Seed Dormancy Imposed by Covering Tissues Interrelates to Shattering and Seed Morphological Characteristics in Weedy Rice

Xing-You Gu, Shahryar F. Kianian, and Michael E. Foley*

ABSTRACT

Seed dormancy, a major adaptive trait in plants, facilitates the survival of weeds and provides for resistance to preharvest sprouting (PHS) in cereal crops. Seventeen weedy strains and 24 cultivars of rice (Oryza sativa L.) were evaluated for germinability to screen for donors of dormancy genes. Extremely dormant genotypes were identified from the weedy strains. These genotypes displayed hull and pericarp/testa-imposed dormancy. Three dormant weedy strains, LD, TKN12-2, and SS18-2, were crossed and backcrossed with the nondormant breeding line EM93-1 to determine the relationship between dormancy and the shattering, awn, hull color, and pericarp/testa color characteristics. All these characteristics interrelated to the covering-imposed dormancy; the weedy forms of the characteristics significantly reduced germination in the BC₁F₁ populations. Moreover, multiple linear regression analyses revealed significant effects of interaction between the characteristics on dormancy in the populations. The interrelation and interaction reflect the importance of combined effects of dormancy and other weedy characteristics in the adaptation of weedy populations to agroecosystems, and suggest that domestication and breeding activities have eliminated dormancy alleles at loci near the genes for shattering and the morphological characteristics from improved cultivars.

Weeds are organisms adapted to human disturbances (Harlan, 1965). Many characteristics contribute to the adaptation and persistence of weeds (Baker, 1974). For example, shattering enables weed seeds to escape harvest, and dormancy promotes survival in the soil seed bank. Other characteristics, such as grain type and awns in wild oat (Avena fatua L.) (Johnson, 1935; Simpson, 1992) and dark seed coat color in proso millet (Panicum miliaceum L.) contribute to weed persistence (Khan et al., 1996), but their adaptive significance has not been extensively examined.

Outcrossing frequently occurs between conspecific weeds and crops, sometimes yielding fertile hybrids (Harlan et al., 1973; Langevin et al., 1990). Outcrossing facilitates gene flow from crop to weed populations and initiates hybridization-differentiation cycles (Ladizinsky, 1985; Oka, 1988). It is these cycles that allow populations of weeds to generate types that are better adapted to compete with or mimic improved cultivars. For example, researchers are now concerned with gene flow between herbicide-resistant cultivars and conspecific weeds such as rice to weedy or red rice (Oryza spp.) (Oard et al., 2000; Gealy et al., 2003; Zhang et al., 2003). Systematic research is required to understand how seed dormancy and other characteristics such as awns, hull and pericarp/testa colorations, herbicide resistance, and shattering influence fitness in weed/cultivar hybrid-derived offspring.

Weedy strains are hypothesized to be intermediate between wild species and cultivars, and thus weeds are considered as part of the primary gene pool for crop breeding (Harlan et al., 1973). It is assumed that weedy races harbor genes for tolerance to various adverse conditions, but their breeding potential has not been well explored (Harlan, 1965; Oka, 1988). New genetic and genomic approaches will facilitate discovery of novel genes in nondomesticated germplasm for major advances in crop improvement ( Tanksley and McCouch, 1997). We are utilizing weedy rice as a genetic system to explore fundamental and applied aspects of seed dormancy because weedy strains generally have a higher level of dormancy compared with cultivars (Oka, 1988; Tang and Morishima, 1997). Additionally, rice is a model system with a small genome size (430 Mbp) that has been sequenced (Goff et al., 2002; Yu et al., 2002).

Weedy rice occurs in areas with and without wild rice relatives (Oryza spp.) (Oka, 1988). Previous research has characterized the level and type of seed dormancy for several weedy and cultivated genotypes (Gu et al., 2003). Seed dormancy was associated with the presence of an awn, and black hull or red pericarp/testa colorations in two weedy strain-derived F₁ populations, but the degree of association varied with the cross or genetic background (Gu et al., 2003). In this research, we screened additional weedy strains, and traditional and improved cultivars for dormant genotypes. Three strongly dormant weedy strains were crossed and backcrossed with a breeding line to synchronize the genetic background of dormancy genes. Thus, the objectives of this research were to use primary segregation populations (BC₁F₅) to establish the co-adaptive relationships between dormancy and other weedy characteristics, and demonstrate how domestication and breeding have resulted in a reduction of seed dormancy.

