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Weedy rice, a hidden gold mine in the paddy field

WEEDY RICE IS A NOVEL ECOTYPE OF RICE

Weedy rice (*Oryza* spp.) is an increasingly invasive paddy weed, which mimics cultivated rice at the seedling stage but is distinguished from cultivated rice with strong seed shattering and seed dormancy, which are typical phenotypic characteristics of wild rice. On the origins of this conspecific form of cultivated rice (*Oryza sativa*), four hypotheses have been proposed and debated for decades: (1) origination from wild rice (*Oryza rufipogon* or possibly other wild *Oryza* species); (2) origination following hybridization between wild and cultivated rice; (3) direct descent from escaped cultivated rice; and (4) intervarietal hybridization between different domesticated rice varieties (Ellstrand et al., 2010). Recent population genomic investigations based on whole-genome variation provide powerful phylogenetic and demographic evidence for the de-domestication origination of weedy rice (Li et al., 2017; Qiu et al., 2017, 2020; Sun et al., 2019). Global sampling and genome analyses of weedy rice have revealed that de-domestication of cultivated rice (including modern cultivars and landraces) is the major pathway to produce weedy rice worldwide, with secondary roles for gene flow from local wild rice (e.g., weedy rice in Southeast Asia) and subspecies hybridization (e.g., weedy rice in Brazil) (Song et al., 2014; Qiu et al., 2020). Notably, de-domestication events have occurred recurrently during the history of rice domestication (Figure 1A). While some strains appear to have emerged early in the history of rice agriculture (Li et al., 2017), others have origins in the elite cultivars that were developed during the Green Revolution of the 1960s (Song et al., 2014; Qiu et al., 2020). For example, one of the most recent de-domestication events has its origins in the widely grown modern dwarf Chinese rice cultivar Nanjing11 (Qiu et al., 2020). Years of accumulation of seeds in fields result in a large and diverse gene pool, reflecting the genetic legacy of cultivated rice from the past. Interestingly, modern de-domestication events have been also observed in other crops (e.g., wheat and barley), as evidenced by population genomics studies (Wu et al., 2021).

Despite the complicated evolutionary relationships among weedy, cultivated, and wild rice, their ecological niches are well defined. Weedy rice conceals itself among cultivated rice plants by crop mimicry at the vegetative growth stage in the agroecosystem. To escape from being harvested and removed along with cultivated rice, mature seeds of weedy rice fall off from spike rachis (i.e., shatter) early and easily (Qi et al., 2015; Qiu et al., 2017). Weedy rice also shows a higher degree of seed dormancy compared with cultivated rice, with buried seeds remaining viable for several or more years (Gu et al., 2004).

As for how the causative variations underlying the acquisition of wild-like characteristics in weedy rice emerge, spontaneous *de novo* mutation or introgression from wild rice are all possible (Song et al., 2014; Qiu et al., 2017). Resembling wild rice in seed features increases the fitness of weedy rice in paddy fields. The adaptively differentiated genomic regions between weedy and cultivated rice overlap a little with rice domestication regions, implying that rice de-domestication occurred mostly through novel genomic changes unrelated to domestication (Sun et al., 2019; Qiu et al., 2020). In several thousand years of accumulation in fields, weedy rice has apparently generated genetic novelty and diversity from cultivated rice, particularly in those weeds with mixed genetic background of different types (*indica*, *japonica*, and *aus*) (Figure 1B). Thus, as a novel ecotype of rice, weedy rice contains a rich pool of potentially useful genetic resources.

WEEDY RICE PROVIDES RESOURCES FOR RICE FUNCTIONAL GENOMIC STUDIES AND BREEDING

Successful reproductive advantages of weedy rice in paddy fields have inspired researchers to explore the genetic mechanisms. Using weedy rice as key parental lines, a series of quantitative trait locus (QTL) mapping trials for important traits have been carried out for over two decades, especially on rice seed dormancy and seed shattering (Gu et al., 2004; Qi et al., 2015; Sun et al., 2021). Several QTLs for the shattering in weedy rice have been identified and, however, not located at the well-characterized shattering loci of *sh4* and *qSH1* (Qi et al., 2015). A recent study revealed that the Kasalath-type (*aus*) *qSH1* allele, underlying high shattering, was fixed in the *japonica* weedy rice population from northern China and highly differentiated from local cultivated rice with derived alleles; this suggests that Kasalath-type *qSH1* may be involved in shattering alteration in *japonica* weedy rice from northern China (Sun et al., 2019). For seed dormancy and red pericarp, several associated QTLs were identified. The major effect loci (*qSD7-1* and *qPC7*) overlap with the *Rc* locus (Gu et al., 2004, 2011; Qi et al., 2015) and the causative effect of a functional *Rc* allele (lacking the 14-base-pair frameshift deletion found in most domesticated rice) was confirmed by subsequent population genomics studies (Li et al., 2017; Qiu et al., 2017). However, whether the reversion of *Rc* to functionality is due to spontaneous back mutations, gene flow from wild rice, or standing variation from older landraces that lack the domestication allele remains uncertain. *Rc* contributes to the seed dormancy by promoting the production of abscisic acid (ABA) and positively regulating the biosynthesis of proanthocyanidin, which have antioxidant properties to improve the seed storage duration (Gu et al., 2011). *GD1*, a B3 domain-containing transcription factor, is putatively associated with seed germination in *japonica* weedy rice (Qiu et al., 2020).

