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Genetic variability analysis of 26 sheep breeds in the Czech Republic

Karolína Machová[a*], Barbora Hofmanová[a], Jana Rychtářová[b], Luboš Vostrý[a], Nina Moravčíková[c], Radovan Kasarda[c]

[a] *Czech University of Life Sciences, Faculty of Agrobiology, Food and Natural Resources, Prague – Suchdol, Czech Republic*

[b] *Institute of Animal Science, Prague – Uhříněves, Czech Republic*

[c] *Slovak University of Agriculture in Nitra, Slovak Republic*

In this study, the intra- and inter-population level of genetic diversity of 26 transboundary and local sheep breeds reared in the Czech Republic was analysed. A total of 14,999 animals genotyped for 11 microsatellite markers were included to describe the gene pool of the breeds. The level of genetic diversity was derived from the proportion of heterozygous animals among and within breeds. The average polymorphic information content (0.745) and Shannon's index (1.361) showed a high genetic variability of the applied set of genetic markers. The average observed heterozygosity (0.683 ± 0.009), as well as F_{IS} index (-0.025 ± 0.004), pointed to a sufficient proportion of heterozygotes concerning the loss of genetic diversity. The deficit of heterozygotes was most evident in Cameroon sheep (F_{IS} = 0.036). The Nei's genetic distances and Wright's F_{ST} indexes showed that the analysed breeds are genetically differentiated to separate clusters with Cameroon sheep as the most genetically distant breed. Individual variation accounted for 83.2 % of total diversity conserved across breeds, whereas 16.8 % of genetic similarity resulted from the inter-population reduction in heterozygosity.

Keywords: microsatellite analysis, genetic diversity, sheep, transboundary and local breed

1 Introduction

Ancient European sheep population was created through two main immigration events from Southwest Asia during the 4th and 5th millennium B.P.. During the first one, primitive breeds came in, which were pushed out and crossed by breeds specialised on the secondary production in the second wave (Chessa et al., 2009). Along with the development of society and agriculture, more productive sheep have been bred and then spread during the European colonisation over the world (Taberlet et al., 2008). Two centuries ago, a great turnout of breeding practices occurred, when bigger selection affords started unifying many populations into breed standards (Taberlet et al., 2008). This selection pressure is now even enhanced by modern reproductive biotechnologies (Taberlet et al., 2008). Nevertheless, artificial insemination with frozen-thawed semen is not widely used in sheep so far (Faigl et al., 2012; Raoul and Elsen, 2020). Current inter- and intra-continental transmission of livestock genotypes still accelerates in the direction from developed to developing countries. Higher sheep products demand initiates breeding of high-yielding sheep breeds, and their commercial use all over the world threatens local genetic sources (FAO, 2007).

Transboundary breeds are usually not endangered by low numbers of individuals or population fragmentation. However, they could be threatened by the loss of genetic diversity as well as

* **Corresponding author**: Karolína Machová. Czech University of Life Sciences, Faculty of Agrobiology, Food and Natural Resources, Department of Genetic and Breeding, Kamýcká 129,165 00 Praha 6 – Suchdol, Czech Republic. E-mail: machovakarolina@af.czu.cz

indigenous breeds. Assessment of their genetic variability could identify more valuable animals or lineages for breeding. In the Czech Republic, there are 28 FAO registered transboundary sheep from a total of 36 registered breeds (FAO, 2020). After the year 1989, most of the breeds imported from western Europe were bred with local populations by absorbent crossing. Czech populations of the same breeds could be so quite genetically distant from western populations and more diverse in comparison to western countries. This study aimed to investigate the genetic diversity through microsatellite (STR) markers analysis of sheep breeds in the Czech Republic.

