Population Genomics of Weedy Crop Relatives: Insights from Weedy Rice

Lin-Feng Li and Kenneth M. Olsen

Abstract Weedy crop relatives can evolve as a byproduct of the domestication process, and most modern crop species have conspecific or congeneric weedy relatives. These weedy relatives invade crop fields and aggressively outcompete desirable cultivars through a suite of weediness traits. Weedy rice (*Oryza sativa* f. *spontanea*) is a highly morphologically diverse group of undesirable rice strains that infest rice production areas and causes heavy yield loss worldwide. In this chapter, we focus on recent phenotypic and genomic characterizations of weedy rice, with special emphasis on its evolutionary origins and adaptive mechanisms. While weedy rice strains can be broadly divided into "crop mimic" and "wild-like" forms, genetic surveys around the world have revealed that most strains have evolved through de-domestication from cultivated rice and that this process has occurred multiple times from different genetically distinct rice varieties. Weedy strains have further evolved and adapted with varying degrees of input from domesticated and wild *Oryza* populations. The weediness traits can evolve independently in weedy rice through a combination of de novo mutation, standing genetic variation, and adaptive introgression. Recent advances in high-throughput sequencing platforms have made it possible to perform genome-enabled QTL mapping and comparative population genomics approaches to identify weediness-related genes in independently evolved weedy strains. We hope that perspectives raised in this review can provide a point of comparison for future studies of other weedy species.

Keywords Adaptive introgression · Agricultural weeds · Comparative population genomics · De novo mutation · De-domestication · Standing genetic variation · Weediness trait · Weedy rice

L.-F. Li
Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, and Coastal Ecosystems Research Station of the Yangtze River Estuary, School of Life Sciences, Fudan University, Shanghai, China

K. M. Olsen (✉)
Department of Biology, Washington University in St. Louis, St. Louis, MO, USA
e-mail: kolsen@wustl.edu

1 Introduction

1.1 Weedy Crop Relatives: Plants at the Margins of the Domestication Process

The domestication of wild plants is one of the most pivotal achievements in human history, having led to the development of agricultural settlements and ultimately the emergence of urban centers and civilization (Hilbert et al. 2017). Modern humans still rely almost entirely on a handful of staple food crop species that were domesticated approximately 10,000 years ago in several geographical centers of domestication around the world (Larson et al. 2014). Archaeobotanical remains and other data suggest that domestication was likely a protracted process (Allaby et al. 2008; Larson et al. 2014), with its origins in the harvesting of wild cereals and other plants (Hillman et al. 2001; Weiss et al. 2006; Willcox et al. 2008). Over time, wild plant gathering would have shifted from reliance on wild populations, whose growth was tolerated or encouraged (e.g., through burning or clearing of competing vegetation), to active cultivation of wild species, to farming of protodomesticates bearing some traits that distinguished them from their wild relatives (e.g., reduced seed shattering and dormancy), to farming of fully domesticated landraces that were dependent on human cultivation for their perpetuation. Subsequent to these initial steps in the domestication process, later selective breeding gave rise to crop varieties with varietal-specific improvement and diversification traits (e.g., fruit color, starch and cooking quality, local climatic adaptation) (Meyer and Purugganan 2013; Li et al. 2017).

Humans can take credit not only for crop domestication but also for the emergence of agricultural weeds that have plagued farmers' fields ever since. Agricultural weeds arose as byproducts of the shift to subsistence farming and have evolved to exploit the agricultural habitat (De Wet and Harlan 1975; Warwick and Stewart 2005; Stewart 2017). Among agricultural weed species, those that are closely related to crop species can pose especially difficult challenges for weed detection and control. It is very likely that these weedy crop relatives have formed a part of the agricultural weed assemblage since the earliest days of agriculture (see, e.g., Fig. 1). Weedy crop relatives infest crop fields and aggressively outcompete desirable cultivars through a combination of weediness traits, such as rapid growth, efficient seed dispersal, and persistent seed dormancy (Baker 1965; Vigueira et al. 2013). Most contemporary crop species have conspecific or congeneric weedy relatives (Ellstrand et al. 1999); some of the best known examples include weedy beet (*Beta vulgaris*), weedy sorghum (shattercane) (*Sorghum bicolor*), and weedy rice (*Oryza sativa* f. *spontanea*) (Arnaud et al. 2003; Barnaud et al. 2009; Stewart 2017). While weedy crop relatives often possess some traits that are more characteristic of wild species than domesticates (e.g., seed shattering and dormancy), they are specifically adapted to agroecosystems and typically are not found outside of crop fields (Stewart 2017).
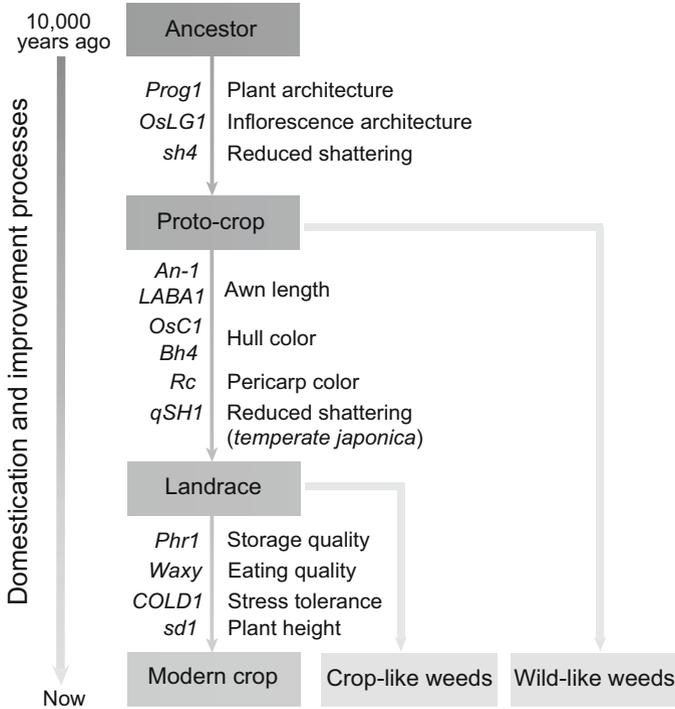
Fig. 1 Origin models of different weedy rice types

Among weedy crop relatives, weedy rice is the species that is by far the best characterized through genomic analyses. For this reason, we focus specifically on weedy rice in this chapter, with the hope that the research reviewed here can provide a point of reference for future genomic characterizations of other weedy crop relatives. Weedy rice infests rice production areas and causes crop yield losses worldwide (Delouche et al. 2007; Qiu et al. 2014; Song et al. 2014). As described below, it includes various forms of undesirable rice strains that occur in cultivated rice fields and possess characteristics intermediate between wild and domesticated rice (De Wet and Harlan 1975; Oka 1988; Delouche et al. 2007). Key features of weedy rice include highly shattering seed, deep seed dormancy, dark-pigmented pericarps (a trait associated with seed dormancy), rapid vegetative growth, and the ability to aggressively outcompete the crop for nutrients and light (De Wet and Harlan 1975; Basu et al. 2004; Estorninos et al. 2005; Burgos et al. 2006; Xia et al. 2011).

Weedy forms of rice have likely been present at the margins of rice fields for thousands of years. Written documentation of weedy rice extends back at least as far as the ancient Chinese book "Huainanzi"《淮南子》, which dates to 2,200 years ago. However, it has only gained worldwide attention as a major agricultural weed in recent decades (Gressel and Valverde 2009). This change is primarily due to the worldwide agricultural shifts away from hand-transplanting of paddy-grown rice

seedlings (which, while time-consuming and laborious, has the advantage of providing ample opportunities for hand weeding of rice fields), to mechanized, direct-seeded farming (Hill et al. 1994; Chauhan 2013; Ziska et al. 2015). In China, for example, weedy rice infestations now affect up to three million ha of rice production areas, with annual yield losses exceeding 3.4 billion kg (Liang and Qiang 2011). Similarly, weedy rice infestations have been estimated to cause grain yield losses of more than $20 and $45 million in the United States and Peninsular Malaysia, respectively (Estorninos et al. 2005; Gealy et al. 2012).

Weedy rice strains are highly morphologically variable, but strains have been proposed to fall into two broad adaptive strategies (Ling-Hwa and Morishima 1997; Suh et al. 1997; Federici et al. 2001): a "crop mimic" form (characterized by short stature, low degree of shattering, and overall similarity to the crop), which persists via crypsis in rice fields, and a more wild-like form, which aggressively outgrows its domesticated relative and then lodges, scattering its seed into the soil where they can remain viable for 20 years or more. Morphological and molecular-based surveys around the world suggest that different weedy rice types have evolved independently from genetically distinct domesticated and wild relatives and that diverse genetic mechanisms have contributed to the formation of weediness traits (Song et al. 2014; Qi et al. 2015; Huang et al. 2017; Li et al. 2017; Qiu et al. 2017). This chapter focuses on recent phenotypic and population genomic insights into the evolutionary origins of weedy rice and introductions out of the center of rice domestication in Asia to rice production areas worldwide.

