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Identification of genetic factors controlling domestication-related traits of rice using an F_2 population of a cross between *Oryza sativa* and *O. rufipogon*

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Abstract Domesticated rice differs from the wild progenitor in large arrays of morphological and physiological traits. The present study was conducted to identify the genetic factors controlling the differences between cultivated rice and its wild progenitor, with the intention to assess the genetic basis of the changes associated with the processes of rice domestication. A total of 19 traits, including seven qualitative and 12 quantitative traits, that are related to domestication were scored in an F_2 population from a cross between a variety of the Asian cultivated rice (*Oryza sativa*) and an accession of the common wild rice (*O. rufipogon*). Loci controlling the inheritance of these traits were determined by making use of a molecular linkage map consisting of 348 molecular-marker loci (313 RFLPs, 12 SSRs and 23 AFLPs) based on this F_2 population. All seven qualitative traits were each controlled by a single Mendelian locus. Analysis of the 12 quantitative traits resolved a total of 44 putative QTLs with an average of 3.7 QTLs per trait. The amount of variation explained by individual QTLs ranged from a low of 6.9% to a high of 59.8%, and many of the QTLs accounted for more than 20% of the variation. Thus, genes of both major and minor effect were involved in the differences between wild and cultivated rice. The results also showed that most of the genetic factors (qualitative or QTLs) controlling the domestication-related traits were concentrated in a few chromosomal blocks. Such a clustered distribution of the genes may provide explanations for the genetic basis of the "domestication syndrome" observed in evolutionary studies and also for the "linkage drag" that occurs in many breeding programs. The information on the genetic basis of some desirable traits possessed by the wild parent may also be useful for facilitating the utilization of these traits in rice-breeding programs.

Key words Common wild rice · Cultivated rice · Evolution · Genetic analysis · Molecular marker

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Introduction

The genetic basis of evolutionary changes associated with domestication and adaptation is an old and long-standing issue in the evolutionary study of crop plants. For long it has been noted that cultivated plants and their wild progenitors differ in large arrays of morphological and physiological characteristics, which were collectively referred to as the "domestication syndrome" (Harlan 1975). There have been a large number of studies addressing the genetic differentiation between cultivated plants and their wild progenitors. The differences that have been detected range from morphological characters (e.g. Harlan 1975), to allozymes (Kahler and Allard 1981; Second 1982) and to DNA restriction fragments and sequences (Khairallah et al. 1992; Saghai Maroof et al. 1994, 1995; Liu et al. 1996). However, data remain scarce pertaining to the genetic components controlling the differences that distinguish cultivated plants from their wild ancestors. Thus, the amounts and kinds of genetic effects underlying the changes associated with the domestication processes are still largely unknown.

Recent advances in genome mapping, which have resulted in high-density molecular-marker linkage maps in most crop species, and mapping techniques (e.g. Lander and Botstein 1989), have provided tools for dissecting the genetic basis underlying complex traits into their individual components. Such developments have provided necessary tools for the characterization

of genetic differences between cultivated plants and their wild ancestors, in terms of the numbers and chromosomal locations of the genes as well as quantitative estimates of the kinds and amounts of genetic effects associated with individual loci. In common bean, for example, a comprehensive analysis was performed by making use of a molecular linkage map that resolved the genetic components controlling a number of traits distinguishing between the wild progenitor and the cultivated descendant (Koinange et al. 1996).

Rice is one of the most important crops in the world and has now become a model system in genome studies among monocot species, because of its small genome size and the availability of high-density molecular-marker linkage maps (Causse et al. 1994; Kurata et al. 1994). There are two cultivated rice species, *Oryza sativa* L., or Asian cultivated rice and *O. glaberrima* Steud., or African cultivated rice, that are widely distributed all over the world. It is known that *O. sativa* originated from Asian common wild rice (*O. rufipogon* Griff.) while *O. glaberrima* originated from African wild rice (*O. barthii* A. Chev.) (Oka 1988). In general, cultivated rice shows marked differences from the wild progenitor in many morphological and physiological traits that are related to adaptation to cultivated environments. These differences, commonly observed in traits such as growth habitat, plant gigantism, photoperiod sensitivity and seed dispersal or shattering, can also be found in other crops with similar trends of domestication (Harlan 1975). However, little is known regarding the genetic basis of the differences that transformed wild rice into cultivated rice.

