

REGISTRATION

Mapping Population

Registration of two rice mapping populations using weedy rice ecotypes as a novel germplasm resource

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Abstract

Two mapping populations were developed from crosses of the Asian *indica* rice (*Oryza sativa* L.) cultivar ‘Dee Geo Woo Gen’ (DGWG; PI 699210 Parent, PI 699212 Parent) and two weedy rice ecotypes, an early-flowering straw hull (SH) biotype AR-2000-1135-01 (PI 699209 Parent) collected in Arkansas and a late-flowering black hull (BHA) biotype MS-1996-9 (PI 699211 Parent) collected in Mississippi. The weed and crop-based rice recombinant inbred line (RIL) mapping populations have been used to identify genomic regions associated with weedy traits as well as resistance to sheath blight and rice blast diseases. The mapping population consists of 185 (DGWG/SH; Reg. no. MP-9, NSL 541035 MAP) and 234 (BHA/DGWG; Reg. no. MP-10, NSL 541036 MAP) F₈ RILs, of which 175 (DGWG/SH) and 224 (BHA/DGWG) were used to construct two linkage maps using single nucleotide polymorphic markers to identify weedy traits, sheath blight, and blast resistance loci. These mapping populations and related datasets represent a valuable resource for basic rice evolutionary genomic research and applied marker-assisted breeding efforts in disease resistance.

1 | INTRODUCTION

Weedy rice, composed of plants in the genus *Oryza*, is a major agricultural pest worldwide. Weedy rice is a highly troublesome, widespread, and persistent weed of rice; it is often the same species as the crop (*Oryza sativa* L.) but can also have origins in wild *Oryza* species. Weedy rice is often taller than cultivated rice, resulting in crop lodging; has strong seed dor-

mancy and grain shattering, resulting in persistence in the soil; and has red bran grains that reduce grain quality; all these factors reduce crop value. For more than a century weedy rice has infested rice fields throughout the Mississippi River Valley and Gulf Coast of the southern United States in the states of Arkansas, Louisiana, Mississippi, Texas, and Missouri, where ~80% of the country’s rice is grown (Delouche et al., 2007; Jia & Gealy, 2018; Ziska et al., 2015). Recently, weedy rice has been identified as a resurging problem in a few isolated areas in California after it had been nearly eliminated by the mid-1950s using water seeding cultural management practices and certified seed programs (Delouche et al., 2007; Jia

Abbreviations: BHA, MS-1996-9; DAH, days after harvest; DGWG, ‘Dee Geo Woo Gen’; RIL, recombinant inbred line; SH, AR-2000-1135-01; SNP, single nucleotide polymorphism; SSD, single seed descent.

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& Gealy, 2018; Kanapeckas et al., 2016; Karn et al., 2020). In Arkansas alone, where nearly half of all U.S. rice is produced, weedy rice consistently ranks among the three most important weeds in rice cultivation, after barnyardgrass and pigweed (Gealy et al., 2019; Norsworthy et al., 2007; Norsworthy et al., 2013; Smith, 1988). Yield loss due to weedy rice varies according to plant type, density, duration of competition, and rice variety. One weedy rice m⁻² has been reported to reduce the yield of a modern rice cultivars ‘CL161’ and ‘Cocodrie’ by 10% in Arkansas (Ottis et al., 2005). Total annual economic losses due to this weed have been estimated at US\$93 million in Arkansas (Burgos et al., 2008).

The accumulated data show that weedy rice most commonly evolves from domesticated rice, either directly via de-domestication or with varying degrees of hybridization with wild rice species (Li & Olsen, 2020; Qiu et al., 2020). The two major groups of weedy rice genotypes infesting modern day rice fields of the southern United States are straw hull (with no awns) and black hull (with long awns) for the general coloration of the seed hulls (Shivrain et al., 2010b). These genotypes were probably introduced into the United States independently from different regions of Asia and at different times in the distant past (Londo & Schaal, 2007; Reagon et al., 2010). It is thought that weedy rice likely first arrived in what is now the United States in 1698 or earlier as contaminants in rice seed when rice was first being introduced into the colony of South Carolina for cultivation. It later became well documented that weedy rice was a serious problem in rice in North Carolina and South Carolina by the mid-1800s, that the problem had expanded into all of the newer rice-producing states (Georgia, Louisiana, and Arkansas) by 1900, and that by the early 1920s was a serious problem in all of the major present-day rice-producing states (Arkansas, Louisiana, Mississippi, Missouri, Texas, and California) (Delouche et al., 2007).

Straw hull genotypes are genetically closely related to cultivated *indica* rice, whereas black hull genotypes are more closely related to cultivated *aus* rice, and both apparently evolved primarily through de-domestication processes from cultivated rice in these subpopulations, with the black hull type arising several thousand years earlier than the straw hull type (Li et al., 2017; Londo & Schaal, 2007; Reagon et al., 2010; Shivrain et al., 2010a). Since their initial introduction into southern U.S. rice fields in the last several hundred years, these two weedy rice genotype groupings have evolved into more morphologically diverse populations via low-level hybridization between themselves or with the crop, but they are still largely identifiable as distinct straw hull and black hull groups (Delouche et al., 2007; Gealy et al., 2012; Londo & Schaal, 2007; Reagon et al., 2010; Shivrain et al., 2010b). The weedy rice types recently identified in California have genetic backgrounds quite different from, and evolutionarily more recent than, those in the southern United States (De Leon et al., 2019; Kanapeckas et al., 2016).

Core Ideas

- Weedy rice competing with cultivated rice is a major pest.
- Weedy rice can benefit germplasm improvement and weed control.
- Two contrasting crop–weed populations are ideal for basic evolutionary genomic research.
- Abundant genotypic and phenotypic data are ready for the users to analyze.
- SNP-linked traits are useful for marker assisted breeding.

To understand the molecular basis of the evolutionary dynamics of the important genes underlying weedy traits, two recombinant inbred line (RIL) mapping populations were developed using a single seed descent (SSD) breeding method. Two weedy rice ecotypes, an early-flowering straw hull type AR-2000-1135-01 (PI 699209 Parent) from Arkansas (SH) and a late-flowering black hull type MS-1996-9 (PI 699211 Parent) from Mississippi (BHA), were crossed with the Asian *indica* rice cultivar ‘Dee Geo Woo Gen’ (DGWF), a putative evolutionarily close relative (Liu et al., 2015a). DGWG is the carrier for semidwarf 1 gene *SD1*, and this rice cultivar played an important role in the development of Green Revolution cultivars (Liu et al., 2015a). The populations derived from the cross of DGWG (PI 699210 Parent) and SH (DGWG/SH; Reg. no. MP-9, NSL 541035 MAP) and the cross of BHA and DGWG (PI 699212 Parent) (BHA/DGWG; Reg. no. MP-10, NSL 541036 MAP) consist of 185 and 234 RILs, respectively.

