Genetic diversity and relationships of wheat landraces from Oman investigated with SSR markers

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Abstract

Little is known about genetic diversity and geographic origin of wheat landraces from Oman, an ancient area of wheat cultivation. The objectives of this study were to investigate the genetic relationships and levels of diversity of six wheat landraces collected in Oman with a set of 30 evenly distributed SSR markers. The total gene diversity, (H_T) , conserved in the three durum wheat (*Triticum durum desf.*) landraces $(H_T = 0.46)$ was higher than in the three bread wheat (*Triticum aestivum* L.) landraces $(H_T = 0.37)$, which were similar to Turkish and Mexican bread wheat landraces calculated in previous studies. Genetic variation partitioning (G_{ST}) showed that variation was mainly distributed within rather than among the durum $(G_{ST} = 0.30)$ and bread wheat $(G_{ST} = 0.19)$ landraces. Based on modified Rogers' distance (MRD), the durum and bread wheat landraces were distinct from each other except for a few individuals according to principal coordinate analysis (PCoA). One bread wheat landraces of worldwide origin revealed that Omani bread wheat landraces were different from other landraces. However, two landraces from Pakistan were grouped somewhat closer to Omani landraces indicating a possible, previously unknown relationship. Implications of these results for future wheat landrace collection, evaluation and conservation are discussed.

Introduction

Wheat (*Triticum* ssp.) has been cultivated in Oman for more than 3000 years (Guarino 1990). While wheat landraces are still grown in many remote oases of Oman's Al-Hajar mountain range and Musandam, their geographic origin remains unknown. Surveys by the Omani Ministry of Agriculture indicate that in recent years modern cultivars of this crop are rapidly replacing Omani landraces, which has led to a decline in the total area cultivated by the latter from 1000 ha in 1988 to 238 ha in 1996 (Anonymous 1995, 2000).

Given the fast rate of disappearance of indigenous wheat germplasm, a mission for the collection of wheat landraces in Oman was initiated in 2001. The collected landraces were studied for morphological traits (Al-Maskri et al. 2003). However, the genetic diversity within and relationships among these Omani landraces have not been investigated. It is conjectured that Omani wheat landraces are distinct from those of other geographic regions, because of the political and geographical isolation of the country, but there is no evidence to support this hypothesis.

Molecular markers are a powerful tool to study the genetic structure of plant populations. Molecular markers can also aid in tracing the geographic origin of accessions by comparing genetic fingerprints of the unknown accession with those of diverse germplasm from different known regions (Salamini et al. 2002; Baek et al. 2003). More information about the genetic diversity within and relationships among germplasm would be invaluable for future collection trips and also for the conservation and utilization of existing genetic resources (Karp et al. 1997; Warburton and Hoisington 2001; Matus and Hayes 2002). PCR-based molecular markers such as SSRs can generate large datasets in a short period of time and, thus, facilitate the evaluation of large numbers of germplasm accessions in seed banks (Rebourg et al. 2001; Huang et al. 2002; Tang and Knapp 2003).

In the present study, we analyzed six Omani wheat landraces described by Al-Maskri et al. (2003) with a set of 30 SSR markers. The objectives were to (1) investigate the level of molecular diversity within and among these six Omani wheat landraces, (2) compare the level of diversity and trace the origin of these Omani landraces by a joint analysis with other wheat landraces of world-wide origin from the CIMMYT seed bank, and (3) discuss implications for future collection and conservation strategies of wheat landraces.

Materials and methods

Plant materials

Five Omani landraces were collected in the mountain oases of Balad Seet and Maqta in northern Oman, (Figure 1) where a hyperarid climate characterizes agriculture on tiny man-made terraces (Luedeling et al. 2005). Approximately 500 g of recently harvested seed were sampled from the stock of a farmer known to grow a specific landrace (identified by its vernacular name). Missani I, Sarraya, and Greda were collected from Balad Seet (23.19° N, 57.39° E; 1000 m asl) and Missani II and Walidi from Maqta (22.83° N, 59.00° E; 1050 m asl). Because the two Missanis were collected from different oases, they were designated and analyzed separately. The sixth accession studies was Cooley, which was originally collected from farmers in the Batinah, the northern costal area of Oman and stored at Sultan Qaboos University near Muscat. Morphologically the two Missanis and Sarraya were classified as predominantly durum wheat containing landraces, whereas Walidi, Cooley and Greda were classified as bread wheat landraces (Al-Maskri et al. 2003). A subsequent survey showed that some of these landraces were widespread within northern Oman but their names were poorly associated with morphological traits such as head characteristics or grain color (Alkhanjari, unpublished data). When the six Omani wheat landraces of this study were grown at CIMMYT, Mexico in 2002, the Missanis were found to be mixtures containing up to 5% bread wheat individuals (B. Skovmand, unpublished data). During the course of this study, a cytological analysis was conducted for the two Missanis and Sarraya to verify these findings. Twenty-five individuals were tested for each landrace, and all had 28 chromosomes except one sample from Missani II, which possessed 42 chromosomes. Therefore, these three landraces were considered as durum wheats, mixed with a few bread wheat individuals.

