Front. Agr. Sci. Eng. 2015, **2**(2): 115–123
DOI : 10.15302/J-FASE-2015055

REVIEW

Approaches to achieve high grain yield and high resource use efficiency in rice

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Abstract This article discusses approaches to simultaneously increase grain yield and resource use efficiency in rice. Breeding nitrogen efficient cultivars without sacrificing rice yield potential, improving grain fill in later-flowering inferior spikelets and enhancing harvest index are three important approaches to achieving the dual goal of high grain yield and high resource use efficiency. Deeper root distribution and higher leaf photosynthetic N use efficiency at lower N rates could be used as selection criteria to develop N-efficient cultivars. Enhancing sink activity through increasing sugar-spikelet ratio at the heading time and enhancing the conversion efficiency from sucrose to starch though increasing the ratio of abscisic acid to ethylene in grains during grain fill could effectively improve grain fill in inferior spikelets. Several practices, such as post-anthesis controlled soil drying, an alternate wetting and moderate soil drying regime during the whole growing season, and non-flooded straw mulching cultivation, could substantially increase grain yield and water use efficiency, mainly via enhanced remobilization of stored carbon from vegetative tissues to grains and improved harvest index. Further research is needed to understand synergistic interaction between water and N on crop and soil and the mechanism underlying high resource use efficiency in high-yielding rice.

Keywords rice, nitrogen-efficient cultivar, grain fill, harvest index, nitrogen use efficiency, water use efficiency

1 Introduction

Rice (*Oryza sativa*) is one of the most important food crops in the world, providing 35%–60% of the dietary calories consumed by approximately 3 billion people[1]. Rice in China is the staple food for more than 65% of the population[2,3]. To meet the population growth, China has paid great attention to increase rice yield, from 2.1 $t \cdot hm^{-2}$ in 1950 to 6.5 $t \cdot hm^{-2}$ in 2012[4]. The national average rice yield was 6.7 $t \cdot hm^{-2}$ in 2013, which was 56% higher than the world average (4.3 $t \cdot hm^{-2}$). These great advances in rice production in China have been important for increasing food supply and security. However, such advances result partly from high inputs of water and chemical fertilizers especially over-use of nitrogen fertilizer. In China today the average N application rate in rice is about 180 $kg \cdot hm^{-2}$, which is 75% above the world average[2,3]. Excessive fertilization with N results in decreased N use efficiency (NUE). It is reported that recovery efficiency of N fertilizer (the percentage of fertilizer N recovered in aboveground plant biomass at the end of the cropping season) in China is only 30%–35%, which is 15%–20% below that in other major rice growing countries[3,5]. In the high yielding area of Taihu Lake, the average N input is 300 $kg \cdot hm^{-2}$, and the average agronomic N use efficiency (AE_N, increase in grain yield per kilogram N applied) is only 12 $kg \cdot (kg\ N)^{-1}$, less than half of that in the developed countries[6,7]. Excessive N input not only results in lodging, severe occurrences of diseases and insects, and poor grain quality in rice, but also pollutes the environment[2,8,9]. Moreover, in spite of a continuous increase in fertilizer input to rice production in China, the rice yield increase has slowed since the 1990s, as reflected by the sharp drop in the annual yield increase rate from 3.7% in the 1980s to 0.9% in the 1990s[10], and 0.5% between 2000 and 2007[11].

Water shortage and low water use efficiency (WUE) are

Received February 25, 2015; accepted May 20, 2015

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two other problems affecting rice production in China. Water resource per capita in China is 23 ML, only a quarter of the world average, and 60%–70% of this is used agriculture. Rice production is the biggest water user, and consumes about 60%–70% of the total irrigation water in agriculture[12]. During the past 20 years, the annual water shortage for irrigation in China's agriculture was 3×10^{12} L, and drought occurred over 2.0×10^8–2.6×10^8 hm^2. Even in the southeast of China, which is usually considered as a water-rich area, 1.6×10^6–2.0×10^6 hm^2 of rice suffered seriously from seasonal drought[13,14]. Furthermore, WUE for rice irrigation (grain yield over amount of irrigation water) is rather low in China, where irrigation water consumption is 30%–40% higher, while WUE is 40%–50% lower, than in the United States of America under similar seasonal rainfall conditions[15]. Low resource use efficiency has been a major factor restricting sustainable agricultural development in China.