The main objective of the present study was to characterize the genetic components underlying the differences between cultivated rice and its wild progenitor. Making use of a high-density molecular-marker linkage map, we investigated the genetic basis of a large number of traits that provide major differences between Asian cultivated rice and common wild rice. The results establish that both major and minor genes have played important roles in the domestication process.

Materials and methods

Plant materials

An F_2 population containing 172 individuals was developed from a cross between an indica (*O. sativa* ssp. *indica*) cultivar 'Aijiao Nante' and a common wild rice (*O. rufipogon*) accession named 'P16', and served as the mapping population (Xiong et al. 1998). This F_2 population was permanently maintained on Hainan (South China Sea) Island using vegetative tissues and was also propagated vegetatively in a greenhouse in Wuhan over-winter. For obtaining data for most of the traits from each F_2 genotype, ten fresh shoots of each F_2 individual were collected in the spring, transplanted to a one-row-block and grown under natural long-day conditions in Wuhan. The same experiment was also repeated under natural short-day conditions on Hainan Island for observing heading date and panicle characters, since a small fraction of the F_2 individuals did not flower in Wuhan due to the high sensitivity of the wild parent to photoperiod.

Scoring and measurement of domestication-related traits

An array of morphological differences exists between the two parents, most of which are also characters that distinguish cultivated rice from its wild progenitor. In this study, we scored a total of 19 morphological traits, most of which represented typical phenotypic differences between cultivated and wild rice (see Table 1).

Four qualitative traits, namely anthocyanin pigmentation on the apiculus (actually the pigment was simultaneously present or absent on other parts of the plant, such as leaf sheath and stigma etc.), awn, lax panicle and extruding stigma, were directly observed in the field according to the presence or absence of the trait. Three additional traits, lazy plant type, twisted culm and drooping leaf, were also scored as qualitative traits because of the lack of intermediate phenotypes. The lazy plant type was determined by the skewness ($>30^\circ$) of the main culm from the upright direction. Twisted phenotype was scored if the angle between the adjacent internodes in the culm was more than 15°. A plant was scored as drooping leaf if the angle between the flag leaf and the panicle axis exceeded 90°.

For most of the quantitative traits listed in Table 1, the scoring methods were essentially the same as those commonly used in genetic and rice-breeding studies. A few traits that are not frequently used in genetic and breeding analyses are described in what follows. Regeneration ability was evaluated based on the numbers of shoots obtained from 1 to 3 internodes that were cut from each plant and planted in wet soil for 3 weeks. Anther length was measured using a fine-scale ruler based on anthers taken from spikelets immediately before flowering. Culm circumference was based on the circumference of the third internode from the panicle. Panicle neck length was the distance between the top of the flag leaf sheath and the first branching site of the panicle. Shattering was measured as the percentage of fallen spikelets in the total spikelets of each panicle. Measurements for all the traits of each F_2 individual were based on the means of at least eight plants.

Linkage-map construction

A subset of data for molecular markers that have distinct positions in our previously published molecular-marker linkage map (Xiong et al. 1998) were chosen for gene mapping and genetic analyses in this study. A molecular-marker linkage map was reconstructed using MAPMAKER/EXP 3.0 (Lincoln et al. 1992 a) based on this data subset consisting of 348 marker loci, including 313 RFLPs, 12 SSRs and 23 AFLPs. The locations of the qualitative traits were determined by using the 'try' command of the Mapmaker program, which placed the morphological markers in their most-likely intervals. The map distances were converted to centi-Morgans (cMs) using the Kosambi function (Kosambi 1944).

QTL mapping

The chromosomal locations of QTLs for domestication-related traits were resolved by interval mapping using MAPMAKER/QTL 1.1 (Lincoln et al. 1992 b). A LOD threshold of 2.4 was used for declaring the existence of a putative QTL. Transformation of the original data for some traits was conducted to reduce skewness and kurtosis of the distribution, but the results of mapping were the same as those obtained using untransformed data.

Results

Population segregation of domestication-related traits

Significant differences ($P < 0.05$) were detected between the two parents for all the quantitative traits listed in Table 1. The F_1 showed nearly the same appearance as the wild parent, except that it displayed an upright plant and a straight culm, and was awnless. Thus, most wild phenotypes are dominant, or at least partly dominant.

