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Heredity and genetic mapping of domestication-related traits in a temperate *japonica* weedy rice

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Abstract Rice is often found as various weedy forms in temperate or newly cultivated rice growing regions throughout the world. The emergence of these forms in the absence of true wild rice remains unclear. A genetic analysis of domestication-related traits (weed syndrome) has been conducted to better understand the appearance of these plants in rice fields. A doubled haploid (DH) population was derived from a cross between a *japonica* variety and a weedy plant collected in Camargue (France) to set up a genetic linkage map consisting of 68 SSR and 31 AFLP loci. Five qualitative traits related to pigmentation of different organs and 15 developmental and morphological quantitative traits were scored for genes and QTLs mapping. Despite a good reactivity in anther culture and a high fertility of the DH lines, segregation distortions were observed on chromosomal segments bearing gametophytic and sterility genes and corresponded to various QTLs evidenced in *indica* × *japonica* distant crosses. Mapping of the coloration genes was found to be in agreement with the presence of several genes previously identified and according to the genetic model governing the synthesis and distribution of anthocyan pigment in the plant. In addition, the main specific traits of weedy forms revealed the same genes/QTLs as progeny derived from a cross between *Oryza sativa* and its wild progenitor *O. rufipogon*. A large variation for most characters was found in the DH population, including transgressive variation. Significant correlations were observed between morphology and traits related to weeds and corresponded to a distinct colocalization of most of the QTLs on a limited number of chromosomal regions. The significance of these results on the origin of weedy forms and the de-domestication process is discussed.

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Introduction

Rice is often associated with weedy forms which are genetically related (Harlan 1965; Harlan et al. 1972). These weedy forms show intermediate characteristics between wild rice *Oryza rufipogon* and cultivated *indica* or *japonica* varieties of *O. sativa* L., and are highly adapted to disturbed habitats (Oka 1988). Molecular analysis has shown that these weedy forms have played a important role in increasing the genetic diversity of cultivated rice (Second 1985). Recently, a new emerging form of weedy rice has appeared in temperate regions, although no wild relative is occurring in these areas. This phenomenon has been observed in many different areas of the world (USA, Brazil, Europe) where conditions of direct seeding and intensive irrigation prevail. These weedy forms relate to both *indica* and *japonica* varieties and show many traits common to Asian weedy forms: phenotypic plasticity, a high seed dispersal ability and dormancy recovery. Plants usually show a red pericarp (they are also called ''red rice''), earlier tillering and flowering habits with various anthocyanin pigmentations of organs (collar, ligule, grain apiculus, stigma, awns) (Marie et al. 1986; Cho et al. 1995; Suh et al. 1997). Experimental observations have been made on weedy rice in France (Marie et al. 1986), Spain (Catala-Forner 1995), USA (Diarra et al. 1985a, b) and Korea (Suh and Ha 1994; Cho et al. 1995). Several studies of their genetic characteristics have been reported; weedy rice strains also appear to be differentiated into *indica* and *japonica* types based on morphological and physiological traits, isozymes, restriction fragment length polymorphism (RFLP) and random amplified polymorphic DNA (RAPD) markers (Cho et al. 1995; Suh et al. 1997).

In the investigation reported here we developed a genetic linkage map based on a doubled haploid (DH) population resulting from a cross between a weedy plant col-

lected in France and a *japonica* variety to localize genes and quantitative traits loci (QTLs) involved in the variation of weedy characteristics via linkage to molecular markers. Our objective was to gain a better understanding of the origin of weedy rice in temperate regions by comparing a weedy rice form with true wild rice *O. rufipogon* with respect to the inheritance of domestication traits.

Materials and methods

Plant material

A cross between Miara, a temperate *japonica* variety cultivated in France, and C6′, a weedy plant collected in a rice field cultivated with Thaibonnet (temperate *japonica* variety also cultivated in France) was performed. A DH population was derived from the F_1 anther culture. C6′ was selected because it was harbors all the attributes of Mediterranean weed (awns, shedding, deep pigmentation in different parts of the plant). DH lines were developed by CIRAD-Guadeloupe in 1996, and more than 500 lines have been released. A subset of 151 DH lines was sown at the Centre Français du Riz (Arles) in the 1997 growing season.

