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Combining Ability and Molecular Marker Approach Identified Genetic Resources to Improve Agronomic Performance in *Coffea arabica* Breeding

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Plant breeding aims to develop cultivars with good agronomic traits through gene recombination and elite genotype selection. To support *Coffea arabica* breeding programs and assist parent selection, molecular characterization, genetic diversity (GD) analyses, and circulating diallel studies were strategically integrated to develop new cultivars. Molecular markers were used to assess the GD of 76 candidate parents and verify the crossing of potential F_1 hybrids. Based on the complementary agronomic traits and genetic distance, eight elite parents were selected for circulating diallel analysis. The parents and 12 hybrids were evaluated based on 10 morpho-agronomic traits. For each trait, the effects of general and specific combining abilities, as well as the averages of the parents, hybrids, and predicted hybrids, were estimated. Crosses that maximize the genetic gains for the main agronomic traits of *C. arabica* were identified. Joint analysis of phenotypic and molecular data was used to estimate the correlation between molecular GD, phenotypic diversity (PD), phenotypic mean, and combining ability. The selection of parents that optimize the allele combination for the important traits of *C. arabica* is discussed in detail.

Keywords: coffee breeding program, microsatellite markers, genetic diversity, hybrid certification, diallel analyses

INTRODUCTION

Coffee breeding programs aim to develop cultivars with agronomic and technological traits demanded by producers, combined with high productive potential, adaptation to different producing regions, and better cup quality (De Paiva Barbosa et al., 2019a). However, the genetic gain obtained through *Coffea arabica* selection is limited, mainly due to its low genetic variability (Setotaw et al., 2013). The recent origin, preferentially autogamous reproduction, and limited dispersion of the species are the primary reasons for this narrow genetic basis (Merot-L'anthoene et al., 2019; Scalabrin et al., 2020). Thus, efficient strategies to explore genetic variability are crucial for the parent selection and the success of *C. arabica* breeding programs (Alkimim et al., 2017). An

alternative would be to estimate and explore genetic variability through molecular markers (Sousa et al., 2019; Alkimim et al., 2020).

Molecular markers are of great use for genetic improvement and selection because they allow precise access to information at the DNA level (Ferrão et al., 2015). In *C. arabica*, these markers have been used successfully for germplasm and cultivar fingerprinting, genetic diversity (GD), genetic mapping, and marker-assisted selection (Missio et al., 2011; Alkimim et al., 2017; Setotaw et al., 2020). Molecular markers also facilitate controlled crossbreeding certification in breeding programs. *Coffea arabica* is an autogamous species and hybridized artificially. In this process, selfing must be prevented using a secure sterility system (Longin et al., 2012). However, female coffee plants are emasculated near the flower opening when the stigma is ripe and pollination proceeds. Therefore, true hybrid assessment is difficult because self-fertilization may occur before out-of-crossing prevention. It provides inaccurate progenies that can adversely affect all stages of future breeding programs. These problems can be overcome with molecular marker assistance (Caballo et al., 2018; Chauhan et al., 2021). By analyzing the allelic profile of the parents, molecular markers quickly and accurately identify self-fertilized progenies, distinguishing them from hybrid progenies (Conceição et al., 2011; Stetter et al., 2016). This strategy is particularly important for breeding perennial and long-cycle species with low genetic variability, such as *C. arabica*.

Another strategy to explore GD among individuals and select genetic resource to be included in breeding programs is to use diallel crosses. Diallel analysis evaluates the general and specific combining abilities of the parents and predicts the average behavior of the hybrids (Kaushik and Dhaliwal, 2018; Maioli et al., 2020). This approach is widely used to identify elite parents for developing hybrids or cultivars for use in breeding programs, understand hybrid heterosis, and provide information about gene action (Moura et al., 2016; Pereira et al., 2017; Ofori and Padi, 2020; Olivo et al., 2020). For coffee, diallel study was carried out to compare the performance of parent lines and hybrids of *C. arabica* (Cilas et al., 1998) and *Coffea canephora* (Cilas et al., 2003, Cilas and Bouharmont, 2005) and the data was used to assist the Cameroon breeding program (Cilas et al., 1998). In addition to its usefulness in breeding, diallel data also has been used to study the heritability of physical and mechanical properties of coffee wood (Cilas et al., 2006).