The populations were evaluated for nine agronomic traits that include seedling growth rate (i.e., days to emergence), phenology (i.e., days to heading), plant height, canopy structure (tiller angle), number of tillers, and awnedness. Weedy rice generally grows faster and taller and produces more tillers that occupy more space because of wider culm angles; these traits increase the competitive ability of weedy rice. Some physiological traits were also evaluated, including seed dormancy and reactions to rice blast (caused by *Magnaporthe oryzae*) and sheath blight (caused by *Rhizoctonia solani*) fungi in replicated field plots and greenhouse experiments in the summers of 2012–2018. All RILs, including parents, were sequenced using the genotyping × sequencing method. A total of 6,016 single nucleotide polymorphism (SNP) markers between DGWG and SH and 13,730 between BHA and DGWG were used to construct densely covered marker linkage maps. Important genomic regions associated with weedy traits, including resistance to rice blast disease, were established by associating phenotypic data and SNP genotypical

data. Thus far, these two mapping populations have been used to understand evolutionary mechanisms of weedy rice (Qi et al., 2015) and to identify rice blast disease resistance genes (Liu et al., 2015a, 2015b), genes controlling root system architecture in weedy rice (Wedger et al., 2019), and sheath blight disease resistance genes (Goad et al., 2020) as well as the genetic bases of U.S. weedy rice evolution based on weedy traits, including shattering (Qi et al., 2015; Thurber et al., 2013).

2 | METHODS

2.1 | Parents

An early-flowering straw hull genotype, AR-2000-1135-01 (PI 653435), from Arkansas (SH) and a late-flowering black hull genotype, MS-1996-9 (PI 653419), from Mississippi (BHA) were used as weedy rice parents for the populations developed in this study (Jia & Gealy, 2018). Mature plant heights and times to 50% heading were 149 cm and 71 d, respectively, for the straw hull genotype and 169 cm and 85 d, respectively, for the black hull genotype. Both SH and BHA were crossed with DGWG to produce two comparative mapping populations.

2.2 | Population development

The *indica* cultivar DGWG was the female parent in the DGWG × SH cross, whereas the weedy rice BHA was the female parent in the BHA × DGWG cross. The crosses of weed and crop accessions were made in 2009 at the Department of Biology, University of Massachusetts, Amherst, MA. Bulk seeds from F₁ plants verified with a SNP marker were used to produce the F₂ population in 2010. Subsequently, the population was advanced using the SSD breeding method in greenhouses at the Dale Bumpers National Rice Research Center near Stuttgart, AR. The population was advanced two generations in each year from 2011 to 2012 using SSD. A single seed derived from each F₇ individual harvested in a greenhouse in April 2013 was grown in the field in 2013, and single plants were bulk harvested for germplasm release at the F₈ generation. Information on the time of measurement and replication of both mapping populations is provided in Supplemental Figure S1.

2.3 | Rice blast disease evaluation

Blast disease reactions of the mapping population were performed as previously described (RoyChowdhury et al., 2012). Specifically, four to seven rice seedlings at 3–4 leaf stages

were inoculated with freshly prepared blast spores. After inoculation, plants were sealed in plastic bags overnight. Then inoculated plants were removed from the bag and moved to a blast developing room in a greenhouse at 80% relative humidity and 26.7 °C for an additional 6 d prior to scoring disease reactions. A single score was given to each RIL for the reaction of the second youngest leaf of four to seven seedlings. The disease reaction was evaluated based on a 0–5 scale, where 0–2 represents different levels of resistance and 3–5 represents different levels of susceptibility (0, no visible disease lesion; 1, one to five brown spots without any fungal mycelia; 2, more than five brown spots without any fungal mycelia; 3, at least one lesion with visible fungal mycelia; 4, more than five lesions with fungal mycelia; and 5, more than 10 lesions with fungal mycelia).

2.4 | Sheath blight disease reactions

The field isolate *Rhizoctonia solani* (AG1-IA) RR0134 (Wamishie et al., 2007), grown on a mixture of sterilized corn chops and rye, was used for field inoculation and evaluation as described (Goad et al., 2020; Liu et al., 2013). Specifically, each line of the mapping populations was planted in three replicates using a complete block design. The susceptible cultivar ‘Lemont’ was used as a border. Rice plants with a main tiller one-half inch in diameter (approximately at the late tiller stage) in a three-row plot with the center row were inoculated with a mixture of air-dried mycelia and sclerotia of *R. solani*. Approximately 3 wk after inoculation, the plants in the middle row were scored from the base of the plant to the panicle for disease lesions. For each 10% of the plant with lesions, the score was increased by an increment of 1 (10% = 1, 20% = 2... 90% = 9), with a lesion at the panicle being scored as 9. The sheath blight evaluation under field conditions was conducted in 2015 and 2016.

2.5 | Agronomic traits

Phenotypic data for seven traits were collected from 2012 to 2016, either in field plots or in the greenhouse, at the Dale Bumpers National Rice Research Center (Stuttgart, AR). The following traits were assessed: seedling emergence, heading date, plant height, tiller number, leaf relative chlorophyll content, plant type, and awns. Seedling emergence date was counted as the number of days from sowing to 50% seedling emergence. Heading date was calculated as the number of days from sowing to ≥50% of plants within a RIL having one or more tillers with an inflorescence at anthesis. Plant height was measured from the tip of panicle to the ground of a mature plant at harvest. The number of productive tillers (with filled grain) was counted with the average of four plants per

