Genetic architecture underlying the evolutionary change of competitive ability in Asian cultivated and wild rice

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ABSTRACT
Breeding of competitive cultivars has long been fraught with difficulty owing to limited knowledge of the genetic basis of competitive ability. In this study, we examined the diversity of competitive ability in Asian rice and the genetic basis of this variation. Cultivated strains and wild perennial strains have higher competitive ability than wild annual strains. Quantitative trait locus (QTL) analysis of competitive ability for three weed species was conducted in the cross between cultivated and wild annual strains, and three QTLs for general competitive ability (GCA) were identified. GCA-QTLs conferred higher competitive ability by the cultivated rice alleles and were co-located with QTLs for plant architecture and root growth, detected in the same mapping population. Furthermore, a significant change in GCA was achieved by accumulation and epistatic interaction of three QTLs. Further studies on the genetic control of competitive ability would facilitate the breeding of competitive cultivars in rice.

Introduction
Competitive interactions between crops and weeds are a pervasive feature in the agro-ecosystem, and cause significant losses of crop yields (Neve et al. 2009). Weed control using herbicides has been used in modern agriculture, and is one of major factors for contributing to incremental crop productivity; however, the negative consequences of using herbicides, such as the emergence of herbicide-resistant weeds in various weed species, necessitate a reconsideration of current weed control strategies (Yu and Powles 2014; Owen et al. 2015). The use of competitive cultivars could be an alternative approach to weed control (McDonald and Gill 2009; Owen et al. 2015). To breed commercial varieties with higher competitive ability, it is necessary to understand the genetic basis of competitive abilities in crop plants.

Studies have revealed a wide range of variation of competitive abilities in crop species such as rice, wheat, and barley (Oka 1960; Haelele et al. 2004; Murphy et al. 2008). Crop competitive ability has been evaluated as weed tolerance, the ability to maintain the growth and yield of crops under competition with weeds, and weed-suppressive ability, the ability to suppress the growth of weed. The former refers to competitive response and the latter to competitive effect (Goldberg 1996). Competitive abilities are genetically complex traits involving a number of genes for multiple traits (Subrahmaniam et al. 2018). They are the weighted sum of a range of traits, such as plant architecture, growth habit and vigor, nutrient acquisition capacity, nutrient efficiency, and allelopathy (Goldberg 1996; McDonald and Gill 2009).

In addition, competitive interactions are determined not only by genetic factors of the target plant, but also, to a large extent, by the environmental conditions in which the plant grows, as well as the identities (species or genotype) of neighbor plants (Fasoula and Fasoula 1997; Keddy 2001; McDonald and Gill 2009; Baron et al. 2015). Therefore, competitive ability is an elusive feature, which makes it difficult to analyse its genetic basis.

Competition is recognized as a major evolutionary force that structures variation and communities in plants and animals, including crop species (Keddy 2001; Mutic and Wolf 2007; Crawley 2009; Willis et al. 2010; Subrahmaniam et al. 2018). During the domestication of crop species, several morphological, physiological, and developmental characteristics, such as seed shattering, seed dormancy, and yield-related traits, including plant architecture, were changed by human selection to increase harvest efficiency (Harlan 1975; Doebly et al. 2006). Because weeds were difficult to control by weeding in primitive agriculture, competition against weed species in rice was suggested to be one of factors influencing the phenotypic changes among subspecies of cultivated rice (Jennings and Aquino 1968); however, it is unclear until now whether the evolutionary changes of competitive ability were involved in the process of domestication.

In the present study, we focused on Asian rice to verify the evolutionary changes of competitive ability between cultivated and wild forms. First, the diversity of competitive ability was surveyed in cultivated and wild rice strains. In addition, quantitative trait locus (QTL) analysis for competitive abilities was carried out using recombinant inbred lines (RILs) of a cultivated rice strain and an annual wild rice strain to understand the genetic basis of their competitive abilities. Preliminary results of QTL analysis was
published before (Onishi and Sano 2007), but new data for diversity of competitive ability in Asian rice strains and comprehensive analysis of effects of QTLs and their interactions are reported here.

