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AN ASSESSMENT OF PHYSIOLOGICAL EFFECTS OF SYSTEM OF RICE INTENSIFICATION (SRI) PRACTICES COMPARED WITH RECOMMENDED RICE CULTIVATION PRACTICES IN INDIA

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SUMMARY

An evaluation was conducted in eastern India over three years, 2005–2007, to compare the performance of certain System of Rice Intensification (SRI) practices: transplanting single, young (10-day-old) seedlings in a square pattern; no continuous flooding; and use of a mechanical weeder – with those currently endorsed by the Central Rice Research Institute of India, referred to here as recommended management practices (RMP). All plots received the same fertilization, a combination of organic and inorganic nutrients, and the SRI spacing used was 20% less than usually recommended. Accordingly, the results reported here are designated as a modification of SRI recommendations (SRI_m). The objective of this research was to understand the benefits in terms of yield and other physiological parameters, if any, from using most if not all recommended SRI practices compared to RMP. These selected SRI practices out-yielded RMP by 42%, with the higher yield associated with various phenotypical alterations, which are reported here. Significant measurable changes were observed in physiological processes and plant characteristics, such as longer panicles, more grains panicle^{-1} and higher % of grain-filling. The decreased plant density with SRI_m management was compensated for by increased per-plant productivity. SRI_m hills with single plants were found to have deeper and better-distributed root systems, higher xylem exudation rates, more open plant architecture with more erect and larger leaves, and more tillers than did RMP hills having multiple plants. Due to the reduction in number of hills m^{-2} in SRI_m plots compared to RMP, no significant difference was found in root dry weight or leaf number, tillers or panicle number on an area basis. Nevertheless, in spite of SRI_m having fewer hills and fewer tillers per unit area, the leaf area index (LAI) with SRI_m practice was greater due to larger leaves. These together with altered plant architecture, contributed to more light interception by SRI_m plants. The higher leaf chlorophyll content at ripening stage reflected delayed senescence and the greater fluorescence efficiency (Fv/Fm and ΦPS II) associated with SRI_m practices contributed to more efficient utilization of light and a higher rate of photosynthesis, which was probably responsible for the observed increase in grain filling and heavier grains compared to RMP plants. The higher photosynthesis rate coupled with lower transpiration in SRI_m plants indicated that they were using water more efficiently than did RMP plants. The latter produced 1.6 μ mol CO_2 fixed per m mol water transpired, compared to 3.6 μ mol CO_2 in SRI_m plants.

INTRODUCTION

The System of Rice Intensification (SRI) has been promoted for more than a decade as a set of agronomic management practices for rice cultivation that enhances yield

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(Ceesay *et al.*, 2006; Kabir and Uphoff, 2007; Namara *et al.*, 2008; Sato and Uphoff, 2007; Senthilkumar *et al.*, 2008; Sinha and Talati, 2007; Uphoff *et al.*, 2002; Yuan, 2002; Zhao *et al.*, 2009), reduces water requirements (Satyanarayana *et al.*, 2007), raises input productivity (Sinha and Talati, 2007), is accessible to smallholders (Stoop *et al.*, 2002), and is more favorable for the environment than conventional practice with its continuous flooding of paddies and heavy reliance on inorganic fertilization (Uphoff, 2003). Given that water scarcity at field level affects more and more rice-growers around the world, SRI has attracted considerable interest, particularly in Asian countries.

The basic claim made for SRI is that making changes in the cultural practices for growing irrigated rice – altering the ways in which rice plants, soil, water and nutrients are managed – can lead to much more productive phenotypes (Uphoff, 1999; Uphoff and Randriamiharisoa, 2002). These changes include the use of much younger seedlings than are normally transplanted; planting them singly and carefully in a square pattern with wide spacing; in soil that is kept moist but not continuously saturated; and with increased soil amendments of organic matter and active aeration of the soil during weed control operations.

However, these recommendations have encountered controversy, and SRI reports of yield benefits and phenotypical changes with SRI management have been challenged on various grounds (Dobermann, 2004; Latif *et al.*, 2005; McDonald *et al.*, 2006; Sheehy *et al.*, 2004, Sinclair, 2004; Sinclair and Cassman, 2004). The debate has been one of the most contentious in recent agronomic forums. For instance, Sheehy *et al.* (2004), based on a theoretical model for predicting maximum yields attainable and on the results from a few field trials, concluded that the reported high yields under SRI must be due to measurement errors and that 'SRI has no major role in improving rice production generally'. SRI results have been characterized by Sinclair (2004) and Sinclair and Cassman (2004) as 'unconfirmed field observations', with the admonition that SRI offers no shortcuts to achieving large yield increases. Sheehy *et al.* (2005) argued that the energy requirements for achieving such high yield in SRI are beyond the thermodynamic capabilities of rice plants' photosynthesis and the crop's use of solar energy. Commenting on the effects of SRI practices, Sinclair (2004) contended that SRI's very low plant densities would lead to poor light interception, whereas high plant density is a prerequisite for enhanced light interception, growth and yield. While Dobermann (2004) accepted SRI as possibly a 'niche innovation' for improving rice production on poor, acidic soils with potential for Fe toxicity, but asserted it had little potential for improving yield in intensively irrigated systems with more favourable soils. More recently, the debate has focused on comparison of SRI performance with available 'best management practices' (BMPs) (McDonald *et al.*, 2008; Uphoff *et al.*, 2008). McDonald *et al.* (2008) have insisted that no significant yield advantages for SRI over BMPs have been documented experimentally except from the Madagascar trials.

Thus, significantly higher yields reported with SRI management have been dismissed as impossible or at least not scientifically demonstrated. Both the claims of SRI and the grounds for rejecting these are matters that can be empirically tested and should be investigated systematically. Some evaluations of this sort have been done previously in China (Tao *et al.*, 2002; Wang *et al.*, 2002; Zhu *et al.*, 2002). But quantified physiological evaluations have not been published on the results of SRI management, comparing them with what are considered by some rice scientists to be the BMPs for rice cultivation.

SRI is referred to as methodology, not a technology or fixed set of practices (Uphoff, 2003), to be tested and optimized under a range of different agro-ecological environments (Stoop *et al.*, 2002). This study was not designed to assess the full set of recommended SRI practices, as this would have required a more complicated set of factorial trials. Some of the management practices of recommended SRI were adopted in this study, while others were adapted to the local conditions. What is assessed here was thus not the full set of practices, which some may consider 'original SRI', but instead the effects of a specified sub-set of practices.

This evaluation was conducted with the same variety over three years to assess the performance of rice plants managed with these alternative practices – referred to here as modified SRI (SRI_m) to indicate that this is not identical to the recommendations of SRI's originator (Laulanié, 1993). A systematic comparison is made with rice plants grown according to recommended management practices (RMP) for India. This study examines the extent to which making certain changes in crop management can alter phenotypical characteristics and induce physiological changes in rice plants, assessing the effects, in any, of alternative management practices on root growth and activity, canopy development, light interception and its utilization, which contribute to differences in yield and components of yield.

