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REVIEW

Water-saving and drought-resistance rice: from the concept to practice and theory

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Abstract The resource and environmental challenges faced by rice production call for resource-saving and environment-friendly rice varieties. Water-saving and drought-resistance rice (WDR) is a new type of cultivated rice combining both high yield potential and acceptable grain quality as a current lowland paddy rice, as well as water-saving and drought resistance as a traditional upland rice. The lowland and upland rice are two ecotypes adapted to contrasting soil water status, originating mainly because of their differentiated drought resistance. Upland rice, domesticated in a water–limited environment and experiencing a bidirectional selection process, has better drought resistance and especially better drought avoidance. Though the potential tradeoff between drought resistance and productivity is very common in rice, the bidirectional selection could overcome this tradeoff and accumulate recombination genotypes. It is very important to choose elite parents on the basis of studies on the great genetic diversity of rice yield and drought resistance among the rice germplasm resources and adapt the bidirectional selection strategies to especially integrate drought avoidance, drought tolerance, high water use efficiency, and productivity in WDR breeding. The breeding history and genomic studies indicated that lowland paddy rice and upland rice hybridization breeding with suitable selection in different environments is an effective approach to improving complex traits such as yield potential and drought resistance. Meanwhile, molecular technology shows higher efficiency on value-added breeding such as transferring and pyramiding pest- and disease-resistant genes, which helps WDR obtain other green characters. Twenty-two WDR varieties were registered and distributed to farmers in recent years and could be planted in both irrigated and rainfed ecosystems, thus showing promising application prospects. The major crop management technology of WDR in lowland paddy fields with water-saving cultivation and in rainfed fields by dry seeding with aerobic cultivation were also discussed in this article.

Keywords Water-saving and drought-resistance rice · Drought avoidance · Drought tolerance · Water use efficiency · Productivity · Bidirectional selection

Abbreviations

GSR	Green super rice
WDR	Water-saving and drought-resistance rice
WUE	Water use efficiency
CMS	Cytoplasmic male sterility
PTSGMS	Photo-thermosensitive genic male sterile

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Introduction

Rice is the most important staple food for more than one-half of the global population. As the population increases, continuous improvement of yield potential has been the priority of virtually all Chinese rice breeding programs. Decades of breeding efforts, including the Green Revolution and successful utilization of heterosis, have greatly increased the yield potential of rice in China. However, sustainable rice production in China is now facing three major problems. First, as a half-aquatic plant, rice requires large amounts of water. In fact, rice production consumes approximately 55% of China's total freshwater resources (Zhang 2007). China is a large water-deficient country. The amount of water for irrigation only maintains at the current level or even decreases (Liu 2006), which means its water resources can no longer meet the needs of rice production. Furthermore, drought occurs more frequently and becomes an increasingly important factor limiting rice yield in China in the face of global climate change. The average yield loss of rice due to drought is approximately 143–250 kg/hm^2 (Chen and Ding 2009). Second, excessive irrigation combined with the increasing application of chemical fertilizers and pesticides in the current rice production system has resulted in serious agricultural surface pollution (Zhuo et al. 2018). Third, continually flooded rice production in paddy fields has generated large amounts of greenhouse gas emissions. For example, methane emissions from rice paddy fields account for 9–30% of the total emissions in China (Zhang et al. 2004). To solve the disharmony between rice yield and environment, Zhang (2007) proposed the concept of green super rice (GSR) aiming to integrate all the green characters into the rice variety. GSR shall realize less pesticide; less chemical fertilizer, water saving, and drought resistance; and acceptable grain quality and high-yield in the production process. (Zhang 2007; Wing et al. 2018). Following the idea of GSR and as an essential part of the GSR program, water-saving and drought-resistant rice (WDR) has been developed to improve water use efficiency (WUE) and drought resistance in the first for solving the greatest challenge caused by water shortage (Luo 2010).

When WDR came to our minds as a new concept at the end of last century, it had taken us almost 20 years to convert this idea into reality. Clearly, to develop WDR cultivars, one has to improve the three major traits of yield potential, drought resistance and WUE in the breeding program, all of which are genetically and physiologically complex. During the evolution of Asian-cultivated rice (*Oryza sativa* L.) from its wild ancestor (*Oryza rufipogon*), yield potential has been improved continuously by long-term natural and artificial selection, particularly in the past 60 years along with continued improvement in the irrigation system. In China, most rice paddy fields have been cultivated for hundreds and even thousands of years and formed a layer of soil-pan to prevent water leaking. As a result, almost all today's high yielding paddy rice cultivars have a shallow but expansive root system associated with their high yield potential. In contrast, the upland rice, a unique rice ecotype adapted to rainfed conditions, has a high level of drought resistance with a strong and deep-root system but with lower yield due to lack of breeding efforts. Thus, developing WDR cultivars introduces high levels of drought resistance of upland rice compared with the modern and high yield potential lowland varieties. This article aims to summarize our research progress in understanding the genetic basis of drought-resistant rice, the practice and theory in developing WDR cultivars, and the application of WDR in China.

The genetic and physiological mechanisms of rice adaptation to drought

It is now known that the adaptability of rice to water-deficient conditions consists of at least two major components, drought resistance and water saving, each of which is genetically and physiologically complex. Genetically, drought resistance and water saving are two interrelated but different concepts. Water saving refers to the effective utilization of rainfall and higher WUE during plant growth and development, while drought resistance refers to the ability of plants to maintain higher water potential and maintain normal physiological function under drought conditions. The water requirement of rice in different growth/development stages varies considerably. There is sufficient evidence that drought stress at the seedling and adult stages has different effects on yield (Boonjung and Fukai 1996; Farooq et al. 2009). Better synchronization of plant growth stages with seasonal rainfall is considered as a good measure for water saving. Effective uses of rainfall during the water-sensitive period can realize the purpose of saving water. On the other hand, WUE is defined as the economic production per unit water consumption. It may or may not be related to drought resistance. WUE was widely used as one of the breeding objectives in water-saving agriculture (Condon et al. 2004).

Drought resistance is a very complex plant trait. It refers to the survival ability and production capacity of a plant under a water stress environment. Drought resistance involves at least three important physiological components of a plant: (1) the ability to maintain high plant water status under drought conditions, (2) the ability to maintain its physiological functions in the case of low water status, and (3) the ability to recover water status and function after drought stress (Blum 1999). According to the plant responses to drought stress, drought resistance can be classified into four types: drought avoidance, drought tolerance, drought recovery, and drought escape.