Phenotypic evaluation

The segregation of morphological traits related to weeds was observed in all DH lines. A total of 20 traits, including five qualitative traits and 15 quantitative traits were evaluated for each DH line: apiculus coloration (APC), node coloration (NC), leaf coloration (LC), stem coloration (SC), pericarp coloration (PC), auricle coloration (AUC), tiller number (TN), plant type (PT), awning (AWN), shaterring (SHT), plant height (PH), heading date (HD), leaf width (LW), panicle length (PL), total number of spikelets/panicle (TNS), number of primary branches/panicle (NPB); number of secondary branches/panicle (NSB), grain length (GL), grain width (GW), Grain Pilosity (GP). For APC, NC, LC, SC, PC and AUC, the presence or absence of organ coloration was noticed. AWN was measured as the absence or presence of awns, with three classes of awn length (short, medium or long awns). SHT was measured by scoring the number of fallen spikelets for each panicle, and nine classes were defined. PT refers to the vegetative aspect of the plant at the end of tillering stage (open, intermediate or erected plant type). GP was measured as the absence *versus* the presence pilosity intensity, with six classes being defined (from glabrous to extremely pilose). For the other quantitative traits, the scoring system was essentially the same as that usually used in genetic and breeding analysis. Measurements were determined on the basis of the average values of 10 individual plants from each line.

Molecular analysis

DNA was isolated from lyophilized leaves using the CTAB method (Hoisington et al. 1994). Sixty-eight simple-sequence repeats (SSRs) described by Wu and Tanksley (1993), Akagi et al. (1996), Panaud et al. (1996) and Chen et al. (1997), all showing polymorphism between the parents, were mapped in the DH population. Polymerase chain reaction (PCR) amplifications were performed as described in Chen et al. (1997) and Lorieux et al. (2000). AFLP were amplified following the standard protocol (Vos et al. 1995).

Statistical analysis

Spearman rank correlation analyses were performed on all characters measured using Statistica software. Normality for each quantitative trait was tested with the Shapiro-Wilks W-test on the same software.

Segregation data for the 104 loci (68 microsatellite loci, 31 AFLP loci and five genes) were obtained from the 151 DH lines. Chi-square tests were performed to examine if the observed allelic and genotypic frequencies of the marker loci deviated from the expected ratio (1:1). Computations were done using MAPDISTO 1.0 (http://www.mpl.ird.fr/~lorieux).

The map was constructed with MAPMAKER 3.0 (Lander et al. 1987) using the Kosambi mapping function. The genetic maps of Akagi et al. (1996) and Chen et al. (1997) were used to assign linkage groups or markers to their corresponding chromosomes. The ''ripple'' test was used to confirm marker orders.

The chromosomal locations of putative QTLs were determined by Interval Mapping (Lander and Botstein 1989) using MAPMAKER/QTL (Lincoln et al. 1993). A LOD threshold of 2.6 was selected for declaring the significance of a putative QTL. A non-parametric Kruskall-Wallis analysis was performed using the MAPQTL 2.4 program (van Ooijen 1992) with a probability level of 0.001 for confirming the results of interval mapping. QTLs identified by both Interval Mapping and the Kruskall-Wallis test are highlighted in this paper.

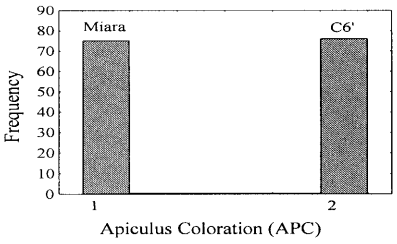
Results

Distribution and correlation among traits

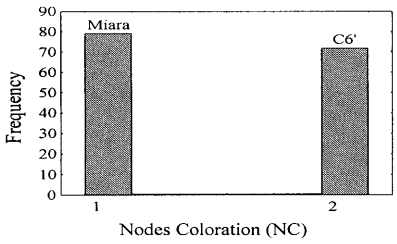
The frequency distributions of phenotypes for each trait in the 151 DH lines are shown in Fig. 1. Traits controlling coloration were bimodally distributed, suggesting a monogenic determinism. Frequencies were equivalent in the two classes except for SC which showed a deficit in Miara class. SHT and AWN data revealed a main class corresponding to the cultivated parent representing about 50% of the DH lines, accompanied by a range of intermediate variation. The distribution is in favor of an oligogenic determinism involving a major gene and interactions with other genes according to the genetic background of the parents. PT data revealed an important unexpected proportion of plants having a more contracted plant aspect at tillering stage. Other traits were characterized by continuous variation, which is typical of quantitative inheritance, and showed approximately normal distributions. HD showed a continuous variation and a bimodal distribution. Three traits (HD, PH and LW) showed transgression, giving a large apparent variation in the DH population.

