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Evaluation of genetic diversity and linkage disequilibrium in Korean-bred rice varieties using SSR markers

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Abstract

Background: In order to evaluate the variation among different rice types, the genetic diversity in a rice collection composed by 59 breeding lines, 23 landraces, 18 weedy rice lines, and 35 introduced lines that collected from countries worldwide was analyzed using 134 simple sequence repeat markers.
Results: In total, 1264 alleles were identified (average, 9.43 per locus). Rare alleles made up a large portion (58.4%) of the detected alleles, and 29 unique alleles associated with rice accessions were also discovered. A model-based structural analysis revealed the presence of three subpopulations. The genetic relationships revealed by the neighbour-joining tree method were fairly consistent with the structure-based membership assignments for most of the accessions. A total of 105 accessions (79.5%) showed a clear relationship to each cluster, while the remaining 27 accessions (20.5%) were categorized as admixtures. Linkage disequilibrium (LD) patterns and distributions are of fundamental importance for genome-wide association mapping. The mean r^2 value for all intrachromosomal loci pairs was 0.1286. The LD between linked markers decreased with the genetic distance between pairs of linked loci.
Conclusions: These results will provide an effective aid for future allele mining, association genetics, mapping and cloning gene(s), germplasm conservation, and improvement programs.

Keywords: landraces, linkage disequilibrium, population structure, rice, simple sequence repeats.

INTRODUCTION

Rice (*Oryza sativa* L.) feeds more than 50% of the world's population; thus, it is one of the most important crops in the world. Rice productivity has been improved dramatically through the efforts of breeders across the globe. However, an estimated 70-100% increase in food production relative to current levels will be required to meet the demands of the ever-increasing population over the next 40 years (Godfray et al. 2010). Crop breeding is important for improving yield and tolerance to existing and emerging biotic and abiotic stresses (Abe et al. 2012). Rice germplasm diversity is the mainstay for rice breeding and is important for global wealth creation and food security. Assessments of genetic diversity and population structure have been carried out in recent decades using diverse approaches (Maurya et al. 1988; Xiao et al. 1996; Davierwala et al. 2000). Two of the most widely grown rice subspecies in the world, *japonica* and *indica*, can be clearly distinguished based on their geographical and ecological characters (Yang et al. 1994). An analysis of genetic structure using 234 rice varieties

revealed five distinct groups (*indica*, *aus*, *aromatic*, *temperate japonica*, and *tropical japonica*) (Garris et al. 2005).

The loss of genetic diversity in cultivated rice during domestication may have had serious consequences for its tolerance to diseases and adaptability to different environments (Londo et al. 2006; Pusadee et al. 2009). To maintain genetic diversity in a rice germplasm, rice accessions with significant genetic variation should be included. Landraces harbour a great amount of genetic diversity and can be used as valuable resources in constructing a germplasm (Ebana et al. 2008). Due to their adaptability to unique environments, widespread distribution, and enormous numbers of collections, landraces are considered critical sources of genetic variation for improving cultivated rice varieties (Yang et al. 1994; Pusadee et al. 2009). Abundant rice germplasm resources, including landraces, maintained in genebanks have a great role in the preservation of genetic diversity and provide considerable materials for genetic research and breeding (Wang et al. 2007; Zhao et al. 2011).

Molecular markers are useful and informative tool for estimating the genetic diversity and genetic relationships in germplasm. In rice, techniques for analyzing genetic markers such as restriction fragment length polymorphisms (Sun et al. 2001), the random amplification of polymorphic DNA (Qian et al. 2001), amplified fragment length polymorphisms (Ipek et al. 2005), microsatellite or simple sequence repeats (SSRs) (Yan et al. 2007), and single nucleotide polymorphisms (Hayashi et al. 2004) have been widely used. SSR markers have been shown to be a powerful tool for this kind of research due to their abundance in eukaryotic genomes, co-dominance, and high polymorphisms (Gwag et al. 2010; Zhang et al. 2011). To date, SSR markers have been used as allele-specific and co-dominant markers in population genetic and evolutionary studies of many plants (McKhann et al. 2004; Upadhyaya et al. 2006).

Association analysis based on linkage disequilibrium (LD) has emerged as an effective approach for mapping quantitative trait loci (Pritchard and Przeworski, 2001; Famoso et al. 2011). LD, the non-random association of alleles at different loci, plays a central role in association analysis, and determines the resolution of association studies (Flint-Garcia et al. 2003). Association analysis has the potential to identify a single polymorphic locus within a gene that is responsible for a difference in phenotype. The distance over which LD persists determines the number and density of markers, and the experimental design needed to achieve reasonable resolution in mapping studies (Jia et al. 2012). The extent of LD may vary among different genomic regions and different groups (*temperate japonica*, *tropical japonica*, *indica*, and *Oryza rufipogon*) (Mather et al. 2007).

Association analysis, or LD mapping, has been used extensively to dissect human diseases (Kerem et al. 1989; Corder et al. 1994). In plants, LD-based association mapping started with the model organism *Arabidopsis* (Nordborg et al. 2002). Patterns of LD have been characterized in several crop species and their relatives. It is suggested that outcrossing between varieties may result in rapid LD decay (Tenaillon et al. 2001). In selfing species such as wild barley (*Hordeum vulgare* ssp. *spontaneum*), LD decays intragenically, with a range of only a few kilobases (kb) (Morrell et al. 2005). Garris et al. (2003) carried out LD analysis in the candidate region for the disease resistance locus and found significant LD decay around 100 kb. More recently, (Rakshit et al. 2007) reported an LD decay around 50 kb in *indica* and of around 5 kb in *O. rufipogon*. Numerous studies on global germplasm collections have indicated 25 cM as a reasonable resolution for association mapping in rice (Agrama et al. 2007; Li et al. 2011).

Information on population structure and LD can be useful for further research such as association mapping. In the present study, we assessed the genetic diversity and the extent of LD in a rice collection containing various accessions using microsatellite markers located on all 12 chromosomes.

MATERIALS AND METHODS

Plant materials

In total, 132 rice accessions were used, including 56 breeding lines, 23 landraces, 18 weedy rice lines, and 35 introduced lines. Of these, the breeding lines, landraces, and weedy rice lines were from Korea while the introduced lines were rice lines collected from countries worldwide by IRRI. Information on these rice accessions is given in Table 1. The *tongil* rice lines were breeding lines derived from

indica/japonica crosses. Young plant leaves were sampled and stored at -80ºC until genomic DNA extraction using the CTAB method (Guillemaut and Maréchal-Drouard, 1992) was performed.

