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Genetic Diversity of Ex-situ Conserved Arabica Coffee (*Coffea arabica* L.) Accessions in Ethiopia as Revealed by Simple Sequence Repeats Markers

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Abstract

So far, there has been limited use of molecular markers in arabica coffee breeding program in Ethiopia. The objectives of this study were to explore the effectiveness of simple sequence repeats markers (SSRs) in detecting polymorphism and to assess the extent of genetic diversity and relationships among ex-situ conserved Arabica coffee accessions. Sixty-two forest coffee accessions planted in the experimental plot of the Ethiopian coffee breeding program were evaluated using 14 SSR markers. These markers amplified a total of 100 alleles, varying from four to ten alleles per locus, with an average of 7.2 across all loci. The rate of polymorphism ranged from 75 to 100, with a mean value of 96.4 across the accessions. The polymorphic information content (PIC) varied from 0.26 to 0.92, with a mean value of 0.70. The genetic similarity coefficient values between 72% possible pair-wise combinations ranged from 0.18 to 0.50, with overall mean value of 0.44. The unweighted pair group method with arithmetic mean (UPGMA) dendrogram based on Jaccard's genetic similarity grouped the accessions into five main clusters and two singletons at ≤0.47 similarity coefficient value. These results indicate the effectiveness of the SSR markers in detecting polymorphism and the presence of a high level of genetic diversity and distant relatedness among the studied coffee accessions. The observed diversity could be exploited in the future coffee breeding program to develop heterotic hybrid coffee varieties through crossing of divergent parental lines. The highly informative SSRs markers can be also used in genetic analysis of Arabica coffee germplasm conserved in the field gene bank at Jimma Agricultural Research Center (JARC) to establish core collections for effective conservation, management and utilization purposes.

Keywords: Coffee accessions, genetic relationships, germplasm conservation, similarity coefficient, SSRs markers

INTRODUCTION

Coffee is one of the most popular beverages and a major foreign exchange earning agricultural export commodity for many countries in the developing world. Of the 124 species only two viz., *Coffea arabica* L. which is the only tetraploid (2n = 4x = 44) and *Coffea canephora* Pierre (Robusta coffee), among the rest of the diploids (2n = 2x = 22), are commercially cultivated in over 80 countries (Davis *et al.,* 2011; Tesfaye *et al*., 2014). *Coffea arabica* is by far the most important economic and widely cultivated species that accounts for two-third of the world coffee production due to its superior cup quality accompanied with appreciable flavor and low caffeine content (Mekbib *et al.,* 2022). The South-western highlands of Ethiopia are the center of origin and genetic diversity for *C. arabica* L. This part of the country represents the potential gene pool reservoir that could be exploited for genetic improvement of the crop (Tesfaye *et al.,* 2014). The three Coffee Forest Biosphere Reserves (Yayu, Kaffa, and Shaka) that are registered by the United Nations Educational, Scientific and Cultural Organization (UNESCO) (www.coffee.uni-bonn.de) are also situated in this part of the country.

Cognizant of its economic importance and the available genetic diversity, Jimma Agricultural Research Center (JARC) has assembled nearly 7000 coffee germplasm accessions collected from different parts of the country including the coffee forest biosphere sites with the aim of developing improved coffee varieties to coffee farmers (Benti, 2017). It is well known that the efficiency of developing improved varieties of any crop species including coffee is determined, among others, by the availability of genetic diversity in the breeding populations. Several researchers have carried out genetic diversity assessments in arabica coffee accessions conserved in the field gene bank in Ethiopia based on morphological characters (Lemi *et al*., 2017, 2020; Masreshaw *et al.,* 2020). These authors reported the presence of moderate to a high level of genetic diversity among the studied coffee samples. It has been reported that selection of genetically diverse parental lines based on morphological characters is often difficult because of a high degree of morphological similarities (Jingade *et al.*, 2019).

Currently, molecular markers have been increasingly used in germplasm diversity assessment of various crops (Garrido-Cardenas *et al*., 2018). The molecular information allows gaining insight into the genetic structure of individual genotypes and eventually helps in accurate selection of superior genotypes for maximizing selection gains (Tiago *et al.*, 2017) suggesting the complementarily of the morphological and molecular marker systems. Previously, numerous studies have been carried out on genetic diversity of Arabica coffee accessions conserved in field gene bank outside of Ethiopia using molecular markers such as RAPD (Anthony *et al.,* 2001; Selveira *et al.,* 2003), AFLP (Anthony *et al.,* 2001), SSR (Anthony *et al*., 2001; Moncada & McCouch, 2004; Silvestrini *et al.,* 2007). Most of the results obtained from these studies have shown that the genetic diversity of Arabica coffee is low due to its narrow genetic base associated with autogamy, evolutionary and domestication history. Furthermore, in a recent assessment of 800 Arabica coffee accessions using SSR markers, the World Coffee Research reported the presence of the least genetic diversity of Arabica coffee compared to other major crops (WCR, 2014).

Molecular diversity studies conducted in Ethiopia so far are mostly focused on

forest coffee populations with inclusion of few samples from garden coffee production system, released varieties and accessions conserved in field gene bank of Ethiopian Biodiversity Institute (EBI). Accordingly, varying results that indicate the presence of low to a high level of genetic diversity were reported using RAPD and ISSR (Aga *et al.*, 2003, 2005), AFLP and SSR (Dessalegn *et al.*, 2009), ISSR (Tesfaye *et al.,* 2014), SSR (Teressa *et al.,* 2010; Aerts *et al.,* 2012) and SNP (Mekbib *et al.,* 2022) markers.

In the context of exploiting the observed genetic diversity, except the study conducted by Benti *et al*. (2021, 2022), neither the evaluated accessions nor their fingerprints from the previous studies were documented in the data base system and, thus, has not been utilized in the Ethiopian coffee breeding program. Moreover, the use of molecular makers has long been identified as one of the major research gaps of the coffee breeding program (Benti, 2017). Among the molecular markers, the powerfulness and cost-effectiveness of SSRs markers have been proofed in several studies carried out on Arabica coffee (Tiago *et al*., 2017; Baltazar & Fabella., 2020; Benti *et al.,* 2021, 2022). Moreover, it was reported that SSR markers were also found to be comparable or more effective than SNP markers in other crops such as grapevine and rice when the objective was mainly focused on the study of genetic diversity (Emanuelli *et al*., 2013; Singh *et al*., 2013). Hence, the present study was undertaken with the objectives: (1) to explore the possibility of using SSRs markers in detecting polymorphism in some ex-situ conserved Arabica coffee accessions, (2) to assess the extent of genetic diversity and relationships among the coffee accessions for future breeding and conservation purposes.

