



Structure and genetic relationships between Brazilian naturalized and exotic purebred goat domestic goat (*Capra hircus*) breeds based on microsatellites

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Abstract

The genetic relationships and structure of fourteen goat (*Capra hircus*) populations were estimated based on genotyping data from 14 goat populations ($n = 410$ goats) at 13 microsatellite loci. We used analysis of molecular variance (AMOVA), principal component analysis (PCA) and F statistics (F_{IS} , F_{IT} and F_{ST}) to evaluate the genetic diversity (H_o , H_e and ad) of the goats. Genetic distances between the 14 goat populations were calculated from allelic frequency data for the 13 microsatellite markers. Moderate differentiation was observed for the populations of the undefined breeds (including the Anglo-Nubian-M breed), the naturalized Brazilian breeds (Moxotó, Canindé), the exotic purebred breeds (Alpine, Saanen, Toggenbourg and Anglo-Nubian) and the naturalized Brazilian Graúna group. Our AMOVA showed that a major portion (88.51%) of the total genetic variation resulted from differences between individual goats within populations, while between-populations variation accounted for the remaining 11.49% of genetic variation. We used a Reynolds genetic distance matrix and PCA to produce a phenogram based on the 14 goat populations and found three clusters, or groups, consisting of the goats belonging to the undefined breed, the naturalized breeds and the exotic purebred breeds. The closer proximity of the Canindé breed from the Brazilian state of Paraíba to the Graúna breed from the same state than to the genetically conserved Canindé breed from the Brazilian state of Ceará, as well as the heterozygosity values and significant deviations from Hardy-Weinberg equilibrium suggests that there was a high number of homozygotes in the populations studied, and indicates the importance of the State for the conservation of the local breeds. Cataloguing the genetic profile of Brazilian goat populations provides essential information for conservation and genetic improvements programs.

Key words: goat, microsatellite, genetic distance, PCA, AMOVA, genetic relationships, genetic diversity, F statistics.

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Introduction

Microsatellite polymorphisms have proved to be a useful tool for the analysis of genetic structure and the genetic divergence between populations and is also important for verifying pedigree relationships and providing fundamental information for the preservation of breeds.

Compared with other farm animals, few studies have been conducted using microsatellite markers to investigate genetic distance in domesticated goats (*Capra hircus*)

(Saitbekova *et al.*, 1999; Yang *et al.*, 1999; Barker *et al.*, 2001; Kim *et al.*, 2002; Li *et al.*, 2002; Baumung *et al.*, 2004). In Brazil, caprine breeds have been studied using morphological characters (Machado *et al.*, 2000), protein markers (Igarashi *et al.*, 2000) and random amplified polymorphic DNA (RAPD) markers (Oliveira *et al.*, 2005).

According to the Brazilian Geographic and Statistics Foundation (Instituto Brasileiro de Geografia e Estatística -IBGE), the vast majority of Brazilian goats (93%) are located in the northeastern region of Brazil where two groups can be identified, naturalized goats and goats of undefined breed. The naturalized goats tend to be small and highly heterogeneous, especially for coat colors. There are four major breeds, Moxotó, Canindé, Repartida and Marota, along with the Graúna group formed by goats with black

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coat color (Santos, 1987) but which has not yet been regarded as a Brazilian breed by the Brazilian Goat Breeders Association (Associação Brasileira de Criadores de Caprinos – ABCC) because this association requires other standardized characteristics in addition to coat color. The goats of undefined breed (UDB) constitute the largest group in the Brazilian northeast, and includes all goats that cannot be assigned to any other breed. This group comprises goats with diverse coat color patterns as well as various degrees of crossing with exotic purebred goats such as those of the Toggenbourg, Anglo-Nubian, Alpine and Saanen breeds, such crossings having been made to improve milk and meat production (KP Pant, personal communication). The crossing of diverse breeds interferes with genetic conservation programs for naturalized and UDB breeds and affects the genetic structure and relationships among the breeds. Assessing the genetic composition of Brazilian naturalized, UDB and exotic purebred goats is important for determining the current genetic structure of these populations and would provide substantial information for genetic improvement and conservation programs. The objective of the present study was to investigate the genetic structures of 14 goat populations and to analyze the genetic relationship between them using 13 microsatellite markers. We included the Graúna group in our investigation to compare our results with those reported by Igarashi *et al.* (2000). To increase the understanding about the diversity of these goat populations we also compared our results to those of Araújo *et al* (2006) who also used microsatellite loci to investigate the genetic diversity between Alpine, Saanen and Moxotó goats.

Material and Methods

DNA extraction and amplification conditions

A total of 410 goats (*Capra hircus*) from a blood sample collection previously obtained by Igarashi *et al.* (2000) was used (Table 1).

We extracted DNA from 300 µL of goat blood according to the method of Higuchi (1989) with some modifications. Amplification reactions were done in a TGradient (Biometra, Germany) thermocycler in a final reaction volume of 15 µL containing 0.2-0.5 µg of template DNA, 0.1 mM of each dNTP, 0.5 U of Taq DNA polymerase (Life Technologies, EUA), 1X reaction buffer (50 mM KCl, 2 mM MgCl₂, 20 mM Tris-HCl, pH 8.4) and 10 pmol of primers. A two-stage touchdown amplification program was designed for DNA amplification. An initial denaturation step of 4 min at 94 °C was used in all programs, followed by amplification cycles in which the annealing temperature (Tm) was gradually decreased by 1 °C every amplification cycle. This treatment was followed by a second stage consisting of either 28 or 30 amplification cycles, in which the Tm remained constant. Denaturation and elongation steps were held constant for

Table 1 - List of the goat populations studied.

Breed, cross or group	Population code	Number of animals	State hosting the population
Exotic purebreds			
Alpine and German Alpine ¹	ALP	119	Minas Gerais
Anglo-Nubian	AGN-P	16	Minas Gerais
Saanen	SAA	35	Minas Gerais
Toggenbourg	TOG	28	Minas Gerais
Brazilian naturalized breed			
Canindé	CAN-PB	19	Paraíba
Canindé	CAN-CE	24	Ceará
Canindé	CAN-RN	29	Rio Grande do Norte
Moxotó	MOX-PB	8	Paraíba
Moxotó	MOX-CE	23	Ceará
Undefined breeds			
Undefined breed	UDB-NE	19	Ceará, north-eastern
undefined breed	UDB-CL	16	Ceará, middle-eastern
undefined breed	UDB-S	20	Ceará, southern
Crossbred goats			
Anglo-Nubian crossbred	AGN-M	43	Ceará
Not yet recognized as a Brazilian breed			
Graúna group	GRA-PB	11	Paraíba

¹German Alpine and the Alpine breed animals were grouped together due to their small sample size.

45 s at 94 °C and 72 °C, respectively, during both stages. An elongation step of 10 min at 72 °C was performed in all programs after stage 2. The 13 microsatellite markers selected for assessing genetic diversity in the goat populations described in Table 1 were: INRA011, INRA040, BM3517, ILST030, ILST028, UWCA46, TEXAN02, ILST011, INRA023, SRCRSP9, MHCIIDR, INRA006 and IDVGA37. These markers were originally described in cattle, with the exception of the caprine SRCRSP9 markers. One PCR primer from each pair was labeled with an appropriate dye, 6FAM, HEX or NED (PE Biosystems, USA) and the polymerase chain reactions (PCR) were carried out as described above resulting in strong and specific PCR products which were analyzed in an ABI PRISM 377 automatic DNA sequencer using standard loading conditions and a 2 h electrophoresis run on 5% (w/v) Long Ranger gel. Alleles were sized relative to a ROX GS 500 internal size standard (Applied Biosystems, USA) and analyzed with the Applied Biosystems GENESCAN program version 2.1. Size estimates, in base pairs (bp), were manually checked for genotyping errors.