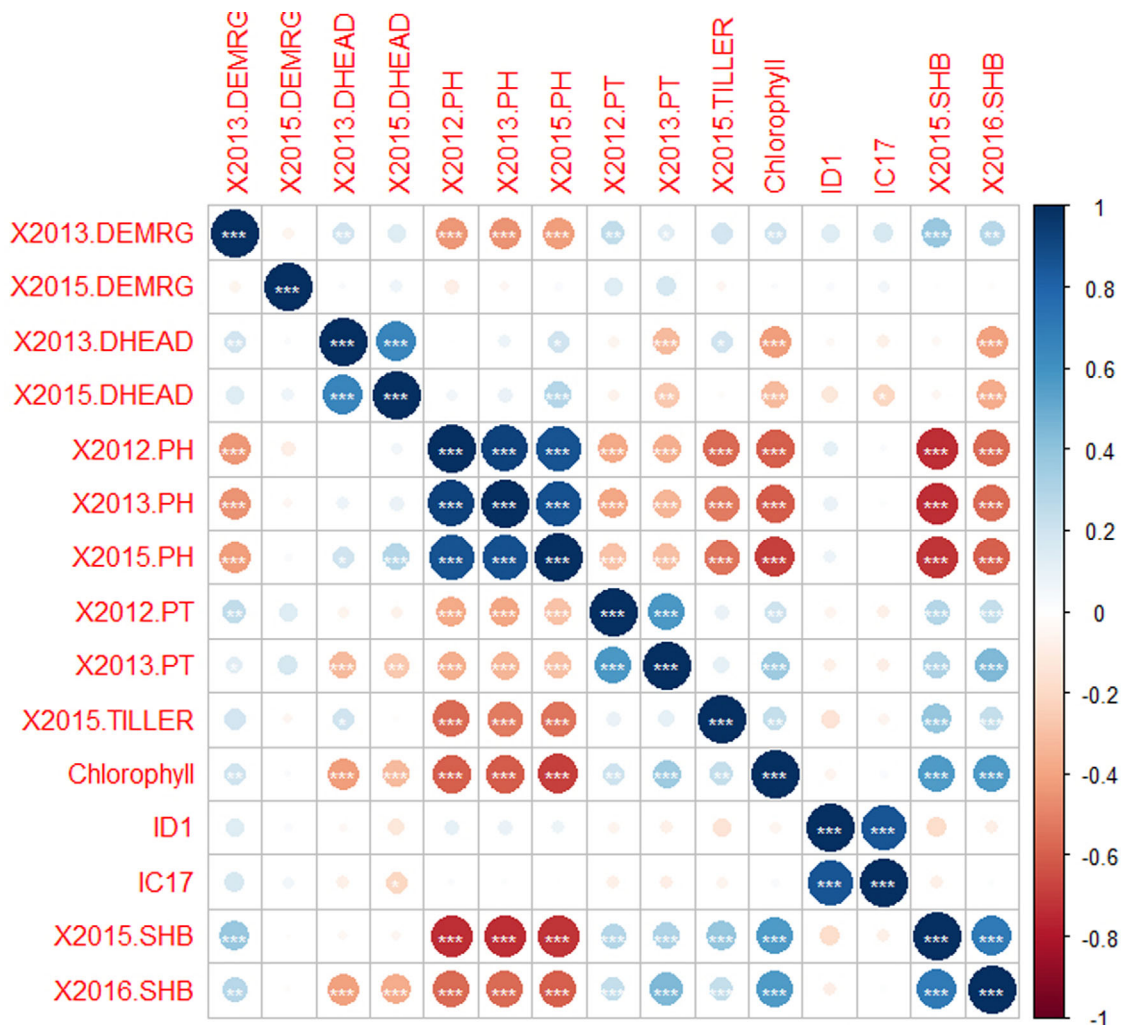


FIGURE 1 Pearson's correlation matrix for all traits in the Table 1. The shaded scale refers to the strength of correlation. Significance levels (*95%, **99%, ***99.9%) are indicated. DEMRG, days to emergence; DHEAD, days to heading; ID1, IC17, blast races; PH, plant height; PT, plant type; SHB, sheath blight reaction; TILLER, number of tillers. Years are indicated after X

pot for SH and three plants per pot for BHA mapping populations at maturity in a greenhouse in 2015. The leaf relative chlorophyll content (unitless) was determined in 2013 (Zhu et al., 2012). Specifically, at 6 d after heading, flag leaves per line per replication were measured, and data from three replications per RIL were collected in the field in 2013 using a LEAF chlorophyll meter that evaluates transmittance of light wavelengths associated with chlorophyll absorbance. Unitless rice descriptors established by the International Rice Research Institute were used to describe the plant type (tiller angle scale of 1 = erect, 3 = intermediate, 5 = open, 7 = spreading, or 9 = procumbent) and to describe the awns on spikelets (on a scale of 0 = absent, 1 = short and partly awned, 5 = short and fully awned, 7 = long and partly awned, 9 = long and fully awned). The data for awn were not collected from DGWG/SH

mapping population because both parents and progeny were awnless.

A randomized complete block design with three replicate blocks was used for field studies. For each replication, several seeds per RIL were sown in a single hill plot using a drill planter, and five plants were kept for each RIL. Fields were flooded when the seedlings reached the 4- to 7-leaf stage. Plants were spaced 30 cm apart within and 61 cm between rows. Each replicate block had five hill plots per row for each RIL, and all were contained within a bay measuring ~40 m by ~16 m.

A total of 10 panicles were bulk harvested for each RIL of two populations, including 234 RILs derived from the cross of BHA × DGWG and 185 RILs derived from the cross of DGWG × SH between October and November in 2012 and 2013.

2.6 | Dormancy

The mapping populations were evaluated in the field in the summer of 2012, and the harvested F_7 seeds were tested for dormancy 150 d after harvest (DAH). Similarly, F_8 seeds were harvested from RILs in the fall of 2013, and a dormancy test was conducted at 90 DAH. Samples were air-dried in paper bags for 5 mo at room temperature for F_7 seeds (2012) and 3 mo for F_8 seeds (2013). Seeds of F_7 and F_8 RILs and parental materials (SH, BHA, DGWG) were tested in batches according to the respective harvest week of each plant. Twenty seeds from each RIL and field replication were placed in a Petri dish (9 cm diameter), replicated three times, moistened with 6 ml deionized water, and dark-incubated in a growth chamber at 30 °C. The Petri dishes were placed in trays, and the trays were arranged in a randomized complete block design in the growth chamber. The trays were covered with a plastic sheet to prevent desiccation and were re-watered every 4 d until termination of the study on the 12th day. A germination count was conducted at 6 and 12 d after placing in the growth chamber. Seeds were considered germinated when the radicle protruded from the caryopsis. A subsample of 10 RILs was tested for viability using the tetrazolium test and compared with the seed-firmness test for dormancy (Singh et al., 2017). Both tests produced the same viability results; thus, firm, non-germinated seeds were counted as viable, dormant seeds. The objective of the study was to differentiate dormancy levels among the RILs within a generation, not to compare dormancy at different times after harvest. In 2012, we tested F_7 seeds at 150 DAH to ensure that the dormancy phenotype was already set. With this seed storage duration, the dormancy among RILs did not differ, but the variation within RILs was high. It seemed like plants within RIL were still segregating. During the same period, dormancy experiments had been conducted on a large number of weedy rice populations from Arkansas, which showed that the dormancy phenotype is already optimally set at 90 DAH. Therefore, in 2013, we tested the dormancy of F_8 seeds at 90 DAH with the expectation of finding significant differences in dormancy among RILs. The differences in generation (F_7 and F_8) and test timings were collectively considered as experiment run or repetition for analysis.