MATERIALS AND METHODS

Plant Materials and Cultivation

Seventeen weedy strains and 24 cultivars of Asian rice (O. sativa L.) and four cultivars of African rice (O. glaberrima Steud.) were screened for strongly dormant and nondormant genotypes. The weedy strains originated from Bhutan (BT1Ac,
Table 1. Species, types, and phenotypic variation in weedy characters of the genotypes used in this research.

<table>
<thead>
<tr>
<th>Species</th>
<th>Types</th>
<th>Number of genotypes in each category (present/absent)</th>
<th>Percentage germination&lt;sup&gt;‡&lt;/sup&gt; mean ± SD (range)</th>
</tr>
</thead>
<tbody>
<tr>
<td>O. sativa</td>
<td>weeds</td>
<td>17/10</td>
<td>11:6 ± 161 (11)</td>
</tr>
<tr>
<td></td>
<td>Indica cultivars</td>
<td>0:16/0:10</td>
<td>0:16 ± 1:1 (0:15)</td>
</tr>
<tr>
<td></td>
<td>Japonica cultivars</td>
<td>0:8/0:8</td>
<td>0:8 ± 0:8 (0:8)</td>
</tr>
<tr>
<td></td>
<td>cultivars</td>
<td>0:4/1:3</td>
<td>0:4 ± 2:2 (0:3)</td>
</tr>
<tr>
<td>O. glaberrima</td>
<td></td>
<td>21 (25–90)</td>
<td>39 ± 39 (2–92)</td>
</tr>
</tbody>
</table>

<sup>‡</sup> Superscripts † and ‡ indicate that the genotypes have seeds with a long (>3 cm) and short (<1 cm) awn, respectively.

BT2Cb, and BT8Acb, Brazil (W1713), China (C9587, C9588, C9589, and LD), India (W1670-14), Korea (C9541, S434, and Hapcheon 3), Nepal (C9520, TKN5-3, and TKN12-2), Thailand (SS18-2), and the USA (US1). The majority of weedy strains were selected based on their origin and morphophysiological characteristics (Suh et al., 1997; Tang and Morishima, 1997). The cultivars of Asian rice included 16 O. sativa subsp. indica [e.g., CO39 (PI 597037), Dular (PI 180861)], EM93-1, IR36 (PI 408586), IR64 (PI 497682), Nanjing 11, N22 (PI 461046), Peta, Pokkali, PTB10 (PI 400144), Seri Raja (PI 233660), Taichung Native 1 (PI 400158) and Teqing (PI 536047) and eight O. sativa subsp. japonica [i.e., Lemont (PI 475833), Mahsuri (PI 400130), Milyang23 (PI 464609), Moroberekan (PI 434632), Nipponbare (PI 514663), Taichung65 (PI 275428), Todorokawase (PI 458775), and WJX] cultivars or breeding lines. These cultivars or lines range from dormant to nondormant based on scattered reports in the literature (Chang and Tagumpay, 1973; Seshu and Sorrel, 1986; Siddique et al., 1988; Wan et al., 1997; Lin et al., 1998) or preliminary observations.

The four African cultivars (O. glaberrima) are Kebra 60 (PI 69463), Kebra 80 (PI 369480), Saka (PI 369481), and NSGC5945 (PI 590414). All weedy strains display seed shattering and most of them have a long awn, a black hull color, and a red pericarp/testa color (Table 1). Several traditional cultivars, such as Pokkali, Kebra 60, and Kebra 80, retain the red pericarp and/or a short awn. The other cultivars or breeding lines have the domesticated form of the traits (Table 1).

