Weed Science

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Weedy rice (*Oryza* spp.): what's in a name?

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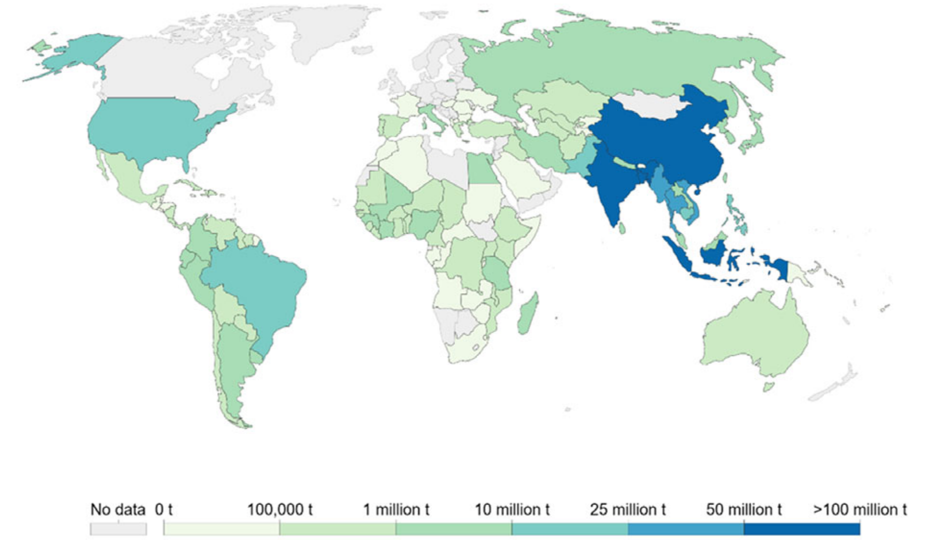
Abstract

There are two species of cultivated rice in the world—*Oryza sativa* L. from Asia and *Oryza glaberrima* Steud. from Africa. The former was domesticated from the wild progenitor *Oryza rufipogon* Griff. and the latter from the African wild rice species *Oryza barthii* A. Shiv. The first known center of rice cultivation in China generated the *O. sativa* subspecies *japonica*. The *indica* subspecies arose from the second center of domestication in the Ganges River plains of India. Variants of domesticated lines and the continuous hybridization between cultivated varieties and the wild progenitor(s) resulted in weedy rice types. Some weedy types resemble the wild ancestor, but the majority of weedy rices today bear close resemblance to cultivated rice. Weedy rice accompanies rice culture and has increased in occurrence with the global shift in rice establishment from transplanting to direct-seeded or dry-drill-seeded rice. Weedy rice (*Oryza* spp.) is the most difficult weed to control in rice, causing as much as 90% yield loss or abandonment of severely infested fields. The gene flow continuum between cultivar and weedy rice or wild relative, crop de-domestication, and regionalized adaptation have resulted in a myriad of weedy rice types. The complex lineage of weedy rice has resulted in confusion of weedy rice nomenclature. Two names are generally used for weedy rice—*Oryza sativa* L. and *Oryza sativa* f. *spontanea*. Genomic data show that *O. sativa* L. applies to weedy rice populations derived from cultivated *O. sativa*, whereas *O. sativa* f. *spontanea* applies only to weedy types that primarily descended from *O. rufipogon*. Neither of these names applies to African weedy rice, which is of African wild rice or *O. glaberrima* lineage. Therefore, unless the lineage of the weedy population in question is known, the proper name to use is the generalized name *Oryza* spp.

Introduction

The most problematic weedy species are those that are most like the crops they infest in terms of morphology, biology, and resource needs. Because weeds are generally more competitive than crops and are often better able to tolerate stress, crop-like weeds are the most difficult species to manage. Such is the case with weedy rice (*Oryza* spp.). Rice is grown in 120 countries (Figure 1), and weedy rice is a problem wherever rice is grown (Delouche et al. 2007). Because the rice crop has been domesticated from wild *Oryza* species, that is, *Oryza rufipogon* Griff. in Asia and *Oryza barthii* A. Shiv. in Africa (Molina et al. 2011), it is ecologically logical for the epicenters of rice cultivation to have weedy types that are admixtures of the wild relative, offtypes of the selected and cultivated strains, and various outcrosses, as the crop, weedy, and wild relative coexist in adjoining habitats (Pusadee et al. 2013; Veltman et al. 2019). Rice cultivation originated in the middle region of the Yangtze River basin in China about 8,000 YBP, or possibly as early as 14,000 YBP (Yasuda 2008). It was deduced that this anthropological development followed the climate warming that favored the growth and expansion of wild rice progenitor populations. Ancient rice cultivation was also evident in the Indo-Gangetic Plain of India around 7,000 to 6,000 YBP (http://ricepedia.org/culture/history-of-rice-cultivation). Integrating genetics and historical linguistics into archaeological data revealed two centers of origin of rice cultivation in China—the middle and lower Yangtze valleys and a separate center of domestication in the Ganges Plain of India (Fuller et al. 2010; Silva et al. 2015). Weedy rice would then eventually accompany rice culture, via seed-mediated gene flow, around the world into regions with or without wild rice species. Although rice cultivars produced around the world are primarily of Asian lineage and are descendants of *O. rufipogon*, other wild rice species with the same AA genome as *Oryza sativa* L. exist in Africa (*Oryza longistaminata* A. Chev. & Roehr. besides *O. barthii* A. Chev.), Australia (*Oryza meridionalis* N. Q. Ng), and Latin America (*Oryza glumipatula* Steud.) (Vaughan 1994). As *O. sativa* cultivars were eventually introduced into Africa, the coexistence of the Asian rice with the locally domesticated rice *Oryza glaberrima* Steud. and the two