With the continuing population growth and economic development in China, food consumption will continue to increase. It is estimated that, by the year 2025, China needs to produce about 20% more rice than is currently produced to meet the food needs of a growing population[2,3]. The questions are whether continuous increases in crop yield can be sustained by simultaneous increases in inputs of water and fertilizer and resource use efficiency. These are contentious issues of agricultural science and remain unresolved[16,17]. The developed countries usually adopt the principle of giving priority to environmental protection. However, simultaneous increase in crop yield and resource use efficiency is the only option in China due to its higher population relative to availability of land and other resources. Therefore, this paper discusses approaches to achieve the dual goal of high yield and high resource use efficiency in rice.

2 Approaches to achieve high grain yield and high resource use efficiency

2.1 Breeding N-efficient rice cultivars without sacrificing grain yield potential

Development of semi-dwarf rice cultivars during the Green Revolution substantially increased N fertilizer rates and grain yield because of their lodging resistance at high N inputs[18–20]. To breed rice with higher yield and stronger lodging resistance, progeny with high N tolerance rather than high N responsiveness are selected in the breeding nursery under high N rates[20]. As a result, high grain yield must be at the cost of higher amount of N application, which leads to a lower NUE. The contradiction between high yield and high NUE for a lodging-resistant cultivar was evident in super rice cultivars, which have larger panicle size, greater yield potential, better grain quality, and stronger tolerance to biotic and abiotic stresses than standard cultivars[21,22]. When compared to standard cultivars, super rice cultivars produced higher grain yield only at the very high N rate (360 $kg\cdot hm^{-2}$), and both grain yield and AE_N were comparable when the N rate was 270 $kg\cdot hm^{-2}$, and showed a lower grain yield and lower AE_N at lower N rates (90 and 180 $kg\cdot hm^{-2}$) (Fig. 1). It is easy to understand that the newly released cultivars have low NUE because of their reduced responsiveness to N. It is hypothesized that the newly released cultivars bred under high N rates have lower NUE than the older cultivars that were bred under low N rates, and future breeding nurseries should be limited to lower N rates such as 120 to 150 $kg\cdot hm^{-2}$[20]. However, such a hypothesis needs to be tested in field experiments.

It needs to be determined if it is possible to develop a super rice cultivar with high grain yield and high NUE.

