Plant Soil
DOI 10.1007/s11104-013-1612-5

REGULAR ARTICLE

Differential responses of system of rice intensification (SRI) and conventional flooded-rice management methods to applications of nitrogen fertilizer

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Received: 6 November 2012 / Accepted: 23 January 2013

Abstract

Background Rising food demand, slowing productivity growth, poor N-use efficiency in rice, and environmental degradation necessitate the development of more productive, environmentally-sound crop and soil management practices. The system of rice intensification (SRI) has been proposed as a methodology to address these trends. However, it is not known how its modified crop-soil-water management practices affect efficiency of inorganic nitrogen applications.

Methods Field experiments investigated the impacts of SRI management practices with different N-application rates on grain yield, root growth and activity, uptake of N and its use-efficiency, leaf chlorophyll content, leaf N-concentration, and photosynthetic rate in comparison with standard management practices for transplanted flooded rice (TFR).

Results Overall, grain yield with SRI was 49 % higher than with TFR, with yield enhanced at every N application dose. N-uptake, use-efficiency, and partial factor productivity from applied N were significantly higher in SRI than TFR. Higher leaf nitrogen and chlorophyll contents during the ripening-stage in SRI plants reflected delayed leaf-senescence, extension of photosynthetic processes, and improved root-shoot activities contributing to increased grain yield.

Conclusions Rice grown under SRI management used N fertilizer more efficiently due to profuse root development and improved physiological performance resulting in enhanced grain yield compared to traditional flooded rice.

Keywords Cultivation practices · Grain yield · Nitrogen use efficiency · *Oryza sativa* · Root growth · System of rice intensification

Abbreviations

SRI	System of rice intensification
TFR	Transplanted flooded rice
AWD	Alternate wetting and drying
ANUE	Agronomic nitrogen use efficiency
PFP	Partial factor productivity
CP	Cultivation practice
MG	Milk grain
LR	Late ripening

Introduction

Rice (*Oryza sativa* L.) is the foremost staple food for more than 50 % of the world's population. It is estimated that by the year 2025, the world's farmers should be producing about 60 % more rice than at present to meet the food demands of the future world

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Responsible Editor: Matthias Wissuwa.

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population (Fageria 2007). In the Green Revolution era, global rice production increased remarkably, largely due to the widespread adoption of high-yielding varieties and increased use of chemical fertilizers in Asia (Tong et al. 2003).

Nitrogen (N) is the main yield-limiting nutrient in rice cropping systems worldwide (Jiang et al. 2004), and the application of chemical nitrogen fertilizer is considered one of the main ways to improve yield (Zhu and Chen 2002). However, since the 1990s, large N fertilizer applications have contributed to severe degradation in the quality of air, soil and water, and there is high potential of N losses through various pathways (Ju et al. 2009). Several studies in rice have focused on the consequences of excessive use of N fertilizer, including decreases in crop quality, decreases in N use efficiency, and creation of environmental hazards (Aparicio et al. 2008; Ju et al. 2009; Shindo et al. 2006; Tian et al. 2007; Yang et al. 2010; Zhao et al. 2009).

Increased fertilization rates have encountered demonstrably diminishing returns with reduced fertilizer use efficiencies. The marginal gain in grain yield per kilogram of N nutrients applied has decreased, from 15 kg in the 1950s to 8–10 kg in the 1970s, to only 6–7 kg in the 1990s (Xie 1998). In China, the productivity of N fertilizer has declined from 15 to 20 kg of paddy rice per 1 kg of N before the Green Revolution to about 5 kg now (Peng et al. 2010). One earlier projection indicated that N fertilizer applications would need to *triple* by 2030 to meet a target of 60 % increase in paddy production that would satisfy consumption demand (Cassman and Harwood 1995). This estimate did not attempt to assess fully the economic and environmental costs of such an expanded use of fertilizer, to ascertain whether such an increase would be in any way feasible.

Further increases in N application rates to meet future food demand therefore are hardly an option unless present production strategies are changed. Nitrogen losses will have to be reduced and fertilizer-N use efficiency increased so that the environmental costs associated with denitrification and leaching of NO_3 are controlled (George et al. 1993). The development of efficient and environmentally-sound practices for N fertilizer use is of utmost importance, which requires improved crop and soil management practices (Cassman et al. 1998).

The system of rice intensification (SRI) could potentially be a sustainable approach to enhance rice productivity with reduced rates of external inputs (Stoop et al. 2002; Stoop 2011). SRI principles focus on neglected potentials to raise yields by changing farmers' agronomic practices towards more efficient use of natural resources (Uphoff and Randriamiharisoa 2002). SRI was developed in Madagascar during the 1980s, and by now is being promoted in over 50 countries by governmental and non-governmental organizations (http://sri.ciifad.cornell.edu/). It has generated considerable interest among farming communities and simultaneously intensive debates among agricultural scientists. Studies on SRI have frequently pointed to positive environmental and resource-conserving effects due to a reduced use of external inputs. The methods raise rice yield (Thakur et al. 2010a, 2011; Zhao et al. 2010) concurrently with a considerable reduction in crop water requirements (Satyanarayana et al. 2007; Thakur et al. 2011), while enhancing the productivity of applied inputs (Sinha and Talati 2007).

Greater reliance on organic sources of nutrients is one of the SRI recommendations, seeking to enhance soil structure and functioning as well as soil microbial abundance and activity. However, organic fertilization is an option, rather than a requirement (Stoop et al. 2002). Where the availability of organic manure is limited by insufficient supply of biomass and/or labor, mineral fertilizers can be used beneficially with the other SRI practices, in addition to or instead of organic material.

One way to reduce N loss through leaching and washing away from rice fields might be to practice alternate wetting and drying (AWD) forms of irrigation, maintaining a shallow water depth with intermittent drying rather than continuous flooding. Reports indicate that the AWD method of irrigation enhances the grain yield with significant water savings as compared with traditional irrigation that uses 5–9 cm of standing water (Lin et al. 2005, 2006). However, the impact of the overall set of SRI practices on N-uptake and on the efficiency of N use by the crop (i.e. the relationship between leaf chlorophyll and leaf-N contents in relation to photosynthetic activity) is still not known. Hence, there is a need to establish how a modified crop-soil-water management regime as proposed by SRI theory and practice will affect N uptake by the root systems of SRI plants.

As compared with standard practices, SRI plants have been shown to develop a profuse root system (Thakur et al. 2011; Barison and Uphoff 2011), which is likely to affect both nutrient (N) uptake and utilization.