Data analysis

Allelic frequencies, observed heterozygosity (H_o), expected heterozygosity (H_e) and exact tests of genotypic frequencies for deviation from Hardy-Weinberg equilibrium (HWE) were carried out using the GENEPOP v.3.4 program (Raymond and Rousset, 1995). The exact test of Hardy-Weinberg proportion for multiple alleles (Guo and Thompson, 1992) was performed using the Markov chain procedure (1,000 batches, 5,000 iterations, 10,000 de-memorization steps). The number of private alleles and allelic diversity were assessed using the FSTAT program v.2.9.3 (Goudet, 2001). A principal component analysis (PCA) was performed on the populations using the PCAGEN program (J.Goudet, unpublished). Populations were ordered according to the first and second PCA axes. The significance of each principal component was assessed from 5,000 randomizations. The F-Statistics (Wright, 1951) were calculated by the method of Weir and Cockerham (1984) using the GDA program (Lewis and Zaykin, 1997) and the significance of the F values were estimated from 10,000 replicates by bootstrapping, with confidence intervals not including zero being considered significantly different from zero.

The groups obtained from the PCA analyses were subjected to analysis of molecular variance (AMOVA; Excoffier *et al.*, 1992) using the ARLEQUIN 3.0 program (Excoffier *et al.*, 2005). Significance was determined from 10,000 permutations. Reynolds distances (Reynolds *et al.*, 1983) between populations were generated from allelic frequency data using the PHYLP package, v.3.65 (Felsenstein, 2005). Genetic distances were calculated using the GENDIST program and used to construct a Neighbor-Joining (NJ) tree in the NEIGHBOR program. To test the robustness of tree topologies, 1,000 bootstrap replicates of the allele frequency file were generated in the SEQBOOT program and analyzed using GENDIST. Tree topologies were created for all replicates using NEIGHBOR and a consensus tree was generated by the CONSENSE program. These programs are incorporated in the PHYLP package, v.3.65 (Felsenstein, 2005).

Results

Genetic diversity within and between populations

All 13 loci were polymorphic, showing an average of 15.6 alleles per locus (min = 9, max = 26 alleles; Table 2). Allelic diversity was lowest for the MOX-PB (4.5) population and highest for ALP (12.8) population. The mean H_o value varied from 0.28 to 0.46 and H_e from 0.64 to 0.80. The MOX-PB population was the least variable (H_e = 0.64), while the ALP (H_e = 0.80) and TOG (H_e = 0.79) populations showing the highest H_e values. In a total of 203 alleles we detected 10 private alleles (5%) over all the populations (Table 2) and the average private allele frequency was 0.075 (min = 0.004, max = 0.0425).

We detected 38 non-significant deviations from HWE from a total of 182 loci/population ($p > 0.01$). In contrast, the remaining loci/populations (144) showed Hardy-Weinberg disequilibrium ($p < 0.01$; Table 2). The populations presenting loci with no significant deviations were: MOX-C (UWCA46, TEXAN02); MOX-PB (INRA040, BM3517, ILST030, UWCA46, TEXAN02, ILST011, INRA023, SRCRSP9, MHCIIr); CAN-CE (ILST028, TEXAN02); GRA-PB (ILST028, ILST011, INRA023, IDVGA37); AGN-M (ILST011, INRA023); AGN-P (BM3517, TEXAN02); TOG (BM3517, ILST028, ILST011, INRA023); SAA (BM3517, ILST011); UDB-NE (BM3517, ILST028, ILST011); UDB-CL (ILST028, TEXAN02, INRA023, IDVGA37); UDB-S (ILST028, TEXAN02, ILST011, INRA023). When either all populations or all loci were pooled, significant differences between H_o and H_e ($p < 0.001$) were detected (Table 2). Allele frequencies are available as supplementary material (Table S1).

Genetic differentiation and PCA

The pattern of genetic differentiation was represented by a plot of scores based on allelic frequency from 14 goat populations (Figure 1). The first principal component axis (PC1) accounted for 32.72% ($p = 0.000$) of the total genetic diversity, and the second (PC2), for 13.72% ($p = 0.056$, not significant). The PCA plot gives the position of the populations according to either their known or apparent origins (historical data; Igarashi *et al.*, 2000). The PC1 axis represents the differentiation between exotic purebred populations (AGN-P, SAA, TOG and ALP) and native and UDB populations (MOX-CE, MOX-PB, CAN-CE, CAN-RN, CAN-PB, GRA-PB, AGN-M, UDB-NE, UDB-CL and UDB-S) whereas the PC2 axis, although not significant, apparently distinguishes native and UDB populations. From this, a primary structuring suggested three major groupings of populations: (1) AGN-P, SAA, TOG and ALP, (2) MOX-CE, MOX-PB, CAN-CE, CAN-RN, CAN-PB and GRA-PB, and (3) AGN-M, UDB-NE, UDB-CL and UDB-S.

Genetic relationship

The neighbor-joining phenogram (Saitou and Nei, 1987) based on genetic distance of Reynolds (1983), divided the populations into three branches similar to the historical data: (1) AGN-M, AGN-P, TOG, SAA and ALP, (2) MOX-CE, MOX-PB, CAN-CE, CAN-RN, CAN-PB and GRA-PB, and (3) UDB-NE, UDB-CL and UDB-S (Figure 2). The most consistent groupings were: UDB-S and UDB-CL (99%); ALP and SAA, TOG, and AGN-P (95%); and GRA-PB and CAN-PB (91%). The detected groupings were as expected and consistent with the historical data of the origin of these populations and breeds. These groupings confirm the PCA primary structuring, except for the position of the AGN-M population.

Table 2 - Summary of observed (H_o), expected (H_e), mean (H) heterozygosity, allelic diversity (ad) and number of private alleles (pa) over all goat populations. At the single-population single-locus levels a total of 38 non-significant deviations from HWE were detected. Significant deviations from HWE were detected when either all populations or all loci were pooled ($p < 0.001$). * = no significant difference between H_o e H_e ($p > 0.01$).