MATERIALS AND METHODS

Coffee Germplasm Accessions and Sample Collection

A total of 62 Arabica coffee germplasm accessions (Table 1) were used in this study. The coffee accessions were collected from Yayu Coffee Forest Biosphere Reserve site located in Yayu district, Ilubabor zone, Oromia regional state, South west Ethiopia (Figure 1). The collection sites are closer to each other having similar agroecology where no population structure/differentiation due to geographical isolation is expected. Collection of the accessions was made based on pointed collection strategy targeting to variation in specific traits of breeding interest such as yield, disease resistance, leaf, fruit, and stem etc. characters. All accessions were planted in experimental plot at Mettu sub-center of the JARC to evaluate their performance for various agronomic characteristics. Young and healthy leaf samples were collected from each accession as described by Benti *et al*. (2021).

Table 1. Summary of Arabica coffee accessions included in the present study

Acc. code	Area of collection		Number of acc.
	District	Specific site	
Y1-Y35	Yayu	Wabo	35
Y36-Y51	Yayu	Bundawo	16
Y52-Y62	Yayu	Gechi	11
Total			62

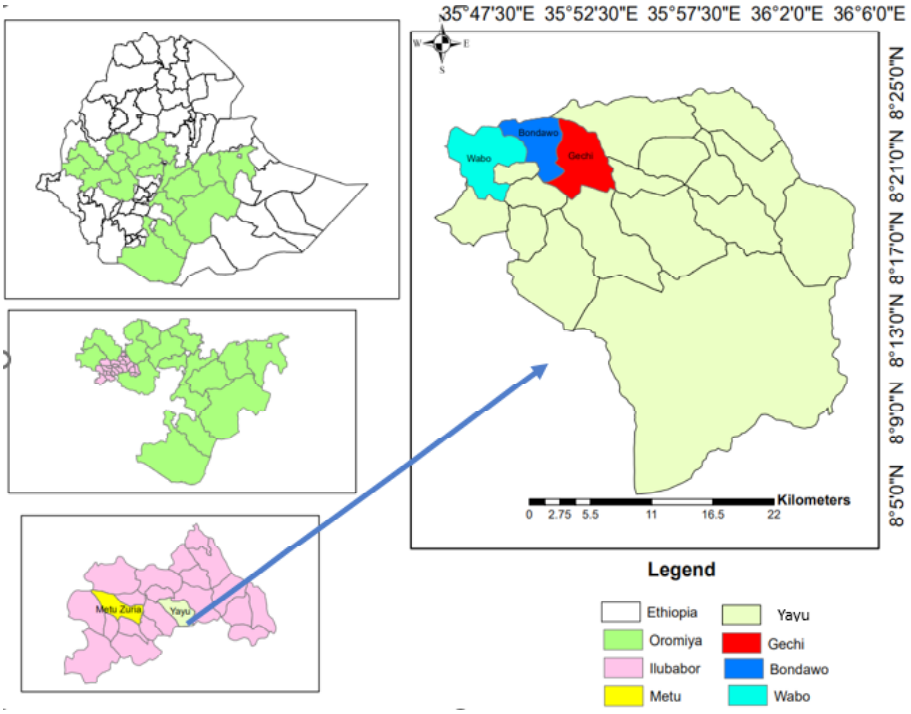

Figure 1. Map showing location of the trial site and Yayu district in Ilubabor Zone, Oromia regional state, South-west Ethiopia

DNA Extraction and Polymerase Chain Reactions (PCRs) with SSRs Markers

Total DNA was extracted from silica gel dried leaf tissue at molecular laboratory of Holetta biotechnology research center, Ethiopia, following a modified version of CTAB (Borsch *et al.,* 2003). DNA purification, quantification and the PCRs with the SSR markers (Table 2) were performed at Biosciences for eastern and central Africa-International Livestock Research Institute (BecA-ILRI) Hub molecular laboratory, Nairobi Kenya, following the step-wise procedures described by Benti *et al.* (2021).

Genotyping and Data Analysis

The same procedure used by Benti *et al.* (2021) was also followed for checking the reputability of amplicons, genotyping the evaluated coffee accessions and the subsequent data analysis.

RESULTS AND DISCUSSION

SSRs-Markers Polymorphism and Genetic Diversity

The genetic parameters calculated from the allelic data of the 14 SSRs markers are summarized in Table 3. The SSRs markers amplified a total number of 100 alleles of which 97 were polymorphic. The number of alleles per primer varied widely, ranging from 4 to 10, with an average of 7.2 total and 6.9 polymorphic alleles over all loci. Rate of polymorphism (Pr) ranged from 75 to 100, with an average of 96.4 percent. The PIC

Table 2. List of primer-pairs and sequences used to amplify the simple sequence repeats (SSRs) loci of the *Coffea arabica* L. accession along with their annealing temperature (Ta)

Code	Locus name	Primer sequence (5' to 3')		Ta [^{0}C]
		Forward + Dye	Reverse	
P1	AJ-250254*	GGCTCGAGATATCTGTTTAG -VIC	TTTAATGGGCATAGGGTCC	58
P2	AJ-250255*	CCCTCCCTGCCAGAAGAAGC-NED	AACCACCGTCCTTTTCCTCG	58
P3	AJ-250260*	TGATGGACAGGAGTTGATGG-6 -FAM	TGCCAATCTACCTACCCCTT	58
P4	Sat-237**	CAAGAGCAGACGATTCTCAATCT -6-FAM	TTGGGGTTAGGAAATCACAAT	58
P5	Sat-171**	TTCCCCCATCTTTTTCTTTC-VIC	TTGTATACGGCTCGTCAGGT	58
P6	CFGA-465	ACCCTTTACTACTTATTTACTCTC -6-FAM	ACATCCCCTTGCCATTTCTTC	62
P8	AJ-250257*	GACCATTACATTTCACACAC-NED	GCATTTTGTTGCACACTGTA	58
P9	Sat-235**	TCGTTCTGTCATTAAATCGTCAA -PET	GCAAATCATGAAAATAGTTGGTG	58
P10	MR-054**	TGATGTGGAAGGCCATTG-VIC	GCCCCTATTATGACCCATGC	62
P11	Sat-180**	CATGTGTAATACATTCAACAGTGA -NED	GCAATAGTGGTTGTCATCCTT	60
P12	AJ-250258*	AAC TCT CCA TTC CCG CAT TC -PET	CTG GGT TTT CTG TGT TCT CG	62
P13	Sat-41**	AGTGTAACTTTAGTTCTTGC-PET	ATTTAATGGGCATAGGGTC	58
P15	AJ-250253*	CTTGTTTGAGTCTGTCGCTG-VIC	TTTCCCTCCCAATGTCTGTA	58
P16	MR-336**	GAGTCGTCCACACTGCTTGA -6-FAM	CATCTGCTTTGGTCCCTGAT	60