2 Evolutionary Origins of Domesticated and Weedy Rice

2.1 Origins of Domesticated Rice

As the evolution of weedy rice is fundamentally intertwined with the domestication history of its cultivated relative, we first provide a brief overview of the current state of knowledge on rice domestication origins. Asian cultivated rice (*Oryza sativa* L.) is one of the world's oldest and most important crop species, serving as the primary staple crop for more than one-third of the global population. As the first crop species to have a reference genome published (Goff et al. 2002; Yu et al. 2002), it has also become an important model system for plant biology research (Sasaki 2005; IRRI 2006). There are two genetically diverged subspecies in cultivated rice, namely *indica* and *japonica*, and each subspecies comprises two or more genetically distinct varietal subgroups within it (Garris et al. 2005; Sweeney and McCouch 2007; Zhao et al. 2011). *Aus* and *indica* are the two major subgroups within the *indica* subspecies, and *aromatic, tropical japonica* and *temperate japonica* are the major subgroups within the *japonica* subspecies. The two subspecies are morphologically distinct and tend to be grown in different geographical regions, with *indica* rice predominating in the tropics and *japonica* varieties cultivated in more temperate climates; they also show partial reproductive isolation (Huang et al. 2012a;

Ouyang and Zhang 2013). Genome-wide sequence divergence between the *indica* and *japonica* subspecies indicates a divergence time of some 200,000–400,000 years ago, which is long before origins of agriculture and thus predates the domestication process; this divergence is also present among individuals within the wild progenitor species, *O. rufipogon* (Ge et al. 1999; Zhu and Ge 2005).

It is widely accepted that *indica* and *japonica* rice were domesticated from *O. rufipogon* in Asia and that this domestication occurred around 10,000 years ago (Oka 1988; Cheng et al. 2003; Fuller et al. 2010). However, there is no consensus on the exact domestication history and the origin(s) of the present-day varietal groups. Two primary alternative hypotheses have been proposed. A single-origin model proposes that rice was domesticated from its wild ancestor only once, and the two cultivated subspecies, *japonica* and *indica*, emerged during the domestication process. Genetic evidence for this model comes from a number of domestication genes where *japonica*-derived domestication alleles are fixed in most or all crop varieties across both subspecies (e.g., *sh4*, controlling reduced seed shattering; *prog1,* controlling erect plant growth; and *rc*, controlling white pericarp/reduced dormancy) (Li et al. 2006; Sweeney et al. 2006; Jin et al. 2008; Tan et al. 2008). Demographic modeling based on SSRs and genome-wide SNPs also supports a single domestication origin (Gao and Innan 2008; Molina et al. 2011).

In contrast, a series of other studies based on phylogenetic and population genetic analyses have proposed that *indica* and *japonica* rice were domesticated independently from different subgroups of *O. rufipogon*. Support is provided by phylogeographic analyses indicating that *indica* and *japonica* are associated with geographically distinct populations of *O. rufipogon*, with *japonica* rice most closely related to populations in southern China and *indica* rice closest to populations in South and Southeast Asia (Cheng et al. 2003; Zhu and Ge 2005; Londo et al. 2006). Population genomic analyses based on ~1,500 wild and cultivated rice accessions similarly indicate that *japonica* was first domesticated from the *O. rufipogon* populations near to the middle area of Pearl River in southern China and that *indica* was subsequently developed from crosses between domesticated *japonica* and local populations of *O. rufipogon* in Southeast and South Asia (Huang et al. 2012a). Consistent with the dual-origin domestication hypothesis, archaeological data provides evidence for early rice cultivation both in the Yangtze Valley (China) and the Ganges Valley (India) beginning at ~8,000–9,000 and ~4,000 years ago, respectively (Fuller et al. 2010; Gross and Zhao 2014; Zuo et al. 2017). In contrast to the demographic models supporting a single origin (Gao and Innan 2008; Molina et al. 2011), gene genealogies across the rice genome indicate that that majority of the *indica* and *japonica* genomes appear to be of independent origin (He et al. 2011). Genomic regions with shared domestication alleles appear to be the rare exception to this pattern and are interpreted under the dual-origin model as evidence of occasional selective introgression during the domestication process (He et al. 2011). Regardless of the number of geographically distinct domestication events, all evidence suggests that *indica* and *japonica* rice are descended from pre-differentiated ancestral *O. rufipogon* populations.

2.2 Evolutionary Roots of Weedy Rice in Different World Regions

As reviewed in the sections below, genetic surveys around the world have revealed multiple independent origins of weedy rice (Reagon et al. 2010; Huang et al. 2017; Li et al. 2017). While different weed strains are all characterized by some weed-adaptive traits (such as seed shattering and dormancy), they also show a broad range of phenotypic variation in both vegetative and reproductive features (Cao et al. 2007; Song et al. 2014; Qiu et al. 2017). This diversity has led to the hypothesis that different weeds may have evolved through different degrees of input from various domesticated and wild *Oryza* populations. Several non-mutually exclusive hypotheses have been proposed, including (1) direct descent from wild rice that adapted to crop fields (De Wet and Harlan 1975; Harlan 1992), (2) intervarietal hybridization within the crop species (Qiu et al. 2014), (3) interspecies hybridization between cultivated and wild rice (Tang and Morishima 1996), and (4) direct de-domestication from cultivated *O. sativa* (including potentially protodomesticates, landraces, or modern varieties) (Li et al. 2017; Qiu et al. 2017).

In considering the evolution of weed strains in different geographical regions of rice cultivation, one of the most important distinctions is whether rice fields occur in proximity to reproductively compatible wild *Oryza* species. If present, wild *Oryza* populations could potentially contribute to the evolution of weed strains – either directly through wild-weed hybridization or indirectly through crop-wild hybridization followed by feralization. In the sections below, we first discuss weedy rice strains in world regions where wild *Oryzas* are absent and then move to the potentially more complex situation of weed strains that co-occur with reproductively compatible wild rice populations. Where data are available, we include comparisons of insights from neutral markers and from candidate genes for weed-associated traits.

2.2.1 No Wild Oryza Species Present

United States

While rice of the *indica* subspecies provides over 70% of total rice production and is genetically more diverse (Huang et al. 2010; Zhang et al. 2016), the *japonica* subspecies is the major crop of temperate zones in the northern hemisphere, including in North America, southern Europe, and northeast Asia. In the United States, *tropical japonica* cultivars are grown in the southern Mississippi River flood plain, which is the primary region of US rice farming (Arkansas, Louisiana, Mississippi, southern Missouri, and eastern Texas) (Gealy 2005). *Temperate japonica* varieties are farmed in the secondary rice growing region in northern California. The earliest available record of weedy rice in the United States dates from 1846 (Allston 1846; Craigmiles 1978). Early studies conducted in the 1850s divided US weeds into four different weedy biotypes (Craigmiles 1978).

In the present day, weedy rice is present in both of the US rice cultivation areas. In the southern US rice belt, two major weedy morphotypes are generally recognized based on grain characteristics (Londo and Schaal 2007; Reagon et al. 2010). The strawhull (SH) form shares many domestication traits with cultivated rice and potentially corresponds to the proposed "crop mimic" ecotype described in Sect. 1 above; its defining traits include short stature and straw-colored grain hulls that lack awns. In contrast, the blackhull awned (BHA) form more closely resembles wild *Oryza* species in some traits, including tall stature and seeds that have dark hulls with long awns; however, unlike true wild *Oryza* species, BHA weeds also share a number of crop-like traits with the SH form, including erect growth and reproduction solely by seed with no vegetative propagation (Noldin et al. 1999; Kelly Vaughan et al. 2001; Gealy 2005; Olsen et al. 2007). Both strains are widely distributed through the southern US rice belt, and they are estimated to occur in at least 30% of rice production areas there (Gealy 2005).

In California, a strawhull awned (SHA) morphotype is the major weedy rice type that infests rice fields. This form infested rice fields there from the 1920s to the 1940s (Kennedy 1923; Bellue 1932; Willson 1979), but was completely eliminated in the 1970s. However, new SHA weeds have re-emerged in California since 2003 (Kanapeckas et al. 2016).

Insights from Neutral Markers

As no wild *Oryza* species are native to the United States, hypotheses for the origin of weedy rice strains there have included de-domestication from US cultivars or introduction of an already established weedy rice strain through contamination of seed stock (Londo and Schaal 2007; Reagon et al. 2010; Kanapeckas et al. 2016). Assessments of the evolutionary origin and genetic background of southern US weedy rice have relied primarily on SSRs and DNA sequencing (Estorninos et al. 2000; Kelly Vaughan et al. 2001; Gealy et al. 2002; Londo and Schaal 2007; Reagon et al. 2010). These studies revealed that despite some phenotypic similarity to wild rice, BHA weeds are clearly genetically more closely related to cultivated rice – specifically, *aus* varieties within the *indica* subspecies – than to the wild progenitor. SH weeds are similarly of crop origin; they are genetically most similar to *indica* varieties (sensu stricto). Neither weed strain is genetically similar to the *tropical japonica* cultivars grown in the southern US, although a recent rise in herbicide-resistant rice farming has selectively favored some weeds derived from crop-weed hybridization (Burgos et al. 2014; reviewed in Vigueira et al. 2019) (discussed in Sect. 3).

As neither *aus* nor *indica* varieties have ever been grown commercially in the United States, both weed forms are thought to have originated in Asia and been introduced as weeds through accidental import in contaminated seed stocks. Using genome-wide patterns of single nucleotide polymorphism (SNP) diversity, Reagon et al. (2010) demonstrated that genetic diversity within SH and BHA weeds is very low compared to *aus* and *indica* rice, which is consistent with severe genetic bottlenecks in their establishment in North America. The de-domestication origin

of US weeds was recently reconfirmed with whole-genome sequence analyses, which again show that the SH and BHA weedy strains are phylogenetically close to *indica* and *aus* crop ancestors, respectively (Li et al. 2017). With regard to the timing of divergence between weeds and their crop ancestors, BHA weedy rice appears to have diverged from *aus* much earlier than SH from *indica* rice (Reagon et al. 2010; Li et al. 2017 discussed below).