Locus	N. of alleles	Size range	MOX-CE (n = 23) ^a		MOX-PB (n = 8)		CAN-CE (n = 24)		CAN-RN (n = 29)		CAN-PB (n = 19)		GRA-PB (n = 11)		AGN-M (n = 43)	
			<i>Ho</i>	<i>He</i>	<i>Ho</i>	<i>He</i>	<i>Ho</i>	<i>He</i>	<i>Ho</i>	<i>He</i>	<i>Ho</i>	<i>He</i>	<i>Ho</i>	<i>He</i>	<i>Ho</i>	<i>He</i>
INRA011	26	196-250	0.22 (0.000) ^b	0.73	0.00	0.41	0.13 (0.000)	0.63	0.17 (0.000)	0.82	0.21 (0.000)	0.74	0.18 (0.000)	0.82	0.26 (0.000)	0.59
INRA040	25	166-258	0.17 (0.000)	0.80	0.50	0.70	0.26 (0.212)*	0.79	0.41 (0.000)	0.81	0.31 (0.000)	0.82	0.27 (0.000)	0.79	0.26 (0.000)	0.83
BM3517	14	100-138	0.45 (0.000)	0.82	0.50	0.62	0.57 (0.378)*	0.79	0.35 (0.006)	0.88	0.43 (0.000)	0.89	0.33 (0.000)	0.82	0.47 (0.001)	0.74
ILST030	14	142-181	0.22 (0.000)	0.79	0.38	0.73	0.38 (0.041)*	0.83	0.43 (0.000)	0.82	0.32 (0.000)	0.81	0.09 (0.000)	0.73	0.58 (0.000)	0.82
ILST028	14	111-164	0.35 (0.000)	0.57	0.25	0.67	0.58 (0.002)	0.53	0.45 (0.319)*	0.73	0.31 (0.000)	0.75	0.45 (0.000)	0.50	0.51 (0.232)*	0.72
UWCA46	17	97-140	0.52 (0.123)*	0.55	0.50	0.69	0.42 (0.036)*	0.87	0.11 (0.000)	0.76	0.29 (0.000)	0.85	0.09 (0.000)	0.76	0.40 (0.000)	0.74
TEXAN02	9	105-133	0.09 (0.068)*	0.12	0.50	0.68	0.21 (0.393)*	0.26	0.28 (0.198)*	0.62	0.37 (0.000)	0.74	0.27 (0.000)	0.64	0.30 (0.009)	0.61
ILST011	9	262-284	0.18 (0.000)	0.64	0.50	0.47	0.33 (1.000)*	0.57	0.46 (0.003)	0.69	0.35 (0.000)	0.68	0.38 (0.000)	0.72	0.74 (0.027)*	0.67
INRA023	12	191-217	0.13 (0.000)	0.49	0.38	0.41	0.17 (0.385)*	0.31	0.32 (0.005)	0.74	0.37 (0.000)	0.68	0.50 (0.000)	0.74	0.60 (0.011)*	0.74
SRCRSP9	18	106-137	0.52 (0.000)	0.79	0.88	0.84	0.54 (0.450)*	0.85	0.59 (0.000)	0.84	0.37 (0.000)	0.81	0.55 (0.000)	0.82	0.23 (0.001)	0.75
MHCIIR	14	193-228	0.39 (0.000)	0.81	0.25 (0.021)*	0.57	0.21 (0.000)	0.80	0.22 (0.000)	0.82	0.13 (0.000)	0.78	0.09 (0.000)	0.77	0.23 (0.000)	0.80
INRA006	19	95-137	0.30 (0.000)	0.78	0.25 (0.003)	0.74	0.58 (0.000)	0.89	0.59 (0.001)	0.82	0.39 (0.001)	0.67	0.45 (0.001)	0.83	0.51 (0.000)	0.77
IDVGA37	12	192-216	0.57 (0.000)	0.78	0.25 (0.000)	0.73	0.38 (0.000)	0.86	0.52 (0.000)	0.85	0.53 (0.000)	0.82	0.73 (0.131)*	0.85	0.51 (0.000)	0.75
Mean H	15.6		0.32 (0.000)	0.67	0.39 (0.000)	0.64	0.37 (0.000)	0.69	0.38 (0.000)	0.78	0.34 (0.000)	0.77	0.34 (0.000)	0.75	0.43 (0.000)	0.73
<i>ad</i>				7.1		4.5		7.9		9.0		7.8		7.1		9.3
<i>pa</i>				2		0		1		0		1		1		0

We verified the undefined position of AGN-M and confirmed it similarity to the UDB goats by calculating the F_{ST} values from AGN-M grouped with either the UDB goats or the exotic purebreds. In the first case, the F_{ST} value was lower and significant (unpublished data), so we grouped the AGN-M population with the UDB goats for the F-statistics analysis. The F-values (F_{IS} and F_{ST}) were significant for all populations and groupings (UDB, native and exotic breeds; $p < 0.01$) and the F_{IS} values were high and

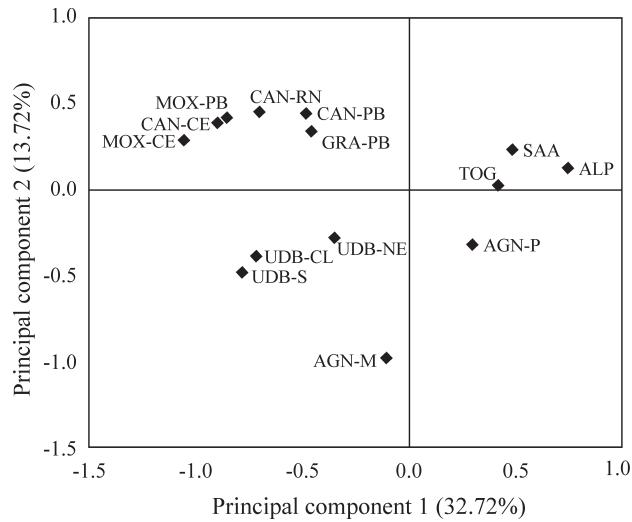


Figure 1 - Plot of scores of principal component analysis based on allele frequency of 14 populations of goats. 1: Moxotó Ceará (MOX-C); 2: Moxotó Paraíba (MOX-PB); 3: Canindé Ceará (CAN-CE); 4: Canindé Rio Grande do Norte (CAN-RN); 5: Canindé Paraíba (CAN-PB); 6: Graúna Paraíba (GRA-PB); 7: In absorbent crossing with Anglo-Nubian purebred (AGN-M); 8: Alpine and German Alpine (ALP); 9: Anglo-Nubian (AGN-P); 10: Toggenbourg (TOG); 11: Saanen (SAA); 12: northeastern undefined breed (UDB-NE); 13: middle-eastern undefined breed (UDB-CL); 14: southern undefined breed (UDB-S).

positive for all the populations while the F_{ST} value (0.105) was moderate (Table 3). When the F-values were estimated by grouping according to historical data, the values did not change considerably, the F_{IS} mean values being high and

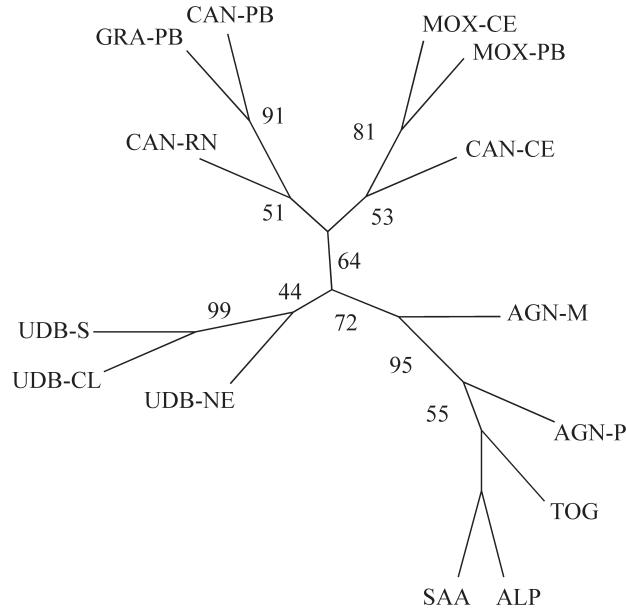


Figure 2 - Phenogram showing the relationship among 14 Brazilian goat populations using genetic distance of Reynolds based on 13 microsatellites loci and Neighbor-Joining method (Saitou and Nei, 1987). Numbers at nodes are the percentages of 1,000 bootstrap replicates in which these nodes appeared. This is an unrooted tree. 1: Moxotó Ceará (MOX-C); 2: Moxotó Paraíba (MOX-PB); 3: Canindé Ceará (CAN-CE); 4: Canindé Rio Grande do Norte (CAN-RN); 5: Canindé Paraíba (CAN-PB); 6: Graúna Paraíba (GRA-PB); 7: In absorbent crossing with Anglo-Nubian purebred (AGN-M); 8: Alpine and German Alpine (ALP); 9: Anglo-Nubian (AGN-P); 10: Toggenbourg (TOG); 11: Saanen (SAA); 12: northeastern undefined breed (UDB-NE); 13: middle-eastern undefined breed (UDB-CL); 14: southern undefined breed (UDB-S).