Drought avoidance refers to the plant's capacity to sustain high water status by increasing water uptake or reducing water loss under drought conditions. It is achieved by capturing water from deep soil layers through a large and deep root system as well as by reducing transpiration through the closure of the stomata or a nonpermeable leaf cuticle. Drought tolerance is defined as the relative capacity of a plant to maintain its function under low leaf water status. It refers to the active accumulation of osmotic adjustment molecules in plant cells, thus increasing the capacity of osmotic adjustment to maintain a high turgor and also includes materials such as antioxidation molecules that can enhance capacity in the removal of harmful substances accumulated in plant cells. Drought recovery refers to plant recovery capability after a period of severe drought causing complete cessation of growth, complete loss of turgor, and leaf desiccation. It is mainly related to the ability of plants to tolerate drying and dehydration. Drought escape refers to the ability of plants to avoid drought effects by regulating the growth process. The specific performance of drought escape may include accelerated flowering/ripening to minimize the drought damage on yield during the most water sensitive stages, staying green for an extended period of time until rain comes and coinciding with the peak of the rainy season to avoid drought. In fact, drought escape also reflects the ability of plants to utilize rainwater, which is the water-saving capability. Although drought avoidance, drought tolerance, and drought recovery possess various connotations, they usually occur together as the phenotypic responses of plants to drought. Drought avoidance is the major factor in plants' adaptation to drought, while drought tolerance is seen as the second line of defense after dehydration avoidance (Blum 2005).

Since the 1970s, studies on rice morphology and physiology have revealed a large number of morphological and physiological characteristics related to the drought resistance of rice (Turner 1997). At the phenotypic level, drought avoidance is associated with specific morphological characteristics of roots (deep rooting rate, root length and diameter, etc.) and physiological traits (stomatal conductance, leaf water potential, leaf relative water content, water loss rate, photosynthetic rate, canopy temperature, etc.). Drought tolerance is associated with the cell contents of specific plant hormones and metabolites (ABA, proline, soluble sugars, etc.) for cell osmotic adjustment, activities of specific enzymes (peroxidase, superoxide dismutase, etc.), chlorophyll content, etc. In recent years, with the development of modern molecular biology, the molecular genetics and functional genomics of drought resistance is receiving increasing attention. A large number of drought-related QTLs and candidate genes were mapped and isolated (Yue et al. 2006; Xiong 2009; Ma et al. 2016a; Guo et al. 2018), and the functions of several genes in drought resistance have been revealed (Uga et al. 2013).

Differentiation of drought resistance among lowland–upland rice germplasm

After a long history of domestication, Asian-cultivated rice, *O. sativa L.*, has expanded to a wide range of environments in subtropical and temperate areas with considerable variation in water availability. The long-term selection of this cultivar since domestication had produced abundant and diverse germplasm resources within *O. sativa*, including two major ecotypes with differentiated adaptation to water conditions (Luo et al. 2002). The predominant ecotype is the lowland paddy rice adapted to a more aquatic environment with greater geographic distribution. After undergoing long-term selection for increased productivity along with continuously improved irrigation, particularly during the modern breeding of the past 60 years, the current paddy rice cultivars have very high yield potential under well-irrigated conditions. The other ecotype is the upland rice which adapts to the rainfed drought-prone upland agro-ecosystems of the hilly areas of Southeast Asia and Southwest China. Currently, most upland rice varieties grown today are still landraces occupying a small acreage in the mountainous areas of Asia. These upland landraces are normally low-yielding but highly water-saving and drought-resistant. The in-depth studies showed that the differentiation between upland and lowland rice is mainly due to their differences in drought resistance (Xia et al. 2019).

The differentiation between the lowland paddy ecotype and upland ecotype are reflected at both phenotypic and genetic levels. Upland rice is usually more drought resistance with deeper and thicker rooting systems, taller plant height, fewer tillers, and low productivity, while the lowland paddy rice normally has poor drought resistance with shallow, abundant, and thinner roots; more tillers; and higher productivity (Turner 1997; Xia et al. 2014). Previous genetic analyses using DNA markers have shown that the morphological differences between the lowland and upland rice ecotypes involved large numbers of QTLs (Yue et al. 2006; Xiong 2009; Ma et al. 2016; Guo et al. 2018), and these QTLs differentiating the two rice ecotypes appeared to be under divergent selections (Xia et al. 2015). We also detected some highly differentiated epiloci between the upland and lowland ecotypes using methylation-sensitive amplified polymorphism, and upland rice accessions have accumulated drought-induced transgenerational epimutations, which could result from their adaptation to drought-prone environments for thousands of generations (Xia et al. 2016; 2017).

The long-term genetic and epigenetic differentiation has produced abundant and diverse drought-resistant germplasm resources. Generally, upland rice, which was domesticated in the field without plough pan, usually has better drought avoidance; however, some lowland rice shows some degree of drought tolerance. In fact, drought resistance shows a variety of types; the different drought-resistant germplasms show advantages in different types of drought resistance. Figure 1 shows the performance and responses of 11 rice accessions of diverse origins to variable water conditions based on six traits related to their adaptation to drought; this revealed interesting differences in their responses to

