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Rice root growth, photosynthesis, yield and water productivity improvements through modifying cultivation practices and water management



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ABSTRACT

Achieving higher productivity in irrigated rice production is becoming ever-more important. A modified rice-cultivation method, the System of Rice Intensification (SRI), recommends keeping rice fields moist but unflooded during the crop's vegetative stage, usually with alternate-wetting-and-drying (AWD), then maintaining shallow flooding during the post-vegetative stage of crop growth. However, no evidence is available on how flooding paddy fields continuously vs. alternately during the post-vegetative stage under SRI might influence the crops' physiology, root growth, grain yield, and water productivity.

Field experiments were conducted to investigate the impacts of two alternative crop management systems, namely, SRI and conventional management practice (CMP) under different water management treatments during the vegetative stage [continuous flooding (CF) vs. AWD] and then during post-vegetative stage: CF vs. AWD @ 1-DAD (days after disappearance of ponded water), 3-DAD or 5-DAD.

SRI practices, compared to CMP methods, significantly improved plants' root growth and xylem exudation rate, leaf area index and light interception by the crop canopy, plus photosynthesis rate at the grain-filling stage, resulting in higher grain yield. Overall, this modified method of rice crop management produced 58% higher grain yield with 16% less water. Across all water management treatments, significantly more grain was produced per unit of water applied with SRI management (6.3 kg ha-mm $^{-1}$) compared to CMP (3.3 kg grain ha-mm $^{-1}$). The highest grain yield with SRI (6.2 t ha $^{-1}$), and the greatest water productivity (6.7 kg ha-mm $^{-1}$) were obtained with SRI and 3-DAD post-vegetative irrigation. With CMP, highest grain yield (4.1 t ha $^{-1}$) and water productivity (3.5 kg ha-mm $^{-1}$) were with 1-DAD irrigation.

Differences measured in plants' response to modified management practices and alternative irrigation schedules indicated how phenotypic and physiological performances can be improved for a given genotype. Combining changes in crop and water management can improve water productivity as well as grain yield.

1. Introduction

Feeding the world's growing population is a major challenge (Godfray et al., 2010). Present standard methods for growing rice (Oryza sativa L.), a staple food for billions, requires large amounts of water. By 2035, the world will need to produce 116 million additional tons of rice for its greater population (GRiSP, Global Rice Science Partnership, 2013), and this must be achieved under conditions of greater water scarcity and climate change (FAO, 2012; Godfray, 2011). The currently prevailing system for growing irrigated rice is to flood paddy fields, maintaining standing water throughout the crop's growth cycle, and then to drain water from the fields 1–2 weeks before harvesting (Bouman et al., 2007). In flooded rice paddies, a large amount

of the water supplied is non-productive due to large losses through runoff, evaporation, seepage, and percolation (GRiSP, 2013). In the future there simply will not be enough water in many areas to sustain this kind of irrigated rice production. Producing more grain with reduced amounts of water must be done in a sustainable way and without environmental harm (Yang and Zhang, 2010).

Researchers have been developing a number of water-saving technologies such as alternate wetting and drying (Belder et al., 2004; Bouman and Tuong, 2001), saturated soil culture (Tuong et al., 2004), direct dry-seeding (Tabbal et al., 2002), aerobic rice culture (Kato et al., 2009), and drip/sprinkler systems (Sharda et al., 2017). These methods have been found to reduce water use and improve water productivity, but their effects on grain yield have remained uncertain (Bouman et al.,

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2007), and the extent to which these techniques are economically remunerative remains unclear.

The System of Rice Intensification (SRI), a modified rice cultivation methodology developed in Madagascar, has been introduced in many rice-producing countries (Uphoff, 2012). SRI practices include transplanting younger seedlings with wider spacing than in conventional methods, leading to much reduced plant densities (by 4/5th to 9/10th less); active soil aeration; and keeping paddy fields unflooded, just moist, during the vegetative stage of crop growth (Stoop et al., 2002). This combination of practices has been reported to increase the yields of irrigated rice by 20–50% or more, while reducing water requirements by 20–35% (Jagannath et al., 2013; Kassam et al., 2011; Thakur et al., 2011; Wu and Uphoff, 2015).

Originally, SRI as developed empirically in Madagascar recommended applying small amounts of water each day to well-leveled fields, just enough water to keep the soil moist and meet the plants' (and soil organisms') basic needs - le minimum de l'eau (Laulanié, 1993). While such careful daily water management contributed to increased grain yields, it required considerable additional efforts by farmers. Therefore, many developed their own labor-reducing schedules of alternative wetting and drying (AWD). A study of SRI water management in Madagascar found that farmers who used SRI methods varied the length of their alternating wet and dry periods between 1-10 days (McHugh et al., 2002). Moreover, these schedules were developed more for farmers' convenience than for calculated productivity. As initially developed, SRI recommended maintaining just a thin layer of water (2-3 cm) on fields after the crop's panicle initiation (Stoop et al., 2002). However, this specification has never been tested systematically, while previous research (Stoop et al., 2009) would question its effectiveness. Under conditions of limited water supplies and hence a need to maximize water productivity (as in major parts of India), any possible savings in water use become increasingly important.

Most evaluations on the effects of different water management regimes for SRI have tested AWD irrigation practices or maintaining saturated soil just during the vegetative stage, comparing it with conventional flooding, the conventional management practices (CMP) approach (Chapagain and Yamaji, 2010; Krupnik et al., 2012; Lin et al., 2009; Singh, 2013; Thakur et al., 2014; Zhao et al., 2009). In some cases, significant savings in irrigation water have been reported while yield differences remained negligible (Chapagain and Yamaji, 2010; Krupnik et al., 2012; Singh, 2013). Other studies have reported both significant yield increase and water savings under SRI management (Lin et al., 2009; Thakur et al., 2014; Zhao et al., 2009). Stoop et al. (2009) have suggested that the responses have often been misinterpreted because of confounding between experimental (and non-experimental) factors, for instance, between the irrigation regime being evaluated and certain non-experimental factors, like plant density and/or the age of transplanted seedlings.

There could be considerable savings of irrigation water in the post-vegetative stage with some optimization of AWD as compared with continuous flooding. For SRI, an irrigation regime providing water at 3-DAD (days after disappearance of ponded water) has been recommended for the vegetative phase, followed then by shallow flooding of the field with 2–3 cm water during the post-vegetative stage (Thakur et al., 2014). In view of the attractive yields reported for SRI in general, there is reason to consider whether water use could be further optimized by keeping SRI fields just moist or AWD instead of being flooded, also during the post-vegetative stage.

Post-vegetative stage of water management deserves systematic investigation because in many countries, it is during the latter stages of rice plant growth that the crop encounters greater water scarcity and stress. In India, this can be due either to lesser rainfall during the rainy season (July-October) or higher temperatures during the winter season (October-March). These stresses have crucial impacts on eventual yield. As water scarcity is becoming a major concern in so many countries, the question arises whether any further reductions can be made in the

amount of water applied during the post-vegetative stage under SRI management without incurring some grain yield loss. Making modifications in the water management regime during the post-vegetative phase could greatly increase water-use efficiency.

