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REVIEW PAPER

Crop management techniques to enhance harvest index in rice

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Abstract

A major challenge in rice (*Oryza sativa* L.) production is to enhance water use efficiency (*WUE*) and maintain or even increase grain yield. *WUE*, if defined as the biomass accumulation over water consumed, may be fairly constant for a given species in given climate. *WUE* can be enhanced by less irrigation. However, such enhancement is largely a trade-off against lower biomass production. If *WUE* is defined as the grain production per unit amount of water irrigated, it would be possible to increase *WUE* without compromising grain yield through the manipulation of harvest index. Harvest index has been shown to be a variable factor in crop production, and in many situations, it is closely associated with *WUE* and grain yield in cereals. Taking rice as an example, this paper discussed crop management techniques that can enhance harvest index. Several practices such as post-anthesis controlled soil drying, alternate wetting and moderate soil drying regimes during the whole growing season, and non-flooded straw mulching cultivation, could substantially enhance *WUE* and maintain or even increase grain yield of rice, mainly via improved canopy structure, source activity, sink strength, and enhanced remobilization of pre-stored carbon reserves from vegetative tissues to grains. All the work has proved that a proper crop management holds great promise to enhance harvest index and, consequently, achieve the dual goal of increasing grain production and saving water.

Key words: Alternate wetting and drying, controlled soil drying, harvest index, non-flooded mulching cultivation, rice, water use efficiency.

Introduction

Global agriculture in the 21st century faces two major challenges. Total food production needs to increase to feed a still-growing world population and this increase needs to be accomplished under increasing scarcity of water resources (Bouman, 2007). Rice (*Oryza sativa* L.) is one of the most important crops in the world and is the foremost staple food in Asia, providing 35–60% of the dietary calories consumed by nearly three billion people (Fageria, 2003). By the year 2025, it will be necessary to produce about 60% more rice than is currently being produced to meet the food needs of a growing world population (Fageria, 2007). Rice is also the greatest consumer of water among all crops and consumes about 80% of the total irrigated fresh water resources in Asia (Bouman and Tuong, 2001; Maclean *et al.*, 2002). Fresh water, however, is becoming increasingly scarce because of the global weather changes, population growth, increasing urban and industrial development, and the decreasing availability resulting from pollution and resource depletion (Belder *et al.*, 2005; Bouman, 2007).

Abbreviations: ABA, abscisic acid; AGP, ADP glucose pyrophosphorylase; AWD, alternate wetting and drying; CI, conventional irrigation; HI, harvest index; MD, moderate soil drying; NM, no mulching cultivation; NSC, non-structural carbohydrate; PM, plastic film mulching cultivation; ψ_{soil}, soil water potential; SBE, starch branching enzyme; SD, severe soil drying; SM, straw mulching cultivation; SRI, system of rice intensification; StS, starch synthase; TF, traditional flooding; WMD, alternate wetting and moderate soil drying; WSD, alternate wetting and severe soil drying; WUE, water use efficiency.

The challenge to produce more food under increasing water scarcity has led to the notion that crop water productivity (economic yield over the amount of water consumed) needs to increase (Kijne *et al.*, 2002, 2003). However, how to increase water productivity is still being debated (Kijne *et al.*, 2003; Bouman, 2007). In cereals and at the crop level it is proposed that water productivity can be defined as the ratio of grain yield over amount of water transpired (WP_T) (Bouman, 2007). As the grain yield is the product of harvest index (*HI*) and total above-ground biomass, the WP_T in rice could be expressed as

$$WP_T = Y/T = HI \times B/T$$

where WP_T is the grain yield per unit water transpired (kg grain kg^{-1} water), Y is the grain yield (kg), T is the amount of water transpired (kg), *HI* is the harvest index (kg kg^{-1}), and B is the above-ground biomass (kg).

The fraction *B*/*T* is sometimes known as transpiration efficiency. The *HI* is the grain yield over total above-ground biomass. The grain yield and water productivity would be improved by either an increase in transpiration efficiency or an increase in *HI*. However, the ratio of biomass production over transpiration (*B*/*T*) has been shown to be fairly constant for a given species in a given climate (Ehlers and Goss, 2003), and can be selected for in plant breeding (Bouman, 2007). Plant biomass production is linearly coupled with the amount of water transpired, and a higher water use efficiency (*WUE*) is often a trade-off against lower biomass production (Zhang and Yang, 2004). In agriculture, many ways of conserving water have been investigated and techniques such as alternate partial root-zone irrigation, deficit irrigation, and drip irrigation, have shown that *WUE* can be enhanced (Graterol *et al.*, 1993; Zhang *et al.*, 1998; Kang *et al.*, 2000; Tabbal *et al.*, 2002; Li *et al.*, 2010). In general, these techniques are a trade-off: a lower yield for a higher *WUE* (Zhang and Yang, 2004).

On the other hand, *HI* has been shown to be a variable factor in crop production (Table 1). Variations in harvest index within a crop are mainly attributed to differences in crop management (Yang *et al.*, 2000; Guo *et al.*, 2004; Kemanian *et al.*, 2007; D'Andrea *et al.*, 2008; Peltonen-Sainio *et al.*, 2008). A water and/or nitrogen management system that could increase growth rate during grain growth and/or enhance the remobilization of assimilates from vegetative tissues to grains during the grain-filling period usually leads to a higher *HI* within a crop (Xue *et al.*, 2006; Zhang *et al.*, 2008*b*; Bueno and Lafarge, 2009; Fletcher and Jamieson, 2009; Ju *et al.*, 2009). In many situations, *HI* is closely associated with *WUE* and grain yield in wheat (*Triticum aestivum* L.) and rice (Ehdaie and Waines, 1993; Yang *et al.*, 2000, 2001*b*, 2002*b*, 2003*a*, 2007; Zhang *et al.*, 2008*a*, *c*). The question arises as to whether it is possible to achieve the dual goal of increasing food production and saving water through the manipulation of *HI* in crop production. Research in rice related to this question is the focus of this paper.

Table 1. Variations of harvest index in crop production

The values are from four, five, three, and five growing seasons, respectively, for rice, wheat, barley, and maize.

