Journal of Agronomy and Crop Science

J. Agronomy & Crop Science (2010) ISSN 0931-2250

MISCELLANEOUS

Comparative Performance of Rice with System of Rice Intensification (SRI) and Conventional Management using Different Plant Spacings

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Keywords
leaf area index; light interception; plant spacing; rice; SRI

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Accepted August 26, 2009

doi:10.1111/j.1439-037X.2009.00406.x

Abstract

The System of Rice Intensification (SRI) reportedly enhances the yields of rice (*Oryza sativa* L.) through synergy among several agronomic management practices. This study was conducted to investigate the effects on rice plant characteristics and yield by comparing the plants grown with different methods of cultivation – SRI vs. recommended management practices (RMP) focusing on the impact of different plant spacings.

Performance of individual hills was significantly improved with wider spacing compared with closer-spaced hills in terms of root growth and xylem exudation rates, leaf number and leaf sizes, canopy angle, tiller and panicle number, panicle length and grain number per panicle, grain filling and 1000-grain weight and straw weight, irrespective of whether SRI or RMP was employed. Both sets of practices gave their highest grain yield with the spacing of 20 × 20 cm; however, SRI yielded 40 % more than the recommended practice. At this spacing, canopies also had the highest leaf area index (LAI) and light interception during flowering stage. The lowest yield was recorded at 30 × 30 cm spacing under both the practices, as a result of less plant population (11 m^{-2}), despite improved hill performance.

During the ripening stage, hills with wider spacing had larger root dry weight, produced greater xylem exudates, and transported these towards shoot at faster rates. These features contributed to the maintenance of higher chlorophyll levels, enhanced fluorescence and photosynthesis rates of leaves and supported more favourable yield attributes and grain yield in individual hills than in closely-spaced plants.

Moreover, these parameters further improved in SRI, apart from the enhanced percentage of effective tillers and showed substantial and positive impacts on grain yield (17 %) compared with recommended practice. In conclusion, wide spacing beyond optimum plant density, however, does not give higher grain yield on an area basis and for achieving this, a combination of improved hills with optimum plant population must be worked out for SRI.

Introduction

System of Rice Intensification (SRI) was developed in Madagascar during the 1980s based on certain modifications in standard production methods (Laulanié 1993). Its divergences from conventional agronomic management for irrigated rice include: (a) transplanting young seedlings, preferably 8–12 days old (at 2–3 leaf stage), quickly, carefully and at shallow depth (1–2 cm deep), (b) transplanting single seedlings in a square pattern, with inter-row and inter-plant spacing of 25 cm or possibly more, (c) maintaining mostly aerobic soil conditions rather than continuous flooding of fields during the vegetative growth period, (d) adding organic manures like compost or mulch, and (e) controlling weeds with a mechanical hand weeder that actively aerates the soil (Stoop et al. 2002).

System of Rice Intensification practices and research have been attempted in different countries like Madagascar (Uphoff 1999, Barrett et al. 2004), Bangladesh (Husain et al. 2004), China (Wang et al. 2002, Yuan 2002, Zhao et al. 2009), Gambia (Ceesay et al. 2006), India (Satyanarayana et al. 2007, Sinha and Talati 2007, Senthilkumar et al. 2008), Indonesia (Sato and Uphoff 2007), Myanmar (Kabir and Uphoff 2007), Nepal (Neupane 2003), Sri Lanka (Namara et al. 2008) and reported to enhance yield and save water compared with farmers' practices. Most of these studies assessed phenotypical impacts of alternative management systems and have focused on structural differences (e.g., tiller number and panicle length) rather than on physiological changes that can be induced in the same genotype by altering the growing environment.

Claims of very high grain yields with SRI have, however, been dismissed by some scientists as unconfirmed field observations (Sinclair and Cassman 2004), as lacking supporting information (Sheehy et al. 2005), or involving measurement error (Sheehy et al. 2004). McDonald et al. (2008) assert that there is still not adequate evidence of a yield advantage with SRI over best management practices (BMP). So it demands more systematic research to validate the advantages of SRI practice over currently recommended practice, if any.

One of the elements of SRI practice is planting at wider spacing to expose rice plants to more light and air (Satyanarayana et al. 2007). This proposition has been challenged by Sinclair (2004) who contends that SRI's lower plant densities compared with conventional practice must suffer from poorer light interception, which will have a direct and adverse impact on plant growth and yield. Some experiments with SRI methods have also showed wider spacing of SRI practice to be disadvantageous when compared with the closer spacing of conventionally-grown rice (Sheehy et al. 2004, Menete et al. 2008). Wide spacing of SRI improve the productivity of individual hills (Menete et al. 2008), but not sufficiently to compensate for the higher yield in area basis as achieved with the lower spacing of conventional cultivation (Sheehy et al. 2004, Latif et al. 2005). However, these experiments, which used 30 × 30 cm spacing, interpreted as the SRI principle of 'wider spacing' to mean greater distance than recommended for SRI – start with 25 × 25 cm spacing, and increase or decrease this empirically according to the fertility of the soil (Stoop et al. 2002, Uphoff 2003). Further, none of these critical evaluations addressed the effects of spacing on variations in the physiology of rice plants, to understand how spacing affects rice plants' growth response to modifications in their above- and below-ground environment.

This study examined how plant spacing affects root development, canopy structure and light interception, plant growth and yield under SRI management conditions compared with standard cultural methods. In addition, it compares SRI practice with currently recommended practice at different spacings, to know whether other SRI component practices have any demonstrable impact on yield, and to find out what extent individual plant productivity can compensate for reductions in plant population.

Materials and Methods

Experimental site and soil

The experiments were conducted in 2007 and 2008 at the Deras Farm, Mendhasal in Khurda district, Orissa, India (20°30′N, 87°48′10″E) during the dry season (January–May) with a medium-duration rice variety, Surendra (130–135 days), which normally give yields of 3.5–5.0 t ha^{-1} (DRD, 2006).

Soils at the experimental site are classified as Aeric Haplaquepts, sandy clay-loam in texture (63 % sand, 16 % silt, and 21 % clay) with pH of 5.5. Organic carbon content was moderate (1.13 %). The mineral content was as follows: total nitrogen 0.08 %, available P (Olsen) 9 ppm, exchangeable K 0.20 meq per 100 g soil, exchangeable Ca 4.5 meq per 100 g soil, available S 14 ppm, Zn 10 ppm, and Fe 370 ppm.

Experimental design and treatments

The experimental design was a split-plot design with three replications and subplot sizes of 10 × 5 m. In the main plots, rice was grown under the two alternative crop management systems being assessed: the SRI, and recommended management practices (RMP) proposed by Central Rice Research Institute (http://crri.nic.in). Five different plant spacings were used in the subplots: 30 × 30 cm, 25 × 25 cm, 20 × 20 cm, 15 × 15 cm, and 10 × 10 cm. The number of hills/m^2 in the respective treatments was: 11 at 30 × 30 cm, 16 at 25 × 25 cm, 25 at 20 × 20 cm, 44 at 15 × 15 cm and 100 at 10 × 10 cm. All plots were surrounded by 50-cm wide bunds to prevent lateral water seepage and nutrient diffusion between plots, followed by 50-cm wide channels for irrigation.