Research done thus far on water optimization under SRI crop management has not focused on how to reduce water applications after panicle initiation without suffering yield loss, and possibly making some gains in yield. This investigation was designed to assess the impacts of two alternative crop management systems, namely, SRI and conventional management practice (CMP) under different water management during, first, the vegetative stage – continuous flooding (CF) with CMP and 3-DAD with SRI – and then during the post-vegetative stage, either CF or irrigation at 1-DAD, 3-DAD or 5-DAD.

2. Materials and methods

2.1. Experimental site

A field experiment was conducted for two *rabi* dry seasons (January-May) during the years 2014 and 2015 at the Research Farm of the ICAR-Indian Institute of Water Management, Mendhasal in Khurda district of Odisha state, India (20° 30′ N/87° 48′ 10^{2} E). The soils at the experimental site have been classified as *Aeric Haplaquepts*, sandy clay-loam (61% sand, 17% silt, and 22% clay), with a pH of 5.9.

2.2. Experimental design and treatments

The design was constructed to evaluate the physiological and morphological effects of different crop and water management practices in irrigated rice production. The split-plot design had three replications with sub-plot sizes of $20\times10\,\mathrm{m}$. All sub-plots were surrounded by bunds 30-cm wide followed by irrigation channels 50-cm wide, then again by bunds 30-cm wide to prevent lateral water seepage and nutrient diffusion between plots.

The two crop production systems were assessed in the main plots: the System of Rice Intensification (SRI), and conventional management practice (CMP). In the sub-plots within each block, four different water management treatments were implemented during the post-vegetative growth stage: CF (continuous flooding) and water applications either 1, 3, or 5 days after disappearance (DAD) of ponded or standing water in the field. During the preceding vegetative stage, the CMP plots were kept continuously flooded, while the SRI plots received irrigation water following 3 DAD schedule. Treatment details are described in Table 1.

2.3. Crop management with different cultivation practices

The experiment used a medium-duration rice cv. Surendra, 130-135 days duration, a popular photo-insensitive variety grown by farmers in the eastern part of India. Seeds were germinated in the shade and then broadcasted on nursery beds on January 10, 2014 in the first year and January 12, 2015 in the second year. In the SRI plots, 12-dayold single seedlings at a spacing of $20 \times 20 \, \text{cm}$ were transplanted within 30 min after removal from the nursery on January 22, 2014 and January 24, 2015. In the CMP plots, 25-day-old seedlings, three per hill, were transplanted at a spacing of 20×10 cm on February 4, 2014 and February 6, 2015. Plant densities for the two crop production systems were thus, respectively, 25 and 150 plants m⁻² for the SRI and CMP plots, giving the CMP plots six times more plants than SRI on an area basis. It should be noted that the SRI spacing used in this experiment was 20% closer than usually recommended for SRI because earlier studies in this location had shown 20 × 20 cm spacing to be optimum with this particular medium-duration variety under the local soil and climatic conditions (Thakur et al., 2010a). On the SRI plots, weeds were removed by using a mechanical weeder at 10, 20 and 30 days after transplanting (DAT), while in CMP plots, three hand weedings were done at the same DAT intervals.

 Table 1

 Details of crop management practices in experimental treatments.

Management practices	Conventional management practices (CMP)	System of rice intensification (SRI)
Planting Spacing Number of seedlings Nutrient management	25-day-old seedlings transplanted from conventional nursery $20 \times 10 \mathrm{cm}$ 3 seedlings hill $^{-1}$ (150 seedlings m $^{-2}$) Fully decomposed farm yard manure (FYM) was applied @ 5 t ha $^{-1}$ along with chemical fertilizers recommended amount of 80 kg N, 40 kg P_2O_5 and 40 kg R_2O_5 ha $^{-1}$ applied in split doses	12-day-old seedlings transplanted from raised nursery $20\times20\mathrm{cm}$ Single seedling hill $^{-1}$ (25 seedlings m $^{-2}$) The same as conventional
Weed management	Weeds removed by manual weeding, three times at 10, 20 and 30 days after transplanting (DAT)	Weeds mechanically incorporated in soil with a mechanical weeder, crisscross, three times at 10, 20 and 30 days after transplanting (DAT)
Water management	Vegetative stage Continuous flooding with 5 cm of standing water	Vegetative stage Irrigation to 5 cm depth three days after the disappearance of ponded water (3-DAD)
	Post-vegetative stage Continuous flooding (CF) with 5 cm of standing water Irrigation to 5 cm depth one day after the disappearance of ponded water (1-DAD) Irrigation to 5 cm depth three days after the disappearance of ponded water (3-DAD) Irrigation to 5 cm depth five days after the disappearance of ponded water (5-DAD)	Post-vegetative stage Continuous flooding (CF) with 5 cm of standing water Irrigation to 5 cm depth one day after the disappearance of ponded water (1-DAD) Irrigation to 5 cm depth three days after the disappearance of ponded water (3-DAD) Irrigation to 5 cm depth five days after the disappearance of ponded water (5-DAD)
	Drained 7 days before harvesting	Drained 7 days before harvesting

Fertilizer use was standard across all the plots since, as noted above, nutrient management was not made a factor in this experiment. Fully-decomposed farmyard manure (FYM) was applied @ $5\,\mathrm{tha}^{-1}$ along with chemical fertilizers @ $80\,\mathrm{kg}$ N, $40\,\mathrm{kg}$ P₂O₅ and $40\,\mathrm{kg}$ K₂O ha^{-1} , using urea, diammonium phosphate, and muriate of potash as sources. The entire amount of phosphorus was applied at the time of final land preparation, while N and K were applied in three splits, i.e., 25% at $10\,\mathrm{days}$ after transplanting (DAT), 50% at tillering stage, and 25% at panicle initiation (PI) stage. The SRI recommendation favors organic over chemical fertilization, but we did not make this practice an additional factor in the present trials.

2.4. Water management treatments

A cemented distribution channel was used to supply water to the main plot channel and subsequently to the respective plots. The first irrigation for the SRI plots was applied at 5 days after transplanting to moisten the field without ponding; then at 10 days after transplanting a second irrigation of 5 cm water depth was applied. After that, water was applied at 3 DAD of ponded water during the entire vegetative stage of crop growth, up to the panicle initiation (PI) stage. In an earlier study, it had been found that highest crop productivity for SRI was achieved with irrigation at 3 DAD under SRI management during the vegetative stage of crop growth (Thakur et al., 2014). In the comparable CMP treatments, 5 cm of standing water was maintained throughout the vegetative period, from transplanting to the crop's PI stage.

Then after panicle initiation (65 days after sowing, DAS), four different water management treatments were implemented during the post-vegetative stage: continuous flooding (CF), and irrigation at 1, 3, or 5 days after the disappearance (DAD) of standing water in the field. All plots were drained 7 days before harvesting.