To investigate possible origins of the Omani bread wheats, two sets of bread wheat landraces from CIMMYT studied by Dreisigacker et al. (2004b) were used in a combined analysis with the three Omani bread wheat landraces. 'Set 1' included 36 landrace accessions, which were collected either as a bulk or in an unknown manner, from different regions world-wide; 'Set 2' consisted of supplementary individual plant collections of five Mexican and four Turkish landraces included in Set 1. Bulked accessions consisted of a random sample of spikes per landrace, which were harvested and stored together in one bag, whereas individual plant collections were harvested as a collection of sub-populations based on morphology, and seeds of each subpopulation were stored separately as described in detail by Dreisigacker et al. (2004b).



Figure 1. Map of Oman indicating the location of the two mountain oases of Balad Seet and Maqta where the wheat germplasm was collected and the climatic conditions of the mountain oases (climate diagram of Buraimi after Lieth et al. 1999).

Marker analyses

Thirty-five plants of each of the six Omani landraces were harvested individually in 2002 and used for DNA fingerprinting. Extraction of genomic DNA from single young plants was performed according to Saghai-Maroof et al. (1984) and modified according to CIMMYT protocols (http://www.cimmyt.cgiar.org/ABC/Protocols/manualABC.html).

A set of 30 SSRs was employed, 10 of which mapped to the A genome, 12 to the B genome, and 8 to the D genome. The SSRs covered all chromosomes except 5A and 5D. The markers provided by Dupont (DuPw) were EST-derived SSRs, while those from IPK were genomic-derived. Detailed information about each SSR is available on the web at http://www.cimmyt. org/english/ webp/support/publications/support_materials/ssr_ mw1. htm. PCR conditions were described by Dreisigacker et al. (2004a). SSRs were multiplexed and multiloaded for maximum efficiency, with an average of 2 primers amplified in the same PCR tube and an average of 3.5 SSRs run in the same lane of the gel (by combining 1 or more multiplexed PCRs). PCR products were run on an ABI Prism 377 DNA Sequencer (Perkin Elmer/Applied Biosystems). Fragments were sized using Genescan 3.1 and assigned to allele categories using the software package Genotyper 2.1 (Perkin Elmer/Applied Biosystems).

Statistical analyses

Proportion of polymorphic loci, average number of alleles per locus, number of unique alleles per landrace (present in only one landrace), and percentage of heterozygosity of each SSR locus on the basis of individual plants were determined. The maximum likelihood estimate of outcrossing rate of the final generation (t_0) and mean outcrossing rates of preceding generations (t_p) using multilocus individual heterozygosity were computed for each landrace according to Enjalbert and David (2000), who assume that t_p estimates are complimentary to $F_{\rm is}$ values. Polymorphic information content (PIC) values were calculated according to Anderson et al. (1993). Total gene diversity (H_T) and gene diversity within landraces (H_S) based on SSR data were determined according to Nei (1987). Confidence intervals for H_S values were obtained using a bootstrap procedure with resampling across markers and individuals. The genetic differentiation between landraces (G_{ST}) was calculated according to Nei (1987)

$$G_{\rm ST} = (H_{\rm T}\bar{H}_{\rm S})/H_{\rm T}$$

where H_s is the mean of H_S values within land-races.