Materials and methods

Study species and genetic stocks

The strains used in this study included 10 strains of cultivated rice (Oryza sativa L.) and nine strains of wild rice (O. rufipogon Griff.). These strains were selected from a wide range of geographical origins (Table 1). They were derived from genetic stocks at the National Institute of Genetics (Mishima) and the Plant Breeding Laboratory of Hokkaido University (Sapporo) in Japan. Four O. sativa spp. temperate japonica strains, two tropical japonica strains, and four indica strains were used. O. rufipogon Griff. is the wild progenitor of Asian cultivated rice, and ecotypic differentiation in annual and perennial types is found in the species (Oka 1988). Six annual strains and three perennial strains were used in this study.

The RILs were developed from a cross between a landrace in Hokkaido, Japan (A58) and an annual wild rice strain from India (W107) by the single seed descent method (Onishi et al. 2007). Eighty of 89 lines of the F2 generation were used for the evaluation of competitive abilities.

Experimental design and measurement of competitive ability

Competitive abilities were evaluated by additive design experiments (Keddy 2001). The values of competitive response (CR) and competitive effect (CE) (Goldberg 1996) were evaluated for each weed species by using the ratio of shoot dry weights (DWs) between the pure and mixed stands, as follows: 

\[ CR = \ln (DW \text{ of rice in the mixed stand}/DW \text{ of rice in the pure stand}) \]

\[ CE = - \ln (DW \text{ of weed species in the mixed stand}/DW \text{ of weed species in the pure stand}) \]

The variation of competitive ability was evaluated in 10 cultivated and nine wild rice strains. The CR and CE were evaluated using Echinochloa oryzicola as a competitor. For investigation of the genetic architecture of competitive ability, QTL analysis was performed in RILs developed from A58 × W107. QTL analysis was performed to investigate whether the genetic factors for competitive abilities in rice differed under competitive interaction with three weed species: E. oryzicola, Monochoria korsakowii, and Schoenoplectus juncoides. Weed species used in this study are major weeds in Hokkaido, Japan, and their seeds were collected in paddy fields in Hokkaido.

Seeds of the rice strains (RILs) were germinated in Petri dishes and sown in a seedling case. Weeds were sown in 200-cell flats, in which each 15-mL cell was filled with soil from the paddy fields. Seeds of both rice and weed species were sown at the end of May. After about three weeks, the rice and weed seedlings were transplanted to plastic pots (12 cm in diameter, 860 mL in capacity). Fertilizer (N, 0.10 g; P, 0.10 g; K, 0.06 g per pot) was supplied three times throughout the experiment. In pure stands, three plants of a single rice strain (or RIL) or weed species were grown in a pot. In mixed stands, three plants of a weed species were added to a pure stand of rice plants. Three replicates for cultivated and wild rice strains and two replicates for RILs of each line × treatment combination were grown. In sum, 19 strains × two treatments (mix and pure stand) × three replicates (pots) were used to evaluate the natural variation in 2006 and 80 RILs (and two parental strains) × four treatments (three weed species plus pure stand) × two replicates (pots) were used for QTL analysis in 2004. The DWs of the above-ground parts were measured at seven weeks after transplanting. Replicates in which experimental plants of rice and weed species showed aberrant growth were excluded from subsequent analysis. The plants were grown in a vinyl greenhouse in Sapporo, Hokkaido, Japan (43°N), to avoid low temperatures.