Significant ($P < 0.01$) correlations were observed between many traits (Table 1). The strongest positive correlations were observed between all of the traits involved in pigmentation and provided from the same parent, such as SC, NC, AUC and LC with correlation coefficients ranging from $r = 0.3$ for LC and NC to $r = 1$ for AUC and NC. Positive correlations also were observed between grain characteristics determining the weed attributes (AWN, APC and GP). Significant correlations also were found between traits involved in plant development and panicle structure, including characters showing

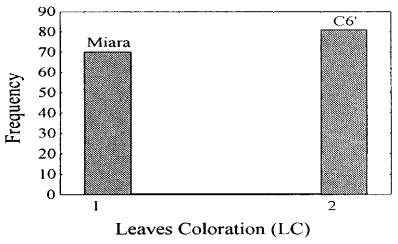
Fig. 1 Frequency distribution of phenotypes for each trait in the 151 DH lines. Phenotypes of Miara and C6' are indicated by the name of the parent when data are available. The *vertical axis* of each figure represents a class effective ▶



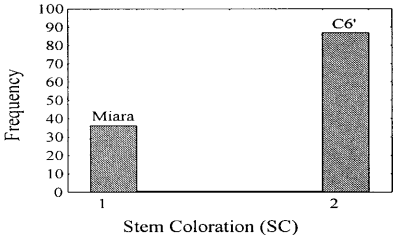
Apiculus Coloration (APC)



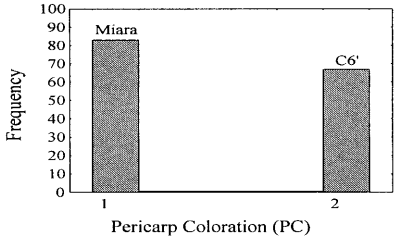
Nodes Coloration (NC)



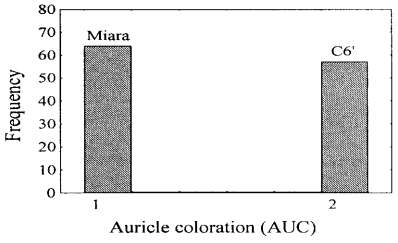
Leaves Coloration (LC)



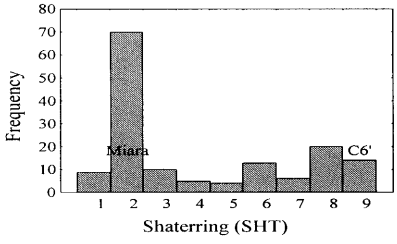
Stem Coloration (SC)



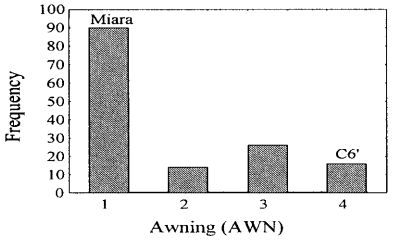
Pericarp Coloration (PC)



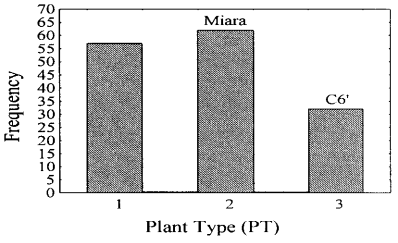
Auricle coloration (AUC)



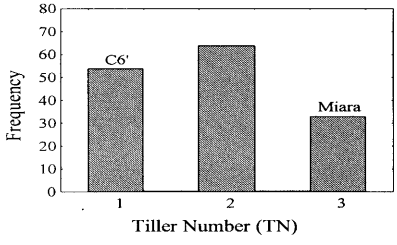
Shaterring (SHT)



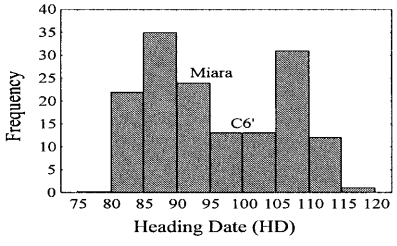
Awning (AWN)



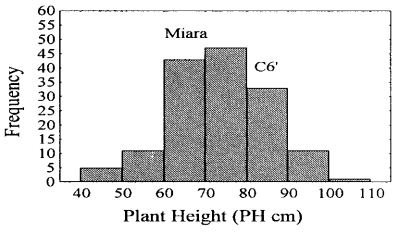
Plant Type (PT)



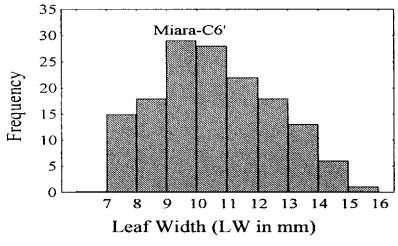
Tiller Number (TN)



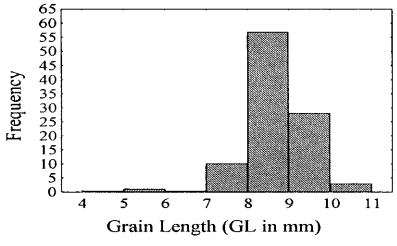
Heading Date (HD)