This study compares rice yields and factor productivity for plants grown with SRI methods with those under standard management practices of transplanted flooded rice (TFR), assessing the effects of different N-fertilizer application rates on these parameters. Possible cultivation system × N interaction effects that would bear on N uptake and N-use efficiencies were also studied to assess whether N-fertilizer applications could be reduced through SRI methods without sacrificing grain yield.

Materials and methods

Study site and soil

The experiments were conducted over two seasons in 2009 and 2010 at the Deras Experimental Research Farm (20° 30′ N, 87° 48′ 10″ E), Mendhasal in Khurda district, Orissa, India, during the dry season (January–May). Soils at the experimental site are classified as *Aeric Haplaquepts*, sandy clay-loam in texture (63 % sand, 16 % silt, and 21 % clay) with a pH of 5.6. Organic carbon content was moderate (11.8 $\mathrm{g kg^{-1}}$). The nutrient content of the soil was as follows: total nitrogen 1.03 $\mathrm{g kg^{-1}}$, available P (Olsen) 12 $\mathrm{mg kg^{-1}}$, exchangeable K 0.24 cmol $\mathrm{kg^{-1}}$ soil, exchangeable Ca 4.7 cmol $\mathrm{kg^{-1}}$ soil, available S 18 $\mathrm{mg kg^{-1}}$, Zn 12 mg $\mathrm{kg^{-1}}$, and Fe 390 $\mathrm{mg kg^{-1}}$.

Experimental design and treatments

The experimental design was a split-plot with three replications. In the main plots, there were two alternative crop management systems: the System of Rice Intensification (SRI), and transplanted flooded rice (TFR) based on standard management practices (ICAR 2006). Sub-plot treatments were four nitrogen rates: no N fertilizer (N_0), 60 kgN $\mathrm{ha^{-1}}$ (N_{60}), 90 kgN $\mathrm{ha^{-1}}$ (N_{90}), and 120 kgN $\mathrm{ha^{-1}}$ (N_{120}). Nitrogen was applied in the form of urea. Phosphorus and potassium fertilizers were applied at same rate to all plots: 40 kg P_2O_5 $\mathrm{ha^{-1}}$ as single super phosphate (16 % P_2O_5), and 40 kg K_2O $\mathrm{ha^{-1}}$ as muriate of potash (60 % K_2O). Fully decomposed cow dung manure (0.37 %N, 0.19 % P_2O_5 and 0.17 % K_2O) was applied at the rate of 5 $\mathrm{t ha^{-1}}$ at the time of land preparation for both SRI and TFR plots, as was the entire amount of P, while the N and K were applied in three installments: 25 % at 10 days after transplanting, 50 % at maximum tillering stage, and 25 % at panicle initiation stage. The plot sizes were 10 m×5 m.

Crop management and irrigation

The rice variety used in the experiment was medium-duration, *Surendra* (IET-12815; 130–135 days), which usually gives yields of 3.5–5.0 $\mathrm{t ha^{-1}}$ (DRD 2006). Germinated seeds were broadcasted for nursery establishment on January 4, 2009 in the first year and on January 3, 2010 in the second year. Twelve-day-old single seedlings were transplanted 1–2 cm deep (shallow) into puddled SRI plots without any standing water on January 16, 2009 and January, 15, 2010 at spacing of 20×20 cm (25 plants $\mathrm{m^{-2}}$). Based on results in an earlier study with the same rice variety under the local soil conditions (Thakur et al. 2010b), it was decided to make the plant spacing under SRI 20×20 cm as compared with the original recommendation of 25×25 cm (Stoop et al. 2002). For the TFR plots, 25-day-old seedlings (three seedlings per hill) were transplanted 2–5 cm deep into a puddled field with 5–6 cm of ponded water at a spacing of 20×10 cm (150 plants $\mathrm{m^{-2}}$) on January 29, 2009 and January 28, 2010. The SRI plots were weeded by mechanical weeder (cono-weeder) at 10, 20 and 30 days after transplanting, and the TFR plots had three hand weedings at the same intervals, so there was active soil aeration along with weed control under SRI method, and only removal of weeds under TFR.

The TFR plots were kept continuously flooded (5–6 cm depth of water) during the entire vegetative stage. In SRI plots, intermittent irrigation was followed, with irrigation water applied 2–3 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 were fully drained at 15 days before harvest in both SRI and TFR. Crops were harvested on May 18 and May 14 during 2009 and 2010, respectively.

Sampling and analysis

Root samples were collected from each sub-plot of three randomly-selected hills with an average number of tillers at flowering stage (105 days after germination; 16–

18 April), using a core sampler (diameter: 10 cm) which removed 30-cm deep soil cores along with the hills to take a uniform soil volume from each treatment. Roots were carefully washed, and dry weights were measured.

Xylem exudation rates were measured at the flowering stage, as a parameter that reflects the activity of the plants' root systems (Soejima et al. 1995). Three hills each with an average number of tillers were selected from each sub-plot. 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 tape. After 24 h, each bag was detached, sealed and weighed, and the weight of the exudates was calculated by subtracting the weight of the bag and pre-weighed cotton wool (San-oh et al. 2004).

In order to assess N utilization in relation to photosynthetic activity, three hills with an average number of panicles were selected from each sub-plot. For each hill, 3 flag leaves and 3 fourth-leaves were selected at the milk-grain stage (111 days after germination; 22–26 April) and late-ripening stage (123 days after germination; 4–6 May) to measure the photosynthetic rate by using a portable photosynthesis system (CIRAS-2; PP Systems Ltd., Hertfordshire, UK). Measurements were taken on a clear sunny day (solar radiation >1,200 μmol $m^{-2}s^{-1}$) between 10:30 and 11:00 a.m. before the mid-day reduction in photosynthesis. Next, the same leaves were collected and used for determining chlorophyll content through dimethyl sulfoxide extraction method (Hiscox and Israelstam 1979) and were expressed as mg g^{-1} fresh leaf weight (FW). Leaf samples were dried in an oven at 60 °C for 4 days. After weighing, dried samples were powdered, and the total N concentration of each sample was determined using the standard Kjeldahl's method.

All plants in an area of 3 m×3 m for each sub-plot were harvested (excluding the border rows) for determination of straw and grain yield per unit area. Dry weight of plant samples was determined at harvest after oven-drying at 80 °C for 72 h to reach a constant weight. Final grain yield was adjusted to 14.5 % seed moisture content.

Panicle numbers, spikelet number per panicle, and number of filled grains were determined at harvesting for one square meter area of each sub-plot. The percentage of filled spikelets was calculated by dividing the number of filled spikelets by the number of total spikelets panicle^{-1}.