SSR genotyping

A total of 134 SSR markers located on all 12 chromosomes were used (Table 2). The SSR markers were obtained from Gramene (http://www.gramene.org/). A three-primer system (Schuelke, 2000) was used that included a universal M13 oligonucleotide (TGTAAAACGACGGCCAGT) labeled with one of three fluorescent dyes (6-FAM, NED, or HEX), which allowed the products to be triplexed during electrophoresis; a special forward primer composed of a concatenation of the M13 oligonucleotide; and the normal reverse primer for SSR PCR amplification. All amplification reactions were carried out in a total volume of 20 µL containing 20 ng template DNA, 1 x PCR buffer, 0.2 mM each dNTP, 1 U *Taq* DNA polymerase, 8 pmol each of the reverse and fluorescently labeled M13 (-21) primers, and 2 pmol forward primer with the M13 (-21) tail at its 5'-end. The reaction conditions were as follows: 94ºC for 3 min, followed by 30 cycles of 94ºC (30 sec), 60ºC (45 sec), and 72ºC (1 min), with 10 subsequent cycles of 94ºC (30 sec), 53ºC (45 sec), and 72ºC (1 min), and a final extension at 72ºC for 10 min. Information on the primer sequences and amplification conditions for each set of primers is available at http://www.gramene.org/. The SSR alleles were resolved on an ABI Prism 3100 DNA sequencer (Applied Biosystems, Foster City, CA, USA) using GeneScan 3.7 software, and sized precisely using GeneScan 500 ROX (6-carbon-X-rhodamine) molecular size standards (35-500 bp) with Genotyper 3.7 software (Applied Biosystems).

Data analysis

The *MAF*, number of alleles, *GD*, and *PIC* value were determined using the genetic analysis package PowerMarker ver. 3.25 (Liu and Muse, 2005). The *PIC* value can be used to evaluate diversity effectively by using the formula:

$$PIC_i = 1 - \sum_{i=1}^{n} {p_{il}}^2$$

[Equation 1]

where p_{il} is the allele frequency of the *ith* allele at *l* th marker, and summed over *n* alleles. The genetic distance among accessions was calculated as Nei's distance (Nei et al. 1983) using the neighbour-joining method, and an unrooted phylogram was constructed using MEGA4 software as implemented in PowerMarker (Tamura et al. 2007). Genetic distances between groups of varieties, as per Nei and Li (1979), were calculated using the equation:

$$\mathrm{GD}_{XY} = 1 - \left(\frac{2N_{XY}}{[N_X + \mathrm{N_Y}]}\right)$$

[Equation 2]

in which N_X and N_Y are the numbers of alleles in groups X and Y, respectively, and N_{XY} is the number of alleles shared between the two groups. The model-based program Structure 2.2 (Pritchard et al. 2000) was used to identify the population structure of the accessions by implementing a Bayesian clustering approach. Four independent replications were performed for each run, with *K* ranging from 2 to 8 using a burn-in of 100,00 and run length of 50,000. The most probable number (*K*) was calculated based on the method of (Flint-Garcia et al. 2003) using a model allowing for admixtures and correlated allele frequencies. An inferred ancestry of ≥75% was used to assign rice accessions of the same subgroup, while <75% was assigned to an admixture group.

Level of LD among intrachromosomal SSR loci

LD was estimated as the correlation coefficient r^2 between all pairs of SSRs using the package TASSEL ver. 2.1 (Bradbury et al. 2007), with the rapid permutation test in 10,000 shuffles (Churchill and Doerge, 1994). The extent of LD was estimated separately for loci on the same chromosome. Only alleles with a frequency ≥0.05 were considered for the calculation of LD because r^2 exhibits large variance with rare alleles (Wen et al. 2009). The decay of LD with genetic distance was estimated as described in Mather et al. (2007). Pairs of loci were considered to have significant LD if $P < 0.01$. The r^2 value for a marker distance of 0 cM was assumed to be 1 (Yan et al. 2009), and a curve was drawn to describe the trend of LD decay using the nonlinear regression model. The estimated genetic distance (cM) between loci was inferred from http://www.gramene.org

RESULTS

Overall SSR diversity

All the 134 SSR used were polymorphic across the 132 rice accessions, and 1264 alleles were identified. Of the 1264 alleles, 445 (35.2%) were common, with a frequency of 0.05-0.5; 748 (59.2%) were rare (frequency <0.05); and 71 (5.6%) were abundant (frequency >0.5). These results reveal a large proportion of rare alleles among the accessions studied (Figure 1). The number of alleles detected per locus ranged from 2 to 33, with an average of 9.43 per locus, whereas the number of rare alleles identified among these loci varied from 0 to 28, with a mean of 5.53 per locus. Positive correlations were found between the number of alleles and the maximum number of repeated units in the microsatellite. Twenty-nine rare alleles were found exclusively in single accessions. The major allele frequency (*MAF*) ranged from 0.12 to 0.99 with a mean of 0.51. The genetic diversity (*GD*) and polymorphism information content (*PIC*) varied from 0.02 to 0.94 and 0.02 to 0.93, with an average of 0.63 and 0.59, respectively (Table 2).

Genetic diversity and population structure

As shown in Table 3, the highest *MAF* was detected in the breeding line accessions, followed by landraces, weedy rice lines, and introduced lines. This result could be partially due to the higher number of accessions, whereas a very small number of alleles and the lowest *GD* value were identified in the breeding lines. Compared to the breeding lines and weedy rice lines, the landraces possessed relatively high *GD* values and a high number of alleles with a small number of accessions. Both the number of alleles and *GD* value were highest in the introduced accessions. Landraces also possessed relatively high H_E compared to that of breeding lines and weedy rice.

Population structure analysis was carried out using Structure 2.2 software (Pritchard et al. 2000), which implements a Bayesian approach to identify subpopulations with distinct allele frequencies and places individuals into K clusters. The distribution of L (*K*) revealed a continuously increasing curve without a clear maximum for the true *K*, while ΔK did show a clear peak at the true value of $K = 3$ (Figure 2), indicating that the rice accessions could be grouped into three main subpopulations (Evanno et al. 2005).

As shown in Figure 3, 132 rice accessions were distributed across three subpopulations, which were denoted S1, S2, and S3, respectively. A total of 105 accessions (79.5%) showed a clear relationship to each cluster based on their inferred ancestry value (>75%), while the remaining 27 accessions (20.5%) were categorized as admixtures. The breeding lines showed relatively concentrated distributions, with 37 accessions in S1 and 19 accessions in S6; none of the breeding line accessions was classified as an admixture. Weedy rice lines were also distributed in S1 and S2, with eight accessions classified as admixtures. However, both the landraces and introduced lines were present in all three subpopulations. Eight landrace accessions and ten introduced accessions were categorized as admixtures (Figure 3 and Table 4).