Source: UN Food and Agriculture Organization (FAO)

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Figure 1. Global map of rice production, 2018 (https://ourworldindata.org/grapher/rice-production?time=2018).

wild rice species made the diversification of cultivated rice and weedy rice in Africa even more complex (Veltman et al. 2019).

Hybridization between crop, weedy populations, and genetically compatible wild rice species, together with de-domestication (Gealy et al. 2012, 2015; Goulart et al. 2014; Grimm et al. 2020; Hoyos et al. 2020; Huang et al. 2017; Kanapeckas et al. 2016; Subudhi et al. 2014; Sun et al. 2013; Xia et al. 2011), would spur extensive diversification of weedy populations wherever rice is grown. Morphological and genetic studies of weedy rice around the globe reveal that after having been introduced into areas without wild rice, the introduced weedy types had diversified greatly after centuries of coexistence (Fogliatto et al. 2012; Kanapeckas et al. 2018; Shivrain et al. 2010).

Weedy rice is a global problem in modern rice culture that is threatening food security (Ziska et al. 2015). Its persistence is aided by the high shattering of grains (Nunes et al. 2014; Shivrain et al. 2010; Thurber et al. 2010) coupled with protracted germination behavior (Shivrain et al. 2009b) and long life span and deep dormancy of seeds (Baek and Chung 2012; Fogliatto et al. 2011; Goss and Brown 1939; Tseng et al. 2013). Weedy rice is managed traditionally by transplanting rice seedlings into puddled fields, followed immediately by permanent flooding and hand weeding as needed. Centuries of hand weeding produced weedy rice populations that are morphologically most similar to cultivated rice, making the weed very difficult to distinguish, leaving several escapes to replenish the seedbank. Also, water shortages and human migration to urban areas spurred the development and large-scale adoption of direct seeding and related technologies to make rice production more efficient and economical. Weedy rice infestation rose with the adoption of direct seeding in Japan (Imaizumi 2018), Italy (Ferrero and Vidotto 1998), Malaysia (Abdullah et al. 1996), Thailand (Maneechote et al. 2004), the Philippines (Juliano et al. 2020), Vietnam (Chauhan et al. 2015), and other countries in Asia and elsewhere (Chauhan 2012; Shekhawat et al. 2020).

Rice yield losses from weedy rice interference could range from 10% to 90% depending on the weedy rice type, rice cultivar, duration of competition, level of infestation, and environment (Table 1). The type of cultivated rice has a large influence on the magnitude of yield loss from weedy rice competition. Hybrid rice is generally more competitive than inbred rice cultivars, and contemporary varieties are more competitive than old ones (Ottis et al. 2005; Shivrain et al. 2009b). In addition to loss of production, high weedy rice infestation results in reduction of farm gate price of rice due to seed contamination (Ottis et al. 2005). There are cases where farmers have had to abandon their fields because of severe weedy rice infestation. The great need for alternative tools to manage weedy rice spurred the development and commercialization of non-transgenic herbicide-resistant (HR) rice technologies, Clearfield® rice in 2002 and Provisia$^{\mathrm{TM}}$ rice in 2018 (Anonymous 2018; Tan et al. 2005). The former carries resistance to imidazolinone (Group 2) herbicides and the latter to aryloxyphenoxypropanoates (Group 1). The Clearfield® rice technology has met unprecedented level of adoption in the Americas, Europe, and Asia wherever it was introduced (Sudianto et al. 2013, 2014). Despite stringent stewardship policies based on scientific data, it was inevitable that HR weedy rice would evolve, for various controllable and uncontrollable reasons. In fact, HR weedy rice populations had evolved in all countries where Clearfield® rice is grown due to pollen- and seed-mediated gene flow, thus reducing the utility of the technology in many places. Rice growers are greatly anticipating Provisia$^{\mathrm{TM}}$ rice to remedy the problem. The adoption of this new technology is limited only by the low yield potential of current Provisia$^{\mathrm{TM}}$ varieties (Roma-Burgos et al. 2021). This short review discusses the origin of weedy rice, gene exchange between crop and weed and its impact on the weedy populations, nomenclature associated with weedy rice in the literature, and our recommendation for a unified, scientifically supported nomenclature for weedy rice.