The weedy strains and some cultivars were self-pollinated with a single plant selected for one or more generations to purify the genotypes before experimentation. Three strongly dormant weedy strains, LD, TKN12-2, and SS18-2, were crossed with the nondormant breeding line EM93-1 to develop backcross F<sub>1</sub> (BC<sub>1</sub>F<sub>1</sub>) populations. EM93-1 was chosen as the recipient parent to simplify the genetic background because the pericarp/testa removed, and excised embryos to estimate the effect of tissue components on dormancy. Caryopses, caryopses and 1 wk for pericarp/testa-removed caryopses and excised embryos. There were about 50 caryopses and 1 wk for pericarp/testa-removed caryopses and excised embryos. There were about 50 caryopses or 20 embryo per treatment with three replications. Caryopsis germination for the LD-derived BC<sub>1</sub>F<sub>1</sub> population also was evaluated using the same method as that for the intact seeds, except that the sample size was 30 caryopses.

Seed Shattering and Morphological Characters

Seed shattering was quantified with the shattering rate on the basis of air-dried weight. Panicles were cut from the plant and immediately shaken gently for about 20 s over a container to collect shattered seeds, and then hand-threshed to collect the nonshattered seeds. The seeds were cleaned by removal of empty spikelets and dried in a greenhouse for 3 d. Shattering rate was calculated as percentage of the shattered to the total seed weight. The awn characteristic was quantified as the percentage of seeds with an awn in a random sample of 50...
seeds from a plant and expressed as the mean of three samples. Black hull and red pericarp/testa colors were classified as present and absent, with the presence of black or red colors rated as 1 and the absence as 0.

Data Analysis

Primary germination data (y) collected from the BC1F1 populations at different DAR was transformed by sin^{-1}(y/100) for statistical analysis. The relationship between two characteristics was determined by a simple linear correlation (CORR) analysis (SAS Institute, 1999). Effects of the characteristics, awn, black hull color, red pericarp/testa color, and seed shattering and the two-way interactions on seed dormancy were estimated based on the multiple linear regression model:

\[ y_i = m + b_1x_{1i} + b_2x_{2i} + b_3x_{3i} + b_4x_{4i} + b_{51}x_{1i}x_{2i} + b_{52}x_{1i}x_{3i} + b_{53}x_{2i}x_{3i} + b_{54}x_{4i} + e_i \]

where \( y_i \) is the mean germination of seeds at 1, 11, or 21 DAR from the \( i \)th plant; \( m \) is the mean of the model; \( x_1, x_2, x_3, \) and \( x_4 \) are the variables for percentage of seeds with an awn, hull color, pericarp color, and shattering rate, respectively; \( x_{1i}, x_{12i}, x_{13i}, x_{14i}, x_{23i}, x_{24i}, \) and \( x_{34i} \) are the interactions between variables \( x_1 \) and \( x_2, x_1 \) and \( x_3, x_1 \) and \( x_4, x_2 \) and \( x_3, \) and \( x_2 \) and \( x_4, \) and \( x_3 \) and \( x_4, \) respectively; \( b_1, b_2, b_3, b_4, b_{51}, b_{52}, b_{53}, b_{54}, \) and \( b_{55} \) are the partial regression coefficients corresponding to the regressor variables \( x_1, x_2, x_3, x_4, x_{12}, x_{13}, x_{14}, x_{23}, x_{24}, x_{34}, \) and \( x_{134}, \) respectively; \( e_i \) is the residual effect including the random error and the genetic effect that is not explained by the above main and two-way interaction effects; and \( N \) is the number of plants in the BC1F1 population. The regression (REG) analysis was complemented by the SAS procedure REG (SAS Institute, 1999). The variables retained in the final model were determined by stepwise selection at a probability level of 0.05.

RESULTS

Strength and Types of Seed Dormancy

It took 3 and 4 wk of incubation for nonafterripened dried seeds and caryopses, respectively, to approach their maximum germination potential (data not shown). However, the variances in cumulative germination of seeds and caryopses at 7 d accounted for about 95% (\( r = 0.973 \)) and 73% (\( r = 0.852 \)), respectively, of the variances at 30 d (Fig. 1). Apparently, the commonly used incubation time of 7 d is appropriate for evaluating dormancy with intact seeds from weedy strain-derived populations. Compared with intact seeds, caryopses were much more vulnerable to contamination, especially after several days of incubation. Thus, as a compromise and for consistency, we limited the germination period in our experiments to 7 d for both seeds and caryopses from the BC1F1 populations.