MATERIALS AND METHODS

Experimental site and soil

Experiments were conducted at the Deras Farm, Mendhasal in Khurda district, Orissa, India (20°30′N, 87°48′E) during the wet season (July–November) in 2005, 2006 and 2007. Soils of the experimental site have been classified previously as Aeric Haplaquepts (Thakur *et al.*, 2004), being sandy clay-loam in texture (63% sand, 16% silt, and 21% clay) with pH of 5.5. The soil at the study site had organic carbon content 1.13%, total nitrogen 0.08%, available P (Olsen) 9 ppm, exchangeable K 0.20 meq/100 g soil, exchangeable Ca 4.5 meq/100 g soil, available S 14 ppm, Zn 10 ppm, and Fe 370 ppm.

Experimental design and cultural practices

The experiments were conducted using randomized complete block designs with five replicates and plot sizes of 20 m × 10 m. All the plots were surrounded by 50-cm wide bunds to prevent lateral seepage between plots, with 50-cm wide channels for irrigation and drainage. The cultivar used, Surendra (OR158–5 × Rasi), is a medium-duration (130–135 days) semi-dwarf rice variety which was released in 1999 and is recommended for Orissa state (DRD, 2006). This improved variety, which normally yields 3.5–5.0 t ha^{-1} (http://dacnet.nic.in/rice/RiceVarieties-09.htm), was grown under the two alternative systems of crop management: the SRI_m, and the RMP proposed by India's Central Rice Research Institute at Cuttack (http://crri.nic.in/).

The SRI practices assessed in this study differed from original SRI practice in two ways, in the use of both organic manures and inorganic fertilizers and in plant spacing. All SRI_m and RMP plots had the same soil amendments, a combination of chemical fertilizer and organic matter, and SRI_m plots had somewhat closer spacing (20 × 20 cm) than original recommendations for SRI (25×25 cm) (Senthilkumar *et al.*, 2009; Thakur *et al.*, 2009). There was limited local availability of large amounts of organic material, so reliance only on organic fertilization was not considered feasible; and the spacing reflected earlier evaluations of optimum plant distances under local soil and other conditions. Details of the two sets of management practices evaluated here are given in Table 1.

For nursery establishment, germinated seeds were broadcasted on 5, 4 and 7 July in 2005, 2006 and 2007, respectively. In the SRI_m plots, 10-day-old seedlings were transplanted on 14, 13 and 16 July in these years, respectively, while in the RMP plots, seedlings from the same nurseries, when 21 days old, were transplanted on 25, 24 and 27 July in 2005, 2006 and 2007, respectively. While the seeds for both SRI_m and RMP plots were germinated at the same time, the respective seedlings were planted into the main field at different times. The aim was to have the plants under both treatments reaching similar stages of growth at the same time, receiving similar sunshine hours, day length, and temperatures, and with harvesting on the same date, respectively, 18 November 2005, 16 November 2006, and 21 November 2007.

RMP plots were kept continuously flooded and irrigated whenever required in order to maintain a ponded layer of 5–6 cm depth during the vegetative stage. SRI_m plot soils were kept saturated but with no standing water during the vegetative stage. Stagnant rain water from these plots was drained out, collected in a refuge, and used for irrigating these plots. After panicle initiation, both sets of plots had 2–3 cm depth of water maintained on them, and plots were drained 15 days before harvest. Weeding in SRI_m plots was performed by cono-weeder to incorporate weeds into the soil and for soil aeration; RMP plots were hand-weeded. To describe rice growth stages, a rice growth staging system was followed (Counce *et al.*, 2000).

Measurements of root dry weight and xylem exudation rate

Three hills from each replicate were randomly selected at grain depth expansion stage (R6, 110 days after germination, DAG), and root samples were collected by removing a cylinder of soil along with the hill using an auger 10 cm in diameter and 45 cm depth (Kawata and Katano, 1976). Roots were carefully washed, and their length and dry weight were measured (Yoshida, 1981). Root volume was measured by the water displacement method of putting all roots in a measuring cylinder.

Table 1. Crop management practices for comparative evaluation of modified SRI and recommended management practices.

Practices	Modified SRI method†	Recommended management‡
Seedling age at transplanting	10-day-old seedlings	21-day-old seedlings
Plant spacing and density	One seedling per hill was transplanted in a square pattern at spacing of 20 cm × 20 cm quickly after uprooting	Three seedlings per hill were transplanted at spacing of 20 cm × 10 cm
Weed control	Three weedings by cono-weeder were performed at 10, 20 and 30 DAT§ to aerate the soil	Hand (manual) weeding at 10, 20 and 30 days DAT
Water management	Seedlings were transplanted 1–2 cm deep into a puddled field without any standing water. During the vegetative growth phase, plots were kept saturated (not flooded) and after panicle initiation (R0) stage, 2–3 cm of standing water was maintained on the field and drained 15 days before harvest	Seedlings were transplanted 2–5 cm deep into a puddle field with 5–6 cm of ponded water, and water level was maintained during the vegetative stage. After panicle initiation (R0) stage, 2–3 cm of standing water was kept on the field and drained 15 days before harvest
Nutrient management	For both sets of methods, organic manure (mixture with cow dung and straw) was applied at the rate of 5 t ha^{-1} along with chemical fertilizers (urea, single super phosphate, and muriate of potash at the rate of 80 kg N ha^{-1}, 40 kg P_2O_5 ha^{-1}, and 40 kg K_2O ha^{-1}). The entire amount of P was applied at the time of final land preparation, while N and K were applied in three splits, i.e. 25% at 10 DAT, 50% at tillering stage (30 DAT), and 25% at panicle initiation stage (60 DAT).	

†SRI_m practices differ from those reported in Stoop *et al.* (2002) only in spacing of 20×20 cm (instead of 25×25 cm) and in fertilization.
‡Based on recommendations of the Central Rice Research Institute, Cuttack, India; full description of these can be found at http://crri.nic.in/
§DAT: days after flowering.

Xylem exudation rate was measured using the method of San-oh *et al.* (2004) at grain depth expansion stage (R6) on 23–26 October each year. From each replicate, three hills were selected, each with an average number of panicles (17±1 from SRI_m and 8±1 from RMP plots). Stems were cut 10 cm from the soil surface, and pre-weighed cotton wool packed in a polythene bag was attached to the cut end of each stem with tape. After 24 hours, each bag was detached, sealed and weighed, and the weight of the exudates was calculated by subtracting the weight of the bag and pre-weighed cotton wool.