2.5. Sampling and measurements

We evaluated the effects of the differing treatments on agronomic/morphological and physiological parameters that are closely associated with rice plant growth and crop performance: root dry weight, xylem exudation rate, leaf area index (LAI), light interception by canopy (LIC), leaf greenness (SPAD), leaf photosynthetic rate, grain-filling rate, yield components, and water productivity (Yoshida, 1981; Fageria, 2007).

2.5.1. Measurement of root weight density and xylem exudation rate

Three hills with average number of tillers were selected at the panicle initiation (65 DAS) and grain-filling stages (110 DAS) from each replicate plot for root sampling. Root samples were collected through the monolith method, each sampler centered over one transplanted hill. The dimensions of the monolith sampler used were $20 \times 20 \, \mathrm{cm}$ to 45-cm depth for the SRI crop, and $20 \times 10 \, \mathrm{cm}$ to 45-cm depth for CMP crops. Therefore, the soil volume excavated to collect root samples under SRI was $18,000 \, \mathrm{cm}^3$ and $9000 \, \mathrm{cm}^3$ under CMP. Root samples were washed carefully in a bucket, separating entire roots by straining. Roots were dried in an oven at $70 \, ^{\circ}\mathrm{C}$ for 48 h, and root weight was recorded at the constant weight (Shashidhar et al., 2012). Root weight density (RWD) was calculated by dividing the root dry weight by the soil volume and expressed as $\mathrm{mg} \, \mathrm{cm}^{-3}$.

The amount of xylem exudates transferred upward from roots to shoots and the rate of exudation is a reflection of plant size as well as of the level of physiological activity of roots. Amounts of xylem exudates were measured at both the PI and grain-filling stages from three hills having an average number of tillers in each plot using the methodology described in San-oh et al. (2004). All the tillers of a hill were cut at 10-cm above the soil surface, and pre-weighed cotton wool along with a polythene bag was wrapped to the cut end of each tiller and secured with tape. After 24 h, the polythene bag with cotton wool was detached and weighed. The amount (weight) of xylem exudate was calculated by subtracting the weight of the bag with cotton wool (initial) from the weight of the bag with cotton wool (after 24 h). Exudation rate was calculated by dividing xylem exudation amount by the time period.

2.5.2. Measurement of leaf area index and light interception by the canopy Leaf area of five hills from each plot was measured during the grainfilling stage (110 DAS) using a leaf area meter (Model: LICOR-3100 Area Meter, USA). Leaf area index was then calculated by dividing the leaf area by the land area. Light interception by the canopy was measured with a line quantum sensor (400–700 nm) (Model: LI-1400; LI-COR, USA) on a bright sunny day between 11:30 a.m. to 12:00 noon at the same stage by following methods described by San-oh et al. (2004) and Thakur et al. (2011).

2.5.3. Measurement of SPAD and leaf photosynthesis rate

Soil-Plant Analyses Development (SPAD) values – an indirect measurement of greenness, or leaf chlorophyll content (Uddling et al., 2007) – and the photosynthesis rates of leaves were measured during

the grain-filling stage (110 DAS) in 10 flag leaves and 10 fourth leaves of plants in every replicated plot by using a chlorophyll meter (Model: SPAD-502 Plus, Konica Minolta Sensing, Japan) and a portable photosynthesis system (Model: CIRAS-2, PP Systems, U.K.), respectively.

2.5.4. Measurement of grain-filling rate of main panicle

In each plot, 30 main tillers, excluding border rows, were tagged as panicles emerged from the flag leaf sheaths. Panicles were removed from the base point of three randomly-selected main tillers at 7-d intervals after flowering until maturity. To monitor post-flowering changes in main panicle weight, panicle dry weight was measured after drying in a forced-air drier at 80°C for 48 h at each date of harvest between flowering and physiological maturity. Beyond flowering, there was no further significant increase in chaff weight (i.e., rachis and glumes without grain); the final grain yield per panicle was calculated as the difference between panicle dry weight at maturity and at flowering. Grain-filling rate was calculated by subtracting the dry weight of main panicles at maturity, divided by the number of days in between (Ehdaie et al., 2008).

2.5.5. Measurements of yield and yield components

In each plot, an area 3×3 m (excluding border rows) was harvested to determine yield per unit area, with harvested paddy grain yield adjusted to 14.5% grain moisture content. Before harvesting, the average numbers of panicles was determined from a representative square-meter area from each plot. The number of grains per panicle and the number of filled grains were counted for each panicle individually, harvested from a square-meter area. Ripening percentage of grains was calculated by dividing the number of filled grains by the total number of grains.

2.5.6. Measurement of water applied and water productivity

To measure the amount of water applied to plots during each irrigation, trapezoidal RBC flumes (13.17.02 RBC, Eijkelkamp Agrisearch Equipment, The Netherlands) were installed in the cemented channel, and water flow was measured. The amount of water applied during each irrigation was calculated using water flow rate and the duration of water application. The total quantity of water applied throughout the cropping season was summed, and water productivity was calculated by a standard methodology reported in detail elsewhere (Thakur et al., 2014). Rainfall during the experimental periods of 2014 and 2015 was

207.0 and 197.6 mm, respectively, a variance of only 5%. Water productivity was estimated as grain yield divided by total water used (rainfall + irrigation) and expressed as kg ha-mm⁻¹.

2.6. Statistical analysis

Experimental data obtained for different parameters were analyzed statistically using the analysis of variance (ANOVA) technique as applicable to split-plot design (Gomez and Gomez, 1984). Duncan's multiple range test (DMRT) was employed to assess differences between the treatment means at a 5% probability level. All statistical analyses were performed using SAS 9.2 for Windows (SAS Institute Inc., Cary, NC, USA).

All the data were statistically analyzed considering 'year' as a source of variation in addition to cultivation system (CS) and water management (W) treatments. The main effects of year (Y) and the interaction effects between year and CS (Y \times CS), year and water management (Y \times W), and three-factor interaction (Y \times CS \times W) were all non-significant at P < 0.05 for all parameters considered in the present study. This with the year effect being non-significant, accordingly the data reported in this paper are averages from the two years of trials.

3. Results

3.1. Effects on grain yield, water requirements, and water productivity

Cultivation systems and post-vegetative phase water-management treatments were both found to have significant impacts on grain yield, water use, and water productivity. For CMP, grain yield was the highest with the 1-DAD treatment (4.06 t ha⁻¹), while the yield under SRI methods was highest with 3-DAD irrigation intervals (6.21 t ha⁻¹). Across the various water management treatments evaluated, SRI methods gave 58% higher average yield than CMP practices; total water use with CMP was 1128 mm, while water use with SRI management during the whole crop cycle was 939 mm (Table 2). With SRI compared to CMP, there was thus a saving of 189 mm water (16%). This water saving was mainly due to differences in the vegetative stage treatments, i.e., 3-DAD under SRI management vs. continuous flooding under CMP. The range of water saving estimated under post-vegetative stage treatments of 5-DAD vs. CF under the two cultivation systems was 63–100 mm. If a comparison is made between conventional flooded rice

Table 2Effects of rice cultivation systems and post-vegetative water management on grain yield, water use and its productivity.