2 Material and methods

2.1 Animal sampling and molecular analysis

Data were from parentage testing, which was going on in the Czech Republic from 2010 to 2015. The original dataset consisted of 15,041 animals representing 30 sheep breeds. Four of them were excluded from the analysis due to the low number of animals (<25). The reduced dataset included 14,999 individuals from 26 breeds: Alpine (AL, n = 106), Berrichon du Cher (BE, n = 251), Cameroon (CA, n = 225), Clun Forest (CF, n = 364), Dorper (DP, n = 34), East Frisian (EF, n = 491), German Black-headed (GB, n = 88), German Grey Heath (GG, n = 297), Hampshire (HA, n = 116), Charollais (CH, n = 764), Jacob (JA, n = 40), Kent (KE, n = 1,288), Kerry Hill (KH, n = 59), Lein (LE, n = 37), Lacaune (LA, n = 1,085), Merinolandschaf (ML, n = 324), Oxford Down (OD, n = 458), Ouessant (OU, n = 88), Romanov (RO, n = 764), Sumava (SU, n = 474), Skudde (SD, n = 31), Shetland (SH, n = 54), Suffolk (SF, n = 5,343), Valachian (VA, n = 340), Texel (TE, n = 1,269), and Zwartbles (ZW, n = 609).

The minimum animal genotyping call rate for STR markers was set to 99.5%. Of the 25 STR markers used in parentage testing, only 11 (CSRD247, D5S2, INRA005, INRA063, MAF065, MAF209, MAF214, MCM527, OARCP049, OARFCB020, and SPS115) met this threshold. Except for SPS115, all listed STR markers are recommended by ISAG/FAO for parentage testing in sheep.

2.2 Statistical analysis

Most of the basic genetic diversity estimators including the effective number of alleles, observed heterozygosity, expected heterozygosity, mean number of alleles per locus, Wright's F statistics and Shannon's information index were computed using GenAlEx 6.5 (Peakall and Smouse, 2006; Peakall and Smouse, 2012). Polymorphic information content was calculated by Cervus 3.0.7 (Kalinowski et al., 2007). Test of Hardy-Weinberg equilibrium was performed in the internet version of GENEPOP (Raymond and Rousset, 1995; Rousset, 2008) by Markov Chain Monte Carlo method (dememorisation 1,000, batches 100, iterations per batch 5,000). Subsequently, Wright's F_{ST} index according to Weir and Cockerham (1984), Nei's standard genetic distance described by Nei (1978) and G_{ST} as an analogue to F_{ST} adjusted for bias were calculated by GenAlex 6.5 (Peakall and Smouse, 2006; Peakall and Smouse, 2012). The F_{ST} and G_{ST} were calculated using 999 permutations and 1,000 bootstraps.

3 Results and discussion

In this study, 26 sheep breeds reared in the Czech Republic were investigated through STR markers analysis. A total of 180 alleles across the 11 analysed STR markers were detected. All of them indicated deviation from Hardy-Weinberg equilibrium (Table 1), which signalises a high impact of factors such as migration, gene flow or relatives mating on the genetic variability conserved in the dataset. Evaluation of each locus in concrete population revealed that less than 26 % of deviations were significant ($P < 0.05$) (data not shown). The number of alleles per locus ranged from 8 (D5S2) to 27 (OARCP049) (data not shown). All the studied loci were polymorphic in each breed, except for locus CSRD247 in DP population (data not shown). Only 27 private alleles were found in 16 breeds, 10 of them exceeded more than 0.5 % frequency. The highest frequency of private alleles, approximately 45 %, was detected in LA. The highest number of private alleles (5) was reported for loci INRA063 and OARCB020 (data not shown).

The mean number of alleles ranged from 3.727 (KH) to 12.273 (SF) (Table 2). Mean number of alleles per breed was similar to the study of Tolone et al. (2012), who analysed Comisana, Pinzirita, Sarda and Valle del Belice Sicilian breeds and reported values from 5.66 to 9.44. Mean number of alleles per locus across analysed breeds was also in agreement with the study of Naqvi et al. (2017) in Pakistan breeds (5.73 to 7.62), Othman et al. (2016) in local Egyptian breeds (5.82 to 8.18) and Loukovitis et al. (2016) in 13 local Greek breeds (4.59 to 7.34).