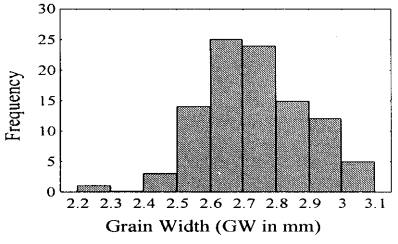
Plant Height (PH cm)



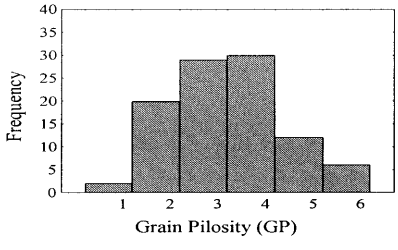
Leaf Width (LW in mm)



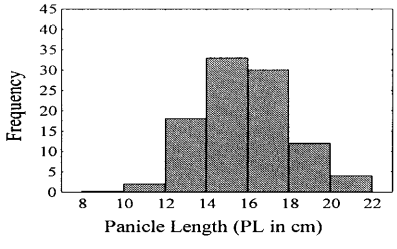
Grain Length (GL in mm)



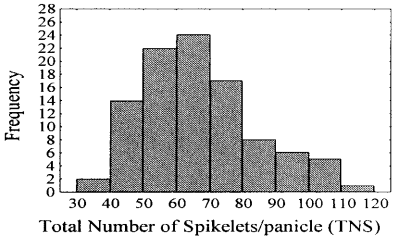
Grain Width (GW in mm)



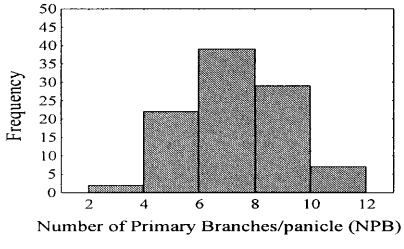
Grain Pilosity (GP)



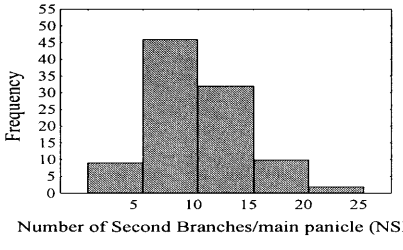
Panicle Length (PL in cm)



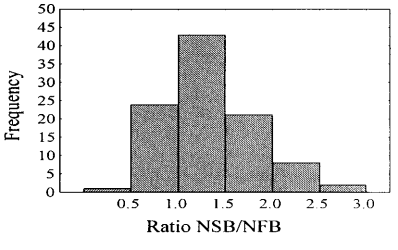
Total Number of Spikelets/panicle (TNS)



Number of Primary Branches/panicle (NPB)



Number of Second Branches/main panicle (NSB)



Ratio NSB/NFB

Table 1 Spearman correlation coefficients among weedy traits in the doubled-haploid population generated from the cross between Miara (cultivated *japonica* variety) and C6' (1 single *japonica* weedy plant. Only significant correlations are shown ($P < 0.01$)

	Coloration traits[a]						Plant morphology[b]							Panicle traits[c]					Grain traits[d]	
	APC	NC	LC	SC	PC	AUC	TN	PT	AWN	SHT	PH	HD	LW	PL	TNS	NPB	NSB	NSB/NPB	GL	GW
APC																				
NC																				
LC		0.3																		
SC		0.38																		
PC																				
AUC		1	0.35	0.38																
TN																				
PT							–0.21													
AWN	0.31																			
SHT																				
PH								0.49	0.34											
HD								0.43	0.32		0.76									
LW	–0.26	0.22	0.23			0.22		0.38			0.59	0.72								
PL											0.48	0.3								
TNS			0.27								0.38	0.43	0.59							
NPB	–0.28							0.42			0.66	0.68	0.74	0.26	0.7					
NSB		0.31	0.38			0.38					0.3	0.39	0.55		0.81	0.57				
NSB/NPB			0.36			0.31				–0.3					0.49		0.81			
GL			–0.41		–0.26						0.4			0.49				–0.32		
GW																				
GP	0.32								0.37				–0.24						–0.3	

[a] APC, apiculus coloration, NC, node coloration, LC, leaf coloration, SC, stem coloration, PC, pericarp coloration, AUC, auricle coloration
[b] TN, tiller number, PT, plant type, AWN, awning, SHT, shattering, PH, plant height, HD, heading date, LW, leaf width
[c] PL, panicle length, TNS, total number of spikelets/panicle, NPB, number of primary branches/panicle, NSB, number of secondary branches/panicle
[d] GL, grain length, GW, grain width, GP, grain pilosity