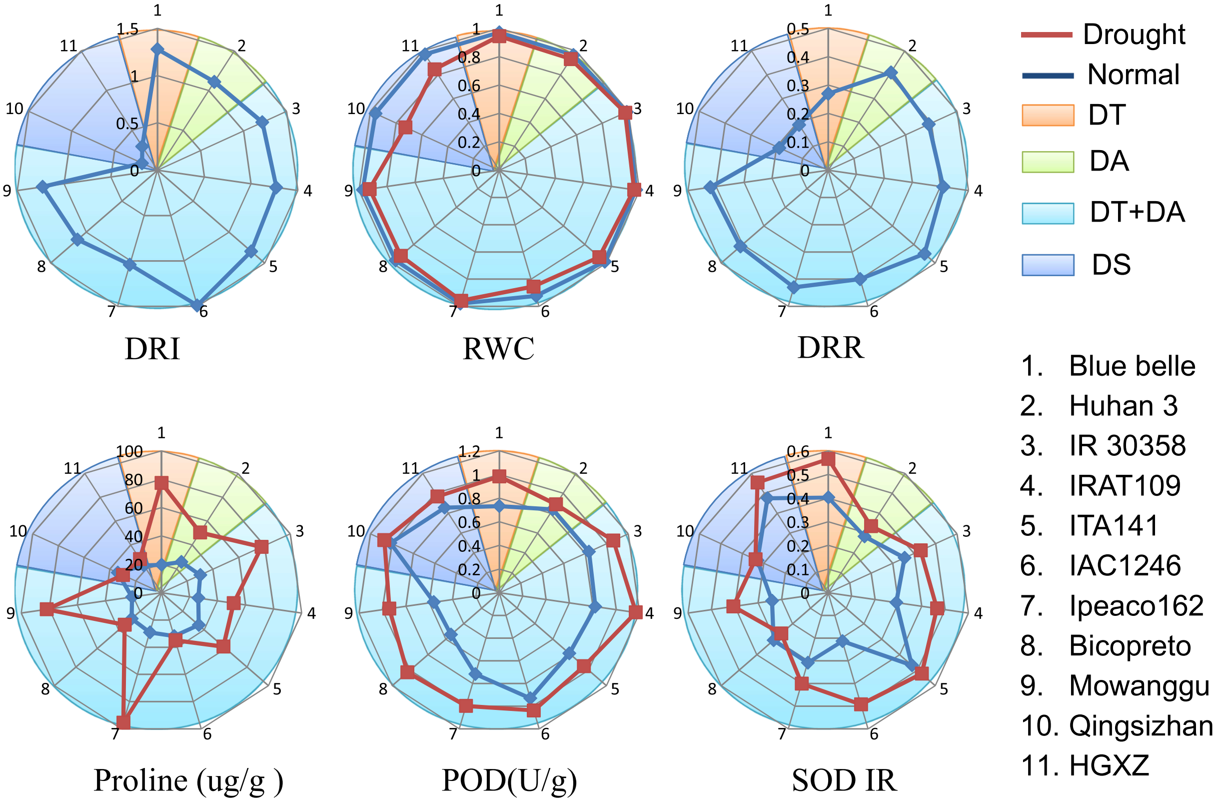


Fig. 1 The classification by different mechanisms of drought resistance for eleven rice genotypes. DRI, drought resistance index; RWC, relative water content; DRR, deep root ratio; SOD IR, SOD inhibit rate; DT, drought tolerance; DA, drought avoidance; DS, drought sensitive

drought stress (Liu et al. unpublished). The upland rice lines (such as IRAT109) usually have better drought avoidance reflected by their deep and strong roots, while the lowland rice lines (such as Bluebelle) tend to show a better level of drought tolerance reflected by their enhanced ability of osmotic adjustment and anti-oxidation. For example, the drought resistant index of Bluebelle was same as that of IRAT 109, but their mechanisms of drought resistance are completely different; Bluebelle showed a higher SOD inhibition rate than IRAT 109 in water stress despite it possess a lower deep root ratio.

The upland rice line IAC 1246 showed the highest drought resistance index because it processes both drought avoidance and drought tolerance. Phenotypic, transcriptomic, and metabolomic studies indicated that IAC1246 shows an enhanced drought tolerance (osmotic adjustment and anti-oxidation) over IRAT09. It could be helpful to maintain normal life activities at the early stages of drought. The improved drought resistance of IAC1246 could be, at least in part, attributed to its differential expression of many photosynthesis-related genes and the dramatic increase of a photosynthetic protective substance, ferulic acid, under drought (Ma et al. 2016b). We further compared IRAT109 with a lowland variety, Zhanshan97B, a maintain line of hybrid rice Shanyou 63 having the largest growing area in China, and found that it has much better drought tolerance than IRAT109 (unpublished data). Genetic analyses of a mapped population derived from the cross of Zhenshan97B/IRAT09 indicated that QTL alleles for better drought avoidance were from IRAT109 (Yue et al. 2005, Lou et al. 2015), while transcription factor *OsGRAS1* from Zhengshen97B could increase drought tolerance by regulating the expression of anti-oxidant enzyme–related genes (Xu et al. 2015).

Tradeoff between yield potential and drought resistance results in bidirectional selection during domestication of upland rice

It is known that plants can activate many acclimation responses to ensure improved survival under drought. These acclimation responses can harm plants' growth, development, and reproduction. For example, a smaller plant or leaf area and limited tillers are components of dehydration avoidance in order to maintain high water status under stress. However, these traits are in contrast to a high yield potential (Blum 2005). Stomatal closure to conserve water status is often at the expense of reduced carbon assimilation and productivity (Zhang and Chen 2005). Thus, there is a certain tradeoff between drought resistance and productivity. Genetically, this physiological tradeoff can result either from genetic pleiotropy or from tight linkage (Xia et al. 2019). One may perceive that during evolution, the upland rice would have gone through two types of directional selection under rainfed drought-prone environments: selection for improved productivity in rain-sufficient years and for drought resistance in drought years. This process would have accumulated recombinants between drought-resistant genes and those for productivity in which the tradeoff due to the linkage was broken, but the rare recombinant genotypes with high levels of drought resistance and productivity would have been easily lost in the lowland rice environments in which drought resistance is neutral (Xia et al. 2019). Thus, one may perceive that the traditional upland rice usually grows on mountainous slope lands without plow soles, in which the root system of the upland rice would penetrate downwards to absorb water in the deep soil layer when encountering drought stress. In contrast, the lowland rice varieties grow in paddy fields with plow soles, under which their root systems cannot penetrate the soil pan to absorb the moisture. This soil pan was formed from plow soles in most paddy fields during the long period of rice cultivation. Thus, lowland rice plants have to depend on drought tolerance to survive. This was the primary reason why upland rice usually possesses strong drought avoidance, while some lowland rice varieties have a certain degree of drought tolerance. This finding encourages us to develop WDR by utilizing drought avoidance from upland rice and drought tolerance from lowland rice.