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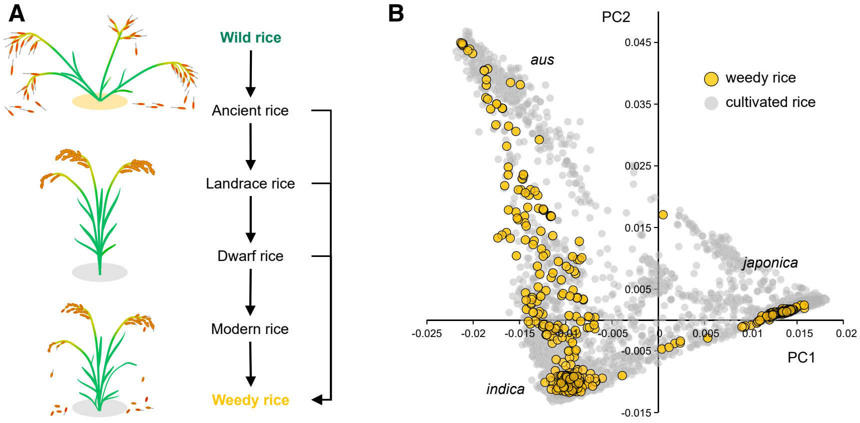

Figure 1. Origin and genetic diversity of weedy rice.

(A) De-domestication events of cultivated rice in paddy field during the evolutionary history of rice. In the present paddy field, weedy rice is composed strains from different historic times or types of rice.

(B) Genetic diversity of cultivated and weedy rice based on their genomic data, presented by the first two principal components (PCs) of PC analysis. Data source: weedy rice, 524 accessions (Li et al., 2017; Qiu et al., 2020); cultivated rice: 4,481 accessions (Wang et al., 2018).

Recently, Zhang et al. identified diverse genes in weedy rice that confers anaerobic germination and anaerobic seedling development tolerance, by comparative multi-omics analysis (Zhang et al., 2021). They helps rice to improve flood adaptation by several ways, such as by enhancing gibberellic acid synthesis and reducing ABA sensitivity. enhancing gibberellic acid synthesis and reducing ABA sensitivity. The inhibition of ABA would increase the risk of pre-harvest sprouting given that the dormancy is largely determined by ABA. To balance the fitness, *Rc* is responsible for reducing the risk of pre-harvest sprouting by regulating the ABA signaling pathway. The findings suggest weedy rice can serve as unique resources for the genetic improvement of direct-seeding rice.

Stronger tolerance to biotic and abiotic stress than cultivated rice is observed in some weedy rice strains, such as high tolerance to salinity (Zhang et al., 2018), blast disease (Liu et al., 2015), and herbicides (Qiu et al., 2020). By regulating the Na^+/K^+ ratio and absorption and transport of other ions, some weedy rice strains show stronger tolerance to salt stress than cultivated rice during seed germination and seedling growth (Zhang et al., 2018), which offers breeders a resource for improving salt tolerance in cultivated rice. Liu et al. (2015) reported that weedy rice in the United States exhibited a broad resistance spectrum to the fungus *Magnaporthe oryzae*, the most important and destructive disease of cultivated rice worldwide, and 28 resistance QTLs were identified, which are potential genetic sources of novel blast *R* genes for rice resistance breeding. Herbicide resistance is crucial for the survival of weedy rice in paddy fields, especially with the promotion of herbicide-resistant rice resistant to acetolactate synthase (ALS) inhibiting herbicides. Besides the causative mutations (Ala122Thr, Ser653-Asn, and Gly654Glu) that have been applied in developing herbicide-resistant rice cultivars, a novel mutation (Ala205Val) conferring strong resistance to ALS inhibitor is observed in weedy rice, which has never been reported in cultivated and wild rice before (Qiu et al., 2020).

Against the global climate change, breeding rice varieties with high adaptation to abiotic stress (e.g., drought, salinity, heat, and flooding) is urgent. As a conspecific, reproductively compatible plant of cultivated rice, weedy rice could be used as parental lines and donor of superior alleles for rice breeding directly. In sum, weedy rice is a gold mine to be exploited as a rich genetic resource for rice functional genomics studies and breeding.

FUTURE DIRECTIONS OF WEEDY RICE GENOMIC STUDIES

The pan-genome of cultivated rice has been constructed recently, which provides a more precise way to interrogate genetic information of cultivated rice, for guiding gene mining and molecular breeding by design (Qin et al., 2021). In the currently available rice pan-genome, weedy rice was missed. It can be expected that more *de novo* assemblies of weedy rice genomes will enhance the size of rice pan-genome, deepen our understanding of rice de-domestication, and facilitate the mining of superior alleles.

Multi-omics approaches will further accelerate the understanding of trait evolution and environmental adaptation of weedy rice. Currently, genomic studies of weedy rice mainly concentrate on the origin and adaptive genomic differentiation by using whole-genome resequencing approaches. Genetic mechanisms underlying the alteration of some traits in weedy rice are still unresolved. For example, the loci controlling shattering of weedy rice identified by QTL mapping remain unknown for most weedy rice populations. Genotyping by high-depth resequencing also reveals no obvious differences in allele frequency between weedy and cultivated rice at the known shattering-related genes (Wu et al., 2021). It is possible that there are undetected but crucial genomic sequence differences or epigenetic changes including three-dimensional genome organization alterations between the genomes of weedy and cultivated rice, underlying the phenotypic variations. Integration of multi-omics data can be implemented to make novel discoveries and provide innovative means for identifying the mechanisms ascribing to these adaptive de-domesticated traits.

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