Most of the *temperate japonica* rice lines showed regular distributions. All 37 *temperate japonica* rice from the breeding lines were distributed in S1, while *temperate japonica* from the weedy rice lines, landraces, and introduced lines were spread across the other two subpopulations, and some of them

were present in admixtures. All *tongil* rice lines were included in S2, whereas those accessions with subspecies of *wild*, *tropical japonica*, and *indica* showed a relatively complicated distribution (Table 1).

An unrooted neighbour-joining tree was constructed by UPGMA based on Nei's genetic distance to show the genetic relationships among the 132 rice accessions (Figure 4). Our results were fairly consistent with the Structure-based membership assignment for most of the accessions. Except for the admixtures, almost all the accessions assigned to the same subpopulation by Structure 2.2 were clustered together (same colour). All 56 breeding lines, including 37 *temperate japonica* and 19 *tongil* rice lines, were clustered into two subgroups in accordance with the results produced using Structure 2.2. Two of the subgroups were constructed from *wild* rice, in which most of the accessions were weedy rice. Landraces and introduced lines were distributed across most of the subgroups. *Temperate japonica* and *tropical japonica* showed a relatively close genetic distance, and both showed a distinct distance with *indica*. Two *wild* rice subgroups were clustered together with *japonica* and *indica*,respectively. *Tongil* rice lines, produced by crossing *japonica* and *indica*, clustered closely with *indica*. Since some of the accessions were displayed as admixtures in different clusters, not all of the accessions clustered exactly with their subspecies type. However, one of the subgroups, displayed as admixtures, consisted of accessions that belonged to *wild* rice lines (coloured black).

LD

Squared allele frequency correlations (r^2) were obtained by an analysis of 729 intrachromosomal locus pairs using the 134 selected SSR markers. The r^2 values ranged from 0.0009 to 0.7548 for all intrachromosomal pairs of loci, with an average of 0.1286. Only around 2% of the global marker pairs had a significant LD ($P < 0.01$), indicating that the LD level was low in the rice accessions included in this study. The distribution of data points in the plot of LD (r^2) decay against distance (cM) within the 12 chromosomes (Figure 5) showed that LD was not a simple monotonic function of the distance between markers. However, r^2 decreased as the genetic distance between the pairs of loci increased, indicating that the probability of LD was low between distant locus pairs.

DISCUSSION

Genetic diversity is critical in crop breeding. Strong genetic diversity means diverse morphological traits and potentially valuable genetic information. Rice varieties with high levels of genetic variation are beneficial resources for broadening the genetic base of the germplasm, and therefore laying a good foundation for rice breeding (Upadhyay et al. 2012).

The objective of this study was to assess the genetic diversity in a rice germplasm from Korea and introduced lines from the International Rice Research Institute (IRRI). A considerable number of rare alleles were identified, making up a large portion of the total, indicating that rare alleles made a major contribution to the overall genetic diversity of the germplasm (Roussel et al. 2004; Yifru et al. 2006). SSR markers identified 29 unique alleles, which may be associated with special traits and which could be useful for distinguishing those special varieties.

The collection of rice accessions is critical for constructing a rice germplasm. The landraces displayed a greater level of genetic variation, among the germplasm studied, in terms of number of alleles and *GD* with a smaller number of accessions compared to the breeding lines, consistent with the findings of Yang et al. (1994). Weedy rice lines, categorized taxonomically as cultivated rice, are one of the most problematic weeds found in rice fields because the grains can be easily shattered and the seeds exhibit long-term dormancy (Cao et al. 2006). However, a number of valuable genes harboured in weedy rice lines such as disease resistance may seep into cultivated rice through natural hybridization and introgression (Chen et al. 2004). In this study, weedy rice lines showed a relatively higher degree of *GD* value, similar to the results of Shivrain et al. (2010). The introduced lines used here showed the highest level of *GD*, possibly due to their diverse geographic origins. It is worth noting that the landraces had a high number of alleles and *GD* value relative to the sample size (Table 3). Including landraces in a rice germplasm should be helpful in raising the genetic variation and assist in laying the foundation for breeding elite cultivars.

In the context of breeding, understanding the population structure is of great importance to confirm the correlation between phenotype and genotype, and it is a precondition for choosing accessions

appropriately. Population structure in plants has been analyzed using different methods, including model-based methods implementing a Bayesian clustering approach (Moe et al. 2010; Zhao et al. 2010). The results of our structure analysis and neighbourhood-joining tree were in good agreement. Accessions distributed in the same subpopulations by Structure 2.2 were clustered together in the dendrogram (Figure 4). However, a relatively large number of accessions were categorized as admixtures (Table 2). The abundance of admixtures indicates that the accessions used here were rich in genetic variation.

It was shown that *temperate*and *tropical japonica* showed a very close genetic relationship and an overall lower *GD* than *indica* (Figure 4). This result is inconsistent with previous findings (Ni et al. 2002; Garris et al. 2005). Interestingly, *tongil*, which was produced from a cross between *japonica* and *indica*, showed a close genetic distance with *indica*. Hybrid rice lines are superior in terms of heterosis and yield potential; therefore, they contribute greatly to the global food supply (Xiao et al. 1996, Wang and Lu, 2006). It has been reported that farmers play an important role in the management of rice landraces and can greatly influence the process of seed selection and exchange (Kumar et al. 2010). Anthropic factors in the collection may be responsible for the small number of biased clusters in the subspecies.

LD is the nonrandom association of alleles between two loci in a population (Flint-Garcia et al. 2003). The extent of LD, affected mainly by factors such as genetic drift, population structure, and selection, is crucial to determine the marker density necessary for association mapping analyses. The extent of LD was relatively low in the present study, possibly due in part to the nature of the plant material. Most of the materials were composed of breeding lines with a strongly homologous genetic background and wild accessions. Landraces resulting from human selection tend to exhibit greater LD (Sakiroglu et al. 2012). Remington et al. (2001) suggested that intragenic LD generally declined rapidly with the genetic distance between loci, but the rates of decline were highly variable among genes. Combined with the results of *GD* and rare alleles, useful information could be found. Further analysis of special genes ought to be carried out.

In conclusion, SSR markers are an effective tool for identifying the *GD* in rice collections. Landraces are important for enhancing the genetic variation in rice germplasms and are of great value as resources in breeding programs.