The Rise of Weedy Rice

Four non–mutually exclusive hypotheses have been proposed to explain weedy rice origins, as supported by recent genetic studies: (1) *de-domestication*: feralization of cultivated rice into the weedy form (e.g., Ellstrand et al. 2010; Kanapeckas et al. 2016; Li et al. 2017; Qiu et al. 2017); (2) *intervarietal hybridization*: weed emergence via hybridization between different cultivated rice varieties (e.g., Ishikawa et al. 2005; Pusadee et al. 2013; Qiu et al. 2014); (3) *wild-derived origin*: incidental selection on the wild ancestor of rice (*O. rufipogon*, known as common wild rice) or possibly

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Table 1. Rice yield losses due to weedy rice.

Location	Cultivar	Weedy rice type	Weedy rice density	Duration of competition[a]	Yield loss	Reference
			plants m^{-2}		%	
Malaysia	'MR 219'	—	200 g seed m^{-2}	Full season	77	Azmi et al. 2007
Arkansas	'CL161'	Strawhull	1	Full season	10	Ottis et al. 2005
Arkansas	'Lemont'	Strawhull	2	Full season	24	Kwon et al. 1991
Arkansas	'Cocodrie'	Strawhull	3	Full season	30	Ottis et al. 2005
China	'Liaojing 294–7'	Strawhull	5	Full season	22	Cao et al. 2007
California	'M-206'	Strawhull	8	12 wk	40	Karn et al. 2020
Greece	'Thaibonnet'	Dark awn	10	Full season	27	Eleftherohorinos et al. 2002
Italy	'Arborio'	Strawhull	10	Full season	23	Vidotto and Ferrero 2009
Louisiana	'CL121'	—	20	Full season	46	Leon 2005
Colombia	'Oryzica 1'	Darkhull	24	6 wk	10	Fischer and Ramirez 1993
Colombia	'Oryzica 1'	Darkhull	24	Full season	75	Fischer and Ramirez 1993
Arkansas	'Kaybonnet'	Katy red rice	25	13 wk	60	Estorninos et al. 2005
Arkansas	'Lemont'	Strawhull	35	Full season	90	Kwon et al. 1992
Greece	'Thaibonnet'	Dark awns	40	Full season	58	Eleftherohorinos et al. 2002
Arkansas	'Kaybonnet'	Louisiana3	51	13 wk	80	Estorninos et al. 2005
China	'Liaojing 294–7'	Strawhull	125	Full season	77	Cao et al. 2007

[a] In competition studies, the duration of competition is generally established from planting and allowed to grow with rice the whole season. In some cases, weedy rice is allowed to compete with rice for only a short period to determine the effect of early-season competition.

other wild *Oryza* species for adaptation to and invasion of rice-planting areas (e.g., Huang et al. 2017); and (4) *crop–wild hybridization*: weed emergence following hybridization between domesticated and wild rice (e.g., Pusadee et al. 2013; Song et al. 2014). Under scenarios 1 and 2, cultivated rice is the sole progenitor of weedy strains, whereas scenarios 3 and 4 both invoke some role for wild *Oryza* in the origins and evolution of weedy rice. This difference has potential taxonomic implications, as discussed in the final section.

Many rice-growing regions of the world, including those both within and outside the geographic range of wild *Oryza*, have two morphologically distinct weedy rice types in terms of seed characteristics: some have seeds resembling cultivated rice (i.e., strawhull awnless, or SH) and others are more wild-like (i.e., blackhull awned, or BHA) (Akasaka et al. 2009; Cao et al. 2006; Chung and Park 2010; Grimm et al. 2013; Reagon et al. 2010; Shivrain et al. 2010; Zhang et al. 2012; Zhu et al. 2012). Because wild *Oryza* species only occur in a subset of the world's rice production regions, the following sections first examine weedy rice evolution in regions without wild *Oryza*, followed by areas where rice crops are planted in proximity to interfertile wild *Oryza* populations.

Regions without Wild Oryza Species

Many of the world's major rice production areas occur outside the range of wild *Oryza* species; these include temperate Asia (northern China, South Korea, and Japan), North America, and Europe. According to a recent global weedy rice population genomics study (Qiu et al. 2020), 112 of the 163 samples (68.7%) collected from regions without wild rice were morphologically characterized as either SH or strawhull awned (SHA), whereas 51 (31.3%) were either wild-like black/brownhull awnless or black/brownhull awned. Most studies of weedy rice origins in these regions support evolution by de-domestication (scenario 1), with independent origins of the morphologically distinct weed forms (reviewed by Li and Olsen 2020). While blackhull awnless (BH) and BHA weed forms in these regions have seeds with morphological resemblance to wild *Oryza* species, the presence of the wild-like traits appears to reflect weed descent from unimproved crop landraces (where features such as awns and dark-pigmented hulls can still be found) rather than any direct role for wild rice.