QTL analysis

A linkage map constructed in the F6 population of the RILs (Shimizu et al. 2010) was used for the analysis. The linkage map comprised 84 public markers (simple sequence repeat, sequence tagged site, and cleaved amplified polymorphic sequence markers) and four markers (three cleaved amplified polymorphic sequence and one sequence tagged site marker) designed by using the genomic sequences available in the public database (Shimizu et al. 2010). QTL analysis was conducted by MQM mapping methods using MapQTL Version 4.0 (Van Ooijen et al. 2000). First, interval mapping was conducted to select putative QTLs. One marker, which was the closest to LOD peak at each putative QTL, was selected as a cofactor for the subsequent MQM mapping. Finally, one cofactor marker per significant QTL was selected to maximize the LOD score. The permutation test (Churchill and Doerge 1994) was performed to estimate the LOD thresholds for significant QTLs. Empirical LOD thresholds corresponding to the significance at the 5% level were estimated to range between 2.7 and 2.8 for the various traits examined.

### Table 1 Variation of competitive response (CR) and competitive effect (CE) against Echinochloa oryzicola in Asian cultivated and wild rice strains.

| Strain Type          | Origin    | CR   | CE   |
|----------------------|-----------|------|------|
| Oryza sativa         |           |      |      |
| A58 J-temp Japan     | -0.27     | 0.65 |
| Nipponbare J-temp    | -0.23     | 0.90 |
| Koshihikari J-temp   | -0.42     | 1.04 |
| T65 J-temp Taiwan    | -0.36     | 1.00 |
| Acc221 J-trop Indonesia | -0.36   | 0.90 |
| Silewah J-trop Indonesia | -0.46   | 0.68 |
| Acc414 I India       | -0.14     | 0.65 |
| IR36 I Philippines   | -0.35     | 0.73 |
| IR108 I Taiwan       | -0.45     | 1.20 |
| Oryza rufipogon      |           |      |      |
| W107 A India         | -0.47     | 0.60 |
| W630 A Myanmar       | -0.59     | 0.65 |
| W1551 A Thailand     | -0.53     | 0.53 |
| W1990 A India        | -0.70     | 0.76 |
| W2002 A India        | -0.53     | 0.85 |
| ACC105451 A Sri Lanka | -0.92   | 0.28 |
| W120 P India         | -0.39     | 1.02 |
| W149 P India         | -0.38     | 0.78 |
| W593 P Malaysia      | -0.30     | 1.08 |

O. sativa mean: -0.34 \( p < 0.05 \) 0.87a
O. rufipogon (annual type) mean: -0.62b 0.61b
O. rufipogon (perennial type) mean: -0.36 0.96a
Statistical analysis

Broad-sense heritability for traits examined in 19 strains (10 cultivated and nine wild rice) and RILs was computed from the ratio of the genetic variance component (\(V_G\)) divided by the total phenotypic variance (\(V_P\)). \(V_G\) and \(V_P\) were estimated by one-way analysis of variance (ANOVA). Mixed-model ANOVAs were used to partition the variance in the traits examined in the RILs into sources attributable to RIL (genotype), weed species, and interactions between RILs and weed species. For each trait, the following model was evaluated:

\[ y = \mu + G + W + G \times W + R, \]

where \(G\) represents the RIL genotype (random effect), \(W\) represents the weed species (fixed effect), \(G \times W\) represents the interaction between RIL genotype and weed species (random effect), and \(R\) represents the residual error (Sokal and Rohlf 1995).

A principal component analysis was conducted based on the correlation coefficient matrix among the CR and CE values for three weed species in RILs. Using principal component scores, the values of general competitive ability (GCA), which defined as the competitive ability affecting both CR and CE for three weed species, was extracted, as explained in Results section.

All statistical analyses were conducted using PASW® Statistics 18 (SPSS Inc., Chicago, IL, USA).

Results

Diversity of competitive ability in cultivated and wild rice strains

The variation of competitive ability against \(E. oryzicola\) was evaluated in 10 cultivated and nine wild rice strains (six annual strains and three perennial strains). Significant variation was observed in 19 strains for both the competitive response (CR) and competitive effect (CE), although broad-sense heritability was relatively low (Table 1). In a comparison of CR and CE among cultivated, wild annual, and wild perennial strains, wild annual strains showed significantly lower values for both CR and CE, and no significant differences were observed between cultivated and wild perennial strains (Table 1).