Cultivation systems	Water management treatments (post-vegetative stage)	Grain yield (t ha ⁻¹)	Total water use (mm) ^a	Water productivity (kg ha-mm ⁻¹)
CMP	CF	3.96 d	1177.5 a	3.37 de
(CF)	1-DAD	4.06 d	1150.4 b	3.53 d
	3-DAD	3.62 e	1106.0 с	3.27 e
	5-DAD	3.30 f	1077.7 d	3.06 f
	Ave.	3.72	1127.9	3.31
SRI	CF	5.88 b	971.5 e	6.05 c
(3-DAD)	1-DAD	5.98 b	949.9 f	6.29 b
	3-DAD	6.21 a	927.7 g	6.70 a
	5-DAD	5.57 c	908.5 h	6.13 c
	Ave.	5.90	939.4	6.29
Analysis of variance				
Cultivation system (CS)		sk sk	会会	**
Water management (W)		*	*	*
CS × W		*	ns	*

Mean values followed by different letter within columns differ significantly at P < 0.05 according to Duncan's range test. CMP: Conventional management practice; SRI: System of rice intensification. CF: Continuous flooding; DAD: Days after disappearance of ponded water. *p < 0.05; **p < 0.01; ns, not significant.

a Total water use includes both rainfall and irrigation applied (rainfall of 2014 and 2015 was 207.0 and 197.6 mm during cropping season, respectively).

Table 3Effects of rice cultivation systems and post-vegetative water management on yield components.

Cultivation systems	Water management treatments (post-vegetative stage)	Panicle number (hill ⁻¹)	Panicle number (m^{-2})	Total no. of grains panicle ⁻¹	Grain filling (%)	1000-grains weight (g)
CMP	CF	6.0 c	300 с	97.4 e	74.5 d	23.7 с
(CF)	1-DAD	6.3 c	315 b	102.1 de	78.7 c	23.8 с
	3-DAD	6.1 c	305 b	92.2 f	72.5 de	23.6 с
	5-DAD	5.8 c	290 с	88.1 f	70.2 e	22.9 d
	Ave.	6.1	302	94.9	74.0	23.5
SRI	CF	12.2 b	305 b	108.1 bc	80.7 bc	24.1 b
(3-DAD)	1-DAD	14.0 a	350 a	112.8 b	82.1 b	24.2 ab
	3-DAD	14.3 a	358 a	118.2 a	85.3 a	24.4 a
	5-DAD	12.5 b	313 b	103.6 cd	79.5 bc	23.8 с
	Ave.	13.3	331	110.7	81.9	24.1
Analysis of variance						
Cultivation system (CS)		*	*	*	*	*
Water management (W)		ns	ns	ns	*	*
CS × W		*	*	*	*	*

Mean values followed by different letter within columns differ significantly at P < 0.05 according to Duncan's range test. CMP: Conventional management practice; SRI: System of rice intensification. CF: Continuous flooding; DAD: Days after disappearance of ponded water. *, p < 0.05; **, p < 0.01; ns, not significant.

and SRI having a 3-DAD irrigation schedule, the best for SRI, a significant amount of water was saved, i.e., 250 mm (20%).

Across all water-management treatments, water productivity was significantly higher under SRI management ($6.3 \, \mathrm{kg \, ha\text{-}mm^{-1}}$) as compared to CMP ($3.3 \, \mathrm{kg \, ha\text{-}mm^{-1}}$). SRI-grown rice plants were thus almost twice as efficient in utilizing water for the production of grain. Under CMP, the highest water productivity was obtained with 1-DAD treatment ($3.5 \, \mathrm{kg \, ha\text{-}mm^{-1}}$), while under SRI, the greatest water productivity was achieved with 3-DAD treatment ($6.7 \, \mathrm{kg \, ha\text{-}mm^{-1}}$), almost double.

3.2. Effects on grain yield components

Grain yield performance is determined by different yield components like number of panicles $\rm m^{-2}$, total number of grains panicle $^{-1}$, grain-filling%, and 1000-grain weight. In the present experiment, all varied significantly (p < 0.05) in response to the method of rice cultivation (Table 3). Cultivation system significantly affected the number of panicles per hill as well as on an area basis. With SRI management, the number of panicles per hill was more than double that for rice grown under CMP. However, on a unit-area basis, panicle numbers were only 9% higher in SRI plots than in CMP plots, mainly due to the greater number of hills and of plants in the latter.

Post-vegetative stage water management treatments had no significant effect on the number of panicles, either per hill or per unit area. Except for panicle number, the other yield components (number of grains/panicle, grain filling, and 1000-grain weight) varied significantly in response to the water management practices imposed after panicle initiation (Table 3). Under CMP, the 3-fold increase in the number of plants per hill and a 6-fold increase in the overall number of plants on a unit-surface-area basis was associated with a highly significant decrease in grain yield.

Under SRI management, grains per panicle and grain-filling were significantly higher with the 3-DAD treatment than with the other water management treatments. Under CMP cultivation, the highest values were recorded with CF and 1-DAD irrigation. Grain-filling under SRI was significantly greater with the 3-DAD treatment, while it was higher with the 1-DAD treatment under CMP. With the increasing moisture stress of 5-DAD irrigation, both grain-filling and grain weight were seen to be reduced with both cultivation systems.

3.3. Effects on root growth, root weight density and xylem exudation rate

Crops grown with SRI practices and 3-DAD alternate wetting and

drying during the vegetative stage had significantly greater weight of roots at the PI stage, both per hill and per unit-area (Table 4). This occurred even though SRI plots had only one plant per hill while CMP plots had three plants per hill and twice as many hills. On average, SRI plants had nearly 2.5-times more roots hills ⁻¹ at the PI stage than did the CMP hills ⁻¹, and on a unit-area basis, the SRI plant roots were 34% more. This reflects among other things the effects of reduced interplant competition due to fewer plants under SRI. No significant effects of the different post-vegetative water management treatments on roots' dry weight were recorded following the PI stage when the four different water treatments were superimposed.

When root growth was measured at the grain-filling stage, after imposing the different post- vegetative water management treatments, there were observable and significant effects of the water management treatments on roots' growth. With SRI methods, the highest root dry weight was observed with the 3-DAD treatment, both per hill and on an area basis. Under CMP management, there were no significant differences found in plant roots' dry weight between continuous flooding and 1-DAD treatments, while there was a decline in roots' dry weight with both the 3-DAD and 5-DAD treatments (Table 4). A similar trend was found with root weight density, which was found to be significantly higher under SRI than CMP at both the PI and grain-filling stages. Also, post-vegetative stage water management significantly affected RWD and was maximum in the 3-DAD treatment of SRI.