Crop management and irrigation

For nursery establishment, germinated seeds were broadcasted on January 10, 2007 in the first year and on January 8, 2008 in the second year. The nursery was adjacent to the main field so that transplanting could be performed quickly to minimize injury. Twelve-day-old single seedlings were transplanted in the SRI plots within 30 min after removal from the nursery on January 22, 2007 and January 20, 2008. After completion of puddling and levelling the field, organic manure was applied after draining excess water. For RMP plots, the recommended practice of using 25-day-old seedlings for a medium-duration variety was followed, and three seedlings hill^{-1} were transplanted on February 4, 2007 and February 2, 2008. SRI plots were weeded by cono-weeder at 10, 20 and 30 days after transplanting (DAT); the RMP plots had three hand weedings at the same interval.

With both cultivation practices, organic manure (mixed with cow dung and straw) was applied at the rate of 5 t ha^{-1} along with chemical fertilizer: urea, single super phosphate (SSP) and muriate of potash (MOP) at the respective rates of 80 kg N ha^{-1}, 40 kg P_2O_5 ha^{-1}, 40 kg K_2O ha^{-1}. All P was applied at the time of final land preparation, while N and K were applied in three instalments, i.e., 25 % at 10 DAT, 50 % at tillering stage (30 DAT), and 25 % at panicle initiation stage (60 DAT). While the SRI recommendation is for organic fertilization in preference to chemical fertilization, in this evaluation we did not make this practice an additional factor to be assessed, so soil nutrient amendments was not a variable in either amount or form.

Recommended management practices plots were kept flooded and were irrigated on alternate days to maintain a ponded layer of 5–8 cm depth of water during the entire vegetative stage. In SRI plots, first irrigation was applied 5 days after transplanting to moisten the field without ponding. A second irrigation was given to the SRI plots on the evening of the 9th day after transplanting at a ponding depth of 2–5 cm, and the next morning a weeding was performed by a cono-weeder. Thereafter, the alternate wetting and drying method of irrigation was followed, and irrigation water was applied 3 days after the disappearance of ponded water. After panicle initiation, all plots were kept flooded with a thin layer of water 1–2 cm, and all were drained at 15 days before harvest. Crops were harvested on May 25 and May 24 during 2007 and 2008 respectively.

Climate data and water measurements

Daily rainfall was recorded at the experimental site using a rainfall gauge. Pan evaporation, daily minimum (T_{min}) and maximum temperature (T_{max}) data were collected from the weather station (Table 1) at our research farm located at 200 m away from experimental plots.

Water was supplied through a cemented channel to a plot channel and subsequently to the plots. Trapezoidal RBC flumes (13.17.02 RBC, Eijkelkamp Agrisearch Equipment, The Netherlands) were installed at the cemented channel and used to estimate the water supplied to the main plots by reading flume water height at 2–5 min intervals, converting to volume and integrating for the irrigation period.

Measurements of root dry weight and xylem exudation rate

Three hills from each replicate were randomly selected at the early-ripening stage on 28–29 April, and root samples were collected by using an auger of 10 cm diameter to remove soil of 15 cm deep along with the hill (Kawata and Katano 1976). A uniform soil volume (1178 cm^3) was excavated to collect root samples from all the treatments. Roots were carefully washed and dry weight measured (Yoshida 1981).

Xylem exudation rate was measured at the early-ripening stage. From each replicate, three hills were selected, each with an average number of panicles: 22 ± 1, 18 ± 1,

Table 1 Climate data for 2007 and 2008 during experimental period at Deras Research Farm, Bhubaneswar

Year	Month	Rainfall (mm month^{-1})	Pan evaporation (mm day^{-1})	T_{min} (°C)	T_{max} (°C)
2007	January	0	2.66	13.99	26.52
	February	64.7	3.71	14.31	30.24
	March	0	4.23	19.63	33.72
	April	26.6	4.82	22.34	35.90
	May	58.2	5.50	25.01	38.68
2008	January	16.0	2.46	12.29	25.83
	February	19.4	2.62	15.13	30.11
	March	7.3	3.98	19.22	31.28
	April	36.4	5.47	23.81	38.24
	May	106.4	5.98	26.21	39.36

14 ± 1, 8 ± 1 and 4 ± 1 in SRI plots; and 17 ± 1, 14 ± 1, 11 ± 1, 6 ± 1, and 3 ± 1 panicles in RMP plots, representing spacing of 30 × 30 cm, 25 × 25 cm, 20 × 20 cm, 15 × 15 cm and 10 × 10 cm respectively. The stems were cut at 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 a tape. After 24 h, each bag was detached, sealed and weighed and the weight of the root exudates was calculated by subtracting the weight of the bag and pre-weighed cotton wool (San-oh et al. 2004).

Measurements of leaf area, light interception by the canopy and canopy angle

To assess the leaf area, three hills were randomly selected from each replicate and the leaf area of 1 m^2 was measured during the flowering stage on 22–24 April, using a leaf area meter (LICOR-3100 Area Meter, LI-COR Inc., Lincoln, Nebraska, USA). Leaf area index (LAI) was calculated by dividing leaf area by the land area. 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 Burrage, Ashford, Kent, UK) on a bright sunny day between 11:30 am to 12:00 noon at flowering stage. 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:

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

Three hills at flowering stage on 22–24 April 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 − (θ_1 + θ_2), where θ_1 and θ_2 are the angles of inclination of the outermost tillers from a horizontal orientation on both sides.

Determination of chlorophyll fluorescence, photosynthesis rate and chlorophyll content

From each plot, flag and fourth leaf (from top) at flowering, middle-ripening and late-ripening stages (24 April, 8 May, and 18 May, i.e. 106, 120 and 130 days after germination, DAG respectively) were marked to measure chlorophyll fluorescence with a Fluorescence Monitoring System (FMS-2, Hansatech Instruments Ltd., Norfolk, UK). 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 management treatments. Prior to each set of Fv/Fm measurements, leaves were dark-adapted for a period of 30 min using leaf clips. Same leaves were also used to measure transpiration rate and photosynthesis rate with the use of a CIRAS-2 Portable Photosynthesis System (PP Systems, Hansatech Instruments Ltd., Norfolk, UK). These measurements were taken on a clear sunny day (solar radiation >1200 μmol m^{-2} s^{-1}) between 10:30 and 11:00 a.m. before the midday reduction in photosynthesis.

Chlorophyll content of flag and fourth leaves was determined at the flowering, middle-ripening and late-ripening stages (106, 120 and 130 DAG). Fresh leaf tissue (200 mg) was taken and cut into small pieces, and chlorophyll pigments were extracted using 10 ml dimethyl sulphoxide (DMSO) solution at 65 °C for 3 h (Hiscox and Israelstam 1979), filtered through Whatman No. 1 filtre paper. Absorption of the chlorophyll extract was measured using a UV-Vis Spectrophotometer (Model: 2600, Chemito, Mumbai, India) at wavelengths of 645 and 663 nm, using DMSO as the blank. Chlorophyll *a*, *b* and total chlorophyll were calculated as suggested by Hipkins and Baker (1986) and expressed as mg g^{-1} fresh leaf weight.

Measurements of plant dry weight, yield and yield components

Dry weight of plant samples was determined at harvest after oven-drying at 80 °C for 72 h to reach a constant weight. All plants in an area of 3 × 3 m for each replicate 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 (HI) was calculated by dividing dry grain yield by the total dry weight of aboveground parts. Average tiller number and panicle number were determined from the crop harvested from a square metre 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 metre area from each replication. The per cent of ripened grains was calculated by dividing the number of filled grains by the number of total grains.