2.7 | Data analysis

Data for sheath blight ratings and agronomic traits were analyzed using SAS Version 9.3, 2002–2010 (SAS Institute Inc.). The analysis was done using Proc GLM (SAS v.9.3). Other statistics, including ANOVA, were performed using Proc Univariate, Proc Freq. The correlation of phenotypic data was analyzed with Pearson's correlation matrix using the R environment correplot package. The ANOVA

was conducted using field replication as random effect, and Tukey's honestly significant difference ($\alpha = .05$) was used to compare the dormancy means. For genotype group comparisons, contrast analysis (e.g., Gonzalez, 2019) was conducted to compare dormancy of RIL group and parent genotypes (SH, BHA, DGWG) and comparisons between parent genotypes (excluding RILs). Significance was evaluated based on F -test ($\alpha = .05$) in JMP Pro (Version 15, SAS Institute Inc.).

3 | CHARACTERISTICS

3.1 | Population properties

Means and ranges for days to heading, plant height, plant type, chlorophyll content, number of tillers, and rice blast and sheath blight reactions of the DGWG/SH and BHA/DGWG populations, as well as the parents, are summarized in Tables 1 and 2, respectively. Correlations among all traits are summarized in Figures 1 and 2. Plant height, plant type, and sheath blight reactions were well correlated among individuals in both mapping populations (Figures 1 and 2). Correlations between disease reaction to the blast races ID1 and IC17 in the SH population and among the races IB33, IC1, IC17, ID1, and IE1 in the BHA population suggest the presence of common blast resistance genes with overlapping resistance spectra exist in these two populations (Liu et al., 2015a). Transgressive segregation was observed among all traits except awns in the BHA/DGWG population (Supplemental Figure S2). Taken together, these findings suggest that both DGWD/SH and BHA/DGWG populations are an excellent resource for identifying novel genes for agronomic, physiologic, and disease-related traits.

3.2 | Dormancy

Approximately 41% of the DGWG/SH RILs in 2012 matured and were harvested during the 42nd Julian week, whereas harvesting of most of the BHA/DGWG RILs (66%) in 2013 was spread over the 42nd and 44th Julian weeks (Figure 3; Supplemental Tables S3–S6).

The viability of RILs, irrespective of population, varied from 75 to 100% in 2012 and 2013 (Figure 4a,c). The F_7 RIL populations indicated that, although the SH parent had higher dormancy (15%) than the BHA parent (8%), the DGWG/SH RILs had high variability in dormancy within the population when evaluated at 150 DAH (Figure 5a). The mean dormancy of F_7 DGWG/SH and BHA/DGWG mapping populations were 16.3 and 8.8%, respectively. In contrast, when dormancy was measured 90 DAH on F_8 seeds, the BHA/DGWG RILs (5.5%) had a greater dormancy than the SH population (3.5%) (Figure 5c,d). The F_8 DGWG/SH RILs

TABLE 1 Agronomic traits and disease reactions for 2012, 2013, 2015, and 2016 for parents and the DGWG/SH mapping population^a

Variable	Mean \pm SE ^b				Range ^b				DGWG ^c				SH ^c			
	2012	2013	2015	2016	2012	2013	2015	2016	2012	2013	2015	2016	2012	2013	2015	2016
Days to emergence	11.3 \pm 0.1	11.3 \pm 0.1	4.4 \pm 0.0	4.4 \pm 0.0	9.7–13.7	9.7–13.7	4–6	4–6	12.7	12.7	5	5	11	11	4	4
Days to heading	97.6 \pm 0.7	97.6 \pm 0.7	90.9 \pm 1.1	90.9 \pm 1.1	73.1–117.1	73.1–117.1	65.0–133.0	65.0–133.0	103.	103.			92.1	92.1	82	82
Plant height, cm	100.7 \pm 1.6	124.8 \pm 1.9	96.9 \pm 2.1	96.9 \pm 2.1	58.8–154.9	78.0–166.7	42.1–148.4	42.1–148.4	73	73	72	72	101	128	93.6	93.6
Plant type	2.9 \pm 0.1	4.8 \pm 0.1			1–7	1–9			5	5	5	5	3	5		
Chlorophyll	41.8 \pm 0.3				34.1–51.8				44.8	44.8			42.3	42.3		
Number of tillers			5.7 \pm 0.2				2.7									6
IC17 ^d	2.7 \pm 0.2				0–5				4				1			
ID1 ^d	3.3 \pm 0.1				1–5				5				2			
Sheath blight (score)			3.6 \pm 0.1	3.8 \pm 0.1			1.7–8.0	2.3–7.0			5.3	4.2		2.5	2.3	

^aData were collected from USDA-ARS, Dale Bumpers National Rice Research Center (USDA-ARS DB NRR), Stuttgart, AR; data were collected from the field for all years, except for rice blast disease data in 2012 and days to emergence, days to heading, plant height, and number of tillers in 2015, which were collected from the greenhouse. All data (Supplemental Table S2) will be deposited at www.ars.usda.gov/GSOR. For the mapping population.

^bParental lines and mean. ^cRice blast disease scoring is from 0 to 5, with 0–2 meaning resistant and 3–5 meaning susceptible. IC17 and ID1 are the names of blast races.

TABLE 2 Agronomic traits and disease reactions for 2012, 2013, 2015, and 2016 for parents and the BHA mapping population^a

Variable	Mean \pm SE ^b			Range ^b			DGWG ^c					BHA ^c				
	2012	2013	2015	2016	2012	2013	2015	2016	2012	2013	2015	2016	2012	2013	2015	2016
Days to emergence	12.0 \pm 0.1	12.0 \pm 0.1	4.6 \pm 0.0	4.6 \pm 0.0	10.0–15.5	4–6			13	5	5		11	5		
Days to heading	102.6 \pm 0.5	102.6 \pm 0.5	96.2 \pm 0.9	96.2 \pm 0.9	84.0–118.1	22–121				103.				104.		
Plant height, cm	104.0 \pm 1.4 ^d	119.3 \pm 0.9	98.4 \pm 1.7	98.4 \pm 1.7	61.3–146.1				73		71.8		146	135		
Plant type (1–9)	2.8 \pm 0.1	4.8 \pm 0.1			1–7	1–9			5	5	5		1	3		
Awns	4.5 \pm 0.3				0–9				0				9			
Chlorophyll	41.1 \pm 0.2				32.7–50.0				43				38.2			
Number of tillers	6.4 \pm 0.1				2.5–16.5				6				5.3			
IB33 ^d	2.9 \pm 0.1				0–5				3				2			
IC1 ^d	3.1 \pm 0.1				0–5				5				2			
IC17 ^c	3.4 \pm 0.1				0–5				5				1			
ID1 ^d	3.2 \pm 0.1				0–5				5				1			
IE1 ^d	2.2 \pm 0.1				0–5				5				2			
IE1K ^d	2.8 \pm 0.1				0–5				5				1			
Sheath blight (score)	4.1 \pm 0.1 ^d	3.7 \pm 0.1			1.8–7.8	2.3–6			5.3	3.7			3.5	2.8		

^aData were collected from USDA-ARS, Dale Bumpers National Rice Research Center (USDA-ARS DB NRRCC), Stuttgart, AR; data were collected from the field for all years, except for rice blast disease data in 2012 and days to emergence, days to heading, plant height, and number of tillers in 2015, which were collected from the greenhouse. All data (Supplemental Table S2) will be deposited at www.ars.usda.gov/GSOR. ^bFor mapping population. ^cParent lines and mean. ^dRice blast disease scoring is from 0 to 5, with 0–2 meaning resistant and 3–5 meaning susceptible. IB33, IC1, IC17, ID1, IE1, are IE1K are the names of blast race.