The xylem exudate data presented in Table 5 show the amounts of exudates that moved upward towards the shoot during a 24 h period of time. The flow when measured on a per-hill basis was significantly higher, even more than double, in SRI plants compared to the plants under conventional flooding method. On an area basis also, the xylem flow was greater under SRI, by 16%, than in crops being grown under CMP (Table 5).

At the grain-filling stage, the amount of xylem exudation in SRI grown plants was 1.5 times more than in CMP plants on a per-hill basis, and 25% greater on an area basis. The different post-vegetative water management treatments had a significant effect on exudate amounts, greatest for SRI with 3-DAD treatment, followed by CMP with 1-DAD and SRI with 1-DAD treatments. On a per-hill basis, xylem exudation rate was nearly 3 times faster under SRI than CMP at both stages of measurements across all water management treatments. Overall, on an area basis, the xylem exudation rate under SRI was calculated to be 25% faster than for crops under CMP: $6.4\,\mathrm{g}\,\mathrm{m}^{-2}\,\mathrm{h}^{-1}$ vs. $5.1\,\mathrm{g}\,\mathrm{m}^{-2}\,\mathrm{h}^{-1}$ during the grain-filling stage.

Table 4Effects of rice cultivation systems and post-vegetative water management on root growth during panicle initiation and grain-filling stages.

Cultivation systems	Water management treatments (post-vegetative stage)	PI stage			Grain-filling stage			
		Root dry weight (g hill ⁻¹)	Root weight density (mg cm ⁻³)	Root dry weight (g m ⁻²)	Root dry weight (g hill ⁻¹)	Root weight density (mg cm ⁻³)	Root dry weight (g m ⁻²)	
CMP	CF	6.04 b	0.67 с	304.7 b	5.89 d	0.65 d	292.6 d	
(CF)	1-DAD	6.17 b	0.69 c	307.9 b	6.14 d	0.68 d	312.2 d	
	3-DAD	6.19 b	0.69 c	308.2 b	5.22 e	0.58 e	267.2 e	
	5-DAD	5.89 b	0.65 c	300.1 b	4.37 f	0.49 f	222.7 f	
	Ave.	6.1	0.68	305.2	5.4	0.60	273.7	
SRI	CF	14.14 a	0.79 b	352.1 b	13.72 с	0.76 с	345.1 c	
(3-DAD)	1-DAD	17.39 a	0.97 a	436.8 a	15.33 b	0.85 b	384.6 b	
	3-DAD	17.12 a	0.95 a	430.1 a	17.11 a	0.95 a	423.8 a	
	5-DAD	16.43 a	0.91 a	422.7 a	13.48 с	0.75 с	334.2 c	
	Ave.	16.3	0.91	410.4	14.9	0.83	371.9	
Analysis of vari	ance							
Cultivation system (CS)		**	**	**	**	**	**	
Water management (W)		ns	ns	ns	*	*	*	
$CS \times W$	$CS \times W$		ns	ns	*	*	ns	

Mean values followed by different letter within columns differ significantly at P < 0.05 according to Duncan's range test. CMP: Conventional management practice; SRI: System of rice intensification. CF: Continuous flooding; DAD: Days after disappearance of ponded water. *, p < 0.05; **, p < 0.01; ns, not significant.

 Table 5

 Effects of rice cultivation systems and post-vegetative water management on xylem exudation amount and rate during panicle initiation and grain-filling stages.

Cultivation systems	Water management	PI stage				Grain-filling stage			
	treatments (post- vegetative stage)	Exudate amount (g hill ⁻¹)	Exudate amount (g m ⁻²)	Exudation rate (g hill ⁻¹ h ⁻¹)	Exudation rate $(g m^{-2} h^{-1})$	Exudate amount (g hill ⁻¹)	Exudate amount (g m ⁻²)	Exudation rate (g hill ⁻¹ h ⁻¹)	Exudation rate (g m ⁻² h ⁻¹)
CMP	CF	3.2 b	160.4 ab	0.13 b	6.68 ab	2.5 e	125.2 cd	0.10 e	5.22 cd
(CF)	1-DAD	3.4 b	170.5 a	0.14 b	7.10 a	3.1 d	155.3 b	0.13 d	6.47 b
	3-DAD	2.9 b	145.7 b	0.12 b	6.07 b	2.2 ef	110.4 e	0.09 ef	4.60 e
	5-DAD	2.9 b	145.3 b	0.12 b	6.05 b	2.0 f	100.1 f	0.08 f	4.17 f
	Ave.	3.1	155.5	0.13	6.48	2.5	122.8	0.10	5.12
SRI	CF	7.5 a	187.2 a	0.31 a	7.80 a	5.5 c	137.5 с	0.23 c	5.73 c
(3-DAD)	1-DAD	6.8 a	170.2 a	0.28 a	7.09 a	6.2 b	155.2 b	0.26 b	6.47 b
	3-DAD	7.2 a	180.7 a	0.30 a	7.53 a	7.1 a	177.6 a	0.30 a	7.40 a
	5-DAD	7.5 a	187.5 a	0.31 a	7.81 a	5.8 c	145.1 c	0.24 c	6.05 c
	Ave.	7.3	181.4	0.30	7.56	6.2	153.9	0.26	6.41
Analysis of va	ariance								
Cultivation sy	rstem (CS)	**	**	**	**	**	*	**	*
Water manage	ement (W)	ns	ns	ns	ns	**	**	**	**
$CS \times W$		*	ns	*	ns	**	**	**	**

Mean values followed by different letter within columns differ significantly at P < 0.05 according to Duncan's range test. CMP: Conventional management practice; SRI: System of rice intensification. CF: Continuous flooding; DAD: Days after disappearance of ponded water. *, p < 0.05; **, p < 0.01; ns, not significant.

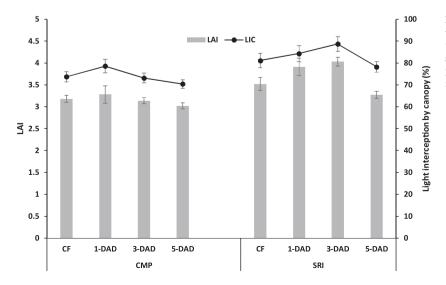


Fig. 1. Effect of rice cultivation systems and post-vegetative water management on LAI and light interception by canopy at the grain-filling stage (110 DAS). Vertical bars represent the standard deviation (n=15). CMP: Conventional management practice; SRI: System of rice intensification; CF: Continuous flooding; DAD: Days after disappearance of ponded water.

SRI

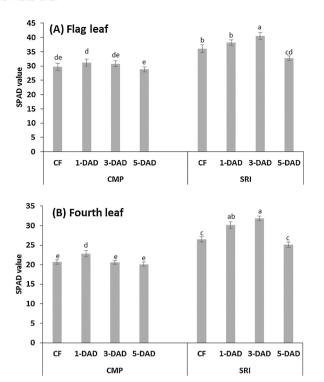


Fig. 2. Effect of rice cultivation systems and post-vegetative water management on SPAD value of flag leaf (A) and fourth leaf (B) at the grain-filling stage (110 DAS). For each replicate, 10 flag leaves and 10 fourth leaves (4^{th} from top) were used for the measurements. Vertical bars represent the standard deviation (n = 30). Bars with a different letter are significantly different at the 5% level. CMP: Conventional management practice; SRI: System of rice intensification; CF: Continuous flooding; DAD: Days after disappearance of ponded water.