Statistical analysis

All data were statistically analysed using analysis of variance (ANOVA) technique as applicable to split-plot design (Gomez and Gomez 1984). The significance of the treatment effect was determined using *F*-test, and to determine the significance of the difference between two treatments means, least significant difference (LSD) was estimated at the 5 % probability level. Regression relationship was developed using the data analysis tool pack of MS-Excel.

The data set for all parameters was statistically analysed considering year as a source of variation in addition to practice and spacing. It has been observed that the main effects of year and interaction effect between year and practice (year × practice), year and spacing (year × spacing) and three-factor interaction (year × practice × spacing) were non-significant at $P < 0.05$ for all parameters considered in the study. Computed-F values for some of the important parameters are shown in Table 2. Thus, it indicates that the year effect was rather negligible, and accordingly the data reported in this study are averages for 2 years of trials.

Results

Dry matter accumulation, grain yield and yield components

The dry weights of aboveground parts of individual hills and in per unit area were significantly greater in SRI than in RMP plants (Table 3). For both practices, dry weight per hill was significantly higher when spacing between plants was wider than with closer spacing. This resulted in straw weight per hill four times greater at 30 × 30 cm compared to 10 × 10 cm spacing. However, on an area basis, straw weight per unit area at 10 × 10 cm was more than double that from 30 × 30 cm spacing. There was no significant difference in straw weight per unit area at 25 × 25 cm and 30 × 30 cm spacing in both SRI and RMP. The interaction effects of neither practice nor spacing on straw weight were significant.

System of Rice Intensification plots produced significantly larger grain yield (17.4 %) than RMP plots and this enhancement was the highest at 20 × 20 cm spacing (40.1 %). Moreover, both cultivation practices produced the highest grain yield with 20 × 20 cm spacing and the lowest with 30 × 30 cm spacing. When spacing was wider or closer than 20 × 20 cm, grain yield decreased with both practices, and no significant differences in grain yield was recorded at 25 × 25 cm and 15 × 15 cm spacings under SRI and at 20 × 20 cm under RMP. The interaction effects of practice and spacing on grain yield were significant ($P < 0.05$). Interestingly, with RMP, grain yield was considerably higher at 25 × 25 cm than at

Table 2 Computed F values from analysis of variance (anova) of straw dry weight m^{-2}, grain yield m^{-2}, Harvest Index (HI), root dry weight m^{-2}, tiller number m^{-2}, panicle number $hill^{-1}$, panicle number m^{-2}, panicle length, leaf area $hill^{-1}$ and leaf area index (LAI)

	Computed F									
Source	Straw dry weight m^{-2}	Grain yield m^{-2}	HI	Root dry weight m^{-2}	Tiller number m^{-2}	Panicle number $hill^{-1}$	Panicle number m^{-2}	Panicle length	Leaf area $hill^{-1}$	LAI
Year (Y)	0.77^{ns}	0.42^{ns}	17.83^{ns}	12.81^{ns}	0.02^{ns}	0.20^{ns}	0.18^{ns}	0.793^{ns}	0.31^{ns}	0.49^{ns}
Practice (P)	9.06*	185.32**	5.40^{ns}	57.87**	16.50*	508.67**	96.54**	229.657**	270.21**	137.20**
Y × P	0.01^{ns}	0.0008^{ns}	0.01^{ns}	0.50^{ns}	0.006^{ns}	2.18^{ns}	1.08^{ns}	0.722^{ns}	6.62^{ns}	4.14^{ns}
Spacing (S)	325.59**	409.71**	328.83**	52.48**	467.0**	1056.19**	84.53**	75.427**	1044.29**	57.26**
Y × S	0.64^{ns}	0.88^{ns}	0.52^{ns}	0.80^{ns}	2.47^{ns}	2.43^{ns}	1.06^{ns}	0.764^{ns}	0.80^{ns}	2.23^{ns}
P × S	1.78^{ns}	47.76**	5.31**	3.02*	0.59^{ns}	14.64**	0.84^{ns}	2.57^{ns}	18.17**	2.25^{ns}
Y × P × S	0.20^{ns}	0.26^{ns}	0.65^{ns}	0.90^{ns}	0.84^{ns}	0.76^{ns}	0.29^{ns}	0.793^{ns}	0.26^{ns}	0.22^{ns}

ns, not significant. * and **, significant at $P < 0.05$ and $P < 0.01$ respectively.

Table 3 Dry matter accumulation, grain yield and Harvest Index at different spacings under SRI and RMP

	Straw dry weight (g $hill^{-1}$)			Straw dry weight (g m^{-2})			Grain yield[1] (g m^{-2})			Harvest Index[2]		
Plant spacing	SRI	RMP	Mean	SRI	RMP	Mean	SRI	RMP	Mean	SRI	RMP	Mean
30 × 30 cm	44.9	41.8	43.4	493.7	460.2	476.9	295.4	247.0	271.2	0.37	0.35	0.36
25 × 25 cm	31.3	28.7	30.0	500.3	459.2	479.7	426.3	397.9	412.1	0.46	0.46	0.46
20 × 20 cm	28.4	24.6	26.5	709.2	615.8	662.5	627.7	448.1	537.9	0.47	0.42	0.45
15 × 15 cm	22.1	20.8	21.4	971.7	913.0	942.3	421.8	403.4	412.6	0.30	0.31	0.30
10 × 10 cm	11.9	10.6	11.2	1191.7	1055.0	1123.3	388.2	342.9	365.6	0.25	0.25	0.25
Mean	27.7	25.3		773.3	700.6		431.9	367.9		0.37	0.36	
	Practice	Spacing	P × S	Practice	Spacing	P × S	Practice	Spacing	P × S	Practice	Spacing	P × S
$LSD_{0.05}$	1.6	1.7	ns	64.8	65.1	ns	18.5	19.4	27.5	ns	0.02	0.03

ns, not significant. [1]Grain yield was measured from crop harvested from 9 m^2 area from each replicate. [2]Harvest Index was calculated by dividing the grain yield weight by the dry weight of aboveground parts.

10 × 10 cm, even though the closer spacing is more common with farmer practice.

With both SRI and recommended practices, harvest index was significantly different with variations in spacing, but was non-significant between SRI and RMP, except at 20 × 20 cm spacing. HI was considerably higher in plants grown at the spacings of 20 × 20 cm and 25 × 25 cm than in plants grown at other spacings. This indicates that differences in grain yield at the various spacings were attributable to differences in dry matter production and harvest index.

Panicle length was significantly higher with SRI practice than with currently recommended practices (Table 4). It was the highest at the spacing of 30 × 30 cm and the lowest at 10 × 10 cm spacing. With both practices, panicle length was greater at wider spacing compared with close spacing. There were no significant differences in panicle length between 25 × 25 cm and 20 × 20 cm spacing plots. Among the yield components, grains/panicle, grain filling percentage and grain weight were significantly ($P < 0.05$) affected by cultivation practice and spacing (Table 4). At wider spacing, there were also more grains per panicle than the closer spacing. SRI panicles had significantly greater number of filled grains than RMP panicles. Closely spaced hills had significantly lower grain filling than widely spaced hills. There was no significant difference in grain filling between 25 × 25 cm and 20 × 20 cm plots. Grain weight was also greater with SRI than RMP. Overall, SRI plots had significant improvement in various yield components than RMP plots.