Informativeness of surveyed loci and breeds was evaluated through Shannon's information index and polymorphic information content (Table 1). Shannon's information index is not so widely used for genetic diversity as for ecology diversity measures possibly due to its difficult interpretation (Hennink and Zeven, 1990). Generally, it reflects the level of genetic markers effectiveness and genetic diversity inside the population (Moravčíková et al., 2016). The average Shannon's information index across loci showed informativeness at level 1.361. Similarly, the polymorphic information content pointed to the high level of polymorphisms across analysed STR markers, and only MAF214 showed a value lower than 0.5.

Average expected heterozygosity over loci ranged from 0.491 (MAF214) to 0.754 (OARFCB020) (Table 1). The highest average expected heterozygosity was observed for SU (0.790) and the lowest for CA (0.509) (Table 2). Similarly, the observed heterozygosity was the highest for SU (0.792) and the lowest for CA (0.493). The fact that SU breed had the greatest heterozygosity is quite surprising. SU is one of the Czech autochthonous breeds and has been included in the program of Czech genetic reserves since 1992, and therefore no hybrids should appear in the studbook since then. This indicates that even if the gene pool of SU is limited by small population size, its management is better compared to evaluated transboundary breeds. Except for CA, GG, CH, OU, RO, and SF, the expected heterozygosity was lower than the observed (Table 2). The level of heterozygosity within breeds was in agreement with previous studies in different sheep breeds (Peter et al., 2007; Jyotsana et al., 2010; Jawasreh et al., 2018; Bravo et al., 2019). In general, the results showed that the heterozygosity across and within breeds was sufficient concerning the potential loss of genetic diversity in the next generations.

Table 1 Mean number of alleles (MNA), effective number of alleles (N_E), Shannon's information index (*I*), polymorphic information content (PIC), observed (H_O) and expected heterozygosity (H_E), F_{IS} index, 95 % confidence interval (F_{IS} 95 %), and Hardy-Weinberg equilibrium (HWE) computed for each locus

Locus	MNA	N_E	*I*	PIC	H_O	H_E	F_{IS}	F_{IS} 95 %	HWE
CSRD247	7.077	2.798	1.142	0.645	0.592	0.582	-0.011	-0.039; 0.041	***
D5S2	4.308	2.640	1.077	0.580	0.624	0.602	-0.034	-0.064; 0.04>	***
INRA005	8.962	4.273	1.612	0.840	0.739	0.736	-0.004	-0.021; 0.025	***
INRA063	8.692	3.611	1.474	0.777	0.720	0.698	-0.032	-0.056; 0.036	***
MAF065	5.731	3.070	1.256	0.758	0.676	0.656	-0.031	-0.056; 0.035	***
MAF209	7.692	3.689	1.454	0.802	0.700	0.680	-0.026	-0.052; 0.040	***
MAF214	4.923	2.214	0.891	0.452	0.500	0.491	-0.018	-0.041; 0.035	***
MCM527	6.000	3.336	1.319	0.773	0.689	0.669	-0.032	-0.060; 0.043	***
OARCP049	9.692	4.561	1.669	0.876	0.773	0.749	-0.034	-0,056; 0.034	***
OARFCB020	8.192	4.360	1.606	0.850	0.776	0.754	-0.029	-0.045; 0.024	***
SPS115	7.346	3.893	1.471	0.841	0.724	0.707	-0.021	-0.052; 0.048	***
Mean	7.147	3.495	1.361	0.745	0.683	0.666	-0.025		
Standard error	0.187	0.080	0.023	0.038	0.009	0.008	0.004		

*** = P < 0.001

Table 2 Number of individuals (N), mean number of alleles (MNA), effective number of alleles (N_E), Shannon's information index (*I*), observed (H_O) and expected (H_E) heterozygosity, and F_{IS} index computed for each sheep breed