For weedy rice in California, genome-wide SNPs indicate that while the SHA strain shows genetic similarity to the *temperate japonica* rice farmed there, it did not evolve directly from US cultivars. Instead, the California weedy strains appear to have originated from *japonicas* outside of the United States and were thereafter introduced into California as weeds; this weed evolution is estimated to have occurred in the relatively recent past (Kanapeckas et al. 2016).

Insights from Candidate Gene Analyses

Whereas genetic surveys using neutral markers can provide a genome-wide perspective of the evolutionary origin and demographic history of US weedy strains, a complementary source of data can be provided by candidate gene analyses – particularly for genes controlling traits related to domestication or weediness. As weedy rice possesses a combination of wild-like traits (e.g., seed shattering, dormancy) and crop-like traits (e.g., annuality, erect growth), sequence variation in the genes controlling these traits can provide insights into the specific mechanisms by which weed strains have adapted to exploit agroecosystems.

Among agronomic traits, the loss of seed shattering is one of the most characteristic features of rice domestication (Konishi et al. 2006; Li et al. 2006; Li and Olsen 2016). Previous archeological and genetic analyses have already provided a wealth of insights into the timing and locations for the occurrence of non-shattering phenotypes in cultivated rice. For example, archaeobotanical remains indicate that the reduced shattering phenotype was likely fixed in cultivated rice about 6,600–6,900 years ago (Fuller et al. 2009, 2010). Genetic analyses of seed shattering revealed that two quantitative trait loci (QTLs), *sh4* and *qSH1*, contributed to >70% of the phenotypic difference between wild and cultivated rice (Konishi et al. 2006; Li et al. 2006). For the *sh4* gene, a single non-synonymous substitution (G → T) in the Myb3 DNA-binding domain results in the incomplete development of the caryopsis abscission zone (reduced shattering phenotype) in cultivated rice (Li et al. 2006). Further population genetic analyses documented that all cultivated rice accessions carry the non-shattering allele (Zhang et al. 2009).

For the SH and BHA weeds in the United States, even though nearly all weedy strains show a similar degree of shattering to wild rice, both strains carry the *sh4* non-shattering allele fixed in cultivated rice (Thurber et al. 2010) (Fig. 1). This finding demonstrates very clearly that both the BHA and the SH strains are descended from ancestors that had passed through the initial stages of domestication and selection for reduced shattering. Genetic mechanisms underlying the apparent phenotypic reversion to shattering are discussed in Sect. 3.

Similar evidence that the SH and BHA weeds are descended from crop ancestors is provided by the *PROG1* and *OsLG1* genes, which are associated with erect plant architecture and closed-panicle inflorescence architecture, respectively (Fig. 1). As with *sh4* and reduced shattering, both of these genes were targets of selection in the initial stages of rice domestication, and both SH and BHA weedy strains share the same haplotypes as cultivated rice at these loci. These patterns further confirm that both the SH and BHA weeds are derived from cultivated ancestors (Li et al. 2017).

In contrast to these early-selected domestication genes, neither the SH nor BHA strains have been found to carry crop-associated alleles at several varietal-specific improvement genes that were likely targets of selection much later in the history of rice domestication; these include *Phr1* (associated with long-term grain storage), *Waxy* (controlling grain amylose content), and *COLD1* (associated with agroecological adaptation to temperate climates) (Li et al. 2017) (Fig. 1). Thus, while the ancestors of US weed strains were clearly domesticated, they were not the improved varieties of the sort most commonly cultivated around the world today.

Perhaps most interesting are the domestication-related genes where SH strains carry crop alleles but BHA weeds do not (e.g., *Bh4*, controlling hull color; *An-1*, controlling awn production) and where neither weed strain possesses the crop-specific allele (*Rc*, controlling pericarp color/seed dormancy) (Fig. 1). For the genes where the two strains differ, this pattern provides phenotypic confirmation of the neutral marker analyses indicating an earlier divergence of BHA weeds from cultivated rice than SH strains (Reagon et al. 2010; Li et al. 2017 see above). In the case of *Rc*, although the loss-of-function *rc* allele that confers white pericarps and reduced dormancy was strongly favored in domesticated rice and is found in most present-day crop varieties, it is absent or nearly absent in all US weeds. We speculate that there may have been strong selection in the SH and BHA weed strains to maintain the wild-type *Rc* allele because of the importance of seed dormancy in weedy rice adaptation (see also Cui et al. 2016; Li et al. 2017).

Europe

Rice was first introduced into Europe via Italy, where *japonica* varieties began to be grown during the Renaissance (thirteen to fifteenth centuries) (Faivre-Rampant et al. 2011). From Italy, rice cultivation spread to other regions of the Mediterranean, including Spain and southern France. Weedy rice was described in Italian rice fields as early as the beginning of the nineteenth century (Biroli 1807), but infestations did not become a severe problem until the 1960s with shifts from hand-transplanting to direct seeding (Tarditi and Vercesi 1993; Vidotto and Ferrero 2005). Nowadays weedy rice is estimated to occur in ~70% of the total rice cultivation area in northern Italy (Grimm et al. 2013). Genetic and morphological analyses of Italian cultivated and weedy rice indicate that despite a great morphological diversity among the weed strains occurring there (including strawhull awnless, blackhull awned, and strawhull awned), all weedy ecotypes apparently share a high level of genetic similarity with *japonica* cultivars (Grimm et al. 2013). However, as all rice accessions used in the

study were collected in Italy only, it remains unclear whether Italian weedy rice evolved through de-domestication from local *japonica* cultivars or was introduced from elsewhere.

Northeast Asia

In Northeast Asia, another region of *japonica* cultivation, weedy rice infestations have also been a relatively recent phenomenon, dating to widespread mechanized rice farming (Sun et al. 2013; Qiu et al. 2014; Kim et al. 2016; He et al. 2017). In South Korea, *temperate japonica* is the dominant group of cultivars, but *tropical japonica* and *indica* rice cultivation were also introduced recently (Kim et al. 2016). The geographic distribution and genetic composition of Korean weedy rice strains have been characterized in several studies (Heu 1988; Hak-Soo and Mun-Hue 1992; Kim et al. 2016; He et al. 2017; Vigueira et al. 2019). Of these weedy strains, "Aengmi" and "Share" type weeds were described, with the latter mainly occurring on Kanghwa Island and geographically isolated from other weedy strains (Chung and Park 2010). Genetic surveys based on genotyping by sequencing (GBS) and whole-genome data demonstrated that Korean weedy accessions cluster together with local *indica* and *temperate japonica* cultivars, respectively, suggesting the possibility of de-domestication origin of these weeds (Kim et al. 2016; Vigueira et al. 2019). It is interesting that the *indica*-like US and South Korean weeds are largely nonoverlapping in genetic cluster analyses, which potentially suggests independent origins for these temperate-adapted *indica*-derived weed strains (Vigueira et al. 2019). In addition to a de-domestication origin, population genomic analyses have also been used to propose a hybrid origin of Korean weedy rice resulting from crosses between modern cultivars and local landraces (He et al. 2017).

In Japan, *temperate japonica* is the dominant crop in most rice fields. Most varieties are the products of modern breeding, but some traditional landraces still exist, and these may have contributed to the origins of Japanese weedy rice. Weedy rice has been observed in the dry and direct-seeded rice fields since the 1940s but only became a serious problem since the 1980s (Ishii and Akazawa 2003; Ushiki et al. 2005). Similar to South Korean weeds, genetic analyses based on neutral markers revealed two genetically distinct weedy types, *indica*- and *japonica*-like weeds (Akasaka et al. 2009). Of the two weedy types, the *japonica*-like weeds show a close phenotypic and genetic resemblance to the local *japonica* varieties such as "Akebono," "Kibinohana," and "Omachi" (Ushiki et al. 2005; Akasaka et al. 2009). The remaining *indica*-like weedy strains are phylogenetically close to the *indica* rice varieties "Kasalath" and "IR36." These attributes clearly demonstrate the de-domestication origin of Japanese weedy rice strains, with a subset likely descended from local landraces. Additional genetic evidence for this de-domestication scenario also comes from domestication and improvement genes. For example, all Japanese weedy rice strains possess the same non-shattering domestication allele of *sh4* gene to cultivated rice (Akasaka et al. 2011). For the two

isozyme loci, *Acp1* and *Sdh1*, *japonica*- and *indica*-like weedy rice strains share the same haplotype with their crop ancestors, respectively, confirming the local de-domestication origin of Japanese weedy rice (Kawasaki et al. 2009).

China

In China, scenarios of weedy rice evolution are more complicated than Korea and Japan, mainly due to the large geographical region and heterogeneous range of environments across which rice cultivation occurs. In general, *japonica* rice is widely cultivated in northern and northeastern China, and *indica* is dominant in southern China. As with other regions of rice cultivation, weedy rice was effectively suppressed in China through traditional hand-transplanted rice farming but has erupted recently because of the adoption of direct-seeding farming (Yu et al. 2005). In northeastern China, cultivated rice was introduced as early as the end of the nineteenth century, but commercial cultivation only occurred there in recent decades (Jin 2010). Although no wild *Oryza* species are naturally distributed in northeastern China, a suite of wild rice traits (e.g., blackhulls and long awns) are found in some weedy rice strains (Qiu et al. 2017). However, population genetic analyses revealed that most of crop- and wild-like weedy rice strains are genetically closer to local *japonica* cultivars rather than *indica* or wild rice, suggesting a role for *japonica* de-domestication in the origin of these Chinese weedy strains (Cao et al. 2007; Sun et al. 2013; Qiu et al. 2017). Similar evidence for de-domestication has been found in other studies in northern and northwestern China, where the weedy rice morphotypes are clustered with either *indica* or *japonica* (Sun et al. 2013; Qiu et al. 2017). Notably, an *indica-japonica* hybridization origin for weedy rice has been described in eastern China where *indica* rice was historically cultivated but has been recently replaced by *japonica* (Qiu et al. 2014). These findings together indicate that de-domestication from different cultivated rice varieties plays the major role in the formation of weedy rice in China, as in other northern temperate rice growing regions.