3.4. Effects on leaf area index and light interception by crop canopy

Leaf area index (LAI) and light interception by canopy (LIC) when measured at the grain-filling stage showed SRI crops to have significantly greater values across all of the treatments. Similar to other parameters measured, under SRI cultivation, the highest LAI and LIC were found with the 3-DAD water management treatment, while under CMP, these values were highest with the 1-DAD treatment (Fig. 1). The lower levels of leaf area and light interception under the water-constrained conditions of the 5-DAD treatment were mainly attributable to greater senescence and dying-off of the lower leaves under both cultivation practices, which caused a decrease in root development as reflected in the data in Table 4.

3.5. Effects on SPAD values and leaf photosynthesis rate

Overall, the leaves of the SRI plants had significantly higher SPAD values than did those of CMP plants, indicating that SRI leaves were greener compared to CMP leaves (Fig. 2). Across all the water management treatments, the flag leaf and the fourth leaf of SRI plants, compared to those of CMP plants, had higher SPAD values, by 22% and 34%, respectively. The SPAD values in both the flag and fourth leaves were found to be the highest with 3-DAD under SRI and with 1-DAD treatments under CMP. The latter were always significantly lower than for the SRI treatment, reflecting differences in the SRI and CMP phenotypes resulting from treatment effects.

During the grain-filling stage, cultivation methods were found to have a significant effect on photosynthesis rates in both flag leaves and fourth leaves (Fig. 3). Overall, the flag leaves of SRI plants had a photosynthesis rate 22% higher and the fourth leaves had a 19% higher rate compared to the flag and fourth leaves of CMP rice plants. Also, the different water management treatments during the post-vegetative

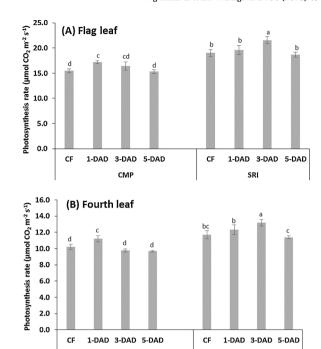


Fig. 3. Effect of rice cultivation systems and post-vegetative water management on rate of photosynthesis of flag leaf (A) and fourth leaf (B) at the grain-filling stage (110 DAS). For each replicate, 10 flag leaves and 10 fourth leaves (4^{th} from top) were used for the measurements. Vertical bars represent the standard deviation (n = 30). Bars with a different letter are significantly different at the 5% level. CMP: Conventional management practice; SRI: System of rice intensification; CF: Continuous flooding; DAD: Days after disappearance of ponded water.

CME

stage had significant impacts on the photosynthesis rates in the flag and fourth leaves during the grain-filling stage under both cultivation systems, an important difference.

In SRI plants, both flag and fourth leaves had significantly higher photosynthesis rates under the 3-DAD treatment compared to others, while with CMP methods, plants under the 1-DAD treatment had a higher photosynthesis rate than with the other irrigation treatments. These trends in leaf photosynthesis rate were consistent with the SPAD values measured for the different treatments.

With both cultivation systems, the lowest rate of photosynthesis was found in rice plants grown under the 5-DAD treatment, which was the treatment with the most water stress. This rate remained significantly higher in SRI treatments than for CMP, which again may be explained by the improved root development and activity (Tables 4 and 5).

3.6. Effects on main stem panicle weight and grain-filling rate (GFR)

There were significant differences between the two crop management systems and the four water management treatments with regard to main panicle dry weight (Fig. 4) and their grain-filling rate (Fig. 5). Overall, at the time of flowering (anthesis), the dry weight of the main panicle that includes empty grains (chaff) was 746 mg under CMP and 929 mg under SRI, so the latter was 25% heavier.

During the initial 7 days after anthesis (DAA), the panicle weight increased at a high rate in all of the treatments. Fig. 4 shows two pairs of curves, distinctly different for SRI and CMP. In panicles grown in CMP plots, the weight of grain increased up to 21 DAA, but after this there were no significant increases. The slopes of the SRI curves show grain-filling continuing at a higher rate and for a longer period than for CMP rice plants. Under SRI practice, in contrast to CMP, the increase in grain weight continued up to 28 or 35 DAA in most of the treatments (except in those with 5-DAD irrigation).

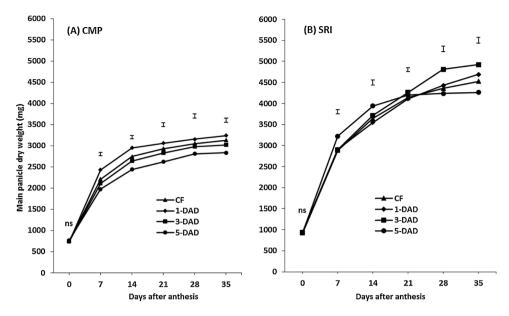


Fig. 4. Effect of rice cultivation systems and post-vegetative water management on changes in the dry weight of main panicle in CMP (A) and SRI (B) during post-anthesis period. Vertical bars represent LSD at 5% level. CMP: Conventional management practice; SRI: System of rice intensification; CF: Continuous flooding; DAD: Days after disappearance of ponded water.

In SRI plots with 5-DAD irrigation, which initially showed the most rapid growth of panicle weight, the curve's leveling off after 21 DAA may be due to unsupportive root functioning and a lower rate of leaf photosynthesis. At the time of harvest, the average main panicle dry weight was 50% more under SRI management than with CMP, i.e., 4599 mg vs. 3056 mg. Among the different water management treatments, the highest main-panicle dry weight with CMP was achieved with 1-DAD water management (3240 mg), and with SRI at 3-DAD scheduling (4921 mg). Similarly, the weight of grain yield per main panicle under CMP was 2310 mg compared with 3670 mg under SRI.

Across all water-management treatments, SRI plants had a GFR of 104.8 mg day⁻¹ panicle⁻¹ for the main panicle, 59% higher than the GFR for CMP plants, which was 66.0 mg day⁻¹ panicle⁻¹. Water management during the post-vegetative stage thus had a significant effect on the grain-filling rate of the main panicle (Fig. 5). Under SRI management, the highest GFR was found with the 3-DAD treatment,

while the highest GFR under CMP methods was achieved with the 1-DAD treatment. This was consistent with the many preceding measurements reported.

4. Discussion

Much of the burden for promoting rice production in the future will rest on developing better-integrated soil-crop management systems (Chen et al., 2011) and promoting water-saving irrigation. The System of Rice Intensification is a method of rice cultivation that can be part of such a strategy (FAO, 2016). Through research and extension over the past decade, it has been extensively documented that SRI ideas and methods can improve productivity by using less external inputs and by reducing the consumption of water (Jagannath et al., 2013; Lin et al., 2009; Satyanarayana et al., 2007; Sinha and Talati, 2007; Thakur et al., 2011, 2014; Uphoff, 2012).