In both China and the United States, where genetics and evolution of weedy rice have been particularly well documented, whole-genome resequencing analyses indicate a clear role for de-domestication of cultivated ancestors in weedy rice origins (Li et al. 2017; Qiu et al. 2020). In the southern United States, the genetic makeup of the two predominant weedy rice morphotypes (SH and BHA) are respectively closest to *indica* and *aus* rice. As neither of these crop varieties are commercially cultivated in the country, it is likely that the U.S. weedy rice forms originally evolved in Asia and were later introduced through contaminated seed stocks (Reagon et al. 2010). Other non-neutral markers, including adaptive genes influencing fitness (*sh4*, conferring shattering; *Bh4*, controlling hull color; *Rc*, conferring pericarp color and seed dormancy), further substantiate the notion that U.S. weeds are genetically close to rice cultivars or landraces (Gross et al. 2010; Thurber et al. 2010; Vigueira et al. 2013).

Interestingly, in China, many of the most prevalent contemporary weeds appear to have evolved through de-domestication from widely grown twentieth-century cultivars, including 'Huk Zo' (temperate *japonica*) and 'Nanjing11' (*indica*) (Qiu et al. 2020). For both U.S. and Chinese weeds, genomic analyses have revealed that the evolution of weedy adaptations during de-domestication has generally not involved genetic changes at loci that were targets of selection during rice domestication (Li et al. 2017; Qiu et al. 2020). This finding points to fundamentally different genetic mechanisms underlying rice domestication versus de-domestication.

Intervarietal hybridization (scenario 2) has been found to be the main mechanism underlying weedy rice evolution in some parts of world without wild *Oryza* species. For example, in northeastern China and Bhutan, weedy populations were found to have evolved from *indica–japonica* hybridizations, creating admixed genomic compositions (Ishikawa et al. 2005; Qiu et al. 2014). In South Korea, similar observations of hybridization between modern cultivars and traditional landraces have been reported (He et al. 2017).

Regions with Wild Oryza Species

Apart from the two domesticated rice species, *O. sativa* and the lesser-known African rice, *O. glaberrima*, there are six wild *Oryza* species that are phylogenetically close to cultivated rice and share the AA genome that potentially allows some degree of interfertility: *O. rufipogon*, *Oryza nivara* S.D. Sharma & Shastry, the annual form of *O. rufipogon* that is sometimes given its own taxonomic standing), *O. barthii* (the wild ancestor of African cultivated rice), *O. longistaminata*, *O. meridionalis*, and *O. glumaepatula* (Khush 1997). Among these wild species, *O. rufipogon* is distributed widely throughout the tropics and subtropics in Asia from western India through Southeast Asia and southern China. The remaining wild rice species are found in Africa, tropical Australia, and South and Central America (Oka 1988; Vaughan et al. 2003).

In regions where wild *Oryza* species are found in proximity to rice-planting areas, most weedy rice evolutionary studies have focused on weed populations where common wild rice (*O. rufipogon*) is present. To date, there is no definitive genetic evidence that any wild *Oryza* other than *O. rufipogon* has contributed to the evolution of weedy rice. Common wild rice has been found to contribute to the evolution of sympatric weedy rice in South and Southeast Asia (Huang et al. 2017; Neik et al. 2019; Pusadee et al. 2013; Song et al. 2014; Sudianto et al. 2016; Vigueira et al. 2019; Wedger et al. 2019).While there is limited evidence in South Asia for weedy rice evolving directly from *O. rufipogon* (scenario 3) (Huang et al. 2017), most studies have proposed that weedy rice in these tropical and subtropical regions is evolving through crop–wild hybridization (scenario 4) (Cui et al. 2016; Neik et al. 2019; Prathepha 2009; Pusadee et al. 2013; Song et al. 2014; Wedger et al. 2019).