Table 3 - Estimates of F_{IS} and F_{ST} calculated by method of Weir and Cockerham (1984) based on allelic frequency of 14 goat populations, using the GDA program.

Locus	Only UDB F_{IS}	Only native F_{IS}	Only exotic purebred F_{IS}	F_{IS} to all the populations	Only UDB F_{ST}	Only native F_{ST}	Only exotic purebred F_{ST}	F_{ST} to all the populations
INRA011	0.567	0.778	0.555	0.620	0.112	0.033	0.031	0.110
INRA040	0.590	0.632	0.602	0.611	0.023	0.003	0.022	0.040
BM3517	0.515	0.480	0.288	0.401	0.044	0.013	0.107	0.095
ILST030	0.592	0.619	0.647	0.639	0.051	0.039	0.074	0.085
ILST028	0.258	0.350	0.262	0.288	0.054	0.243	0.054	0.152
UWCA46	0.477	0.597	0.433	0.491	0.115	0.154	0.080	0.147
TEXAN02	0.443	0.479	0.568	0.535	0.075	0.206	0.052	0.142
ILST011	0.083	0.468	0.211	0.239	0.096	0.061	0.048	0.115
INRA023	0.316	0.524	0.352	0.395	0.179	0.052	0.053	0.125
SRCRSP9	0.584	0.364	0.481	0.471	0.048	0.074	0.080	0.075
MHCIIDR	0.790	0.719	0.796	0.765	0.121	0.044	0.197	0.130
INRA006	0.525	0.444	0.714	0.587	0.073	0.078	0.067	0.093
IDVGA37	0.287	0.413	0.281	0.339	0.053	0.041	0.047	0.073
All loci	0.476	0.531	0.475	0.494	0.078	0.079	0.069	0.105

positive while the F_{ST} mean values were moderate (Table 3).

The AMOVA results for the goat populations without any structuring revealed that most of the total variation occurred within populations (88.51%; Table 4). The remainder variation (11.49%) was significantly different from zero ($F_{ST} = 0.1149$; $p < 0.01$) and resulted from differences among populations. When populations were structured according to historical data, most of the total variation was observed within populations (87.34%). The remaining percentages of variation (4.82% and 7.84%) were significantly different from zero and were attributed to differences among groups ($F_{CT} = 0.0482$; $p < 0.01$) and among populations within groups ($F_{SC} = 0.0824$; $p < 0.01$) respectively (Table 4).

Discussion

Heterozygosity values and significant deviations from HWE suggest a large number of homozygotes in the populations studied. Deviations from HWE at microsatellites loci have been reported in various studies and indicate departure from random mating (Luikart *et al.*; 1999; Laval *et al.*, 2000; Barker *et al.*, 2001). This deviation might be the result of inbreeding, but could also have been caused by the presence of null or non-amplified alleles, allele grouping defects, a sampling structure effect or selection against heterozygotes. Araújo *et al.* (2006) used the INRA006 and ILST011 markers to study the Alpine, Saanen and Moxotó breeds but did not detect any deviations from HWE. This fact could be due to differences in the frequency, number and type of alleles founded in the two investigations, possibly due to a sampling effect. Comparing the remaining loci for the same populations, most of the loci revealed no heterozygote deficit or excess in the study of Araújo *et al.* (2006) but our data indicated a deficit of heterozygotes. We believe that this divergence could have occurred because the remaining loci compared for the same breeds were different in the two studies, suggesting that the choice of different loci can produce different results.

Populations were subjected to PCA for primary structuring, which resulted in a pattern of three major groups

(Figure 1), which is consistent with historical data and the neighbor-joining phenogram. This structuring is comparable to that reported by Igarashi *et al.* (2000) when the same populations were studied with protein markers.

The F-statistics analysis was performed based on established structuring from both analyses and historical data. The F_{IS} statistic is a measure of the extent of genetic inbreeding within subpopulations and can range from -1.0 (all individuals heterozygous) to +1.0 (no observed heterozygotes), while F_{IT} is a measure of the mean reduction in heterozygosity of an individual relative to the total population (Wright, 1951; Weir and Cockerham, 1984). The F_{IS} values detected for either all the populations or for the three groups (UDB, naturalized and exotic purebred) ranged from 0.475 to 0.531 and were high and significant ($p < 0.01$). This indicates an excess of homozygotes due to a high level of inbreeding in the populations. However, Araújo *et al.* (2006) reported a different F_{IS} value (0.0252) when they assessed the Alpine, Saanen and Moxotó breeds. This divergence in results may be understood if we consider that most of the loci analyzed in the two investigations were different.

The F_{ST} value measures the degree of genetic differentiation between populations. Considering the interpretation of F_{ST} , it can be presumed that a value lying in the range 0 to 0.05 indicates little genetic differentiation, 0.05 to 0.15 indicates moderate differentiation, 0.15 to 0.25 a large degree of differentiation and values above 0.25 very great differentiation (Wright 1978; Hartl and Clark, 1997). The F_{ST} values identified for either all the populations or for the three groups fell in the range 0.05 to 0.15, indicating moderate genetic differentiation for both conditions. The F_{ST} value of 0.105 for all populations indicates that 10.5% of the total variability resulted from genetic differences between the populations while the remaining 89.5% was due to the high diversity between individuals within each population.

The AMOVA results without subgroups definition, or when considered a hierarchical structure, revealed genetic differentiation between the 14 populations. When the populations were unstructured the AMOVA F_{SC} value was 0.1149 (Table 4), indicating that 11.49% of the total varia-

Table 4 - AMOVA results for 14 populations of goats based on F_{ST} pairwise distance values using ARLEQUIN program. Populations were assigned according to historical data into three groups: (1) AGN-P, SAA, TOG and ALP; (2) MOX-CE, MOX-PB, CAN-CE, CAN-RN, CAN-PB and GRA-PB; (3) AGN-M, UDB-NE, UDB-CL and UDB-S.

Hierarchical structure	Groups composition	Proportion of variance		
		<i>Among populations</i> (F_{ST})	<i>Within populations</i>	
Not structured	(1) All populations	-	11.49% (0.1149; $p = 0.0000$)	88.51%
		<i>Among groups</i> (F_{CT})	<i>Among populations within groups</i> (F_{SC})	<i>Within populations</i> (F_{ST})
Structured (historical data)	(1) (2) (3)	4.82% (0.0482; $p = 0.0000$)	7.84% (0.0824; $p = 0.0000$)	87.34% (0.1266; $p = 0.000$)

tion could be attributed to differences between populations. This represents a moderate difference between populations and validates the F_{ST} value detected for all populations. When populations were structured according to historical data, the AMOVA confirmed that most (87.34%) of the total variation was caused by differences between individual animals within populations. The differentiation between populations within groups was higher than the differentiation between groups (Table 4), indicating that the UDB, naturalized or exotic purebred populations were highly differentiated.