The F_2 segregation of five qualitative traits, lazy growth, twisted stem, drooping leaf, lax panicle and awn, fit the expected 3 : 1 ratio (Table 2). The segregation of pigmentation (*C* gene) and extruding stigma deviated significantly from the 3 : 1 ratio. In both cases, phenotypes of the cultivated parent were greatly in excess, while those of the wild parent were deficient (see next section for explanation).

All the quantitative traits examined showed transgressive segregation (Fig. 1). Five traits, anther length, spikelet density, tillers per plant, panicle neck length and secondary branches per panicle, displayed more-or-less

Table 1 Domestication-related traits in rice examined in this study and the scores of the parents and F_1

Attribute	Trait	Aijiao Nante	P16	F_1
Growth habit	Lazy growth	Upright	Lazy	Nearly upright
	Twisted culm	Straight	Twisted	Straight
	Drooping leaf	Upright	Drooping	Drooping
	Regeneration ability	1.0	3.8	4.0
Gigantism	Plant height	72.2 cm	215.2 cm	211.8 cm
	Anther length	2.12 mm	5.16 mm	3.42 mm
	Panicle length	21.4 cm	29.8 cm	27.1 cm
	Tillers/plant	12.2	26.7	30.3
	Culm circumference	0.95 cm	1.3 cm	1.31 cm
Panicle and spikelet	Secondary branches/panicle	14.8	2.8	7.6
	Panicle neck length	− 4.57[a] cm	8.2 cm	9.32 cm
	Extruding stigma	Non-extruding	Extruding	Extruding
	Lax panicle	Dense	Lax	Lax
	Awn	Absent	Present	Absent
	Shattering rate	37%	91.8%	86.9%
	Spikelet/panicle	86.5	74.5	97.4
	Spikelet density	40.4	25.2	39.6
Photoperiod sensitivity	Heading date	79 days	155 days	138 days
Anthcyanin pigmentation	Presence vs absence	Absent	Present	Present

[a] The negative value indicated that the first branching site of the panicle was inside the flag leaf sheath

Table 2 Segregation and mapping of qualitative trait loci

Trait (locus)[a]	Phenotypic ratio[b]			Chromosome	Linked markers[c]	Distance (cM)
	D	R	χ^2			
Awn [*an-5* (t)]	121	51	1.74	4	RZ740	21.2
					RG122	24.5
Pigmentation (*C*)	110	62	10.6	6	RZ588	5.8
					RG213	23.7
Drooping leaf [*dl-1*(t)]	112	35	0.06	6	G1314X	26.9
					G12	28.4
Extruding stigma [*es*-1(t)]	114	58	6.52	6	C gene	16.8
					RG213	22.4
Lax panicle (*lax*)	128	32	1.88	1	RG810	27.0
					RG109	15.8
Lazy growth (*la*)	113	46	1.11	11	RG1094	37.4
					RG167	26.9
Twisted stem [*ts*-3(t)]	127	32	1.76	1	RG109	24.2
					RG220	19.7

[a] The 't' in parentheses represents a locus whose identity with published results needs to be confirmed
[b] The phenotypes of cultivated parent are dominant (D) for three traits, awn, lazy growth and twisted culm, and the phenotypes of the wild parent are dominant for the remaining four traits
[c] Only the two adjacent markers are listed