Notes: *Combes *et al*. (2000); **Institute for Research and Development (IRD).

values also ranged from 0.28 to 0.92 with an average value of 0.70 per locus. The results of the study indicate that all the 14 SSRs markers were found to be polymorphic and detected high percent of polymorphism, suggesting the presence of high genetic variation among the studied coffee accessions. According to Botstein *et al*. (1980), the PIC values observed for all primers sets were high (>0.50) except for primers AJ-250257 and MR-336 that showed moderate values (between 0.50 and 0.25) indicating the effectiveness of the markers in discriminating and exploring genetic diversity among the evaluated coffee accessions. This result is in agreement with results of several researchers who previously reported the high discriminative power of the SSRs markers and their suitability in genetic diversity analysis of Arabica coffee genetic resources (Pruvot-Woehl *et al*., 2020; Montagnon *et al.,* 2021; Benti *et al.,* 2021, 2022). Thus, the SRRs markers with high PIC values could be used to assess the level of genetic diversity to make available the structural image of the whole ex-situ conserved large number of Arabica coffee germplasm collections in Ethiopia.

Furthermore, the results of the mean values for all indices of the genetic diversity were also closer to similar indices detected in commercial varieties (Benti *et al*., 2021) and elite breeding lines (Benti *et al*., 2022) of Arabica coffee using the same sets of SSRs markers. These suggest that the suitability of the markers in genetic analysis of different categories/breeding populations of Arabica coffee genetic resources. On the other hand, the mean values for diversity indices detected in the present study were much higher than those previously detected in spontaneous (forest) and sub-spontaneous (semi-forest) Arabica coffee accessions reported by several authors using different

Table 3. Indices of genetic diversity in 62 Arabica coffee accession using 14 SSRs markers

Code	Locus name	Na[a]	Pa[b]	Pr (%)[c]	PIC[d]
P1	AJ-250254	10	10	100	0.92
P2	AJ-250255	4	4	100	0.73
P3	AJ-250260	8	7	87.5	0.64
P4	Sat-237	7	7	100	0.62
P5	Sat-171	7	7	100	0.82
P6	CFGA-465	7	7	100	0.88
P8	AJ-250257	7	7	100	0.28
P9	Sat-235	7	7	100	0.81
P10	MR-054	8	7	87.5	0.60
P11	Sat-180	5	5	100	0.56
P12	AJ-250258	10	10	100	0.78
P13	Sat-41	8	8	100	0.82
P15	AJ-250253	8	8	100	0.87
P16	MR-336	4	3	75	0.46
Total	100	97			
Average	7.2	6.9	96.4	0.70	

Notes: [a] = number of total alleles, [b] = number of polymorphic alleles, [c] = rate of polymorphism, and [d] = Polymorphic information content.

sets of SSRs markers (Anthony *et al.,* 2002; Moncada & McCouch, 2004; Dessalegn *et al.,* 2009; Teressa *et al*., 2010; Al-Murish *et al*., 2013; Baltazar *et al.*, 2020). These authors detected average values of 2.0 to 5.9 alleles, 0.50 to 0.93 polymorphism and 0.25 to 0.40 PIC values per locus among the coffee samples analyzed. Moreover, majority of them reported the presence of low level of genetic diversity and the narrow genetic base in Arabica coffee. Hence, the results of our study demonstrated not only the high polymorphic nature of the SSR markers but also the presence of a high level of genetic diversity among the studied coffee accessions which could be exploited in the breeding program. One of the factors for the differences between the results of present and previous studies could be variation in samples size and genetic base of the source populations from where the studied materials were collected. Majority of the previous studies were conducted on a small number of samples representing FAO and ORSTOM collections (FAO, 1968; Guillaumet & Halle, 1978). These early collections made from Ethiopia were comprised of wild coffee and landraces where genetic bottleneck is expected in the later case due to selection for few traits derived by coffee farmers. The coffee accessions evaluated in the present study, however, were collected only from natural coffee forest (wild coffee) where human interference has less impact on selection for any traits. The other factors that may explain some of these differences are variations in the number and type of SSRs markers employed in the studies (Jingade *et al.,* 2019).

Genetic Similarity Among Coffee Accessions

A further result of this study is the estimation of the genetic similarity coefficients (Annex 1). The Jaccard's (Jaccard, 1908) similarity coefficient values between all possible pairs of accessions were ranged from 0.18 between Y25 and Y08 to 0.91 between Y43 and Y45 with an average value of 0.44 (Annex 1). The most genetically similar accessions were Y43 and Y45 with a similarity coefficient of 0.91, followed by accessions Y27 and Y62 (0.77), Y31 and Y52 (0.76), Y32 and Y44 (0.76), Y10 and Y13 (0.75), Y12 and Y40 (0.75), Y26 and Y53 (0.74) and Y05 and Y23 (0.74). In general, 1359 (72%) pair-wise combinations showed a range of 0.18 to 0.50 genetic similarity coefficient values.