2.2.2 No *O. rufipogon* but Other Wild *Oryza* Species Present

The genus *Oryza* consists of 23 species that are widely distributed in pantropical areas (Vaughan 1994; Vaughan et al. 2003, 2005). Most members of the genus possess genomes that are diverged from the AA genome that characterizes *O. sativa* and its wild ancestor (*O. rufipogon*) and are thus not interfertile with cultivated rice. However, reproductively compatible wild *Oryza* species besides *O. rufipogon* can be found in several regions where weedy rice occurs, including the neotropics and Africa, and these wild *Oryzas* could in principle contribute to the evolution of local weed strains.

Africa

In Africa, the AA genome-cultivated rice *O. glaberrima* was domesticated from *O. barthii* in the Niger River delta around 3,000 years ago and was disseminated from there to other parts of West Africa (Harlan 1976; Linares 2002; Wang et al. 2014). The concept of "weedy rice" in Africa is different from other world regions, as it collectively refers to the native weedy forms of *O. glaberrima*, *O. barthii*, *O. longistaminata*, and *O. punctata* as well as weedy strains of the introduced Asian *O. sativa* (Delouche et al. 2007). All these weedy forms co-occur in rice fields with cultivated African and Asian rice and cause serious reductions of rice production in West and North Africa, in particular those areas where traditional farming has been replaced by intensification and commercialization of rice agriculture (Delouche et al. 2007). To our knowledge, no detailed genetic characterizations of African weedy rice have been published; the exact origin model and adaptive evolution of these African weedy forms thus remain uninvestigated so far.

Latin America

In Central and South America, the AA genome species *O. glumaepatula* can be found growing in proximity to Asian cultivated and weedy rice. However, studies in Costa Rica based on morphological and genetic analyses do not suggest any direct contribution of this native *Oryza* species to the genetic composition of local weed strains (Arrieta-Espinoza et al. 2005). Similarly, weedy rice strains in South America appear to be descended primarily from domesticated *O. sativa* ancestors (Federici et al. 2001; Andres et al. 2013). In Uruguay and Brazil, different morphotypes of weedy rice have been reported, including blackhull awned and strawhull awnless forms (Federici et al. 2001; Andres et al. 2013). Molecular genetic analyses have suggested that Uruguayan weedy rice is genetically close to local cultivated rice, indicating the possibility of de-domestication (Federici et al. 2001). However, a role for native wild *Oryza* species has not been explicitly assessed in the evolution of weedy rice in South America. Further investigations based on comparative genomics might reveal some role for the native wild species in local adaptation of weedy rice in Latin America.

2.2.3 *O. rufipogon* Present

The wild ancestor of rice (*O. rufipogon*) occurs widely throughout tropical and subtropical regions of southern Asia (Oka 1988; Vaughan 1994; Vaughan et al. 2008), and these wild rice populations are characterized by wide genetic and phenotypic variability (Grillo et al. 2009; Huang et al. 2012b; Civáň et al. 2015). Two wild rice ecomorphs are sometimes recognized based on life history (perennial vs. annual), with the annual form sometimes designated a separate species (*O. nivara*); however, there is no clear evidence for evolutionary divergence between

annual and perennial ecotypes, and we refer to both as *O. rufipogon*. As the center of rice domestication, southern Asia is also home to the highest crop varietal diversity, with all five major subgroups cultivated in various parts of this region. This combination of highly diverse crop germplasm and reproductively compatible wild relatives creates an environment in which weedy rice origins could be particularly complex and the genetic diversity of weed strains especially high.

Like other regions of traditional rice cultivation, weedy rice in southern Asia was traditionally kept in check by hand weeding during transplanting of rice seedlings. With shifts to direct seeding, weedy rice infestation has become a serious threat to rice production in South and Southeast Asia in the last several decades (Chauhan 2013; Song et al. 2014). The recent and pervasive emergence of weedy rice is especially well documented in Malaysia and Thailand.

Malaysia

In the last two decades of the twentieth century, 90% of the rice cultivation in Malaysia shifted from traditional transplanting to direct-seeding farming. Weedy rice was first reported in Malaysian rice fields in 1988 (Wahab and Suhaimi 1991), and this was followed by rapid proliferation throughout production areas (Karim et al. 2004). Malaysian weedy rice strains are highly morphologically diverse (Sudianto et al. 2016), with a gradation of grain characters ranging from strains closely resembling cultivated rice (strawhull, awnless) to those showing close similarity to wild rice (brown or blackhulls with awns). Studies using a combination of microsatellites (Song et al. 2014; Neik et al. 2019), genotyping by sequencing (Vigueira et al. 2019), and candidate gene analyses of weed-associated traits (Song et al. 2014; Cui et al. 2016; Neik et al. 2019) have revealed a major role for both domesticated rice, including modern elite *indica* cultivars, and wild rice in the evolution of Malaysian weed strains. Introgression from wild populations is especially evident in candidate gene analyses. For example, whereas the domestication allele of the *sh4* shattering gene is completely fixed in US and northern Asian weedy rice populations (Thurber et al. 2010; Zhu et al. 2012) (Fig. 1), the functional wild-type allele is present at high frequencies in Malaysian weeds, particularly those strains with grain phenotypes similar to wild rice (Song et al. 2014). Interestingly, a high proportion of strains with the wild allele were found to be *sh4* heterozygotes, suggesting recent hybridization between domesticated (or de-domesticated) and wild rice populations. Similar patterns are also found for allelic variation at the hull color gene *Bh4* (Song et al. 2014) and the *An-1* gene controlling presence/absence of awns (Cui et al. 2016; Neik et al. 2019). Malaysian weeds carry disproportionately higher frequencies of the wild-type allele at the *Rc* gene, which controls pericarp color and seed dormancy; this may reflect strong selection for seed dormancy in weedy populations (discussed by Cui et al. 2016).

Thailand

In Thailand, weedy rice also became a serious problem in recent decades, in particular within the commercial *Thai Hom Mali* rice cultivation area (Prathepha 2009a). Genetic investigations based on domestication genes suggested the possibility of gene introgression from both wild and cultivated rice (Prathepha 2009a, b; Wedger et al. 2019). For example, while the Thai weedy rice accessions with red pericarp carry the functional allele of *Rc* gene, the white pericarp accessions share a common genotype with cultivated rice. Similarly, the *badh2* allele (8 bp deletion) of *fgr/BADH2* gene was proven to be responsible for rice fragrance (Bradbury et al. 2005). As expected, three genotypes (*BADH2/BADH2*, *BADH2/badh2*, and *badh2/badh2*) were identified in Thai weedy rice strains (Prathepha 2009a). It should be noted that the domestication allele *badh2* is absent in wild rice but persists at high frequency (54.7%) in the weedy rice population (Prathepha 2009b), indicating the possibility of a wild-crop hybridization origin of weedy rice.

South Asia

In South Asia, weedy rice also exhibits a high level of phenotypic diversity, such as straw and blackhull, white and red pericarp, and awned and awnless (Ishikawa et al. 2005; Rathore et al. 2016; Huang et al. 2017). As in Southeast Asia, independent de-domestication from different cultivated varieties is the major origin model of South Asian weedy rice (Ishikawa et al. 2005; Huang et al. 2017). Interestingly, while the blackhull awned strains there show similarity to the wild-like BHA type found in the United States and South and Southeast Asia, distinct genetic backgrounds have been clearly revealed in several studies (Thurber et al. 2010; Song et al. 2014; Huang et al. 2017). Moreover, as with weed strains in other world regions, the weedy rice strains in this region appear to have evolved independently from crop ancestors, providing further evidence for the parallel evolution of weedy rice worldwide. In addition, however, population genomic analyses have shown that some wild-like weedy strains in South Asia show genetic similarity to wild rice (Huang et al. 2017), suggesting the possibility of weed adaptation through introgression from wild populations as in Southeast Asia. Taken together, these observations suggest that weedy rice can evolve repeatedly worldwide through different genetic mechanisms, which provides an extreme system to address molecular bases underlying recurrent evolution.

3 Insights on Molecular Mechanisms of Weedy Rice Adaptation

Morphological and genetic surveys around the world have clearly established that while weedy rice strains evolved independently in different geographic areas, parallel evolution has resulted in a common suite of weediness traits. These traits collectively consist of adaptations referred to as the "agricultural weed syndrome" (Vigueira et al. 2013; Huang et al. 2017; Li et al. 2017; Qiu et al. 2017). They include features that facilitate escape from dependence on human cultivation for reproduction and propagation, and adaptations to survive, proliferate, and outcompete crops within the agroecosystem. The mechanisms by which weediness traits may emerge could potentially include any of the following: (1) de novo mutations during the process of de-domestication; (2) emergence of weediness traits by recombining standing genetic variation that was already present in crop varieties (e.g., if there is weed evolution through hybridization of genetically distinct crop varieties); (3) adaptive introgression from wild populations (e.g., for traits such as seed shattering and dormancy); and (4) adaptive introgression from crop varieties (e.g., for herbicide resistance). We highlight recent findings for these different mechanisms below.