Variation of competitive ability in RILs

For investigation of the genetic basis of competitive ability, the CR and CE values for three weed species were evaluated in RILs developed from A58 × W107. A58, a cultivated strain, and W107, a wild annual strain, showed contrasting competitive ability (Table 1). The CR and CE values of A58 were higher than those of W107 for all weed species (Figure 1). The CR and CE values for three weed species in the RILs were distributed between the parental values, whereas transgressive segregation was observed between cultivated and wild perennial strains (Figure 1).

QTL analysis

QTL analysis was conducted for each value of CR and CE for the three weed species and GCA (Table 5, Figure 3). In total, seven QTLs were detected in the four chromosome regions on chromosomes 1 (qCA1), 2 (qCA2), 7 (qCA7), and 12 (qCA12). Although six of the seven QTLs increased the competitive ability by the A58-derived alleles, CE for \(M. korsakowii\) was increased by the W107-derived allele at qCA7, which could cause the transgressive segregation of competitive ability in RILs. QTLs were detected for \(E. oryzicola\) and \(M. korsakowii\), but not for \(S. juncoides\), and QTLs for \(E. oryzicola\) and \(M. korsakowii\) were not detected in the same chromosome regions. In addition, qCA1 and qCA2 only had an effect on the CR or CE, whereas QTLs of both CR and CE were detected in qCA7. For GCA, three significant QTLs were identified on chromosomes 1, 7, and 12. The QTLs for GCA on chromosomes 1 and 7 were in the same region as at least one of the QTLs for CR and CE; however, QTL for GCA on chromosome 12 was detected in a region where no QTLs for CR and CE were found. Percentages of variance explained by the detected QTLs were relatively low, indicating that a number of genes with small effects might be included in the competition.

Previously, we reported QTL analysis for domestication-related traits and phenotypic plasticity in response to nutrient and density change, using the same mapping population (Onishi et al. 2007; Shimizu et al. 2010). Traits such as plant growth and architecture, organ size, and biomass production were inferred to be associated with competitive ability (McDonald and Gill 2009). The QTLs for competitive ability-related traits, co-located in the region of QTLs for competitive ability, are shown in Table 5. qCA1 and qCA7 were co-located with QTLs for traits associated with plant architecture above ground, and qCA12 was co-located with QTL for root biomass.

Epistatic interaction among three QTLs for general competitive ability

To evaluate the genetic interaction of the three QTLs for GCA, the RILs were classified into eight genotypes based on the alleles of the three QTL regions. Alleles of the three
QTLs were estimated by the flanking markers RM431 and RM1387 for qCA1, RM481 for qCA7, and RM247 for qCA12. A three-way ANOVA for the effects of the three QTLs on GCA indicated that interaction among the three QTLs (qCA1 × qCA7 × qCA12) in addition to the main effects of each QTL were significant (Figure 4). The genotypes having one or two competitive (A58) allele(s) at the three QTLs, with the exception of Type III, were not significantly

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**Table 2. Two-way ANOVA for competitive response (CR) and competitive effect (CE) in RILs.**

| Factor          | df | CR  |   |      |      | CE  |   |      |
|-----------------|----|-----|---|------|------|-----|---|------|
| RIL genotype (G) | 79 | 0.16| 4.18 | <0.001*** | 0.34 | 2.99 | <0.001*** |
| Weed species (W) | 2  | 69.07 | 1815.55 | <0.001*** | 44.45 | 388.65 | <0.001*** |
| G × W           | 158 | 0.05 | 1.27 | 0.046* | 0.11 | 0.99 | 0.519NS |
| Error           | 240 | 0.04 |      |      | 0.11 |      |      |

*, **Indicate significance at the 5% and 0.1% levels, respectively. NS indicates non-significance.

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**Figure 1.** Segregation of competitive response (CR) and competitive effect (CE) against three weed species (A: Echinochloa oryzicola, B: Monochoria korsakowii, and C: Schoenoplectus juncoides) in RILs from the A58 × W107 cross. $h^2$ is broad-sense heritability. *** and NS indicate significance at the 0.1% level and non-significance, respectively.
different from the genotype having no competitive allele (Type VIII); however, the combination of all three competitive alleles at the three QTLs (Type I) significantly increased competitive ability (Figure 4).