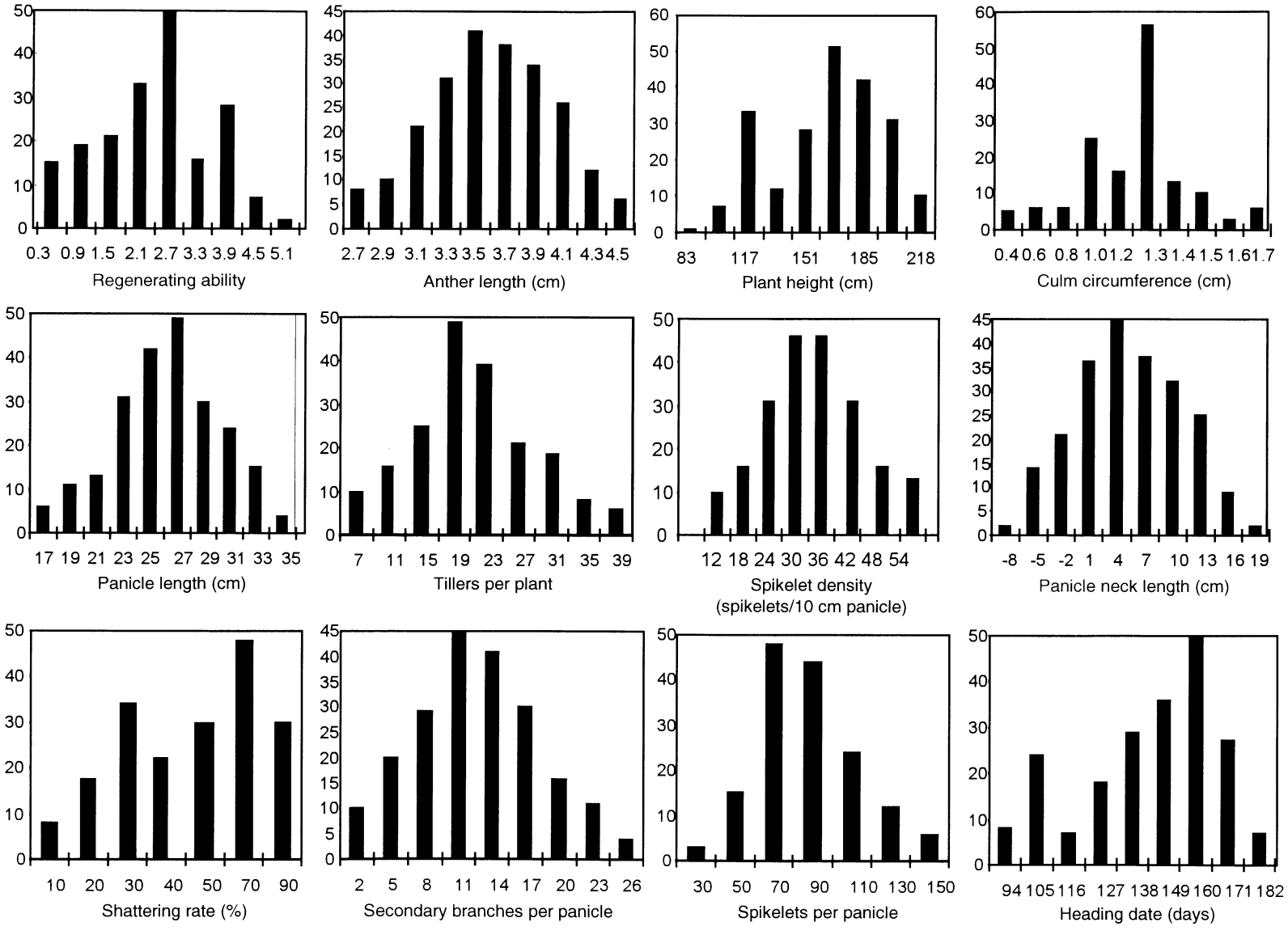


Fig. 1 The distribution of 12 quantitative traits in the F_2 population of the (Aijiao Nante × P16) cross. The *vertical axis* of each figure represents number of F_2 individuals

normal distributions (Fig. 1). Multiple peaks were observed for plant height, heading date, culm circumference and shattering rate, suggesting that genes with major effects were involved in the genetic control of these traits in this population.

