Therefore, flooded soil condition with conventional methods has been considered as a wastage of water because the excessive supply of water exceeds the needs of the rice plants. SRI methods were more efficient in using water, however (Ndiiri et al. 2012). Leaf temperature was also not significantly different between SRI and conventional methods, although the soil in the conventional method was kept flooded (Figure 2B). Leaf temperature is strongly influenced by air temperature, wind speed, and air humidity (Martin et al. 1999). These factors were the same for both sets of plants in this study because the SRI and conventional methods were used in the same area.

The increased rate of photosynthesis, high chlorophyll content, and increased nutrient uptake with SRI methods likely caused the rice plants to function more optimally in converting most of the tillers into productive ones (Table 2). The increased number of productive tillers and greater panicle length, as well as the decreased percentage of empty grains, contributed to an increased number of filled grains and to total number of grains, therefore, this could increase the grain dry weight per hill, grain dry weight at harvest, and grain dry weight per square-meter (grain yield) with SRI methods (Table 4). Zhang et al. (2008) reported that higher grain yield in the rice plants is because of the improvement in the root growth and shoot growth, which contributes to remobilization of carbon reserves from vegetative tissues to grains. Thakur et al. (2011) reported that the improvement in grain yield under SRI cultivation was mainly due to improved morphology and physiological features of the rice plant. This study also showed that the improvement in vegetative and generative growth of rice plants under SRI method was due to increasing of photosynthesis rate, high chlorophyll content, and increased nutrient uptake. Therefore, it caused increase in grain yield. Besides that, transpiration and leaf temperature were not significantly different in the two cultivation methods and could be asserted that rice cultivation did not need to be flooded irrigation during the period of 80 days after planting (along with vegetative and generative growth of rice plants) in conventional method.

The result of this study contradicts the statement of Sheehy *et al.* (2004) which states that SRI didn't have a major role in increasing rice production. It also refuted the statement of McDonald *et al.* (2005) which states that the SRI method did not fundamentally change the physiological yield potential of rice. The results of this study proved that the SRI method affects the physiology of rice plants especially in increasing photosynthesis, which ultimately affects the increase in yield.

Conflict of interest

There is no conflict of interest.

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