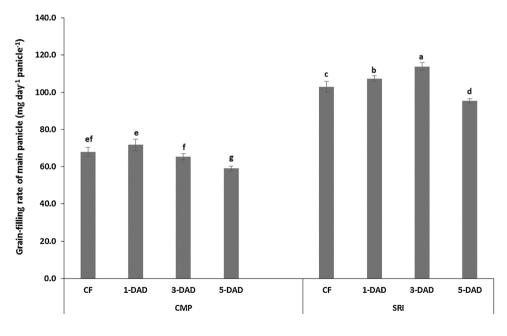


Fig. 5. Effect of rice cultivation systems and post-vegetative water management on grainfilling rate of the main panicle. Vertical bars represent the standard deviation. Bars with a different letter are significantly different at the 5% level. CMP: Conventional management practice; SRI: System of rice intensification; CF: Continuous flooding; DAD: Days after disappearance of ponded water.

The purpose of this investigation was to evaluate whether further water savings might be possible within the SRI management framework particularly during the post-vegetative stage, and whether observed yield and water productivity improvements could be explained through demonstrable impacts on crop growth and physiology. In the present trials, SRI produced 58% higher grain yield compared with CMP (Table 2). Many earlier studies have also shown SRI methods giving 20-50% higher yield, and even more (Jagannath et al., 2013; Satyanarayana et al., 2007; Sinha and Talati, 2007; Thakur et al., 2011). Obviously, the percentage increase will vary depending on the cultivation systems with which it is compared, the latter varying greatly between regions and farmers. However, increases of more than 20% over already-high levels have been reported on a large scale in China (Wu and Uphoff, 2015; Zheng et al., 2013). These yield increases are achieved, while water consumption is greatly reduced, particularly important in a water-scarce country like Iraq (Hameed et al., 2013).

The present study recorded similar results that can be explained by the morphological and physiological changes associated with changes in plant phenotypes under SRI practices. The changes in water management practices during the post-vegetative stage had a significant impact on grain-filling rate, and hence on panicle dry weight. Moisture reduction beyond a certain point during the post-vegetative stage was seen to set in on all plants, however cultivated, but this was evident earlier with CMP-grown plants, whose root systems were less well-developed and less functional.

Rice plants grown with CMP methods having less root growth evidently started experiencing moisture stress beyond 1-DAD irrigation, while for SRI plants this constraint set in beyond 3-DAD irrigation. This effect correlated with measurements on declining root growth and root activity, decreasing green leaf area, lowered photosynthesis rate, and enhanced senescence. These morpho-physiological changes led to a lowering of dry weight of the main panicle, to a slowing down of the grain-filling rate, and ultimately to less grain yield.

It is interesting to note that even at 5-DAD, the SRI plots still yielded significantly more than from any of the CMP treatments (Table 2). This indicates a greater resilience of SRI plants to withstand moisture stress. These results may have relevance also to the widespread rainfed rice systems which experience water stress mostly during their post-vegetative stage of crop growth and which will have more resilience if they grow larger root systems.

The significantly larger root systems that had been developed during the vegetative phase up to the PI stage resulted from the preceding practices that are introduced under SRI. These include transplanting young, single seedlings at wider spacing; enhancing soil fertility with organic amendments; regular mechanical weeding; and alternate wetting and drying irrigation during the vegetative-growth stage rather than continuous flooding. A major factor will have been the greatly reduced plant density that has been responsible for a relatively unrestricted and remarkable root development (Table 4). But aerobic soil conditions and active soil aeration that promote the growth and functioning of beneficial soil organisms, including possibly as symbiotic endophytes (Uphoff et al., 2013), could be playing a role in this better crop performance, a hypothesis that warrants more investigation.

Under conventional cultivation, in contrast, older seedlings are transplanted, 3 or 4 together in more closely-spaced hills, with the field kept flooded throughout the vegetative stage. These practices result in poor root growth under CMP, both on a per-hill basis and on an area basis, which accelerates the degeneration of rice root systems (Kar et al., 1974), with obviously adverse effects on root activity (Yang et al., 2004). This is reflected in reduced exudation rates and quantities (Table 5). Under SRI management, greater root growth and activity of individual plants and of the crop as a whole become much more efficient in using the natural resources as well as in plants' uptake of mineral fertilizer (Thakur et al., 2013).

SRI practices presumably establish a more favourable root-soil interface in terms of soil microbiology and aeration. However, there is not

much research on this or on how alternate wetting-and-drying irrigation facilitates better root growth under SRI compared to CMP. In terms of grain yield, different researchers comparing AWD with CF have reported some contradictory results. For example, Yao et al. (2012) found no difference in yield between AWD and continuously flooded rice; however, AWD in their evaluation saved 24–38% irrigation water and had higher water productivity than continuously flooded rice. Recently, Carrijo et al. (2017) found no significant yield reductions under mild AWD with 23.4% water saving, but a 22.6% yield penalty under severe AWD compared with continuous flooding in rice.

These comparisons were made, however, without taking into account the probably confounding effects of plant density and moisture stress factors (Stoop et al., 2009) and without considering the impact of greater root growth as results under SRI due to its management modifications. Wang et al. (2016) and Yang et al. (2017) have reported, without reference to or use of SRI methods, that alternate-wetting-and-moderate-drying is better for rice crop growth than either continuous flooding or alternate-wetting-and-severe-drying in terms of higher grain yield and greater water use efficiency (WUE) in rice. According to Yang et al. (2017), moderate AWD enhances grain yield and WUE mainly due to improved vegetative growth, root growth, canopy structure, and enhanced carbon remobilization from vegetative tissues to grain. Also, elevated phyto-hormonal levels particularly increase in abscisic acid (ABA) levels during soil drying and then cytokinin levels during rewatering.

Transplanting young seedlings under SRI methods influences their quick establishment in the main field by avoiding trauma to their roots and canopies during their uprooting from the nursery. This helps the seedlings to resume their growth quickly and grow greater root mass (Pasuquin et al., 2008). Also, transplanting single seedlings with wider spacing minimizes competition for nutrients, water, solar energy and other requirements. Such practices create more favourable environments for plant growth.

The significance of the expanded root systems was illustrated in our trial by the increase in xylem exudates transported from the roots upward towards the shoots during the grain-filling stage. These were significantly more under SRI than under CMP. The greater root growth and activity in addition to better extraction of water and nutrients also improves the transport of cytokinins towards the shoot (San-oh et al., 2004, 2006).

It is well known that cytokinins delay leaf senescence and maintain the greenness of leaves, as was recorded in both the flag leaf and the fourth (lower) leaf of SRI plants in this study (Fig. 2). Also cytokinins are associated with increased chlorophyll content in the leaves (Thakur et al., 2010b, 2011). Maintenance of a higher leaf chlorophyll level results in higher rates of photosynthesis during grain-filling (Fig. 3). The incipient grains received a greater supply of carbohydrates from photosynthesis, while also more of these were sent to the roots for the maintenance of their activity (metabolism).