Measurements of plant dry weight, leaf area and crop growth rate

Dry weight of plant samples was determined at harvest after oven-drying at 80 °C for 72 h to reach a constant weight. To assess leaf area, three hills were randomly selected from each replicate, and the leaf area of 1 m^2 ground area was measured at anthesis (R4, 105 DAG) using a leaf area meter (LICOR-3100 Area Meter). Specific leaf weight (SLW) was calculated by dividing the leaf dry weight by leaf area. Leaf area index (LAI) was calculated by dividing leaf area by the land area. Area of flag leaves, collected from three hills, was measured at grain dry down stage (R7) on 3–4 November. Three hills were collected randomly during each sampling at 10-day intervals from each replicate to calculate crop growth rate (CGR), starting from 30 DAG to 70 DAG. Crop growth rate is the gain in the weight of plants on a unit of land within a unit of time, calculated from the following equation:

$$\text{CGR} = 1/\text{G}_\text{A} \times (\text{W}_2 - \text{W}_1)/(\text{T}_2 - \text{T}_1),\ \text{where GA} = \text{ground area},$$
$$\text{W} = \text{weight of crop},\ \text{and T} = \text{time}.$$

Measurements of light interception by the canopy

The light intensity above the canopy (I_0) and at the surface of the soil under the canopy (I_b) was measured with a line quantum sensor (400–700 nm) (Model: EMS 7; SW & WS Company) on a bright sunny day between 11:30 hours and 12:00 noon at 10-day intervals from each replicate starting from planting to panicle initiation stage (R0, 70 DAG). The light intensity at the surface of the soil relative to the intensity above the canopy was measured at consecutive points at intervals of 1 m apart in the inter-row space and in the inter-hill space, respectively (San-oh *et al.*, 2004). Light interception by the canopy (LIC) was calculated, as a percentage, from the following equation:

$$\text{LIC} = \left(1 - \frac{I_b}{I_0}\right) \times 100$$

Measurements of leaf inclination and canopy angle

Three hills at the grain dry down stage (R7, 120 DAG) were selected randomly from each replicate for measurements of canopy angle. The canopy angle (CA) was measured with a protractor using the following equation: CA (in degrees) = 180 – ($\theta_1 + \theta_2$), where θ_1 and θ_2 are the angles of inclination of the outermost tillers from a horizontal orientation on both sides. The leaf inclination was calculated after measuring the angle between the leaf blade and stem for each leaf from top to bottom (1st to 5th leaf) of a tiller.

Determination of chlorophyll in leaves

Chlorophyll (Chl) content was determined in the flag leaf at the grain dry down stage (R7, 120 DAG). Two hundred mg of fresh leaf tissue was taken and cut into small pieces, and chlorophyll pigments were extracted using 10 ml dimethyl sulfoxide (DMSO) solution at 65°C for 3 hours (Hiscox and Israelstam, 1979), filtered through Whatman No. 1 filter paper. Absorption of the chlorophyll extract was measured using a UV-Vis Spectrophotometer (Model: Chemito, 2600) at wavelengths of 645 and 663 nm, using DMSO as the blank. Chlorophyll *a*, *b* and total chlorophyll were calculated (Hipkins and Baker, 1986) and expressed as mg g^{-1} fresh leaf weight.

Measurement of chlorophyll fluorescence and photosynthesis rate

Flag leaves at the grain dry down stage (R7) on 4–5 November from each plot were marked to measure chlorophyll fluorescence with a Fluorescence Monitoring System (FMS-2, Hansatech). The chlorophyll fluorescence parameters measured were dark-adapted maximum photochemical efficiency (Fv/Fm) and ΦPS II at the same stage of the crop under both treatments. Prior to each set of Fv/Fm measurements, leaves were dark adapted for a period of 30 min using leaf clips. The same flag leaves were also used to measure transpiration rate, photosynthesis rate, stomatal conductance and internal CO_2 concentration, using a CIRAS-2 Portable Photosynthesis System (PP Systems, U.K.). These measurements were taken on a clear sunny day (solar radiation $> 1200\ \mu mol\ m^{-2}\ s^{-1}$) between 10:30 and 11:00 hours before any marked reduction in photosynthesis at midday occurred.

Measurements of yield and yield components

The stage of phyllochron was determined on the basis of the number of total tillers in a hill and was adapted from the analysis of Laulanié (1993). Five hills in each plot were randomly marked at the time of planting for counting tiller number periodically at the interval of 10 days up to panicle initiation stage (R0, 70 DAG). The average number of tillers was extrapolated into phyllochrons based on the relationship between phyllochrons and tiller numbers given by Laulanié (1993), Nemoto *et al.* (1995), Matsuo *et al.* (1997) and Stoop *et al.* (2002).

All plants in an area of 5 m × 5 m for each replicate (25 m^{-2}) were harvested (excluding the border rows) for determination of yield per unit area, and grain yield was adjusted to 14.5% seed moisture content. Harvest index was calculated by dividing dry grain yield by the total dry weight of aboveground parts. Average tiller number and panicle number were determined from crop harvested from a square meter area from each replication. Panicle length, number of grains per panicle and number of filled grains were measured for each panicle individually harvested from a square meter area from each replication. The percentage of ripened grains was calculated by dividing the number of filled grains by the total number of grains. All panicles from a square meter area were categorized according to their length, and a frequency distribution was plotted.

Statistical analyses

All data were statistically analysed using analysis of variance (ANOVA) as applicable to a split-plot design (Gomez and Gomez, 1984). The significance of the treatment effect was determined using an F-test, and to determine the significance of the difference between the means of the two treatments, least significant differences (LSD)

Table 2. Mean squares from analysis of variance (ANOVA) of root dry weight hill^{-1}, root dry weight m^{-2}, photosynthesis rate, leaf area index (LAI), panicle number m^{-2}, straw weight m^{-2} and grain yield m^{-2}.

	Mean squares						
Source	Root DW hill^{-1}	Root DW m^{-2}	Photosynthesis rate	LAI	Panicle number m^{-2}	Straw weight m^{-2}	Grain yield m^{-2}
Year (Y)	0.045ns	348.76ns	26.43ns	0.04ns	825.43ns	19710.2ns	253.03ns
Practice (P)	249.697**	921.30ns	893.26**	5.41**	520.83ns	315187.5**	267907.5**
Y X P	0.318ns	3168.11ns	6.04ns	0.05ns	287.23ns	17366.9ns	919.9ns

DW: dry weight
ns: Not significant
* and **: Significant at $p < 0.05$ and $p < 0.01$, respectively

Table 3. Comparison of dry matter accumulation, grain yield, and harvest index in modified SRI and RMP.

Cultivation method	Dry weight (g hill^{-1})	Dry weight (g m^{-2})	Straw weight (g m^{-2})	Grain yield (g m^{-2})	Harvest index
SRI_m	54.58 (6.52)	1364.6 (162.9)	726.7 (161.8)	637.9 (22.1)	0.47 (0.06)
RMP	27.61 (4.61)	1380.6 (230.3)	931.7 (230.5)	448.9 (20.5)	0.33 (0.05)
$LSD_{0.05}$	3.58	ns	124.9	17.5	0.04

Standard deviations are given in parentheses (n = 15).

were calculated at the 5% probability level. Regression relationships were determined using the data analysis tool pack of MS-Excel.

The data set for all the parameters was statistically analysed considering year as a source of variation in addition to the treatment (practice). The main effect of year and interaction effects of year × practice were not significant at $p < 0.05$ for any of the parameters, so the data reported in this paper are averages for three years. Mean squares for some of the important parameters are presented in Table 2.

RESULTS

Dry matter accumulation, yield and crop growth rate

The dry weight of aboveground parts of individual hills under SRI_m was significantly greater than that of RMP hills, although it was non-significant on a per unit area basis, when compared between the two cultivation methods (Table 3). The straw weight per unit area was significantly higher in RMP than SRI_m plots but grain yield was 42% more in SRI_m than in RMP. Further, harvest index was significantly higher for SRI_m than RMP. Differences in grain yield between these two methods of cultivation were due principally to differences in the harvest index rather than because of differences in dry matter production.