Total N content in the above-ground parts were determined using the standard Kjeldahl's method, and the following parameters (Zhao et al. 2009) were calculated:

$$\text{Agronomic N use efficiency}(\text{ANUE}:\ \text{kg grain/kg N applied}) = (\text{GY}_\text{F} - \text{GY}_0)/\text{N}_\text{F}$$
$$\text{Partial factor productivity of applied N}(\text{PFP}:\ \text{kg grain/kg N applied}) = \text{GY}_\text{F}/\text{N}_\text{F}$$

Where:

GY_0 grain yield without N application (N_0)
GY_F grain yield with fertilizer N application (N)
N_F fertilizer N applied.

Statistical analyses

All data were statistically analyzed using procedures described by Gomez and Gomez (1984). The analysis of variance (ANOVA) was conducted using SAS 9.2 for Windows (SAS Institute Inc., Cary, NC, USA). Significance of the treatment effect was determined by using F-test. Mean differences between treatments were compared using the least significant difference (LSD) method, and the ordering of treatments was done after Duncan's range test. The data sets for all parameters were statistically analysed considering *year* as a source of variation in addition to *practice* (SRI vs. TFR) and *N application rates*, as well as the interaction between these factors. Correlation and regression analysis for selected variables was conducted by using the data analysis tool pack of MS-Excel. To understand the difference in the slope of the regression line between cultivation practices, a homogeneity test of regression coefficients was conducted.

Results

The main effects of year and of interaction effects between "year × practice", "year × nitrogen" and three-factor interaction (year × practice × nitrogen) were not significant at 5 % probability for any of the parameters considered in the study (Table 1). Therefore, the data reported in this paper are calculated as the averages for the 2 years of field trials.

Grain yield, straw production and yield components

Grain yield of SRI was significantly ($p<0.05$) greater than that of transplanted flooded rice at all levels of nitrogen application (Fig. 1). Over the whole range of N application rates, average yield under SRI management increased by 49 % as compared with TFR. N fertilizer applications always increased the grain yields over the zero-N control. Among N treatments, the maximum yield under SRI was 6.31 tha^{-1} with 90 kgN ha^{-1}, while the maximum yield under TFR was 4.37 tha^{-1} with 120 kgN ha^{-1}. The grain yield achieved under TFR with application of 90–120 kgN ha^{-1} was equivalent to the yield achieved with half or two-thirds as much N fertilizer under SRI method, i.e., 60 kgN ha^{-1}. Average TFR yield was within the expected range for Surendra variety, while average yield with SRI was 26 % above the expected maximum.

Under TFR, nitrogen applications increased the straw weight at a greater rate than did grain weight. In contrast, with SRI management, nitrogen applications proportionately increased the production of both grain and straw. Under both cultivation practices, straw weight significantly increased with increases in N fertilizer rate. Yet, the effect of the cultural practices on straw production was non-significant. As a consequence the Harvest index (HI) was significantly higher under SRI (ave. 0.46; range: 0.43–0.49) as compared with TFR management (ave. 0.37; range: 0.35–0.38).

Number of panicles m^{-2} increased significantly under SRI methods, by 15.5 % compared with TFR (Table 2). Other yield components like spikelet number panicle^{-1}, % of filled spikelets, and 1,000-grain weight were also significantly greater with SRI methods, by 27.8 %, 9.7 % and 3.5 %, respectively, compared with TFR. There were differences in the recorded grain yield and calculated yield for all the treatments, mainly because various yield components were measured on smaller area basis than the area from which actual grain yield was recorded.

Nitrogen application rate had a significant impact on yield components under both cultivation methods. Panicle number was significantly higher with increasing N doses from 0 to 90 kgha^{-1} under SRI, and from 0 to 120 kgha^{-1} under TFR. However, spikelet number panicle^{-1} and 1,000-grain weight only increased up till 90 kgN ha^{-1} under both sets of practices and beyond this application rate, there were no significant changes. It did not significantly affected grain-filling.

Root development: dry weights and root activity

Roots collected from similar soil volumes under both methods showed that with SRI practices, hills had a significantly larger amount of roots as indicated by increased root dry weight per hill. Root dry weight per hill was 66 % higher for SRI compared to TFR at the flowering stage (Table 3), even though SRI had only one plant hill^{-1} whereas TFR had three plants. Root

Table 1 Computed F values from analysis of variance (ANOVA) of major parameters measured in this study

Source of variation	Computed F					
	Grain yield ha^{-1}	Straw dry weight ha^{-1}	Panicle number m^{-2}	Root dry weight hill^{-1}	Root dry weight m^{-2}	N uptake ha^{-1}
Year (Y)	13.14^{ns}	17.92^{ns}	2.3^{ns}	0.00^{ns}	0.01^{ns}	0.46^{ns}
Cultivation practice (CP)	1459.56**	2.04^{ns}	3406.2**	816.59**	147.96**	29.99**
Y × CP	0.13^{ns}	0.04^{ns}	3.34^{ns}	0.02^{ns}	0.05^{ns}	0.02^{ns}
Nitrogen level (N)	2230.43**	896.25**	266.6 **	263.13**	166.21**	2565.62**
Y × N	1.50^{ns}	0.77^{ns}	0.03^{ns}	2.36^{ns}	2.40^{ns}	0.41^{ns}
CP × N	47.77**	43.78**	6.11**	57.83**	4.32*	2.21^{ns}
Y × CP × N	0.03^{ns}	2.81^{ns}	0.68^{ns}	0.45^{ns}	0.90^{ns}	2.71^{ns}

ns not significant

* and **significant at $P<0.05$ and $P<0.01$ respectively

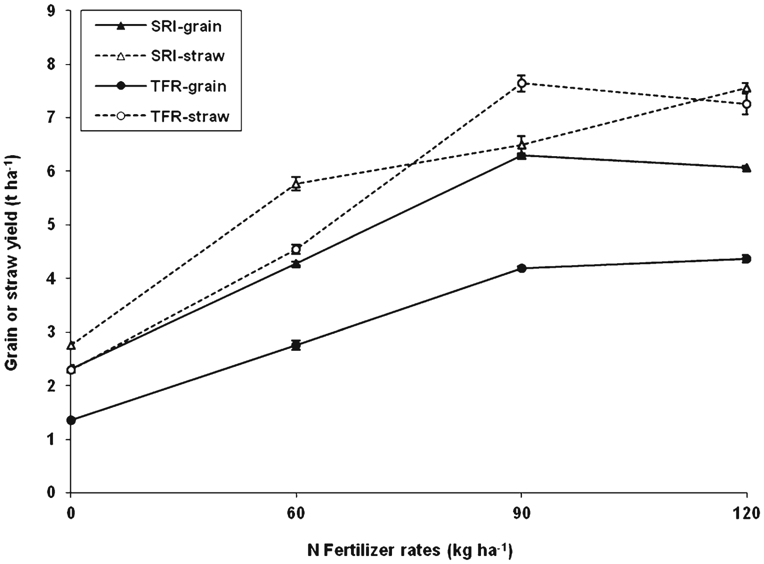

Fig. 1 Effect of fertilizer N rates on grain yield and straw weight under SRI and TFR management. *Vertical bars* represent standard errors of the means ($n=6$)

dry weight was significantly increased at 90 kgN ha^{-1} under SRI. Under TFR, no significant increase in root dry weight per hill was observed beyond 60 kgN ha^{-1}.