In Malaysia and Thailand, where the occurrence and spread of weedy rice have been extensively studied, simple sequence repeats and genome-wide single-nucleotide polymorphisms (SNPs) revealed natural gene flow and hybridization between common wild rice and cultivated rice (Neik et al. 2019; Pusadee et al. 2013; Song et al. 2014; Vigueira et al. 2019; Wedger et al. 2019). Such similar crop–wild intercrossing was also found in South Asia (Huang et al. 2017). The observations of a heterozygous state for several adaptive genes, including *sh4*, *Bh4*, *Rc*, and *An-1* (controlling awn development), found in Malaysian weed samples further support crop–wild hybridization evolutionary mechanisms in weedy rice populations (Cui et al. 2016; Neik et al. 2019; Song et al. 2014). Interestingly, these studies also revealed that the genomes of the Malaysian common wild rice and modern elite cultivars have both been recently introgressed into the local weedy rice populations. Particularly, the brown-striped-like (BR-like) and BHA-like weedy rices have been found to harbor abundant segments of the common wild rice genome. On the other hand, wild introgression detected at domestication genes of the Thai weedy rice samples were likely to be historical gene flow rather than recent introgression (Wedger et al. 2019).

While weedy rice from the tropics and subtropics in Asia has been extensively studied using molecular markers, limited weedy rice population studies have been conducted in regions where wild *Oryza* other than *O. rufipogon* is present. For instance, in Central and South America, where rice is planted in proximity to the interfertile wild rice *O. glumaepatula*, gene flow has been speculated to play a role in local weedy rice evolution. Nevertheless, genome-wide SNP analyses found no evidence for contributions from this native wild *Oryza* to the co-occurring weedy populations (Hoyos et al. 2020; Qiu et al. 2020). Instead, the evolutionary trajectory of these Latin American weeds is similar to those of weed populations from the temperate regions without wild *Oryza* species, wherein intervarietal hybridization between *aus* and *indica* is predominant (Hoyos et al. 2020; Qiu et al. 2020). In Africa, *O. barthii* and *O. longistaminata* have been reported to grow sympatrically with cultivar planting areas. As such, the occurrence of weedy rice, some of which have the wild-like feature of red pericarps, may point toward the role of these wild African *Oryza* species as the weeds' origin (Delouche et al. 2007). Comprehensive analysis of genomic data resolved five subpopulations of wild rice in Africa with which *O. glaberrima* grown in some regions singularly clustered (Wang et al. 2014). African weedy rice is, consequentially, a mixture of wild and cultivated species in the region (Orjuela et al. 2014) and genetically distinct from Asian weedy rice, which descended from *O. rufipogon* or *O. sativa* cultivars. Local adaptation, or ecotypic evolution, is yet another means by which rice types could diverge, as demonstrated by the polycentric, geographically influenced divergence of African rice (Meyer et al. 2016; Veltman et al. 2019). Coastal rice, for example, is adapted to a high salt environment and could give rise to a distinct ecotype of weedy rice. Thus, although wild AA genome *Oryza* species have some degree of interfertility with cultivated rice, they may not contribute to the occurrence of the weedy rice in Latin America and Africa. What has been confirmed, however, is that the closest wild relative of rice, *O. rufipogon*, does play an important role in the evolution and adaptation of weedy rice in South and Southeast Asian regions.

Crop–Weed–Wild Relative Gene Flow and Weed Population Diversification

The genetic structure of weedy rice as it relates to the crop or wild rice is supported by field-collected gene flow rate data. Numerous pollen flow experiments have been conducted using herbicide-resistance traits as markers to estimate detectable gene flow in "real time." The gene flow rate from crop to weed is generally low, ranging from 0% to 1.26% (Table 2). The majority of weedy rice used in outcrossing experiments were *indica* strains. In two studies conducted in China and Korea where the pollen source was an *indica* cultivar and the recipients were different accessions of *japonica* weedy rice, the outcrossing rate ranged from 0% to 0.046% (Chen et al. 2004). Gene flow data from the United States were derived from *indica* and *aus* weedy rice (strawhull and blackhull) with generally *tropical japonica* rice cultivars as pollen donors. Reverse gene flow from weedy rice to cultivars could range from 0.01% to 0.2% in Arkansas, USA (Shivrain et al. 2009a). Two exceptions are notable. In Malaysia, the outcrossing rate between the two Clearfield® rice varieties and four unspecified weedy rice accessions ranged from 7% to 28%, averaged across distances of 1 to 5 m from the pollen source (Engku et al. 2016). These numbers are the highest on record, globally. Another notable situation is a study conducted in three localities in China (Xia et al. 2011). Xia and colleagues collected 11 weedy rice accessions from rice fields infested with 2 to 60 weedy rice plants m^{-2} and determined that the outcrossing rates between these accessions and various rice cultivars ranged from 0.4% to 11.7%. In one study in China where the recipient was wild rice (*O. rufipogon*) and the pollen donor was an *indica* cultivar and a glufosinate-resistant transgenic line, the detectable pollen flow was 1.2% to 2.2% (Chen et al. 2004). Conversely, *O. rufipogon* can hybridize with rice cultivars, as demonstrated in controlled crosses with four Thai cultivars as female parents, resulting in 6% to 62% seed set (Niruntrayakul et al. 2009). These studies show that pollen flow occurs between crop and weed and between crop and wild relative and vice versa. By extension, one can also expect gene exchange between weedy rice and wild relatives. In rice fields in the United States, populations of tall, pink-awned weedy rice are occasionally spotted. These are outcrosses between blackhull weedy rice and *tropical japonica* rice cultivars (Vigueira et al. 2018) and are potentially bridging gene exchange between the crop and other weedy plants.