Mean germination of nonafterripened seeds was considerably lower in weedy strains than in African and Asian cultivars, although both the weedy and cultivated types contain dormant (<5% germination) and nondormant (90% or higher germination) genotypes (Table 1 and Fig. 2A). Compared with japonica cultivars, indica cultivars had a lower mean and a larger variation for germination percentage (Table 1). Seed germination for all cultivars and a few weedy strains increased following 11 DAR (Fig. 2A and B). With highly dormant seeds, an afterripening treatment is required to distinguish genotypic differences in dormancy strength and to realistically estimate genetic variance (Gu et al., 2003). The extremely dormant genotypes, defined by <5% germination at 11 DAR, were all weedy strains (Fig. 2B). These strains included LD, SS18-2, and TKN12-2 (Table 2). Of the remaining weedy strains, six exhibited strong dormancy (<35% germination at 11 DAR), the other two (BT1Ac and BT2Cb) showed weak and essentially no dormancy (73 and 92% germination at 11 DAR), respectively. Several traditional indica cultivars had strongly to moderately dormant seeds with 20 to 40% germination at 11 DAR. The degree of dormancy in some of the dormant cultivars, including N22, Peta, and PTB10, was similar to that in previous reports (Chang and Tagumpay, 1973; Seshu and Sorrells, 1986; Siddique et al., 1988). However, some previously reported dormant cultivars, such as Milyang 23 and IR36, displayed a relatively low level of dormancy in this experiment (data not shown). The remaining indica and all japonica cultivars had weak dormancy or nondormancy. The four African cultivars ranged from strongly or moderately to weakly dormant, to nondormant (Fig. 2B).

Dehulling nonafterripened seeds did not completely eliminate dormancy in all the dormant weedy strains and cultivars. Moderate to strong dormancy still occurred in 10 weedy strains including LD, and one African (Kebraba 80) and three Asian (N22, Peta, and Pokali) cultivars as indicated by 8 to 55% germination of caryopses (Fig. 2C). Caryopses with the pericarp/testa removed and excised embryos from all the dormant genotypes displayed >90% germination after seven and four d of incubation, respectively (data not shown). These results support our previous observation that seed dormancy is imposed by the covering tissues of the hull and/or pericarp/testa in the weedy rice strains that have been evaluated to date (Gu et al., 2003).

Interrelation between Dormancy and the Other Weedy Characteristics

A wide range of variation in degree of seed or caryopsis dormancy was observed in the weedy strain-derived
**Fig. 2.** Distribution for germination of (A) nonafterripened seeds, (B) 11-d afterripened seeds, and (C) nonafterripened caryopses for genotypes from weedy and cultivated rice. Only the moderately to strongly dormant genotypes were further evaluated for caryopsis germination.

**Table 2.** Germination of seeds at different days of afterripening (DAR) or nonafterripened caryopses and the characteristics shattering, awn, and black hull and red pericarp colors in weedy strain-derived BC1F1 populations.