Breed	N	MNA	N_E	I	H_O	H_E	F_{IS}
AL	106	5.091	3.218	1.305	0.738	0.671	-0.096
BE	251	6.909	3.264	1.319	0.682	0.662	-0.028
CA	225	5.545	2.280	0.987	0.493	0.509	0.036
CF	364	6.545	3.352	1.324	0.658	0.653	-0.005
DP	34	4.636	3.123	1.181	0.628	0.614	-0.021
EF	491	6.182	2.439	1.080	0.558	0.556	-0.002
GB	88	7.636	3.997	1.476	0.736	0.703	-0.049
GG	297	8.000	4.013	1.533	0.723	0.725	0.001
HA	116	6.909	4.015	1.486	0.726	0.702	-0.036
CH	764	9.636	3.685	1.508	0.694	0.698	0.004
JA	40	4.636	2.892	1.171	0.625	0.612	-0.019
KE	1,288	9.636	4.117	1.547	0.714	0.711	-0.003
KH	59	3.727	2.571	1.032	0.630	0.572	-0.094
LE	37	4.636	2.906	1.167	0.683	0.610	-0.110
LA	1,085	10.000	4.522	1.653	0.744	0.735	-0.012
ML	324	10.000	4.552	1.676	0.766	0.759	-0.009
OD	458	7.000	3.449	1.345	0.694	0.680	-0.018
OU	88	4.818	3.073	1.208	0.634	0.649	0.022
RO	764	7.727	3.571	1.373	0.675	0.680	0.008
SU	474	10.273	5.024	1.810	0.792	0.790	-0.002
SD	31	4.364	2.862	1.141	0.654	0.608	-0.075
SF	5,343	12.273	3.783	1.469	0.672	0.673	0.001
SH	54	5.727	3.763	1.434	0.785	0.717	-0.094
TE	1,269	9.000	3.221	1.375	0.674	0.667	-0.011
VA	340	8.273	3.777	1.495	0.732	0.715	-0.024
ZW	609	6.636	3.403	1.292	0.649	0.641	-0.009

AL – Alpine; BE - Berrichon du Cher; CA – Cameroon; CF – Clun Forest; DP – Dorper; EF – East Frisian; GB – German Black-headed; GG – German Grey Heath; HA – Hampshire; CH – Charollais; JA – Jacob; KE – Kent; KH - Kerry Hill; LE – Lein; LA – Lacaune; ML – Merinolandschaf; OD – Oxford Down; OU – Ouessant; RO – Romanov; SU – Sumava; SD – Skudde; SH – Shetland; SF – Suffolk; VA – Valachian; TE – Texel; ZW – Zwartbles

The average F_{IT} value (0.146) showed the prevalence of homozygotes in the analysed dataset (Table 3). However, the F_{IS} values indicated that at the intra-population level most of the breeds were not significantly affected by inbreeding (mean F_{IS} = -0.025) (Table 2). Only six breeds (CA, GG, CH, OU, RO, and SF) showed a slight deficiency of heterozygotes, with CA exhibiting the strongest decrease of heterozygosity (F_{IS} = 0.036) (Table 2). Such value close to zero could be hardly considered as inbreeding. More interesting is that most of the F_{IS} values were negative (Table 2), similarly to the study of Niu et al. (2012). This point to prevailing outcrossing within breeds.

The genetic differences among breeds were quite remarkable, according to average F_{ST} (0.168) and G_{ST} (0.164) (Table 3). Individual variation affected 83.2% of total diversity, and 16.8% of genetic similarity was caused by inter-population reduction in heterozygosity. Genetic differentiation among the analysed breeds was higher than that reported in five Moroccan sheep breeds (3.6%; Gaouar et

al., 2016), Saudi Arabia sheep (3.6 %; Mahmoud et al., 2020), three Colombian indigenous sheep (5.4 %; Ocampo et al., 2017) and 10 Iranian fat-tailed breeds (2 %; Vahidi et al., 2016). Our results are similar to values reported for breeds reared in Kosovo and Albania (13.9 %; Hoda and Bytyqi, 2017), Namaqua Afrikaner sheep from South Africa (10.6 %; Qwabe et al., 2013), or to a comparative study focused on Punjab Urial sheep (15.9 %; Pichler et al., 2017).