Crop	Harvest index (kg kg^{-1})	Source
Rice (*Oryza sativa* L.)	0.17 – 0.56	Bueno and Lafarge, 2009; Ju *et al.*, 2009
Wheat (*Triticum aestivum* L.)	0.31 – 0.53	Yang *et al.*, 2000; Zhang *et al.*, 2008*b*
Barley (*Hordeum vulgare* L.)	0.30 – 0.62	Kemanian *et al.*, 2007; Peltonen-Sainio *et al.*, 2008
Maize (*Zea mays* L.)	0.25 – 0.58	Guo *et al.*, 2004; D'Andrea *et al.*, 2008

The dominant system of paddy rice production in Asia is transplanting or direct-seeding in a field that is kept continuously flooded with 5–10 cm water throughout the growing season (Bouman and Tuong, 2001). To reduce water use in irrigated rice, water-saving regimes have been introduced such as an aerobic rice system (Bouman *et al.*, 2005; Singh *et al.*, 2008; Lampayan *et al.*, 2010), a system of rice intensification (SRI) (Uphoff and Randriamiharisoa, 2002), alternate wetting and drying (AWD) irrigation (Bouman and Tuong, 2001; Belder *et al.*, 2004 2005, 2007; Zhang *et al.*, 2008*a*), controlled soil drying during grain filling (Yang *et al.*, 2002*b*, 2003*a*; Yang and Zhang, 2006), and non-flooded mulching cultivation (Liu *et al.*, 2005; Tao *et al.*, 2006; Xu *et al.*, 2007; Zhang *et al.*, 2008*c*, 2009*b*). In the aerobic rice system, rice is grown under non-flooded, non-puddled, and non-saturated soil conditions (Bouman, 2001). Although aerobic rice needs less water at the field level than conventional lowland rice, it could not replace lowland rice in most of the rice-growing areas due to its lower grain yield and poorer taste and eating qualities (Zhang and Yang, 2004; Lampayan *et al.*, 2010). It is suggested that the aerobic rice system could be an option for farmers in rainfed lowlands with a limited or an erratic distribution of rainfall (Bouman *et al.*, 2005; Altin *et al.*, 2006). The SRI is characterized by a set of basic management practices including transplanting young seedlings with 2–4 phyllochrons, planting a single seeding per hill, wide space planting, daily or intermittent irrigation before panicle initiation, hand or mechanical weeding, and applying nutrients to soil preferably in an organic form (Stoop *et al.*, 2002; Uphoff and Randriamiharisoa, 2002). Uphoff and Randriamiharisoa (2002) claimed that double or triple yields over those of conventional rice cultures were attained by SRI in Madagascar. Rafaralahy (2002) reported yields over 15 t ha^{-1} or even above 20 t ha^{-1} by SRI in the highlands of Madagascar. Criticisms of these reports on SRI were made by Sheehy *et al.* (2004), Dobermann (2004), and Sinclair and Cassman (2004) for the extraordinary high yield, effectiveness of SRI practices, experimental procedures, and publications. The intermittent irrigation of SRI would reduce water use in rice, but the intensive labour requirement and the high level of skill needed are likely to limit the adoption of SRI in rice production (Horie *et al.*, 2005). There are reports that the practices of controlled soil drying during grain filling, alternate wetting and moderate soil drying, and non-flooded straw mulching cultivation could not only increase *WUE*, but also maintain or even increase grain yield (Yang *et al.*, 2002*b*, 2003*a*, 2006; Zhang *et al.*, 2008*a*, *c*, 2009*a*, *b*). It would be interesting to know if and how such practices manipulate *HI* and, consequently, increase *WUE* and grain yield. Therefore the discussions in this review cover: (i) post-anthesis controlled soil drying improves the remobilization of carbon reserves and grain filling; (ii) a moderate wetting drying regime reduces redundant vegetative growth and increases grain yield; and (iii) non-flooded wheat straw mulching cultivation maintains a high grain yield and increases *WUE*.

To investigate the performances of *HI*, grain yield, and *WUE* under these crop management systems, three experiments of post-anthesis soil drying, AWD, and non-flooded mulching cultivation were conducted at the research farm of Yangzhou University, Jiangsu Province, China (32°30′ N, 119°25′ E, 21 m altitude) during the rice growing season (May–October). Two high-yielding rice cultivars currently used in local production, Zhendao 88 (*japonica*) and Liangyoupeijiu (LYPJ, *indica* hybrid), were grown in the field. Each experiment was repeated for three or five growing seasons. The methodologies applied in the experiments were described previously (Yang *et al.*, 2001*c*, 2003*a*; Zhang *et al.*, 2008*c*, 2009*a*). Briefly, in the experiment of post-anthesis soil drying, two levels of nitrogen treatments were applied. Half the plots were top-dressed with either 15 g N m^{-2} (normal amount, NN) or 30 g N m^{-2} (high amount, HN) as urea. From 9 d post anthesis to maturity, three levels of soil water potential (ψ_{soil}) were imposed on the plants of both NN and HN treatments. The well-watered (WW) treatment kept a water depth of 1–2 cm ($\psi_{soil}=0$) in the field by manually applying water every day. The moderate soil drying (MD) treatment maintained ψ_{soil} at –25 kilopascal (kPa), and the severe soil drying (SD) treatment maintained ψ_{soil} at –50 kPa. The ψ_{soil} in the MD and SD treatments was monitored with tension meters buried in the 15–20 cm soil depth. Tension meter readings were recorded twice a day at 10.00 h and 16.00 h. When the reading dropped to the designed value, 0.23 cm and 0.12 cm of irrigation per plot was added manually to the MD and SD treatments, respectively (Yang *et al.*, 2003*a*). A rain shelter consisting of a steel-frame covered with plastic sheet was used in each block to protect the plot during rains. Grains that developed from spikelets of 15 panicles were sampled at 4 d intervals from anthesis to maturity, dried at 70 °C to constant weight for 72 h, and weighed. The grain-filling process was fitted by the Richards' growth equation (Richards, 1959) as described by Zhu *et al.* (1988):

$$W = A/\left(1 + \mathrm{B}e^{-\mathrm{kt}}\right)^{1/\mathrm{N}}$$

where *W* is the grain weight (mg), *A* is the final grain weight (mg), *t* is the time after anthesis (d), and B, k, and N are coefficients determined by regression. The active grain-filling period was defined as that when *W* was 5% (t1) to 95% (t2) of *A*. The average grain-filling rate during this period was calculated from t1 to t2.