The amount of xylem exudates and the exudation rate are parameters that indicate the extensiveness and activity of root systems. Under SRI, the amounts of exudates hill^{-1} and the rate of exudate transport were twice as high as for TFR (having 3 plants hill^{-1}). Under both cultivation practices, the exudate amount and its rate of transport towards the shoot significantly increased with increasing N doses up to 90 kgha^{-1}.

Root dry weights per unit area were 20 % higher in TFR compared to SRI, mainly resulting from the TFR plant population being six times higher. However, the total amount of exudates and rate of transport per m^2 were higher in SRI plots than TFR plots, by 7 %. These parameters significantly increased up to N_{90} doses under SRI.

Nitrogen uptake, use efficiency, and factor productivity

The N uptake by rice plants differed significantly according to cultivation practices and N application rates. N uptake across the four N rates was significantly higher under SRI management than with TFR, by 51.8 %

Table 2 Effects of cultivation practices and fertilizer N rates on yield components in rice crop

N rate	Panicle number m^{-2}		Spikelet number panicle^{-1}		% Filled spikelets		1000-grain weight (g)	
	SRI	TFR	SRI	TFR	SRI	TFR	SRI	TFR
N_0	202.3 d	183.8 e	111.8 c	79.8 e	71.4 d	66.1 e	23.45 d	22.15 e
N_{60}	274.2 b	243.8 c	126.2 b	101.3 d	79.2 b	72.3 d	24.19 bc	23.50 d
N_{90}	327.3 a	269.2 b	147.2 a	115.7 c	83.4 a	73.1 cd	24.66 a	23.88 cd
N_{120}	330.0 a	285.3 b	145.9 a	118.7 c	80.4 b	75.1 c	24.62 ab	24.06 c
Av.	283.5	245.5	132.8	103.9	78.6	71.7	24.23	23.40
Analysis of variance								
Cultivation practice (CP)	**		**		**		*	
Nitrogen level (N)	**		**		**		*	
CP × N	**		**		**		ns	

Mean values followed by different letters denote significant ($P<0.05$) difference between treatments by DMRT

ns not significant

* and **significant at $P<0.05$ and $P<0.01$ respectively

Table 3 Effects of cultivation practices and fertilizer N rates on root dry weight and xylem exudation rates at flowering stage of rice crop

N rate	Per hill						Per unit area					
	Root dry weight (g hill^{-1})		Exudate amount (g hill^{-1})		Rate (g hill^{-1}h^{-1})		Root dry weight (gm^{-2})		Exudate amount (gm^{-2})		Rate (gm^{-2}h^{-1})	
	SRI[a]	TFR[b]	SRI	TFR	SRI	TFR	SRI	TFR	SRI	TFR	SRI	TFR
N_0	5.9 d	4.8 e	2.4 d	1.4 e	0.10 d	0.06 e	147.4 e	237.8 d	59.4 f	67.8 e	2.5 f	2.8 e
N_{60}	11.6 b	6.8 c	6.6 b	2.5 d	0.27 b	0.10 d	290.2 c	338.4 b	164.9 c	124.8 d	6.9 c	5.2 d
N_{90}	12.7 a	7.3 c	8.7 a	4.2 c	0.36 a	0.17 c	318.5 b	363.9 a	218.2 a	207.8 b	9.1 a	8.7 b
N_{120}	12.9 a	7.3 c	8.9 a	4.4 c	0.37 a	0.18 c	324.3 b	364.8 a	221.6 a	220.5 a	9.2 a	9.2 a
Av.	10.8	6.5	6.6	3.1	0.28	0.13	275.1	326.2	166.0	155.2	6.9	6.5
Analysis of variance												
Cultivation practice (CP)		**		**		**		**		**		**
Nitrogen level (N)		**		**		**		**		**		**
CP × N		**		**		**		*		**		**

Mean values followed by different letters denote significant ($P<0.05$) difference between treatments by DMRT

[a] SRI refers to 1 plants hill^{-1} and 25 plants m^{-2}

[b] TFR to 3 plants hill^{-1} and 150 plants m^{-2}

* and **significant at $P<0.05$ and $P<0.01$ respectively

(Table 4), and this with an SRI plant population six times lower. As N application rates increased, total N uptake by rice plants under both SRI and TFR increased significantly. Agronomic N use efficiency (ANUE) ranged from 31.3 to 44.3 kg grain kg^{-1}N under SRI, and from 23.3 to 31.6 kg grain kg^{-1}N under TFR. ANUE with SRI was 34–40 % higher than in TFR plants (Table 4). Highest ANUE was found with the application rate of 90 kgN ha^{-1} under both SRI and TFR.

Partial factor productivity (PFP) from applied nitrogen was estimated to be 49 % higher with SRI management when compared to TFR. Under SRI, 64 kg grain was produced with the application of 1 kgN, whereas with TFR, only 43 kg grain resulted per kgN applied,

Table 4 Effects of cultivation practices and fertilizer N rates on N uptake, agronomic N use efficiency (ANUE), and partial factor productivity of applied N (PFP) in rice crop

N rate	N uptake (kgNha^{-1})		ANUE (kg grain kg^{-1}N)		PFP (kg grain kg^{-1}N)	
	SRI	TFR	SRI	TFR	SRI	TFR
N_0	27.4 g	24.2 h	–	–	–	–
N_{60}	71.2 d	38.6 f	32.6 b	23.3 c	71.2 a	45.9 c
N_{90}	98.3 b	64.3 e	44.3 a	31.6 b	70.1 a	46.6 c
N_{120}	102.5 a	76.8 c	31.3 b	25.1 c	50.6 b	36.4 d
Av	77.4	51.0	36.1	26.6	63.9	42.9
Analysis of variance						
Cultivation practice (CP)		**		**		**
Nitrogen level (N)		**		**		**
CP × N		**		**		**

Mean values followed by different letters denote significant ($P<0.05$) difference between treatments by DMRT

**significant at $P<0.01$

one-third less. PFP from applied N did not vary between 60 and 90 kgN ha^{-1} rates for either SRI or TFR. The interaction effect of cultivation systems and N application rates was significant for N uptake, ANUE and PFP, indicating that applied N fertilizer was already effective at lower rates under SRI than for TFR.