The structuring seen in the phenogram confirmed the expected relationship of the populations (Figure 2). Igarashi *et al.* (2000) investigated these populations with protein markers and reported similar structuring. The grouping of the UDB populations with the exotic purebred populations can be explained by some crossbreeding (Igarashi *et al.*, 2000). Native and exotic breeds, including the Anglo-Nubian, may influence UDB populations, especially the UDB-NE and UDB-CL populations (Machado *et al.*, 2000).

The branching pattern within the three major groups also showed considerable similarity to the results described by Igarashi *et al.* (2000), the similarities being as follows: As expected, the UDB populations were grouped in the same branch since they indirectly belong to the same group; the MOX-CE and CAN-CE populations were grouped in a separate branch, either due to the fact that they are Brazilian naturalized breeds or due to a derivative process through the isolation of the local population (Igarashi *et al.*, 2000). According to Silva Neto (1950) the Moxotó breed may have already been brought from Portugal to Brazil in a standardized form; A branch with the TOG, ALP and SAA exotic purebred populations occurred. In this branch, the TOG population was set apart in a single branch, while the ALP and SAA populations were closer, probably reflecting the same origin (Igarashi *et al.*, 2000); and the exotic purebred AGN-P population was separated from the other populations. This fact can be explained because such a breed, unlike the others, does not have an essentially European origin, instead it is a European (English), Middle-Eastern (Nubian) and maybe Asian (Indian) synthetic goat breed (Jeffery, 1977). In contrast to Igarashi *et al.* (2000) and our PCA results, our AGN-M population was connected to the exotic purebreds via a single branch. However, F_{ST} analysis confirmed the similarity of the AGN-M population to the UDB populations.

Finally, the phenogram presented a branch including three populations, the Canindé and Graúna populations from the state of Paraíba and, more separately, another Canindé population from the state of Rio Grande do Norte. The clustering of these populations can be easily explained by the fact that they are regarded as populations of Brazilian naturalized breeds (Igarashi *et al.*, 2000). The CAN-PB and GRA-PB grouping reveals that the CAN-PB popula-

tion is less similar to the genetically conserved CAN-CE population. In some locations there are problems related to the crossing of goats and, due to lack of information about standardized characteristics, some farmers are making crossings based only on coat color. Since the CAN-PB population also presents a black coat as GRA-PB, we believe that this process may be occurring between the GRA-PB and CAN-PB populations, explaining the similarity among these populations. This highlights the importance of an official government role in the conservation of local goat breeds.

All the analyses showed consistency and reliability, and reproduced the geographic and genetic reports of the population studied. They established the genetic structure of the populations in three major groups and showed that the populations in these groups were highly differentiated due to high inbreeding, indicating that the preservation of these breeds and the genetic diversity among them is extremely important.

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Internet Resources

- FSTAT Software, <http://www.unil.ch/izea/softwares/fstat.html>.
- FUNDAÇÃO IBGE. Pesquisa Pecuária Municipal (PPM), <http://www.sidra.ibge.gov.br/> (February 10, 2006).
- GDA Software, <http://hydrodictyon.eeb.uconn.edu/people/plewis/software.php>.
- PCAGEN Software, <http://www2.unil.ch/popgen/softwares/pcagen.htm>.
- PHYLIP Software, <http://evolution.gs.washington.edu/phylip.html>.

Supplementary Material

- The following online material is available for this article:
Table S1.
This material is available as part of the online article from <http://www.scielo.br/gmb>
Associate Editor: Luiz Lehmann Coutinho

Table S1 – Allele Frequencies for the Polymorphic Loci for Each Goat population Sampled.

L o c u s	Allele	UDB-NE	UDB-CL	UDB-S	AGN-M	MOX-C	MOX-PB	CAN-C	CAN-RN	CAN-PB	GRA	ALP	SAA	AGN-P	TOG
INRA011	196	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.000	0.156	0.018
	198	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.013	0.000	0.156	0.000
	200	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.031	0.000	0.125	0.054
	202	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.018	0.100	0.063	0.036
	204	0.059	0.000	0.158	0.012	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.029	0.000	0.000
	206	0.059	0.219	0.184	0.023	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.063	0.000
	208	0.088	0.063	0.053	0.012	0.000	0.000	0.000	0.000	0.000	0.000	0.004	0.000	0.000	0.018
	210	0.059	0.188	0.053	0.012	0.000	0.000	0.000	0.034	0.000	0.000	0.000	0.000	0.000	0.000
	212	0.000	0.000	0.053	0.000	0.000	0.000	0.043	0.000	0.000	0.000	0.000	0.029	0.000	0.000
	214	0.147	0.000	0.000	0.000	0.022	0.000	0.000	0.000	0.000	0.091	0.000	0.029	0.094	0.000
	216	0.000	0.000	0.053	0.221	0.043	0.000	0.043	0.155	0.000	0.091	0.094	0.014	0.250	0.071
	218	0.206	0.063	0.053	0.000	0.109	0.000	0.087	0.034	0.263	0.091	0.174	0.186	0.000	0.054
	220	0.029	0.000	0.000	0.023	0.000	0.000	0.000	0.000	0.000	0.000	0.018	0.043	0.000	0.000
	222	0.088	0.156	0.289	0.593	0.022	0.125	0.239	0.017	0.053	0.045	0.045	0.000	0.000	0.018
	224	0.206	0.219	0.079	0.093	0.435	0.750	0.543	0.328	0.421	0.364	0.027	0.000	0.031	0.018
	226	0.059	0.031	0.026	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.027	0.057	0.000	0.125
	228	0.000	0.063	0.000	0.000	0.109	0.000	0.000	0.052	0.053	0.045	0.067	0.043	0.000	0.125
	230	0.000	0.000	0.000	0.000	0.239	0.000	0.000	0.000	0.000	0.000	0.031	0.086	0.000	0.143
	232	0.000	0.000	0.000	0.000	0.000	0.000	0.043	0.017	0.053	0.045	0.027	0.043	0.000	0.036
	236	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.103	0.053	0.000	0.027	0.014	0.000	0.000
	238	0.000	0.000	0.000	0.012	0.022	0.000	0.000	0.034	0.000	0.000	0.013	0.000	0.000	0.071
	240	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.155	0.079	0.091	0.009	0.100	0.000	0.071
	242	0.000	0.000	0.000	0.000	0.000	0.125	0.000	0.000	0.000	0.045	0.040	0.157	0.000	0.036
	244	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.034	0.026	0.000	0.156	0.071	0.000	0.071
	246	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.112	0.000	0.063	0.018
	250	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.034	0.000	0.091	0.049	0.000	0.000	0.018
INRA040	166	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.093	0.094	0.045	0.009	0.000	0.000	0.000
	172	0.000	0.000	0.000	0.000	0.000	0.043	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	196	0.063	0.031	0.053	0.107	0.000	0.000	0.000	0.000	0.063	0.045	0.004	0.043	0.000	0.018