Genetic distances within and between landraces were calculated using the modified Rogers' distance (MRD; Wright 1978)

MRD =
$$\sqrt{\frac{1}{1}} 2m \sum_{i=1}^{m} \sum_{j=1}^{a_i} (p_{ij} - q_{ij})^2$$
,

where p_{ij} and q_{ij} are the frequencies of the *j*th allele at the *i*th locus in the two taxonomic units under consideration, a_i is the number of alleles at the *i*th locus, and *m* refers to the number of loci. Standard errors were calculated via bootstrapping using 5000 repetitions and the significance of associated MRD was subsequently tested. The unweighted pair group method with arithmetic averages (UPGMA) cluster analysis (Sneath and Sokal 1973) and principal coordinate analysis (PCoA; Gower 1966) were used to reveal associations between landraces based on the MRD matrices.

All calculations were carried out separately for the three durum wheat landraces using the 22 SSRs mapping to the A and B genomes, and the three bread wheat landraces using all 30 SSRs.

To trace the geographic origin of the Omani landraces, a comparison was made with 'Set 1' of 36 CIMMYT landraces. A comparison of allelic diversity between the Omani landraces and the 36 landraces studied previously, and a UPGMA cluster analysis of the Omani plus 36 landraces, were calculated using 19 SSRs that were scored in both data sets (the Omani and the 36 landraces). In addition, a combined analysis was performed to compare the genetic diversity between the three Omani bread wheat landraces and 'Set 2' of the CIMMYT landraces using a common set of 28 SSRs. In order to eliminate any bias in the diversity statistics arising from different sample sizes in the Omani (n = 105), Turkish (n = 20) and Mexican (n = 99) landraces, a random sample of 18 individuals was taken without replacement from each sample for calculating the above statistics and results were averaged across 5000 bootstrap repetitions. All necessary calculations were performed with the PLABSIM software (Frisch et al. 2000) except for the calculation of outcrossing rate, which followed Enjalbert and David (2000).

Results

Marker information in Omani landraces

The number of alleles per SSR marker found across all three durum wheat landraces averaged 5.7 and varied between 2 and 13. By comparison, the three bread wheat landraces had on average 4.6 alleles per SSR marker with a range between 1 and 10 (Table 1). A high proportion of alleles was unique in the durum (54.4%) and bread wheat (45.3%) landraces. PIC values averaged 0.45 and 0.37 for the durum and bread wheat landraces, respectively.

The proportion of polymorphic SSR loci per landrace averaged 68.2% in the durum wheat landraces and 76.6% in the bread wheat landraces (Table 1). The level of heterozygosity per SSR per individual averaged 2.4 and 1.0%, ranging from 0.9 to 3.1% and from 0.7 to 1.4%, in the durum and bread wheat landraces, respectively (data not shown). The genomic-derived SSRs showed much higher values of H_T , H_S and G_{ST} than the correspondent EST-derived SSRs both in bread and durum wheat landraces (data not shown).

Table 1. Modified Rogers' distances (MRD), total gene diversity (H_T), gene diversity within (H_S) and proportion of genetic differentiation (G_{ST}) among landraces as well as average number of alleles per locus (A), unique alleles, proportion of polymorphic loci (P) and outcrossing rate of the final generation (t_0), a mean of outcrossing rates of the preceding generations (t_p) identified for each landrace.

No.	Landrace	MRD		$H_{\rm S}$	А	Unique Alleles	Р	Outcrossing rate	
		1	2					t_0	tp
Durum	wheat								
1	Missani I			0.41a ^b	3.8	33	81.8	0.00	0.17
2	Missani II	0.50^{a}		0.21c	2.6	22	54.5	0.00	0.08
3	Sarraya	0.42 ^a	0.58^{a}	0.27b	3.0	13	63.6	0.00	0.27
	Mean			0.29	3.1	22.7	68.2		
				$H_{\rm T} = 0.4$	6	$G_{\rm ST} = 0.30$			
Bread v	wheat								
1	Walidi			0.32a	3.6	35	83.3	0.00	0.11
2	Cooley	0.42 ^a		0.17b	2.4	7	63.3	0.00	0.07
3	Greda	0.42^{a}	0.26^{a}	0.34a	2.6	20	83.3	0.00	0.08
	Mean			0.28	2.9	20.7	76.6		
				$H_{\rm T} = 0.3$	7	$G_{\rm ST} = 0.19$			

All calculations were based on 22 and 30 SSRs for durum wheat and bread wheat landraces from Oman, respectively.

^aSignificant at the 0.05 probability level according to a bootstrap procedure.