Hence, an expanded and active root system, as developed under AWD methods of irrigation with moderate drying of the soil, significantly affects a crop's above-ground physiology and performance. Zhang et al. (2009), for example, have reported similar effects of a moderate wetting and drying regime when compared with continuous flooding. They also showed the significant effects of water management on root oxidation activity, cytokinin concentrations in the roots and shoots, leaf photosynthetic rate, and the activities of key enzymes involved in sucrose-to-starch conversion in grains. A resultant effect of root growth and physiology on crop grain yield was an increase of 11% with AWD practices and in water use efficiency of 55% (Zhang et al., 2009). Similarly, other researchers also found that post-anthesis alternate-wetting-and-moderate-soil-drying elevates cytokinin levels in the rice shoot, at the same time improving sink strength, grain-filling rate, and grain weight of inferior spikelets (Zhang et al., 2010, 2012). All this ultimately resulted in higher grain yield.

The amount of light intercepted by the canopy is positively

correlated with the leaf area of the crop, and this relates directly to plant growth (San-oh et al., 2004). In this present study, rice plants grown with SRI methods had significantly greater leaf area as well as more light interception by the canopy compared with the CMP crop during the grain-filling stage. This was achieved in spite of the six-fold reduction in plant density m⁻² in the SRI treatments. The higher leaf area with SRI management was mainly due to delayed senescence of the lower leaves and to greater leaf size, which resulted in increased light interception (Thakur et al., 2011). The SRI-grown plants also had a more open canopy with more erect leaves, a structure that facilitated higher light interception and minimized shading of the lower leaves of the crop (Thakur et al., 2016). All these effects are associated with the drastic reduction in the number of plants per unit area, which allows the rice plants to function physiologically more efficiently than under conventional management.

During the vegetative growth phase and subsequent panicle initiation, the plant's potential yielding capacity is determined. The post-vegetative phase that follows determines the extent to which this potential gets realized. Unconstrained grain-filling is the decisive process which correlates with the crop's yield performance. Many researchers have explored the relationship between photosynthesis and related parameters in the leaves (i.e., source factors) vis-à-vis the grain-filling process (sink factors) which determines ultimate grain yield. We have observed that under SRI management, higher leaf chlorophyll content and a faster rate of photosynthesis led to more rapid grain-filling, by about 59% (Fig. 5). This relationship also confirmed that leaf photosynthetic rates are positively related with chlorophyll meter values (Park and Lee, 2003a).

The stay-green characteristics of SRI plants during grain-filling (reflected in their SPAD values) contributed to higher grain yield. Delayed senescence of both upper and lower leaves as analyzed by Park and Lee (2003b) is associated with the higher grain yield observed under SRI management (Figs. 2 and 3). Enhanced photosynthetic rate in the lower leaves also provides an increased supply of carbohydrates to the roots, thereby enhancing their metabolism and prolonging their longevity. Improved shoot characteristics and functioning due to the receipt of more nutrients, water, and plant hormones then translates into an overall increase in biomass production and in plants' grainfilling processes (Samejima et al., 2004; Zhang et al., 2009). A similar result has been reported by Chen et al. (2013) on increases in biomass accumulation before the heading stage and the subsequent improved utilization of photosynthates during the grain-filling stage.

The underlying reasons might be due to some reorientation in the translocation process in plants. Earlier, Yang et al. (2003) demonstrated that a properly-controlled 'water deficit' during grain-filling could enhance the remobilization of pre-stored carbon in the stems, which greatly increased the plant's grain-filling rate. In our study, a controlled but not excessive water deficit had no yield-constraining effect up to 1-DAD irrigation for the CMP plants nor up to 3-DAD irrigation for the SRI crop. However, remobilization of carbohydrate reserves stored in the leaf sheath and stem for grain-filling under SRI management has not been studied specifically. This is an important area of research for making crops more heat- or drought-resistant through modifications in irrigation and other crop management practices.

Apart from the rate of grain-filling, variations in the duration of grain-filling are also an important factor that can account at least in part for differences in grain yield. Extension of the grain-filling period can provide rice plants with more access to ambient resources for prolonged grain growth, in this way achieving higher yield (Yang et al., 2008). Although it is clear that SRI practices have an effect on the grain-filling rate (see Fig. 4), it would be good to know more about how the duration of grain-filling is affected by crop or water management practices.

Yield components such as the number of panicles and the number of grains per panicle are determined mostly by growth processes that begin before anthesis. In our study, when alternative water

management practices were introduced during the post-vegetative stage, there were no significant differences detected in the numbers of panicles per plant and grains per panicle. However, our trials showed a consistent pattern of better crop performance and higher grain yield from SRI compared with CMP crop management; and best CMP performance was consistently with irrigation provided at 1-DAD in the post-vegetative phase rather that maintaining continuous flooding, and for SRI the best scheduling was with 3-DAD during both the post-vegetative and vegetative phases.

5. Conclusions

Enhancing water productivity in rice production will continue to be a matter of great concern to researchers, farmers and policy-makers in order to produce 'more grain with less water' – more crop per drop. In the present study, we demonstrated that SRI practices induce rather different phenotypic responses in rice plants both morphologically and physiologically. One of the most important findings was that water productivity could be enhanced by about 90% when using the suite of practices that constitute SRI. In our trials, these methods reached a productivity of 6.3 kg ha-mm⁻¹ compared to 3.3 kg ha-mm⁻¹ with CMP. Under SRI management, with 16% less irrigation water there was, on average, a 58% enhancement of grain yield.

Alternate wetting and drying together with SRI management practices had significant and multiple beneficial effects on grain yield as well as on water saving and water productivity. SRI crops were able to achieve greater grain yield even with reduced applications of water due to their more vigorous root growth, greater root activity, delayed leaf senescence and higher photosynthetic rate, and greater rate of grainfilling compared with CMP rice crops.

These results were obtained in spite of the drastic six-fold reduction in the number of plants m⁻² under SRI practice. Under such management, the best results in terms of yield, water saving and productivity from sandy clay-loam soil with a medium-duration variety were obtained by maintaining a 3-DAD irrigation regime throughout the entire cropping season, instead of flooding the rice field continuously including during the post-vegetative stage. Based on our results, the current SRI recommendation for maintaining a shallow layer of water on the field after panicle initiation could well be revised. This would further increase SRI's water saving without any yield penalty, indeed with an enhancement of yield.

Further studies are required regarding the effect of SRI on the remobilization of carbohydrate reserves stored in leaf sheaths and stems during grain-filling, especially during terminal heat or water stress. The impact of crop management practices on grain-filling duration under SRI management should also be researched. Studies on SRI's yield and water productivity performance using other water-saving irrigation methods like drip or sprinkler systems should also be investigated. Possibly together with SRI management, both of these methods and new irrigation technology could be made more productive in terms of their use of land, labor and (especially) water.

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