<table>
<thead>
<tr>
<th>Populations/parents†</th>
<th>1 DAR</th>
<th>11 DAR</th>
<th>21 DAR</th>
<th>Caryopsis germination (%)</th>
<th>Shattering rate</th>
<th>Awned seeds (%)</th>
<th>Hull color ratio</th>
<th>Pericarp color ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>BC1F1s</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>EM93-1/EM93-1/LD</td>
<td>21 (0–67)</td>
<td>43 (1–89)</td>
<td>61 (1–99)</td>
<td>75 (5–100)</td>
<td>61 (3–92)</td>
<td>31 (0–100)</td>
<td>86:78§</td>
<td>51:113¶</td>
</tr>
<tr>
<td>EM93-1/EM93-1/SS18-2</td>
<td>20 (0–85)</td>
<td>55 (6–98)</td>
<td>74 (10–100)</td>
<td>NA†</td>
<td>55 (3–95)</td>
<td>33 (0–100)</td>
<td>135:63</td>
<td>91:107</td>
</tr>
<tr>
<td>EM93-1/EM93-1/TKN12-2</td>
<td>12 (0–68)</td>
<td>57 (14–98)</td>
<td>67 (17–100)</td>
<td>NA†</td>
<td>65 (8–100)</td>
<td>0 (0–0)</td>
<td>45:37</td>
<td>27:55</td>
</tr>
<tr>
<td>Parents</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>EM93-1</td>
<td>76</td>
<td>96</td>
<td>98</td>
<td>97</td>
<td>4</td>
<td>0</td>
<td>straw</td>
<td>white</td>
</tr>
<tr>
<td>LD</td>
<td>0</td>
<td>1</td>
<td>6</td>
<td>11</td>
<td>95</td>
<td>100</td>
<td>black</td>
<td>red</td>
</tr>
<tr>
<td>SS18-2</td>
<td>0</td>
<td>1</td>
<td>3</td>
<td>83</td>
<td>91</td>
<td>100</td>
<td>black</td>
<td>red</td>
</tr>
<tr>
<td>TKN12-2</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>77</td>
<td>100</td>
<td>0</td>
<td>black</td>
<td>red</td>
</tr>
</tbody>
</table>

† EM93-1 is a breeding line; LD, SS18-2, and TKN12-2 are weedy strains originating from China, Thailand, and Nepal, respectively.

‡ NA, germination was not evaluated because of the relatively small difference between the parents.

§ Observed ratio of the plants with and without black hull colors in the population.

¶ Observed ratio of the plants with and without red pericarp color in the population.

The seed shattering and awn characteristics, as expressed by the shattering rate and percentage of seeds with an awn, also displayed continuous variation (Table 2). The black hull and red pericarp/testa color characteristics were relatively easy to group into presence and absence categories (Table 2).
Table 4. Summary of the components retained in the multiple linear regression model based on the data from the BC1F1 populations.

<table>
<thead>
<tr>
<th>Populations</th>
<th>DAR or caryopsis†</th>
<th>m</th>
<th>b1</th>
<th>b2</th>
<th>b3</th>
<th>b4</th>
<th>b12</th>
<th>b14</th>
<th>b24</th>
</tr>
</thead>
<tbody>
<tr>
<td>EM93-1/EM93-1/LD</td>
<td>1</td>
<td>0.554***</td>
<td>−0.247***</td>
<td>−0.227***</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>11</td>
<td>0.833***</td>
<td>ns</td>
<td>−0.134*</td>
<td>−0.309***</td>
<td>ns</td>
<td>ns</td>
<td>−0.158*</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>21</td>
<td>1.097***</td>
<td>ns</td>
<td>−0.132**</td>
<td>ns</td>
<td>ns</td>
<td>−0.291***</td>
<td>−0.162*</td>
<td>ns</td>
</tr>
<tr>
<td>Caryopsis</td>
<td>1</td>
<td>1.247***</td>
<td>ns</td>
<td>−0.252**</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>11</td>
<td>0.496***</td>
<td>−0.293***</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>−0.132**</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>21</td>
<td>1.227***</td>
<td>−0.315***</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>−0.102*</td>
<td>ns</td>
</tr>
<tr>
<td>EM93-1/EM93-1/SS18-2</td>
<td>1</td>
<td>0.424***</td>
<td>NA§</td>
<td>−0.213***</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>−0.118**</td>
</tr>
<tr>
<td></td>
<td>11</td>
<td>1.138***</td>
<td>NA</td>
<td>−0.270**</td>
<td>−0.220***</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>21</td>
<td>1.226***</td>
<td>NA</td>
<td>−0.304***</td>
<td>−0.170**</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
</tr>
</tbody>
</table>

* Significant at the P = 0.05 level.
** Significant at the P = 0.01 level.
*** Significant at the P = 0.001 or < 0.0001 levels.
† DAR, days of afterripening before the seed germination; caryopsis, germination of nonafterripened caryopses.
‡ See the description in Materials and Methods for the linear model and the meanings of the partial regression coefficients.
§ ns, nonsignificant at the P = 0.05 level.