In the AWD experiment, three irrigation regimes including alternate wetting and moderate soil drying (WMD), alternate wetting and severe soil drying (WSD), and conventional irrigation (CI), were applied from 10 d after transplanting to maturity. In the WMD regime, fields were not irrigated until ψ_{soil} reached –15 kPa at 15–20 cm depth. While in the WSD regime, water was withheld until ψ_{soil} reached –30 kPa at 15–20 cm depth. The CI regime was maintained as plots with a continuous flood with a water depth of 2–3 cm until one week before harvest, which are the recommended farming practices.

The experiment of non-flooded mulching cultivation comprised four treatments: traditional flooding (TF) as control, and plastic film mulching (PM), wheat straw mulching (SM), and no mulching (NM) as non-flooded cultivation systems. The TF treatment was continuously flooded with 2–3 cm water level over the plot until one week before rice harvest in line with traditional farming practices. Plastic film, 0.007 mm thick and 1.8 m wide, was used to cover the soil in the PM treatment. Wheat straw harvested from the same field in the wheat season was used to cover the soil in the SM treatment. In all the non-flooded treatments, plots were flooded only for 6–8 d after transplanting for the re-greening of seedlings. After that, the amount of water applied to PM, SM, and NM plots was controlled at 380–440 m^3 ha^{-1} at each stage of mid-tillering, booting, flowering, and early grain-filling, respectively, when ψ_{soil} had reached –25 kPa at 15–20 cm depth and if there was no precipitation at this time.

Post-anthesis controlled soil drying improves remobilization of carbon reserves and grain filling

Grain filling is the final stage of growth in cereals when fertilized ovaries develop into caryopses and depends on carbon from two resources: current assimilates and assimilates redistributed from reserve pools in vegetative tissues either pre- or post-anthesis (Kobata *et al.*, 1992; Schnyder, 1993; Samonte *et al.*, 2001). The contribution of reserved assimilates in culms and leaf sheaths of rice plants is estimated at 10–40% of the final yield, depending on the cultivar and the environmental conditions (Gebbing and Schnyder, 1999; Takai *et al.*, 2005). Remobilization of reserves to the grain is critical for grain yield if the plants are subjected to water stress or if the yield potential is largely based on the high biomass accumulation (Yoshida, 1972; Ehdaie and Waines, 1996; Asseng and van Herwaarden, 2003; Plaut *et al.*, 2004).

Remobilization and transfer of the stored assimilates in vegetative tissues to the grain in monocarpic plants such as rice and wheat require the initiation of whole plant senescence (Gan and Amasino, 1997; Noodén *et al.*, 1997). Delayed whole plant senescence (i.e. plants remain green when grains are due to ripen) results in much non-structural carbohydrate (NSC) left in the straw and leads to a low *HI*. Slow grain-filling can often be associated with the delay of whole plant senescence (Zhu *et al.*, 1997; Mi *et al.*, 2002; Gong *et al.*, 2005). In China, there are currently at least three common cases where plant whole senescence is unfavourably delayed: the over-use of nitrogen fertilizers (Buresh *et al.*, 2004; Peng *et al.*, 2006), adoption of lodging-resistant cultivars that stay 'green' for too long (Yuan, 1994, 1998; Zhu *et al.*, 1997), and the introduction of hybrid rice which is too vigorous (Yang *et al.*, 2002*a*; Yuan, 2003). Their senescence is defined as unfavourably delayed because the gain from the extended grain-filling period is less than the loss due to slow grain filling and unused assimilates left in the straw (Yang and Zhang, 2006).

Usually, water stress at grain-filling time induces early senescence and shortens the grain-filling period but increases the remobilization of assimilates from the straw to grains (Kobata and Takami, 1981; Nicolas *et al.*, 1985; Palta *et al.*, 1994; Asseng and van Herwaarden, 2003; Plaut *et al.*, 2004). Can the advantage of soil drying-induced whole plant senescence and better carbon remobilization be taken to improve grain yield in situations where unfavourably delayed senescence is a problem? It has been found that a controlled soil drying or a moderate soil drying, namely plants can rehydrate overnight (Fig. 1A, B) and photosynthesis is not severely inhibited (Fig. 1C, D), imposed at mid and late grain-filling stages (from 9 d post-anthesis until maturity) can greatly enhance assimilate remobilization from vegetative tissues to grains and also accelerate the grain-filling rate (Table 2). Such a controlled soil drying does not necessarily reduce grain yield even when plants are grown under normal nitrogen conditions. Furthermore, in cases where plant senescence is unfavourably delayed, such as by the heavy use of nitrogen, the gain from enhanced remobilization and accelerated grain-filling rate can outweigh the loss of reduced photosynthesis and a shortened grain-filling period, leading to an increased grain yield and higher *HI* and *WUE* (Table 3).

The mechanism by which post-anthesis-controlled soil drying enhances the utilization of pre-stored assimilates is not fully understood. Many processes are likely to be involved, including the hydrolysis of stored carbohydrate, phloem loading, long-distance translocation, and phloem unloading into the kernels. It was observed that, in rice stems, both α- and β-amylase activities were enhanced by the soil drying treatment, with the former enhanced more than the latter, and significantly correlated with the concentrations of soluble sugars in the stems. The other two possible starch-breaking enzymes, α-glocosidase and starch phosphorylase, showed no significant differences in the activities between well-watered and soil drying treatments. Soil drying also increased the sucrose-phosphate synthase activity that is responsible for sucrose production (Yang *et al.*, 2001*a*). In grains, the activities of four enzymes involved in sucrose-to-starch conversion: sucrose synthase, ADP glucose pyrophosphorylase (AGP), starch synthase (StS), and starch branching enzyme (SBE), were significantly enhanced by soil drying, and positively correlated with the starch accumulation rate in grains (Yang *et al.*, 2003*b*). These results suggest that, in the source (stems), enhanced activities of α-amylase and sucrose-phosphate synthase contribute to the fast hydrolysis of starch and