Discussion

Breeding of competitive cultivars has long been fraught with difficulty owing to limited knowledge of the genetic architecture for competitive ability in crop species, including rice (Fasoula and Fasoula 1997; McDonald and Gill 2009; Owen et al. 2015; Subrahmaniam et al. 2018). In this study, we focused on Asian cultivated and wild rice to examine whether the evolutionary changes of competitive ability were involved in the process of domestication. Significant difference of competitive ability was observed between the cultivated and wild annual rice strains, and QTLs were successfully identified in their RILs. These results may be simply because a landrace, AS8, have accumulated genes for competitive ability against coexisted weed species and showed higher competitive ability under the environment where it grows; however, cultivated strains of diverse origins tended to have higher competitive ability than wild annual strains. These results suggested that genetic changes responsible for competitive ability have occurred between cultivated and wild annual rice, although further analysis using weed species of different origins should be needed. Therefore present results imply that competitive ability is a genetic trait and could be the target of selection, not only in the evolutionary process, but also in current breeding programs. Understanding of the genetic control of competitive ability will facilitate the breeding of new varieties with higher competitive ability.

One of the complex aspects of genetic control of competitive ability highlighted in this study is that QTLs for CR and CE were not always identical and the effects of QTLs changed depending on the identities of neighbor species. Such complicated genetic effects at each genetic locus make competitive ability elusive as a genetic trait and lead to the diverse patterns of interaction in the agro-ecosystem observed in nature. CR and CE are not necessarily positively correlated, as has frequently been reported (Goldberg and Landa 1991; Keddy et al. 1994; Cahill Jr et al. 2005; Baron et al. 2015). However, the suppression of weed growth (higher CE) is expected to reduce the effect of weeds, which might result in increased crop growth (higher CR). Higher CR indicates that the crop can acquire more resources, which might suppress weed growth (higher CE). Although neighbor identities greatly affect the magnitude of competition, ranking of competitive ability among different species has been reported to be generally consistent in spite of differences in neighbor identities (Goldberg 1996). In fact, CR and CE for all weed species loosely and positively contributed to GCA in this study and three QTLs for GCA could be identified, suggesting the presence of common genetic mechanisms affecting competition despite the differences in CR and CE ability and neighbor identity.

The identification of the traits associated with competitive ability is important for the elucidation of mechanisms including competitive interactions between plants. In addition, it should facilitate breeding for competitive ability

Table 3. Correlation coefficients among competitive response (CR) and competitive effect (CE) for three weed species evaluated in RILs and their parental strains.

| Trait | CR | CE |
|------|----|----|
| CR for | | |
| Eo | Mk | Sj | Eo | Mk | Sj |
| **0.604*** | | | **0.583*** | **0.283*** | **0.202*** |
| **0.356*** | **0.589*** | | | | |
| CE for | | |
| Eo | Mk | Sj | Eo | Mk | Sj |
| **0.689*** | **0.517*** | **0.248*** | | | |
| **0.547*** | **0.471*** | **0.251*** | | | |

Eo, Echinochloa oryzicola; Mk, Monochoria korsakowii; Sj, Schoenoplectus juncoides.

* and ** indicate significance at the 5% and 1% levels after Bonferroni correction, respectively.

Table 4. Principal component analysis of competitive response (CR) and competitive effect (CE) for three weed species in RILs and their parental strains.

| Trait | PC1 | PC2 |
|------|-----|-----|
| CR for | | |
| Eo | 0.87 | -0.11 |
| Mk | 0.69 | -0.44 |
| Sj | 0.78 | 0.45 |
| CE for | | |
| Eo | 0.80 | -0.23 |
| Mk | 0.55 | -0.72 |
| Sj | 0.75 | -0.22 |

Eigenvalue 3.3 1.0 = % of variance explained 55.6 17.2

Factor loadings are listed for principal component 1 (PC1) and 2 (PC2).