Tillers and panicles number

The number of tillers and panicles per hill was significantly ($P < 0.05$) larger in SRI than the RMP (Table 5). At wider spacing with both practices, both tiller and panicle number per hill were significantly increased compared with closer spacing. At 30 × 30 cm spacing, plants had

Table 4 Panicle length and yield components with different spacings under SRI and RMP

	Panicle length[1] (cm)			Grain number/panicle[1]			Grain filling[2] (%)			1000-grain weight[3] (g)		
Plant spacing	SRI	RMP	Mean	SRI	RMP	Mean	SRI	RMP	Mean	SRI	RMP	Mean
30 × 30 cm	22.86	22.09	22.47	184.3	165.5	174.9	87.87	82.66	85.26	25.35	24.84	25.09
25 × 25 cm	22.28	21.14	21.71	178.4	149.8	164.1	85.13	80.01	82.57	25.11	24.81	24.96
20 × 20 cm	22.22	20.00	21.11	163.4	142.5	153.0	84.04	78.43	81.23	24.95	24.29	24.62
15 × 15 cm	20.30	19.04	19.67	151.9	125.8	138.9	71.81	70.40	71.11	24.39	24.17	24.28
10 × 10 cm	19.13	18.22	18.67	124.8	105.2	115.0	68.46	63.12	65.79	24.18	23.96	24.07
Mean	21.36	20.10		160.5	137.8		79.46	74.92		24.79	24.41	
	Practice	Spacing	P × S	Practice	Spacing	P × S	Practice	Spacing	P × S	Practice	Spacing	P × S
$LSD_{0.05}$	0.33	0.72	ns	3.8	4.5	ns	2.73	3.34	ns	0.16	0.22	0.31

ns, not significant. [1]Panicle length and grains per panicle were measured from one square metre area from each replicate. [2]Grain-filling percentage was calculated by dividing the number of filled grains by the number of total grains. [3]1000-grain weight was calculated for a seed moisture content of 14.5 %.

Table 5 Tiller, panicle numbers and percent effective tillers at different spacings under SRI and RMP

	Av. tiller number ($hill^{-1}$)			Tiller number (m^{-2})			Av. panicle number ($hill^{-1}$)			Panicle number (m^{-2})			Effective tillers[1] (%)		
Plant spacing	SRI	RMP	Mean	SRI	RMP	Mean	SRI	RMP	Mean	SRI	RMP	Mean	SRI	RMP	Mean
30 × 30 cm	24.0	21.7	22.8	266.0	240.5	253.3	22.5	17.8	20.1	249.6	197.0	223.3	93.9	82.2	88.1
25 × 25 cm	18.8	17.9	18.4	301.3	286.1	293.7	18.0	14.7	16.3	287.2	234.9	261.1	95.3	82.1	88.7
20 × 20 cm	14.6	14.1	14.4	365.8	352.1	359.0	13.6	11.1	12.3	339.2	277.5	308.3	92.8	78.8	85.8
15 × 15 cm	9.2	8.8	9.0	404.1	385.0	394.5	8.3	6.4	7.3	364.5	280.1	322.3	90.3	72.9	81.6
10 × 10 cm	5.1	5.0	5.1	510.0	503.3	506.7	4.3	3.7	4.0	426.7	366.7	396.7	83.8	73.0	74.8
Mean	14.3	13.5		369.5	353.4		13.3	10.7		333.4	271.3		91.2	77.8	
	Practice	Spacing	P × S	Practice	Spacing	P × S	Practice	Spacing	P × S	Practice	Spacing	P × S	Practice	Spacing	P × S
$LSD_{0.05}$	0.8	0.7	1.0	15.5	18.5	ns	0.5	0.8	1.2	24.8	29.2	ns	9.0	7.1	ns

ns, not significant. [1]Effective tillers was calculated by dividing the panicle number by tiller number m^{-2}.

four to five times as many tillers and panicles per hill as plants at 10 × 10 cm spacing.

At all spacings, the number of tillers and panicles m^{-2} was significantly larger in SRI than RMP. However, there were significantly more tillers, nearly twice as many, at 10 × 10 cm vs. 30 × 30 cm spacing, mainly because there were so many more plants with closer spacing, i.e., 100 vs. 11.1 m^{-2}. In SRI plots, panicles per hill ranged respectively between 13–36, 8–24, 6–22, 3–14 and 2–11, for the spacings of 30 × 30 cm, 25 × 25 cm, 20 × 20 cm, 15 × 15 cm and 10 × 10 cm respectively.

The percentage of tiller-bearing panicles, i.e., effective tillers, was considerably higher in the SRI plots (91.2 % average for all spacings). The RMP plots, on the other hand, had lower percentages of effective tillers (only 77.8 %). Among different spacings, the lowest effective tillering was found in 10 × 10 cm plots. This highest percentage of effective tillers in RMP matched with the lowest effective tillering rate under SRI management. This difference in effective tillering associated with SRI management was thus one of the factors most clearly contributing to higher SRI yields.

Leaf area and light interception by the canopy

We examined how leaf area and light interception by the canopy varies with planting spacing under both cultivation practices. At the flowering stage, the number of leaves per hill with wider spacing was significantly larger ($P < 0.05$) than in the more closely-spaced plots, irrespective of the practices used. This resulted in higher leaf area in the hills more widely spaced (Table 6). Leaf area per hill was also significantly different between both practices, and it was higher in SRI than RMP mainly as a result of a significant increase in leaf size. The size of leaves increased significantly with wider spacing than with closer spacing in both SRI and RMP plots.

We compared the canopy angle at the flowering stage, on 22–24 April, as this has a significant effect on light interception. With both practices, there was wider canopy angle of plants in hills with wider spacing than in hills of more closely-spaced plants, mainly because of higher tiller numbers and spaces between hills. Those plants in hills with the same spacing had wider canopy angles when coming from SRI rather than RMP plots which may be attributed to the shallower planting practiced with SRI.

Leaf area index (LAI) and interception of light at flowering stage were both significantly higher in SRI than that in RMP plots (Fig. 1), and these parameters were the highest at the spacing of 20 × 20 cm with both practices. Plots with plant spacing more or less than this had lower LAI and light interception. A close relationship (r = 0.91) was observed between LAI and light interception for plants in all plots (Fig. 2).

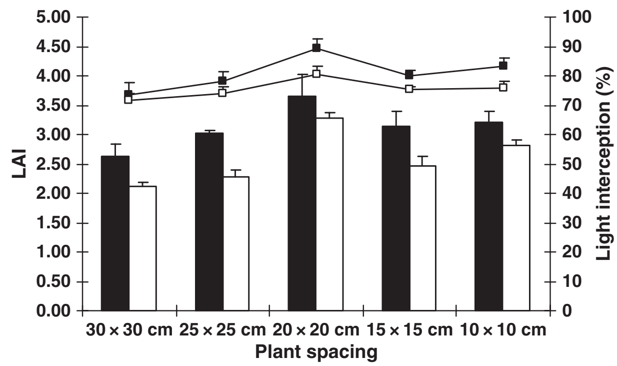

Fig. 1 Leaf area index (LAI) and light interception by canopy at flowering stage on 22-24 April. Black and white bars represent LAI in SRI and RMP plots respectively. Closed and open squares represent light interception in SRI and RMP plots respectively. Vertical bars represent the standard deviation (n = 6). Practice, spacing and its interaction were significantly different at 5 % level of significance for both LAI and light interception.