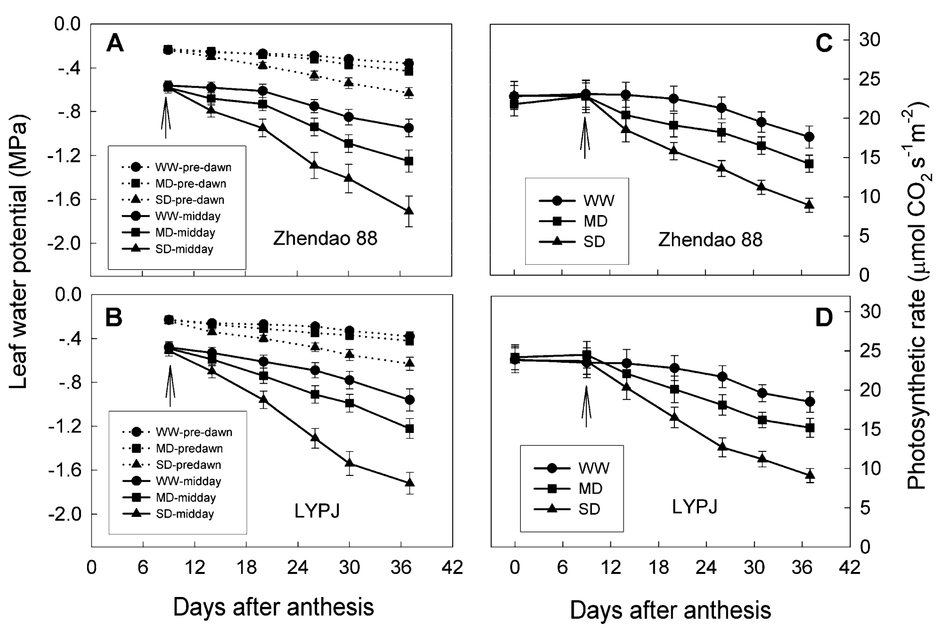

Fig. 1. Leaf water potential (A, B) and photosynthetic rate (C, D) of the flag leaf of rice. The *japonica* cultivar Zhendao 88 (A, C) and *indica* hybrid Liangyoupeijiu (LYPJ) (B, D) were field grown. WW, MD, and SD are well watered [soil water potential (ψ_{soil})=0 kPa, moderate soil drying (ψ_{soil}= –25 kPa), and severe soil drying (ψ_{soil}= –50 kPa) treatments during grain filling. Measurements of leaf water potentials were made on the flag leaves at pre-dawn (06.00 h) and at midday (11.30 h). The photosynthetic rates were measured during 09.00–11.00 h. Arrows indicate the start of soil drying treatments. Values are averages across the three years (2005–2007). Vertical bars represent ±SE of the mean (n=12) where these exceed the size of the symbol.

Table 2. Remobilization of pre-stored assimilates in straws and grain filling rate of rice subjected to various nitrogen and soil moisture treatments

Both cultivars Zhendao 88 (*japonica*) and Liangyoupeijiu (LYPJ, *indica* hybrid) were field grown. WW, MD, and SD are well-watered, moderate soil drying, and severe soil drying treatments during grain filling. NN and HN indicate normal and high amounts of nitrogen application. Values of remobilized C reserve and contribution to grain are calculated according to the following formulas: remobilized C reserve (%) =[non-structural carbohydrate (NSC) in straws at heading time–NSC in straws at maturity]/NSC in straws at heading time×100; contributed to grain (%)=(NSC in straws at heading time–NSC in straws at maturity)/grain yield×100. Active grain-filling period and grain-filling rate were calculated according to the Richards equation (Richards, 1959). Values are averages across the three years (2005–2007). Letters after the values indicate the least significant difference (LSD) at the P=0.05 level within the same column and the same cultivar.

Cultivar	Treatment	Remobilized C reserve (%)	Contribution to grain (%)	Total dry matter (g m^{-2})	Active grain-filling period (d)	Grain-filling rate (mg d^{-1} $grain^{-1}$)
Zhendao 88	WW-NN	28.08 d	8.78 e	1857 a	23 b	1.02 d
	WW-HN	7.72 e	2.62 f	1867 a	27 a	0.84 e
	MD-NN	66.17 b	21.14 c	1684 b	18 d	1.31 b
	MD-HN	52.94 c	16.07 d	1828 a	21 c	1.17 c
	SD-NN	74.81 a	28.61 a	1358 d	13 f	1.65 a
	SD-HN	68.66 b	24.43 b	1506 c	16 e	1.38 b
LYPJ	WW-NN	11.89 d	3.89 e	1998 ab	26 b	0.88 d
	WW-HN	2.96 e	1.05 f	2069 a	32 a	0.69 e
	MD-NN	59.11 b	18.34 c	1914 b	20 d	1.17 b
	MD-HN	49.83 c	15.27 d	1991 ab	24 c	0.99 c
	SD-NN	66.78 a	24.55 a	1572 d	17 e	1.28 a
	SD-HN	60.96 b	21.37 b	1735 c	19 d	1.16 b
$LSD_{0.05}$		5.31	2.45	72	1	0.11

Table 3. Grain yield, harvest index, and water use efficiency (*WUE*) for irrigation of rice subjected to various nitrogen and soil moisture treatments

Both cultivars Zhendao 88 (*japonica*) and Liangyoupeijiu (LYPJ, *indica* hybrid) were field grown. WW, MD, and SD are well-watered, moderate soil drying, and severe soil drying treatments during grain filling. NN and HN indicate normal and high amounts of nitrogen application. Values are averages across the three years (2005–2007). Letters after the values indicate least significant difference (LSD) at the P=0.05 level within the same column and the same cultivar.

Cultivar	Treatment	Total number of spikelets ($\times 10^3$ m^{-2})	Filled grain (%)	Grain weight (mg $grain^{-1}$)	Grain yield (g m^{-2})	Harvest index (kg kg^{-1})	*WUE* (kg grain m^{-3})
Zhendao 88	WW-NN	38.23 a	85.59 ab	26.1 b	854 b	0.46 c	1.12 c
	WW-HN	38.31 a	83.51 b	25.1 c	803 c	0.43 d	0.98 d
	MD-NN	38.45 a	83.90 b	26.1 b	842 b	0.50 ab	1.32 b
	MD-HN	38.28 a	86.05 a	27.2 a	896 a	0.49 b	1.31 b
	SD-NN	38.04 a	77.98 d	23.8 d	706 e	0.52 a	1.41 a
	SD-HN	38.19 a	80.48 c	24.5 c	753 d	0.50 ab	1.39 a
LYPJ	WW-NN	47.79 a	72.41 b	25.4 b	879 b	0.44 b	1.11 c
	WW-HN	47.65 a	69.12 c	24.5 c	807 cd	0.39 c	0.95 d
	MD-NN	47.54 a	76.18 a	25.9 ab	938 a	0.49 a	1.36 ab
	MD-HN	47.86 a	75.66 a	26.4 a	956 a	0.48 a	1.33 b
	SD-NN	47.44 a	68.75 c	24.1 c	786 d	0.50 a	1.40 a
	SD-HN	47.59 a	71.44 b	24.5 c	833 c	0.4 a	1.39 a
$LSD_{0.05}$		1.85	2.09	0.5	38	0.02	0.04

increased carbon remobilization, and in the sink side (grains), an increased grain-filling rate is mainly attributed to the enhanced sink activity by regulating key enzymes involved in sucrose-to-starch conversion, when subjected to a mild soil drying during the grain-filling period.