Table 3 Wright's F statistics and Nei's G_{ST}

Locus	F_{IS}	F_{IT}	F_{ST}	G_{ST}
CSRD247	-0.017	0.224	0.237	0.234
D5S2	-0.035	0.122	0.152	0.148
INRA005	-0.003	0.160	0.163	0.159
INRA063	-0.032	0.127	0.154	0.151
MAF065	-0.030	0.139	0.164	0.161
MAF209	-0.030	0.136	0.161	0.157
MAF214	-0.018	0.162	0.177	0.174
MCM527	-0.030	0.139	0.164	0.161
OARCP049	-0.032	0.134	0.160	0.157
OARFCB020	-0.029	0.106	0.131	0.128
SPS115	-0.025	0.161	0.181	0.178
Mean	-0.026	0.146	0.168	0.164
Standard error	0.003	0.009	0.008	0.025

Table 5 Comparison of pairwise F_{ST} between the same breeds in the present study (CZ) and in the Hungarian study (HU) of Neubauer et al. (2015)

Breeds	CZ	HU
CH vs. LA	0.047	0.730
CH vs. ML	0.058	0.118
CH vs. GB	0.052	0.076
CH vs. SF	0.054	0.084
CH vs. TE	0.059	0.149
LE vs. ML	0.082	0.067
LE vs. GB	0.050	0.051
LE vs. SF	0.052	0.066
LE vs. TE	0.060	0.071
ML vs. GB	0.041	0.094
ML vs. SF	0.054	0.099
ML vs. TE	0.063	0.122
GB vs. SF	0.049	0.052
GB vs. TE	0.054	0.096
SF vs. TE	0.065	0.111

GB – German Black-headed; CH – Charollais; LA – Lacaune; LE – Lein; ML – Merinolandschaf; SF – Suffolk; TE – Texel

Pairwise F_{ST} values among all breeds are reported in Table 4 (see page 46). The F_{ST} showed that, overall, LA, SU, and ML are less distinctive than any other breed. Neubauer et al. (2015) studied genetic diversity of CH, LA, ML, GB, SF, and TE breeds based on STR markers and they reported

different genetic relationships among breeds compared to our study (e.g. CH vs. TE). A full comparison is provided in Table 5.

According to Nei's genetic distances (Table 4, see page 45), the highest genetic similarity was found between ML and LA breeds (0.179), while the genetically most distant breeds were ZW and CA (1.838). The CA seems the most distant to other breeds followed by SD, OU and DP. However, results should be interpreted with caution because some genotypes were missing (8 % in KH, locus D5S2; 25 % in OU, locus MCM527; 25 % SU, locus MCM527). Jawasreh et al. (2018) observed similar genetic distances for SF vs. RO (0.42), but different for CH vs. SF (0.41) and RO vs. CH (0.24). Nevertheless, this could be caused by a partially divergent set of STR markers.

4 Conclusions

In summary, this study through 11 highly polymorphic STR markers revealed good genetic management in most of the studied sheep breeds. Negative values of Wright's fixation indexes indicated breeding of genetically distant animals or exchange of unrelated individuals between populations and farms. Only CA, GG, CH, OU, RO, and SF breeds deviated from this scheme. For these populations, it would be beneficial to reconsider existing breeding schemes or introduce genetic material from abroad. Analysed breeds were genetically distinguishable from each other. However, some of them (LA, SF, and ML) exhibited a high level of similarity. Generally, the monitored breeds showed sufficient genetic variability that reflects correct breeding practices in particular farms. However, it is necessary to consider that the genotyping data come from parentage testing (production of breeding rams), which may bias the overall view on the gene pool of selected breeds in the Czech Republic.