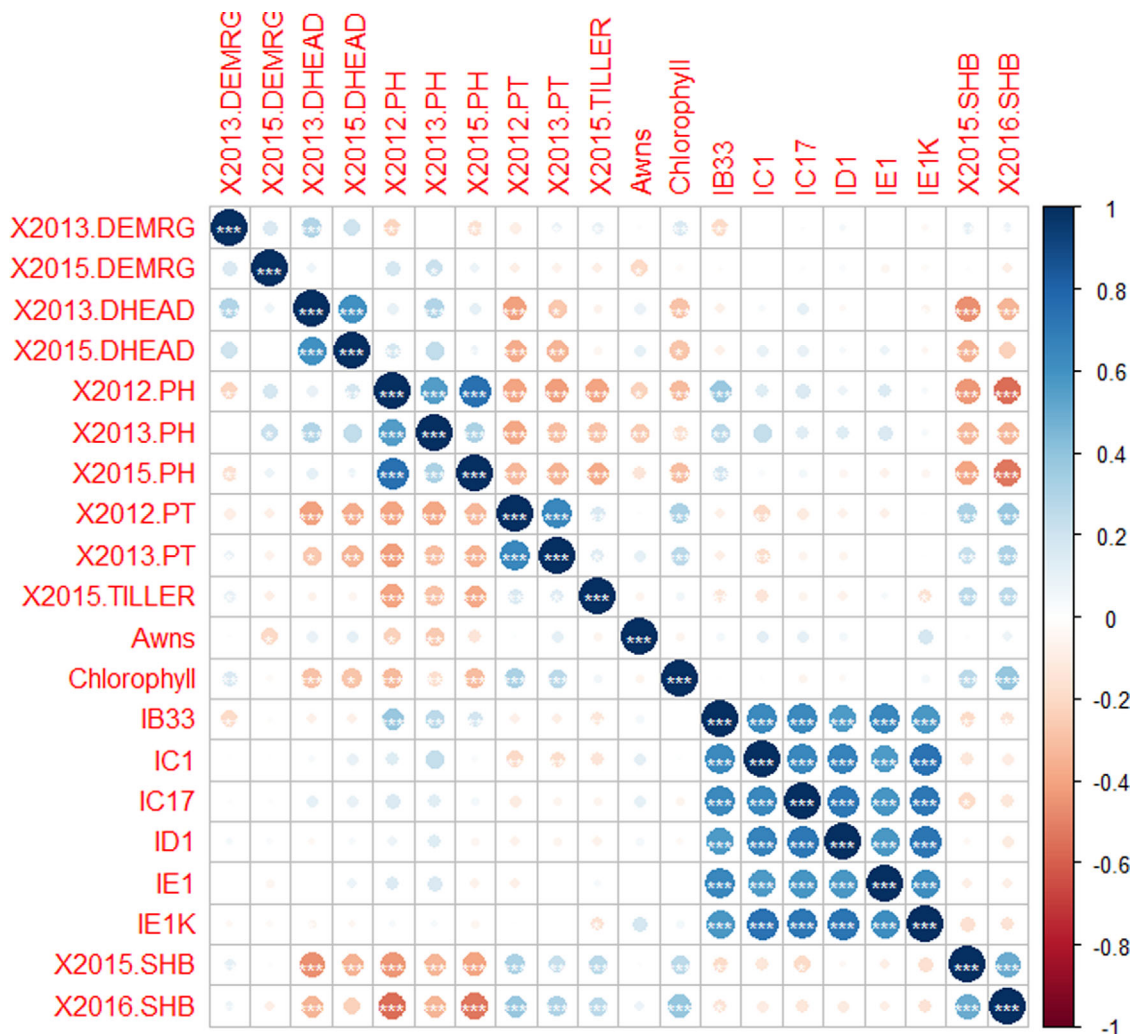


FIGURE 2 Pearson's correlation matrix for all traits in the Table 2. The shaded scale refers to the strength of correlation. Significance levels (*95%, **99%, ***99.9%) are indicated. DEMRG, days to emergence; DHEAD, days to heading; IB33, IC1, IC17, ID1, IE1, IE1k, blast races; PH, plant height; PT, plant type; SHB, sheath blight reaction; TILLER, number of tillers. Years are indicated after X

were more similar to one another, and the majority of the them did not show greater dormancy than the parent population (Figure 5c). The dormancy percentage was greater and more variable in F_7 RILs than in F_8 RILs (Figure 5). However, no significant differences in dormancy were observed among inbred lines, except for F_8 BHA/DGWG RILs (Figure 5d), when analyzed separately for each population in a year. A contrast analysis indicated consistent differences in dormancy between both weedy rice parents SH or BHA and DGWG.

4 | DISCUSSION

Combinations of numerous traits and characteristics such as dormancy have helped weedy rice persist as a dominant weed in rice fields. In general, straw hull and black hull ecotypes are phenotypically and genotypically different (Shivrain et al.,

2010a, 2010b; Tseng et al., 2018). Previous studies have indicated that contemporary black hull ecotypes have higher intrapopulation variation in terms of dormancy than straw hull ecotypes (Do Lago, 1982; Tseng et al., 2013). It has been observed that black hull ecotypes require longer after-ripening time to release dormancy (Tseng et al., 2013). However, the hybrids of weedy rice and rice cultivars are expected to show >90% germination irrespective of hull color due to the introgression of crop alleles (Shivrain et al., 2009b; Singh et al., 2017).