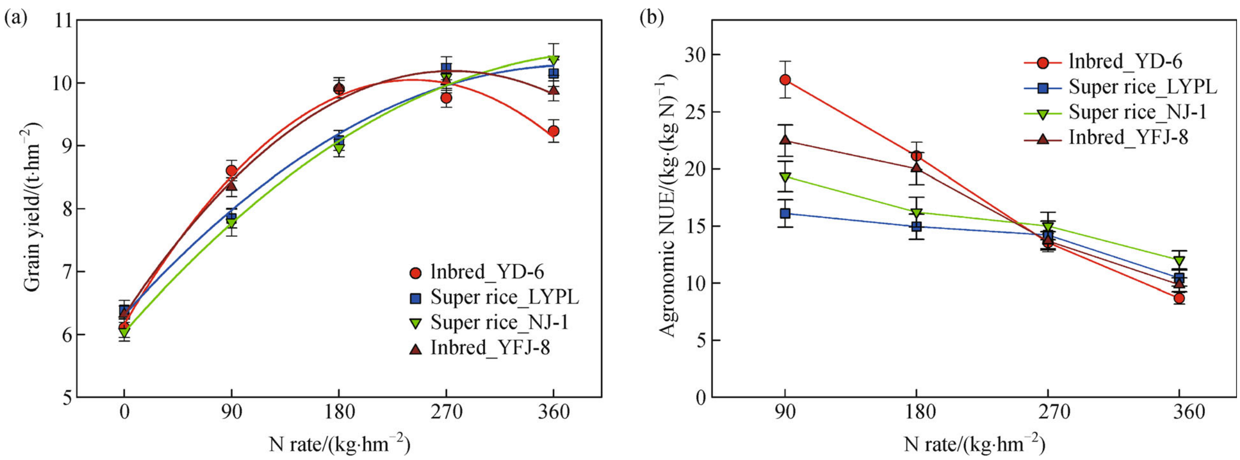

Fig. 1 Responses in grain yield (a) and agronomic nitrogen use efficiency (NUE) (b) of inbred and super rice cultivars to five nitrogen application rates. Vertical bars represent±standard error of the mean ($n = 4$) where these exceed the size of the symbol. Data are adapted from Liu et al.[21] and Fan[22].

Recently it has been observed that there is a large difference in NUE among newly bred super rice cultivars[23]. Two super rice cultivars, Huaidao 5 and Lianjing 7, produced higher grain yield, absorbed higher amounts of N from the soil, and exhibited higher NUE than other super rice cultivars at lower N rates (0, 100 or 200 $kg \cdot hm^{-2}$). The grain yield and NUE of both cultivars were comparable with those of other cultivars at the N rate of 300 $kg \cdot hm^{-2}$. These results suggest that Huaidao 5 and Lianjing 7 are N-efficient cultivars without sacrificing grain yield potential.

Understanding plant traits that are associated with high grain yield and high NUE is crucial for breeding programs aimed at developing N-efficient cultivars. Compared with N-inefficient cultivars, N-efficient cultivars have longer root length, greater root length per volume of soil, root oxidation activity and leaf photosynthetic NUE, and more nonstructural carbohydrate (NSC) remobilization at lower N rates[23]. The agronomic and physiological indices for N-efficient rice cultivars are shown in Table 1. These plant traits, especially deeper root distribution, greater root oxidation activity and higher photosynthetic NUE at lower N rates, could be used as selection criteria in a breeding program to develop N-efficient rice cultivars that have high yield and high NUE.

2.2 Improving grain fill in later-flowering inferior spikelets

In rice and other cereal crops, grain yield can be defined as the product of yield sink capacity and filling efficiency[24]. To further increase yield and break the yield ceiling, breeding efforts have expanded yield sink capacity, the maximum size of sink organs to be harvested, mainly by increasing the number of spikelets per panicle[25,26]. As a result, cultivars with large panicles or extra-heavy panicle types, namely numerous spikelets per panicle, have become available, such as the New Plant Type of the International Rice Research Institute[27], hybrid rice and super rice in China[28,29]. These cultivars, however, frequently do not exhibit their high yield potential due to their poor grain fill, due to slow grain filling rate and many unfilled grains[26,30,31].

The degree and rate of grain fill in rice differs largely with the position of the spikelet in the panicle. In general, earlier-flowering superior spikelets, usually located on apical primary branches, have fast-filling and heavier grains. Later-flowering inferior spikelets, on the other hand, are usually located on proximal secondary branches, and are either sterile or have poor and slow-filling grains that are unsuitable for human consumption[32,33]. The problem of slow-filling grain in inferior spikelets is even worse in newly bred super rice cultivars, although they generally show a yield potential of 8%–20% more than other rice cultivars[28,34]. For example, 20 super rice cultivars grown in the Lower Yangtze River Basin were found to have an average grain filling proportion and grain weight in inferior spikelets of 21.8% and 20.1%, respectively, which was lower than those in superior spikelets (Fig. 2). In contrast, these values for 20 standard cultivars were only 8.6% and 10.9%, respectively. Poor grain fill in inferior spikelets not only reduces yield potential and grain quality, but also decreases WUE and NUE, because inferior spikelets consume much water and nutrients during their development[35–37].