We proposed a model for adaptive differentiation between the upland and lowland rice during domestication (Fig. 2, Xia et al. 2019). In this model, there is a common genetic tradeoff between drought resistance and productivity due largely to the linkage between genes for drought resistance and genes for higher productivity in the rice genome (a). Early domestication of the lowland rice in the paddy fields focused primarily on improved productivity resulting from directional selection on productivity (b). Domestication of the upland rice had gone through bidirectional selection for improved productivity under favorable environments and for yield stability (or drought resistance) under drought conditions that would have retained considerable

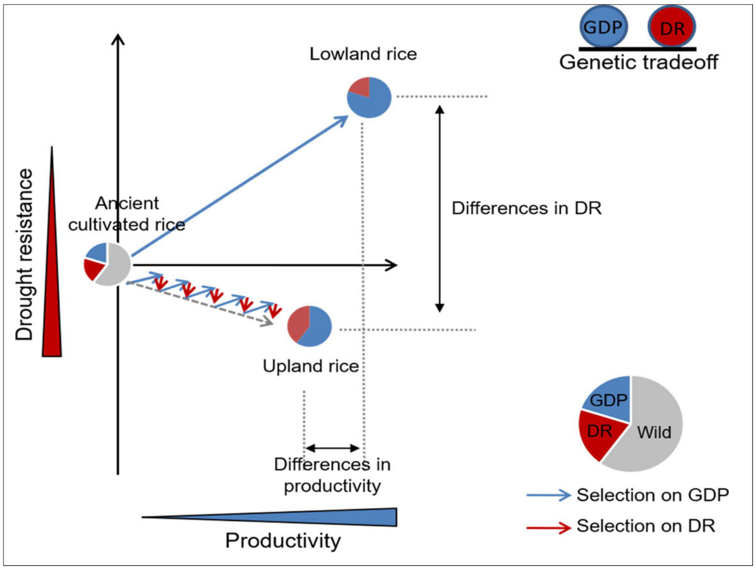


Fig. 2 A model describing adaptive differentiation between upland and lowland rice ecotypes for drought resistance. Due to the genetic tradeoff between GDP and DR, upland rice receives a bidirectional selection between them, which leads to its differences from lowland rice. GDP (growth, development, and reproduction) and DR (drought resistance)

genetic diversity in drought resistance and beneficial recombinant genotypes in the upland rice gene pool (c). Divergent selections (bidirectional selection in the upland rice but directional selection in the lowland rice) would have led to adaptively differentiated ecotypes, particularly for drought resistance (d). This model for the evolution of drought resistance in the upland rice and its balance with productivity has been partially proven to be true in our efforts for developing WDR cultivars, where the bidirectional selection is applied to obtain both high yield potential and good drought resistance in WDR. We have found the induction of many upland-specific/preferential alleles of drought resistance genes (Wei et al. 2016), as well as some recombination events (Xia et al. 2019), in the WDR verities. The further efforts for us are to disclose how these introduced alleles of drought resistance genes work systematically to improve drought resistance and how recombination events break the potential tradeoff between drought resistance and yield potential in WDR. This knowledge could promote the development of WDR.

The concept of water-saving and drought-resistant rice (WDR)

As mentioned above, WDR is needed for sustainable rice production in China. Here, WDR is defined as a new type of rice cultivar that has both high yield potential and good grain quality comparable with the current paddy rice cultivars, as well as the capacity of water saving and/or drought resistance. In this concept, WDR's water saving capacity mainly refers to a higher WUE and more effective use of rainfall during the water-sensitive periods of rice development. In this regard, WUE can be divided into two categories: one is a low physiological water requirement for a plant to maintain its normal physiological metabolic activities and the other is the increased production capacity under a given water supply. The first category of low physiological water requirement could be found mainly in the upland rice, which is adapted to water-limited agro-ecosystems. For example, a WDR cultivar could maintain its yield potential at the irrigation of 360 tons water per mu, while an elite paddy rice variety decreases its yield by 16.9% at this irrigation (Bi et al. 2019). This result indicates WDR possesses better WUE than the paddy rice variety. The second category of WUE mainly depends on the yield potential of a given variety. When comparing the WUE of a drought-resistant upland variety and a current rice hybrid with high yield potential, we found that the hybrid showed much higher WUEs than the upland one (Zou et al. 2006), thus indicating that strong drought resistance does not necessarily mean a high WUE. Furthermore, this indicated that to have a higher WUE, improving yield potential is more important than improving drought resistance (Luo 2010). As a result, WDR combines the low physiological water requirement from upland rice and high yield potential from lowland rice, forming its water-saving character.

Moreover, the effective use of rainfall mainly depends on whether a rice variety could meet the rainfall at appropriate time in the different regions, particularly during its seeding, flowering, and maturity. For example, there is usually high rainfall in late May to August in regions along the Yangtze River in China, where farmers can directly sow dry seeds in the field and depend on rainfall for germination. In addition, the most sensitive stage of rice development (the panicle initiation stage) to drought should be arranged in late August to receive the abundant rainfall in the season.

On the other hand, drought resistance in WDR mainly refers to the capacity of maintaining high water status to achieve normal metabolism in water-limited environments, i.e., to maintain a high-water status under drought via drought avoidance (absorb more water through deep rooting) and drought tolerance (osmotic adjustment, anti-oxidation, etc.). In addition, WDR cultivars should also possess superior characteristics of the current elite modern paddy rice cultivars such as high yield potential, desirable grain quality, good pest and disease resistance, lodging resistance, reasonable tolerance to low or high temperature, etc. Thus, WDR cultivars conceptualized with the characteristics described above should have several advantages in rice production. First, under the well-irrigated conditions, they should have the same high yields and desirable grain quality as the modern lowland paddy cultivars, while saving more than 50% of the irrigation water in production. Second, under rainfed conditions, they can be planted like upland crops such as wheat and maize (directly seeded with dry seeds). Third, WDR normally requires simple and easy crop management practices. Thus, WDR can not only be used for water-saving cultivation in the paddy fields but can also be directly planted in the drylands for realizing a new low-carbon, energy-saving, and environmentally friendly rice production system (Luo 2010).

Development of WDR

Before the WDR concept was fully developed, our breeding practices for developing WDR cultivars already started simultaneously with our efforts in theoretical studies on drought resistance of rice approximately 20 years ago. The original idea was simple and straightforward, i.e., to combine the high yield potential of the modern lowland rice varieties with the high level of drought resistance from the upland rice such that the resultant WDR cultivars would be both high yield potential and drought resistance with the abovementioned traits. However, this was a great challenge to breeders because all the traits related to yield potential and drought resistance are complex; each trait is controlled by large numbers of genes and complicated pathways.