^bMeans followed by different letters were significantly different (P < 0.05) according to a bootstrap procedure.

Genetic differentiation within and between landraces

Estimates of $H_{\rm S}$ differed significantly (P < 0.05) among the three durum wheat and three bread wheat landraces (Table 1). The values ranged from 0.21 (Missani II) to 0.41 (Missani I) in the durum landraces and from 0.17 (Cooley) to 0.34 (Greda) for the bread wheat landraces. The proportion of genetic differentiation among landraces (G_{ST}) was 30% for the durum wheat and 19% for the bread wheat landraces. Outcrossing rates (t_0) for the current generation of the 6 Omani landraces was 0.00, indicating no seed mixing since collection, but outcrossing rates of previous generations (t_p) ranged from 0.08 to 0.27 for the durum landraces and 0.07 to 0.11 for the bread wheat landraces. A $t_{\rm p}$ value of 0.27 is quite high, and may indicate seed mixing in the manner that the durum landraces were handled by the farmers. Outcrossing due to crosspollination between different landraces is not supported because of the very low number of heterozygous individuals in all of the landraces.

MRD values averaged 0.50 and 0.37 for durum wheat and bread wheat landraces, respectively (Table 1). MRD values among durum wheat and among bread wheat landraces were all significant (P < 0.05) indicating that these landraces are genetically distinct from each other.

Principal coordinate analysis (PCoA)

In the PCoA based on MRD for the three durum wheat landraces, the first and second principal coordinate (PC) accounted for 27.8 and 13.9% of the total variation, respectively (Figure 2). The two Missanis were clearly separated from each other and from Sarraya along both PCs except for one individual from Missani II, which was adjacent to Missani I. For the bread wheat landraces, the first two PCs explained 25.3 and 16.8% of the total variation, respectively (Figure 3). Walidi was distinguished from Cooley and Greda mainly along PC1, and the latter two landraces overlapped slightly. In addition, Greda was separated into two distinct sub-populations along both PC1 and PC2: Greda-a with 28 individuals, which overlapped with Cooley, and Greda-b with 7 individuals, positioned far away from all other individuals.

Comparison of Omani bread wheat landraces with other well-characterized landraces

The three Omani bread wheat landraces displayed a lower average number of alleles and H_S value (Table 1) than values found in the Mexican and Turkish landraces ('Set 2') given by Dreisigacker



Figure 2. Principal coordinate analysis of three Omani durum wheat landraces based on modified Rogers' distance calculated from allele frequencies at 22 SSRs. PC1 and PC2 are the first and second principal coordinates, respectively. Missani I (\Diamond), Missani II (\Box), Sarraya (\blacktriangle).



Figure 3. Principal coordinate analysis of three Omani bread wheat landraces based on modified Rogers' distance calculated from allele frequencies at 30 SSRs. PC1 and PC2 are the first and second principal coordinates, respectively. Walidi (∇), Cooley (\star), Greda (\bigcirc).

et al. (2004b). However, based on a comparison of resampled values, these differences were not significant (data not shown).

A dendrogram of the three Omani bread wheat landraces and 36 CIMMYT landraces ('Set 1') from various countries demonstrated that the three Omani bread wheat landraces clustered closely together (Figure 4). However, they were fairly distant from all landraces from the other regions. Only two landraces from Pakistan, No. 10 and 11 (Shorewaki and 86PK1317) were merged with Omani bread wheat landraces in a fairly heterogeneous cluster. Fifty-one unique alleles in 6 Omani wheat landraces were revealed by a comparative analysis with the landraces of 'Set 1', accounting for 29% of the total alleles; 36 of them were rare alleles (< 0.05), while 4 common rare alleles between 6 Omani wheat landraces and 3 Pakistani landraces included in 'Set 1' were found (data not shown).

Discussion

SSR polymorphism in Omani wheat landraces

The results of the SSR analysis demonstrated that fingerprinting 35 individuals per Omani landrace were sufficient to characterize and discriminate the landraces. Many previous studies used 1 to 10 plants (individually or in a bulk) to characterize landrace accessions (Gilbert et al. 1999; Kim and Ward 2000; Eujayl et al. 2002). Although this reduces the amount of laboratory work, the information gathered in the diversity studies is usually insufficient (Gilbert et al. 1999; Treuren et al. 2001; Dreisigacker et al. 2004b).