The mechanism underlying poor grain fill in inferior spikelets remains unknown. Recent research has shown

Table 1 Agronomic and physiological indices for N-efficient rice at the N rate of 200 $kg \cdot hm^{-2}$

Agronomic and physiological traits	Index
Grain yield/($t \cdot hm^{-2}$)	⩾9.5
N uptake/($kg \cdot hm^{-2}$)	⩾140.0
Internal N use efficiency/($kg \cdot kg^{-1}$)	⩾67.0
Apparent recovery efficiency of N fertilizer/(%)	⩾34.8
Agronomic N use efficiency/($kg \cdot kg^{-1}$)	⩾19.5
Shoot biomass at heading/($t \cdot hm^{-2}$)	9.9–10.3
Crop growth rate from panicle initiation to maturity/($g \cdot m^{-2} \cdot d^{-1}$)	⩾14.5
Specific leaf N content at heading/($g \cdot m^{-2}$)	2.2–2.3
Photosynthetic nitrogen use efficiency at heading/($\mu mol \cdot g^{-1} \cdot s^{-1}$)	⩾10.5
Root biomass in 10.1–20.0 cm soil layer at heading/($g \cdot m^{-2}$)	44.5–46.5
Root length at heading/($km \cdot m^{-2}$)	24.2–26.5
Root length density at heading/($cm \cdot cm^{-3}$)	12.8–14.2
Root oxidation activity at heading/(μg α-NA$\cdot g^{-1} \cdot DWh^{-1}$)	450.0–500.0
Nonstructural carbohydrate in the stem at heading/($g \cdot m^{-2}$)	⩾285.0
Nonstructural carbohydrate remobilization during grain filling/%	57.5–58.5

Note: Data are adapted from Ju et al.[23].

that there are two important causes for poor grain fill in inferior spikelets: one is low sink activity (low ATP content, cytokinin concentration, mRNA level, etc.) at the initial grain filling stage, and the other is low ratio of abscisic acid (ABA) to ethylene during the grain filling period[35,38]. The low sink activity at the initial grain filling stage can result in a slow division rate of endosperm cells, leading to fewer endosperm cells, smaller sink capacity and grain weight[39,40]. Also, a low ratio of ABA to ethylene during grain fill can inhibit activities of the key enzymes involved in sucrose-to-starch conversion in grains and thereby reducing the efficiency of this process, and consequently, lead to poor grain fill[41,42]. Further studies showed that super rice has a lower NSC (sugar) to spikelet ratio at heading time, and this ratio was positively and significantly correlated with sink activity at the initial grain filling stage[36,38]. Application of potassium at the panicle initiation stage and/or N fertilizer at the spikelet differentiation stage can significantly increase the sugar-spikelet ratio at the heading time through increasing NSC accumulation in stems 0–15 days before heading, and consequently, increase sink activity at the initial grain filling stage, leading to an improvement in grain fill in inferior spikelets[38,43]. Therefore, increasing sugar-spikelet ratio at heading can be considered as an important approach to improving grain fill in inferior spikelets. The technique and mechanism involved in the improvement in grain fill by increasing the sugar-spikelet ratio are summarized in Fig. 3.

An important question is how to increase the ratio of ABA to ethylene in grains during the grain filling period so that filling of the inferior spikelets can be improved. There are reports showing that an alternate wetting and moderate drying regime (AWMD) can significantly decrease ethylene evolution rate and increase the ratio of ABA to ethylene, and enhance the activities of key enzymes involved in sucrose to starch conversion and expressions of the genes encoding enzymes involved in starch synthesis in rice grains[44–46]. These processes increase the fill and weight of grain in inferior spikelets, so increasing the ratio of ABA to ethylene in grains by AWMD during grain fill is an important approach, to enhance filling of inferior spikelets. The technique and mechanisms involved in these improvements in grain fill through increasing the ratio of ABA to ethylene are summarized in Fig. 4.