Among weediness traits, reacquisition of seed shattering is among the most critical steps in the establishment of weedy rice populations, as seed dispersal would be required for persistence in rice fields (De Wet and Harlan 1975; Thurber et al. 2010). In domesticated rice, by contrast, artificial selection for reduced shattering greatly facilitates the harvesting efficiency and renders domesticated rice primarily dependent on humans for survival and propagation (Li and Olsen 2016). Previous studies have identified six shattering-related genes (*sh4*, *qSH1*, *OsSh1*, *SH5*, *OsCPL1*, and *SHAT1*) in cultivated rice, of which *sh4* has been inferred to be a major causative gene that resulted in the phenotypic shift from shattering to non-shattering during rice domestication (Li and Olsen 2016). Consistent with this conclusion, genetic analyses of the *sh4* gene around the world revealed that most of the weedy strains carry the non-shattering *sh4* allele (Thurber et al. 2010; Akasaka et al. 2011; Zhu et al. 2012; Song et al. 2014; Nunes et al. 2015). The fact that weedy rice is highly shattering despite carrying the *sh4* domestication allele strongly suggests a role for either novel mutations or recombined standing variation in the re-emergence of seed shattering in weedy rice. In regions of Southeast Asia where weedy rice occurs in proximity to *O. rufipogon*, the weedy rice shattering phenotype has also been found to be attributable in part to adaptive introgression of the wild-type *sh4* allele from local wild populations (Song et al. 2014; Vigueira et al. 2019).

As a step toward identifying the genetic basis of shattering in US strains of weedy rice, the shattering phenotype was mapped in two recombinant inbred line populations derived from crosses between an *indica* crop cultivar (Dee Geo Woo Gen) and a representative accession of the SH and BHA weed strains (Thurber et al. 2013; Qi et al. 2015). QTL mapping and linkage analyses identified two

and five statistically significant QTLs in the SH and BHA mapping populations, respectively, of which *qSH2S* and *qSH3Bb* are estimated to account for 51.7% and 14.1% of the total phenotypic variances in the SH population (Qi et al. 2015). Importantly, these shattering QTLs do not overlap with the genomic locations of previously identified shattering-related genes in cultivated rice, which points to genetic mechanisms other than second-site mutational suppression in the phenotypic reversions to shattering. Equally importantly, the QTL locations do not co-localize between the two US weed-crop mapping populations, indicating different underlying genetic bases for shattering in the two major US weed strains. In a similar study conducted on Chinese weedy rice, Yao et al. (2015) analyzed F₂ offspring derived from the crosses between an *indica* variety Minghui86 and a high shattering Chinese weedy accession. The three shattering-related QTLs (*wd-qsh1*, *wd-qsh3*, and *wd-qsh5*) identified show no overlap with the previously reported shattering-related genes (e.g., *sh4*, *qSH1*, *sh-h*, and *SHAT1*). In addition, eight shattering QTLs were also identified in two RIL populations developed from the crosses between two *japonica* cultivars and a weedy accession (Subudhi et al. 2013). It is interesting to note that although the major-effect QTL identified in that study, *qSH4BR*, overlaps with the *sh4* gene, there is no evidence that mutations within *sh4* itself are responsible for the phenotypic reversion to shattering.

To persist in the agroecosystem, weedy rice must possess sufficient seed dormancy to remain viable in the soil seed bank. Like seed shattering, seed dormancy is a complex trait that is controlled by multiple genes (Gu et al. 2004, 2011; Sugimoto et al. 2010; Ye et al. 2013), and the emergence of shattering in weedy rice remains largely uncharacterized beyond the resolution of QTLs. Among the genetically best-characterized dormancy genes is *Rc*, which encodes a transcription factor that pleiotropically controls both pericarp pigmentation and ABA-mediated seed dormancy. Whereas most modern cultivated rice varieties carry a loss-of-function *rc* allele that confers a white pericarp and reduced dormancy, weedy rice strains worldwide are largely characterized by the presence of functional *Rc* alleles. In the case of US weedy rice, these functional alleles are proposed to be derived from the red-pericarp protodomesticates or landraces that gave rise to the weeds (Gross et al. 2010). In tropical Asia, introgression from hybridizing wild rice populations has also likely played a role in the presence of functional *Rc* alleles in weed strains (Song et al. 2014; Cui et al. 2016; Vigueira et al. 2019). As noted above, in Malaysia, where introgression from both wild and domesticated rice has shaped recent weedy rice evolution, the white pericarp *rc* allele appears to be disproportionately underrepresented in weed strains, which is consistent with selection favoring weed strains that have sufficient seed dormancy to allow seed persistence in crop fields over multiple seasons (Cui et al. 2016).

Over the last two decades, the rice production industry has adopted the widespread use of imidazolinone herbicide-resistant crop varieties as a means of controlling weedy rice and other agricultural weeds (Croughan 2003). Resistance is largely acquired through selection for amino acid variants at the *ALS* (*acetolactate synthase*) gene. As herbicide-resistant rice varieties have increased in use throughout the world, resistant weedy rice strains have begun to proliferate (Olguin et al. 2009;

Azmi et al. 2012; Burgos et al. 2014; Merotto et al. 2016). Crop-weed hybridization appears to be the primary mechanism by which weed populations are acquiring this trait (Roso et al. 2010; Andres et al. 2014; Burgos et al. 2014). This widespread selection for crop introgression will likely have a major impact in reshaping the weedy rice genome in coming decades.

4 Current Advances in Weedy Rice Population Genomics and Future Directions

The availability of an annotated rice reference genome and an abundance of well-characterized domestication-related genes offer an efficient platform to address the genetic mechanisms underlying weedy rice adaptation. However, studies of the functional identification of weediness-related genes lag far behind those of cultivated rice. Fortunately, recent comparative genomics studies have promoted our understanding of the formation of weediness traits in weedy rice. For example, Qi et al. (2015) employed QTL mapping identified a series of QTLs associated with diverse adaptive traits, such as seed shattering, heading date, and emergence data. By comparing the physical positions of these weed-associated QTLs with known functional genes, several domestication-related genes were confirmed to be causally related to the observed phenotypic variation; these include genes for heading date (*Hd1* and *DTH8*), awn length (*An-1*), and pericarp color (*Rc*).

Complementing QTL mapping approaches, population genomics provides an alternative strategy to detect weediness-related genes at the genome-wide level. For example, Li et al. (2017) analyzed the genomes of 183 wild, cultivated, and weedy rice accessions and, through genome scans for signatures of weed-specific adaptation, identified 178 and 307 annotated genes in 2 US weedy strains, SH and BHA, respectively. Interestingly, while some of these genomic regions co-localize to known QTLs for weediness traits (including a major-effect QTL for shattering), many others do not. Likewise, genome-wide scanning based on whole-genome data was also performed in Chinese and Korean weedy rice strains in which a large number of candidate genes were identified (He et al. 2017; Qiu et al. 2017). Collectively these findings suggest that there is a rich pool of candidate genes that can be explored in future studies aimed at characterizing the mechanisms underlying weediness evolution. It seems likely that some key genes underlie phenotypes whose functions have not previously been associated with weediness or competitive ability. Further investigations focusing on functional analyses of weediness candidate genes will play a critical role in advancing our knowledge of weedy rice adaptation.

5   Future Perspectives

With the rapid advance in next-generation sequencing technologies and accumulated genomic resources, pan-genomic analyses may provide an efficient strategy to identify candidate genes related to the weediness traits. Models for such studies can already be found in recent research on the wild-cultivated rice complex, where both single nucleotide polymorphisms (SNPs) and structural variations (SVs) have been shown to underlie important phenotypes (Zhao et al. 2018). In addition, epigenetic control is an important regulatory mechanism that contributes to the phenotypic diversity of plant species. The role of epigenetic regulation in the control of complex phenotypes has been well-documented in cultivated rice (Deng et al., 2016). However, investigations of epigenetic mechanisms underlying weediness traits lag far behind cultivated rice phenotypes. Collectively we propose that future studies should not only focus on the single base-pair DNA sequence variations (e.g., SNPs) and large-scale structural variation (e.g., copy number polymorphisms) but also integrate both genetic and epigenetic regulatory networks to understand the genotype-phenotype connection.

6   Conclusions

Weedy crop relatives have likely been present in and around agricultural fields since the dawn of agriculture. In the case of weedy rice, recent research has revealed that this this major agricultural pest is by no means a single evolutionary entity. Rather, it is a complex assortment of lineages that have arisen multiple times independently and that have evolved and adapted over time with varying levels of genetic input from domesticated and wild rice populations. Population genetics and genomics studies suggest that the adaptations that characterize weedy rice can evolve through a variety of molecular mechanisms; this has almost certainly facilitated the process of convergent weed evolution. It remains to be seen whether these findings for weedy rice are shared with other major weedy crop relatives. While extensive, the research findings reviewed in this chapter are perhaps best considered a good starting point for more detailed characterizations of weediness traits and the mechanisms by which they evolve in weedy rice and other agricultural weed species.

References

Akasaka M, Ushiki J, Iwata H, Ishikawa R, Ishii T. Genetic relationships and diversity of weedy rice (*Oryza sativa* L.) and cultivated rice varieties in Okayama Prefecture, Japan. Breeding Sci. 2009;59(4):401–9.

Akasaka M, Konishi S, Izawa T, Ushiki J. Histological and genetic characteristics associated with the seed-shattering habit of weedy rice (*Oryza sativa* L.) from Okayama, Japan. Breeding Sci. 2011;61(2):168–73.

Allaby RG, Fuller DQ, Brown TA. The genetic expectations of a protracted model for the origins of domesticated crops. Proc Natl Acad Sci U S A. 2008;105(37):13982–6.

Allston RFW. The rice plant. DeBow's Review. 1846;1:320–56.

Andres A, Concenço G, Theisen G, Vidotto F, Ferrero A. Selectivity and weed control efficacy of pre-and post-emergence applications of clomazone in Southern Brazil. Crop Prot. 2013;53:103–8.