The results of similarity coefficient values observed among the majority (72%) of possible pair-wise combinations and the overall average (0.44) indicate the presence of distant genetic relatedness and broad genetic diversity among the studied coffee accessions. This is expected because the studied materials were derived from Yayu coffee forest biosphere site where moderate to a high level of genetic diversity in the coffee populations was reported in previous studies using ISSR marker (Tesfaye *et al.,* 2014). Similar results have been reported by Benti *et al.* (2021; 2022) among commercial varieties and elite breeding lines of Arabica coffee in Ethiopia using the same sets of SSRs primer combinations. In contrast to our study, high genetic similarity coefficient values, most of which ranged from 0.60 to 1.0, were reported previously among different samples of Arabica coffee accessions using different number of SSRs (Al-Murish *et al*., 2013; WCR, 2014; Tiago *et al.,* 2017; Baltazar *et al*., 2020) and other marker systems such as SRAP and TRAP (Al-Murish *et al*., 2013; Jingade *et al*., 2019).

In coffee, identification of genotypes for crossing is mainly based on the variation in quantitative characters. On the other hand, it has been reported that parental distance resulted from molecular markers implies a great number of contrasting alleles at the desired loci, and then to the extent that these loci recombine in the F_2 and F_3 generations following crossing of distantly related parents (Ghaderi *et al.,* 1984). This will also provide greater opportunities for breeders to make effective selection for yield and its components among the segregants. In this context, the wider genetic distance among the majority of the pair-wise combinations, particularly the low similarity coefficient values (0.18 to 0.50) detected between 72.0% pairs of accession, suggest the presence of sufficient genetically divergent accessions to be selected as complementary parental lines for crossing to develop heterotic hybrid coffee varieties resilient to climate change in future improvement program.

Clustering Pattern Among Coffee Accessions

The most probable genetic relationship among the evaluated coffee accessions was represented by the UPGMA dendrogram resulting from a SAHN clustering analysis on the basis of Jaccard's similarity coefficients (Figure 2). The 62 coffee accessions evaluated in the present study were classified into five main clusters and two singletons at a genetic distance of $\geq$ 0.47 (Figure 2). Cluster I contained eight accessions collected from Wabo and a single accession from Gechi. Cluster II contained 12 accessions collected from Wabo (5), Bondawo (4), and Gechi (3) sites. The third cluster consisted of 23 accessions and divided into two sub clusters and a single accession stand alone. The sub cluster III-a consisted of nine accessions of which six were collected from Bondawo and the remaining three accessions from Wabo. The sub-cluster III-b was dominated by accessions collected from Wabo with inclusion of three accessions from Gechi and a single accession from Bondawo. Accession Y48 which was collected from Bondawo site stand independently of the accessions grouped in the main cluster III. Cluster IV consisted of nine of which five were collected from Wabo, three from Gechi and one accession from Bondawo sites. Cluster V consisted of six accessions collected from Wabo (4) and Gechi (2). Accession Y60 and Y25 which were collected from Gechi and Wabo were classified as singleton. The accessions were distributed into the five clusters regardless of their collection sites. However, accessions from the same site were grouped more closely to each other than those from different sites.

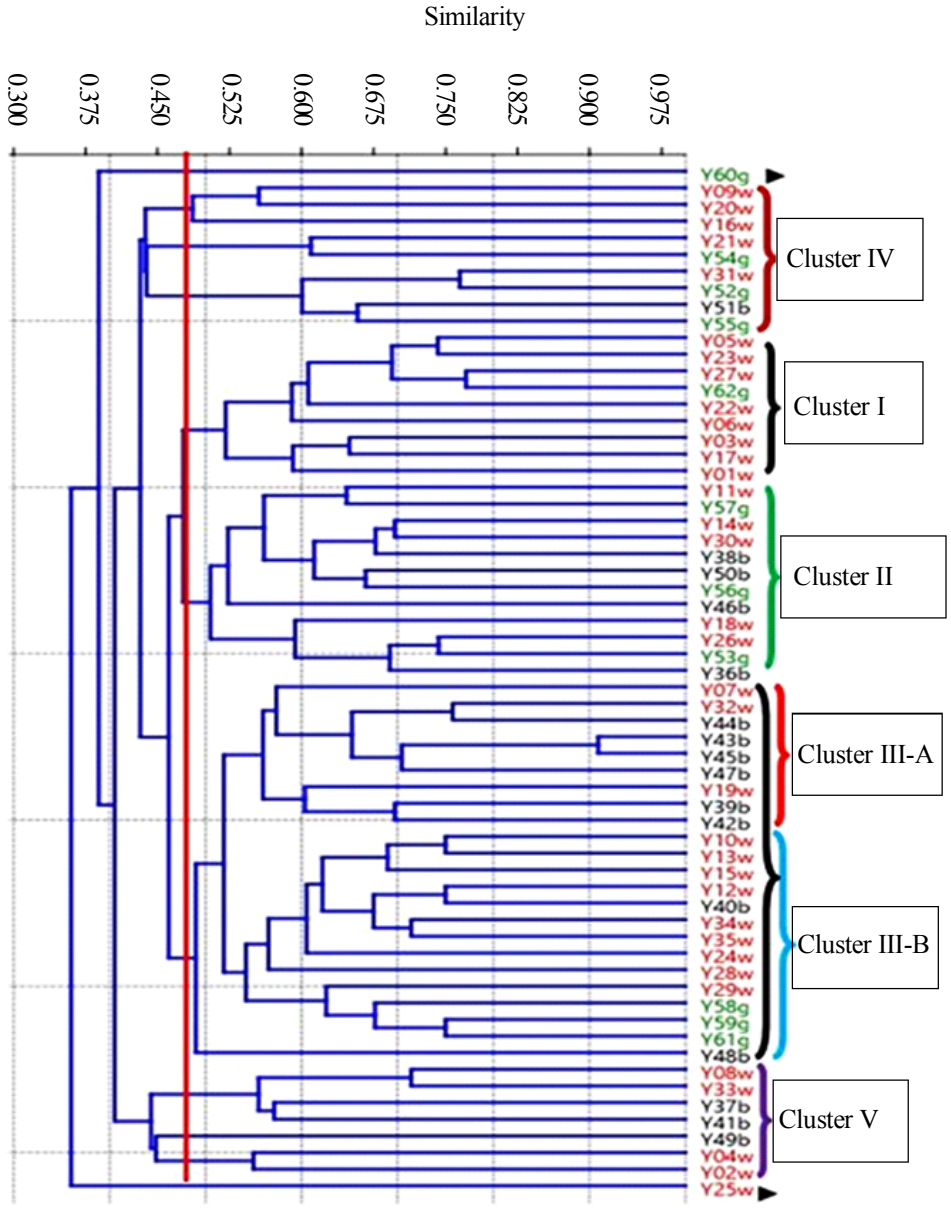

Figure 2. UPGMA cluster dendrogram showing genetic relationships among 62 ex-situ conserved Arabica coffee accessions based on 14 SSRs markers

Notes: b, g, and w, respectively, indicate the specific sites; Bundawo, Gechi, and Wabo, from where the accessions were collected.