2.3 Enhancing harvest index to increase grain yield and water productivity

Global agriculture in the Twenty-First Century faces two major challenges: total food production needs to increase to feed a growing world population, and this increase needs to be accomplished as water resources become increasingly scarce[47]. The challenge to produce more food under increasing water scarcity has led to the conclusion that crop water productivity (economic yield over amount of water consumed) needs to increase[48,49]. However, the ways to increase water productivity remain unclear[47,49]. In cereals and at the crop level, it is proposed that water productivity can be defined as the ratio of grain yield to water transpired (WP_T)[47]. As the grain yield (Y) is the product of harvest index (HI) and total above-ground biomass (B), that is, Y = HI × B, the WP_T in rice can be expressed as:

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

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

The ratio B/T is sometimes known as transpiration efficiency. HI is the grain yield over total above-ground biomass. The grain yield and water productivity can be improved by either increased transpiration efficiency or increased HI. However, the ratio of biomass production over transpiration (B/T) has been shown to be relatively constant for a given species in given climate[50], and can be

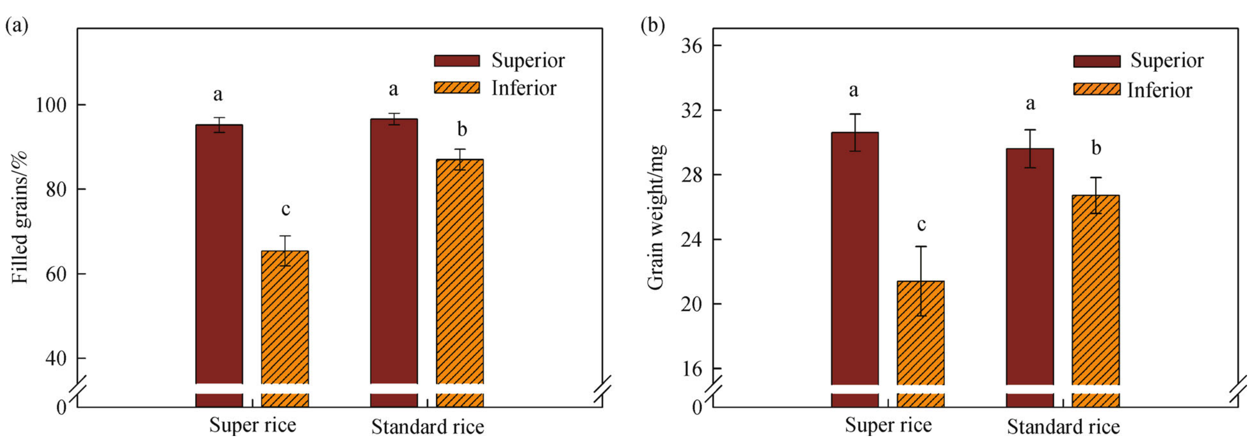

Fig. 2 Mean filled grain percentage (a) and grain weight (b) in superior and inferior spikelets for 20 super rice and 20 standard rice cultivars. Vertical bars represent±standard error of the mean (n = 60) where these exceed the size of the symbol. Different letters above the column indicate statistical significance at the P = 0.05 level. Data are adapted from Yang et al.[26], Yang[35] and Fu[36].

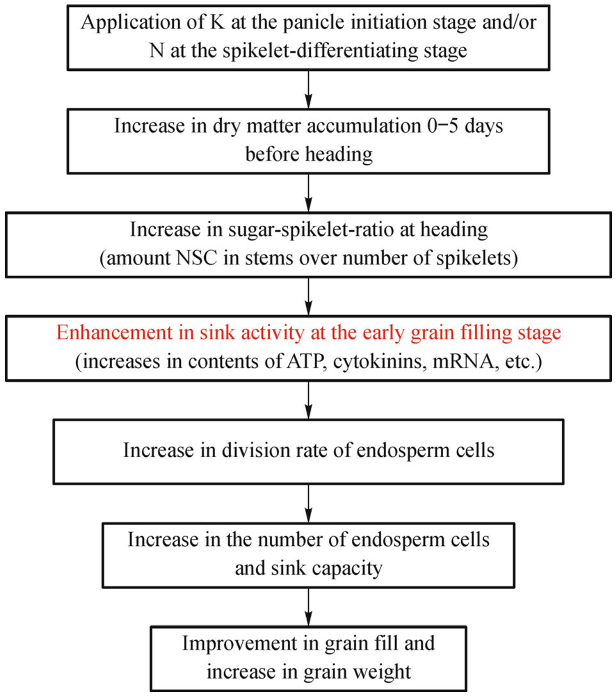

Fig. 3 The technique and mechanism involved in improvement in grain fill in inferior spikelets through increasing sugar-spikelet-ratio at the heading time