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Tables

Table 1. List of the 132 rice accessions and their model-based groupings.

Serial No	Types	Subspecies	Countries of origin	Subpopulation ownership [1]
1	Breeding line	*Temperate japonica*	Korea	S1
2	Breeding line	*Temperate japonica*	Korea	S1
3	Breeding line	*Temperate japonica*	Korea	S1
4	Breeding line	*Temperate japonica*	Korea	S1
5	Breeding line	*Temperate japonica*	Korea	S1
6	Breeding line	*Temperate japonica*	Korea	S1
7	Breeding line	*Temperate japonica*	Korea	S1
8	Breeding line	*Temperate japonica*	Korea	S1
9	Breeding line	*Temperate japonica*	Korea	S1
10	Breeding line	*Temperate japonica*	Korea	S1
11	Breeding line	*Temperate japonica*	Korea	S1
12	Breeding line	*Temperate japonica*	Korea	S1
13	Breeding line	*Temperate japonica*	Korea	S1
14	Breeding line	*Temperate japonica*	Korea	S1
15	Breeding line	*Temperate japonica*	Korea	S1
16	Breeding line	*Temperate japonica*	Korea	S1
17	Breeding line	*Temperate japonica*	Korea	S1
18	Breeding line	*Temperate japonica*	Korea	S1
19	Breeding line	*Temperate japonica*	Korea	S1
20	Breeding line	*Temperate japonica*	Korea	S1
21	Breeding line	*Temperate japonica*	Korea	S1
22	Breeding line	*Temperate japonica*	Korea	S1
23	Breeding line	*Temperate japonica*	Korea	S1
24	Breeding line	*Temperate japonica*	Korea	S1
25	Breeding line	*Temperate japonica*	Korea	S1
26	Breeding line	*Temperate japonica*	Korea	S1
27	Breeding line	*Temperate japonica*	Korea	S1
28	Breeding line	*Temperate japonica*	Korea	S1
29	Breeding line	*Temperate japonica*	Korea	S1
30	Breeding line	*Temperate japonica*	Korea	S1
31	Breeding line	*Temperate japonica*	Korea	S1
32	Breeding line	*Temperate japonica*	Korea	S1
33	Breeding line	*Temperate japonica*	Korea	S1
34	Breeding line	*Temperate japonica*	Korea	S1
35	Breeding line	*Temperate japonica*	Korea	S1
36	Breeding line	*Temperate japonica*	Korea	S1
37	Breeding line	*Temperate japonica*	Korea	S1
38	Breeding line	*Tongil*	Korea	S2
39	Breeding line	*Tongil*	Korea	S2
40	Breeding line	*Tongil*	Korea	S2
41	Breeding line	*Tongil*	Korea	S2
42	Breeding line	*Tongil*	Korea	S2
43	Breeding line	*Tongil*	Korea	S2
44	Breeding line	*Tongil*	Korea	S2
45	Breeding line	*Tongil*	Korea	S2
46	Breeding line	*Tongil*	Korea	S2

47	Breeding line	*Tongil*	Korea	S2
48	Breeding line	*Tongil*	Korea	S2
49	Breeding line	*Tongil*	Korea	S2
50	Breeding line	*Tongil*	Korea	S2
51	Breeding line	*Tongil*	Korea	S2
52	Breeding line	*Temperate japonica*	Korea	S2
53	Breeding line	*Tongil*	Korea	S2
54	Breeding line	*Tongil*	Korea	S2
55	Breeding line	*Tongil*	Korea	S2
56	Breeding line	*Tongil*	Korea	S2
57	Landrace	*Temperate japonica*	Korea	Admixture
58	Landrace	*Temperate japonica*	Korea	S1
59	Landrace	*Temperate japonica*	Korea	S1
60	Landrace	*Temperate japonica*	Korea	S1
61	Landrace	*Temperate japonica*	Korea	Admixture
62	Landrace	*Temperate japonica*	Korea	Admixture
63	Landrace	*Temperate japonica*	Korea	S1
64	Landrace	*Temperate japonica*	Korea	S1
65	Landrace	*Temperate japonica*	Korea	S3
66	Landrace	*Temperate japonica*	Korea	S1
67	Landrace	*Indica*	Korea	S2
68	Landrace	*Wild*	Korea	S2
69	Landrace	*Indica*	Korea	Admixture
70	Landrace	*Temperate japonica*	Korea	S1
71	Landrace	*Temperate japonica*	Korea	S1
72	Landrace	*Temperate japonica*	Korea	Admixture
73	Landrace	*Temperate japonica*	Korea	Admixture
74	Landrace	*Temperate japonica*	Korea	S3
75	Landrace	*Temperate japonica*	Korea	S1
76	Landrace	*Temperate japonica*	Korea	Admixture
77	Landrace	*Temperate japonica*	Korea	Admixture
78	Landrace	*Indica*	Korea	S2
79	Landrace	*Indica*	Korea	S3
80	Weedy rice	*Wild*	Korea	Admixture
81	Weedy rice	*Wild*	Korea	Admixture
82	Weedy rice	*Wild*	Korea	Admixture
83	Weedy rice	*Wild*	Korea	S2
84	Weedy rice	*Wild*	Korea	S2
85	Weedy rice	*Wild*	Korea	S2
86	Weedy rice	*Wild*	Korea	S2
87	Weedy rice	*Wild*	Korea	S2
88	Weedy rice	*Wild*	Korea	S2
89	Weedy rice	*Wild*	Korea	S2
90	Weedy rice	*Temperate japonica*	Korea	S1
91	Weedy rice	*Temperate japonica*	Korea	S1
92	Weedy rice	*Wild*	Korea	Admixture
93	Weedy rice	*Wild*	Korea	Admixture
94	Weedy rice	*Wild*	Korea	Admixture
95	Weedy rice	*Wild*	Korea	Admixture
96	Weedy rice	*Wild*	Korea	Admixture
97	Weedy rice	*Temperate japonica*	Korea	S1
98	Introduced lines	*Tropical japonica*	Nigeria	S3
99	Introduced lines	*Tropical japonica*	Burkina Faso	Admixture
100	Introduced lines	*Indica*	India	S2