197	0.000	0.125	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.085	0.057	0.000	0.018				
198	0.031	0.000	0.000	0.012	0.022	0.000	0.000	0.000	0.000	0.000	0.000	0.049	0.000	0.000	0.018				
202	0.000	0.000	0.026	0.012	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.013	0.000	0.067	0.000				
210	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.014	0.100	0.018				
214	0.063	0.156	0.053	0.012	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000				
216	0.063	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004	0.000	0.067	0.000				
222	0.000	0.125	0.132	0.000	0.022	0.000	0.065	0.000	0.000	0.000	0.000	0.027	0.029	0.067	0.000				
225	0.031	0.031	0.026	0.012	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.027	0.029	0.000	0.089				
226	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.085	0.114	0.000	0.054				
228	0.000	0.000	0.071	0.000	0.000	0.022	0.000	0.000	0.000	0.000	0.009	0.014	0.067	0.089					
230	0.094	0.031	0.026	0.012	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.018	0.029	0.000	0.161				
232	0.094	0.063	0.079	0.024	0.087	0.250	0.261	0.130	0.000	0.091	0.049	0.029	0.200	0.036					
234	0.188	0.031	0.105	0.333	0.283	0.188	0.283	0.204	0.250	0.273	0.080	0.100	0.033	0.036					
236	0.000	0.156	0.053	0.024	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.114	0.000	0.018					
238	0.219	0.094	0.053	0.083	0.043	0.000	0.043	0.111	0.000	0.000	0.027	0.229	0.133	0.179					
240	0.031	0.063	0.132	0.071	0.283	0.438	0.217	0.296	0.219	0.273	0.058	0.043	0.000	0.036					
242	0.094	0.094	0.132	0.179	0.174	0.125	0.022	0.000	0.156	0.045	0.152	0.114	0.100	0.071					
244	0.000	0.000	0.105	0.036	0.043	0.000	0.043	0.000	0.000	0.000	0.112	0.014	0.067	0.107					
246	0.031	0.000	0.026	0.012	0.043	0.000	0.000	0.148	0.031	0.227	0.080	0.029	0.067	0.000					
248	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.019	0.188	0.000	0.013	0.000	0.033	0.054					
256	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.036	0.000	0.000	0.000					
258	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.054	0.000	0.000	0.000					
BM3517	100	0.000	0.025	0.000	0.000	0.000	0.000	0.065	0.143	0.000	0.017	0.000	0.067	0.018					
	103	0.118	0.000	0.000	0.023	0.000	0.000	0.022	0.000	0.000	0.111	0.009	0.000	0.000	0.018				
	107	0.059	0.219	0.075	0.070	0.182	0.188	0.261	0.130	0.179	0.333	0.248	0.500	0.633	0.143				
	110	0.000	0.000	0.047	0.045	0.000	0.000	0.022	0.143	0.056	0.052	0.182	0.033	0.143					
	111	0.088	0.031	0.075	0.035	0.068	0.313	0.196	0.196	0.071	0.111	0.052	0.076	0.067	0.196				
	113	0.000	0.000	0.150	0.093	0.023	0.000	0.000	0.000	0.107	0.000	0.035	0.000	0.000	0.071				
	115	0.471	0.188	0.300	0.477	0.045	0.000	0.000	0.043	0.000	0.000	0.404	0.076	0.100	0.036				
	117	0.000	0.000	0.025	0.047	0.114	0.000	0.065	0.043	0.071	0.000	0.000	0.000	0.000	0.018				
	119	0.059	0.000	0.000	0.023	0.068	0.000	0.043	0.087	0.071	0.111	0.004	0.015	0.000	0.036				
	121	0.059	0.125	0.075	0.070	0.341	0.500	0.304	0.130	0.107	0.111	0.026	0.045	0.000	0.018				

	123	0.088	0.438	0.250	0.070	0.091	0.000	0.000	0.152	0.036	0.000	0.013	0.091	0.033	0.089
ILST030	128	0.059	0.000	0.025	0.047	0.023	0.000	0.022	0.022	0.036	0.111	0.083	0.015	0.067	0.214
	132	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.052	0.000	0.000	0.000
	138	0.000	0.000	0.000	0.000	0.000	0.000	0.087	0.109	0.036	0.056	0.004	0.000	0.000	0.000
	142	0.000	0.000	0.000	0.000	0.065	0.000	0.000	0.018	0.000	0.000	0.017	0.000	0.000	0.000
	150	0.000	0.000	0.158	0.035	0.109	0.000	0.188	0.250	0.289	0.455	0.000	0.029	0.000	0.000
	151	0.053	0.000	0.053	0.000	0.000	0.000	0.000	0.071	0.105	0.091	0.294	0.200	0.000	0.000
	155	0.053	0.000	0.026	0.070	0.022	0.125	0.000	0.000	0.053	0.000	0.063	0.086	0.000	0.054
	161	0.158	0.031	0.079	0.081	0.304	0.188	0.104	0.036	0.000	0.000	0.025	0.086	0.125	0.018
	163	0.211	0.000	0.132	0.256	0.000	0.063	0.208	0.018	0.053	0.045	0.324	0.329	0.000	0.464
	165	0.289	0.125	0.026	0.047	0.087	0.063	0.083	0.071	0.263	0.091	0.101	0.186	0.094	0.214
	167	0.000	0.250	0.053	0.256	0.087	0.000	0.063	0.143	0.053	0.182	0.067	0.029	0.063	0.107
	169	0.053	0.125	0.026	0.000	0.043	0.000	0.000	0.036	0.105	0.000	0.017	0.000	0.406	0.018
	170	0.105	0.188	0.105	0.023	0.283	0.438	0.250	0.286	0.053	0.091	0.017	0.029	0.000	0.018
	171	0.000	0.188	0.105	0.000	0.000	0.000	0.063	0.071	0.000	0.000	0.008	0.029	0.000	0.000
	173	0.079	0.031	0.237	0.174	0.000	0.000	0.042	0.000	0.000	0.045	0.021	0.000	0.250	0.089
	175	0.000	0.063	0.000	0.058	0.000	0.125	0.000	0.000	0.026	0.000	0.000	0.000	0.063	0.018
	181	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.046	0.000	0.000	0.000
ILST028	111	0.000	0.000	0.000	0.000	0.425	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	129	0.000	0.000	0.000	0.000	0.000	0.000	0.042	0.121	0.156	0.000	0.000	0.000	0.000	0.000
	130	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.013	0.029	0.031	0.018
	140	0.000	0.000	0.000	0.000	0.000	0.188	0.667	0.466	0.031	0.000	0.000	0.000	0.000	0.036
	141	0.706	0.531	0.639	0.384	0.500	0.500	0.000	0.052	0.313	0.136	0.134	0.114	0.438	0.125
	143	0.029	0.094	0.000	0.081	0.000	0.063	0.000	0.000	0.000	0.000	0.147	0.057	0.063	0.375
	145	0.029	0.000	0.056	0.035	0.000	0.000	0.000	0.069	0.000	0.000	0.042	0.043	0.000	0.018
	148	0.059	0.000	0.000	0.023	0.000	0.000	0.000	0.000	0.031	0.136	0.088	0.014	0.031	0.054
	150	0.088	0.031	0.139	0.337	0.025	0.188	0.083	0.138	0.344	0.682	0.134	0.271	0.094	0.179
	152	0.029	0.063	0.083	0.058	0.000	0.000	0.042	0.000	0.000	0.000	0.181	0.243	0.031	0.107
	154	0.059	0.031	0.000	0.023	0.000	0.000	0.000	0.069	0.063	0.000	0.004	0.086	0.281	0.000
	156	0.000	0.063	0.056	0.047	0.025	0.063	0.042	0.069	0.000	0.000	0.155	0.000	0.000	0.000
	158	0.000	0.063	0.028	0.012	0.025	0.000	0.125	0.000	0.063	0.045	0.071	0.100	0.031	0.089
	164	0.000	0.125	0.000	0.000	0.000	0.000	0.000	0.017	0.000	0.000	0.029	0.043	0.000	0.000