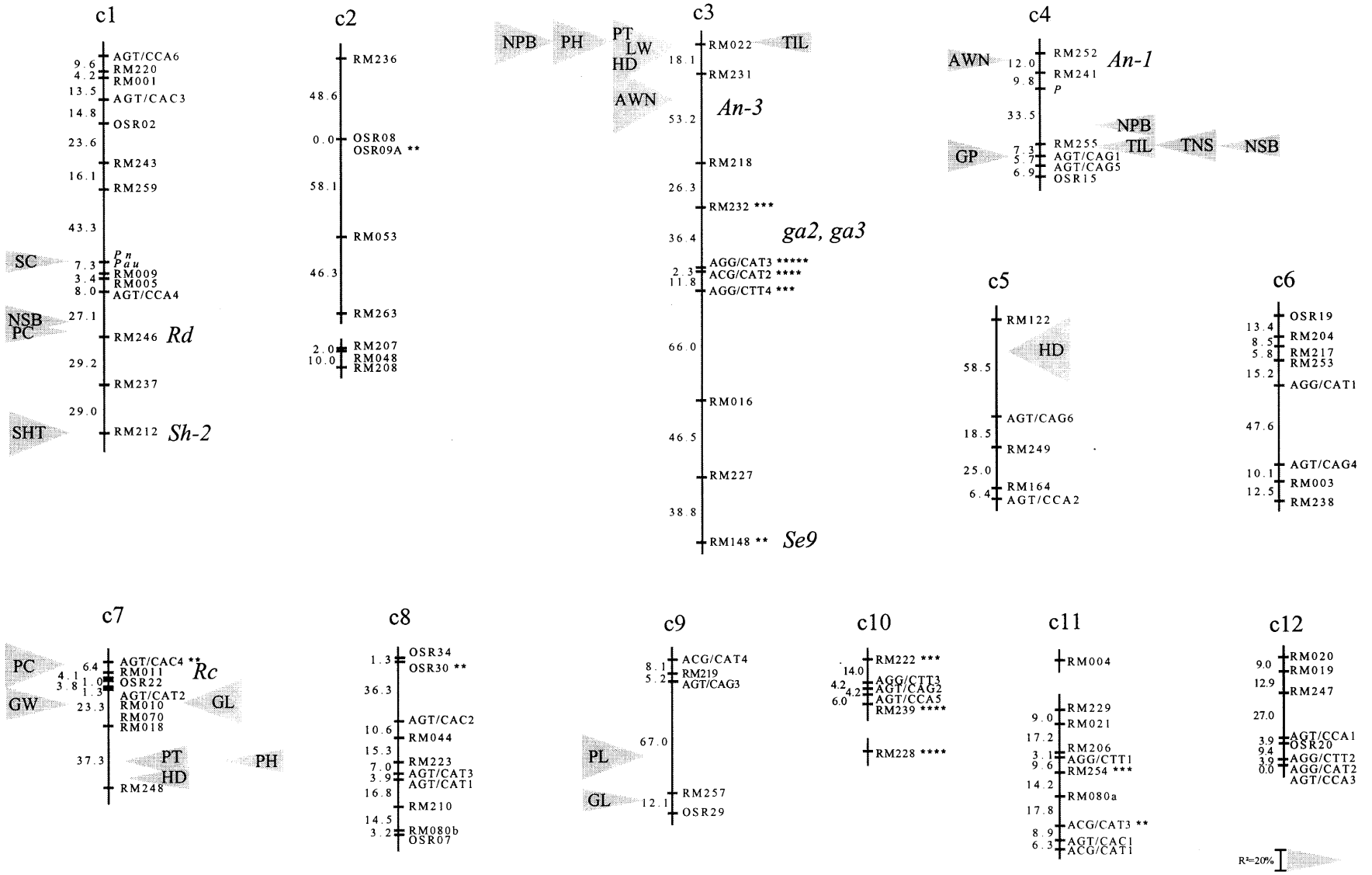

c1
AGT/CCA6
RM220
RM001
AGT/CAC3
OSR02
RM243
RM259
Pn
Pau
RM009
RM005
AGT/CCA4
RM246 Rd
RM237
RM212 Sh-2
SC
NSB
PC
SHT
c2
RM236
OSR08
OSR09A **
RM053
RM263
RM207
RM048
RM208
c3
NPB
PH
PT
LW
HD
AWN
RM022
TIL
RM231
An-3
RM218
RM232 ***
ga2, ga3
AGG/CAT3 *****
ACG/CAT2 ****
AGG/CTT4 ***
RM016
RM227
RM148 ** Se9
c4
AWN
RM252 An-1
RM241
P
NPB
TIL
TNS
NSB
GP
RM255
AGT/CAG1
AGT/CAG5
OSR15
c5
RM122
HD
AGT/CAG6
RM249
RM164
AGT/CCA2
c6
OSR19
RM204
RM217
RM253
AGG/CAT1
AGT/CAG4
RM003
RM238
c7
PC
GW
AGT/CAC4 ** Rc
RM011
OSR22
AGT/CAT2
RM010
RM070
RM018
GL
PT
HD
PH
RM248
c8
OSR34
OSR30 **
AGT/CAC2
RM044
RM223
AGT/CAT3
AGT/CAT1
RM210
RM080b
OSR07
c9
ACG/CAT4
RM219
AGT/CAG3
PL
GL
RM257
OSR29
c10
RM222 ***
AGG/CTT3
AGT/CAG2
AGT/CCA5
RM239 ****
RM228 ****
c11
RM004
RM229
RM021
RM206
AGG/CTT1
RM254 ***
RM080a
ACG/CAT3 **
AGT/CAC1
ACG/CAT1
c12
RM020
RM019
RM247
AGT/CCA1
OSR20
AGG/CTT2
AGG/CAT2
AGT/CCA3
R²=20%

Table 2 Summary of major genes and putative QTL controlling weedy traits

Traits[a]	Chromosome	Marker interval	Parent contributing allele value	LOD	%PVE[b] score	Corresponding major gene[c]
SC	1	*Pn*	C6'	4.23	14.7	
PC	1	AGT/CCA4-RM246	C6'	2.58	11.8	*Rd*
	7	AGT/CAC4-RM11	C6'	8.79	26.7	*Rc*
PT	3	?-RM022	C6'	5.68	20.1	
	7	RM018-RM248	Miara	3.7	23.0	
AWN	3	RM231-RM218	C6'	17.97	85.9	*An-3*
	4	RM252-RM241	C6'	4.65	16.1	*An-1*
SHT	1	RM212- ?	C6'	8.6	30.2	*Sh-2*
PH	3	?-RM022	C6'	9.87	31.1	
	7	RM018-RM248	Miara	3.88	19.0	
HD	3	RM022-RM231	C6'	30.62	82.5	
	5	RM122	Miara	2.62	9.2	
	7	RM018-RM248	Miara	2.76	10.7	
TIL	3	?-RM022	Miara	2.81	10.7	
	4	RM255-AGT/CAG1	Miara	2.82	10	
LW	3	RM022-RM231	C6'	9.51	37.0	
PL	9	AGT/CAG3-RM257	C6'	4.68	36.5	
TNS	4	RM255-AGT/CAG1	Miara	4.76	21.8	
NPB	3	?-RM022	C6'	7.15	32.7	
	4	*P*-RM255	Miara	3.76	18.2	
NSB	1	AGT/CCA4-RM246	C6'	3.5	23.6	
	4	RM255-AGT/CAG1	Miara	3.17	15.6	
GL	7	RM070-RM018	Miara	5.58	31.2	
	9	RM257-OSR29	C6''	2.59	12.3	
GW	7	RM070-RM018	C6'	3.56	25.1	
GP	4	AGT/CAG1	C6'	4.51	21.2	