The designed WDR cultivars in our breeding program were expected to have high levels of drought resistance (including drought avoidance and drought tolerance) and high WUE targeted at both irrigated and rainfed ecosystems of China. Thus, all crosses of our breeding program used the upland rice accession with strong drought resistance as one parent and a high-yielding lowland modern variety as the other parent so that transgressive segregations with high yield potential, drought resistance and WUE could be identified in the progeny of the crosses. It is noteworthy that drought tolerance is most important for the WDR specifically growing in irrigated ecosystems because the plow sole limits downwards root growth, which allows the absorption of the deep soil moisture. To increase the WUE, the high yield potential variety is also very important. For example, by crossing drought-resistant varieties (Huhan 3 and Huhan 11) and high-yielding varieties (Wuyugeng 3 and Xiushui 128), we bred a new japonica/geng WDR inbred variety "Huhan 61", which was registered and released in 2015. Huhan 61 showed strong drought resistance and high WUE, and yielded 10.8 t/ha in the water-saving cultivation model (seeding directly on a wet bed, decreasing over 50% irrigation in growth duration). Its utilization rate of irrigation water (excluding precipitation) reached 3.42% or 128% higher than the best cultivar "Xiushui 134" (Gao et al. 2017).

Two common breeding procedures based on strong phenotypic selection were used to manage the progenies for developing WDR cultivars in our breeding program.The first procedure was the conventional pedigree breeding combined with strong and different types of phenotypic selection for specific drought resistance/yield potential traits under either natural and controlled drought stress and normal irrigated conditions (Luo 2018). In the breeding procedure, segregated F2 populations derived from crosses between high-yielding lowland varieties and upland ones were first screened in the mountainous areas (without plow soles) under natural drought for selecting drought avoidance. The selected F3 progeny were then screened under fully irrigated conditions for selecting high yield potential and under the shielded paddy fields with severe water stress for selecting high drought tolerance and WUE (Luo 2018). In this way, all selected breeding lines from our breeding program would have gone through strong phenotypic selection under at least three types of environment. The uniform and advanced lines from this procedure were progeny tested in replicated experiments under the same three environments; this was done to identify promising WDR lines that performed the best under all three conditions to be nominated to multilocational yield trials. Using this approach, we have developed and released many WDR-inbred varieties, cytoplasmic male sterility (CMS) lines, and restorer lines since 2003 (Table 1). The WDR varieties were high yielding with excellent levels of drought avoidance, drought tolerance, and WUE, as well as good grain quality (Luo et al. 2011).

This conventional breeding approach based on strong phenotypic selection in different stress and nonstress environments allows drought resistance genes and their networks to be accumulated across generations in breeding lines. In an effort to understand what genetic and genomic changes would result from the conventional breeding for drought resistance, we compared the

Table 1 The WDR cultivars and sterile lines released for the rainfed and irrigated areas since 2003

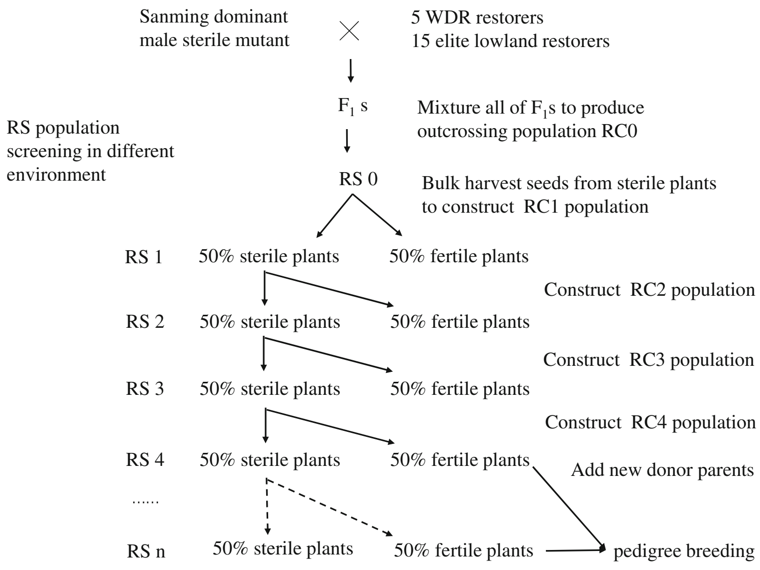
Cultivar name	Type	Subspecies	Release year	Release region
Zhonghan 3	Inbred	Xian	2003	China national released
Huhan 3	Inbred	Geng	2004	China national released
Huhan 7	Inbred	Xian	2004	Shanghai, China
Huhan 15	Inbred	Xian	2005	Shanghai, China
Huhan 19	Inbred	Xian	2017	Shanghai, China
Huhan 1509	Inbred	Xian	2017	Shanghai, China
Zaoyuxianggeng	Inbred	Geng	2012	Shanghai, China
Huhan 61	Inbred	Geng	2016	Shanghai, China
Huhan 68	Inbred	Geng	2019	Shanghai, China
WDR48	Inbred	Geng	2016	Hubei, China
Hanyou 2	Hybrid	Xian	2010	China national released
Hanyou 3	Hybrid	Xian	2006, 2008	Shanghai and Guangxi, China
Huyou 8	Hybrid	Geng	2010	Shanghai, China
Hanyou 113	Hybrid	Xian	2014	Shanghai and Guangxi, China
Hanyou 73	Hybrid	Xian	2014-2017	Anhui, Hunan, Jiangxi, Henan China
Hanyou 737	Hybrid	Xian	2018	Yunnan, China
Hanyou 780	Hybrid	Xian	2018	Shanghai, China
Hanyou 127	Hybrid	Xian	2018	Shanghai, China
Hanyou 540	Hybrid	Xian	2019	Shanghai, China
SAGC 4	Inbrid	Xian	2015	Laos national release
SAGC 7	Inbrid	Xian	2017	Bangladesh national release
Huhan 1A	CMS	Xian	2003	Shanghai, China
Huhan 2A	CMS	Geng	2010	Shanghai, China
Huhan 5A	CMS	Xian	2012	Shanghai, China
Huhan 7A	CMS	Xian	2012	Shanghai, Anhui of China
Huhan 11A	CMS	Xian	2013	Shanghai, China
Shenhan 5A	CMS	Xian	2016	Shanghai, China
Huhan 1S	PTSGMS	Xian	2016	Shanghai, China
Shenhan 1S	PTSGMS	Xian	2016	Shanghai, China
Huhan 9S	PTSGMS	Xian	2018	Shanghai, China
Huhan 74S	PTSGMS	Xian	2018	Shanghai, China