Both abscisic acid (ABA) and cytokinins are generally believed to be two major regulators of plant senescence (Biswas and Choudhuri, 1980; Noodén, 1988; Noodén *et al.*, 1997; Haberer and Kieber, 2002). However, their regulatory roles in the remobilization of carbon reserves are not clear. The work of Yang *et al.* (2003*c*, 2004) on rice and wheat showed that the soil drying treatments substantially increased ABA accumulation (concentration) in the leaves and stems or root exudates, and markedly reduced cytokinins [zeatin (Z)+zeatin riboside (ZR)] in the leaves. Elevated ABA levels in the stems or root exudates were associated with the partitioning of pre-feed ^{14}C in the grains under soil-drying treatments. ABA in both the leaves and stems, but not cytokinins, was significantly and positively correlated with the remobilization of pre-stored carbon, and such remobilization was enhanced by exogenous ABA, suggesting that enhanced remobilization by soil drying during grain filling can be attributed, at least partly, to an elevated ABA concentration in the plant.

A moderate wetting drying regime reduces redundant vegetative growth and increases grain yield

Sufficient water supply under the irrigated lowland rice system often leads to excessive vegetative growth which may result in less root activity, unhealthy canopy structure, and Lower *HI* (Li, 2001, Zhang and Yang, 2004). To reduce water use in irrigated rice, an alternate wetting and drying (AWD) irrigation system has been developed and is being adopted in countries of East Asia such as Bangladesh, India, Vietnam, and China (Belder *et al.*, 2004; Bouman, 2007, Zhang *et al.*, 2009*a*). In AWD, irrigation is applied a few days after water has disappeared from the surface so that periods of soil submergence alternate with periods of non-submergence during the whole growing season (Belder *et al.*, 2007). In studies on AWD irrigation, grain yield of rice was increased (Li, 2001; Tuong *et al.*, 2005; Yang *et al.*, 2007; Zhang *et al.*, 2008*a*, 2009*a*) but reduced in others (Mishra *et al.*, 1990; Tabbal *et al.*, 2002; Belder *et al.*, 2004) when compared with continuously submerged conditions. The discrepancies between the studies are probably attributed to the variations in soil hydrological conditions and the timing of the irrigation method applied (Belder *et al.*, 2004). It has been shown that an alternate wetting and moderate soil drying (WMD) regime could significantly increase both grain yield and *WUE*, and an alternate wetting and severe soil drying (WSD) regime increased *WUE*, but markedly reduced grain yield when compared with the conventional irrigation (CI) (Table 4). Increase in grain yield and *WUE* under the WMD regime could be attributed to several reasons:

First, the WMD regime reduced redundant vegetative growth and improved canopy structure (Table 5). Compared with the CI regime, the WMD regime reduced the maximum number of tillers by 21–23% and total leaf area by 14%, but the number of productive tillers and effective leaf area (leaf area of productive tillers) showed no significant difference between the two regimes (Table 5). As a result, the WMD regime significantly increased the percentage of productive tillers and the percentage of effective leaf area. The improved canopy quality would reduce the water used in the production of unproductive tillers and transpiration from redundant leaf area. Furthermore, the WMD regime significantly reduced the leaf angle of the top three leaves at heading time (Table 5). The improved leaf architecture would allow more radiations to penetrate the canopy, which is very important to maintain a healthy canopy during grain filling (Fageria, 2007). Although the WSD regime also reduced redundant vegetative growth and improved leaf architecture, it significantly decreased the number of productive tillers and the effective leaf area (Table 5), which may contribute to the reduction in biomass and, consequently, in grain yield.

Second, the WMD regime enhanced root and shoot activities. It was observed that the WMD regime enhanced root oxidation activity, either during the soil drying period or at the time when plants were re-watered (Fig. 2A, B), and the enhancement was more during the re-watering time. The photosynthetic rate of leaves under the WMD regime was not significantly reduced during the soil drying period, but it was significantly increased when the plant was re-watered (Fig. 2C, D). In contrast to the WMD, the WSD regime reduced the root oxidation activity and leaf photosynthetic rate, especially during the soil drying period (Fig. 2A–D). It is little understood whether the changes in photosynthetic rate are due to changes in leaf water relations, or whether there is a role for root-sourced chemical signals that alter in response to AWD. Zhang *et al.* (2009*a*) observed that changes in leaf photosynthetic rate were closely associated

Table 4. Grain yield and water use efficiency (*WUE*) for irrigation of rice under various irrigation regimes

Both cultivars Zhendao 88 (*japonica*) and Liangyoupeijiu (LYPJ, *indica* hybrid) were field grown. CI, WMD, and WSD indicate conventional irrigation, alternate wetting and moderate soil drying, and alternate wetting and severe soil drying during the rice growing season. Values are averages across the three years (2006–2008). Letters after the values indicate least significant difference (LSD) at the P=0.05 level within the same column and the same cultivar.

Cultivar	Treatment	Number of panicles (m^{-2})	Number of spikelets per panicle	Filled grains (%)	Grain weight (mg $grain^{-1}$)	Grain yield (g m^{-2})	*WUE* (kg grain m^{-3})
Zhendao 88	CI	322 a	114 a	85.6 b	26.2 b	825 b	0.91 c
	WMD	319 a	116 a	90.5 a	27.2 a	908 a	1.39 a
	WSD	246 b	106 b	80.4 c	25.1 c	526 c	1.15 b
LYPJ	CI	256 a	196 a	78.6 b	25.3 b	997 b	1.01 c
	WMD	251 a	192 a	84.3 a	26.2 a	1065 a	1.51 a
	WSD	202 b	181 b	73.7 c	24.1 c	649 c	1.29 b
$LSD_{0.05}$		37	6	3.4	0.6	42	0.06

Table 5. Maximum number of tillers, the number of productive tillers, the percentage of productive tillers, total leaf area index (*LAI*), effective *LAI*, percentage of effective *LAI*, and mean leaf angles of the top three leaves of rice under various irrigation regimes

Both cultivars Zhendao 88 (*japonica*) and Liangyoupeijiu (LYPJ, *indica* hybrid) were field grown. CI, WMD, and WSD indicate conventional irrigation, alternate wetting and moderate soil drying, and alternate wetting and severe soil drying during the rice growing season. The maximum number of tillers was measured at the joining stage, and the number of productive tillers, total *LAI*, effective *LAI* (*LAI* of productive tillers), and mean leaf angles of the top three leaves were determined at the full heading time (95% panicles headed). The percentage of productive tillers was defined as the number of productive tillers as a percentage of the maximum number of tillers. The percentage of effective *LAI* was defined as the effective *LAI* as a percentage of total *LAI*. The leaf angle was defined as an angle between the leaf and its stem. Values are averages across the three years (2006–2008). Letters after the values indicate least significant difference (LSD) at the P=0.05 level within the same column and the same cultivar.