Molecular-marker linkage map

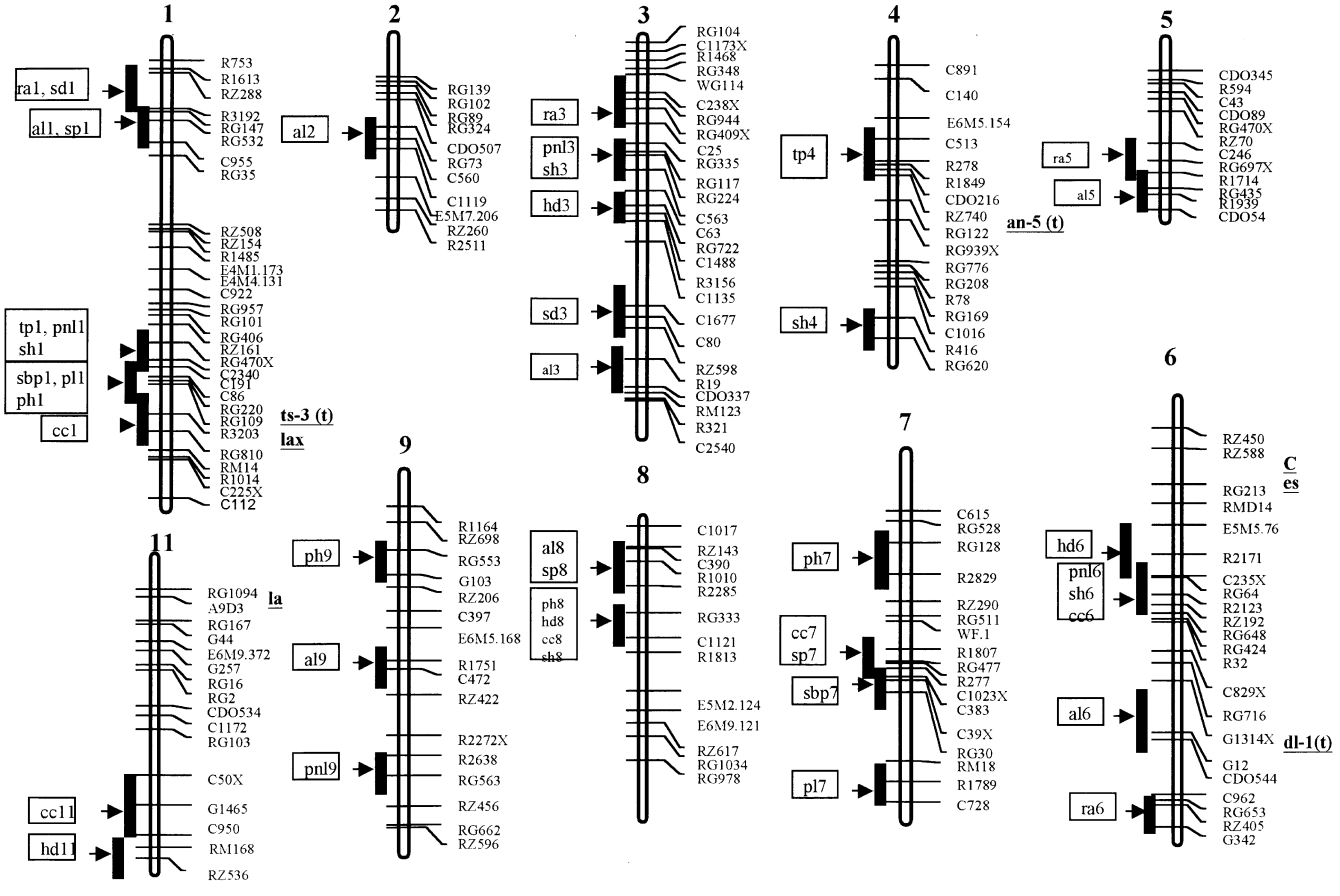
The map (data not shown), constructed using the subset of molecular-marker data, was 1820 cM in length with an average distance 5.2 cM between adjacent markers. The length and the structure of the map are essentially the same as the one we published previously (Xiong et al. 1998).

Fig. 2 Locations of genes for domestication-related traits in the molecular linkage map. Only the chromosome segments containing QTLs (to the left of chromosome segments) or morphological trait loci (to the right) are displayed. The chromosome numbers are shown at the top of the segments. The 1 LOD-supporting interval for each QTL is indicated by a *black bar* on the left of chromosome segment and the position of the peak LOD is shown by an *arrow*. QTLs that mapped in the same intervals are placed in a *box*

Mapping of qualitative-trait loci

Although the distances between qualitative-trait loci and molecular-marker loci can be calculated for all seven traits, the insertion of these morphological-trait loci into the map would severely alter the frame of the map, as most of the calculated distances were larger than 15 cM (Table 2). Therefore, we placed these morphological-trait loci at the most probable intervals rather than inserting them into the map (Fig. 2).

Comparison of the mapping with previous results revealed that the chromosomal locations for lax panicle (*lax*), lazy growth (*la*) and anthocyanin pigmentation (*C* gene) coincided exactly with the positions reported previously (Yu 1991; Causse et al. 1994). The locus for extruding stigma (*es*), a valuable trait for hybrid production, has not been reported previously and was found to be linked to the *C* locus at a distance of 16.8 cM. Both *C* and *es* were mapped in the segregation-distortion region of chromosome 6 (Xiong et al. 1998), which provided the explanation for the observed deviation from the expected 3 : 1 ratio. The loci for twisted culm (*ts*), drooping leaf (*dl*) and awn (*an*) have not been mapped previously, although they have been the subject of inheritance studies (Hsieh 1960; Nagao and Takahashi 1963; Iwata and Omura 1971).