In the current study, we found different seed dormancies of DGWG/SH and BHA/DGWG populations, and the dormancy differed between different time intervals of germination after harvest. However, lack of significant segregation at F_7 and F_8 might have led to the more uniform expression of dormancy among the RILs. Consistent with these results, >96% of the genome in F_7 or higher generation RILs often becomes homozygous and provides genetic stability (Al-kordy et al.,

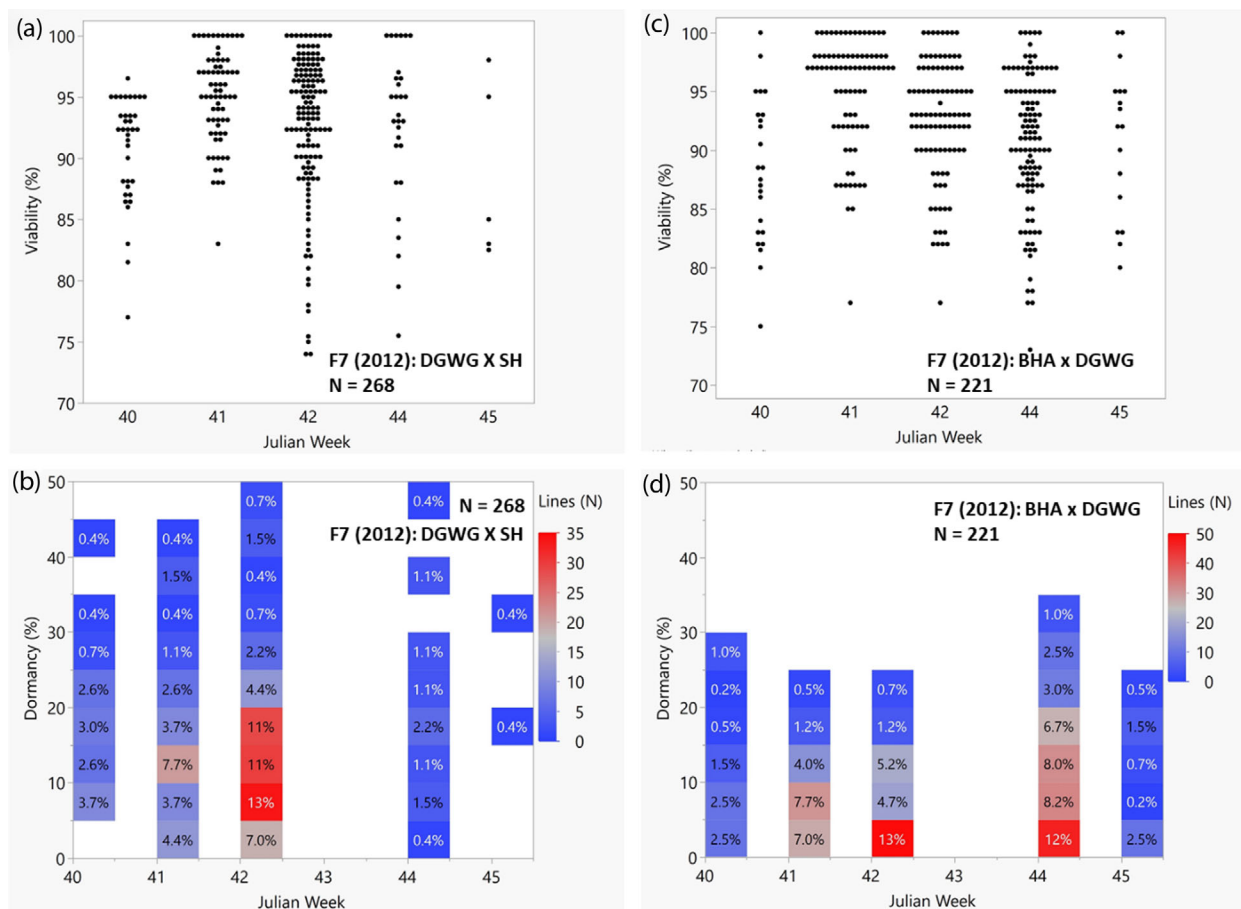


FIGURE 3 Viability and dormancy of F₇ DGWG/SH and BHA/DGWG mapping populations. Individual plants and seeds were harvested from October to November in 2012, and dormancy was measured at 150 d after harvest (~20 wk) with respect to harvesting date (Julian week). (a) Viability and (b) dormancy of F₇ DGWG/SH and (c) viability and (d) dormancy of F₇ BHA/DGWG were plotted with respect to Julian week. For viability, each dot represents a seed from an individual plant of F₇ DGWG/SH and F₇ BHA/DGWG. For dormancy, the color scheme and percentages in the boxes represent the number of recombinant inbred lines (RILs; percent of total) with a particular combination of Julian week and dormancy, where red highlights a greater number of RILs with corresponding dormancy level indicated by y-axis. All data will be deposited at www.ars.usda.gov/GSOR

2019; Zhang et al., 2006). This might have resulted in non-significant differences in dormancy among the RILs in the current study.

Transgressive segregation in these two mapping populations is useful to dissect genetic and epigenetic bases underlying weedy traits (Qi et al., 2015; Thurber et al., 2013). The weedy parents BHA and SH are taller than the *indica* parent DGWG and most cultivated rice in the southern United States, enabling lodging that reduces crop yield. Identified resistance genes to blast and sheath blight diseases are consistent with correlations of blast and sheath blight reactions we observed (Goat et al., 2020; Liu et al., 2015a). These newly identified resistance genes are new sources for breeders to use for marker-assisted breeding and for elucidating adaptive innate immunity in weedy rice. Among the most interesting of these traits are superior vigor and competitiveness throughout its life, population diversity and changeability facilitated by natural crossing with cultivars or other weedy

rice genotypes, abundant production of seed, and high levels of seed shattering and dormancy, which assure deposition of large numbers of weedy rice seed into the soil, where they can infest the next crop or a future crop following multiple years of dormancy (Delouche et al., 2007). Some genes for seed shattering appear to be closely linked with a major gene for red bran color and quantitative trait loci for seed dormancy (Ji et al., 2006). From the mapping populations presented here, it is shown that weed-associated traits such as seed shattering are controlled by multiple quantitative trait loci, whereas awn length and seed bran color are mostly attributable to individual loci; the genetic “weedy” alleles derived from the two weedy rice genotypes have evolved in parallel through independent mechanisms (Qi et al., 2015). Much of the competitiveness of weedy rice is attributable to aggressive emergence and growth relating to profuse tillering; nitrogen fertilizer uptake; production of root, shoot, and seed biomass; and greater plant height (which causes lodging), all of which