Table 6 Leaf development at different spacings under SRI and RMP at flowering stage[1]

	Leaf number ($hill^{-1}$)			Leaf area (cm^2 $hill^{-1}$)			Area of single leaf (cm^2)			Canopy angle (°)		
Plant spacing	SRI	RMP	Mean	SRI	RMP	Mean	SRI	RMP	Mean	SRI	RMP	Mean
30 × 30 cm	126.0	119.2	122.6	2371.95	1899.28	2135.6	18.85	15.97	17.4	44.6	36.5	40.6
25 × 25 cm	103.3	85.2	94.3	1871.28	1407.62	1639.5	18.18	16.55	17.4	37.2	32.1	34.6
20 × 20 cm	83.0	86.0	84.5	1462.27	1289.60	1375.9	17.68	15.02	16.4	32.0	23.8	27.9
15 × 15 cm	47.5	48.2	47.8	704.47	554.83	629.7	14.94	11.52	13.2	25.1	19.1	22.1
10 × 10 cm	31.3	29.3	30.3	319.93	280.98	300.5	10.31	9.60	10.0	21.1	16.8	18.9
Mean	78.2	73.5		1346.0	1086.5		16.0	13.7		32.0	25.7	
	Practice	Spacing	P × S	Practice	Spacing	P × S	Practice	Spacing	P × S	Practice	Spacing	P × S
$LSD_{0.05}$	3.8	5.5	7.7	62.0	94.4	133.5	0.9	1.7	ns	2.1	3.4	ns

ns, not significant. [1]Measurements were taken on 23–24 April in both years.

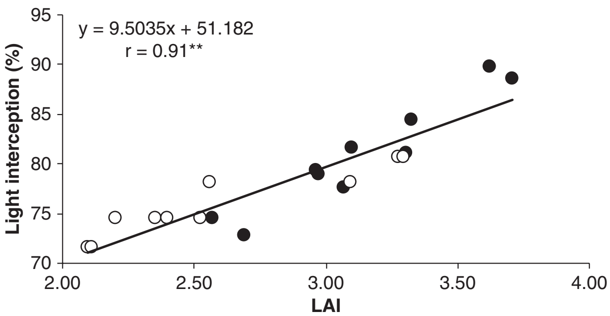

Fig. 2 Relationships between leaf area index (LAI) and light interception by the canopy. Closed and open circles represent plots from SRI and RMP respectively. **significant at 1 % level

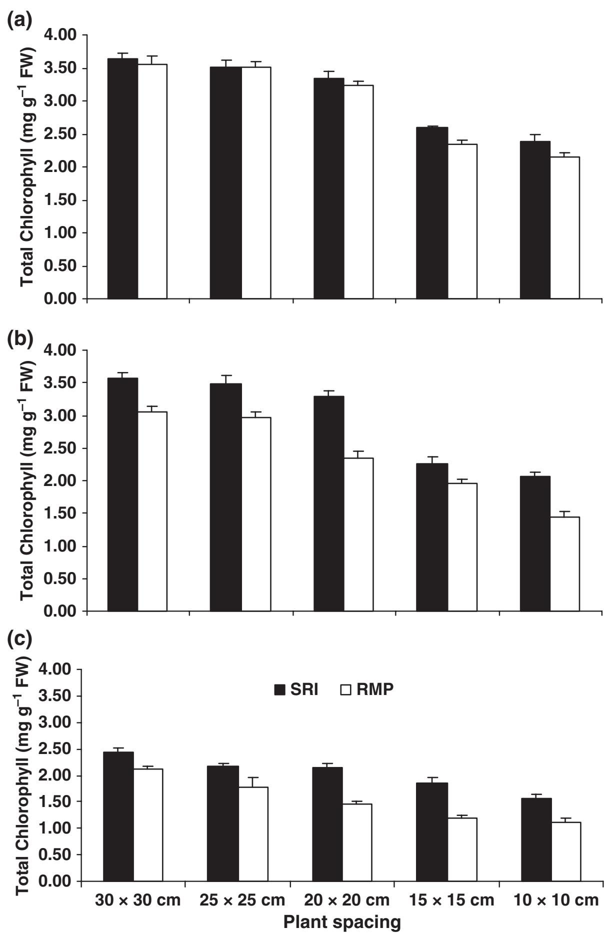

Fig. 3 Total chlorophyll content of leaves at flowering (a), middle ripening (b) and late ripening (c) stages for SRI and RMP plants. Black and white bars represent SRI and RMP management respectively. For each replicate, three flag and fourth leaf (from top) were used for the measurements. Vertical bars represent the standard deviation (n = 6). Practice, spacing and its interaction were significantly different at 5 % level of significance.

Chlorophyll content and fluorescence in leaves

Chlorophyll content and fluorescence in flag leaf and fourth leaf at flowering stage (24–25 April), at the middle-ripening stage (8–9 May), and at the late-ripening stage (May 18–19) for plants from SRI and RMP plots grown at the five different spacings. The chlorophyll contents in leaves produced with both practices at all spacings decreased at the middle-ripening stage and further at the late-ripening stage (Fig. 3). The decrease in chlorophyll content from flowering to late-ripening stage was observed to be greater in RMP than SRI plants. However, at all three stages with both practices, the chlorophyll content of leaves was significantly higher ($P < 0.05$) in plants growing at wider spacing than in the more closely-spaced plants. When comparing cultivation systems, the following differences were observed. The chlorophyll content of leaves decreased significantly below 20×20 cm spacing for both SRI and RMP at the flowering stage, while during the middle-ripening stage, chlorophyll loss was observed to be less for SRI plants with the spacing of 20×20 cm or above and for RMP plants at 25×25 cm or above. Overall, the leaf chlorophyll contents were more in SRI compared with RMP plants.

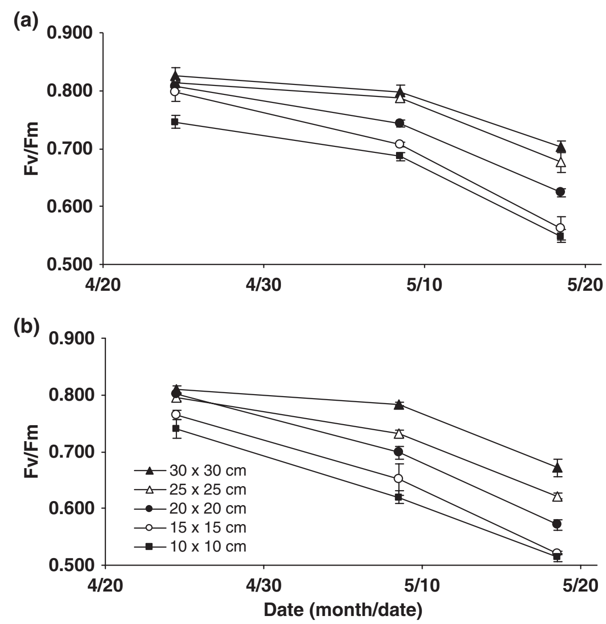

Fig. 4 Changes in Fv/Fm ratio of the flag leaves of SRI (a) and RMP (b) plants at different spacings. Measurements were taken at flowering, middle-ripening and late-ripening stages. For each replicate, three flag leaves and fourth leaf (from top) were used for the measurements. Vertical bars represent the standard deviation (n = 6). Practice, spacing and its interaction were significantly different at 5 % level of significance.