Table 2. Some gene flow statistics from cultivated rice to weedy rice.

Location	Pollen source[a]	Recipient weedy rice[b]	Outcrossing rate (%)	Comments	Reference
Spain	Glufosinate-resistant rice with *bar*	Unspecified type	0.036	Encircle test, average of all wind directions	Messeguer et al. 2004
Chaling, Hunan Province, China	Nam29/TR18, Minghui-63 (*indica*)	*O. rufipogon* (wild rice)	1.2–2.19	Pollen flow at closest distance	Chen et al. 2004
		Lu-tao (*japonica*)	0		
		Ch79-1 (*indica*)	0		
		Heidiaogu (*indica*)	0.011		
Kyongsan, South Korea	Nam29/TR18, Minghui-63 (*indica*)	Slashare (*japonica*)	0	Pollen flow at closest distance	Chen et al. 2004
		Seongjuaeng (*japonica*)	0.026		
		Galsaegshare (*japonica*)	0.046		
Valle del Cauca, Colombia	CF205 (*indica*)	Various, not described	<1%		Fory et al. 2005, 2007
Santa Maria & Rio Grande do Sul, Brazil	IRGA 422CL (*indica*)	Various, not described	0.065		Villa et al. 2006
Louisiana, USA	CL121, CL141, CL161 (*japonica*)	Strawhull	0.17		Zhang et al. 2006
Arkansas, USA	CL-XL8 (*indica*)	7 strawhull	0.139 (0–1.26)	2 locations, 4 planting dates, mid-April to late May, 2 yr	Shivrain et al. 2009b
		3 blackhull	0.154 (0–0.34)		
		2 brownhull	0.286 (0.01–1.26)		
	CL161	7 strawhull	0.068 (0–0.22)		
		3 blackhull	0.125 (0–0.22)		
		2 brownhull	0.032 (0.01–0.09)		
	CL161	7 strawhull	0.044 (0.03–0.26)	Same as above, highest flowering synchrony 40%–100%	Shivrain et al. 2008
		3 blackhull	0.120 (0.03–0.21)	Same as above, highest flowering synchrony 70%–100%	
		2 brownhull	0.014 (0.01–0.02)	Same as above, highest flowering synchrony 25%–100%	
	CL121	Strawhull	0.003	2 planting dates, 2 yr	Shivrain et al. 2007
	TeQing (*indica*)	Blackhull	0.002	Weedy rice planted in a row between two rows of rice cultivars, 2 yr	Gealy et al. 2015
	PI 615022 (*indica*)	Blackhull	0.017		
	Kaybonnet (*japonica*)	Blackhull	0.032		
Heilongjiang, Jilin, and Jiangsu provinces, China	Various cultivars	11 weedy rice populations	4.1 (0.4–11.7)	From rice fields; infestation level of 2–60 weedy rice 100 m^{-2}	Xia et al. 2011
Malaysia	CL1	Four types, not described	11–20	Encircle design; average of 1 to 5m from source	Engku et al. 2016
	CL2		7–28		

[a] CL, Clearfield® rice.

[b] U.S. weedy rice in these studies was strawhull or blackhull *indica*.

The lineage of weedy rice, the continuous interaction between crop and weed or crop, weed, and wild relative, and the evolution of some weedy traits from de-domesticated cultivars have led to the remarkable diversification of weedy rice populations regionally and globally. Weedy rice differs from cultivated rice in many morphological (i.e., height; tiller number; color of leaf, hull, and kernel pericarp; awnedness; grain traits) and physiological (i.e., seed dormancy, emergence, flowering time, grain shattering, stress tolerance, photosynthetic capacity) traits. As a consequence of the gene flow continuum, weedy rice populations have also diversified greatly in various regions with or without wild rice. Weedy rice diversity has been documented in various countries in Asia (Chauhan and Johnson 2010; Prathepha 2009; Pusadee et al. 2013; Sudianto et al. 2016), Colombia (Hoyos et al. 2019), Costa Rica (Arrieta-Espinoza et al. 2005), Italy (Fogliatto et al. 2012), the United States (Kanapeckas et al. 2018; Karn et al. 2020; Noldin et al. 1999; Shivrain et al. 2010; Tseng et al. 2013), and other parts of the world (Delouche et al. 2007). Globally, strawhull weedy rice is the predominant type. In Asia, awned and awnless strawhull populations occur in high proportions, but in North America, strawhull weedy rice is predominantly awnless. Brownhulls and grayhulls also exist but occur less frequently. Generally, weedy rice populations are taller than cultivars and have an open canopy, droopy leaves, high tillering potential, a wide range of flowering phenologies, open panicles, high seed shattering, red pericarps, and high seed dormancy. However, closer inspection reveals great variability in these and other traits within the strawhull or blackhull group. Vegetative and reproductive traits vary significantly within each hull-color group, creating subgroups based on various combinations of certain key variant traits, such as plant height, maturation, grain shattering, awn length, pericarp color, or grain size. These generalizations also obscure the fact that some weedy rice types are as short or shorter than the cultivars they infest, flower earlier, and have crop-like grain traits (i.e., long grain with white pericarp, low shattering, not dormant). Atypical weedy rice types may arise from weed–weed gene exchange. For example, genetic analysis of short-awned, intermediate-height weedy rice in Arkansas, USA, indicated that such types could have arisen from