genomic and transcriptomic differences between two highly related lines, Huhan 2B and Hanfeng B. Huhan 2B is a newly developed *Geng* CMS maintainer, developed in a BC breeding program using Hanfeng B (a high yield CMS maintainer) as the recipient and a drought-resistant line and Huhan 3 as the donor. Huhan 3 was developed from a cross involving three parents: a Chinese lowland landrace Ma-Wan-Nuo, an upland variety IRAT109, and high-quality rice P77. Under drought-stress conditions, Huhan 2B had much better drought resistance than Hanfeng B, and its yield was equivalent to that of Hanfeng B under well-irrigated conditions. The genomic similarity between Huhan 2B and Hanfeng B was 84% with differential SNPs at 7256 loci. As expected, the differential responsive genes for drought were significantly enriched in the transcriptional regulatory biological pathways in Huhan 2B, which were regulated by three transcription factor families (Wei et al. 2016). Another major difference between Huhan 2B and Hanfeng B was reflected at the level of posttranscriptional modification, in which the expression of variable splicing genes in Huhan 2B was significantly different from that of Hanfeng B and enriched in the transcription regulatory networks (Wei et al. 2017). These results indicated that under strong phenotypic selection in drought environments for the conventional breeding strategy, large numbers of genes in transcription regulatory networks for drought adaptation and drought resistance were retained and aggregated across the genomes of the breeding progeny, resulting in greatly improved drought resistance of Huhan 2B (Wei et al. 2016, 2017).

In addition to the genetic difference involving large numbers of genes and complex gene networks in newly developed drought resistant lines from our conventional breeding program, epi-mutation accumulation was another aspect we observed with the drought resistant lines developed from strong phenotypic selection. As mentioned above, drought-induced transgenerational epimutations of DNA methylation was a unique characteristic of the upland rice. In fact, we also observed that inbred rice varieties showed improved drought resistance when they were grown under long-term dryland conditions, and this “induced” drought resistance of inbred rice varieties was apparently associated with transgenerational variations of DNA methylation in these inbred varieties under six successive generations of drought (Zheng et al. 2013). To disclose the potential role of drought-induced, transgenerational, and inherited epimutations in drought resistance, we established two rice epimutation accumulation lines through exerting 11 successive generations of drought imposition. Based on the highly integrated DNA methylome maps generated by whole-genome bisulfite sequencing, we found that the stress-induced epimutations occurred preferentially in some “hot spots” in the genome that are associated with drought tolerance. These drought-induced transgenerational epimutations included differentially methylated positions, single-cytosine methylation polymorphisms, and differentially methylated regions. Furthermore, genes showing transgenerational epimutations directly participate in stress-responsive pathways, indicating that transgenerational epimutations are able to contribute to improved drought resistance in drought-treated rice lines (Zheng et al. 2017). Thus, the inheritable epigenetic variations induced by drought can provide a new way to develop drought-resistant rice varieties.

As we have known, most rice-breeding programs usually involve a limited number of elite germplasm, resulting in the reducing genetic diversity. Meanwhile, as yield potential and drought tolerance are highly complex and quantitative traits that are determined by multiple genes/QTLs, it is difficult and time-consuming to pyramid all of these genes (Pang et al. 2017). In order to solve the above problems, we adopted the strategy of recurrent selection. Recurrent selection involving dozens of parents and multiple cycle of trait selection is an effective breeding approach to simultaneously broad genetic diversity and improve the quantitative traits. In RS procedure, the Sanming dominant male sterile (SDMS) mutant was used as an outcrossing tool (Huang et al. 2008), and different types of RS populations were developed. For example, we developed successfully a restorer RS population used the SDMS mutant as female parent and 20 restorers as male parents (Fig. 3): Firstly, a total of 15 lowland restorers and 5 WDR restorers was crossed with SDMS mutant respectively and produce the F1generation. The restorers have advantages on different characteristics, such as high yield potential, drought resistance, excellent grain quality, and resistant to pest and disease. Secondly, all of F1 were planted together to form the RS 0 population and only harvested seeds from sterile plants at mature stage. These seeds were planted together to form the RS 1 population. The same step was repeated to advance to RS 4 population. Thirdly, in RS cycle, the population was screened under various adverse environments with

Fig. 3 The scheme of recurrent selection (RS)



different stresses (drought, blast, and high temperature). Finally, after four recurrent selection cycles, we began to add the new donor parents and select target phenotype in fertile plants for pedigree breeding. Using this procedure, we successfully developed many WDR restorer lines, such as Hanhui780 and Hanhui839, showing water saving and drought resistance as well as multi-disease resistance and high yield.

Another breeding approach we used was the value-added breeding by marker-assisted selection. Actually, the drought resistance of a plant is extremely complex and related to many genes and interactions among genes and environments. Although finding drought-resistant genes and applying them to breeding practice has always been a popular research topic, so far, there are few reports of using these genes to breed drought-resistant varieties and applying them to production. Actually, as Pennisi (2008) argued, of the large number of published candidate drought resistance genes revealed by genomics, almost none had shown any impact in field performance. This is because drought resistance is a complex trait compromised by thousands of drought resistant genes and their interactions with environments (Shinozaki and Yamaguchi-Shinozaki 2007; Hadiarto and Tran 2011). In other words, the formation of drought resistance is resulted from a systematic network by many interacted drought resistance genes, rather than a single drought–resistant gene. For this reason, a strategy of pyramiding drought-resistant genes of different mechanisms in breeding has been proposed by many researchers (Ali et al. 2017; Cui et al. 2018). The success of WDR breeding by introducing drought avoidance form upland rice and drought tolerance from lowland rice via conventional breeding approach is just the case. As the evolution of drought resistance is a systematic process, it is necessary for us to learn the formation of drought avoidance in upland rice and drought tolerance in lowland rice during their adaptation. Meanwhile, we should also disclose how these drought avoidance and drought tolerance genes work together in WDR (Zhou et al. 2016). Once we learn the systematic network among several key genes, we can efficiently apply marker-assistant selection in WDR breeding. However, the conventional breeding approach of RS is still the first choice for developing WDR currently.