In addition to measuring leaf chlorophyll content, we also measured dark-adapted potential quantum yield (Fv/Fm) and actual quantum yield (ΦPS II) of leaves at the same three stages to understand what was the light utilization during photosynthesis. Fv/Fm was higher in leaves grown at wider spacing than in leaves of closely-spaced plants with both practices (Fig. 4a, b). When compared for similar spacings, SRI leaves had higher Fv/Fm than RMP leaves. The Fv/Fm of flag leaves decreased from flowering stage to late-ripening stage in all the treatments, but with a higher rate of decrease in closely-spaced plants than in leaves from more widely-spaced plots. A similar decreasing trend from flowering to late-ripening stage was also found for ΦPS II (Fig. 5a, b). This decrease was more in RMP leaves and in the leaves of SRI grown in 15 × 15 cm and 10 × 10 cm plots than in the leaves of widely-spaced SRI plants.

Rate of photosynthesis

Rates of photosynthesis of the flag and fourth leaves were significantly higher in plants from SRI plots than in plants from RMP plots at flowering, middle- and late-ripening stages (Fig. 6). Plants grown at wider spacing had higher photosynthesis rates than plants at closer spacing under both SRI and RMP management. Rates of photosynthesis of leaves decreased from flowering stage to late-ripening stage in all plants. These decreases in the rate of photosynthesis were, however, more in RMP plants than in SRI plants. A close linear relationship was observed between the chlorophyll content and Fv/Fm (Fig. 7a; r = 0.92), the chlorophyll content and PS II (Fig. 7b; r = 0.85), and the chlorophyll content and the rate of photosynthesis (Fig. 7c; r = 0.96) of leaves. This relationship was independent of cultivation practices and the spacing of plants.

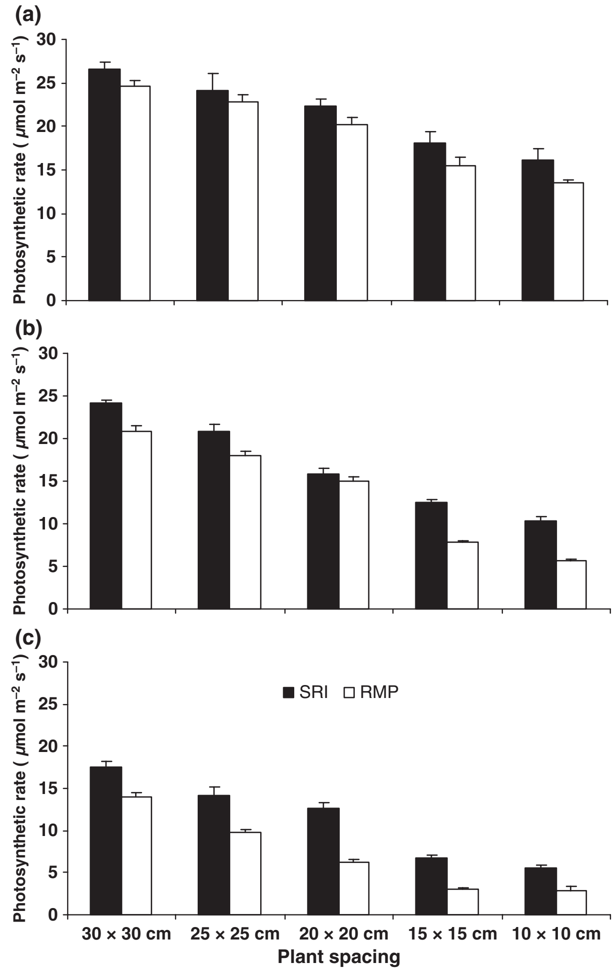

Fig. 6 The rate of photosynthesis of flag leaves at flowering (a), middle-ripening (b) and late-ripening (c) stages for SRI and RMP plants. Black and white bars represent SRI and RMP management respectively. For each replicate, three flag leaf and fourth leaf (from top) were used for the measurements. Vertical bars represent the standard deviation (n = 6). Practice, spacing and its interaction were significantly different at 5 % level of significance.

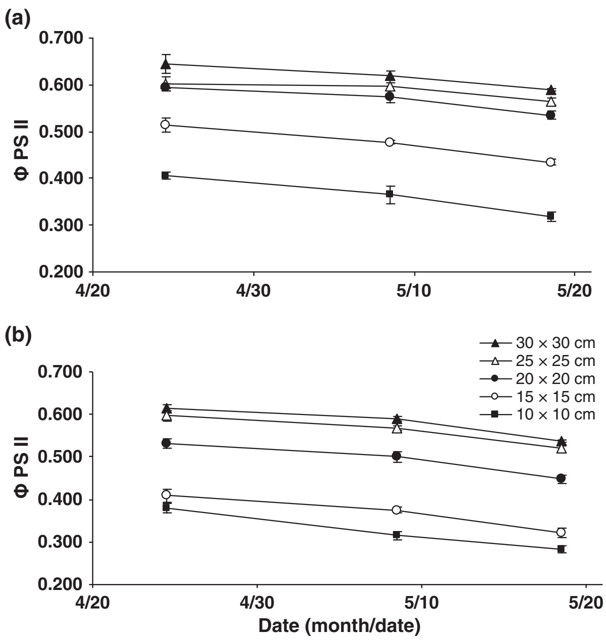

Fig. 5 Changes in ΦPS II of the flag leaves of SRI (a) and RMP (b) plants at different spacings. Measurements were taken at flowering, middle-ripening and late-ripening stages. For each replicate, three flag and fourth leaf (from top) were used for the measurements. Vertical bars represent the standard deviation (n = 6). Practice, spacing and its interaction were significantly different at 5 % level of significance.

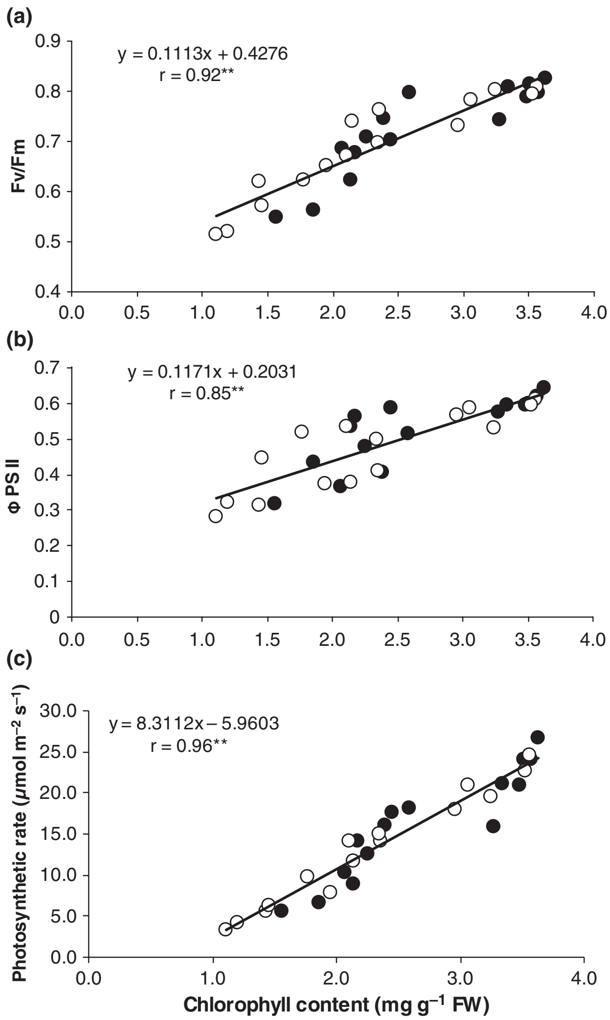

Fig. 7 Relationships between chlorophyll content and Fv/Fm (a), ΦPS II (b),and with rate of photosynthesis (c) of rice leaves. Closed and open circles represent the leaves of plants from plots under SRI and RMP management respectively. **significant at 1 % level.