Andres A, Fogliatto S, Ferrero A, Vidotto F. Susceptibility to imazamox in Italian weedy rice populations and Clearfield® rice varieties. Weed Res. 2014;54(5):492–500.

Arnaud JF, Viard F, Delescluse M, Cuguen J. Evidence for gene flow via seed dispersal from crop to wild relatives in *Beta vulgaris* (Chenopodiaceae): consequences for the release of genetically modified crop species with weedy lineages. Proc Roy Soc Lond B Biol. 2003;270(1524):1565–71.

Arrieta-Espinoza G, Sánchez E, Vargas S, Lobo J, Quesada T, Espinoza AM. The weedy rice complex in Costa Rica. I. Morphological study of relationships between commercial rice varieties, wild *Oryza* relatives and weedy types. Genet Resour Crop Evol. 2005;52(5):575–87.

Azmi M, Azlan S, Yim K, George T, Chew S. Control of weedy rice in direct-seeded rice using the Clearfield production system in Malaysia. Pak J Weed Sci Res. 2012;18:49–53.

Baker HG. Characteristics and modes of origin of weeds. In: Baker HG, Stebbins GL, editors. The genetics of colonizing species. London: Academic Press; 1965. p. 141–72.

Barnaud A, Deu M, Garine E, Chantereau J, Bolteu J, Koïda EO, McKey D, Joly HI. A weed-crop complex in sorghum: the dynamics of genetic diversity in a traditional farming system. Am J Bot. 2009;96(10):1869–79.

Basu C, Halfhill MD, Mueller TC, Stewart CN. Weed genomics: new tools to understand weed biology. Trends Plant Sci. 2004;9(8):391–8.

Bellue MK. Weeds of California seed rice. Calif Dept Agri Bull. 1932;21:290–6.

Biroli G. Del riso. Milan: Tipografia Giovanni Silvestri; 1807. 151pp.

Bradbury LM, Henry RJ, Jin Q, Reinke RF, Waters DL. A perfect marker for fragrance genotyping in rice. Mol Breed. 2005;16(4):279–83.

Burgos NR, Norman RJ, Gealy DR, Black H. Competitive N uptake between rice and weedy rice. Field Crop Res. 2006;99(2):96–105.

Burgos NR, Singh V, Tseng TM, Black H, Young ND, Huang Z, Hyma KE, Gealy DR, Caicedo AL. The impact of herbicide-resistant rice technology on phenotypic diversity and population structure of United States weedy rice. Plant Physiol. 2014;166(3):1208–20.

Cao QJ, Li B, Song ZP, Cai XX, Lu BR. Impact of weedy rice populations on the growth and yield of direct-seeded and transplanted rice. Weed Biol Manage. 2007;7(2):97–104.

Chauhan BS. Strategies to manage weedy rice in Asia. Crop Prot. 2013;48:51–6.

Cheng C, Motohashi R, Tsuchimoto S, Fukuta Y, Ohtsubo H, Ohtsubo E. Polyphyletic origin of cultivated rice: based on the interspersion pattern of SINEs. Mol Biol Evol. 2003;20(1):67–75.

Chung JW, Park YJ. Population structure analysis reveals the maintenance of isolated sub-populations of weedy rice. Weed Res. 2010;50(6):606–20.

Cíváň P, Craig H, Cox CJ, Brown TA. Three geographically separate domestications of Asian rice. Nat Plants. 2015;1:15164.

Craigmiles JP. Introduction. Pages 5-6 in red rice research and control. Texas Agric Exp Stn Bul. 1978;1270:46.

Croughan TP. Clearfield rice: it's not a GMO. La Agric. 2003;46(4):24–6.

Cui Y, Song BK, Li LF, Li YL, Huang Z, Caicedo AL, Jia Y, Olsen KM. Little white lies: pericarp color provides insights into the origins and evolution of southeast Asian weedy rice. G3. 2016;6(12):4105–14.

De Wet JM, Harlan JR. Weeds and domesticates: evolution in the man-made habitat. Econ Bot. 1975;29(2):99–108.

Delouche JC, Burgos NR, Gealy DR, de San Martin GZ, Labrada R, Larinde M, Rosell C. Weedy rices: origin, biology, ecology and control, vol. 188. Rome: Food and Agriculture Organization of the United Nations; 2007.

Ellstrand NC, Prentice HC, Hancock JF. Gene flow and introgression from domesticated plants into their wild relatives. Annu Rev Ecol Syst. 1999;30(1):539–63.

Estorninos LE Jr, Gealy DR, Gbur EE, Talbert RE, McClelland MR. Rice and red rice interference. II. Rice response to population densities of three red rice (*Oryza sativa*) ecotypes. Weed Sci. 2005;53(5):683–9.

Estorninos LE, Gealy DR, Talbert RE, Wells BR. Rice research studies 1999. Fayetteville, AR, USA. 2000. p. 463–8.

Faivre-Rampant O, Bruschi G, Abbruscato P, Cavigiolo S, Picco AM, Borgo L, Lupotto E, Piffanelli P. Assessment of genetic diversity in Italian rice germplasm related to agronomic traits and blast resistance (*Magnaporthe oryzae*). Mol Breed. 2011;27(2):233–46.

Federici MT, Vaughan D, Norihiko T, Kaga A, Xin WW, Koji D, Francis M, Zorrilla G, Saldain N. Analysis of Uruguayan weedy rice genetic diversity using AFLP molecular markers. Electron J Biotechnol. 2001;4(3):5–6.

Fuller DQ, Qin L, Zheng Y, Zhao Z, Chen X, Hosoya LA, Sun GP. The domestication process and domestication rate in rice: spikelet bases from the Lower Yangtze. Science. 2009;323(5921):1607–10.

Fuller DQ, Sato Y-I, Castillo C, Qin L, Weisskopf AR, Kingwell-Banham EJ, Song J, Ahn S-M, Van Etten J. Consilience of genetics and archaeobotany in the entangled history of rice. Archaeol Anthrop Sci. 2010;2(2):115–31.

Gao L, Innan H. Nonindependent domestication of the two rice subspecies, *Oryza sativa* ssp. *indica* and ssp. *japonica*, demonstrated by multilocus microsatellites. Genetics. 2008;179(2):965–76.

Garris AJ, Tai TH, Coburn J, Kresovich S, McCouch S. Genetic structure and diversity in *Oryza sativa* L. Genetics. 2005;169(3):1631–8.

Ge S, Sang T, Lu BR, Hong DY. Phylogeny of rice genomes with emphasis on origins of allotetraploid species. Proc Natl Acad Sci U S A. 1999;96(25):14400–5.

Gealy D. Gene movement between rice (*Oryza sativa*) and weedy rice (*Oryza sativa*): a US temperate rice perspective. In: Gressel J, editor. Crop ferality and volunteerism. London: CRC Press; 2005. p. 323–5.

Gealy DR, Tai TH, Sneller CH. Identification of red rice, rice, and hybrid populations using microsatellite markers. Weed Sci. 2002;50(3):333–9.

Gealy DH, Agrama H, Jia MH. Genetic analysis of atypical US red rice phenotypes: indications of prior gene flow in rice fields? Weed Sci. 2012;60(3):451–61.

Goff SA, Ricke D, Lan T-H, Presting G, Wang R, Dunn M, Glazebrook J, Sessions A, Oeller P, Varma H. A draft sequence of the rice genome (*Oryza sativa* L. ssp. *japonica*). Science. 2002;296(5565):92–100.

Gressel J, Valverde BE. A strategy to provide long-term control of weedy rice while mitigating herbicide resistance transgene flow, and its potential use for other crops with related weeds. Pest Manag Sci. 2009;65(7):723–31.

Grillo MA, Li C, Fowlkes AM, Briggeman TM, Zhou A, Schemske DW, Sang T. Genetic architecture for the adaptive origin of annual wild rice, *Oryza nivara*. Evolution. 2009;63(4):870–83.

Grimm A, Fogliatto S, Nick P, Ferrero A, Vidotto F. Microsatellite markers reveal multiple origins for Italian weedy rice. Ecol Evol. 2013;3(14):4786–98.

Gross BL, Zhao Z. Archaeological and genetic insights into the origins of domesticated rice. Proc Natl Acad Sci U S A. 2014;111(17):6190–7.

Gross BL, Steffen FT, Olsen KM. The molecular basis of white pericarps in African domesticated rice: novel mutations at the *Rc* gene. J Evol Biol. 2010;23(12):2747–53.

Gu XY, Kianian SF, Foley ME. Multiple loci and epistases control genetic variation for seed dormancy in weedy rice (*Oryza sativa*). Genetics. 2004;166(3):1503–16.

Gu XY, Foley ME, Horvath DP, Anderson JV, Feng J, Zhang L, Mowry CR, Ye H, Suttle JC, Kadowaki K-I. Association between seed dormancy and pericarp color is controlled by a pleiotropic gene that regulates abscisic acid and flavonoid synthesis in weedy red rice. Genetics. 2011;189(4):1515–24.

Hak-Soo S, Mun-Hue H. Collection and evaluation of Korean red rices I. Regional distribution and seed characteristics. Korean J Crop Sci. 1992;37(5):425–30.

Harlan JR. Origins of African plant domestication. The Hague: Mouton; 1976.

Harlan JR. Crops and man. Madison: American Society of Agronomy; 1992.

He Z, Zhai W, Wen H, Tang T, Wang Y, Lu X, Greenberg AJ, Hudson RR, Wu C-I, Shi S. Two evolutionary histories in the genome of rice: the roles of domestication genes. PLoS Genet. 2011;7(6):e1002100.