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Table 3. Scientific names associated with weedy rice in journal articles on the Web of Science and their frequency of use.

	Frequency of use						
	1991–2000		2001–2010		2011–2020		
Name	*N*	%	*N*	%	*N*	%	Total
Oryza sativa	10	100	103	87.3	244	79.2	357
Oryza sativa f. spontanea	0	0	12	10.2	55	17.9	67
Oryza spp.	0	0	3	2.5	9	2.9	12
Total	10		118		308		436

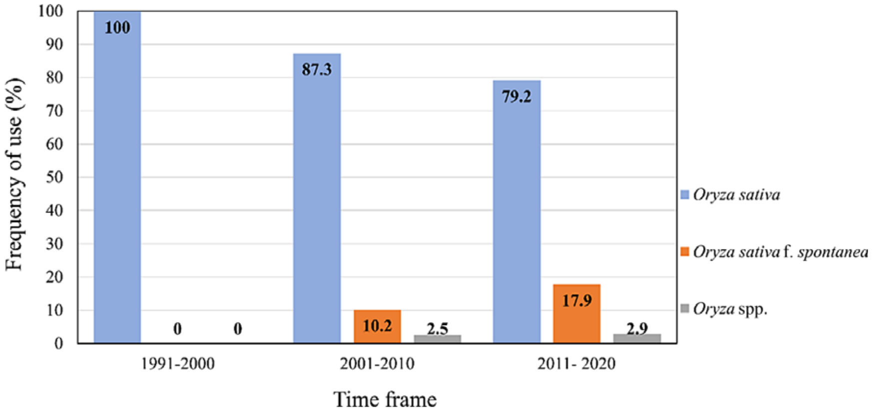

Figure 2. Scientific names associated with weedy rice in the literature between 1991 and 2020.

hybridization between awned and awnless weedy rice (Gealy et al. 2012). Apart from pollen-mediated gene flow, crop-like weedy rice could have arisen from feralization of cultivars planted, as was the case of most weedy rice in Taizhou, China (Zhang et al. 2008); rice in abandoned fields of Sri Lanka (Marambe 2005); or the first-detected weedy rice in California, USA, after decades of having eradicated the weed (Kanapeckas et al. 2016).

The hybridization of HR rice with weedy populations, and subsequent selection with the technology-associated herbicides, has further expanded weedy rice diversity. In the southern United States, for example, where the genetic population structure of weedy rice historically consisted of distinct strawhull and blackhull populations, it presently consists of diversified populations of HR strawhull, blackhull, brownhull, and other hull colors containing a significant portion of the crop genome (Burgos et al. 2014). The majority of HR weedy rice in Arkansas rice fields with a history of Clearfield® rice are crop-like in terms of plant morphology, flowering phenology, and seed dormancy (Singh et al. 2017). Besides having grains with a variety of hull colors, the HR weedy rice populations also have a range of pericarp colors from red, brown, and light brown to white (Singh et al. 2017), in contrast to historically being all red (Shivrain et al. 2010). The hidden consequence of such “disguised” weedy plants is yield loss from competition and loss of grain quality from seed contamination. Overall, this kaleidoscope of traits (crop-like, wild-like, and all sorts in between) is reflected in the confused nomenclature of weedy rice in the literature.

Names Associated with Weedy Rice

As discussed in the previous section, worldwide, weedy rice can be morphologically and genetically classified into two main lineages: crop- and wild-like weedy rice. Based on a literature search, we learned that regardless of the types of weedy rice, the weed has been often referred to as *O. sativa*. The other commonly used term to describe weedy rice is “*O. sativa* f. *spontanea*,” which technically indicates that *O. rufipogon*, but not other wild species, has contributed wild genetic material to the weedy rice strain. These two names to describe weedy rice could be misleading if the forms and origins of the weeds have not been confirmed. The other less commonly used term is “*Oryza* spp.,” which refers collectively to multiple undetermined *Oryza* species.