All four characteristics were significantly correlated with seed dormancy in the three populations, with the presence of black hull color, red pericarp color, a high percentage of seeds with an awn, and a high shattering rate reducing germination (Table 3). Caryopsis dormancy in the LD-derived BC1F1 population was significantly correlated with red pericarp and black hull color, but not with shattering rate or percentage seed with an awn (Table 3), which is similar to an observation made for the LD/WYJ-derived F2 population (Gu et al., 2003). The variance in degree of dormancy explained by the linear relationship varied with the characteristic. For example, red pericarp color in LD-, awns in SS18-2, and black hull color and shattering in TKN12-2-derived populations accounted for about 25% (r = −0.5), 16% (r = −0.4), and 25% (r = −0.4 to −0.6) of the phenotypic variation in seed or caryopsis germination, respectively.

Multiple linear regression analysis detected significant main and two-way interaction effects on seed dormancy in all BC1F1 populations and a main effect of red pericarp color on caryopsis dormancy in the LD-derived population (Table 4). However, the occurrence of the main and interaction effects on seed dormancy varied with the characteristic and population. For example, a significant main effect of shattering was not detected in the three populations, and the main effects of black hull and red pericarp colors were not significant in the SS18-2-derived population. Black hull color influenced seed dormancy by interacting with the awn, red pericarp color, or shattering characteristics in the populations (Table 4). Theoretically, the variation between the populations and characteristics is because one or more of the four variables in the linear model do not independently influence seed dormancy.

Correlation analysis detected significant positive associations between any two of the three characteristics (awn, black hull color, and shattering) in the three weedy strain-derived BC1F1 populations (Fig. 3). Red pericarp color appeared weakly correlated to black hull color and independent of the awn and shattering characteristics in these populations (Fig. 3). The results from the correlation analysis confirm that the main and/or interaction effects of a characteristic on seed dormancy could be masked by or included in its interrelated characteristic(s).

DISCUSSION

The most dormant genotypes were weedy strains rather than the Asian and African cultivars. There appear
to be some novel alleles underlying the strong dormancy in weedy rice that are not present in domesticated cultivars. Nondormant and weakly dormant genotypes also were identified in weedy strains (Fig. 2A), such as BT1Ac and BT2Cb, respectively. These weakly dormant or nondormant strains are similar to cultivars in a number of morphological characteristics. For example, both BT1Ac and BT2Cb have a straw-colored hull and awnless seeds, and BT2Cb also has a white-colored pericarp/testa. Considering their morphological characteristics and degree of dormancy, it is possible that the original seeds of these strains were collected from nondormant or weakly dormant variants in segregation populations derived from hybridization between cultivars and their accompanying weedy plants.

Only seed-covering (i.e., hull- and/or pericarp/testa)-imposed dormancy was identified in the weedy strains. This is consistent with previous research (Gu et al., 2003). The covering tissues have been hypothesized as a physical barrier to germination of dormant seeds, or they may contain inhibitors of germination (Bewley and Black, 1982). Removal of the hull and/or pericarp/testa alters the environment of the embryo (Leather et al., 1992). As such, germination inhibitors might be partly released from the endosperm or embryo, or embryo excision could induce production of chemicals in the embryo that stimulate germination. Therefore, we cannot rule out the existence of embryo or endosperm-imposed dormancy in weedy rice, which has been suggested for wild rice (*Oryza* spp.) (Takahashi, 1963). We are developing near-isogenic lines using some of the extremely dormant genotypes to determine mechanisms underlying seed dormancy.