Cultivars	Treatment	Maximum number of tillers m^{-2}	Productive tillers		Total *LAI*	Effective leaf area		Leaf angles (°)
			(Number m^{-2})	(%)		(*LAI*)	(%)	
Zhendao 88	CI	450 a	302 a	67 c	8.4 a	6.4 a	76 b	23.5 a
	WMD	345 b	297 a	86 a	7.2 b	6.3 a	88 a	20.2 b
	WSD	276 c	224 b	81 b	5.1 c	4.5 b	89 a	19.8 b
LYPJ	CI	334 a	237 a	71 c	7.8 a	5.6 a	72 b	24.2 a
	WMD	268 b	235 a	88 a	6.7 b	5.8 a	87 a	21.3 b
	WSD	224 c	184 b	82 b	4.8 c	4.1 b	86 a	20.8 b
$LSD_{0.05}$		32	16	4	0.5	0.3	2	1.1

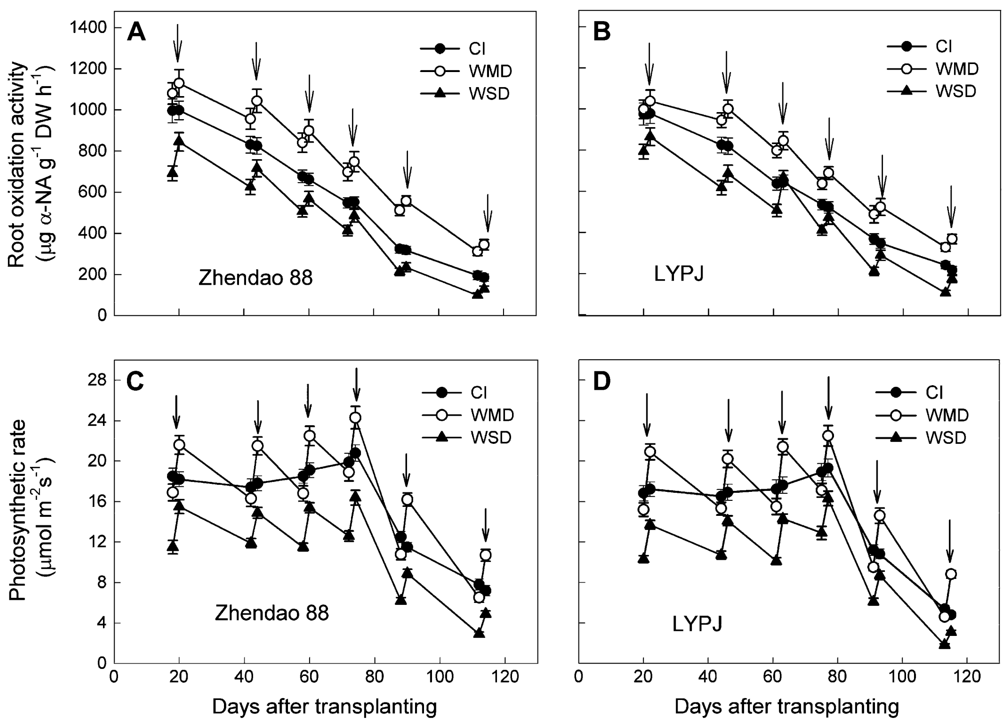

Fig. 2. Root oxidation activity (A, B) and leaf photosynthetic rate (C, D) of rice. The *japonica* cultivar Zhendao 88 (A, C) and *indica* hybrid Liangyoupeijiu (LYPJ) (B, D) were field grown. CI, WMD, and WSD indicate conventional irrigation, alternate wetting and moderate soil drying, and alternate wetting and severe soil drying during the rice growing season. The photosynthetic rate was measured on the upper surface of the top fully expanded leaves at 09.00–11.00 h. Measurements of both root oxidation activity and photosynthetic rate were made when soil water potentials were –15 kPa in WMD and –30 kPa in WSD and when plants were rewatered (indicated by arrows). Values are averages across the three years (2006–2008). Vertical bars represent ±SE of the mean (n=12) where these exceed the size of the symbol.

with changes in Z+ZR concentrations in roots under WMD and WSD regimes, implying that root-derived cytokinins may play a role in regulating leaf photosynthesis under the AWD system.

It was also observed that under the WMD regime, the activities of three key enzymes involved in starch synthesis, AGP, StS, and SBE, in grains during the grain-filling period could be maintained or increased during soil drying, and were markedly enhanced when plants were re-watered (Table 6). The increased sink strength through enhancement in the activities of these enzymes under the WMD regime may contribute to a greater percentage of filling grains and a higher grain weight, and, consequently, to a higher grain yield. On the other hand, the reduction in grain yield under the WSD regime may be attributed to the reduced root and shoot activities and sink strength (Fig. 2; Table 6).

Third, the WMD regime increased pre-stored carbon remobilization and *HI*. Biomasses showed no significant difference between CI and WMD regimes (Table 7). However, the WMD regime significantly facilitated the reallocation of pre-anthesis assimilates from straws to grains. From anthesis to maturity, the remobilized C reserves from vegetative tissues for plants under the WMD regime was as 2.5–3.0-fold that of plants under the CI regime (Table 7). The contribution of remobilized C reserves to the grain for plants under the WMD regime was increased by 10.0–12.9% when compared with that under the CI regime. The enhanced remobilization by the WMD regime led to a higher *HI* (Table 7). Although the WSD regime significantly increased pre-stored carbon remobilization and *HI*, it markedly reduced biomass production (Table 7). The loss from biomass production could not compensate the gain from the partitioning or remobilization of assimilates, leading to the reduction in grain yield.