UWCA46	97	0.000	0.000	0.000	0.000	0.022	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	99	0.000	0.000	0.000	0.000	0.609	0.438	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	110	0.000	0.000	0.000	0.000	0.283	0.313	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	113	0.000	0.000	0.000	0.000	0.000	0.042	0.000	0.000	0.000	0.000	0.000	0.129	0.000	0.000	0.000
	114	0.206	0.250	0.079	0.047	0.043	0.125	0.125	0.018	0.029	0.000	0.000	0.000	0.000	0.000	0.000
	115	0.000	0.063	0.000	0.023	0.000	0.000	0.083	0.000	0.059	0.000	0.004	0.000	0.000	0.000	0.000
	117	0.324	0.313	0.368	0.128	0.000	0.000	0.188	0.339	0.176	0.273	0.214	0.129	0.094	0.268	
	118	0.088	0.094	0.289	0.000	0.000	0.063	0.042	0.089	0.118	0.091	0.021	0.029	0.000	0.054	
	119	0.029	0.000	0.000	0.442	0.000	0.063	0.188	0.143	0.147	0.000	0.000	0.000	0.000	0.000	0.000
	122	0.088	0.031	0.000	0.081	0.022	0.000	0.083	0.000	0.000	0.000	0.008	0.043	0.031	0.125	
	124	0.000	0.094	0.158	0.000	0.000	0.000	0.042	0.000	0.000	0.045	0.063	0.200	0.188	0.054	
	125	0.059	0.000	0.000	0.000	0.000	0.000	0.042	0.000	0.000	0.000	0.029	0.000	0.031	0.000	
	126	0.206	0.031	0.053	0.186	0.000	0.000	0.021	0.036	0.029	0.136	0.084	0.157	0.125	0.196	
	127	0.000	0.063	0.053	0.081	0.022	0.000	0.146	0.000	0.029	0.000	0.164	0.229	0.031	0.304	
	130	0.000	0.063	0.000	0.012	0.000	0.000	0.000	0.000	0.029	0.000	0.412	0.086	0.469	0.000	
	136	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.304	0.176	0.364	0.000	0.000	0.000	0.000	
	140	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.071	0.206	0.091	0.000	0.000	0.031	0.000	
TEXAN02	105	0.000	0.063	0.000	0.035	0.022	0.000	0.000	0.000	0.105	0.045	0.000	0.000	0.219	0.000	
	113	0.632	0.781	0.816	0.523	0.935	0.375	0.854	0.534	0.263	0.318	0.286	0.514	0.281	0.357	
	115	0.079	0.031	0.053	0.326	0.043	0.188	0.083	0.138	0.000	0.091	0.298	0.243	0.469	0.518	
	117	0.132	0.094	0.132	0.000	0.000	0.375	0.063	0.017	0.211	0.000	0.269	0.243	0.031	0.089	
	119	0.000	0.000	0.000	0.035	0.000	0.063	0.000	0.034	0.026	0.000	0.134	0.000	0.000	0.000	
	121	0.158	0.031	0.000	0.081	0.000	0.000	0.000	0.276	0.368	0.500	0.008	0.000	0.000	0.036	
	129	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.026	0.000	0.000	0.000	0.000	0.000	
	131	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004	0.000	0.000	0.000	
ILST011	133	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.045	0.000	0.000	0.000	0.000	0.000
	262	0.000	0.000	0.000	0.000	0.023	0.000	0.042	0.000	0.000	0.000	0.004	0.000	0.000	0.000	
	268	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.030	0.000	0.000	0.179	
	270	0.536	0.267	0.294	0.209	0.545	0.375	0.604	0.442	0.353	0.375	0.205	0.214	0.063	0.000	
	272	0.000	0.067	0.000	0.012	0.045	0.000	0.000	0.000	0.000	0.000	0.205	0.114	0.063	0.375	
	276	0.000	0.000	0.000	0.091	0.000	0.000	0.096	0.088	0.000	0.000	0.000	0.000	0.000	0.000	
	278	0.250	0.100	0.294	0.488	0.023	0.000	0.063	0.038	0.412	0.188	0.397	0.514	0.469	0.286	

	280	0.214	0.567	0.412	0.186	0.227	0.625	0.250	0.288	0.000	0.313	0.111	0.100	0.406	0.125		
	282	0.000	0.000	0.000	0.105	0.045	0.000	0.042	0.000	0.000	0.063	0.047	0.057	0.000	0.036		
	284	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.135	0.147	0.063	0.000	0.000	0.000	0.000		
INRA023	191	0.000	0.000	0.000	0.012	0.000	0.000	0.000	0.000	0.053	0.000	0.021	0.000	0.000	0.107		
	195	0.000	0.000	0.000	0.000	0.043	0.000	0.000	0.000	0.000	0.000	0.013	0.029	0.094	0.018		
	197	0.563	0.917	0.947	0.384	0.674	0.750	0.826	0.411	0.526	0.450	0.218	0.271	0.031	0.214		
	199	0.219	0.000	0.053	0.140	0.239	0.125	0.087	0.143	0.000	0.100	0.357	0.229	0.063	0.125		
	201	0.031	0.000	0.000	0.291	0.000	0.000	0.000	0.089	0.053	0.050	0.000	0.043	0.156	0.036		
	203	0.094	0.083	0.000	0.081	0.000	0.000	0.022	0.000	0.000	0.000	0.004	0.000	0.344	0.000		
	205	0.000	0.000	0.000	0.000	0.022	0.063	0.000	0.089	0.132	0.200	0.000	0.057	0.125	0.089		
	207	0.031	0.000	0.000	0.023	0.000	0.000	0.043	0.000	0.000	0.050	0.034	0.000	0.000	0.071		
	211	0.000	0.000	0.000	0.012	0.000	0.000	0.000	0.000	0.000	0.000	0.059	0.043	0.031	0.071		
	213	0.063	0.000	0.000	0.058	0.022	0.063	0.022	0.232	0.132	0.050	0.206	0.314	0.063	0.268		
	215	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.053	0.050	0.059	0.014	0.063	0.000		
	217	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.036	0.053	0.050	0.029	0.000	0.031	0.000		
SRCRSP9	106	0.000	0.000	0.000	0.012	0.239	0.250	0.021	0.052	0.000	0.000	0.000	0.000	0.000	0.000		
	109	0.000	0.000	0.000	0.000	0.152	0.188	0.042	0.017	0.000	0.000	0.000	0.000	0.000	0.000		
	110	0.028	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.129	0.000	0.125		
	111	0.000	0.000	0.000	0.000	0.022	0.125	0.063	0.190	0.158	0.091	0.000	0.014	0.000	0.000		
	115	0.000	0.000	0.000	0.070	0.000	0.000	0.000	0.017	0.000	0.000	0.059	0.000	0.031	0.000		
	117	0.000	0.000	0.025	0.000	0.000	0.000	0.000	0.017	0.000	0.045	0.050	0.000	0.406	0.000		
	118	0.056	0.000	0.050	0.000	0.000	0.125	0.000	0.000	0.000	0.045	0.063	0.014	0.000	0.036		
	120	0.000	0.000	0.025	0.023	0.239	0.000	0.042	0.017	0.053	0.000	0.000	0.014	0.063	0.018		
	122	0.000	0.031	0.125	0.012	0.087	0.125	0.042	0.017	0.026	0.045	0.008	0.000	0.031	0.000		
	123	0.139	0.094	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.029	0.157	0.375	0.339		
	124	0.194	0.063	0.350	0.047	0.000	0.000	0.125	0.052	0.289	0.318	0.105	0.171	0.000	0.107		
	125	0.000	0.031	0.000	0.000	0.261	0.125	0.000	0.000	0.000	0.000	0.092	0.086	0.000	0.071		
	126	0.111	0.406	0.300	0.430	0.000	0.000	0.125	0.138	0.053	0.227	0.143	0.143	0.031	0.143		
	128	0.250	0.063	0.050	0.163	0.000	0.000	0.104	0.207	0.026	0.045	0.290	0.029	0.000	0.089		
	129	0.000	0.000	0.025	0.035	0.000	0.000	0.063	0.034	0.105	0.091	0.038	0.086	0.000	0.036		
	135	0.194	0.219	0.025	0.174	0.000	0.000	0.083	0.000	0.053	0.045	0.029	0.043	0.063	0.000		
	136	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.029	0.029	0.000	0.000		