Genomic-SSRs showed much higher genetic differentiation than that of EST-SSRs in both durum and bread wheat landraces. This is in contradiction to Dreisigacker et al. (2004a), who observed no significant genetic differentiation in the two kinds of markers among a set of CIMMYT wheat genotypes targeted to different Mega-Environments. The differentiation in Omani wheat landraces could be due to a long history of natural and/or artificial selection, or different mutation rates of EST-SSR loci.

Durum landraces from Oman had a higher genetic diversity than did the bread wheat landraces (Table 1). One explanation might be the different domestication history of durum and bread wheat. Wild forms of tetraploid wheat frequently exchanged genes with emmer wheats at



Figure 4. Dendrogram of three Omani bread wheat landraces and 36 other landraces from West Europe (\Diamond), Turkey (\blacklozenge), Africa (\clubsuit), Central America (\bullet), South America (\bigcirc) and Asia (∇) based on UPGMA cluster analysis of modified Rogers' distance calculated from 19 common SSRs [Numbers refer to landraces in Dreisigacker et al. (2004b)].

the early stages of domestication, and with durum wheat in more recent times, leading to a high level of polymorphism in emmer and durum wheat landraces (Huang et al. 1999). Recent findings of emmer landrace populations from the same area, where the wheat landraces were collected for the present study, may strengthen this hypothesis (Hammer et al. 2004). By comparison, bread wheat evolved by polyploidy from a small number of progenitor individuals (Dvorak et al. 1998). Consequently, isolation of bread wheat from its two ancestral species resulted in a narrow germplasm pool with very restricted genetic variability (Chao et al. 1989; Siedler et al. 1994).

Oman is neither a known center of wheat diversity nor a leading wheat producing country.

Nevertheless, the results of this study indicate that significant molecular diversity has been conserved in the six Omani landraces studied here. The standardized H_S values for Omani bread wheat landraces are comparable to those of Turkish landraces, which come from a primary center of wheat origin, and of the Mexican landraces included in our study. However, H_S values of the landraces were significantly different. Genetic diversity within populations is highly dependent on the founder principle, such as the establishment of a new population by a few individuals (Allard 1970), or a small amount of seed used for multiplication (Brown et al. 1997). Typically, farmers in the two oases of northern Oman grow wheat in small terraces sized 2-100 m² (Nagieb et al. 2004; Siebert et al. 2005). At the time of its collection, Missani II was grown in only one plot at Maqta, which is reflected by the low H_S value for this landrace (Table 1). Cooley has also a low H_S value and number of unique alleles, which may be due to artificial selection during seed multiplication.

Genetic variation is mainly found within rather than among the durum and bread wheat landraces. This might be due to some seed exchanges between farmers, within or between oases, which permit landraces to regain lost within diversity resulting from drift and selection, and to reduce the genetic differentiation between them. Outcrossing, facilitated via seed exchanges or between different fields, could also generate new combinations as shown by the outcrossing rates in Table 1. Estimates of outcrossing in previous generations were high enough to indicate that these landraces were not grown in complete isolation, and migration of alleles between landraces has been a factor in the evolution of the Omani landraces. Considering the very long cultivation history of these landraces, high levels of variation could accumulate within each landrace.

Previous studies of barley and wheat landraces have reported that a high degree of genetic heterogeneity has been conserved within accessions (Parzies et al. 2000; Dakir et al. 2002; Dreisigacker et al. 2004b). This high heterogeneity within landraces is important for genetic buffering and adaptation of landraces to different environments, different conditions from year to year, with various biotic and abiotic stresses, and has implications for conservation of these landraces *ex situ*.

Genetic relationships among Omani landraces

Landraces of durum and bread wheat from Oman were well separated as indicated by MRD values and PCoA. The main reasons for this genetic differentiation among populations are presumably the geographic isolation of the oases Balad Seet and Maqta, and farmer selection. One individual plant of Missani II was positioned close to the individuals from the Missani I (Figure 2). This could be an indication of a seed mixture from Missani I. Likewise, one plant of Cooley was located directly within the plants from Walidi (Figure 3) pointing to the possibility of a seed mixture with Walidi. Greda separated into two distinct sub-populations as revealed by PCoA; the MRD value between them (0.74) is highly significant. This result might indicate that Greda derived from two originally different landraces that have been recently mixed. Based on its similarity to Cooley in Figure 3, it could be a mixture between Cooley and something else, but until more landraces from the area are studies, this conclusion cannot be proven. Further morphological data are required to confirm this hypothesis. The MRD value between Greda-a and Cooley (0.26) was significant, suggesting that they are distinct populations, even though they overlapped in the PCoA graph.