[a] See Materials and methods and Table 1 for the description of the traits

[b] %PVE (R^2) indicates the percentage of phenotypic variation explained by the putative QTL

[c] Corresponding major gene: possible correspondence with known genes localized in other studies (Kinoshita 1995)

transgressive variation. Genetic diversity created by transgressive variation did not appear to be correlated to weed-related traits.

Genetic map

A sufficient level of polymorphism (50% with microsatellites and 14% with AFLPs) between Miara and C6′ allowed us to construct a genetic map.

Segregation data on the 104 loci were obtained from 151 DH lines. Of the 104 loci analyzed in the DH population 19 (18.2%) deviated significantly ($P \leq 0.01$) from the expected 1:1 monogenic ratio. Of these loci, 8 had an excess of Miara genotypes, and 11 had an excess of C6′ genotypes. Most of them clustered at regions on chromosomes 2, 3, 5, 6, 8, 10 and 11, and the markers showing distorted segregation in the same region had an excess of alleles from the same parent (Fig. 2). The linkage map consisted of 99 loci from 17 linkage groups, including a gene for node coloration (*Pn*), a gene for auricle coloration (*Pau*), both of which mapped on chromosome 1, and a gene for apiculus coloration (*P*) that mapped on chromosome 4 (Fig. 2). The insertion of these morphological-trait loci into the map did not significantly alter the map distances. Two microsatellite loci, 1 AFLP locus and 2 major genes were found to be unlinked to the other genes and markers. The total map length was 1239 cM with an average of 18.2 cM between 2 markers. Due to the low level of polymorphism, a large number of gaps were observed, particularly at the extremities of chromosomes. The chromosomal locations for the node coloration (*Pn*), auricle coloration (*Pau*) and apiculus coloration (*P*) loci coincided exactly with positions previously reported (Kinoshita 1995; Redoña and Mackill 1996a).