Crop growth rate (CGR) was higher in RMP than in SRI_m up to 60 DAG. However, after this CGR in RMP declined compared to that observed in SRI_m (Figure 1). In

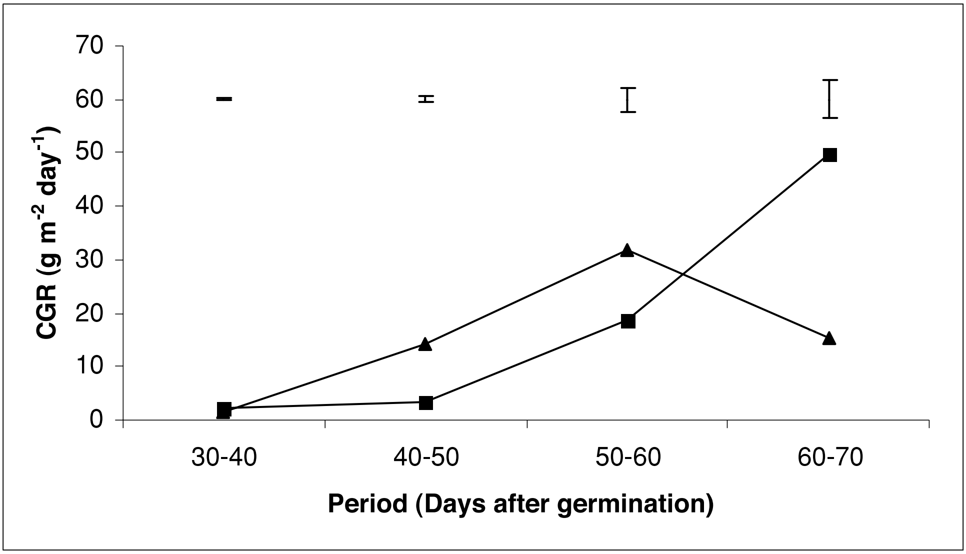

Figure 1. Changes in crop growth rate (CGR) with modified SRI and RMP methods during vegetative stage. Solid squares and solid triangles represent SRI_m and RMP, respectively. Vertical bars represent LSD at 5%.

Table 4. Comparison of yield-contributing characters in modified SRI and RMP.

Cultivation method	Ave. panicle number hill^{-1}	Panicles (m^{-2})	Ave. panicle length (cm)	Grains/ panicle	Unfilled grains/ panicle	Ripened grains (%)	1000-grain weight (g)
SRI_m	16.9 (5.23)	421.7 (15.58)	21.61 (2.26)	141.9 (35.25)	9.80 (3.24)	93.1 (4.68)	22.46 (0.56)
RMP	8.6 (2.84)	430.0 (21.13)	18.77 (2.60)	84.2 (20.53)	8.17 (3.38)	90.3 (6.54)	20.68 (0.53)
$LSD_{0.05}$	0.4	ns	1.18	10.3	1.11	0.7	0.40

Standard deviations are given in parentheses (n = 15).

the latter treatment, CGR showed a continuously increasing trend throughout the vegetative stage.

Yield-contributing characters

The number of panicles per hill was significantly greater in SRI_m (average: 16.9 hill^{-1}; range: 12–30 hill^{-1}) than in hills under RMP (average: 8.6 hill^{-1}; range: 4–12 hill^{-1}). On the other hand, the number of panicles per unit area was not significantly different between the respective systems (SRI_m: 421.7 panicles m^{-2}, RMP: 430.0 panicles m^{-2}) (Table 4). The average panicle length in SRI_m (21.61 cm) was, however, significantly ($p < 0.05$) higher than panicles in RMP (18.77 cm). The longer SRI_m panicles carried nearly 1.7 times more number of grain compared to panicles obtained from RMP plots, and the percentage of ripe grains and 1000-grain weight were also significantly higher in SRI_m plants than RMP plants.

Modified SRI plots had the highest number of panicles per unit area of land that were 23.1–24.0 cm long. This was different from RMP plots whose highest number

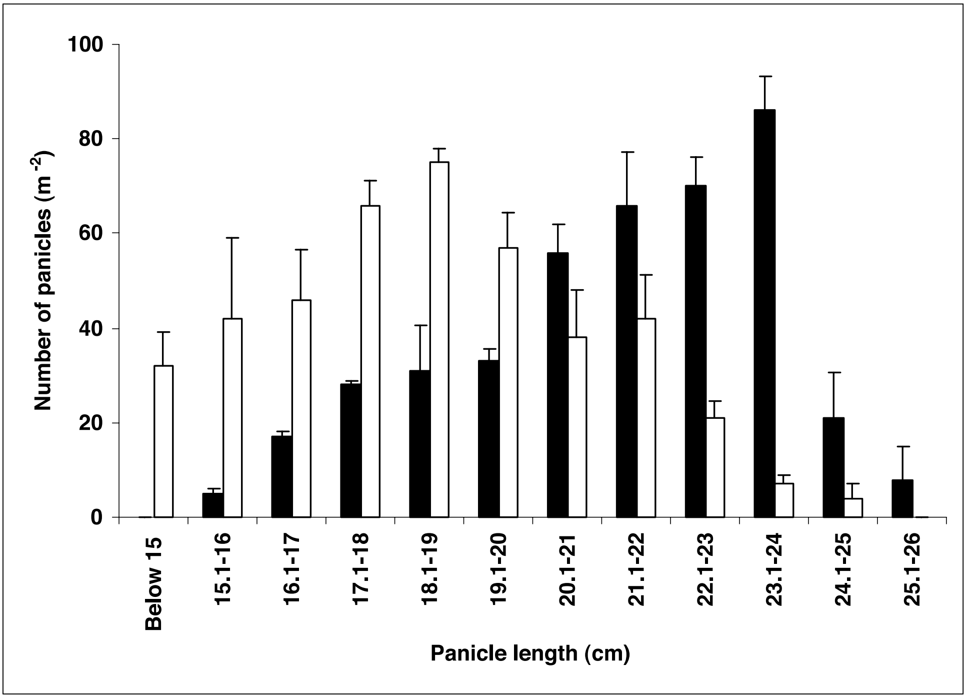

Figure 2. Frequency distribution of panicle length m^{-2} in modified SRI and RMP. Black and white bars represent SRI_m and RMP, respectively. Vertical bars represent standard deviation: n = 421 for SRI, and n = 430 for RMP.

of panicles was 18.1–19.0 cm long (Figure 2). Most of the panicles (66%) in SRI_m were 20.1 cm to 24.0 cm in length, while most RMP panicles (66%) were 15.1 cm to 20.0 cm long. It was noted that, with SRI_m, no panicle was <15 cm length; in contrast, no RMP panicles were >25 cm long.

The relationship between panicle length and grain number in SRI_m and RMP is shown in Figure 3. With SRI_m management, each centimetre of increase in panicle length could accommodate 12 grains, whereas with RMP, only 6 grains could be accommodated by each additional centimetre. The alternative sets of management practices thus produced a difference in the branching of panicles, so that the structure of SRI_m panicles could accommodate more grains.

Number of tillers and phyllochrons

The number of tillers per hill in SRI_m varied from 13 to 36 (average: 17.9 tillers $hill^{-1}$) whereas in RMP the number ranged from 6 to 16 (average: 9.7 tillers $hill^{-1}$). On the other hand, tiller number per unit area was significantly ($LSD_{0.05}$ = 11.7) lower in SRI_m (448.3 tillers m^{-2}; *s.e.m.* ± 4.80) than in the RMP plots (486.7 tillers m^{-2}; *s.e.m.* ± 6.41). Ninety-four percent of all SRI_m tillers produced panicles whereas in RMP effective tillers were significantly ($LSD_{0.05}$ = 1.7) lower (89%).