Mapping of quantitative trait loci (QTLs)

Interval mapping with a LOD threshold of 2.4 resolved a total of 44 putative QTLs for the 12 traits, 3.7 QTLs for each trait on average (Table 3). These 44 QTLs were located in 30 intervals distributed on 10 of the 12 chromosomes (Fig. 2).

Regeneration ability

Four QTLs (*ra1*, *ra3*, *ra5* and *ra6*) were detected for regeneration ability, which jointly explained 36.7% of the total variation. These QTLs appeared to be completely different from those associated with regeneration ability from a seed-derived callus in rice (Taguchi-Shiobara et al. 1997).

Plant height

Plant height is the trait most directly related to gigantism of wild rice. Four QTLs, explaining 72.4% of the total variation, were detected for this trait (Table 3). The QTL *ph1*, accounting for 59.8% of the total variation and located in the interval R3203–RG109 of chromosome 1, coincided with the *sd1* locus for dwarfism (Cho et al. 1994). The QTL *ph7* was located in the same interval as that reported by Yu (1997). Another minor QTL, *ph8*, was located in the interval RG333–C1121 on chromosome 8 where a QTL for plant height was mapped in previous studies (Li et al. 1995; Lu et al. 1996; Xiao et al. 1996). The QTL *ph9* appeared to be a new locus for plant height that was not reported previously.

Tillers per plant

Two QTLs were detected for tillers per plant, which jointly explained 21.2% of the total variation. The QTL on chromosome 1, *tp1*, had a larger effect than *tp4* on chromosome 4. Neither of the two QTLs have been reported in previous studies (e.g. Xiao et al. 1996; Yu et al. 1997).

Panicle length

Two QTLs were detected for panicle length (*pl1* and *pl7*). The position of *pl1* is exactly the same as *ph1*, the major locus for plant height, indicating the likelihood of a pleiotropic effect of this locus. Again, neither of the QTLs have been identified previously for this trait.

Culm circumference

The analysis detected five QTLs (*cc1*, *cc6*, *cc7*, *cc8* and *cc11*) for culm circumference, which jointly explained 52.9% of the total variation. One of the QTLs, *cc8*, demonstrated a major effect on this trait, explaining 28.6% of the variation. Three QTLs, *cc1*, *cc7* and *cc8*, appeared in almost the same intervals as those of the QTLs *ph1*, *ph7* and *ph8* for plant height (Fig. 2).

Panicle neck length

Four QTLs explaining 36.2% of the total variation were detected for panicle neck length (*pnl1*, *pnl3*, *pnl6* and *pnl9*). The QTL with the largest effect on this trait, *pnl1*, was located in the same interval as *tp1*, the main QTL for tillers per plant.

Secondary branches per panicle

Two QTLs for secondary branches per panicle (*sbp1* and *sbp7*) were detected explaining, respectively, 18.0% and 7.8% of the variation. The QTL *sbp1* was mapped in the same interval as *ph1* for plant height and *pl1* for panicle length.

Spikelets per panicle

Three QTLs with small and almost equal effects (explaining 6.9%, 8.0% and 7.9% of the variation) were detected for spikelets per panicle. These three QTLs were mapped to almost the same intervals as the ones reported by Lin et al. (1996), Xiao et al. (1996) and Yu et al. (1997), respectively, for this trait.

Spikelet density

Two QTLs (*spd1* and *spd3*) were detected which accounted for 15.9% of the total variation. Again, *spd1* was located in the same interval as reported by Yu (1997) for this same trait.

Anther length

Seven QTLs explaining 47.3% of total variation were detected for anther length (*al1*, *al2*, *al3*, *al5*, *al6*, *al8* and *al9*); all of them had relatively small effects on the trait. These QTLs were located in intervals that were different from those of QTLs for other traits.