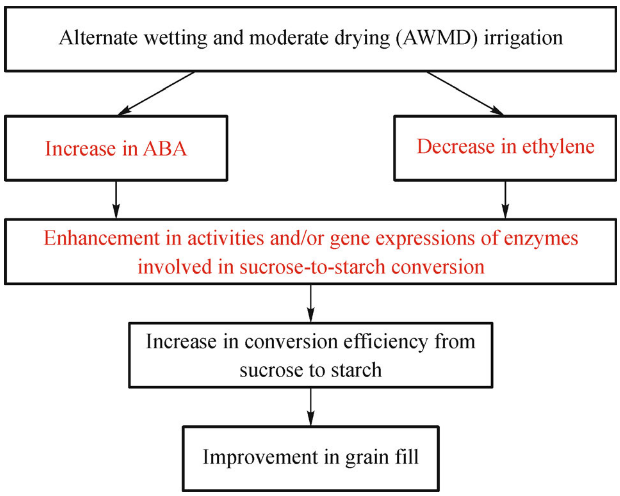

Fig. 4 The technique and mechanism involved in the improvement in grain fill in inferior spikelets through increasing the ratio of abscisic acid (ABA) to ethylene in the grains during the grain filling period

selected for during plant breeding[47]. Plant biomass production is linearly coupled with amount of water transpired, and achieving higher WUE often involves a trade-off with lower biomass production[51]. In agriculture, many ways of conserving water have been investigated and techniques such as alternate partial irrigation of the root zone, deficit irrigation and drip irrigation have been shown to enhance WUE[51,52]. In general, these techniques are a trade-off of lower yield for a higher WUE[51–53].

HI has been shown to be a variable factor in crop production. There are reports that HI can range from 0.17 to 0.56 in rice[54,55], from 0.31 to 0.51 in wheat[56,57] and from 0.25 to 0.58 in maize[58,59]. Increases in grain yield and WUE for a given rice cultivar were mainly achieved through an increase in HI when above-ground biomass was over 18.3 $t\cdot hm^{-2}$ in the inbred rice cv. Yangdao 6 and over 21.8 $t\cdot hm^{-2}$ in the hybrid rice cv. IIyou 084 (Table 2). These results demonstrate that increasing HI is an important approach to increasing grain yield and WUE.

HI increased significantly with the shift from early tall

Table 2 Above-ground biomass, grain yield, harvest index and water use efficiency of rice*

Cultivar	Biomass/($t \cdot hm^{-2}$)	Grain yield/($t \cdot hm^{-2}$)	Harvest index	Water use efficiency/($kg \cdot m^{-3}$)§
Yangdao 6	18.27d#	8.77c	0.48e	0.78e
	19.05b	9.04c	0.50d	0.81d
	18.66c	9.52b	0.51cd	0.82cd
	18.54c	9.64b	0.52bc	0.84c
	18.84c	9.98b	0.53b	0.87b
	19.64a	10.81a	0.55a	0.91a
IIyou 084	23.18a	9.32c	0.40c	0.77c
	23.69a	9.71c	0.41c	0.79c
	21.88b	11.59b	0.53b	0.83b
	21.86b	12.01a	0.55a	0.95a

Note: *, the field experiments were conducted in Yangzhou and Jiangsu, China in 2008 and 2009. Data are means of the two years and unpublished; §, grain yield over the amount of irrigation water and rainfall; #, letters after the values indicate least significant difference (LSD) at the $P = 0.05$ level within the same column and the same cultivar.

cultivars to dwarf cultivars, and declined slightly from dwarf cultivars to modern super rice cultivars[60], implying that increased HI could be achieved mostly through crop management techniques rather than by rice breeding. Actually, several practices, such as post-anthesis controlled soil drying, a moderate wetting drying regime during the growing season and non-flooded straw mulching cultivation, have been developed and can substantially enhance WUE and increase grain yield in rice, mainly through improved canopy structure, source activity, sink strength and enhanced remobilization of stored carbon from vegetative tissues to grains (Table 3). This work has demonstrated that appropriate crop management holds great promise for enhancing HI and consequently achieving the dual goal of increasing grain production and saving water[19,61–71].