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Table 4 Values of F_{ST} (below diagonal) and Nei's genetic distance (above diagonal). AL - Alpine; BE - Berrichon du Cher; CA - Cameroon; CF - Clun Forest; DP – Dorper; EF - East Frisian; GB - German Black-headed; GG - German Grey Heath; HA – Hampshire; CH – Charollais; JA - Jacob; KE - Kent; KH - Kerry Hill; LE – Lein; LA – Lacaune; ML – Merinolandschaf; OD - Oxford Down; OU - Ouessant; RO - Romanov; SU – Sumava; SD - Skudde; SH - Shetland; SF – Suffolk; VA – Valachian; TE – Texel; ZW – Zwartbles

AL	BE	CA	CF	DP	EF	GB	GG	HA	CH	JA	KE	KH	LE	LA	ML	OD	OU	RO	SU	SD	SF	SH	TE	VA	ZW	
0.000	0.473	1.013	0.511	0.671	0.694	0.426	0.424	0.449	0.511	0.463	0.546	0.768	0.629	0.418	0.415	0.618	0.601	0.584	0.488	0.785	0.491	0.447	0.428	0.532	0.610	AL
0.085	0.000	0.790	0.487	0.691	0.573	0.387	0.528	0.422	0.522	0.592	0.518	0.626	0.522	0.360	0.320	0.555	0.832	0.427	0.408	0.740	0.577	0.460	0.399	0.606	0.670	BE
0.184	0.162	0.000	0.905	0.738	0.828	0.949	0.395	0.997	1.025	0.771	0.844	0.686	1.117	0.667	0.522	0.948	1.173	0.715	0.604	0.733	0.934	0.796	1.069	0.661	1.838	CA
0.089	0.089	0.182	0.000	0.706	0.517	0.362	0.447	0.447	0.540	0.690	0.547	0.625	0.403	0.366	0.390	0.444	0.766	0.404	0.501	0.718	0.527	0.559	0.508	0.554	0.537	CF
0.117	0.122	0.172	0.129	0.000	0.570	0.482	0.643	0.696	0.578	0.700	0.714	0.870	0.663	0.544	0.452	0.515	0.930	0.625	0.469	1.029	0.633	0.624	0.555	0.657	0.762	DP
0.132	0.121	0.201	0.113	0.140	0.000	0.342	0.522	0.394	0.432	0.447	0.536	0.619	0.386	0.379	0.500	0.530	0.710	0.364	0.448	0.657	0.282	0.707	0.369	0.359	0.454	EF
0.071	0.067	0.171	0.066	0.092	0.084	0.000	0.414	0.253	0.285	0.453	0.495	0.402	0.405	0.299	0.258	0.315	0.582	0.330	0.353	0.789	0.246	0.349	0.298	0.433	0.393	GB
0.068	0.082	0.101	0.073	0.110	0.106	0.063	0.000	0.404	0.447	0.541	0.473	0.485	0.550	0.270	0.294	0.673	0.525	0.345	0.376	0.496	0.425	0.346	0.632	0.416	0.774	GG
0.074	0.075	0.177	0.078	0.127	0.089	0.046	0.062	0.000	0.285	0.509	0.422	0.728	0.346	0.313	0.384	0.353	0.500	0.431	0.366	0.522	0.192	0.411	0.368	0.458	0.403	HA
0.083	0.088	0.182	0.089	0.109	0.089	0.052	0.068	0.049	0.000	0.456	0.410	0.546	0.351	0.290	0.378	0.383	0.524	0.439	0.317	0.760	0.292	0.488	0.335	0.501	0.413	CH
0.091	0.116	0.173	0.126	0.142	0.110	0.091	0.096	0.095	0.087	0.000	0.443	0.668	0.428	0.405	0.498	0.565	0.686	0.515	0.318	0.736	0.394	0.550	0.397	0.346	0.590	JA