Among the different methods proposed for diallel crossing, circulating diallel (Kempthorne and Curnow, 1961) aims to reduce the number of hybrids to be evaluated and predicts the best unused hybrids. Thus, it is an efficient design and requires little mating efforts and experimental resources for plant material evaluation. It is of particular interest in the breeding programs for commercially important tree species (Tello et al., 2019), such as coffee.

Both molecular markers and diallel crosses have been used in different crops to analyze the relationships between genetic distance, agronomic performance, heterosis, and combining ability of hybrids. The results have been contrasting depending on the crop, genotypes, markers, and traits evaluated (Kaushik et al., 2018). Combining ability and genetic distance is highly correlated when related genotypes are crossed, as observed in the same heterotic group of corn (Makumbi et al., 2011) and related sunflower strains (Reif et al., 2013). Since *C. arabica* has a very narrow genetic base (Setotaw et al., 2013; Sousa et al., 2017b), the association of information on GD using molecular markers and the average behavior of genotypes based on morpho-agronomic traits may be useful in selecting parents.

This study aimed to use different approaches to assist the selection of parents to be introduced in coffee breeding programs for the main agronomic traits. *Coffea arabica* resources were selected based on a circular diallel mating design, for evaluating and predicting the performance of progenies in breeding programs. Diallel analysis and molecular markers genotyping were coupled to ensure the efficiency of coffee selection.

MATERIALS AND METHODS

Genetic Material

For the GD study, 22 coffee genotypes were evaluated, corresponding to cultivars and elite accessions of *C. arabica* breeding programs developed in Brazil. More than one plant from each cultivar/access was analyzed, totaling 76 coffee plants (**Table 1**). Eight genotypes were selected based on the complementary agronomic traits (**Table 2**) and genetic distance. They were crossed according to the circulating diallel model (**Table 3**). The potential hybrids were evaluated with molecular markers for controlled crossbreeding certification, and the true hybrids were planted.

The parents and hybrids were kept in the experimental area of the Department of Plant Pathology of the Universidade Federal de Viçosa (DFP/UFV), Brazil, region located at 20°44′26″S latitude, 42°50′54″W longitude and 665 m altitude. The annual temperature, considering the years of 2013 to 2016, varies from 5.4 to 37.5°C, with annual mean temperature of 20.3°C (20.1°C in the last 30 years) and annual mean precipitation of 1,220.5 mm (1,289.0 in the last 30 years). The seedling (in bags), with three pair of leaves, were planted in January, 2013, following a randomized block design, containing 20 treatments, composed of 12 F_1 hybrids and eight parents, with four replications and three plants per plot. The plants were arranged at a spacing of 3.0 × 0.70 m.

Phenotypic Evaluations

The circulating diallel crosses were phenotypically analyzed by observing and quantifying 10 phenotypic traits (**Table 4**): vegetative vigor (Vig), sprout color (SC), ripening fruit color (RFC), yield (Y), maturation cycle (MC), maturation uniformity (MU), ripening fruit size (RFS), coffee leaf rust (*Hemileia vastatrix)* incidence (CLR), brown eye spot (*Cercospora coffeicola*) incidence (BES), and leaf miner infestation (LM). The evaluations were carried out in May 2016 (41 month after plantation) in the experimental area of the DFP/UFV.

DNA Extraction and Amplification With SSR Markers

The genomic DNA of each plant was extracted from young and fully expanded leaves using a previously proposed method

TABLE 1 | Coffee cultivars and accessions used in the genetic diversity analysis.

Cultivar/Accession	Plant code	Location
Paraíso MG H419-1	1–10	Experimental field (Epamig)—Três Pontas, MG[a]
Catíguá MG2	11–16	Experimental field (Epamig)—Três Pontas, MG
Oeiras MG 6851	17–22	Experimental field (Epamig)—Três Pontas, MG
Acauã Novo	23	Experimental field (Fundação Procafé)—Varginha, MG
Arara	24	Experimental field (Fundação Procafé)—Varginha, MG
H484-2-18-12	25	Experimental field (Epamig)—Três Pontas, MG
Siriema	26	Experimental field (Fundação Procafé)—Varginha, MG
UFV 311-63	27	Experimental field (Epamig)—Três Pontas, MG
Sarchimor MG 8840	28–33	Experimental field (Epamig)—Patrocínio, MG
MGS Paraíso 2	34–37	Experimental field (Epamig)—Patrocínio, MG
Catuaí Amarelo IAC62	38–44	Experimental field (Epamig)—Patrocínio, MG
Bourbon Amarelo MG0009	45–49	Experimental Field (Epamig)—Patrocínio, MG
Híbrido de Timor MG 0357	50–54	Experimental field (Epamig)—Patrocínio, MG
Ibairi IAC 4761	55	Farm pântano—Patos de Minas, MG
Tupi Ferrero	56	Farm pântano—Patos de Minas, MG
Acauã	57	Experimental field of DFT/UFV, MG[b]
IPR103	58	Experimental field of DFT/UFV, MG
Obatã	59–60	Farm Paraíso—Varginha, MG
Obatã Vigoroso	61	Farm Paraíso—Varginha, MG
Catuaí Vermelho IAC144	62–64	Experimental Field (Epamig)—Três Pontas, MG
Topázio MG 1190	65	Experimental Field (Epamig)—Três Pontas, MG
IAC125RN	66–76	Farm Pântano—Patos de Minas, MG