The clustering pattern deployed by the UPGMA dendrogram also provides additional insight into the presence of a high level of genetic diversity among the accessions. The distribution of the accessions into different clusters regardless of the collection sites indicates lack of population differentiation among the sites and the existence of genetic diversity within coffee populations of each site. This could be attributed to lack of targeted human selection process in the biosphere reserve site as well as high gene flow among the coffee population of the collection sites. The presence of gene flow among the sites is expected because the sites are very close to each other. Such gene flow could result in high rate of overlapping or sharing of common alleles among the accessions and the presence of genetically closely related individuals among the populations of the three sites. The expected gene flow might be facilitated by pollen and seed disseminating agents such as wind, insects, wild animals and human being. Similar grouping pattern was reported by other researchers while studying intra-regional variation among forest coffee samples collected from different areas of Ethiopia (Tesfaye *et al*., 2014).

Moreover, majority of the accessions that showed relatively higher pair-wise similarity coefficient values were grouped closely to each other in any of the identified clusters, indicating their close relatedness at DNA level. Therefore, emphasis should be given to the presence of complimenting morphological traits while selecting these accessions for suitable cross combinations and pure line variety development in future breeding program. On the other hand, most of the accessions that showed wider genetic distances were either assigned into different clusters or positioned distantly to each other in the same cluster. This would help easy identification of divergent parental lines for hybridization study to exploit hybrid vigor resulting from recombination of genes responsible for desirable contrasting traits. However, the complementarity of genetic distances and the phenotypic variations should not be overlooked while selecting parental lines for crossing. Different researchers from Ethiopia (Ameha & Bellachew, 1983) and beyond (Silveira *et al*., 2003; Bertrand *et al*., 2005) have also confirmed the association between genetic diversity and heterosis in Arabica coffee for various traits of agronomic and economic importance using morphological markers.

CONCLUSIONS

The SSR markers used in the present study were found to be effective in detecting polymorphism and revealing the presence of a high level of genetic diversity among the studied coffee accessions. The information on the genetic similarity coefficient values will also enable selection of maximized diversity in parents to exploit hybrid vigor. Further, the evaluated accessions could also be conserved in the field gene bank as a source of gene reservoir for future improvement program.

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Conflict of Interest

No potential conflict of interest was reported by the authors.

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Annex 1- Jaccard's genetic similarity coefficient matrix among 62 ex-situ conserved *Coffea arabica* accessions using 14 simple sequence repeats (SSRs) markers

Gen.	y1	y2	y3	y4	y5	y6	y7	y8	y9	y10	y11	y12	y13	y14	y15	y16	y17	y18	y19	y20	y21
	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	0.53	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
y3	0.53	0.51	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
y4	0.46	0.55	0.46	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
y5	0.47	0.36	0.43	0.36	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
y6	0.48	0.46	0.50	0.43	0.63	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
y7	0.43	0.44	0.37	0.49	0.40	0.35	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-
y8	0.38	0.47	0.42	0.51	0.41	0.36	0.38	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-
y9	0.49	0.36	0.48	0.44	0.31	0.30	0.44	0.50	1.00	-	-	-	-	-	-	-	-	-	-	-	-
y10	0.50	0.40	0.45	0.62	0.46	0.43	0.57	0.47	0.61	1.00	-	-	-	-	-	-	-	-	-	-	-
y11	0.38	0.40	0.48	0.40	0.41	0.45	0.37	0.39	0.38	0.56	1.00	-	-	-	-	-	-	-	-	-	-
y12	0.38	0.43	0.48	0.48	0.45	0.42	0.59	0.43	0.43	0.60	0.50	1.00	-	-	-	-	-	-	-	-	-
y13	0.38	0.37	0.39	0.48	0.38	0.33	0.59	0.43	0.68	0.75	0.46	0.62	1.00	-	-	-	-	-	-	-	-
y14	0.49	0.43	0.51	0.56	0.49	0.56	0.40	0.43	0.42	0.61	0.69	0.58	0.50	1.00	-	-	-	-	-	-	-
y15	0.33	0.33	0.32	0.42	0.33	0.40	0.49	0.38	0.51	0.66	0.40	0.55	0.72	0.44	1.00	-	-	-	-	-	-
y16	0.41	0.36	0.48	0.47	0.45	0.39	0.40	0.43	0.46	0.51	0.50	0.43	0.50	0.64	0.37	1.00	-	-	-	-	-
y17	0.65	0.49	0.65	0.33	0.56	0.48	0.36	0.38	0.49	0.42	0.45	0.38	0.38	0.49	0.30	0.53	1.00	-	-	-	-
y18	0.50	0.48	0.49	0.38	0.50	0.54	0.45	0.31	0.37	0.53	0.60	0.48	0.40	0.51	0.36	0.40	0.50	1.00		-	-
y19	0.40	0.33	0.43	0.39	0.56	0.51	0.43	0.38	0.34	0.54	0.49	0.53	0.41	0.49	0.36	0.41	0.40	0.50	1.00	-	-
y20	0.43	0.35	0.52	0.32	0.39	0.40	0.42	0.44	0.56	0.49	0.56	0.40	0.48	0.51	0.36	0.51	0.54	0.53	0.39	1.00	-
y21	0.51	0.46	0.53	0.38	0.48	0.48	0.35	0.43	0.45	0.50	0.60	0.46	0.43	0.56	0.38	0.49	0.59	0.50	0.44	0.50	1.00
y22	0.53	0.47	0.51	0.48	0.53	0.52	0.44	0.33	0.36	0.56	0.54	0.46	0.43	0.68	0.38	0.50	0.53	0.55	0.49	0.40	0.60
y23	0.59	0.44	0.52	0.38	0.74	0.58	0.41	0.37	0.39	0.53	0.56	0.47	0.44	0.61	0.38	0.51	0.69	0.67	0.50	0.53	0.62
y24	0.40	0.30	0.47	0.46	0.47	0.41	0.50	0.38	0.57	0.64	0.41	0.57	0.66	0.53	0.54	0.45	0.44	0.43	0.51	0.43	0.44
y25	0.40	0.33	0.52	0.25	0.37	0.41	0.37	0.18	0.32	0.30	0.44	0.30	0.30	0.35	0.22	0.35	0.50	0.52	0.37	0.39	0.41
y26	0.43	0.51	0.49	0.39	0.43	0.50	0.39	0.32	0.31	0.49	0.59	0.48	0.44	0.51	0.39	0.37	0.43	0.61	0.46	0.42	0.50
y27	0.45	0.43	0.45	0.37	0.66	0.52	0.51	0.33	0.39	0.56	0.46	0.67	0.58	0.54	0.55	0.46	0.53	0.55	0.53	0.40	0.52
y28	0.40	0.41	0.46	0.36	0.46	0.40	0.45	0.35	0.40	0.53	0.44	0.59	0.55	0.44	0.49	0.37	0.43	0.49	0.46	0.36	0.47
y29	0.33	0.45	0.43	0.54	0.37	0.35	0.46	0.41	0.34	0.54	0.45	0.57	0.53	0.57	0.46	0.49	0.33	0.36	0.44	0.33	0.38
y30	0.43	0.35	0.49	0.41	0.46	0.54	0.39	0.37	0.40	0.57	0.60	0.55	0.48	0.70	0.42	0.44	0.43	0.49	0.50	0.57	0.53
y31	0.29	0.40	0.39	0.40	0.35	0.33	0.51	0.43	0.36	0.47	0.50	0.58	0.54	0.50	0.44	0.39	0.29	0.37	0.41	0.44	0.43
y32	0.43	0.51	0.46	0.41	0.43	0.43	0.53	0.34	0.33	0.53	0.56	0.59	0.48	0.47	0.42	0.33	0.39	0.61	0.50	0.38	0.43
y33	0.41	0.40	0.55	0.40	0.35	0.33	0.38	0.71	0.54	0.47	0.33	0.40	0.43	0.36	0.35	0.43	0.49	0.31	0.38	0.44	0.37
y34	0.42	0.44	0.54	0.51	0.49	0.49	0.55	0.40	0.50	0.68	0.58	0.69	0.69	0.62	0.62	0.47	0.42	0.48	0.49	0.41	0.52
y35	0.45	0.50	0.61	0.48	0.42	0.52	0.48	0.35	0.43	0.55	0.54	0.61	0.53	0.58	0.48	0.43	0.45	0.51	0.56	0.41	0.49