Eo, Echinochloa oryzicola; Mk, Monochoria korsakowii; Sj, Schoenoplectus juncoides.

Table 5. Putative QTLs for competitive abilities detected in RILs.

| QTL | Trait | LOD *(PVE %) | add. | Trait | LOD (PVE %) | add. | LOD (PVE %) | add. | Co-located QTL |
|-----|------|--------------|------|------|----------|------|-----------|------|----------------|
| qC1A1 | CR | 4.7 (24.8) | 0.14 | NS | | | 2.7 (10.5) | 0.34 | Culm length * |
| qC1A2 | NS | | | CE | 3.4 (16.5) | -0.18 | NS | | |
| qC1A7 | NS | | | CR | 4.5 (23.8) | 0.08 | 2.8 (11.0) | 0.34 | QTL cluster for plant architecture ab |
| qC1A12 | NS | | | CE | 3.8 (17.3) | 0.17 | | | |
| | | | | | | | 2.7 (10.5) | 0.33 | Root biomass b |

A part of this result was reported in Onishi and Sano (2007). CR, competitive response; CE, competitive effect; Eo, Echinochloa oryzicola; Mk, Monochoria korsakowii; GCA, general competitive ability; PVE, Percentage of phenotypic variance explained by the QTL; add., additive effects. Positive and negative values of the additive effect indicate the effects of QTLs to increase the trait values by the A58- and W107-derived alleles, respectively. Co-located QTLs for competitive ability-related traits are listed. QTLs were detected in the same mapping population reported in a, Onishi et al. (2007) and b, Shimizu et al. (2010).
if plant breeders can conduct indirect selection of specific traits, which is easy to evaluate, for the identification of genotypes with high competitive ability (Caton et al. 2003; Murphy et al. 2008; McDonald and Gill 2009). Our approach was to analyse the association between specific traits and competitive ability by the genetic dissection of multiple traits in the segregating population using a cross between genotypes with contrasting competitive abilities as well as morphological and physiological traits. The results indicated that the three QTLs for GCA were co-located with the QTLs for plant architecture and root growth, suggesting them as plausible traits conferring different competitive abilities among genotypes.

The importance of belowground competition has been illustrated in various plant species (Schenk 2006; Shindo et al. 2008). In this study, qCA12 was revealed to be co-located with the QTL for root biomass, suggesting the occurrence of belowground competition. Higher root biomass should confer higher competitive ability by enhancing foraging ability for space and nutrients (Schenk 2006; McDonald and Gill 2009; Pierik et al. 2013); however, recent advances in our understanding of the mechanisms of interaction among plant individuals indicate that complex communication mediated by root exudates, including phenomena such as allelopathy or kin and non-kin recognition, might be also involved in belowground competition (Schenk 2006; Hodge 2009; Pierik et al. 2013). Although no significant QTLs were found in the qCA12 region when QTL analysis was conducted for CR and CE for each weed species, this might be because plant performance under competition was assessed by measuring the dry weight of only the aboveground architecture, and root traits were not measured.

In contrast to qCA12, qCA1 and qCA7 were co-located with QTLs for the traits associated with plant architecture above ground. In the qCA1 region, the QTL for culm length, in which the allele of wild rice (W107) increased the culm length, was detected (Onishi et al. 2007). In this region, the ‘green revolution’ gene (sd1 gene) locus, which confers the semi-dwarf trait by the recessive (sd1) allele, is known to be

Figure 3. Linkage map showing the position of putative QTLs detected in RILs. QTL positions are represented as boxes with two-LOD support intervals, with the LOD peak indicated by a horizontal bar. Filled and open boxes indicate the effects of QTLs on increasing the competitive abilities of the A58- and W107-derived alleles, respectively.