Table 3 Putative QTLs detected for each trait by Mapmaker/QTL analysis

Trait	QTL	Intervals	Chromosome	Peak LOD	% Var explained		Effect[a]	
					Locus	Trait	Add.	Dom.
Regeneration ability	ra1	R3192–RZ288	1	2.81	13.7		0.15	− 0.90
	ra3	C25–RG409X	3	3.41	15.6		0.61	0.33
	ra5	R1714–RG697X	5	2.65	10.2		− 0.52	0.38
	ra6	RZ405–G342	6	2.72	11.7	36.7	0.62	− 0.16
Plant height	ph1	R3203–RG109	1	26.9	59.8		35.88	18.64
	ph7	RG128–R2829	7	2.46	8.2		− 5.2	18.0
	ph8	RG333–C1121	8	2.87	8.3		14.4	4.55
	ph9	G103–RG553	9	2.76	10.1	72.4	11.5	13.8
Tillers per plant	tp1	RZ161–RG470X	1	5.74	17.7		− 4.68	− 1.84
	tp4	C513–R278	4	2.82	9.0	21.2	− 3.87	− 0.89
Anther length	al1	RG532–RG147	1	2.73	8.3		− 0.17	0.09
	al2	C560–RG73	2	3.79	11.1		0.24	0.08
	al3	CDO337–R19	3	2.55	11.4		0.19	− 0.16
	al5	RG435–R1939	5	2.47	7.4		0.11	0.21
	al6	G1314X–G12	6	4.12	12.8		0.25	− 0.05
	al8	R1010–R2285	8	2.72	8.4		0.12	0.22
	al9	R1751–E6M5168	9	4.43	12.9	47.3	0.23	− 0.06
Panicle length	pl1	RG109–RG220	1	9.1	25.9		2.59	0.57
	pl7	R1789–C728	7	3.51	19.4	34.1	0.13	3.22
Culm circumference	cc1	RG810–R3203	1	4.87	14.7		0.15	0.07
	cc6	R2123–RZ192	6	2.68	8.4		0.08	− 0.15
	cc7	R1807–RG477	7	3.26	11.1		− 0.06	− 0.19
	cc8	RG333–C1121	8	8.35	28.6		0.23	0.11
	cc11	G1465–C950	11	2.75	9.0	52.9	− 0.07	0.16
Panicle neck length	pnl1	RZ161–RG470X	1	6.5	19.1		3.44	1.97
	pnl3	RG117–RG335	3	3.42	10.6		0.24	− 4.17
	pnl6	RG64–R2123	6	3.48	10.8		− 2.46	− 1.43
	pnl9	RG563–R2638	9	2.61	6.7	36.2	2.21	0.76
Secondary branches per panicle	sbp1	RG220–C86	1	6.07	18.0		3.75	0.29
	sbp7	C39X–CDO407	7	2.48	7.8	20.8	− 1.28	− 3.13
Shattering	sh1	RZ161–RG470X	1	3.0	9.4		0.07	0.21
	sh3	RG335–RG117	3	4.14	15.0		0.06	− 0.32
	sh4	RG620–R416	4	7.15	20.8		0.21	0.17
	sh6	RG64–R2123	6	7.37	21.4		− 0.19	− 0.16
	sh8	RG333–C1121	8	2.52	7.6	64.3	2.71	− 0.13
Spikelets per panicle	sp1	RG532–RG147	1	2.61	6.9		− 7.28	− 20.56
	sp7	R1807–RG477	7	2.42	8.0		5.04	− 21.0
	sp8	R2285–RG333	8	2.50	7.9	23.5	11.9	15.0
Spikelet density	sd1	R3192–RZ288	1	2.76	8.6		− 5.50	− 0.74
	sd3	C1677–C80	3	3.14	9.7	15.9	4.8	− 9.2
Heading date	hd3	RG722–C63	3	2.45	6.9		− 23.8	25.5
	hd6	R2171–C235X	6	7.79	2.11		13.4	0.16
	hd8	RG333–C1121	8	22.8	52.3		20.14	15.5
	hd11	RM168–RZ536	11	2.73	8.6	67.5	− 4.53	11.21

[a] A positive value of the additive effect indicates that the genotype of the wild parent is in the direction of decreasing the measurement of the trait, and a negative value indicates that the genotype of the cultivated parent is in the direction of decreasing the measurement of the trait. The units of the genetic effects for the various traits are described in Table 1

Shattering

Five QTLs were detected for shattering and three of them (*sh3*, *sh4* and *sh6*) had relatively large effects on the trait, each explaining more than 15% of the variation. The effects of the remaining two QTLs (*sh1* and *sh8*) were relatively small, accounting for 9.4% and 7.6% of the variation respectively. The QTL *sh3* on chromosome 3 was located in the same region as the locus for shattering reported previously (Paterson et al. 1995).