3 Concluding remarks

A simultaneous increase in crop yield and resource use efficiency is essential for China with its large population and growing shortages of land and resources. Breeding N-efficient cultivars without sacrificing rice yield potential, improving grain fill in later-flowering inferior spikelets and enhancing HI are three important approaches to achieve the dual goal of high grain yield and high resource use efficiency in rice. Deeper root distribution, longer root length, greater root length per volume soil, root oxidation activity and leaf photosynthetic NUE, and more NSC remobilization at lower N rates could be used as selection criteria in the breeding program to develop N-efficient cultivars.

Poor grain fill in inferior spikelets not only limits yield potential, but also decreases resource use efficiency. Enhancing sink activity through an increase in sugar-spikelet ratio during heading and increasing the conversion efficiency from sucrose to starch though increasing the ratio of ABA to ethylene in grains during grain fill could effectively improve grain fill in inferior spikelets.

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 regime during the whole growing

Table 3 Crop management techniques for increasing harvest index in rice

Crop management techniques	Key points of the techniques	Main agronomic and physiological mechanisms involved	References
Post-anthesis controlled soil drying	Soil water potential is kept –15 to –20 kPa at 15–20 cm depth from 7 days after anthesis to maturity	Enhancing remobilization of NSC from stems to grains by regulating enzymes in the stems and grains	[19,61–64]
Alternate wetting and moderate soil drying during the growing season	Except at the stages of re-greening, meiosis and flowering, at which plants are well-watered, fields are not irrigated until soil water potential reached –10 to –15 kPa at 15–20 cm depth	Reducing redundant vegetative growth at early and mid growth stages and enhancing grain fill through balance among hormones during the grain filling period	[19,65–67]
Non-flooded straw mulching cultivation	Wheat or rice straw is used to cover the soil. Fields are only flooded during the re-greening. Water (380–440 $kL \cdot hm^{-2}$) is applied to plants at each stage of mid-tillering, booting, flowering, and early grain fill if soil water potential reached –25 kPa at 15–20 cm depth	Improving canopy structure, maintaining high root activity and enhancing sink activity during the grain filling period	[19,68–71]

season and non-flooded straw mulching cultivation, could substantially enhance WUE and maintain, or even increase, grain yield of rice, mainly via enhanced remobilization of stored carbon from vegetative tissues to grains and improved HI. It is recommended that farmers adopt the technique of post-anthesis controlled soil drying, if they have used excessive N fertilizer or are growing 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 or where water is scarce but temperature is favorable to rice growth. The technique of alternate wetting and moderate soil drying irrigation could be used for all the irrigated lowland system.

Further research is needed to understand: (1) the mechanisms underlying N uptake, assimilation and remobilization in N-efficient cultivars, (2) factors both intrinsic and extrinsic to spikelets that may regulate grain fill and environmental factors that affect grain filling rates in inferior spikelets, and (3) synergistic interaction between water and nitrogen on the crop and in the soil, and the mechanisms underlying resource use efficiency in high-yielding rice.

Acknowledgements The National Natural Science Foundation of China (31461143015; 31271641, 31471438, 91317307), the National Key Technology Support Program of China (2011BAD16B14, 2012BAD04B08, 2014AA10A605), the Priority Academic Program Development of Jiangsu Higher Education Institutions, Jiangsu Creation Program for Post-graduation Students (KYZZ_0364) are thanked for their financial support.

Compliance with ethics guidelines Jianchang Yang declares that there is no conflict of interest or financial conflicts to disclose.

This article is a review and does not contain any studies with human or animal subjects performed by the author.

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