Figure 4. Epistatic interactions among the three QTLs for general competitive ability (GCA) in RILs. (A) Comparison of GCA among eight genotypes having different allele combinations at three QTLs. A and W indicate A58- and W107-derived alleles, respectively. Different letters indicate significant differences by Tukey’s HSD test. (B) Result of ANOVA for the effects of three QTLs on GCA. *, **, and *** indicate significance at the 5%, 1%, and 0.1% levels, respectively. NS indicates non-significance.
located between RM431 and RM471 (Asano et al. 2011; Murai et al. 2011). Allelic differentiation among wild-type alleles at the sd1 locus also confers variation of culm length (Asano et al. 2011; Murai et al. 2011) and is responsible for the reduction in culm length during domestication of japonica rice (Asano et al. 2011). Generally, lower plant height, such as the semi-dwarf trait, is expected to confer lower competitive ability (Jennings and Aquino 1968; Kawano et al. 1974; McDonald and Gill 2009); however, the A58 allele(s) of the qCA1- sd1 region conferred lower culm length but higher competitive ability than the W107 allele(s). Culm length is determined at the reproductive stage, but in this study, competitive ability was evaluated only at the vegetative stage. Further studies are needed to examine whether a causal genetic factor of competitive ability is identical to the gene for culm length.

In the qCA7 region, a QTL cluster for plant architecture, which comprises the QTLs for plant height, tiller angle, leaf angle and tiller number, has been reported (Li et al. 2006; Onishi et al. 2007). The PROSTRATE GROWTH 1 (PROG1) gene was isolated as the causal gene responsible for plant architecture, and the alleles of both spp. japonica and spp. indica were suggested to have a single origin (Jin et al. 2008; Tan et al. 2008). The erect growth with fewer and larger tillers and panicles by the allele of cultivated rice compared with wild rice could improve the grain yield under the cultivated condition of higher density, which might result in strong selection of the allele of cultivated rice in the domestication process (Jin et al. 2008; Tan et al. 2008). In contrast, the prostrate growth trait accompanied with shorter plant height and higher tiller number by the wild rice allele was associated with tolerance to trampling, which could confer the adaptability under disturbed conditions on wild annuals (Onishi et al. 2007). QTLs for competitive ability (qCA7) were detected in the PROG1 region, and the PROG1 gene is a plausible candidate for the causal gene of qCA7. This suggests that the selective advantage of the cultivated allele at the PROG1 locus could be not only increasing yield by improving the yield component but also increasing fitness under competitive environments in primitive agriculture. The trade-off between adaptabilities for competitive and disturbed environments is the most critical factor in life-history strategies in plants (Crawley 2009). The PROG1 region had an antagonistic pleiotropy for competitive ability and disturbance tolerance (trampling), suggesting that allelic differentiation in this region plays a significant role in adaptation to contrast environments as well as domestication. It remains to be studied whether allelic differentiation at the PROG1 locus and distribution are associated with phenotypic variation and habitat environments in the wild rice population.

Epistasis, which refers to non-additive genetic effects between loci, has been suggested to play an important role in phenotypic variation and evolution in plants, including crop species (Lynch and Walsh 1998; Lukens and Doebely 1999; Cooper et al. 2009). We detected epistatic interaction between three QTLs for GCA, and GCA changed drastically with the accumulation of competitive alleles at all QTLs. This indicates that competitive ability is a complex trait of synergetic effects, including various morphological, physiological, and developmental traits. In addition to their genetic complexity, competitive abilities generally have a negative correlation with reproductive traits associated with crop yield (Jennings and Aquino 1968; Kawano et al. 1974; McDonald and Gill 2009), implying the difficulty of breeding for increased competitive ability without sacrificing yield and quality. This study evaluated competitive ability only at the vegetative stage; however, the effects of competitive interaction on yield will be more important in rice production and the genetic effects might differ depending on the developmental stage (Cousens et al. 2003; Shimizu and Itoh 2012). Further detailed analysis of the genetic mechanism is needed to facilitate the breeding of practical rice varieties with high yield and competitive ability.

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Disclosure statement

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