◀ **Fig. 2** Linkage map showing genes/QTL position for weedy plant-related traits based on a DH population between a *japonica* cultivated variety (Miara) and a *japonica* weedy plant (C6'). Kosambi map distances are shown to the *left* of chromosomes; microsatellite and AFLP loci are indicated on the *right*. *Asterisks* to the *right* of markers indicate segregation distortions (**: $P < 0.01$, ***: $P < 0.005$, ****: $P < 0.001$). Putative QTLs are indicated by *arrows* on the *right* or on the *left* according to the parent bearing the favourable allele (*right*: Miara, *left*: C6'). The *width* of the *triangle base* is proportional to percentage of the phenotypic variation (R^2) explained by that QTL. Major genes mapped on previous studies are indicated in *italics* on the *right*

Two traits, PC and SC, could not be mapped in this way and were included in QTL analyses.

Mapping of QTLs

Twenty-three putative QTLs were identified using Interval Mapping at a LOD threshold of 2.6 and confirmed by Kruskall-Wallis analysis (Table 2). Six chromosomes (1, 3, 4, 5, 7 and 9) revealed at least 1 QTL, and most of the concerned determined more than 1 trait. Of the 29 genes/QTLs 26 were found to be clustered only on limited regions of chromosomes 1, 3, 4 and 7. For example, QTL for the SC and AUC and NC traits were located on the same or adjacent intervals on chromosome 1 (Fig. 2). Similarly, QTLs for NSB and PC mapped to adjacent intervals on chromosome 1. QTLs for NPB, PH, PT, LW and HD mapped to adjacent intervals on chromosome 3. QTLs for TIL, NPB, TNS, NSB and GP mapped to adjacent intervals on chromosome 4. QTLs for PT, PH and HD were located on adjacent intervals on chromosome 7.

Thus, 1–3 QTLs were detected for each trait examined in this study. The percentage of trait variation explained by each individual QTL ranged from 9.2% to 85.9%, with most of them accounting for less than 20% of the total variation. Comparison with published results (Xiong et al. 1999) showed that 12 of the genes/QTLs detected in this study of 10 traits corresponded to the QTLs identified in previous studies; the remaining 17 QTLs have not been previously reported.

Segregation of each qualitative trait was controlled by a single Mendelian locus except for pericarp coloration (PC), which is controlled by two genes. These two genes correspond to the *Rc* gene on chromosome 1 and the *Rd* gene on chromosome 7 (Kinoshita 1995) and are complementary. *Rc* is involved in anthocyanin synthesis, and its presence implies the synthesis of brown pigments in the pericarp. *Rd* allows the distribution of the pigment produced by *Rc*. Conjugation *Rd/Rc* has been implicated earlier in the accumulation of red pigments in the pericarp tissue of weedy rice. The complementation between these 2 genes could be explained by the percentage of variance of the 2 QTLs (38.5%). We can suggest that this pigment accumulation is strongly affected by the environment. The anthocyanin gene pigment system consists mainly of three basic genes: *C* (chromogen), *A* (activator) and *P* (distributor), also called the *CAP* system. The tissue-specific distribution and accumulation of anthocyanin pigments are determined by additional loci (Reddy 1995). The known genes can be grouped tentatively into structural and regulatory genes. Among the structural genes, the *C*, *A*, *Rc* and *Rd* genes may encode enzymes of the pathway, whereas the regulatory gene *P* with these diverse alleles determine the temporal and spatial regulation of pigmentation. In our analysis, structural genes *C* and *A* were not revealed, and only regulatory genes and genes encoding for pericarp coloration were detected.

Discussion

In this paper we describe the genetic control of domestication traits based on a cross between a temperate *japonica* weedy plant and a temperate *japonica* cultivar. In our DH population, six independent regions of the genome exhibited distorted segregation ratios. Two of them (chromosomes 3 and 10) showed deviations from Mendelian expectations that are highly significant ($P < 0.005$), while the other regions showed slighter, although still significant ($P < 0.01$), distortions. Segregation distortions have been frequently observed in distant *indica* × *japonica* crosses (McCouch et al. 1988; Kurata et al. 1994; Xu et al. 1997) or interspecific crosses (Causse et al. 1994; Lorieux et al. 2000) and can involve many chromosomal regions. The extent of segregation distortion in our mapping population was found to be greater than that usually observed in *japonica* crosses (Redoña and Mackill 1996b). Moreover, the F_1 hybrids as well as the DH lines of our cross were very fertile, and the anther culture reactivity of the F_1 hybrids was found to be exceptionally high (D. Filloux, personal communication). Consequently, bias due to anther culture or sterility were probably not the primary cause of segregation distortion. The segregation distortion observed in our cross involved chromosomal regions already known for segregation distortion in other crosses (chromosomes 10 and 11) or chromosomes bearing sterility genes (chromosomes 3 and 7; Xu et al. 1997). The mapping of QTLs like plant height and heading date (Li et al. 1995; Albar et al. 1998; Yan et al. 1998) in *indica* and *japonica* crosses corresponded to some of these regions showing distortions in our population.