[a] *MG, state of Minas Gerais, Brazil.*
[b] *DFT/UFV, Department of Plant Pathology, Universidade Federal de Viçosa.*

(Diniz et al., 2005). The quality and quantity of DNA were evaluated using a NanoDrop 2000 spectrophotometer. DNA purity was analyzed using 12 SSR primers (**Table 5**). These markers can distinguish and show the unique molecular profile of the main Brazilian coffee cultivars (Sousa et al., 2017b), including those analyzed in our work. PCR amplification was performed in a 20 μl reaction mix containing 50 ng DNA, 1 U Taq DNA polymerase, 1× enzyme buffer, 1 mM $MgCl_2$, 150 μM each dNTP, and 0.1 μM each primer, the volume was adjusted with sterile milli-Q water, using a PTC-200 thermocycler (MJ Research) and Veriti (Applied Biosystems). The reaction conditions were: initial denaturation at 94°C for 2 min; 10 cycles at 94°C for 30 s, decreased by 1°C each cycle (from 66 to 57°C) for 30 s; and 72°C for 30 s, followed by another 30 cycles of denaturation at 94°C, annealing at 57°C, and extension at 72°C, with 30 s each step. The final extension was performed at 72°C for 8 min. The amplified DNA was separated by electrophoresis in a 6% denaturing polyacrylamide gel and visualized using silver nitrate staining, according to a previously described protocol (Brito et al., 2010).

Genetic Diversity Analyses

Molecular marker data were coded as codominant for the performance of GD analyses. The dendrograms were constructed according to the unweighted pair group method using arithmetic averages (UPGMA) methodology in the MEGA software (7.0) (Kumar et al., 2016). The scores of the genetic dissimilarity matrix were obtained by the arithmetic complement of the weighted index in the GENES software (Cruz, 2013). The genetic distance was calculated as follows:

$$D_{ii'} = 1 - (\frac{1}{2}\sum_{j=1}^{L} p_j c_j)$$

Where:

Dii': genetic distance between the accession pairs i and i';
c_j: number of common alleles between the accession pairs i and i;
$p_j = \frac{a_j}{A}$: weight associated with locus j, determined by:
a_j: total number of alleles of locus j;
A: total number of alleles studied;

$$\sum_{j=1}^{L} p_j = 1$$

Diallel Analysis

The individual variance was analyzed using the data of 10 traits evaluated in the parents and hybrids, according to the following model:

$$X_{(ij)k} = m + g_{(ij)} + b_k + \varepsilon_{ijk}$$

Where:

$X_{(ij)k}$ = phenotypic score of the k-th observation regarding the ij-th genotype in the k-th block
m = general average;
= effect of the ij-th genotype (parent, $i = j$, or hybrid, $i \neq j$);
b_k = fixed effect of the k-th block;
ε_{ijk} = experimental error.

The superiority of the hybrid in relation to the others and/or the parents was evaluated using the Tukey test, with a 5% probability.

The general combining ability (GCA) and specific combining ability (SCA) were estimated using the parent and hybrid data, according to a previously described model (Kempthorne and Curnow, 1961). This diallel analysis was performed according to the following statistical model:

$$Y_{ij} = \mu + g_i + g_j + s_{ij} + \varepsilon_{ij}$$

TABLE 2 | Parents used in the diallel crossing.