The two Missanis are neither duplicates nor redundant landraces according to their MRD value and their positions in the PCoA (Figure 2). This illustrates that the name of a landrace is not a reliable passport criterion to identify duplicates. More detailed information on phenotypic data, collection site, and farmer's knowledge would be highly beneficial for further clarification of the genetic relationships among these landraces. The fact that the SSR data did not confirm the presence of T. aestivum material in Sarraya or T. durum material in Walidi which were detected in the morphological classification of a larger seed sample planted under controlled conditions (Al-Maskri et al. 2003), points to the low frequency of the respective material in these landraces.

Contrary to Rebourg et al. (2001) who suggests classification of populations based on a two-step procedure (first a classification based on molecular data, followed by morphological description), we used morphological and passport data to group wheat landraces in a crude way, and then carried out molecular analyses for refining the genetic structure patterns. In this way, we took full advantage of all available information and reduced the expensive costs for molecular marker analyses (Pardey et al. 2001; Dreher et al. 2003).

Origin of Omani wheat landraces

Wheat landraces have a long history of cultivation in Oman. In ancient times, Maqta had direct access to Indian and Pakistani trade routes via the Arabian Sea. Balad Seet had well established trade relationships to the interior of Oman and Batinah coast connecting the country with Iran and Iraq, the Mediterranean region and with Yemen.

Cluster analysis indicates that Omani bread wheat landraces investigated in this study are not closely related to today's landraces from Africa, Asia, Western Europe, Turkey, Central or South America. Although there is no certainty about the origin of the Omani bread wheat landraces, two landraces (10, 11) from Pakistan did cluster somewhat closer to the Omani landraces (Figure 4), which might indicate a relationship demonstrated by the four common rare alleles. On the other hand, the morphological characteristics of the two bread wheat varieties found within the Sarraya landrace from Balad Seet and Walidi from Maqta indicate an ancient evolutionary origin (Al-Maskri et al. 2003). It may be that the investigated Omani landraces are in fact relics of once much more widespread wheat populations that have been conserved (and continued to evolve) in the isolation of the remote Omani mountain oases. Further efforts to analyze more landraces from Pakistan, India and Iran could lead to a more definitive answer regarding the geographic origin of Omani wheat landraces.

Implications for further collection and conservation of wheat landraces

Wheat landraces have never been systematically collected in Oman and little is known about their genetic diversity. Because they are presently under high risk of extinction, *ex situ* conservation becomes the safest approach for maintenance of these materials. The same situation prevails in other regions of the world, and collection missions

should be sent to these remote areas to rescue the last remnants of crop genetic diversity. Our SSR data reveal that Omani wheat landraces are quite unique and differ from those collected in other regions while harboring a comparable level of genetic diversity. Therefore, more wheat landraces from Oman should be collected. The geographic isolation and the limited exchanges of wheat seed among oases suggest that wheat landraces may widely differ among various oases. The clear separation of the landraces, especially the separation of the two Missanis by SSR data, confirms this hypothesis. Hence, it seems more efficient to investigate more oases and collect more samples from various oases rather than within only one oasis. Furthermore, care should be taken not to rely on pedigree or nomenclature when deciding what might be a duplicate.

Landraces with low H_S values such as Cooley and Missani II could be maintained in the seed bank using a bulk method without risking the loss of diversity. On the other hand, those landraces with high H_S values such as Missani I may benefit more from an individual method of storage and multiplication. As more screening and molecular evaluation information is accumulated, core collections based on ecogeographic origin, distribution of polymorphic loci and the possible value to breeders seem to be a logical step in seed bank management (Brown 1989). Core collections are selected to represent as much of the genetic diversity in the collections of the crop species as possible, which could greatly benefit the conservation and utilization of these collections. Furthermore, it seems promising to compare SSR data of all newly collected accessions with a group of representative landraces from a core collection around the world to elucidate the geographic origin of these materials and to decide whether or not to collect further landraces from that area, and which collection strategy would be most efficient.

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