Dormancy of intact seeds interrelates to shattering, awn, black hull, and red pericarp/testa color characteristics in weedy rice (Table 3). However, not all of these weedy characteristics were significantly correlated with seed dormancy in F1 populations derived from crosses between different weedy strains and cultivars (Gu et al., 2003). Thus, we used a backcross strategy with the breeding line EM93-1 as the recipient genetic background and several different weedy strains to reexamine the relationship of weedy characteristics to seed dormancy. The three weedy strain-derived BC1F1 populations yielded similar correlations between the characteristics and seed dormancy (Table 3). In fact, seed dormancy has been associated with grain type in populations from wild oat/cultivated oat crosses (Johnson, 1935), with red grain color in wheat (*Triticum aestivum* L.) (Gfeller and Svejda, 1960), and with seed shattering in rice wild relative (*O. rufipogon* Griff.) (Oka, 1988; Cai and Morishima, 2000). In all cases, presence of the weedy or wild-type characters enhances the degree of dormancy. Our research supports a conclusion that seed dormancy is a major but not independent factor contributing to adaptation of weeds. Seed dormancy promotes the survival of genotypes with other weedy characteristics, and in turn, the other characteristics help accumulate and maintain dormancy genes in nondomesticated populations. This conclusion has been implied by the concept of *adaptive or domestication syndrome* developed in crop evolution research (Harlan et al., 1973; Oka, 1988). It is well known that seed shattering and dormancy are extremely important adaptive traits in seed-bearing plants in nature. However, morphological characters such as awns, and hull and pericarp/testa colors also have adaptive significance because of their association with both shattering and dormancy. Figure 3 summarizes the relationship between the characters examined in this research.

Previous research focused mainly on the influence of one weedy characteristic on seed dormancy. However, combined effects of shattering and morphological characteristics on seed dormancy should not be neglected in nondomesticated populations. The significant two-way interactions detected in the BC1F1 populations (Table 4) are a simple example. The interaction effects indicate that dormancy genes are better preserved in variants with more than one weedy characteristic in weedy populations. The positive impacts of multiple factors on one another (Fig. 3) are probably near to the natural condition required for survival or persistence of weeds in agroecosystems. Previously, we identified six quantitative trait loci (QTLs) and different epistases that regulate seed dormancy in the SS18-2-derived population (Gu et al., 2004b). The QTL qSDS7-1 is linked to a red pericarp/testa color gene in this population. It is likely that additional dormancy loci link to genes for other adaptive traits, as reported in an accession of *O. rufipogon* (Cai and Morishima, 2002). As a practical
matter when considering the impacts of multiple factors, transfer of herbicide resistance transgenes occurs under natural conditions from rice cultivars to weedy rice (Oard et al., 2000; Zhang et al., 2003), fitness of the weed might be increased, particularly if the transgene is closely linked with one or more genes for other adaptive traits.

Domestication and breeding processes certainly lead to elimination of dormancy alleles, especially at loci near to genes for other weedy characteristics. Some traditional cultivars of rice retain some wild-type characteristics such as a short awn and red pericarp/testa color (Table 1), but improved cultivars lack these wild-type or weedy traits. More QTLs for seed dormancy or PHS have been reported for wild and weedy rice (Cai and Morishima, 2000; Gu et al., 2004b) than for cultivars (Lin et al., 1998; Dong et al., 2003). Selection during early domestication might have focused more on elimination of seed shattering and other undesirable seed morphological characters than on dormancy, or selection for the domesticated form of these traits may have incidentally selected genotypes with a low level of seed dormancy due to such interrelations and interactions detected in this experiment (Fig. 3 and Table 4). Domestication reduced the genetic diversity of crops, and breeding activities have been accelerating this reduction ( Tanksley and McCouch, 1997). The lost diversity can be partly regained from weedy strains to solve practical problems like PHS. Phenotypic associations such as those in this report can result from either genetic linkage or pleiotropic effect. Thus, fine mapping or cloning the loci responsible for interrelated characteristics is required to answer the question: Can dormancy genes whose phenotypes associate with the other weedy characteristics be employed to improve the resistance to PHS?

ACKNOWLEDGMENTS

Teresa Nelson and Cheryl Kimberlin provided technical assistance. Weedy strains were kindly provided by Dr. H.S. Suh and Dr. H. Morishima. The cultivars with a PI number were obtained from the National Small Grains Collection of the United States Department of Agriculture-Agricultural Research Service, and the other cultivars and the weedy strain LD obtained from Yangzhou University, China. This work was supported in part by the grants from USDA-NRI (200068), USA, and from NSF (BJ98111) of Science and Technology Committee of Jiangsu Province, China.

REFERENCES