Root dry weight and xylem exudation rates

At the early-ripening stage, on April 28–29, root dry weight per hill and per unit area was found to be significantly ($P < 0.05$) higher in SRI plants than in RMP plants (Table 7). Moreover, there was significantly more root dry weight per hill at wider spacing compared with more closely-spaced plants, irrespective of cultivation practice. Root dry weight per hill was three times more at 30 × 30 cm spacing than 10 × 10 cm. However, on an area basis the root dry weight were more at closer spacing than with wide spacing of plants in both the practices.

The amount of xylem exudates and the exudation rate were higher in plants grown at wider spacing than in those grown at closer spacing, irrespective of cultivation practice

Table 7 Comparison of root dry weight (g) under SRI and RMP during early ripening stage[1]

	Root dry weight (g hill^{-1})			Root dry weight (g m^{-2})		
Plant spacing	SRI	RMP	Mean	SRI	RMP	Mean
30 × 30 cm	18.7	14.9	16.8	207.0	165.2	186.1
25 × 25 cm	16.1	11.9	14.0	257.3	190.4	223.9
20 × 20 cm	13.0	9.7	11.3	324.2	242.1	283.1
15 × 15 cm	10.0	6.3	8.1	443.3	279.7	361.5
10 × 10 cm	6.8	4.7	5.7	683.3	465.0	574.2
Mean	12.9	9.5		383.0	268.5	
	Practice	Spacing	P × S	Practice	Spacing	P × S
$LSD_{0.05}$	1.1	2.9	ns	59.1	86.7	122.7

ns, not significant. [1]Measurements were taken on 28–29 April in both years.

(Table 8). There were significantly higher amounts of exudate and rate per hill in SRI plants than RMP plants. The amount of exudates and exudation rate m^{-2} was higher in plants with closer spacing, having a greater number of hills in both practices. However, the exudation rate per stem was also significantly ($P < 0.05$) higher in SRI plants than that in RMP plants at all spacings.

Discussion

Planting density in rice is known to play a crucial role for dry matter production and grain yield (Yoshida 1981). The first objective in this evaluation was to know whether wider spacing as part of SRI practice would in fact improve plants' performance in individual hills compared with that with currently recommended practice favouring closer spacing within and between hills, and then to determine whether SRI's lower plant density would be able to compensate for the lower number of hills which would affect yield on an area basis.

At wider spacing, the dry weight of individual hills increased significantly compared with closely-spaced hills, irrespective of practices (Table 3). The factor responsible for increased weight of individual hills' dry matter at wider spacing was greater tiller number with a larger number of leaves (Tables 5 and 6). Further, hills with wider spacing had a greater canopy angle with both management practices than did closely-spaced hills, as a result of their greater number of tillers.

Leaves in plants with wider spacing under both SRI and RMP management, from 30 × 30 to 20 × 20 cm spacing, maintained higher rates of photosynthesis at their middle- and late-ripening stages than did plants with closer spacing (Fig. 6). The slower decrease in chlorophyll content, fluorescence and rate of photosynthesis in leaves during later stages of ripening observed at wider

Table 8 Comparison of xylem exudation rates under SRI and RMP during early ripening stage[1]

	Exudate amount ($g\ hill^{-1}$)			Exudate amount ($g\ m^{-2}$)			Rate per hill ($g\ hill^{-1}\ h^{-1}$)			Rate per stem ($g\ stem^{-1}\ h^{-1}$)			Rate per m^{-2} ($g\ m^{-2}\ h^{-1}$)		
Plant spacing	SRI	RMP	Mean	SRI	RMP	Mean	SRI	RMP	Mean	SRI	RMP	Mean	SRI	RMP	Mean
30 × 30 cm	12.5	8.3	10.4	138.5	91.6	115.1	0.52	0.34	0.43	0.57	0.47	0.52	5.77	3.82	4.79
25 × 25 cm	9.9	6.4	8.2	158.4	102.4	130.4	0.41	0.27	0.34	0.54	0.44	0.49	6.60	4.26	5.43
20 × 20 cm	7.3	5.0	6.2	183.3	124.0	153.7	0.31	0.21	0.26	0.52	0.43	0.47	7.64	5.17	6.40
15 × 15 cm	4.1	2.4	3.3	180.1	107.2	143.7	0.17	0.10	0.14	0.49	0.38	0.43	7.50	4.47	5.99
10 × 10 cm	2.0	1.4	1.7	200.0	137.7	168.8	0.08	0.06	0.07	0.45	0.39	0.42	8.33	5.74	7.03
Mean	7.2	4.7		172.1	112.6		0.30	0.20		0.51	0.42		7.17	4.69	
	Practice	Spacing	P × S	Practice	Spacing	P × S	Practice	Spacing	P × S	Practice	Spacing	P × S	Practice	Spacing	P × S
$LSD_{0.05}$	0.4	0.4	0.6	13.4	8.5	12.0	0.02	0.02	0.02	0.04	0.03	ns	0.56	0.35	0.50

ns, not significant. [1]Measurements were taken on 28–29 April in both years.

spacing may have contributed to the greater dry matter production of individual hills (San-oh et al. 2004).

During the early-ripening stage, the higher dry weight of roots in hills with wider spacing and also their higher amount of exudates and its transportation rate compared with closely-spaced plants could be responsible for more transportation of cytokinins, a phytohormone synthesized in the roots, through the xylem to the shoot. The previous reports have also suggested that a well-developed root system enhances the synthesis of cytokinins in roots (Soejima et al. 1995, San-oh et al. 2004), and the rate of leaf senescence is lower in plants that have larger amounts of cytokinins transported into their canopies from the roots (Soejima et al. 1995). These characteristics were associated with longer panicle length with greater number of grains and with enhanced grain filling and grains weight in widely spaced hills compared with closely spaced hills in both the practices (Table 4). Similar observations of improvement in performance of individual hills at wider spacing in SRI have also been reported earlier (e.g., Latif et al. 2005, Menete et al. 2008).

Crop yields are the result of performance of the total plant community rather than of individual hills. We further examined whether reduced plant density with highly productive hills would be able to compensate for the loss of plant number under both SRI and RMP management. The highest grain yield in these trials was recorded at 20 × 20 cm spacing with both practices, with SRI giving 40 % higher yield than RMP at this spacing. At wider spacing (25 × 25 cm and 30 × 30 cm), despite the longer panicles with more grains, higher grain filling and improvement in grain weight, the decreased plant density was apparently not sufficiently compensated for to achieve higher yield. At closer spacing (<20 × 20 cm), root dry weight, tiller number and panicle number m^{-2} increased significantly, but with more straw weight and less grain yield. This lower grain yield at closer spacing was mainly caused by smaller panicles with lower grain numbers, less filling of grains,and reduction in grain weight (Table 4).