MHCIIR	137	0.028	0.094	0.025	0.035	0.000	0.063	0.292	0.241	0.237	0.045	0.063	0.086	0.000	0.036					
	193	0.000	0.000	0.000	0.000	0.000	0.063	0.083	0.333	0.367	0.136	0.013	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
	194	0.053	0.000	0.000	0.000	0.000	0.125	0.063	0.074	0.100	0.000	0.000	0.000	0.000	0.000	0.000	0.018			
	198	0.526	0.233	0.053	0.244	0.174	0.625	0.292	0.111	0.167	0.273	0.622	0.600	0.000	0.143					
	200	0.000	0.000	0.000	0.047	0.000	0.000	0.042	0.000	0.000	0.000	0.026	0.000	0.156	0.018					
	205	0.000	0.200	0.000	0.093	0.000	0.000	0.000	0.037	0.067	0.000	0.013	0.000	0.563	0.000					
	207	0.053	0.000	0.000	0.314	0.109	0.000	0.000	0.000	0.000	0.000	0.057	0.043	0.063	0.000					
	208	0.263	0.300	0.658	0.128	0.196	0.063	0.292	0.167	0.200	0.273	0.052	0.029	0.094	0.071					
	210	0.000	0.000	0.000	0.000	0.043	0.000	0.000	0.000	0.000	0.000	0.043	0.014	0.000	0.000					
	214	0.053	0.133	0.132	0.105	0.304	0.000	0.125	0.111	0.033	0.091	0.030	0.171	0.000	0.268					
	216	0.000	0.067	0.105	0.023	0.087	0.000	0.000	0.093	0.000	0.227	0.061	0.029	0.063	0.393					
	218	0.000	0.000	0.000	0.012	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.071	0.063	0.036					
	224	0.000	0.000	0.000	0.012	0.022	0.125	0.063	0.019	0.000	0.000	0.004	0.000	0.000	0.000					
	225	0.053	0.067	0.053	0.023	0.022	0.000	0.042	0.037	0.067	0.000	0.009	0.000	0.000	0.054					
	228	0.000	0.000	0.000	0.000	0.043	0.000	0.000	0.019	0.000	0.000	0.070	0.043	0.000	0.000					
INRA006	95	0.053	0.000	0.075	0.000	0.217	0.125	0.104	0.000	0.528	0.091	0.004	0.000	0.000	0.000					
	103	0.000	0.000	0.000	0.198	0.000	0.000	0.000	0.000	0.000	0.045	0.017	0.000	0.000	0.018					
	105	0.026	0.031	0.125	0.058	0.043	0.000	0.000	0.034	0.000	0.000	0.029	0.000	0.375	0.000					
	107	0.263	0.188	0.025	0.419	0.000	0.000	0.042	0.121	0.000	0.000	0.008	0.014	0.031	0.125					
	108	0.000	0.000	0.000	0.012	0.000	0.000	0.000	0.000	0.000	0.000	0.050	0.071	0.094	0.286					
	109	0.368	0.156	0.300	0.070	0.370	0.375	0.125	0.362	0.028	0.136	0.084	0.057	0.000	0.125					
	111	0.000	0.000	0.075	0.023	0.065	0.000	0.000	0.017	0.000	0.000	0.013	0.000	0.063	0.000					
	113	0.026	0.063	0.075	0.012	0.000	0.000	0.083	0.121	0.139	0.318	0.042	0.086	0.063	0.000					
	114	0.000	0.000	0.000	0.070	0.000	0.000	0.000	0.000	0.000	0.000	0.092	0.286	0.000	0.071					
	115	0.132	0.188	0.150	0.058	0.065	0.000	0.063	0.017	0.000	0.091	0.256	0.043	0.063	0.000					
	116	0.000	0.000	0.000	0.000	0.000	0.250	0.000	0.000	0.000	0.000	0.067	0.171	0.063	0.071					
	117	0.026	0.188	0.050	0.047	0.000	0.063	0.042	0.000	0.028	0.091	0.181	0.057	0.063	0.214					
	119	0.000	0.188	0.075	0.012	0.000	0.000	0.104	0.086	0.167	0.136	0.063	0.186	0.188	0.036					
	121	0.105	0.000	0.000	0.012	0.065	0.188	0.188	0.052	0.000	0.091	0.050	0.029	0.000	0.018					
	123	0.000	0.000	0.050	0.012	0.000	0.000	0.021	0.017	0.000	0.000	0.021	0.000	0.000	0.000					
	125	0.000	0.000	0.000	0.000	0.000	0.000	0.021	0.103	0.056	0.000	0.008	0.000	0.000	0.036					
	127	0.000	0.000	0.000	0.000	0.000	0.000	0.146	0.034	0.000	0.000	0.000	0.000	0.000	0.000					

	135	0.000	0.000	0.000	0.000	0.152	0.000	0.042	0.017	0.028	0.000	0.008	0.000	0.000	0.000	0.000
	137	0.000	0.000	0.000	0.000	0.022	0.000	0.021	0.017	0.028	0.000	0.004	0.000	0.000	0.000	0.000
IDVGA37	192	0.000	0.000	0.000	0.000	0.000	0.000	0.238	0.000	0.000	0.045	0.141	0.014	0.000	0.000	0.000
	194	0.000	0.000	0.025	0.012	0.043	0.000	0.000	0.017	0.132	0.091	0.021	0.000	0.000	0.000	0.000
	196	0.000	0.000	0.000	0.000	0.196	0.063	0.048	0.017	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	198	0.000	0.125	0.050	0.073	0.326	0.125	0.024	0.224	0.158	0.182	0.043	0.014	0.031	0.036	
	200	0.026	0.156	0.275	0.000	0.000	0.000	0.000	0.138	0.132	0.000	0.085	0.114	0.281	0.286	
	202	0.132	0.000	0.000	0.037	0.000	0.000	0.119	0.017	0.079	0.045	0.073	0.243	0.219	0.089	
	204	0.105	0.125	0.050	0.012	0.022	0.125	0.167	0.138	0.316	0.227	0.021	0.157	0.031	0.089	
	206	0.132	0.000	0.125	0.061	0.043	0.000	0.071	0.086	0.053	0.045	0.107	0.157	0.000	0.286	
	208	0.158	0.156	0.050	0.341	0.043	0.188	0.071	0.103	0.026	0.182	0.338	0.286	0.250	0.161	
	210	0.132	0.281	0.350	0.329	0.239	0.438	0.143	0.190	0.000	0.091	0.056	0.000	0.188	0.054	
	212	0.026	0.000	0.050	0.024	0.000	0.000	0.048	0.017	0.026	0.000	0.090	0.000	0.000	0.000	
	216	0.289	0.156	0.025	0.110	0.087	0.063	0.071	0.052	0.079	0.091	0.026	0.014	0.000	0.000	