Single seedlings with SRI_m management produced 28 tillers before onset of anthesis; in contrast with RMP, the three plants in each hill together averaged only 13 tillers

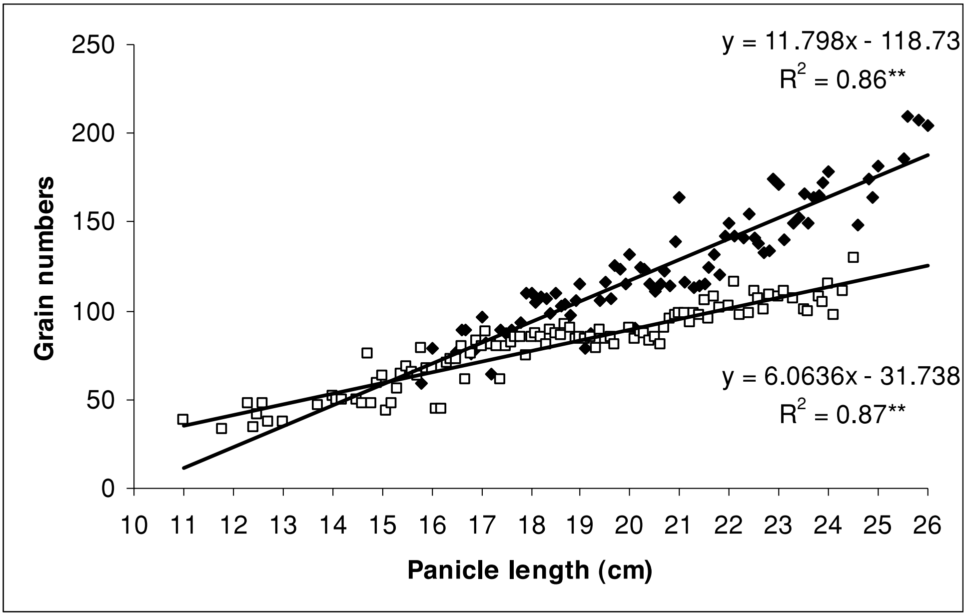

Figure 3. Relationships between the panicle length and grain number with modified SRI (n = 81) and RMP (n = 103). Black and white squares represent SRI_m and RMP, respectively.

per hill (Figure 4). When the transplanting of clumps of more mature seedlings was done in RMP plots (21 DAG), the single seedlings in SRI_m plots had already started their tillering; and at 30 DAG (20 days after transplanting), rapid tillering had begun with SRI_m, soon overtaking the RMP treatment, as seen in Figure 4. The highest number of tillers in an SRI_m hill was 36, whereas with RMP it was 16.

When the mean number of tillers was assessed in terms of phyllochron stages (Table 5), the average number of tillers in SRI_m plots was five at 30 DAG (6th phyllochron, V5 stage). At this date, the transplanted seedlings in RMP plots were still experiencing transplant shock, and active tillering had not yet started. In RMP plots, tillering only started after 30 DAG and reached a total of five tillers by 40 DAG (6th phyllochron, V5 stage).

By the onset of anthesis, SRI_m plants had reached their 10th phyllochron stage (V9 stage) of tillering and root growth, whereas RMP plants by this time had only reached their 8th phyllochron stage (V7 stage), resulting in lower numbers of tillers per hill. RMP plants reached their 8th phyllochron (V7 stage) at about 60 DAG and remained in this same phyllochron interval up to 70 DAG, reflecting a slower rate of development.

Leaf area index and specific leaf weight

At anthesis, the number of leaves and the leaf area per hill in the SRI_m treatment were significantly higher than in RMP. SRI_m hills had more than twice the number

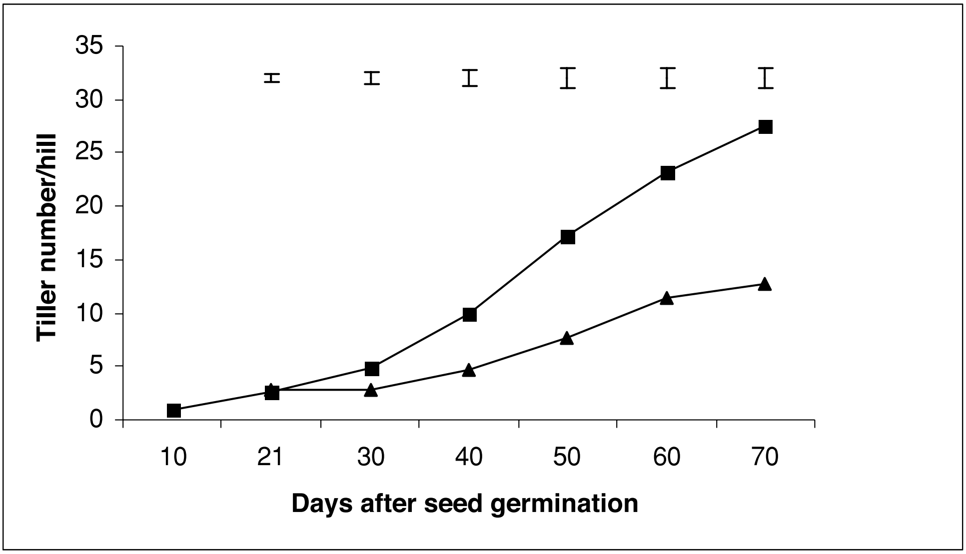

Figure 4. Changes in tiller number per hill in modified SRI and RMP method during vegetative stage. Solid squares and solid triangles represent SRI_m and RMP, respectively. Vertical bars represent LSD at 5%.

Table 5. Comparison between numbers of phyllochrons[a] completed under modified SRI and RMP in trials.

Cultivation method	10 DAG	30 DAG	40 DAG	50 DAG	60 DAG	70 DAG
SRI_m	Transplanted 4th phyllochron (V3)	6th Phyllochron (V5)	7–8th phyllochron (V6-V7)	8–9th phyllochron (V7-V8)	9th phyllochron (V8)	10th Phyllochron (V9)
RMP	In Nursery	Transplanting shock	6th Phyllochron (V5)	7th phyllochron (V6)	8th phyllochron (V7)	8th Phyllochron (V7)

[a]Phyllochron: The period of time in which one or more units of tiller, leaf and roots, each unit constituting a phytomer, emerges from the plant's meristematic tissue as described by Nemoto *et al.* (1995).
DAG: Days after germination of seed.
V-Vegetative development stages with the number of true leaves on the main stem (adapted from rice growth staging system as described by Counce *et al.* 2000).

of leaves and three times the total leaf area of each hill compared to hills under RMP (Table 6). Similarly, flag leaf area per hill at the grain dry down stage (R7 or dough grain stage or middle ripening stage) was significantly higher in SRI_m than in RMP but there were no significant differences between treatments on a per unit area basis. However, SRI_m crops had a significantly higher LAI, mainly because of an increase in the area of single leaves and because the leaves of SRI_m plants had higher SLW than did RMP leaves.