101	Introduced lines	*Temperate japonica*	Egypt	S1
102	Introduced lines	*Tropical japonica*	India	S3
103	Introduced lines	*Tropical japonica*	Honduras	S3
104	Introduced lines	*Tropical japonica*	USA	S3
105	Introduced lines	*Indica*	Vietnam	Admixture
106	Introduced lines	*Temperate japonica*	Taiwan	Admixture
107	Introduced lines	*Wild*	Surinam	S3
108	Introduced lines	*Indica*	Philippines	S2
109	Introduced lines	*Tropical japonica*	USA	Admixture
110	Introduced lines	*Indica*	Bangladesh	Admixture
111	Introduced lines	*Indica*	Pakistan	S3
112	Introduced lines	*Wild*	Pakistan	S3
113	Introduced lines	*Indica*	Iran	Admixture
114	Introduced lines	*Indica*	Portugal	S3
115	Introduced lines	*Temperate japonica*	Taiwan	S3
116	Introduced lines	*Tropical japonica*	Vietnam	S3
117	Introduced lines	*Tropical japonica*	Afghanistan	Admixture
118	Introduced lines	*Indica*	Surinam	S3
119	Introduced lines	*Temperate japonica*	Taiwan	S2
120	Introduced lines	*Temperate japonica*	Taiwan	Admixture
121	Introduced lines	*Indica*	Taiwan	S2
122	Introduced lines	*Temperate japonica*	Pakistan	S1
123	Introduced lines	*Wild*	Afghanistan	S3
124	Introduced lines	*Indica*	Taiwan	S2
125	Introduced lines	*Tropical japonica*	Nigeria	S3
126	Introduced lines	*Indica*	USA	S3
127	Introduced lines	*Temperate japonica*	Taiwan	S1
128	Introduced lines	*Temperate japonica*	Taiwan	S2
129	Introduced lines	*Temperate japonica*	Uzbekistan	Admixture
130	Introduced lines	*Wild*	Uzbekistan	Admixture
131	Introduced lines	*Indica*	Vietnam	S3
132	Introduced lines	*Indica*	Thailand	Admixture

[1]As defined by the STRUCTURE software.

Table 2. Chromosome location, repeat motif and diversity parameters of microsatellite markers used in the study.

Marker	Chromosome	Repeat motif	*MAF*[a]	*NA*[b]	*NAR*[c]	*GD*[d]	*PIC*[e]
MRG2295	5	(CT)14	0.50	11	7	0.69	0.67
MRG2392	3	(CT)17	0.27	11	6	0.82	0.80
MRG5454	12	(CCG)8	0.81	3	1	0.31	0.26
RM10	7	(GA)15	0.44	9	5	0.72	0.68
RM1002	3	(AC)12	0.54	5	1	0.63	0.59
RM1003	1	(AC)12	0.33	8	4	0.74	0.70
RM1022	3	(AC)13	0.52	9	6	0.67	0.64
RM105	9	(CCT)6	0.71	5	1	0.47	0.44
RM1067	1	(AC)20	0.31	19	16	0.84	0.83
RM110	2	(GA)15	0.60	6	3	0.58	0.54
RM1153	4	(AG)13	0.48	14	12	0.65	0.60
RM121	6	(CT)7	0.84	3	0	0.28	0.26
RM1216	1	(AG)14	0.48	8	6	0.63	0.57
RM122	5	(GA)7A(GA)2A(GA)11	0.51	9	5	0.65	0.61
RM127	4	(AGG)8	0.62	4	1	0.52	0.45
RM128	1	(GAA)9	0.63	4	1	0.53	0.47
RM129	1	(CGG)8	0.60	3	0	0.53	0.45
RM1306	7	(AG)18	0.30	22	20	0.81	0.79
RM131	4	(CT)9	0.26	9	4	0.82	0.79
RM1313	2	(AG)19	0.26	11	4	0.81	0.79
RM134	7	(CCA)7	0.75	2	0	0.37	0.30
RM1376	8	(AG)31	0.29	12	7	0.81	0.79
RM1387	1	(AG)44	0.20	24	19	0.90	0.90
RM1388	4	(AG)46	0.17	30	27	0.93	0.92
RM146	5	(CT)11-(CT)7	0.51	6	4	0.60	0.52
RM149	8	(AT)10	0.44	10	5	0.74	0.71
RM160	9	(GAA)23	0.38	12	7	0.76	0.73
RM168	3	T15(GT)14	0.56	6	3	0.61	0.56
RM169	5	(GA)12	0.43	11	8	0.70	0.65
RM170	6	(CCT7	0.69	4	2	0.46	0.40
RM172	7	(AGG)6	0.68	3	1	0.46	0.39
RM174	2	(AGG)7(GA)10	0.42	6	2	0.71	0.67
RM175	3	(CCG)8	0.61	4	2	0.51	0.42
RM1812	11	(AT)16	0.17	22	16	0.89	0.88
RM194	5	(GA)6	0.99	2	1	0.02	0.02
RM2	7	(GA)2A(GA)13	0.59	5	0	0.61	0.58
RM201	9	(CT)17	0.37	8	4	0.73	0.68
RM202	11	(CT)30	0.43	12	5	0.77	0.75
RM204	6	(CT)44	0.12	29	22	0.94	0.93
RM205	9	(CT)25	0.36	10	7	0.73	0.68
RM212	1	(CT)24	0.61	6	2	0.58	0.55
RM2191	11	(AT)23	0.16	33	28	0.93	0.93
RM22	3	(GA)22	0.59	10	5	0.62	0.60
RM220	1	(CT)17	0.29	10	5	0.80	0.77
RM225	6	(CT)18	0.59	8	4	0.59	0.55
RM227	3	(CT)10	0.74	5	1	0.43	0.41
RM229	11	(TC)11(CT)5C3(CT)5	0.17	12	5	0.87	0.86
RM23	1	(GA)15	0.48	12	5	0.73	0.71
RM234	7	(CT)25	0.48	11	7	0.69	0.66