0.086	0.088	0.166	0.089	0.122	0.104	0.079	0.070	0.067	0.062	0.084	0.000	0.663	0.530	0.249	0.350	0.459	0.555	0.498	0.317	0.578	0.355	0.466	0.460	0.385	0.544	KE
0.142	0.128	0.162	0.131	0.168	0.151	0.090	0.098	0.133	0.113	0.142	0.124	0.000	0.697	0.437	0.315	0.572	0.903	0.583	0.547	1.071	0.589	0.538	0.755	0.421	0.890	KH
0.114	0.104	0.217	0.086	0.143	0.094	0.083	0.098	0.069	0.068	0.098	0.093	0.150	0.000	0.340	0.445	0.423	0.797	0.490	0.366	0.624	0.294	0.632	0.350	0.478	0.411	LE
0.066	0.063	0.136	0.063	0.096	0.080	0.050	0.042	0.051	0.047	0.076	0.040	0.091	0.067	0.000	0.179	0.371	0.552	0.380	0.336	0.421	0.297	0.373	0.369	0.329	0.467	LA
0.063	0.055	0.114	0.065	0.081	0.098	0.041	0.042	0.058	0.058	0.087	0.054	0.070	0.082	0.027	0.000	0.344	0.610	0.350	0.344	0.677	0.320	0.402	0.404	0.378	0.531	ML
0.100	0.095	0.175	0.083	0.108	0.117	0.057	0.093	0.064	0.068	0.107	0.076	0.114	0.088	0.061	0.054	0.000	0.786	0.492	0.379	0.980	0.332	0.664	0.282	0.503	0.440	OD
0.103	0.130	0.205	0.123	0.157	0.144	0.094	0.086	0.087	0.090	0.127	0.093	0.158	0.139	0.086	0.089	0.121	0.000	0.650	0.490	1.099	0.481	0.751	0.695	0.723	0.657	OU
0.092	0.077	0.157	0.073	0.116	0.084	0.058	0.057	0.072	0.071	0.097	0.077	0.118	0.094	0.060	0.056	0.085	0.106	0.000	0.403	0.740	0.447	0.523	0.446	0.515	0.590	RO
0.068	0.064	0.120	0.074	0.084	0.090	0.051	0.048	0.052	0.047	0.062	0.046	0.097	0.069	0.044	0.041	0.057	0.072	0.059	0.000	0.651	0.377	0.365	0.255	0.333	0.519	SU
0.129	0.127	0.166	0.129	0.174	0.140	0.128	0.088	0.096	0.120	0.140	0.100	0.184	0.124	0.079	0.105	0.148	0.162	0.122	0.097	0.000	0.601	0.560	0.913	0.581	1.160	SD
0.086	0.101	0.180	0.093	0.127	0.075	0.049	0.071	0.037	0.054	0.083	0.063	0.125	0.065	0.052	0.054	0.062	0.089	0.080	0.059	0.112	0.000	0.517	0.349	0.322	0.308	SF
0.072	0.077	0.152	0.089	0.109	0.131	0.057	0.051	0.066	0.075	0.098	0.071	0.106	0.110	0.056	0.056	0.095	0.109	0.081	0.048	0.100	0.084	0.000	0.549	0.403	0.674	SH
0.075	0.075	0.195	0.088	0.109	0.086	0.054	0.091	0.064	0.059	0.083	0.076	0.142	0.075	0.060	0.063	0.057	0.114	0.076	0.044	0.143	0.065	0.085	0.000	0.454	0.313	TE
0.084	0.095	0.136	0.090	0.115	0.083	0.069	0.061	0.071	0.076	0.071	0.060	0.087	0.091	0.049	0.053	0.079	0.107	0.081	0.046	0.099	0.059	0.062	0.076	0.000	0.668	VA
0.104	0.116	0.248	0.097	0.147	0.103	0.075	0.113	0.071	0.072	0.114	0.090	0.164	0.082	0.078	0.085	0.085	0.118	0.102	0.079	0.169	0.062	0.108	0.063	0.107	0.000	ZW