At very wide spacing (30 × 30 cm), harvest index was reduced as a result of lower grain yield; however, at the spacing below 20 × 20 cm, higher straw weight was responsible for reduction in harvest index. Leaf area index (LAI) and light interception by the canopy were also the greatest at the spacing of 20 × 20 cm in both practices (Fig. 1). Wider plant spacing than this had greater leaf area per hill and larger sizes of individual leaves, but LAI was not found to be as high mainly because of lesser number of hills in unit area. On the other side, at closer spacing despite more number of hills or tillers, LAI and light interception were less than at 20 × 20 cm as a result of a decrease in the size of leaves.

The relationship between tillering and yield in rice has been well studied previously with flooded rice, and several authors have reported that increased tillering was accompanied by decreasing numbers of grains per panicle (De Datta 1981). Similarly, we also observed an inverse relationship between tiller number in unit area and grain yield with both practices, and the spacing with maximum grain yield was found in these trials to be 20 × 20 cm, also reported by Ceesay et al. (2006).

Some of the previous experiments evaluating SRI (Sheehy et al. 2004, Latif et al. 2005, Menete et al. 2008) have compared the performance of SRI methods at 30 × 30 cm with closely-spaced recommended practice (20 × 20 cm) and have found the latter giving higher yield. In these evaluations, the advantages of the other SRI components responsible for enhancing yield were not achieved because the wide spacing used with SRI management exceeded the capacity of those soils.

At the similar spacing, single plants starting as young (12-day) seedlings with SRI practice were able to produce more tillers or panicles per hill, with a greater number of larger leaves, more open canopy structure with wider angles than did three plants that were started as older (25-days) seedlings grown with conventional practice. The percentage of effective tillers was significantly higher with SRI (91.2 %) compared with RMP management (77.8 %) and is one of the factor responsible for overall yield enhancement in SRI practice (17 %). SRI hills had a more open canopy structure with wider angles than RMP, probably because of shallow planting, resulted in minimum shading of lower leaves, which helped lower leaves to remain green and photosynthetically active during the later phases of growth (Figs 3 and 6). The leaves of SRI plants at all spacings had significantly higher chlorophyll content, more light-utilizing capacity (fluorescence) and a greater rate of photosynthesis compared with RMP leaves (Figs 3–6). A strong relationship was observed to exist among these parameters (Fig. 7). During the reproductive stage, maintenance of a high CO_2-assimilation rate via a delay in leaf senescence is one of the important factors that can increase crop yield (Cock and Yoshida 1972) and also evidenced here for SRI plants.

Improvement in root dry weight and xylem exudation rate in SRI than RMP is responsible for delayed senescence, maintaining higher photosynthesis rate during later phase of reproductive growth and improvement in yield components. Earlier reports also shows younger seedlings used with SRI perform better in terms of various root characteristics (root length density and root weight density) than do older seedlings (Mishra and Salokhe 2008). SRI's water management practices (keeping soil mostly aerobic through wetting and drying) also help in improving root systems (Bouman et al. 2007). However, continuous flooding can cause degeneration of as much as three-fourths of roots by the flowering stage (Kar et al. 1974).

As observed from the research of San-oh et al. (2006), when each hill contains a single plant (like SRI) compared with three plants in each hill (like RMP), a greater number of crown roots can maintain higher cytokinin fluxes from roots to shoot (Nooden et al. 1990) during the ripening stage, which is responsible for maintaining higher levels of Rubisco in plant leaves. The highly efficient photosynthetic performance of super high-yielding rice is largely a result of the increased cytokinin content in their roots, contributing to higher grain yield (Shu-Qing et al. 2004). Akenohoshi (a slowly-senescing and high-yielding cultivar) produces high dry-matter production as a result of maintaining a high rate of photosynthesis, which is a consequence of the delayed senescence of its leaves resulting from transport of large amount of cytokinins from the roots to the shoots (Jiang et al. 1988a,b, Soejima et al. 1995). The SRI plant had similar characteristics as that of super high yielding varieties and Akenohoshi.

Apart from rice, alternative agriculture practices when used with tomatoes have been shown to affect the expression of specific classes of genes, with N-responsive genes, cytokinin-responsive genes and key photosynthesis genes up-regulated in response to certain practices (using leguminous hairy vetch in place of black plastic mulch) (Kumar et al. 2004). These genes were responsible for greater root growth and an efficient utilization and mobilization of C and N, with delayed leaf senescence. The effect of SRI practice on the processes and mechanisms involved in the enhancement of root growth and on the maintenance of high levels of nitrogen and Rubisco during ripening caused by the action of cytokinins deserves further investigation.

In this study, SRI practices like transplanting single young seedlings under aerobic field condition enhanced the performance of individual hills more than using three older seedlings in a flooded field, producing higher grain yield when compared at same spacing. One plant per hill produced more dry matter and higher grain yield, as a result of its open canopy structure, enhanced light interception, enhanced root growth, slower leaf senescence and greater photosynthesis during the ripening stage, compared with RMP practice of using three older plants per hill. Optimum plant spacing for higher yield in this experiment was found to be 20 × 20 cm for both SRI and recommended practice, which combines improved hills with optimum plant population. The SRI recommendation is to plant young seedlings singly at wider spacing, preferably 25 cm or more although the optimal spacing will vary according to soil fertility and varietal tillering ability (Satyanarayana et al. 2007, Thakur et al. 2009) with a purpose is to avoid inhibition of root growth and to expose plants to more light and air (Stoop et al. 2002, Satyanarayana et al. 2007).

Conclusions

Before concluding what is the optimum spacing with SRI practices, further evaluations should be performed with similar design (a) to assess the effects, if any, of varying fertilizer applications, comparing the effects of all-organic fertilization with all-chemical and mixed applications, and (b) to assess what spacing would be optimum for different levels of soil fertility, considered not only in soil chemistry terms but also in soil physical and soil biological terms. There are farmer reports, not systematically evaluated, that in the long run, SRI practices improves the fertility of the soil possibly because of adding organic matter to the soil and inducing greater root growth with increased resulting exudation. There is need to do more longitudinal evaluation of SRI practices over 3–5 years or more.

Plant spacing is a factor to be optimized, neither maximized nor minimized, with the aim of maximizing agronomic yield and, indeed, economic returns. Optimum spacing is a dynamic parameter that will be affected considerably by soil fertility, including soil physical and soil biological properties This underscores the importance of addressing whole sets of practices (Uphoff et al. 2008), not just making *ceteris paribus* assessments of the effects of individual parameters, such as spacing, and these effects just within a single season. Plant-soil system interactions are complex and multiply contingent. On the basis of the investigations reported here, we think there are sound agronomic reasons for formulating evaluations in terms of how widely plants should be grown to optimize returns rather than how densely they can (should) be placed. In summary, there are evident benefits from giving plants more space above- and below-ground for roots and canopy to grow rather than from crowding them together.

Acknowledgements

The authors wish to thank Dr Willem A. Stoop, West African Rice Development Association (WARDA), Ivory Coast for reviewing the draft of this manuscript and offering useful comments.

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