Under SRI the increased rates of exudation and quantities of exudates, as well as total uptake of nitrogen were achieved by a far lower number of plants than was present under TFR, which underscores the greater physiological efficiency of low plant densities.

Leaf-nitrogen, leaf-chlorophyll, and rate of photosynthesis measurements

Applied N fertilizer had direct effects on increasing leaf-N and leaf-chlorophyll contents. This is seen from the data comparing leaf N and chlorophyll contents as well as photosynthetic activity in the flag- and fourth leaves, both at the milk-grain (MG) stage and at the late-ripening (LR) stage 2 weeks later.

All three parameters were significantly higher in the leaves of rice plants grown under the SRI cultivation system as compared with TFR plant leaves during the reproductive stage of the crop (Table 5). SRI flag leaves had 17.6 and 30.1 % higher N-concentration at MG and LR stages, respectively, compared to TFR leaves. Similarly, fourth leaves of SRI plants contained 9.5 and 53.2 % higher N compared to TFR leaves at the MG and LR crop stages, respectively. As expected, the N concentration in the leaves decreased with ripening (from MG to LR stage); but importantly, the decrease was more rapid in TFR plants as compared with SRI plants: respectively, 20.1 % vs. 11.5 % in the flag leaf, and 48.7 % vs. 28.2 % in the fourth leaf.

Chlorophyll content generally decreases as rice leaves age and as crop growth advances from milk-grain stage to late-ripening stage. This is a well-established relationship, but the decrease was seen to be more rapid in TFR plants (24 % in flag leaf, and 33.3 % in fourth leaf) than in SRI plants (17.2 % in flag leaf, and 31.6 % in fourth leaf). With increase in N-doses, both leaf-N concentration and chlorophyll contents increased significantly up to 90 kgN ha^{-1} dose.

SRI flag leaves had higher photosynthesis rates during MG and LR stages, respectively, 45 % and 57 % higher than in TFR flag leaves. Similarly, the fourth leaves of SRI plants had photosynthesis rates

Table 5 Effects of cultivation practices and N levels on leaf N-concentration, leaf chlorophyll content, and photosynthetic rate of flag and fourth leaf measured at milk-grain (MG) and late-ripening (LR) stage of the rice crop

Treatments	Flag leaf						Fourth leaf					
	Leaf N-concentration (mgNg^{-1} leaf DW)		Leaf chlorophyll content (mgg^{-1} leaf FW)		Photosynthetic rate (μmolm^{-2}s^{-1})		Leaf N-concentration (mgNg^{-1} leaf DW)		Leaf chlorophyll content (mgg^{-1} leaf FW)		Photosynthetic rate (μmolm^{-2}s^{-1})	
	MG	LR	MG	LR	MG	LR	MG	LR	MG	LR	MG	LR
Cultivation practice (CP)												
SRI	38.1	33.7	2.9	2.4	17.4	13.5	30.1	21.6	1.9	1.3	11.9	10.0
TFR	32.4	25.9	2.5	1.9	12.0	8.6	27.5	14.1	1.2	0.8	9.3	6.0
Nitrogen level (N)												
N_0	28.0	23.6	1.7	1.2	11.0	7.5	25.1	12.6	1.1	0.7	9.3	6.2
N_{60}	35.1	30.8	2.6	2.1	14.0	10.7	28.4	18.4	1.6	1.0	10.5	7.8
N_{90}	38.6	32.1	3.2	2.7	16.4	12.6	30.1	20.0	1.7	1.2	10.9	8.7
N_{120}	39.4	32.8	3.3	2.7	17.5	13.3	31.5	20.4	1.8	1.2	11.7	9.3
Analysis of variance												
CP	*	*	*	**	**	**	*	*	**	**	**	*
N	*	*	*	**	**	**	*	*	**	**	**	*
CP × N	ns	ns	ns	**	**	**	ns	ns	**	**	**	*

ns not significant

* and **significant at $P<0.05$ and $P<0.01$ respectively

28.0 % higher at MG stage, and 66.7 % greater at LR stage than in TFR plants.

Overall, the major effects of crop management were recorded in leaves of SRI crop, which had higher N and chlorophyll contents, and a slower decrease of these contents with leaf-aging than under TFR. Consequently under SRI compared with TFR, there was greater and prolonged photosynthetic activity, due to a delay in leaf senescence. Both flag leaf and fourth leaf showed similar trends, but it is particularly important that the fourth leaf, an older leaf, continued to function physiologically for a prolonged period.

Interrelationships between leaf-N, leaf-chlorophyll, and photosynthetic activity

A close linear relationship was observed between the nitrogen and chlorophyll contents of leaves (Fig. 2a); and between the leaf nitrogen concentrations and the rate of photosynthesis (Fig. 2b). Highly significant correlations were recorded between these parameters under SRI as well as TFR. The test of homogeneity of regression coefficients showed that rate of increase in leaf chlorophyll content (*t*=11.3) and photosynthetic rate (*t*=13.3) due to an incremental change in leaf N-concentration are greater for SRI than for TFR.

Close linear relationships were also observed between the chlorophyll content and photosynthetic rate of leaves (Fig. 2c) under both cultivation practices. Here too, the slope of the regression line and homogeneity of regression coefficients (*t*=14.2) indicated that the rate of photosynthesis in SRI leaves changed more with changes in chlorophyll content than in TFR leaves. A change of 10 mgN concentration g^{-1} leaf dry weight corresponded to 4.8 and 3.2 μmolm^{-2}s^{-1} change in the photosynthesis rate in leaves of SRI and TFR plants,