Continued

Gen.	y1	y2	y3	y4	y5	y6	y7	y8	y9	y10	y11	y12	y13	y14	y15	y16	y17	y18	y19	y20	y21
y36	0.43	0.48	0.43	0.39	0.46	0.43	0.49	0.29	0.28	0.41	0.51	0.44	0.38	0.48	0.33	0.34	0.36	0.56	0.40	0.42	0.38
y37	0.33	0.42	0.35	0.43	0.47	0.41	0.50	0.61	0.34	0.46	0.41	0.45	0.38	0.38	0.33	0.31	0.30	0.39	0.51	0.33	0.33
y38	0.43	0.48	0.49	0.57	0.39	0.54	0.45	0.40	0.37	0.57	0.60	0.55	0.44	0.70	0.39	0.44	0.36	0.49	0.54	0.49	0.47
y39	0.45	0.43	0.41	0.40	0.49	0.45	0.55	0.36	0.38	0.61	0.50	0.58	0.54	0.46	0.48	0.38	0.41	0.56	0.67	0.44	0.42
y40	0.42	0.40	0.45	0.45	0.46	0.40	0.57	0.44	0.51	0.73	0.51	0.75	0.75	0.61	0.66	0.47	0.42	0.45	0.50	0.45	0.47
y41	0.45	0.46	0.41	0.47	0.31	0.36	0.37	0.58	0.42	0.47	0.42	0.39	0.39	0.42	0.34	0.32	0.31	0.40	0.34	0.40	0.36
y42	0.46	0.44	0.43	0.45	0.54	0.47	0.53	0.34	0.47	0.62	0.40	0.51	0.64	0.44	0.53	0.40	0.46	0.49	0.54	0.38	0.43
y43	0.43	0.48	0.40	0.49	0.36	0.38	0.60	0.44	0.37	0.49	0.40	0.55	0.48	0.40	0.42	0.37	0.33	0.42	0.50	0.39	0.35
y44	0.43	0.55	0.43	0.53	0.46	0.43	0.61	0.40	0.37	0.62	0.44	0.69	0.55	0.56	0.49	0.44	0.39	0.49	0.50	0.35	0.43
y45	0.44	0.49	0.41	0.50	0.37	0.38	0.58	0.45	0.41	0.50	0.35	0.56	0.53	0.41	0.43	0.38	0.34	0.40	0.48	0.36	0.36
y46	0.29	0.40	0.31	0.45	0.38	0.40	0.35	0.44	0.36	0.49	0.51	0.44	0.51	0.51	0.41	0.43	0.29	0.38	0.42	0.45	0.40
y47	0.33	0.44	0.40	0.38	0.43	0.37	0.56	0.40	0.37	0.49	0.40	0.55	0.51	0.37	0.42	0.33	0.33	0.45	0.58	0.38	0.38
y48	0.30	0.48	0.40	0.41	0.30	0.34	0.45	0.34	0.27	0.45	0.40	0.51	0.40	0.40	0.42	0.30	0.30	0.35	0.39	0.23	0.38
y49	0.46	0.44	0.56	0.45	0.33	0.40	0.39	0.48	0.37	0.41	0.44	0.44	0.32	0.51	0.28	0.37	0.43	0.42	0.46	0.49	0.41
y50	0.45	0.47	0.51	0.48	0.42	0.52	0.44	0.40	0.40	0.59	0.62	0.47	0.47	0.67	0.41	0.46	0.45	0.55	0.45	0.59	0.49
y51	0.38	0.40	0.31	0.40	0.32	0.31	0.53	0.36	0.42	0.43	0.39	0.36	0.49	0.36	0.38	0.36	0.29	0.37	0.35	0.43	0.39
y52	0.32	0.40	0.42	0.37	0.32	0.31	0.55	0.43	0.43	0.40	0.43	0.50	0.54	0.43	0.38	0.54	0.38	0.37	0.35	0.51	0.43
y53	0.46	0.51	0.43	0.41	0.43	0.47	0.42	0.31	0.30	0.45	0.56	0.40	0.40	0.47	0.36	0.37	0.39	0.61	0.39	0.41	0.40
y54	0.33	0.32	0.31	0.35	0.36	0.34	0.39	0.34	0.37	0.49	0.47	0.44	0.44	0.51	0.36	0.40	0.30	0.35	0.43	0.41	0.61
y55	0.41	0.43	0.44	0.37	0.35	0.39	0.47	0.33	0.42	0.46	0.49	0.42	0.49	0.45	0.38	0.39	0.38	0.50	0.41	0.58	0.45
y56	0.44	0.52	0.47	0.47	0.41	0.48	0.50	0.40	0.36	0.50	0.60	0.49	0.46	0.56	0.44	0.42	0.41	0.47	0.48	0.47	0.45
y57	0.27	0.44	0.43	0.41	0.36	0.37	0.39	0.34	0.27	0.41	0.65	0.48	0.40	0.51	0.36	0.44	0.36	0.49	0.36	0.41	0.43
y58	0.36	0.38	0.49	0.61	0.39	0.40	0.49	0.44	0.44	0.67	0.56	0.55	0.55	0.56	0.49	0.47	0.33	0.49	0.50	0.38	0.43
y59	0.32	0.44	0.45	0.49	0.46	0.40	0.53	0.47	0.36	0.53	0.56	0.65	0.51	0.61	0.45	0.56	0.38	0.41	0.50	0.41	0.47
y60	0.30	0.33	0.35	0.33	0.46	0.47	0.28	0.35	0.28	0.38	0.55	0.38	0.35	0.51	0.31	0.37	0.33	0.42	0.43	0.36	0.44
y61	0.29	0.43	0.45	0.55	0.35	0.36	0.55	0.36	0.36	0.60	0.50	0.58	0.54	0.50	0.48	0.43	0.32	0.40	0.45	0.31	0.40
y62	0.50	0.44	0.56	0.39	0.71	0.69	0.42	0.38	0.40	0.53	0.59	0.55	0.48	0.69	0.42	0.51	0.62	0.61	0.54	0.49	0.64