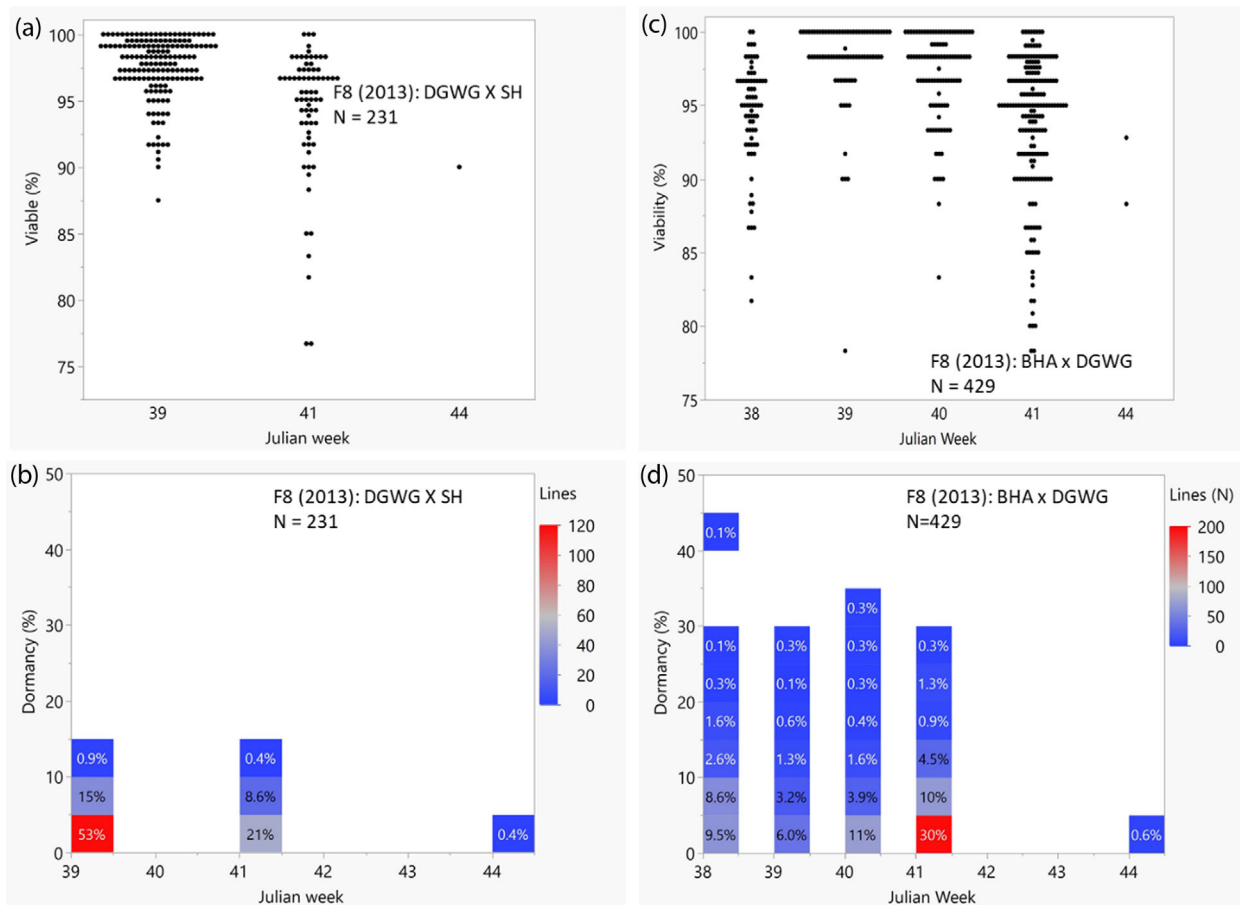


FIGURE 4 Viability and dormancy of F_8 DGWG/SH and BHA/DGWG mapping populations. Individual plants and seeds were harvested from October to November in 2013, and dormancy was measured at 90 d after harvest (~12 wk) with respect to harvesting dates (Julian week). (a) Viability and (b) dormancy of F_8 DGWG/SH and (c) viability and (d) dormancy of F_8 BHA/DGWG were plotted with respect to Julian week of harvest. For viability, each dot represents a seed of an individual plant of F_8 DGWG/SH and F_8 BHA/DGWG. For dormancy, the color scheme and percentages in the boxes represent the number of lines/ individuals (percent of total) with a particular combination of Julian week and dormancy, where red highlights a greater number of lines with corresponding dormancy level indicated by y-axis. All data (Supplemental Tables S3–S6) will be deposited at www.ars.usda.gov/GSOR

confer greater competitiveness in comparison with the crop, resulting in severe yield losses (Burgos et al., 2006; Jia & Gealy, 2018; Sales et al., 2011; Shivrain et al., 2009a, 2009b, 2009c, 2010b). A single weedy rice plant has been shown to have the same yield-reducing potential as up to five cultivated rice plants (Pantone et al., 1992). Weedy rice also reduces grain quality because its red bran color is undesirable and its seeds are difficult and costly to separate from those of the white rice crop, which results in dockage and reduced commercial value (Delouche et al., 2007). Although the species is primarily self-pollinated, rice and weedy rice can intercross at low frequencies (usually <0.5%), sometimes producing new and difficult-to-control “weedy” progeny (Burgos et al., 2014; Gealy et al., 2015; Jia & Gealy, 2018; Jia et al., 2014; Reagon et al., 2010; Shivrain et al., 2007, 2009a, 2009b, 2009c). Weedy rice–cultivated rice outcrosses tend to become even more difficult to manage when rice cultivars carry genes for herbicide resistance, and such herbicide-

resistant rice cultivars now make up more than half of the rice grown in the southern United States (Burgos et al., 2014; Norsworthy et al., 2013; Ziska et al., 2015). Deployment of herbicide-resistant rice cultivars in the southern United States over the past two decades has led to improved management and control of weedy rice but has also resulted in some challenges (Burgos et al., 2008; Norsworthy et al., 2013). New weedy rice genotypes have developed in some fields over time from intercrossing between weedy rice and herbicide-resistant rice cultivars and intense selection from herbicides used with these cultivars, as well as from traditional avenues such as new introductions of weedy rice seed and intercrossing between different genotypes of weedy rice (Burgos et al., 2014; Gealy et al., 2012; Norsworthy et al., 2013). Newer rice cultivars tend to have earlier flowering times than older cultivars, and the earliest-flowering ones exhibit improved flowering synchronization and increased outcrossing with many of the naturally occurring, early-heading straw hull weedy