He Q, Kim KW, Park YJ. Population genomics identifies the origin and signatures of selection of Korean weedy rice. Plant Biotechnol J. 2017;15(3):357–66.

Heu M. Weed rice "Sharei" showing closer cross-affinity to *japonica* type. Rice Genet Newslett. 1988;5:72–4.

Hilbert L, Neves EG, Pugliese F, Whitney BS, Shock M, Veasey E, Zimpel CA, Iriarte J. Evidence for mid-Holocene rice domestication in the Americas. Nat Ecol Evol. 2017;1:1693–8.

Hill J, Smith RJ, Bayer D. Rice weed control: current technology and emerging issues in temperate rice. Aust J Exp Agr. 1994;34(7):1021–9.

Hillman G, Hedges R, Moore A, Colledge S, Pettitt P. New evidence of Lateglacial cereal cultivation at Abu Hureyra on the Euphrates. Holocene. 2001;11(4):383–93.

Huang X, Sang T, Zhao Q, Feng Q, Zhao Y, Li C, Zhu C, Lu T, Zhang Z, Li M. Genome-wide association studies of 14 agronomic traits in rice landraces. Nat Genet. 2010;42(11):961–7.

Huang X, Kurata N, Wang ZX, Wang A, Zhao Q, Zhao Y, Liu K, Lu H, Li W, Guo Y. A map of rice genome variation reveals the origin of cultivated rice. Nature. 2012a;490(7421):497–501.

Huang P, Molina J, Flowers JM, Rubinstein S, Jackson SA, Purugganan MD, Schaal BA. Phylogeography of Asian wild rice, *Oryza rufipogon*: a genome-wide view. Mol Ecol. 2012b;21(18):4593–604.

Huang Z, Young ND, Reagon M, Hyma KE, Olsen KM, Jia Y, Caicedo AL. All roads lead to weediness: patterns of genomic divergence reveal extensive recurrent weedy rice origins from South Asian *Oryza*. Mol Ecol. 2017;26(12):3151–67.

IRRI. Bring hope, improving lives: strategic plan 2007–2015. Los Baños: IRRI; 2006.

Ishii T, Akazawa M. Direct seeding in dry field and weedy rice in Okayama prefecture. Proceedings of the 18th symposium in Japanese Weedy Association. 2003. p. 7–16.

Ishikawa R, Toki N, Imai K, Sato Y, Yamagishi H, Shimamoto Y, Ueno K, Morishima H, Sato T. Origin of weedy rice grown in Bhutan and the force of genetic diversity. Genet Resour Crop Evol. 2005;52(4):395–403.

Jin Y. A study on modern rice introduction into northeastern China and its impact. Agr Hist China. 2010;3:35–41. In Chinese.

Jin J, Huang W, Gao JP, Yang J, Shi M, Zhu MZ, Luo D, Lin HX. Genetic control of rice plant architecture under domestication. Nat Genet. 2008;40(11):1365–9.

Kanapeckas KL, Vigueira CC, Ortiz A, Gettler KA, Burgos NR, Fischer AJ, Lawton-Rauh AL. Escape to ferality: the endoferal origin of weedy rice from crop rice through de-domestication. PLoS One. 2016;11(9):e0162676.

Karim RS, Man AB, Sahid IB. Weed problems and their management in rice fields of Malaysia: an overview. Weed Biol Manage. 2004;4(4):177–86.

Kawasaki A, Imai K, Ushiki J, Ishii T, Ishikawa R. Molecular constitution of weedy rice (*Oryza sativa* L.) found in Okayama prefecture, Japan. Breeding Sci. 2009;59(3):229–36.

Kelly Vaughan L, Ottis BV, Prazak-Havey AM, Bormans CA, Sneller C, Chandler JM, Park WD. Is all red rice found in commercial rice really *Oryza sativa*? Weed Sci. 2001;49(4):468–76.

Kennedy PB. Observations on some rice weeds in California, vol. 27. Oakland, CA: University of California, California Agricultural Bulletin; 1923. p. 356.

Kim T-S, He Q, Kim K-W, Yoon M-Y, Ra W-H, Li FP, Tong W, Yu J, Oo WH, Choi B. Genome-wide resequencing of KRICE_CORE reveals their potential for future breeding, as well as functional and evolutionary studies in the post-genomic era. BMC Genomics. 2016;17(1):408.

Konishi S, Izawa T, Lin SY, Ebana K, Fukuta Y, Sasaki T, Yano M. An SNP caused loss of seed shattering during rice domestication. Science. 2006;312(5778):1392–6.

Larson G, Piperno DR, Allaby RG, Purugganan MD, Andersson L, Arroyo-Kalin M, Barton L, Vigueira CC, Denham T, Dobney K. Current perspectives and the future of domestication studies. Proc Natl Acad Sci U S A. 2014;111(17):6139–46.

Li LF, Olsen K. Chapter three-to have and to hold: selection for seed and fruit retention during crop domestication. Curr Top Dev Biol. 2016;119:63–109.

Li C, Zhou A, Sang T. Rice domestication by reducing shattering. Science. 2006;311(5769):1936–9.

Li LF, Li YL, Jia Y, Caicedo AL, Olsen KM. Signatures of adaptation in the weedy rice genome. Nat Genet. 2017;49(5):811–4.

Liang D, Qiang S. Current situation and control strategy of weedy rice in China. China Plant Prot. 2011;31:21–4.

Linares OF. African rice (*Oryza glaberrima*): history and future potential. Proc Natl Acad Sci U S A. 2002;99(25):16360–5.

Ling-Hwa T, Morishima H. Genetic characterization of weedy rices and the inference on their origins. Breeding Sci. 1997;47(2):153–60.

Londo J, Schaal B. Origins and population genetics of weedy red rice in the USA. Mol Ecol. 2007;16(21):4523–35.

Londo JP, Chiang Y-C, Hung K-H, Chiang T-Y, Schaal BA. Phylogeography of Asian wild rice, *Oryza rufipogon*, reveals multiple independent domestications of cultivated rice, *Oryza sativa*. Proc Natl Acad Sci U S A. 2006;103(25):9578–83.

Merotto A, Goulart IC, Nunes AL, Kalsing A, Markus C, Menezes VG, Wander AE. Evolutionary and social consequences of introgression of nontransgenic herbicide resistance from rice to weedy rice in Brazil. Evol Appl. 2016;9(7):837–46.

Meyer RS, Purugganan MD. Evolution of crop species: genetics of domestication and diversification. Nat Rev Genet. 2013;14(12):840–52.

Molina J, Sikora M, Garud N, Flowers JM, Rubinstein S, Reynolds A, Huang P, Jackson S, Schaal BA, Bustamante CD. Molecular evidence for a single evolutionary origin of domesticated rice. Proc Natl Acad Sci U S A. 2011;108(20):8351–6.

Neik T-X, Chai J-Y, Tan S-Y, Sudo M, Cui Y, Jayaraj J, Teo S-S, Olsen KM, Song BK. When West meets East: the origins and spread of weedy rice between continental and island Southeast Asia. G3. 2019;9:2941–50.

Noldin JA, Chandler JM, McCauely GN. Red rice (*Oryza sativa*) biology. I. Characterization of red rice ecotypes. Weed Technol. 1999:12–8.

Nunes D, Boa-Sorte N, Grassi MFR, Pimentel K, Teixeira MG, Barreto ML, Dourado I, Galvão-Castro B. Evidence of a predominance of sexual transmission of HTLV-1 in Salvador, the city with the highest prevalence in Brazil. Retrovirology. 2015;12(1):O3.

Oka H. Weedy forms of rice. Origin of cultivated rice. Amsterdam: Elsevier and Japan Society Press; 1988. p. 107–14.

Olguin ERS, Arrieta-Espinoza G, Lobo JA, Espinoza-Esquivel AM. Assessment of gene flow from a herbicide-resistant *indica* rice (*Oryza sativa* L.) to the Costa Rican weedy rice (*Oryza sativa*) in Tropical America: factors affecting hybridization rates and characterization of F1 hybrids. Transgenic Res. 2009;18(4):633–47.

Olsen KM, Caicedo AL, Jia Y. Evolutionary genomics of weedy rice in the USA. J Integr Plant Biol. 2007;49(6):811–6.

Ouyang Y, Zhang Q. Understanding reproductive isolation based on the rice model. Annu Rev Plant Biol. 2013;64:111–35.

Prathepha P. Pericarp color and haplotype diversity in weedy rice (*O. sativa f. spontanea*) from Thailand. Pak J Biol Sci. 2009a;12(15):1075.

Prathepha P. The *badh2* allele of the fragrance (*fgr/BADH2*) gene is present in the gene population of weedy rice (*Oryza sativa f. spontanea*) from Thailand. Am Eurasian J Agric Environ Sci. 2009b;5:603–8.

Qi X, Liu Y, Vigueira CC, Young ND, Caicedo AL, Jia Y, Gealy DR, Olsen KM. More than one way to evolve a weed: parallel evolution of US weedy rice through independent genetic mechanisms. Mol Ecol. 2015;24(13):3329–44.

Qiu J, Zhu J, Fu F, Ye CY, Wang W, Mao L, Lin Z, Chen L, Zhang H, Guo L. Genome re-sequencing suggested a weedy rice origin from domesticated *indica-japonica* hybridization: a case study from southern China. Planta. 2014;240(6):1353–63.

Qiu J, Zhou Y, Mao L, Ye C, Wang W, Zhang J, Yu Y, Fu F, Wang Y, Qian F. Genomic variation associated with local adaptation of weedy rice during de-domestication. Nat Commun. 2017;8:15323.