However, the marker-assistant selection approach is very useful to integrate important traits controlled by single major genes such as disease and insect resistance and grain quality. A rice cultivar must have sufficient levels of resistance to major diseases and insects before they can be distributed to farmers. Thus, we used marker-assistant selection to improve qualitative traits such as the pest and disease resistance of WDR varieties. For example, Hanhui 3, an elite drought resistant restorer for 3 released WDR hybrids (Huyou 2, Hanyou 73, and Hanyou 113), is one susceptible to blast and bacterial leaf blight (BLB), which blocks its commercialization. We have successfully transferred two genes (*Pi9* and *Xa234*) resisting to blast into the genetic background of Hanhui 3, forming three isogenic introgression lines (NIL) by the marker assistant selection procedure (Fig. 4) (Zhang et al. 2019). The three Hanhui 3 NILs were then crossed with the drought-resistant CMS lines to produce WDR hybrids of excellent resistance to blast and BLB. Furthermore, we have also transferred 4 genes (*Bph6*, *Bph9*, *Bph14*, and *Bph15*) resisting to brown planthopper into the genetic background of Hanhui 3.

Using the above two breeding approaches, we have developed 20 new WDR cultivars, including eleven WDR inbreds, nine WDR hybrids, and six CMS lines since 2003 (Table 1). These WDR cultivars have been grown in both rainfed and irrigated ecosystems in China. Several varieties were very successful in various Asian and African countries; two inbred lines were released in Laos and Bangladesh, whereas the total accumulated area in China is over million hectares. In 2016, the Chinese Ministry of Agriculture formally implemented the “Water-saving and drought-resistance rice terminology” industry standard (NT/T 2862-2015).

Management technology of WDR

Because WDR represent a new type of rice cultivars, they require different crop management technology in order to maximize their advantages of water saving and adaptation to rainfed environments compared with the conventional modern paddy rice cultivars. In this section, we would like to introduce several common crop management technologies, including both direct seeding and transplanting technologies for different WDR cultivars based on our research results. It should be pointed out that the developed WDR cultivars include four series of WDR cultivars including inbred varieties and hybrids of both *Xian* and *Geng* subspecies registered to farmers in different provinces of China. Although these WDR cultivars have wide adaptability and can be grown in different rice ecosystems, the most suitable crop management practices of a WDR cultivar differ considerably when they are grown under the lowland paddy fields (Fig. 5a, b) and rainfed fields (Fig. 5c). The two cases are discussed in detail below.

Water-saving cultivation in the lowland paddy field

When WDR cultivars are grown in irrigated environments as the current lowland paddy rice is, the following 3 practices should be adopted so as to save over 50% irrigated freshwater by dry management (wet-seeded with aerobic rice cultivation) (Zhao et al. 2018): (1) soaking seeds until the emergence of the white tip of coleoptiles before direct seeding in well-organized and moist fields using mechanical or artificial sowing, (2) spraying herbicides two times (before and after sowing) to remove weeds, and (3) keeping the field soil moist, especially at the plant stages sensitive to drought (panicle initiation). No water layer needs to be retained in the fields during the whole growth period, but timely irrigation is necessary to ensure normal plant growth during the long period of drought.

Wet-seeding with aerobic rice cultivation often produces high yields while saving freshwater resources, reducing the application of chemical fertilizers and pesticides, and minimizing non-point source pollution and carbon emission. For example, in the demonstration of planting Huhan 61 in 2016 in Shanghai, China, Huhan 61

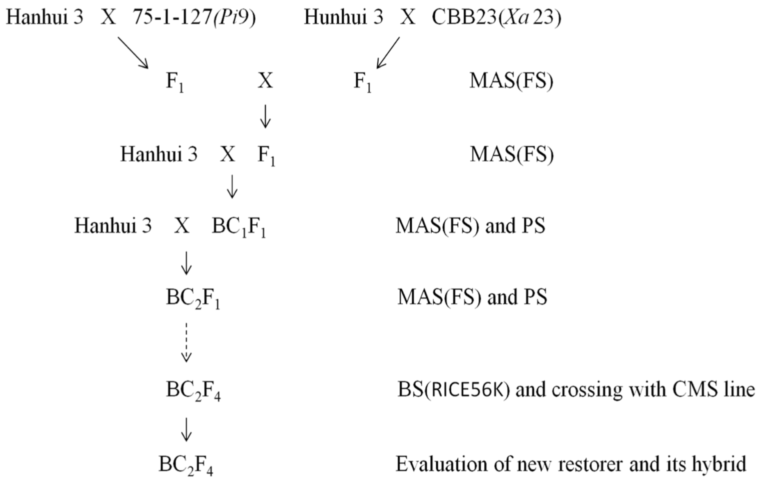


Fig. 4 The diagram for value-added breeding. MAS, maker assistant selection; FS, foreground selection; PS, phenotypic selection; BS, background selection. RICE56K is a rice SNP array containing ~ 60 K SNPs used in BS