Table 6. Comparison of leaf number, leaf area, leaf area index (LAI), and specific leaf weight (SLW) in modified SRI and RMP at anthesis stage (R4).

Cultivation method	Leaf number ($hill^{-1}$)	Leaf number (m^{-2})	Leaf area (cm^2 $hill^{-1}$)	Area of single leaf (cm^2)	Flag leaf area (cm^2 $hill^{-1}$)	Flag leaf area (cm^2 m^{-2})	LAI	SLW (g m^{-2})
SRI_m	103.33	2583.33	1521.21	14.72	282.69	7067.13	3.91	134.16
	(16.95)	(423.70)	(260.71)	(1.00)	(41.21)	(1030.16)	(0.19)	(9.47)
RMP	55.87	2793.33	501.22	9.18	141.96	7098.00	2.34	107.80
	(17.54)	(876.86)	(147.12)	(1.55)	(20.42)	(1020.93)	(0.22)	(11.39)
$LSD_{.05}$	11.02	ns	124.11	0.77	21.83	ns	0.16	5.09

Standard deviations are given in parentheses (n = 15).

Table 7. Comparison of leaf inclination and canopy angle at grain dry down stage (R7) under modified SRI and RMP.

Cultivation method	1st leaf (flag leaf)†	2nd leaf	3rd leaf	4th leaf	5th leaf	Canopy angle
SRI_m	7.5 (1.67)	4.9 (1.39)	7.5 (1.41)	10.7 (1.99)	15.9 (2.63)	34.9 (2.28)
RMP	9.2 (1.20)	7.3 (1.33)	9.9 (1.86)	13.7 (1.65)	19.9 (1.98)	17.5 (5.60)
$LSD_{.05}$	0.8	0.6	0.8	1.3	1.8	2.6

Standard deviations are given in parentheses (n = 15).
†Angle between flag leaf and panicle axis.

Canopy structure and solar radiation interception by the canopy

Canopy structures were compared at the grain dry down stage (R7 or dough grain stage or middle ripening stage), on 3–4 November. New tillers in SRI_m emerged flatter, i.e. with a greater angle from the vertical, whereas new RMP tillers emerged more upright within the clump of plants. This configuration of tiller emergence gave SRI_m hills a more open-plant structure, with greater canopy angle than measured in RMP hills (Table 7). This could be attributed to the shallower planting (1–2 cm) in SRI_m as well as to less crowding of SRI_m plants. At the same time, we found that the angle between the leaf blade and the stem/tiller, flag leaf and panicle axis was lesser in SRI_m plants than RMP plants. This meant that SRI_m leaves were more erect as compared to RMP.

As seen in Figure 5, during the initial growth stages (up to 40 DAG), the RMP canopy intercepted more solar radiation than did the SRI_m canopy. However, beyond 50 DAG light interception in SRI_m plots was significantly more than in the RMP plots. At panicle initiation stage (R0), it reached 90% in SRI_m plots, while light interception by RMP canopies was only 78% at this stage.

Chlorophyll content, chlorophyll fluorescence and photosynthesis

At the grain dry down stage (R7 or dough grain stage or middle ripening stage), on 3–4 November, SRI_m flag leaves had significantly higher 40% more Chl *a*, 14% more Chl *b* and 31% more total Chl than RMP plants, as well as a 23% higher Chl *a*/*b* ratio (Table 8).

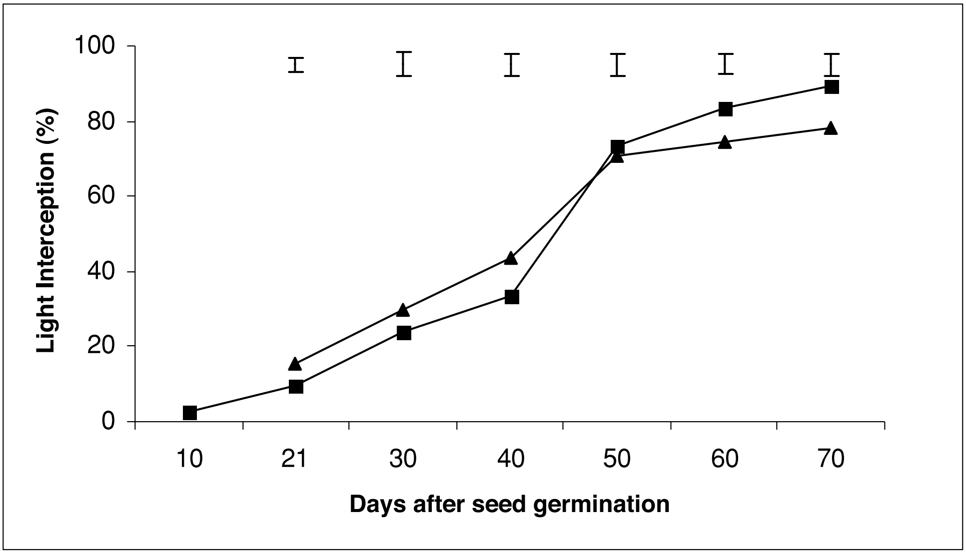

Figure 5. Changes in the interception of solar radiation by the canopy in modified SRI and RMP crops during vegetative stage. Solid squares and solid triangles represent SRI_m and RMP, respectively. Vertical bars represent LSD at 5%.

Table 8. Comparison of chlorophyll content, fluorescence, transpiration rate, net photosynthetic rate, stomatal conductance, and internal CO_2 concentration in modified SRI and RMP at grain dry down stage (R7).

	Cultivation method		
Parameters	SRI_m	RMP	$LSD_{.05}$
Chlorophyll a (mg g^{-1}FW)	2.35 (0.17)	1.68 (0.21)	0.14
Chlorophyll b (mg g^{-1}FW)	1.02 (0.09)	0.90 (0.09)	0.07
Total chlorophyll (mg g^{-1}FW)	3.37 (0.17)	2.58 (0.21)	0.11
Chlorophyll a/b ratio	2.32 (0.28)	1.90 (0.37)	0.29
Fv/Fm ratio	0.796 (0.023)	0.708 (0.023)	0.017
Φ PS II	0.603 (0.026)	0.486 (0.026)	0.020
Transpiration (m mol m^{-2} s^{-1})	6.41 (0.43)	7.59 (0.33)	0.27
Leaf temperature (°C)	34.48 (1.13)	33.09 (0.71)	ns
Net photosynthetic rate (μ mol m^{-2} s^{-1})	23.15 (3.17)	12.23 (2.02)	1.64
Stomatal conductance (m mol m^{-2} s^{-1})	422.73 (34.35)	493.93 (35.93)	30.12
Internal CO_2 concentration (ppm)	292.6 (16.64)	347.0 (19.74)	11.1

Standard deviations are given in parentheses (n = 15).

At this same stage (R7 or dough grain stage or middle ripening stage), the maximum fluorescence efficiency (Fv/Fm) and the actual fluorescence efficiency (ΦPS II) of flag leaves were both significantly higher in the SRI_m crop compared to the RMP crop. The reduction in fluorescence efficiency from maximum to actual was significantly greater in the leaves of the crop grown under RMP compared to SRI_m.

There were significant differences in flag leaf photosynthesis, internal CO_2 concentration, and transpiration rate between SRI_m and RMP. Net photosynthesis

Table 9. Comparison of root depth, root dry weight, root volume, and root length in modified SRI and RMP crops at grain depth expansion stage (R6).