Continued

Gen.	y22	y23	y24	y25	y26	y27	y28	Y29	y30	y31	y32	y33	y34	y35	y36	y37	y38	y49	y40	y41	y42
y22	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
y23	0.65	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
y24	0.49	0.50	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
y25	0.41	0.42	0.34	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
y26	0.51	0.57	0.33	0.46	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
y27	0.58	0.65	0.57	0.44	0.55	1.00			-	-	-	-	-	-	-	-	-	-	-	-	-
y28	0.44	0.49	0.50	0.43	0.52	0.68	1.00		-	-	-	-	-	-	-	-	-	-	-	-	-
y29	0.53	0.38	0.47	0.31	0.50	0.53	0.46	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-
y30	0.51	0.57	0.50	0.36	0.49	0.51	0.45	0.43	1.00	-	-	-	-	-	-	-	-	-	-	-	-
y31	0.46	0.37	0.41	0.27	0.51	0.46	0.44	0.61	0.44	1.00	-	-	-	-	-	-	-	-	-	-	-
y32	0.51	0.49	0.39	0.42	0.69	0.59	0.61	0.58	0.45	0.55	1.00	-	-	-	-	-	-	-	-	-	-
y33	0.30	0.33	0.38	0.27	0.32	0.30	0.35	0.41	0.34	0.36	0.34	1.00			-	-	-	-	-	-	-
y34	0.50	0.51	0.64	0.39	0.62	0.65	0.62	0.52	0.55	0.53	0.59	0.38	1.00		-	-	-	-	-	-	-
y35	0.53	0.51	0.56	0.48	0.62	0.57	0.55	0.56	0.55	0.47	0.55	0.38	0.71	1.00	-	-	-	-	-	-	-
y36	0.51	0.53	0.30	0.49	0.64	0.48	0.42	0.50	0.42	0.51	0.61	0.27	0.51	0.58	1.00		-	-	-	-	-
y37	0.41	0.38	0.37	0.26	0.36	0.38	0.36	0.47	0.36	0.49	0.50	0.53	0.39	0.39	0.46	1.00	-	-	-	-	-
y38	0.59	0.45	0.46	0.36	0.49	0.44	0.39	0.54	0.66	0.55	0.49	0.34	0.51	0.63	0.49	0.46	1.00		-	-	-
y39	0.46	0.47	0.45	0.41	0.59	0.63	0.59	0.53	0.47	0.58	0.65	0.36	0.58	0.62	0.55	0.49	0.56	1.00	-	-	-
y40	0.51	0.49	0.64	0.33	0.49	0.70	0.71	0.64	0.57	0.56	0.57	0.44	0.72	0.68	0.45	0.42	0.53	0.66	1.00	-	-
y41	0.39	0.39	0.34	0.29	0.40	0.33	0.31	0.45	0.44	0.39	0.40	0.50	0.34	0.40	0.40	0.57	0.51	0.38	0.39	1.00	-
y42	0.51	0.53	0.63	0.39	0.53	0.69	0.53	0.58	0.41	0.51	0.61	0.34	0.63	0.55	0.49	0.46	0.41	0.70	0.57	0.37	1.00
y43	0.35	0.38	0.40	0.31	0.45	0.44	0.45	0.54	0.39	0.51	0.61	0.44	0.48	0.48	0.45	0.58	0.42	0.55	0.49	0.48	0.53
y44	0.51	0.49	0.43	0.31	0.56	0.64	0.61	0.68	0.45	0.55	0.76	0.40	0.59	0.55	0.53	0.54	0.49	0.65	0.67	0.40	0.61
y45	0.36	0.39	0.44	0.27	0.43	0.45	0.47	0.51	0.36	0.49	0.54	0.45	0.49	0.49	0.40	0.51	0.40	0.53	0.50	0.45	0.54
y46	0.40	0.37	0.35	0.24	0.53	0.44	0.41	0.50	0.45	0.60	0.45	0.30	0.51	0.48	0.41	0.35	0.57	0.56	0.53	0.33	0.45
y47	0.40	0.41	0.46	0.33	0.49	0.51	0.53	0.58	0.38	0.59	0.66	0.40	0.48	0.51	0.49	0.58	0.45	0.70	0.53	0.40	0.66
y48	0.40	0.31	0.33	0.28	0.45	0.48	0.56	0.54	0.32	0.48	0.57	0.37	0.48	0.48	0.42	0.43	0.41	0.51	0.53	0.30	0.41
y49	0.38	0.38	0.36	0.37	0.39	0.32	0.33	0.36	0.53	0.41	0.39	0.44	0.39	0.45	0.33	0.36	0.61	0.48	0.38	0.48	0.33
y50	0.58	0.51	0.42	0.42	0.55	0.47	0.41	0.53	0.63	0.54	0.55	0.43	0.53	0.57	0.55	0.42	0.68	0.54	0.55	0.43	0.48
y51	0.42	0.36	0.38	0.28	0.38	0.33	0.29	0.38	0.31	0.56	0.37	0.25	0.40	0.40	0.47	0.38	0.47	0.45	0.36	0.36	0.47
y52	0.40	0.37	0.38	0.30	0.41	0.40	0.35	0.45	0.34	0.76	0.40	0.43	0.43	0.40	0.41	0.38	0.44	0.46	0.44	0.33	0.40
y53	0.51	0.49	0.33	0.49	0.74	0.51	0.45	0.50	0.41	0.48	0.66	0.28	0.51	0.55	0.74	0.39	0.45	0.56	0.45	0.44	0.53
y54	0.51	0.38	0.43	0.25	0.36	0.44	0.39	0.43	0.53	0.51	0.38	0.28	0.44	0.38	0.36	0.39	0.49	0.44	0.49	0.33	0.41
y55	0.52	0.46	0.35	0.38	0.53	0.42	0.40	0.44	0.43	0.64	0.47	0.33	0.43	0.52	0.61	0.41	0.54	0.56	0.46	0.42	0.47
y56	0.52	0.50	0.38	0.36	0.57	0.49	0.44	0.51	0.53	0.56	0.53	0.37	0.55	0.66	0.60	0.48	0.61	0.60	0.54	0.45	0.50
y57	0.44	0.45	0.36	0.39	0.56	0.48	0.42	0.58	0.49	0.51	0.57	0.31	0.48	0.51	0.49	0.33	0.49	0.40	0.49	0.37	0.38
y58	0.51	0.45	0.58	0.33	0.49	0.48	0.42	0.58	0.49	0.48	0.49	0.40	0.59	0.51	0.42	0.43	0.57	0.44	0.49	0.47	0.49
y59	0.51	0.49	0.50	0.30	0.49	0.56	0.49	0.64	0.49	0.60	0.53	0.40	0.59	0.55	0.45	0.42	0.53	0.56	0.63	0.39	0.49
y60	0.48	0.45	0.36	0.34	0.42	0.41	0.36	0.40	0.45	0.41	0.45	0.29	0.45	0.39	0.42	0.40	0.45	0.37	0.38	0.28	0.39
y61	0.50	0.37	0.53	0.33	0.48	0.50	0.48	0.66	0.44	0.50	0.55	0.36	0.61	0.61	0.44	0.38	0.55	0.50	0.60	0.36	0.51
y62	0.68	0.76	0.54	0.52	0.60	0.77	0.56	0.46	0.61	0.44	0.53	0.35	0.62	0.58	0.49	0.40	0.53	0.51	0.57	0.37	0.56