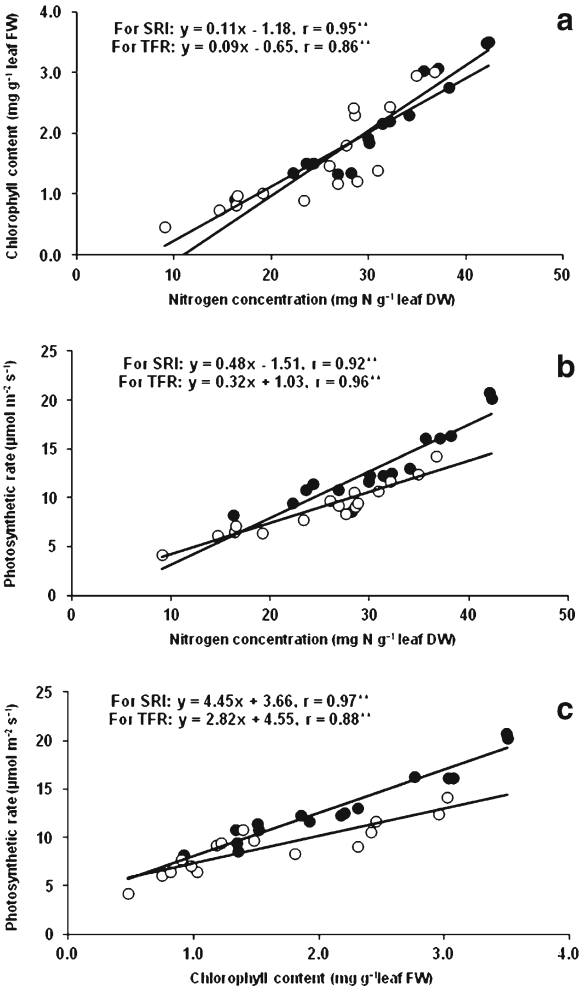

Fig. 2 Relationship between **a** nitrogen concentration and chlorophyll content, **b** nitrogen concentration and the rate of photosynthesis, and **c** chlorophyll content and the rate of photosynthesis. *Closed and open circles* represent the leaves of plants from plots under SRI and TFR management, respectively

respectively. Similarly, a unit change in chlorophyll content of leaves increased 4.45 and 2.82 units in the photosynthetic rate in SRI and TFR leaves, respectively. These results point to a significantly greater photosynthetic efficiency in SRI than in TFR plants.

Discussion

The kinds of physiological changes that are reported above are likely to have contributed to the yield improvements registered with SRI crop management in many countries (Kassam et al. 2011). Various individual practices associated with SRI management have already been identified as conducive for increasing rice yields under irrigated production systems, i.e., single seedlings hill^{-1} (San-oh et al. 2006), young seedlings (Menete et al. 2008; Pasuquin et al. 2008), and moderate wetting and drying (moist) soil conditions (Yang et al. 2004; Zhang et al. 2009; Yang and Zhang 2010; Wang et al. 2011). With SRI the transplanting of young seedlings results in a prolonged period (by nearly 2 weeks) for more root development and tillering. Moreover, with young seedlings the transplanting shock will be minimal, while greatly-reduced plant density (25 in SRI vs. 150 plants/m^2 in TFR) favours the development of a distinctly different plant phenotype. The present data show that this phenotype functions physiologically more efficiently, leading to substantially increased grain yields.

In the present study, SRI practices -on average across the different N-treatments enhanced grain yield by 49 %. This was a significant increase in comparison to conventionally grown flooded rice. However, in terms of straw production the difference between the two sets of cultural practices was not significant, which meant a notable increase in the Harvest Index for SRI plants. This indicates that SRI practices enhanced the translocation processes of assimilates from *source* to *sink*, leading to gains in yield that were supported and explained by the recorded physiological data.

SRI practices cause distinct changes in the plants' growing environment, thereby enhancing both root and tiller development. As a result, the overall efficiencies of N uptake and use, as well as of the photosynthetic process are raised, which had led to increased yields from the same rate of nitrogen applied (Fig. 1). In spite of the reduced number of plants per unit area, total N uptake, as well as in ANUE and PFP, along with exudation rates and quantities of exudates were significantly increased under SRI management. Consequently, the SRI practices produced 64 kg of grain in response to the provision of 1 kgN fertilizer, while only 43 kg of grain resulted from giving 1 kg of N fertilizer under conventional flooded cultivation.

The maximum yield under SRI was 6.31 tha^{-1} with 90 kgN ha^{-1}, while under TFR, the maximum yield was 31 % less, 4.37 tha^{-1} with 120 kgN ha^{-1}. Experiments in China employing nitrogen rates up to 240 kgN/ha also registered a similarly lower optimum N fertilisation rate around 80 kgN/ha under SRI (Zhao et al. 2009). This rate was two-thirds less than the 240 kgN/ha commonly used under flooded conditions with conventional crop management in China.

In spite of the far lower plant population under SRI and the lower quantity of roots per unit area, root functionality in terms of the amounts of exudates per unit area and the transportation rates from roots to stems were significantly superior as compared with TFR (Table 3). By avoiding hypoxic soil conditions from flooding during the vegetative stage, the efficiency of SRI root systems in taking up nutrients as well as moisture from the soil will be enhanced.

Additional observations on root morphology show that approximately 50 % of the roots under TFR had degenerated (as judged by their black color); by contrast, 80 % of SRI roots were whitish and functional at the same stage of crop development (data not shown). A similar result was reported by Chapagain and Yamaji (2010), who recorded that the average proportion of functional to decaying roots was higher (74:26) in SRI compared to conventionally flooded rice (46:54). The maintenance of root activity (see the xylem exudation rates in Table 3) at significantly higher levels under SRI therefore is likely to have contributed to an increase in the biomass productivity of individual hills (22.56 g hill^{-1} in SRI vs. 10.86 g hill^{-1} in TFR).

Together these features have translated into gains both in the number of grains and in heavier individual grains. Further evidence for the enhanced translocation process is provided by significant improvements in the performance of individual hills, both in terms of root growth and above-ground physiological performances. Thus, SRI plants had far more extensive root systems and enhanced xylem exudation rates, which Soejima et al. (1995) and Samejima et al. (2004) have presented earlier as a useful index of root activity.

The recorded yield responses are further explained by the data on leaf-N, leaf-chlorophyll, and photosynthetic rate all of which were significantly higher under SRI management than with TFR practices. With the ageing of plants and their leaves, these parameters normally decrease. However, the rate of decrease over time was more rapidly under TFR than under SRI. Under SRI, leaf senescence therefore is delayed and photosynthetic processes are prolonged. This was confirmed and illustrated by the steeper regression curves presented in Fig. 2. The prolonged and greater photosynthetic activity in SRI leaves will have contributed to larger panicles (more spikelets per panicle), better grain setting (higher percentage of filled grains), heavier individual grains (higher 1,000-grain weight), and ultimately higher grain yield.