Cultivation method	Root depth (cm)	Root dry weight (g $hill^{-1}$)	Root dry weight (g m^{-2})	Root volume (ml $hill^{-1}$)	Root volume (ml m^{-2})	Root length (cm $hill^{-1}$)
SRI_m	32.33 (3.11)	11.10 (2.05)	277.42 (51.21)	47.93 (8.19)	1198.33 (204.74)	7378.53 (1074.65)
RMP	19.61 (2.74)	5.33 (1.06)	266.33 (53.06)	21.47 (3.25)	1073.33 (162.42)	3560.53 (591.82)
$LSD_{0.05}$	2.88	1.47	ns	4.77	ns	566.81

Standard deviations are given in parentheses (n = 15).

Table 10. Comparison of xylem exudation rates in modified SRI and RMP crops at grain depth expansion stage (R6).

Cultivation method	Amount of exudates (g $hill^{-1}$)	Amount of exudates per m^2 (g m^{-2})	Rate per hill (g $hill^{-1}$ h^{-1})	Rate per m^2 (g m^{-2} h^{-1})
SRI_m	6.43 (1.08)	160.70 (26.89)	0.27 (0.04)	6.70 (1.12)
RMP	2.33 (0.34)	116.50 (17.06)	0.10 (0.01)	4.85 (0.71)
$LSD_{0.05}$	0.66	19.61	0.03	0.82

Standard deviations are given in parentheses (n = 15).

rate was significantly higher, and the buildup of internal CO_2 concentration inside the leaf was lower, in SRI_m plants than in RMP (Table 8). Concomitantly, RMP plants had a higher transpiration rate than the SRI_m crop. The ratio of photosynthesis to transpiration (instantaneous water-use efficiency) was accordingly higher in SRI_m compared to RMP. With the loss of one millimol of water, 3.6 and 1.6 μ mol of CO_2 was fixed in SRI_m and in RMP plants, respectively.

Root growth and xylem exudation rates

Root growth and xylem exudation rate were measured at the crop's grain depth expansion stage (R6, milk grain stage or early ripening stage) which is when active grain-filling starts. Roots per hill were nearly twice as heavy, were deeper, more than double the length and double the volume in SRI_m plants (Table 9). But these root parameters were not significantly different on a per unit area basis.

There was significantly more xylem exudate in SRI_m plants at the grain depth expansion stage (R6), both per hill and per unit area (Table 10). Similarly, the rate at which these exudates were transported from the root towards the stem was higher in SRI_m hills. The exudation rate per m^{-2} of land area was also found to be higher in SRI_m plots than the RMP plots.

DISCUSSION

System of rice intensification (SRI) management includes many departures from conventionally recommended methods of rice cultivation. It proposes the use of single young seedlings, drastically lowered plant densities, keeping fields unflooded and use of a mechanical weeder which aerates the soil, all with the aim of providing optimal growth conditions for the plant, to get better performance in terms of yield and input productivity.

The data presented in this paper evaluated the performance of modified SRI plants compared with usual rice cultivation under standard irrigated conditions (RMP), not assessing any effects of organic vs. inorganic fertilization which could have further differentiated the results. The spacing used (20 × 20 cm) was less than that generally recommended for initial SRI spacing, being the distance found previously to be optimum under research-station conditions when used in conjunction with other SRI practices (Thakur *et al.*, 2009).

The basic question investigated was whether some combination of SRI management practices would induce any significant differences in plant growth or physiology that might tap some currently untapped production potential in rice, as suggested by Stoop *et al.* (2002). A detailed comparison has been presented here of the performance of rice plants grown with most of the recommended SRI management practices vis-à-vis that of plants raised under current RMP, having the same soil, climatic conditions, similar fertilization and with the same rice variety (genotype).

A number of previously published reports on SRI have showed enhancement of rice yield (Ceesay *et al.*, 2006; Kabir and Uphoff, 2007; Namara *et al.*, 2008; Satyanarayana *et al.*, 2007; Sato and Uphoff, 2007; Senthilkumar *et al.*, 2008; Sinha and Talati, 2007; Zhao *et al.*, 2009). This study found SRI_m management practices increasing grain yield by 42%, from 4.49 t ha^{-1} to 6.38 t ha^{-1}, while utilizing fewer seeds and less water. The dry weight of aboveground parts at harvest was greater in SRI_m than RMP when compared per hill, but no significant difference was found in dry matter production when the two methods of cultivation were compared on a unit area basis (Table 3).

The divergence in grain yield between SRI_m and RMP was due to differences in harvest index rather than dry matter production. For higher yield, profuse tillering is critical, with yield being determined by the number of panicle-bearing tillers per unit area, the number of grains per panicle and the weight of individual grains (Yoshida, 1981). In SRI_m, the number of panicle-bearing tillers per unit area by itself was not responsible for higher grain yield (Table 4). Even without significant increase in this parameter, SRI_m recorded significantly higher grain yield compared to RMP.

With SRI_m management, the main factors responsible for the yield enhancement in these trials were longer panicles with more grains, better grain filling and a significant increase in grain weight. SRI_m had a greater percentage of longer panicles than did rice grown with recommended practices; on the other hand, RMP produced a greater percentage of shorter panicles (Figure 2). Panicles of SRI_m plants accommodated more grains than RMP. For every centimetre increase in SRI_m panicle length, the number of grains increased by 12, while with RMP, the corresponding increase was only 6 grains (Figure 3). The increased number of grains per unit length was the result of longer primary branches on SRI_m panicles accommodating a greater number of spikelets (data not shown).

The greater straw weight at harvest from RMP plots was due to a greater number of tillers per unit area. However, with RMP the percentage of productive tillers relative to the maximum number of tillers was less than for SRI_m. Using modified SRI management practices, the number of tillers produced in each hill was almost double that of RMP, even though RMP hills contained three plants instead of one. The number of tillers per m^2 was lower with SRI_m mainly because it had only half as many hills per m^2.

When we considered the number of phyllochrons completed under each management system, it was found that many of the hills in the SRI_m plots were able to reach their 9th or 10th phyllochron of growth before anthesis (R4 stage) (Table 5), thereby producing a larger number of tillers (28–34). By comparison, rice plants under conventional RMP cultivation reached only up to 13 tillers before the onset of their reproductive stage, representing the completion of no more than eight phyllochrons before anthesis.

Tillering ability in rice has a close relationship with the number of phyllochrons completed before entering the reproductive stage (Nemoto *et al.*, 1995; Stoop *et al.*, 2002). The duration of phyllochrons is influenced by a number of environmental factors and biophysical growing conditions for the plant: soil and ambient temperature, exposure to sunlight, spacing, nutrient availability, soil friability vs. compaction, soil moisture vs. desiccation, and soil aeration vs. hypoxia (Nemoto *et al.*, 1995). RMP rice plants, with their multiple root systems in each hill, appeared to be constrained by competition for nutrients, space and light during their later stages of vegetative growth, especially beyond 60 DAG (Table 5). RMP canopies and root systems were limited compared to those of SRI_m plants as seen by their not completing more phyllochrons before anthesis. With SRI_m management, individual plants with more favorable growing conditions have shorter phyllochrons, which results in more, and more productive-, tillers and larger root systems (Katayama, 1951). This limitation of growth during the later vegetative stage in RMP was indicated by the slowing of CGR in RMP plants after 60 DAG (Figure 1).