Heading date

Four QTLs (*hd3*, *hd6*, *hd8* and *hd11*), accounting for 67.5% of the total variation, were detected for heading date in this study. All of them were located in regions where QTLs for heading date had been identified previously (Li et al. 1995; Lin et al. 1996; Lu et al. 1996; Xiao et al. 1996; Yano et al. 1997; Yu 1997). Interestingly, *hd8* on chromosome 8 showed a major effect on heading date explaining 52.3% of the variation for this trait. This suggested that a major gene for photoperiod sensitivity exists in the wild rice parent in this genomic region where no gene for photoperiod sensitivity has been reported previously. However, the location for the QTL *hd6* on chromosome 6, showing the second largest effect on the trait, corresponded to *se-1*, a major locus for photoperiod sensitivity (Mackill et al. 1993).

Summary of the QTL mapping

Thus, two to seven QTLs were detected for the various traits examined in this study. The variation explained by individual QTLs ranged from a low of 6.7% to a high of 59.8%, with the majority of them explaining $\leq 20\%$ of the variation. Comparison of these QTLs with published results showed that 12 QTLs detected in this study for five of the traits corresponded to those identified in various studies, while the remaining 32 QTLs have not been reported previously.

Discussion

Several features have emerged from the analyses concerning the genetic differences between the wild and cultivated rice parents used in this study with implications for the domestication and evolution of cultivated rice. The first feature is that the differences involved both major and minor genes. Segregation of all seven qualitative traits was each controlled by a single Mendelian locus. However, the segregation of quantitative traits is not necessarily conditioned by genes of minor effect. Even for the traits that are usually considered as exhibiting quantitative inheritance, the effects of major genes are clearly pronounced: as much as 59.8% of the variation was accounted for by the *ph1* locus for plant height, with 52.3% of the variation explained by the *hd8* locus for heading date. In addition, there were also quite a number of loci each explaining 20% or more of the total variation, which should also be regarded as loci having large effects on the traits. It is evident that the genes conditioning strong photoperiod sensitivity, extreme tallness and shattering were among the first to be eliminated in the domestication process. Most of the qualitative traits are also likely to have been among the first to be changed by domestication. Thus, early domestication is most likely to have been a process involving major genes, while subsequent changes may have occurred by the accumulation of minor mutations.

Another interesting feature is the relatively high concentration of the loci detected in relatively few chromosomes. The results showed that 38 of the 51 loci (qualitative or QTLs) controlling domestication-related traits are located on five chromosomes (numbers 1, 3, 6, 7 and 8). Furthermore, the majority of the loci detected on these five chromosomes are clustered in a few chromosomal blocks. An extreme example is the 16.2-cM segment from RZ161 to RG109 on chromosome 1 in which six QTLs were detected specifying, respectively, tillers per plant, panicle neck length, shattering, secondary branches pre panicle, panicle length and plant height. Another interesting example is the concurrence of QTLs for shattering and panicle neck length that appeared together in the same intervals three times, i.e. RZ161–RG470 on chromosome 1, C25–RG335 on chromosome 3, and RG64–R2123 on chromosome 6. Such clustered distributions of genes may provide an explanation for the genetic basis of the "domestication syndrome" (Harlan 1975) on one hand, and may also serve as the genetic basis for "linkage-drag" on the other hand. It is almost certain that some of the effects detected in the same chromosomal blocks for different traits are pleiotropic whereby one locus exerts significant effects on multiple traits. Such a non-random distribution of QTLs for complex traits involved in domestication has also been observed in the common bean (Koinange et al. 1996).

The results also have some implications for rice breeding programs. Among the characters examined in the present study, extruding stigma is a useful trait for male-sterile lines that can increase outcrossing rate. Long anther is also a useful trait for restorer lines with the potential of increasing the amount of pollen. The single-gene segregation of extruding stigma indicates that it should be easy to transfer this character from the wild parent to cultivated rice. However, the large number and small effects of QTLs for anther size suggests that it will be difficult to increase anther size by transferring the genes from the wild parent. We have also observed that the wild rice parent possesses a number of desirable characteristics, such as tolerance to biotic and abiotic stresses. Further studies should address these genetic basis of those characters in order to use these genes in breeding programs.

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