Rathore M, Singh R, Kumar B, Chauhan B. Characterization of functional trait diversity among Indian cultivated and weedy rice populations. Sci Rep. 2016;6:24176.

Reagon M, Thurber CS, Gross BL, Olsen KM, Jia Y, Caicedo AL. Genomic patterns of nucleotide diversity in divergent populations of US weedy rice. BMC Evol Biol. 2010;10(1):180.

Roso A, Merotto A Jr, Delatorre C, Menezes V. Regional scale distribution of imidazolinone herbicide-resistant alleles in red rice (*Oryza sativa* L.) determined through SNP markers. Field Crop Res. 2010;119(1):175–82.

Sasaki T. The map-based sequence of the rice genome. Nature. 2005;436(7052):793.

Song BK, Chuah TS, Tam SM, Olsen KM. Malaysian weedy rice shows its true stripes: wild *Oryza* and elite rice cultivars shape agricultural weed evolution in Southeast Asia. Mol Ecol. 2014;23(20):5003–17.

Stewart CN. Becoming weeds. Nat Genet. 2017;49(5):654.

Subudhi PK, Singh PK, DeLeon T, Parco A, Karan R, Biradar H, Cohn MA, Sasaki T. Mapping of seed shattering loci provides insights into origin of weedy rice and rice domestication. J Hered. 2013;105(2):276–87.

Sudianto E, Neik T-X, Tam SM, Chuah T-S, Idris AA, Olsen KM, Song B-K. Morphology of Malaysian weedy rice (*Oryza sativa*): diversity, origin and implications for weed management. Weed Sci. 2016;64(3):501–12.

Sugimoto K, Takeuchi Y, Ebana K, Miyao A, Hirochika H, Hara N, Ishiyama K, Kobayashi M, Ban Y, Hattori T. Molecular cloning of *Sdr4*, a regulator involved in seed dormancy and domestication of rice. Proc Natl Acad Sci U S A. 2010;107(13):5792–7.

Suh H, Sato Y, Morishima H. Genetic characterization of weedy rice (*Oryza sativa* L.) based on morpho-physiology, isozymes and RAPD markers. Theor Appl Genet. 1997;94(3–4):316–21.

Sun J, Qian Q, Ma DR, Xu ZJ, Liu D, Du HB, Chen WF. Introgression and selection shaping the genome and adaptive loci of weedy rice in northern China. New Phytol. 2013;197(1):290–9.

Sweeney M, McCouch S. The complex history of the domestication of rice. Ann Bot. 2007;100 (5):951–7.

Sweeney MT, Thomson MJ, Pfeil BE, McCouch S. Caught red-handed: *Rc* encodes a basic helix-loop-helix protein conditioning red pericarp in rice. Plant Cell. 2006;18(2):283–94.

Tan L, Li X, Liu F, Sun X, Li C, Zhu Z, Fu Y, Cai H, Wang X, Xie D. Control of a key transition from prostrate to erect growth in rice domestication. Nat Genet. 2008;40(11):1360–4.

Tang L, Morishima H. Genetic characteristics and origin of weedy rice. Beijing: China Agricultural University Press; 1996. p. 211–8.

Tarditi N, Vercesi B. The *Oryza silvatica* as weed: a problem more and more present in rice-growing. Verona: Informatore Agrario; 1993.

Thurber CS, Reagon M, Gross BL, Olsen KM, Jia Y, Caicedo AL. Molecular evolution of shattering loci in US weedy rice. Mol Ecol. 2010;19(16):3271–84.

Thurber CS, Jia MH, Jia Y, Caicedo AL. Similar traits, different genes? Examining convergent evolution in related weedy rice populations. Mol Ecol. 2013;22(3):685–98.

Ushiki J, Ishii T, Ishikawa R. Morpho-physiological characters and geographical distribution of *japonica* and *indica* weedy rice (*Oryza sativa*) in Okayama Prefecture, Japan. Breed Res. 2005;7:179–87.

Vaughan DA. The wild relatives of rice: a genetic resources handbook. Los Banos: International Rice Research Institute; 1994.

Vaughan DA, Morishima H, Kadowaki K. Diversity in the *Oryza* genus. Curr Opin Plant Biol. 2003;6(2):139–46.

Vaughan DA, Kadowaki K-I, Kaga A, Tomooka N. On the phylogeny and biogeography of the genus *Oryza*. Breeding Sci. 2005;55(2):113–22.

Vaughan DA, Lu BR, Tomooka N. The evolving story of rice evolution. Plant Sci. 2008;174(4):394–408.

Vidotto F, Ferrero A. Modelling population dynamics to overcome feral rice in rice. Crop ferality and volunteerism. Boca Raton, FL: CRC Press; 2005. p. 353–68.

Vigueira C, Olsen K, Caicedo A. The red queen in the corn: agricultural weeds as models of rapid adaptive evolution. Heredity. 2013;110(4):303–11.

Vigueira CC, Qi X, Song BK, Li LF, Caicedo AL, Jia Y, Olsen KM. Call of the wild rice: *Oryza rufipogon* shapes weedy rice evolution in Southeast Asia. Evol Appl. 2019;12:93–104. https://doi.org/10.1111/eva.12581.

Wahab A, Suhaimi O. Padi angin characteristics, adverse effects and methods of its eradication. Teknologi Padi. 1991;7:21–31.

Wang M, Yu Y, Haberer G, Marri PR, Fan C, Goicoechea JL, Zuccolo A, Song X, Kudrna D, Ammiraju JS. The genome sequence of African rice (*Oryza glaberrima*) and evidence for independent domestication. Nat Genet. 2014;46(9):982–8.

Warwick SI, Stewart C. Crops come from wild plants: how domestication, transgenes, and linkage together shape ferality. In: Gressel J, editor. Crop ferality and volunteerism. Boca Raton, FL: CRC Press; 2005. p. 9–30.

Wedger MJ, Pusadee T, Wongtamee A, Olsen KM. Discordant patterns of introgression suggest historical gene flow into Thai weedy rice from domesticated and wild relatives. J Hered. 2019;110:601–9.

Weiss E, Kislev ME, Hartmann A. Autonomous cultivation before domestication. Science. 2006;312:1608–10.

Willcox G, Fornite S, Herveux L. Early Holocene cultivation before domestication in northern Syria. Veg Hist Archaeobotany. 2008;17(3):313–25.

Willson JH. Rice in California. Richvale, CA: Butte County Rice Growers Association; 1979. p. 254.

Xia HB, Xia H, Ellstrand NC, Yang C, Lu BR. Rapid evolutionary divergence and ecotypic diversification of germination behavior in weedy rice populations. New Phytol. 2011;191(4):1119–27.

Yao N, Wang L, Yan H, Liu Y, Lu B-R. Mapping quantitative trait loci (QTL) determining seed-shattering in weedy rice: evolution of seed shattering in weedy rice through de-domestication. Euphytica. 2015;204(3):513–22.

Ye H, Beighley DH, Feng J, Gu XY. Genetic and physiological characterization of two clusters of quantitative trait loci associated with seed dormancy and plant height in rice. G3. 2013;3(2):323–31.

Yu J, Hu S, Wang J, Wong GK-S, Li S, Liu B, Deng Y, Dai L, Zhou Y, Zhang X. A draft sequence of the rice genome (*Oryza sativa* L. ssp. *indica*). Science. 2002;296(5565):79–92.

Yu GQ, Bao Y, Shi CH, Dong CQ, Ge S. Genetic diversity and population differentiation of Liaoning weedy rice detected by RAPD and SSR markers. Biochem Genet. 2005;43(5):261–70.

Zhang LB, Zhu Q, Wu ZQ, Ross-Ibarra J, Gaut BS, Ge S, Sang T. Selection on grain shattering genes and rates of rice domestication. New Phytol. 2009;184(3):708–20.

Zhang J, Chen LL, Xing F, Kudrna DA, Yao W, Copetti D, Mu T, Li W, Song JM, Xie W. Extensive sequence divergence between the reference genomes of two elite *indica* rice varieties Zhenshan 97 and Minghui 63. Proc Natl Acad Sci U S A. 2016;113(35):E5163–71.

Zhao K, Tung C-W, Eizenga GC, Wright MH, Ali ML, Price AH, Norton GJ, Islam MR, Reynolds A, Mezey J. Genome-wide association mapping reveals a rich genetic architecture of complex traits in *Oryza sativa*. Nat Commun. 2011;2:467.

Zhao Q, Feng Q, Lu HY, Li Y, Wang AH, Tian QL, Zhan QL, Lu YQ, Zhang L, et al. Pan-genome analysis highlights the extent of genomic variation in cultivated and wild rice. Nat Genet. 2018;50:278–84.

Zhu Q, Ge S. Phylogenetic relationships among A-genome species of the genus *Oryza* revealed by intron sequences of four nuclear genes. New Phytol. 2005;167(1):249–65.

Zhu Y, Ellstrand NC, Lu BR. Sequence polymorphisms in wild, weedy, and cultivated rice suggest seed-shattering locus *sh4* played a minor role in Asian rice domestication. Ecol Evol. 2012;2(9):2106–13.

Ziska LH, Gealy DR, Burgos N, Caicedo AL, Gressel J, Lawton-Rauh AL, Avila LA, Theisen G, Norsworthy J, Ferrero A. Chapter three-weedy (red) rice: an emerging constraint to global rice production. Adv Agron. 2015;129:181–228.

Zuo X, Lu H, Jiang L, Zhang J, Yang X, Huan X, He K, Wang C, Wu N. Dating rice remains through phytolith carbon-14 study reveals domestication at the beginning of the Holocene. Proc Natl Acad Sci U S A. 2017;114(25):6486–91.