To determine the usage trend of these scientific names, a Boolean search was conducted in the Web of Science database using the key terms “weedy rice,” “*spontanea*,” “*Oryza* spp.,” and “*Oryza sativa*”; the fields searched were abstract, key words, and title. We categorized the weedy rice studies based on the scientific name used and different time frames (1991 to 2000, 2001 to 2010 and 2011 to 2020). The proportion of weedy rice studies that used *O. sativa*, *Oryza* spp., and *O. sativa* f. *spontanea* was quantified for the different time frames (Table 3; Figure 2). “*Oryza sativa*,” as expected, was the most extensively used term in weedy rice studies, while “*Oryza* spp.” was the least used. Interestingly, the proportion of *O. sativa* f. *spontanea* increased from 10.2% (12 papers) in 2001 to 2010 to 17.9% (55 papers) in 2011 to 2020, signifying a growing use of “*spontanea*” in the past two decades.

Oryza sativa f. *spontanea* refers to the “*spontanea*” type of *O. sativa*, which is *Oryza rufipogon* wild-like weedy rice, or a hybrid between wild *O. rufipogon* and *O. sativa*, particularly the type found in Asia (Chang 1975, 1976a, 1976b; Lu et al. 1997; Morishima et al. 1961; Oka and Chang 1959). When the term “*O. sativa* f. *spontanea*” is used to describe weedy rice in general, it implies that all weedy rice populations originate from the common wild rice (*O. rufipogon*) or is a product of a wild-cultivated rice hybrid. However, 39 out of the 45 papers (86.7%) we could access that used *O. sativa* f. *spontanea*, reported cultivar-like weedy rice or weedy rice from regions where

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wild rice does not exist. This observation demonstrated the misuse of *O. sativa* f. *spontanea* in weedy rice studies, which is problematic, as the scientific name of an organism should be precise and true to the evidence provided, allowing people to communicate about the organism without confusion.

Another notable issue with the term "*O. sativa* f. *spontanea*" is that the it does not inherently indicate the involvement of *O. rufipogon*. Readers might mistakenly assume that *O. sativa* f. *spontanea* can be a direct descendant of *O. sativa*, although in fact some role for *O. rufipogon* is required for weedy rice to be correctly classified as *O. sativa* f. *spontanea*. Moreover, a thorough check of various plant databases, including the International Plant Names Index and the World Checklist of Selected Plant Families, also revealed that *O. sativa* f. *spontanea* is not accepted by some databases due to its ambiguous characterizations (Govaerts 2019; IPNI 2020).

The use of the term "*O. sativa*" is less problematic but still not universally appropriate, as it gives the impression that *O. sativa* is the sole contributor to emergence of weedy rice. Given that *O. sativa* is not the only *Oryza* species that contributes to the emergence of weedy rice, one should not assume that all weedy rice is *O. sativa*. We acknowledge that the use of *O. sativa* to describe weedy rice is not wrong in most contexts, as de-domestication of cultivars is the primary contributor to most of the weeds. However, it becomes problematic when *O. sativa* is used to describe worldwide weedy rice indiscriminately. The notions and suggestions mentioned in this section are also endorsed by the experts in the field, as listed in Supplementary Table 1.

Conclusion and Recommendation

The common usage of the term "*O. sativa*" or "*O. sativa* f. *spontanea*" in describing weedy rice has confounded the discrimination between crop- and wild-like forms of the weed and a broad spectrum of all other intermediates. Such generalization in naming creates confusion and hinders the weedy rice community from effective scientific communication. In regions where there are no wild rice species present, and where *O. sativa* is the only *Oryza* species contributing to the evolution of weedy rice, it is reasonable to use the term "*Oryza sativa*" for describing crop-like weedy rice. This, however, may not apply to weedy rice in Africa, where rice-growing areas are planted with both *O. glaberrima* and *O. sativa* cultivated rice species and where two wild rice species unique to Africa exist. The term should also not be used for wild-like weedy rice introduced into the non–wild rice regions. For regions that have wild *Oryza* species, the usage of "*O. sativa* f. *spontanea*" for weedy rice implies that the rice possesses *O. rufipogon* characteristics; hence, this name is not appropriate for crop-like weedy rice in those localities, either. Furthermore, not all databases recognize "*O. sativa* f. *spontanea*" as a valid taxonomic designation, which may lead to further confusion. Therefore, we advise the use of the more general name, "*Oryza* spp.," when describing worldwide weedy rice in general or when the evolutionary history of the weed strain studied is unresolved. As such, authors should be diligent in considering the names to be used when describing weedy rice populations. The precise usage of scientific name not only averts confusion, but also enhances correct understanding by the audience, who may be unfamiliar with weedy rice evolution and biology.

Supplementary material. To view supplementary material for this article, please visit https://doi.org/10.1017/wsc.2021.22

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