As root system development and above-ground shoot growth are highly interdependent, the prolonged physiological activity of the leaves will also affect root growth and its functions through material cycling between roots and shoots (Wang et al. 2006). In rice plants, the main supply of carbohydrates for the roots is derived from the plants' lower leaves (Osaki et al. 1997). To maintain high levels of root activity, sufficient amounts of carbohydrates must be produced by the shoots and subsequently transported to the roots. However, the carbohydrate present in the shoots that is potentially available for the roots decreases during maturation, because of competition for carbohydrates from the panicles. In the present study, the increased photosynthetic rate of the lower leaves of SRI plants will have contributed to a greater transport of photosynthates towards the roots, thereby supporting and extending the roots' metabolic activities. Simultaneously, the extensive root systems of SRI plants might be responsible for an increased transport of cytokinins to the shoots as illustrated by the data on xylem exudates (Table 3), which might explain the delayed leaf senescence and increased leaf N concentration. The effects of cytokinins on the inhibition of leaf senescence and on the promotion of biomass productivity and grain yield have been clearly demonstrated in rice (Ookawa et al. 2004; San-oh et al. 2006; Soejima et al. 1995).

Alternate wetting and moderate drying soil water regimes, as followed in SRI practice, besides enhancing root development (Thakur et al. 2011; Yang et al. 2004; Zhang et al. 2009) also facilitate a host of other physiological processes. Among these are increases in root oxidation activities, in concentrations of cytokinin in roots and shoots, in leaf photosynthetic rates, as well as in the activities of key enzymes involved in sucrose-to-starch conversion in grains (Zhang et al. 2009). Moreover, profuse root systems will also likewise greatly enhance the opportunities for beneficial interactions / associations with soil micro-organisms as elaborated by Naher et al. (2009); a subject that so far has received limited attention from research.

Apart from better root growth and functioning, another factor responsible for decreased nitrogen loss and increased nitrogen efficiency under SRI might be that less water drains away and less stagnant water remains in the field. Wang et al. (2011) reported that compared to flood irrigation, shallow water depth with wetting and drying decreased vertical NH_4^+-N and total nitrogen leaching. TFR plants, on the other hand, were under continuously hypoxic conditions. This limited the ability of the roots to respire, thereby slowing down N-uptake and transport and slowing also the rate of metabolism and growth (Lin et al. 2006).

SRI practices have enhanced the uptake of nitrogen, thereby minimizing losses to the environment and providing economic benefits to farmers. Apart from more efficient utilization of N, SRI also permits farmers to economize on the use of increasingly scarce supplies of irrigation water. However, the effects of alternate wetting and drying method of irrigation in combination with greatly reduced plant densities as followed under SRI, and their effects on N-losses via processes of nitrification-denitrification deserve further investigation.

Conclusions

The results of this study indicated that under SRI management grain yields could be increased significantly, while at the same time greatly economizing on the use of N fertilizer than those raised in conventional flooded rice culture. These responses were attributed to a significantly better root development and a more efficient physiological functioning due to changes in the plants' morphological structure resulting from a modified crop management.

It should be emphasized, however, that the set of SRI practices will require adaptation / fine-tuning in response to local weather / climate and soil fertility conditions. Further adjustments according to the plant characteristics of different varieties and other aspects of rice production systems (e.g. timing of field operations) may likewise be needed. In terms of field testing this requires an understanding and appreciation of the many interactions between experimental as well as non-experimental factors that are involved in comparing different production systems (Stoop et al. 2009). Optimizing the number of plants m^{-2} and appropriate cultural practices, such as AWD water regimes and the use of organic manures, all expected to enhance root and shoot activity would lead to substantial increases in grain yield, as the present study has illustrated. Considerable reductions in N fertilizer rates conjoined with modifications in crop management practices can result in raising yields sustainably; simultaneously the crop water requirements from surface and sub-surface sources are reduced, as are the risks of groundwater pollution. These changes can bring significant environmental as well as economic benefits.

Acknowledgments The authors wish to thank Prof. Norman Uphoff, Senior Advisor for the SRI International Network and Resources Center (SRI-Rice), Cornell International Institute for Food, Agriculture and Development, Ithaca, NY, USA, for reviewing drafts of this manuscript and offering useful comments. We also deeply thank the anonymous reviewers for their very constructive comments.

References

Aparicio V, Costa JL, Zamora M (2008) Nitrate leaching assessment in a long-term experiment under supplementary irrigation in humid Argentina. Agric Water Manag 95:1361–1372

Barison N, Uphoff N (2011) Rice yield and its relation to root growth and nutrient-use efficiency in SRI and conventional cultivation: an evaluation Madagascar. Paddy Water Environ 9:65–78

Cassman KG, Harwood RR (1995) The nature of agricultural systems: food security and environmental balance. Food Policy 20:439–454

Cassman KG, Peng S, Olk DC, Ladha JK, Reichardt W, Dobermann A, Singh U (1998) Opportunities for increased nitrogen-use efficiency from improved resource management in irrigated rice systems. Field Crops Res 56:7–39

Chapagain T, Yamaji E (2010) The effects of irrigation method, age of seedling and spacing on crop performance, productivity and water-wise rice production in Japan. Paddy Water Environ 8:81–90

DRD (2006) Rice varieties released/notified during 1996–2005. Directorate of Rice Development, Department of Agriculture and Co-operation, Ministry of Agriculture, Govt. of India, Patna

Fageria NK (2007) Yield physiology of rice. J Plant Nutr 30:843–879

George T, Ladha JK, Buresh RJ (1993) Nitrate dynamics during the aerobic soil phase in lowland rice-based cropping systems. Soil Sci Soc Am J 57:1526–1532

Gomez KA, Gomez AA (1984) Statistical procedure for agricultural research. Wiley, New York, p 680

Hiscox JD, Israelstam R (1979) A method of extraction of chlorophyll from leaf tissue without maceration. Can J Bot 57:1332–1334

ICAR (2006) Handbook of agriculture, 5th edn. Indian Council of Agriculture Research, New Delhi

Jiang L, Dai T, Jiang D, Cao W, Gan X, Wei S (2004) Characterizing physiological N-use efficiency as influenced by nitrogen management in three rice cultivars. Field Crops Res 88:239–250

Ju XT, Xing GX, Chen XP, Zhang SL, Zhang LJ, Liu XJ, Cui ZL, Yin B, Christie P, Zhu ZL, Zhang FS (2009) Reducing environmental risk by improving N management in intensive Chinese agricultural systems. Proc Natl Acad Sci U S A 106:3041–3046

Kassam A, Stoop W, Uphoff N (2011) Review of SRI modifications in rice crop and water management and research issues for making further improvements in agricultural and water productivity. Paddy Water Environ 9:163–180

Lin X, Zhou W, Zhu D, Zhang Y (2005) Effect of SWD irrigation on photosynthesis and grain yield of rice (*Oryza sativa* L.). Field Crops Res 94:67–75

Lin X, Zhou W, Zhu D, Chen H, Zhang Y (2006) Nitrogen accumulation, remobilization and partitioning in rice (*Oryza sativa* L.) under an improved irrigation practice. Field Crops Res 96:448–454