At anthesis, the number of leaves and the leaf area per hill were both significantly higher in SRI_m than RMP; however, there was no difference in number of leaves per m^2. LAI was significantly higher in SRI_m plots than RMP mainly due to an increase in the size of individual leaves (Table 6). The higher SLW in SRI_m plants also indicated thicker leaves compared to the leaves grown under RMP.

Rice plants under RMP had a more compact structure, with tillers that were less horizontal and leaves that were more spreading (Table 7). This, along with smaller LAI, made RMP plants less efficient in utilizing solar energy given lower light interception (Figure 3). In contrast, the SRI_m plants had more open architecture, with tillers splayed out more widely, covering more ground area and more erect leaves that avoided mutual shading of leaves. These plants also had higher leaf area index due to significant increase in leaf sizes. More erect leaves are known to contribute to a higher LAI and to lead to more nitrogen storage, resulting in increased grain yield (Sinclair and Sheehy, 1999). Sakamoto *et al.* (2006) have also highlighted that erect leaves in rice can increase both biomass production and grain yield. Thus, the more erect leaves and higher LAI with SRI_m appeared to contribute to higher grain production.

We further examined whether the higher solar radiation interception by SRI_m plants was effectively utilized or not by comparing characteristics related to the rate of photosynthesis. A positive correlation was found between chlorophyll content, Fv/Fm and ΦPS II. A change in Fv/Fm derives from a change in the efficiency of non-photochemical quenching. Dark-adapted values of Fv/Fm reflect the potential quantum efficiency of PS II and are used as a sensitive indicator of plant photosynthetic performance. Our results showed that potential quantum yield and actual quantum yield of SRI_m plants were higher than for RMP plants (Table 8). Light is more effectively utilized in the photosynthesis process in SRI_m plants.

ΦPS II also gives an indication of overall photosynthesis performance (Genty *et al.*, 1989). There is a strong linear relationship between ΦPS II and efficiency of carbon fixation according to Maxwell and Johnson (2000). SRI_m plants with dark green leaves had higher chlorophyll content and a higher Chl *a*/*b* ratio than conventionally managed rice. This indicated better nutrient supply received by SRI_m hills compared with conventional RMP rice. This was apparently related to the larger and better functioning root systems of SRI_m plants (Tables 9 and 10). Previous reports also support our finding that lighter green leaves, unless experiencing low light condition (shading), have reduced total Chl/mg fresh weight and higher Chl *a*/*b* ratio (Harper *et al.*, 2004; Leong and Anderson, 1984; Murchie and Horton, 1997).

High photosynthetic rate with lower CO_2 concentration inside the sub-stomatal cavity in SRI_m plants also suggests a more efficient carboxylation system (Table 8). The instantaneous water-use efficiency of the leaf (represented by the ratio of photosynthesis to transpiration) is a measurement of carbon gained through photosynthesis with per-unit water transpired. A higher photosynthetic rate with lower transpiration in SRI_m plants indicates that they are using water more efficiently than conventionally managed, continuously flooded rice plants. There is further need to study the changes in leaf anatomy and stomatal density of SRI plants and their relationship with water and CO_2 diffusion pathways.

At the grain depth expansion stage, SRI_m plants had significantly larger root mass and length per plant compared to conventionally managed rice per hill. However, root mass per unit land area was not significantly different. The amount of xylem exudates and the rate at which exudates are transported from root to shoot during the active grain-filling stage, which was high in SRI_m plants, is an index of root physiological activity and also affects (potentially delays) the onset of leaf senescence (San-oh *et al.*, 2004; 2006).

Research by San-oh *et al.* (2006) found that rice plants with a larger number of crown roots and root apices synthesize larger amounts of cytokinins when each hill contains just one plant compared to each hill containing three plants. Our planting of one seedling per hill with SRI_m methods is similar to the treatments in the experiments of San-oh and associates. It is possible that SRI_m plants with better root growth and higher physiological activity would be transporting larger amounts of cytokinins (not measured here) from roots to shoot, resulting in a lower rate of leaf senescence

(San-oh *et al.*, 2006; Soejima *et al.*, 1992, 1995). In SRI_m plants, delayed senescence could derive from having increased root growth, higher leaf area and chlorophyll content, and perhaps by gene expression of enzymes contributing to photosynthesis during the latter part of the growth cycle (Ookawa *et al.*, 2004; Suzuki *et al.*, 2001).

This study was not designed to achieve or assess maximum potentials with different combinations of alternative management practices. Rather it undertook to determine whether there would be any substantial yield differences and significant phenological variations associated with the alternative management. The data presented here give considerable evidence that alterations in management practices can induce multiple, significant and positive changes in phenotype from a given rice genotype. Similar results have been reported by Zhao *et al.* (2009) with regard to nitrogen use efficiency and water use efficiency. The mechanisms for evoking these changes remain to be studied and determined in satisfactory detail.

CONCLUSIONS

Our results showed that the combination of specific SRI practices, designated here as SRI_m, outyielded currently recommended rice cultivation practices by 42%. Rice plants managed according to SRI precepts were able to complete more phyllochron stages and benefit from substantially larger and more active root systems. SRI_m practices improved the performance of individual hills (plants) in terms of their root growth and root activity, their tillering and grain filling, canopy characteristics, chlorophyll content, light utilization for photosynthesis and water-use efficiency.

These improved characteristics enabled SRI_m hills to produce longer panicles and greater proportions of longer panicles, which accommodated more filled and heavier grains. These changes more than compensated for having fewer hills per unit land area and reduced plant population with SRI_m. On the other hand, crowded environments under RMP conditions both below- and above-ground, evinced more competition during their later stages of vegetative growth, as evidenced by poor root growth and slower crop growth rate. These characteristics resulted in poorer performance of several important physiological processes during reproductive growth stages. These apparently contributed to the shorter panicle length, fewer grains, higher percentage of unfilled grains and smaller-sized grains. These constraints observed in RMP plants were mitigated by a combination of SRI practices.

With SRI management, we found that even the youngest tillers were as productive as the older ones in terms of panicle length, grain number and fewer unfilled grains – something observed by the originator of SRI (Laulanié, 1993). The SRI practices evaluated in this study enabled rice plants to develop more productive phenotypes with deeper roots having greater activity, larger leaves with spreading canopy for greater light interception, and delayed leaf senescence with an elevated rate of photosynthesis that ultimately lead to an improvement in harvest index for better grain yield.

In this study, SRI methods used were more productive than RMP under the conditions of our trials, and the data generated identified physiological mechanisms by which this result could be achieved. However, many further studies will be needed to gain a fuller understanding of how the respective components of SRI individually and collectively contribute to augmented grain yield under different soil and climatic conditions. Knowledge of synergistic effects between and among SRI components may help in breeding or selecting cultivars especially suitable for SRI conditions to maximize the significance of G × E interactions for better performance and greater yield. Also, this research did not investigate the possible contributions that aerobic soil biota make to these results (Randriamiharisoa *et al.*, 2006), so that domain also warrants investigation. Taking the influence of soil biota more explicitly into account could open some promising new opportunities for rice plant breeding.

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