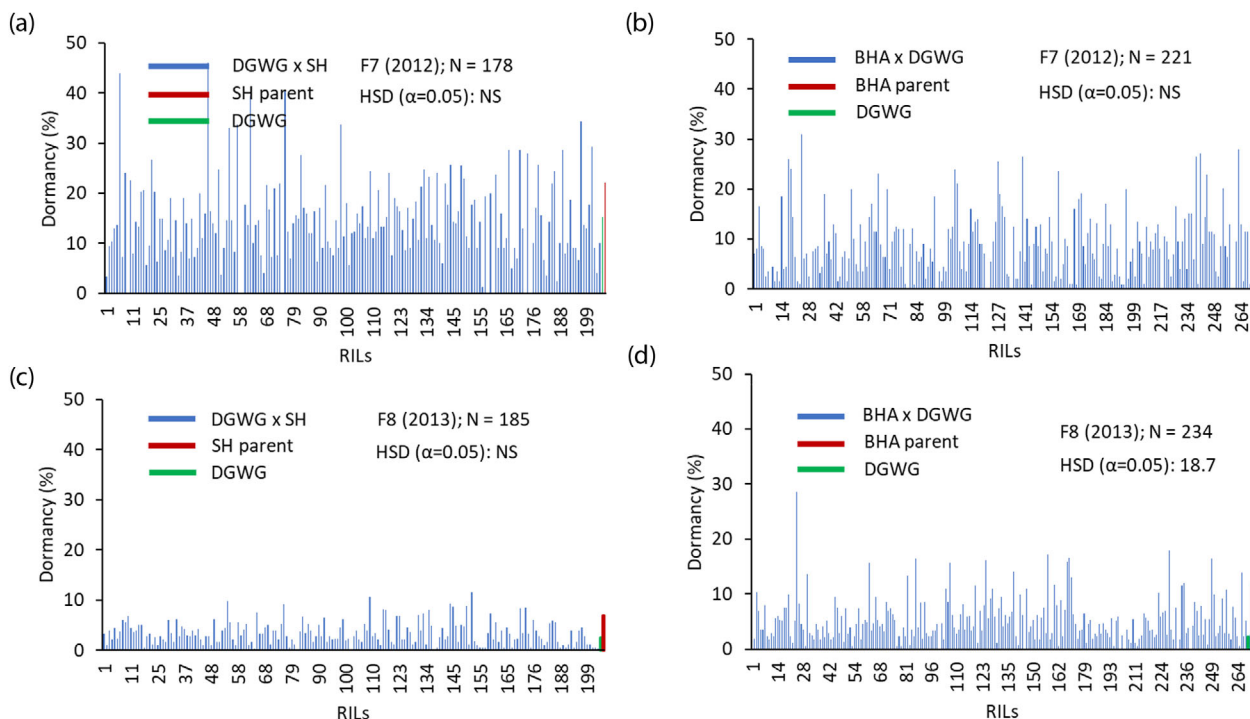


FIGURE 5 Dormancy of F_7 and F_8 mapping populations (DGWG/SH and BHA/DGWG). Individual plants and seeds were harvested from October to November in 2012 and 2013, and dormancy was measured at 150 and 90 d after harvest for F_7 and F_8 recombinant inbred lines (RILs), respectively, based on their harvesting dates (Julian week). Dormancy of (a) F_7 DGWG/SH, (b) F_7 BHA/DGWG, (c) F_8 DGWG/SH, and (d) F_8 BHA/DGWG were plotted for each RIL along with its parents, irrespective of the week of harvest. Dormancy was averaged over three growth chamber replications for each of three field replications. The mean values of dormancy for F_7 DGWG/SH = 16%, F_7 BHA/DGWG = 8.8%, F_8 DGWG/SH = 3.5%, and F_8 BHA/DGWG = 5.5%. All data (Supplemental Tables S3–S7) will be deposited at www.ars.usda.gov/GSOR

rice genotypes. However, a biological bottleneck between outcrossing and permanent gene flow into weedy rice populations apparently has mitigated the impact of this increased outcrossing activity somewhat because F_1 hybrids from crosses with straw hull weedy rice genotypes usually flower extremely late, which largely prevents production of viable F_2 seed (Jia & Gealy, 2018; Shivrain et al., 2009a). There is evidence to suggest that gene flow from rice into modern populations of black hull weedy rice has been greater than into those of straw hull weedy rice (Burgos et al., 2014).

5 | CONCLUSIONS

Future challenges from weedy rice may arise due to shifts in cultural practices or soil microbes or environmental conditions. Negative impacts of weedy rice worldwide have increased in recent years, particularly where direct-seeding or drill-seeding practices have replaced traditional water-seeded or transplanting systems that previously had held weedy rice in check due to the weed control benefits of maintaining permanent flood at planting and throughout the growing season

(Ziska et al., 2012). Weedy rice is likely to become an even greater weed problem under projected future climate conditions because recent research showed that the relative growth aggressiveness of weedy rice and outcrossing between weedy rice and cultivated rice increased under simulated environmental changes, such as increases in ambient CO_2 levels and temperature (Wang et al., 2016; Ziska et al., 2012). Alternative rice irrigation systems such as alternate wetting and drying, which conserves irrigation water and is being developed and deployed in the United States and worldwide, may also result in new and unpredictable interactions between weedy rice and cultivated rice in the fields. Because weed-crop RILs may also cause problems in fields due to the weedy traits, it is preferable to work under highly contained environmental conditions, such as in the greenhouse. Nevertheless, these genetic resources characterized for agronomic traits, including dormancy and disease reactions, along with abundant genetic markers of all RILs and parents are thus important for investigating the genetic interactions of weedy rice and cultivated rice under different cultural practices and changing environments. The resulting knowledge will benefit functional genomics, breeding, and crop protection.

6 | AVAILABILITY

These two mapping populations with the accompanying genetic and phenotypic information provide a valuable foundation for association mapping, understanding the basis of beneficial traits for crop improvement, and insights into the molecular dynamics of the evolution of invasive weed species of rice and their management. The F_8 generation seeds from 2013 are available for distribution. Seeds of two weedy rice mapping populations, the DGWG (GSOR 301040) and straw hull type AR-2000-1135-01 (PI 653435), referred as SH, and the late-flowering black hull type MS-1996-9 (PI 653419), referred as BHA, will be maintained by Dr. Yulin Jia of the USDA-ARS Dale Bumpers National Rice Research Center, Stuttgart, AR. Distribution of seeds will be made by the USDA-ARS Genetic Stock Collection of *Oryza sativa* (<http://www.ars.usda.gov/main/docs.htm?docid=8318>), where they are available for research purposes, including development and commercialization of new materials. It is requested that appropriate recognition of the source be given when these lines contribute to the research or development of improved lines, cultivars, or hybrids.

DATA AVAILABILITY STATEMENT

All phenotypic data and genotypes of these two populations and parents generated by genotyping by sequencing can be accessed at www.ars.usda.gov/GSOR and the DRYAD Digital Repository at <https://datadryad.org/stash/dataset/> <https://doi.org/10.5061/dryad.566h9>, and Illumina HiSeq Raw reads: NCBI SRA accession SRX576894, respectively.

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AUTHOR CONTRIBUTIONS

Yulin Jia: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Resources; Software; Supervision; Validation; Visualization; Writing-original draft; Writing-review & editing. Vijay Singh: Data curation; Formal analysis;


Writing-review & editing. David Gealy: Conceptualization; Data curation; Writing-review & editing. Yan Liu: Data curation; Writing-review & editing. Jianbing Ma: Data curation; Writing-review & editing. Carrie Thurber: Data curation; Writing-review & editing. Nilda Roma-Burgos: Conceptualization; Writing-review & editing. Kenneth M. Olsen: Conceptualization; Resources; Writing-review & editing. Ana Caicedo: Conceptualization; Resources; Writing-review & editing.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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SUPPORTING INFORMATION

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