Table 6. Activities of adenosine diphosphate glucose pyrophosphorylase (AGP), starch synthase (StS), and starch-branching enzyme (SBE) in the grains of rice under various irrigation regimes

Both cultivars Zhendao 88 (*japonica*) and Liangyoupeijiu (LYPJ, *indica* hybrid) were field grown. CI, WMD, and WSD indicate conventional irrigation, alternate wetting and moderate soil drying, and alternate wetting and severe soil drying during the rice growing season. Measurements of enzymatic activities were made when soil water potentials were –15 kPa in the WMD and –30 kPa in the WSD and when plants were rewatered. The activity is expressed as μmol grain^{-1} min^{-1} for AGP and StS and as units grain^{-1} min^{-1}for SBE. Values are averages across the three years (2006–2008). Letters after the values indicate least significant difference (LSD) at the P=0.05 level within the same column and the same cultivar.

Cultivar	Treatment	During the soil drying period			During the rewatering time		
		AGP	StS	SBE	AGP	StS	SBE
Zhendao 88	CI	46 a	8.5 b	685 b	44 b	8.2 b	637 b
	WMD	48 a	12.6 a	767 a	57 a	16.4 a	859 a
	WSD	21 b	4.4 c	389 c	32 c	5.8 c	498 c
LYPJ	CI	42 a	9.3 b	576 b	39 b	8.8 b	554 b
	WMD	45 a	14.5 a	694 a	55 a	17.9 a	796 a
	WSD	25 b	5.7 c	321 c	30 c	7.2 b	432 c
$LSD_{0.05}$		4	1.6	48	5	2.1	57

Non-flooded straw mulching cultivation maintains a high grain yield and increases WUE

Non-flooded mulching cultivation, either non-flooded plastic film mulching cultivation (PM) or non-flooded wheat/rice straw mulching cultivation (SM), has been adopted and developed as a new rice production technique in recent years (Fan *et al.*, 2005; Liu *et al.*, 2005; Lu *et al.*, 2007). Both PM and SM are employed under non-flooded conditions with limited irrigation, and they are substantially different from both traditional flooded rice cultivation and rain-fed rice cultivation (Li *et al.*, 2006). There are reports that the PM, characterized by its striking efficiency in the maintenance of soil moisture, the increase in soil temperature in the early season, and the inhibition of weed growth, has led to an improvement in *WUE* and an increase in grain yield in the mountainous areas where both water shortage and low temperature are limiting factors to rice production (Fan *et al.*, 2005; Liu *et al.*, 2005; Tao *et al.*, 2006). However, there are also reports that the PM decreases both

Table 7. Remobilization of pre-stored assimilates in straws and harvest index of rice under various irrigation regimes

Both cultivars Zhendao 88 (*japonica*) and Liangyoupeijiu (LYPJ, *indica* hybrid) were field grown. CI, WMD, and WSD indicate conventional irrigation, alternate wetting and moderate soil drying, and alternate wetting and severe soil drying during the rice growing season. Values of remobilized C reserve and contribution to grain are calculated according to following formulas: remobilized C reserve (%)=[non-structural carbohydrate (NSC) in straws at heading time–NSC in straws at maturity]/NSC in straws at heading time×100; contributed to grain (%)=(NSC in straws at heading time–NSC in straws at maturity)/grain yield×100. Values are averages across the three years (2006–2008). Letters after the values indicate least significant difference (LSD) at the P=0.05 level within the same column and the same cultivar.

Cultivar	Treatment	NSC in straws at heading (g m^{-2})	NSC in straws at maturity (g m^{2})	Remobilized C reserve (%)	Contribution to grain (%)	Total dry matter (g m^{2})	Harvest index (kg kg^{1})
Zhendao 88	CI	274 a	238 a	13.1 c	4.5 c	1713 a	0.47 b
	WMD	282 a	138 b	51.1 b	15.5 b	1820 a	0.51 a
	WSD	161 b	63 c	60.9 a	18.6 a	1012 b	0.52 a
LYPJ	CI	352 a	289 a	17.9 c	6.6 c	2127 a	0.45 b
	WMD	363 a	155 b	51.3 b	19.5 b	2130 a	0.50 a
	WSD	225 b	71 c	68.4 a	23.7 a	1273 b	0.51 a
$LSD_{0.05}$		26	17	5.3	2.1	110	0.02

grain yield and quality, partly due to too high a temperature in the soil (31.5 °C at 10 cm below the surface) and canopy (32.3 °C) under such a production condition (Xu *et al.*, 2007; Zhang *et al.*, 2008*c*, 2009*b*).

The SM has developed in the Yangtze River Basin in China where rice–wheat rotations are the main cropping system (Fan *et al.*, 2005; Liu *et al.*, 2005; Qin *et al.*, 2006). A major challenge in the rice–wheat cropping system is the disposal of the wheat residue preceding a rice crop. Farmers always burn the crop residue particularly when they want to establish the rice crop rapidly while labour is limited. This leads to a loss of most of the organic C and large losses (up to 80%) of nitrogen (N) (Raison, 1979), 25% of phosphorus (P), and 21% of potassium (K) (Ponnamperuma, 1984) as well as significant air pollution and the death of beneficial soil fauna and micro-organisms. One of the best solutions would be to use crop straw as a soil mulch material in non-flooded rice cultivation in the rice–wheat rotation system. The SM could substantially increase *WUE*, but its effect on grain yield remains disputable (Fan *et al.*, 2005; Liu *et al.*, 2005; Zhang *et al.*, 2008*c*, 2009*b*). The data herein demonstrated that both PM and SM substantially increased *WUE*, but only the SM maintained grain yield as high as the traditional flooding (TF) did (Tapble 8). The PM significantly decreased the yield when compared with the TF. Increase in *WUE* and good performance in grain yield under SM conditions may be attributed to the high biomass, the enhanced remobilization of pre-stored C reserves from vegetative tissues to grains, and increased *HI* (Table 9). The greater percentage of filled grains and higher grain weight under SM also resulted from the increased photosynthetic rate, root oxidation activity, and activities of the key enzymes involved in the sucrose–starch metabolic pathway in grains and a higher ratio of ABA to ethylene in the sink (grains) during the grain-filling period (Zhang *et al.*, 2008*c*, 2009*b*). On the other hand, the loss of biomass due to the decreases in

Table 8. Grain yield and water use efficiency (WUE) for irrigation of rice under non-flooded mulching cultivations

Both cultivars Zhendao 88 (*japonica*) and Liangyoupeijiu (LYPJ, *indica* hybrid) were field grown. TF indicates traditional flooding cultivation, and PM, SM, and NM are plastic film mulching, wheat straw mulching, and no mulching under non-flooded conditions. Values are averages across the five years (2003–2007). Letters after the values indicate least significant difference (LSD) at the *P*=0.05 level within the same column and the same cultivar.