Continued

Gen.	y43	y44	y45	y46	y47	y48	y49	y50	y51	y52	y53	y54	y55	y56	y57	y58	y59	y60	y61	y62
y43	1.00	-	-	-	-	-	-													
y44	0.69	1.00		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
y45	0.91	0.71	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
y46	0.38	0.45	0.39	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
y47	0.69	0.71	0.71	0.49	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
y48	0.49	0.66	0.50	0.38	0.57	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-
y49	0.39	0.39	0.37	0.38	0.39	0.30	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-
y50	0.41	0.51	0.36	0.55	0.44	0.41	0.51	1.00	-	-	-	-	-	-	-	-	-	-	-	-
y51	0.40	0.34	0.38	0.46	0.40	0.29	0.40	0.40	1.00	-	-	-	-	-	-	-	-	-	-	-
y52	0.48	0.44	0.49	0.47	0.48	0.37	0.38	0.40	0.60	1.00	-	-	-	-	-	-	-	-	-	-
y53	0.45	0.49	0.40	0.45	0.45	0.41	0.33	0.51	0.40	0.40	1.00	-	-	-	-	-	-	-	-	-
y54	0.36	0.45	0.36	0.45	0.41	0.41	0.30	0.48	0.40	0.40	0.35	1.00	-	-	-	-	-	-	-	-
y55	0.43	0.43	0.41	0.54	0.47	0.40	0.40	0.56	0.66	0.60	0.58	0.50	1.00	-	-	-	-	-	-	-
y56	0.50	0.50	0.45	0.54	0.47	0.50	0.47	0.67	0.51	0.46	0.53	0.43	0.65	1.00	-	-	-	-	-	-
y57	0.39	0.45	0.33	0.53	0.41	0.41	0.33	0.51	0.34	0.44	0.57	0.35	0.43	0.50	1.00	-	-	-	-	-
y58	0.45	0.49	0.46	0.41	0.49	0.45	0.39	0.44	0.40	0.44	0.49	0.41	0.40	0.40	0.57	1.00	-	-	-	-
y59	0.45	0.57	0.46	0.53	0.57	0.53	0.41	0.48	0.36	0.56	0.49	0.45	0.43	0.54	0.62	0.62	1.00	-	-	-
y60	0.33	0.36	0.29	0.45	0.36	0.30	0.31	0.51	0.35	0.32	0.39	0.39	0.32	0.47	0.45	0.39	0.45	1.00	-	-
y61	0.41	0.55	0.42	0.47	0.51	0.55	0.35	0.47	0.39	0.43	0.48	0.40	0.39	0.49	0.64	0.74	0.75	0.41	1.00	-
y62	0.39	0.53	0.40	0.45	0.45	0.39	0.39	0.59	0.32	0.38	0.53	0.45	0.43	0.50	0.49	0.49	0.53	0.52	0.44	1.00