Our data support the hypothesis that the genetic control of domestication related-traits (domestication syndrome) in the DH population is relatively simple. A few genes with major effects explained most of the variation of the majority of quantitative traits. The quantitative expression of grain pilosity (GP), grain width (GW), total number of spikelets (TNS) and panicle length (PL) appears to be controlled by only 1 QTL. There are two explanations for this observation: some putative QTLs could be undetected due to the distance between markers and QTLs; otherwise, only a subset of QTLs with relatively large effects were detected because of the small population size.

A limited number of chromosomal regions (1, 3, 4 and 7) encompassed most of the genes/QTLs controlling the key differences between weedy and cultivated rice. This apparent concentration of factors can be explained by single QTLs with pleiotropic effects on several traits, by multiple-linked QTLs affecting the individual traits or by a mixture of linkage and pleiotropy. Pleiotropy is more likely when the alleles contributing to the QTLs come from the same parent. If this assumption is correct, then co-localization of QTLs can be expected to be associated with significant correlations between traits. On chromosome 3, the co-localisation of QTLs related to various traits were involved in vegetative and reproductive development (plant height,

heading date, leaf width, panicle length, total number of spikelets, number of primary branches and number of secondary branches). Interestingly, most of these traits showed an significant transgressive variation in the DH population. These observations allow us to suppose that most likely a significant proportion of QTLs have been evidenced despite the possible limitations of population size and numbers of markers. In this cross, small chromosomal segments were found to be exert a great impact on the heredity and diversity of various traits.

The clustering of genes/QTLs in a few chromosomal blocks is very similar to the situation found in the mapping of the domestication syndrome in many cultivated species – a compact genetic structure – especially in allogamous species (maize, pearl millet) but also in autogamous species (common bean, rice). Only a few tightly linked genes are implicated in the domestication syndrome and observed in rice (Xiong et al. 1999), common bean (Koinange et al. 1996), maize (Doebley and Stec 1991) and pearl millet (Poncet et al. 1998). Moreover, there is a global conservation of gene order in the domestication syndrome between cereals. Paterson et al. (1998) observed a correspondence between QTLs that affect domestication characters in crosses between cultivated and wild sorghum, between cultivated and wild maize and between divergent subspecies of cultivated rice. Our results are in good general agreement with the QTLs affecting the domestication characters in a population derived from a cross between *O. rufipogon* and *O. sativa* ssp. *indica* (Xiong et al. 1999). QTLs or genes detected for shattering and awning mapped on the same chromosomal regions, which suggests that the same genes/QTLs are involved in our weed material. With respect to shattering, the putative locus on chromosome 1, located in the neighbourhood of *sh-2*, which was identified by Ogi et al. (1993), corresponds to a major QTL identified by Fukuta et al. (1996) in a F_2 population between Nipponbare (*japonica*) and Kasalath (shattering *indica*) and physically mapped by Konishi et al. (2000). A shattering-resistant mutant gene in a mutant line with special characters of very high resistance to shattering and non-formation of an abscission layer has been located in the same chromosomal region where Ogi et al. (1993) mapped *sh-2* (Fukuta 1995). So it seems that our putative QTL could be provided by an *indica* gene.

Studies on the origin of weedy forms, their genetic origin and its significance in rice domestication provide information for understanding the evolution of rice. Weedy rice populations found in wet tropical regions originated by natural hybridization between wild and cultivated types followed by selection for man-made-disturbed environments. Additionally, markers studies have also shown that some weedy populations can be derived from *indica* × *japonica* crosses. However, beyond the limitations of wild rice, the origin of weedy rice is open to debate. It is known by breeders that distant crosses, either interspecific (*O. sativa* × *O. glaberrima*) or intraspecific (*indica* × *japonica*), could generate some individuals showing wild characteristics. Both segregation distortions and QTL mapping, in particular the shattering QTL in chromosome 1, which seems to correspond to *indica* gene *sh-2*, have to some extent similarities with what happens in *indica* × *japonica* crosses. These observations are also consistent with our results obtained by the analysis of microsatellite genetic diversity in weeds collected in France (unpublished results) and the possibility of *indica* introgression in the weeds collected, even though *indica* rice varieties are not grown in Europe.

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