Cultivar	Treatment	Number of panicles (m^{-2})	Number of spikelets per panicle	Filled grains (%)	Grain weight (mg $grain^{-1}$)	Grain yield (g m^{-2})	*WUE* (kg grain m^{-3})
Zhendao 88	TF	326 b	115 a	85.6 b	26.2 b	841 a	0.91 c
	PM	385 a	98 c	81.2 c	25.1 c	768 b	3.96 a
	SM	324 b	104 b	89.3 a	27.1 a	815 a	3.88 a
	NM	275 c	91 d	72.4 d	24.2 d	483 c	1.72 b
LYPJ	TF	252 b	198 a	78.5 b	25.2 b	987 a	1.02 c
	PM	283 a	176 bc	73.6 c	24.3 c	890 b	4.44 a
	SM	248 b	181 b	82.8 a	26.0 a	966 a	4.21 a
	NM	212 c	172 c	69.5 d	23.5 d	596 c	1.86 b
$LSD_{0.05}$		14	5	2.1	0.6	32	0.26

Table 9. Remobilization of pre-stored assimilates in straws and harvest index of rice under non-flooded mulching cultivations

Both cultivars Zhendao 88 (*japonica*) and Liangyoupeijiu (LYPJ, *indica* hybrid) were field grown. TF indicates traditional flooding cultivation, and PM, SM, and NM are plastic film mulching, wheat straw mulching, and no mulching under non-flooded conditions. Values of remobilized C reserve and contribution to grain are calculated according to the following formulae: remobilized C reserve (%)=[non-structural carbohydrate (NSC) in straws at heading time–NSC in straws at maturity]/NSC in straws at heading time×100; contributed to grain (%)=(NSC in straws at heading time–NSC in straws at maturity)/grain yield×100. Values are averages across the five years (2003–2007). Letters after the values indicate least significant difference (LSD) at the *P*=0.05 level within the same column and the same cultivar.

Cultivar	Treatment	NSC in straws at heading (g m^{-2})	NSC in straws at maturity (g m^{-2})	Remobilized C reserve (%)	Contribution to grain (%)	Total dry matter (g m^{-2})	Harvest index (kg kg^{-1})
Zhendao 88	TF	298 a	243 a	18.5 b	6.5 c	1752 a	0.48 c
	PM	243 b	104 b	57.2 a	18.1 a	1476 b	0.52 a
	SM	257 b	122 b	52.5 a	16.6 ab	1630 ab	0.50 b
	NM	143 c	71 c	50.3 a	14.9 b	966 c	0.50 b
LYPJ	TF	368 a	308 a	16.3 c	6.1 c	2145 a	0.46 c
	PM	315 b	134 c	57.5 a	20.3 a	1745 b	0.51 a
	SM	353 a	184 b	47.9 b	17.5 a	1971 a	0.49 b
	NM	172 c	90 d	47.6 b	13.8 b	1241 c	0.48 b
$LSD_{0.05}$		24	19	7.1	2.9	175	0.01

source capacity and sink strength outweighed the gain from the increased remobilization of pre-stored C reserves under the PM (Zhang *et al.*, 2008*c*, 2009*b*).

The decrease in grain yield under the PM compared with that under the SM may also be attributed to high rootzone temperature, lodging, and less supply of nutrients from the soil. Zhang *et al.* (2008*c*) observed that the average subsurface (10 cm depth) soil temperature was 26.8 °C under the TF and 27.2 °C under the SM which is suitable for the normal growth of rice roots as proposed by Hasegawa *et al.* (2001). Under the PM treatment, the average temperature from transplanting to heading was 31.5 °C in subsurface soil and from panicle initiation to maturity was 32.3 °C in the canopy. Such high temperatures would promote plant growth at the early growing stage but may also inhibit root and micro-organism activity at the mid and late growing stages and accelerate plant senescence (Funaba *et al.*, 2006; Barnabas *et al.*, 2008). Liu *et al.* (2002) observed that lodging of approximately 50% of the plants under the PM, while only 8% of plants under the SM, happened during the late grain-filling period, presumably due to deficiency in silicon in plants and early senescence under the PM. It was reported that organic C and N in the top 5–15 cm soil surface were 15–20% less under the PM than under the SM during the grain-filling period (Rasmussen and Collins, 1991; Liu *et al.*, 2003, 2005; Fan *et al.*, 2005). These observations indicate that the SM would be a better practice than the PM in areas where water is scarce but temperature is favourable to rice growth, such as in Southeast China.

Concluding remarks

Harvest index (*HI*) is a variable factor in crop production. Enhancement in *HI* would increase *WUE* without compromising grain yield. Several practices, such as post-anthesis controlled soil drying, alternate wetting and moderate soil drying regimes during the whole growing season, and non-flooded straw mulching cultivation, could substantially enhance *WUE* and maintain or even increase the grain yield of rice, mainly via the enhanced remobilization of pre-stored carbon reserves from vegetative tissues to grains and improved *HI*. Farmers are recommended to adopt the technique of post-anthesis controlled soil drying if they have over-used nitrogen fertilizers and/or used a hybrid rice cultivar which is too vigorous. It would be a good option for farmers to adopt non-flooded straw mulching cultivation in the areas where rice–wheat rotations are the main cropping system and/or where water is scarce but temperature is favourable for rice growth. The technique of alternate wetting and moderate soil drying irrigation could be used in all the irrigated lowland systems. In recent years, these techniques have been extended into rice production in Southeast China, and effectively enhanced *HI* in the field of commercial crop production (Yang *et al.*, 2007), which has proved that proper crop management can achieve the dual goal of increasing food production and saving water. Several problems, a proper indicator of moderate soil drying during the growing season, soil drying-initiated physiological regulations, the carbon and nitrogen metabolism of plants under the controlled soil drying, moderate soil drying regime, and non-flooded straw mulching cultivation, and the effects of these techniques on nitrogen use efficiency and environment (such as N_2O emission from the soil) are worthy of further investigation.

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