RM236	2	(CT)18	0.79	8	6	0.36	0.34
RM238	6	(CT)15	0.98	2	1	0.04	0.04
RM240	2	(CT)21	0.66	7	4	0.52	0.48
RM242	9	(CT)26	0.42	11	5	0.76	0.73
RM243	1	(CT)18	0.52	12	9	0.68	0.65
RM248	7	(CT)25	0.53	12	8	0.68	0.66
RM250	2	(CT)17	0.31	16	12	0.80	0.78
RM251	3	(CT)29	0.61	15	12	0.61	0.59
RM252	4	(CT)19	0.51	21	18	0.70	0.68
RM255	4	(AGG)5(AG)2-(GA)16	0.42	9	4	0.69	0.64
RM256	8	(CT)21	0.90	6	4	0.19	0.18
RM258	10	(GA)21(GGA)3	0.58	8	5	0.62	0.59
RM26	5	(GA)15	0.52	7	2	0.67	0.63
RM261	4	C9(CT)8	0.70	7	4	0.47	0.44
RM263	2	(CT)34	0.47	14	8	0.74	0.72
RM267	5	(GA)21	0.64	9	6	0.55	0.52
RM274	5	(GA)15-7-(CGG)5	0.76	4	2	0.38	0.34
RM276	6	(AG)8A3(GA)33	0.48	18	15	0.71	0.69
RM278	9	(GA)17	0.55	7	3	0.63	0.59
RM280	4	(GA)16	0.73	9	6	0.44	0.43
RM282	3	(GA)15	0.70	4	0	0.48	0.45
RM293	3	(GT)20	0.62	5	1	0.56	0.52
RM296	9	(GA)10	0.90	3	1	0.19	0.18
RM301	2	(GT)5G2(GT)8T2(GT)3	0.65	3	1	0.46	0.37
RM302	1	(GT)30(AT)8	0.27	12	8	0.82	0.80
RM308	8	(AT)4-6-(GT)2T2(GT)7	0.87	4	1	0.24	0.22
RM309	12	(GT)13	0.67	6	4	0.48	0.41
RM3134	3	(CA)14	0.59	5	2	0.58	0.52
RM315	1	(AT)4(GT)10	0.41	6	2	0.73	0.69
RM316	9	(GT)8-(TG)9(TTTG)4(TG)4	0.55	6	1	0.64	0.61
RM317	4	(GC)4(GT)18	0.63	12	9	0.57	0.54
RM318	2	(GT)15	0.67	6	3	0.49	0.43
RM321	9	(CAT)5	0.71	2	0	0.41	0.33
RM327	2	(CAT)11(CTT)5	0.51	5	2	0.64	0.58
RM3276	4	(CT)13	0.45	9	6	0.67	0.61
RM328	9	(CAT)5	0.66	2	0	0.45	0.35
RM3288	4	(CT)14	0.18	17	9	0.89	0.88
RM3331	12	(CT)15	0.38	9	4	0.76	0.73
RM3337	4	(CT)15	0.67	8	5	0.52	0.49
RM335	4	(CTT)25	0.24	14	9	0.84	0.82
RM341	2	(CTT)20	0.55	10	5	0.64	0.60
RM3436	3	(CT)18	0.39	10	6	0.71	0.66
RM3475	1	(CT)22	0.35	12	5	0.80	0.77
RM348	4	(CAG)7	0.63	4	2	0.48	0.38
RM349	4	(GA)16	0.41	9	5	0.75	0.72
RM3726	12	(GA)16	0.28	10	6	0.79	0.76
RM3766	3	(GA)18	0.20	17	9	0.88	0.87
RM3785	4	(GA)19	0.31	12	7	0.78	0.74
RM3808	9	(GA)20	0.27	18	12	0.85	0.83
RM4	11	(GA)16	0.34	9	5	0.72	0.66
RM403	1	(GA)8	0.71	2	0	0.41	0.33
RM407	8	(AG)13	0.52	6	1	0.67	0.64
RM418	7	(ATT)21	0.21	18	13	0.88	0.87

RM42	8	(AG)6 - (AG)2T(GA)5	0.50	4	1	0.57	0.48
RM444	9	(AT)12	0.47	23	19	0.75	0.74
RM463	12	(TTAT)5	0.71	4	1	0.45	0.40
RM467	10	(TC)21	0.40	9	3	0.75	0.72
RM47	7	(AG)7 - (AG)11	0.80	4	1	0.34	0.31
RM471	4	(GA)12	0.66	7	3	0.53	0.50
RM475	2	(TATC)8	0.46	8	3	0.72	0.68
RM517	3	(CT)15	0.31	12	7	0.78	0.75
RM520	3	(AG)10	0.77	7	5	0.38	0.36
RM523	3	(TC)14	0.67	5	2	0.50	0.45
RM526	2	(TAAT)5	0.66	8	6	0.51	0.46
RM529	1	(CT)12	0.38	5	1	0.73	0.69
RM544	8	(TC)9	0.74	6	3	0.44	0.41
RM5471	10	(TC)20	0.26	9	3	0.81	0.78
RM5503	4	(TC)27	0.38	14	8	0.79	0.77
RM553	9	(CT)10	0.56	4	0	0.59	0.53
RM561	2	(GA)11	0.35	6	2	0.72	0.66
RM5639	3	(AAG)13	0.42	9	5	0.69	0.64
RM5647	8	(AAG)16	0.26	15	9	0.85	0.84
RM569	3	(CT)16	0.41	13	10	0.74	0.70
RM571	3	(GT)11(AG)13	0.58	8	4	0.62	0.59
RM580	1	(CTT)19	0.23	16	10	0.87	0.86
RM589	6	(GT)24	0.43	17	10	0.78	0.76
RM6	2	(AG)16	0.67	5	1	0.51	0.48
RM60	3	(AATT)5AATCT(AATT)	0.90	4	2	0.19	0.18
RM6676	3	(TAA)8	0.27	13	7	0.86	0.84
RM7	3	(GA)19	0.49	12	8	0.69	0.65
RM71	2	(ATT)10T(ATT)4	0.69	5	1	0.50	0.46
RM7376	12	(GAAA)6	0.68	6	3	0.50	0.46
RM80	8	(TCT)25	0.24	17	10	0.87	0.86
RM81	3	(TCT)10	0.66	9	5	0.53	0.50
RM85	3	(TGG)5(TCT)12	0.71	5	3	0.45	0.41
Mean			0.51	9.43	5.53	0.63	0.59

a: Major allele frequency; b: Number of alleles; c: Number of rare alleles; d: Gene diversity; e: Polymorphism information content.

Table 3. Genetic diversity of different classfications.

Type	Sample Size	*MAF*[a]	*NG*[b]	*NA*[c]	*GD*[d]	H_E[e]	*PIC*[f]
Introduced lines	35	0.43	7.65	7.46	0.70	0.05	0.66
Breeding lines	56	0.62	4.42	4.10	0.49	0.02	0.43
Landrace	23	0.58	5.39	5.34	0.56	0.04	0.52
Weedy	18	0.52	4.03	3.99	0.57	0.02	0.51

a: Major allele frequency; b: Genotype number; c: Number of alleles; d: Gene diversity; e: Expected heterozygosity f: Polymorphism information content.

Table 4. Distribution of accessions from different classifications to each population identified by inferred value by STRUCTURE program.