Menete MZL, van Es HM, Brito RML, DeGloria SD, Famba S (2008) Evaluation of system of rice intensification (SRI) component practices and their synergies on salt-affected soils. Field Crops Res 109:34–44

Naher UA, Othman R, Shamsuddin ZHJ, Saud HM, Ismail MR (2009) Growth enhancement and root colonization of rice seedlings by *Rhizobium* and *Corynebacterium* spp. Int J Agric Biol 11:586–590

Ookawa T, Naruoka Y, Sayama A, Hirasawa T (2004) Cytokinin effects on ribulose-1, 5-bisphosphate carboxylase/oxygenase and nitrogen partitioning in rice during ripening. Crop Sci 44:2107–2115

Osaki M, Shinano T, Matsumoto M, Zheng T, Tadano T (1997) A root-shoot interaction hypothesis for high productivity of field crops. Soil Sci Plant Nutr 43:1079–1084

Pasuquin E, Lafarge T, Tubana B (2008) Transplanting young seedlings in irrigated rice fields: early and high tiller production enhanced grain yield. Field Crops Res 105:141–155

Peng SB, Buresh RJ, Huang JL, Zhong XH, Zou YB, Yang JC, Yang GH, Liu YY, Tang QY, Cui KH, Zhang FS, Doberman A (2010) Improving nitrogen fertilization in rice by site-specific nutrient management: a review. Agron Sustain Dev 30:649–656

Samejima H, Kondo M, Ito O, Nozoe T, Shinano T, Osaki M (2004) Root-shoot interaction as a limiting factor of biomass productivity in new tropical rice lines. Soil Sci Plant Nutr 50:545–554

San-oh Y, Mano Y, Ookawa T, Hirasawa T (2004) Comparison of dry matter production and associated characteristics between direct-sown and transplanted rice plants in a submerged paddy field and relationships to planting patterns. Field Crops Res 87:43–58

San-oh Y, Sugiyama T, Yoshita D, Ookawa T, Hirasawa T (2006) The effect of planting pattern on the rate of photosynthesis and related processes during ripening in rice plants. Field Crops Res 96:113–124

Satyanarayana A, Thiyagarajan TM, Uphoff N (2007) Opportunities for water saving with higher yield from the system of rice intensification. Irrig Sci 25:99–115

Shindo J, Okamoto K, Kawashima H (2006) Prediction of the environmental effects of excess nitrogen caused by increasing food demand with rapid economic growth in eastern Asian countries, 1961–2020. Ecol Model 193:703–720

Sinha SK, Talati J (2007) Productivity impacts of the system of rice intensification (SRI): a case study in West Bengal, India. Agric Water Manag 87:55–60

Soejima H, Sugiyama T, Ishihara K (1995) Changes in the chlorophyll contents of leaves and in levels of cytokinins in root exudates during ripening of rice cultivars Nipponbare and Akenohoshi. Plant Cell Physiol 36:1105–1114

Stoop WA (2011) The scientific case for system of rice intensification and its relevance for sustainable crop intensification. Int J Agric Sustain 9:443–455

Stoop WA, Uphoff N, Kassam A (2002) A review of agricultural research issue raised by the System of Rice Intensification (SRI) from Madagascar: opportunities for improving system for resource poor farmers. Agric Syst 71:249–274

Stoop WA, Adam A, Kassam A (2009) Comparing rice production systems: a challenge for agronomic research and for the dissemination of knowledge-intensive farming practices. Agric Water Manag 96:1491–1501

Thakur AK, Uphoff N, Antony E (2010a) An assessment of physiological effects of system of rice intensification (SRI) practices compared with recommended rice cultivation practices in India. Exp Agric 46:77–98

Thakur AK, Rath S, Roychowdhury S, Uphoff N (2010b) Comparative performance of rice with system of rice intensification (SRI) and conventional management using different plant spacings. J Agron Crop Sci 196:146–159

Thakur AK, Rath S, Patil DU, Kumar A (2011) Effects on rice plant morphology and physiology of water and associated management practices of the system of rice intensification and their implications for crop performance. Paddy Water Environ 9:13–24

Tian YH, Bin Y, Yang LZ, Yin SX, Zhu ZL (2007) Nitrogen runoff and leaching losses during rice-wheat rotations in Taihu lake region, china. Pedosphere 17:445–456

Tong C, Hall CAS, Wang H (2003) Land use change in rice, wheat and maize production in China (1961–1998). Agric Ecosyst Environ 95:523–536

Uphoff N, Randriamiharisoa R (2002) Reducing water use in irrigated rice production with the Madagascar system of rice intensification (SRI). In: Bouman BAM (ed) Water-wise rice production. International Rice Research Institute, Los Banos, pp 151–166

Wang H, Inukai Y, Yamauchi A (2006) Root development and nutrient uptake. Crit Rev Plant Sci 25:279–301

Wang X, Suo Y, Feng Y, Shohag MJI, Gao J, Zhang Q, Xie S, Lin X (2011) Recovery of ^{15}N-labeled urea and soil nitrogen dynamics as affected by irrigation management and nitrogen application rate in a double rice cropping system. Plant Soil 343:195–208

Xie JC (1998) Present situation and prospects for the world's fertilizer use. Plant Nutr Fert Sci 4:321–330

Yang J, Zhang J (2010) Crop management techniques to enhance harvest index in rice. J Exp Bot 61:3177–3189

Yang C, Yang L, Yang Y, Ouyang Z (2004) Rice root growth and nutrient uptake as influenced by organic manure in continuously and alternately flooded paddy soils. Agric Water Manag 70:67–81

Yang X, Shang Q, Wu P, Liu J, Shen Q, Guo S, Xiong Z (2010) Methane emissions from double rice agriculture under long-term fertilizing systems in Hunan, China. Agric Ecosyst Environ 137:308–316

Zhang H, Xue Y, Wang Z, Yang J, Zhang J (2009) An alternate wetting and moderate soil drying regime improves root and shoot growth in rice. Crop Sci 49:2246–2260

Zhao LM, Wu LH, Li YS, Lu XH, Zhu DF, Uphoff N (2009) Influence of the system of rice intensification on rice yield and nitrogen and water use efficiency with different N application rates. Exp Agric 45:275–286

Zhao LM, Wu LH, Li YS, Animesh S, Zhu DF, Uphoff N (2010) Comparisons of yield, water use efficiency, and soil microbial biomass as affected by the system of rice intensification. Commun Soil Sci Plant Anal 41:1–12

Zhu ZL, Chen DL (2002) Nitrogen fertilizer use in China-contributions to food production, impacts on the environment and best management strategies. Nutr Cycl Agroecosyst 63:117–127