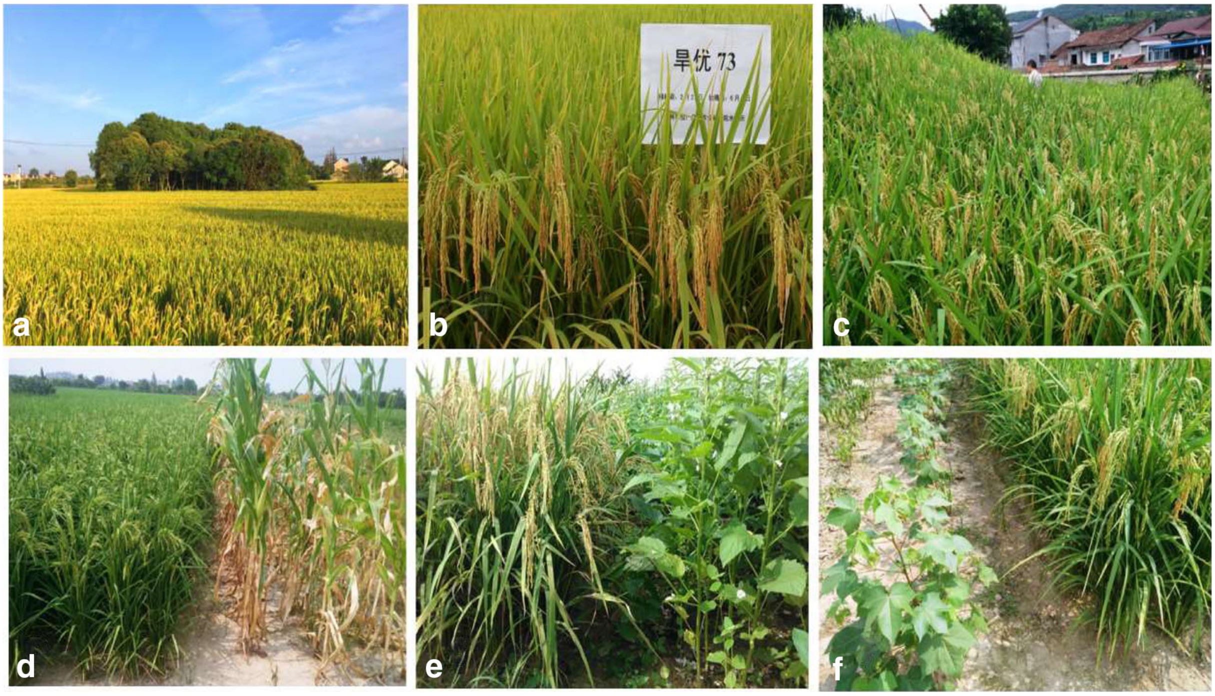


Fig. 5 WDR in fields of different managements. **a** WDR (Huhan 61) in irrigated lowland by mechanical direct seeding. **b** WDR (Hanyou 73) in irrigated lowland by mechanical transplanting. **c** WDR (Hanyou 73) in hillslope by dry seeded with aerobic cultivation. **d-e** the WDR-dry crops intercropping with aerobic cultivation (WDR, maize; WDR, sesame; WDR, cotton)

yielded 10.8 t/ ha, 5.4% higher than that of CK lowland rice Xiushui 134. More importantly, compared with planting Xiushui 134, planting Huhan 61 not only reduced irrigation by 53.3% and urea application by 76% but also significantly reduced agricultural nonpoint source pollution and methane emission (Gao et al. 2017).

Dry seeding with aerobic cultivation in the rainfed field

In rainfed conditions, WDR is planted by dry seeding followed with the aerobic cultivation just as wheat. The farmer usually uses direct sow machine to sow WDR seeds. The machine has two containers, which are filled with fertilizer and dry seed, respectively. With the machine, farmers can sow the seed while simultaneously supplying the fertilizer. The yield with this cultivation mode is approximately 6 t per hectare. Compared with the wet-seeded lowland paddy rice, the weeds in these fields are more complex and additional applications of herbicide must be carried out. However, the dry seeding is much simpler and was actually welcomed by the farmers. The plant areas have increased significantly in recent years in China. As an excellent hybrid in which WDR was combined in over one hundred thousand hectares per year in China, Hanyou 73 was widely planted in the dry-seeded mode in rainfed land and achieved a higher and stable yield. For example, as the demonstration planting in a farmer's field in Funan County, Anhui Province showed, Hanyou 73 yielded 9.3 t/ha through mechanical direct seeding and being twice irrigated with a total irrigation volume of 1200 m^3/ha throughout the growth period (Luo 2018). In practice, the farmer also intercropped WDR with dry crops such as cotton, corn and sesame (Fig. 5d, e).

R&D of WDR in the future

Breeding practice of WDR has achieved great success in China, which has resulted in dozens of WDR varieties and corresponding cultivation technologies. Many efforts have been made to disclose genetic and epigenetic bases of drought avoidance and drought tolerance in WDR, including QTL mapping, functional study of drought resistance genes, and genetic/epigenetic mechanisms of drought resistance evolution in rice. However, there is still great knowledge gap between theoretical research and breeding. First, the acquirement of drought resistance in WDR remains a puzzle. It may refer to the introduction of beneficial alleles of drought-resistant genes from upland donors (Wei et al. 2016), transcriptomic alterations in WDR (Wei et al. 2017), and directional epigenetic changes (Zheng et al. 2013, 2017). Second, WDR breaks the tradeoff between yield potential and drought resistance, which is hypothesized by the accumulated recombinant events during its breeding (Xia et al. 2019). To bridge the knowledge gap, it is very important to identify drought-resistant genes, particularly using plant materials and experimental populations derived in WDR breeding. It is also essential to study the evolution of drought resistance among rice ecotypes, which can provide valuable information for us to understand genetic basis of drought resistance and its roles in WDR. With the accumulation of this knowledge, we can then develop effective molecular markers relevant to drought resistance. They can be applied in marker assistant selection or genome selection to accelerate the WDR breeding. Meanwhile, the sustainable agriculture requires pyramiding of green characters in rice (e.g., nutrient efficiency, simplified, and efficient cultivation, resistance to diseases and insects, etc.), which has been described by Zhang as GSR (Zhang 2007). DR is a vital part of GSR, which focus on enhancing rice drought resistance and water use efficiency in first to meet the increasing challenge of water deficiency and drought. It performs well in the medium-and-low yield field. We have improved insect resistance, disease resistance, and direct-seeding tolerance in WDR by introducing key functional genes via marker-assistant selection. We also begin to improve salt-tolerance and nutrient efficiency by recurrent selection using appropriate donors. Finally, many WDR verities and lines have been under trails at home (e.g., the Huaihe basin, South China, Central China, Northeast China, etc.) and abroad (e.g., The Philippines, Indonesia, India, Nigeria, Algeria, etc.). They are welcomed by local farmers as they are labor saving, environment friendly, and beneficial in economy. However, the economic, ecological, and social benefits of WDR require further rigorous assessment. In summary, WDR has great prospective and calls for global cooperation in development and theoretical research.

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Compliance with ethical standards

Competing interests The authors declare no competing interests.

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