Type	S1	S2	S3	Admixture	Total
Breeding lines	37	19	0	0	56
Landrace	9	3	3	8	23
Weedy rice lines	3	7	0	8	18
Introduced lines	3	6	15	11	35
Total	52	35	18	27	132
	39.4%	26.5%	13.6%	20.5%	

Figures

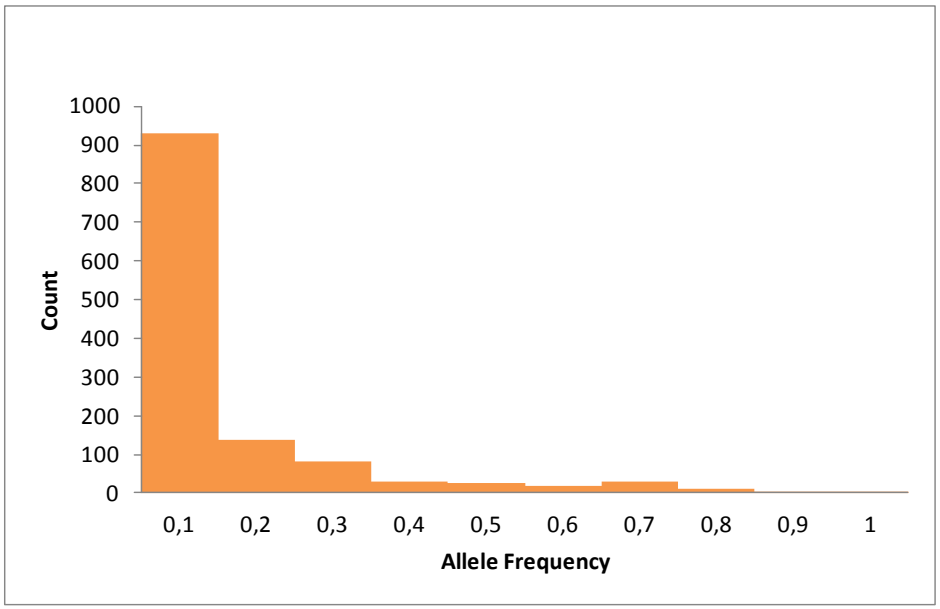

Fig. 1 Histograms of allele frequencies for the 1264 alleles in 132 accessions of rice and its relatives.

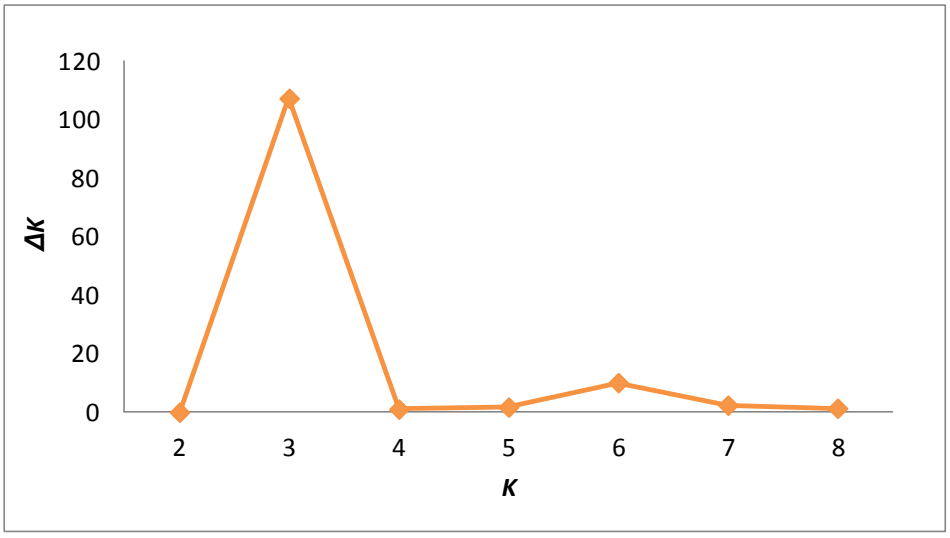

Fig. 2 Magnitude of Δ*K* as a function of *K*. In this case, the maximum value of *ΔK* of the 132 rice accessions was identified at *K* = 3.

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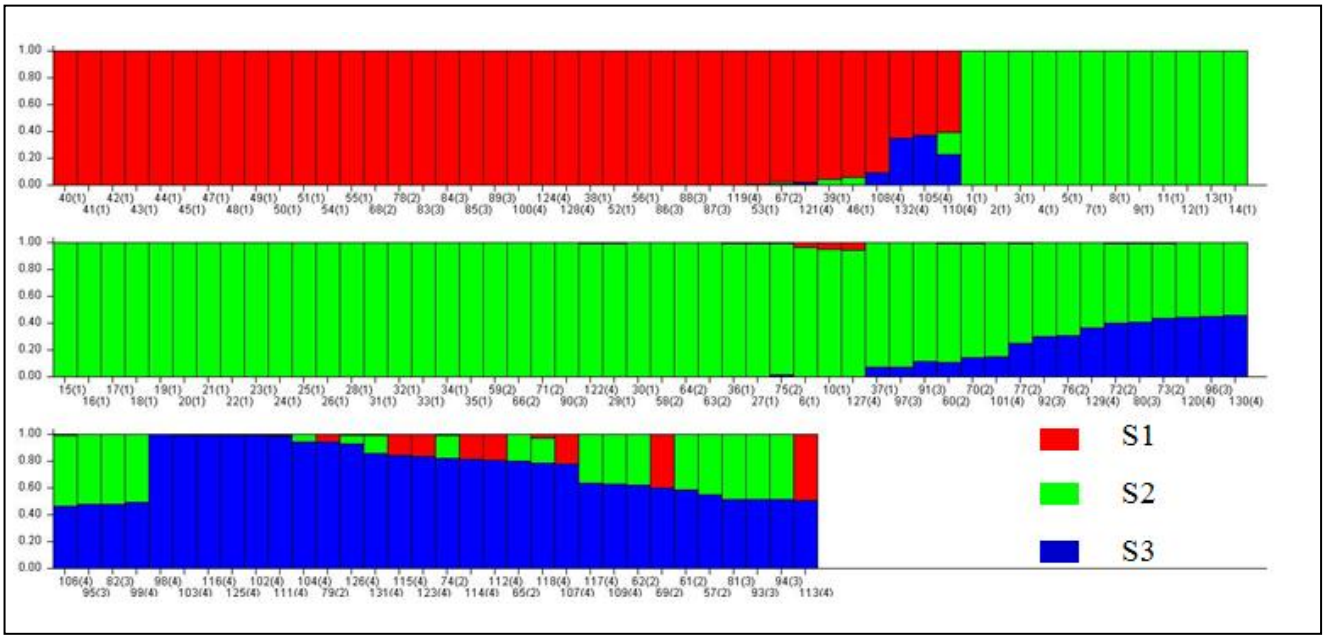

Fig. 3 Model based clustering for each of the 132 rice accessions examined based on 134 SSR markers used to build the Q matrix. Each individual bar represents an accession. The different colour bars refer to three different genetic groups (S1-S3, respectively).

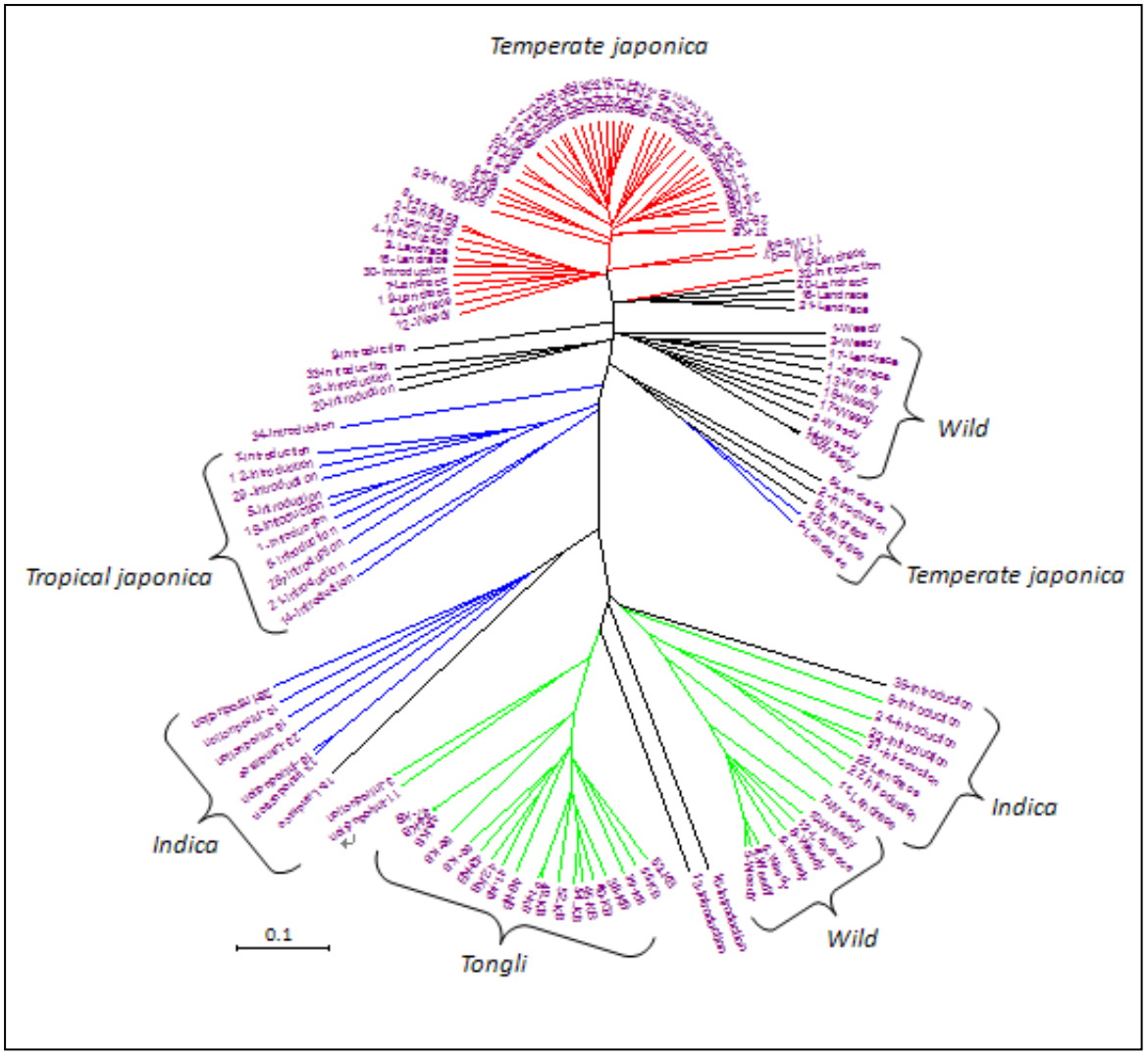

Fig. 4 An unrooted neighbor-joining tree showing the genetic relationships between the 132 rice accessions based on 134 microsatellite markers. The color corresponds to that of model-based populations. At subspecies level, *Temperate japonica* and *tropical japonica* cluster in one group together with one of the *wild* subgroups, whereas *indica*, *tongil* and the other *wild* subgroups clustered together.

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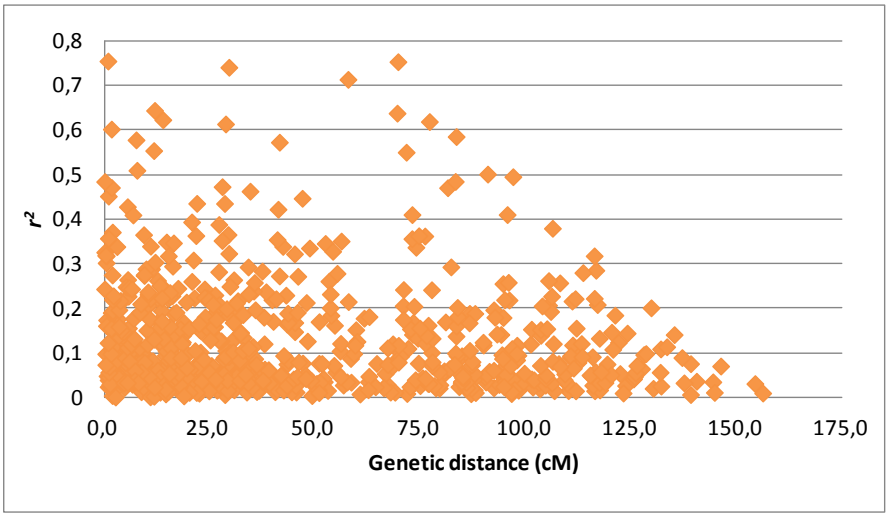

Fig. 5 Pattern of linkage disequilibrium (LD) for 134 simple sequence repeat (SSR) loci indicating the correlation of allele frequency (r^2) values against genetic distance (cM) of linked loci pairs.