N°	Parents	Origin	Main Features/Traits
1	Paraíso MG H 419-1	Catuaí Amarelo IAC30 × Híbrido de Timor UFV445-46	Dwarf cultivar, green sprout (young leaves), yellow ripening fruit, intermediated maturation cycle, large ripening fruit, resistant to coffee leaf rust, and nematode (*Meloydogine exigua)*
2	Catiguá MG2	Catuaí Amarelo IAC86 × Híbrido de Timor UFV440-10	Good cup quality, low nutrient demand, brown and green sprout (young leaves), red ripening fruit, intermediate maturation cycle, medium ripening fruit, coffee leaf rust resistant
3	Oeiras MG 6851	Caturra Vermelho CIFC19/1 × Híbrido de Timor CIFC 832/1	Excellent plant architecture, large grains, uniform fruit maturation, brown sprout (young leaves), red ripening fruit, semi-late maturation cycle, large ripening fruit, partial coffee leaf rust resistant
4	H484-2-18-12	Mundo Novo IAC515-3 × Híbrido Timor UFV443-3	Elite genotype (F_3 generation) with high yield, high vegetative vigor, and resistant to coffee leaf rust
5	UFV 311-63	Caturra CIFC426/2 × S.333 CIFC 254/14	Elite genotype carrying the coffee leaf rust resistance gene S_H3
6	Arara	Obatã × Catuaí Amarelo	High yield, green sprout (young leaves), yellow ripening fruit, late maturation cycle, large ripening fruit, coffee leaf rust resistant
7	Acauã Novo	Mundo Novo IAC388-17 × Sarchimor IAC1668	Drought tolerant, green sprout (young leaves), red ripening fruit, semi-late maturation cycle, medium-size ripening fruit, coffee leaf rust resistant
8	Siriema	[(Blue Mountain *C. racemosa*) × Mundo Novo] × Catimor UFV417	Drought tolerant, green sprout (young leaves), yellow ripening fruit, early maturation cycle, medium-size ripening fruit, partial coffee leaf rust resistant, leaf miner resistant

Where:

Y_{ij} = mean score of the hybrid combination ij ($i \neq j$) or the i-th parent ($i = j$). $Y_{ij} = (1/r)\sum_{k=1}^{r} X_{(ij)k}$, where r is the number of repetitions;
u = overall means of hybrid combinations;
g_i = effects of GCA of the i-th parent;
g_j = effects of GCA of the j-th parent;
s_{ij} = effect of SCA; and
ε_{ij} = mean experimental error.

The potential of hybrid combinations not obtained in the diallel (as the model was circulating diallel) was predicted using the following equation:

$$\hat{Y}_{ij} = u + \hat{g}_i + \hat{g}_j$$

Where:

$\hat{Y}_{ij}$ = predicted score of the hybrid ij;
μ = general average;
$\hat{g}_i$ and $\hat{g}_j$ = estimates of general combining capabilities

To assess the existence of significant differences between the effects of GCA and SCA, confidence intervals with a 95% probability were calculated. In this procedure, the bootstrap approach was adopted with the establishment of 5,000 new data sets obtained from the resampling of the original data. These sets were again submitted to diallel analyzes, generating estimates of the combining ability. The new estimates were ordered and, from the set, 5% of the extreme values were excluded (2.5% at each end), allowing the identification of limit estimates representing the desired confidence intervals.

TABLE 3 | Crossings performed according to the circulating diallel model.

Hybrid code	Female parent	Male parent
H14	Paraíso MG H 419-1	H484-2-18-12
H15	Paraíso MG H 419-1	UFV 311-63
H16	Paraíso MG H 419-1	Arara
H25	Catiguá MG2	UFV 311-63
H26	Catiguá MG2	Arara
H27	Catiguá MG2	Acauã Novo
H36	Oeiras MG 6851	Arara
H37	Oeiras MG 6851	Acauã Novo
H38	Oeiras MG 6851	Siriema
H47	H484-2-18-12	Acauã Novo
H48	H484-2-18-12	Siriema
H58	UFV 311-63	Siriema

Correlation Analysis

Pearson's correlation coefficient among parental GD, parental phenotypic diversity (PD), parental SCA, and hybrid phenotypic mean was estimated. Genetic diversity was obtained using the genetic distance matrix of the parents and analyzed using SSR markers. Phenotypic diversity was calculated by comparing the mean scores of each trait evaluated in the parents. The SCA was estimated using diallel analysis and the phenotypic means using the mean scores of each phenotypic trait evaluated in the

TABLE 4 | Phenotypic traits evaluated in eight progenitors of arabica coffee and 12 F_1 hybrids obtained by crossing in a circulating diallel scheme.

Variable	Description
Vig	Vegetative vigor (score scale ranging from 1 to 10). 1, fully depleted plants (low vigor) and 10, plants with maximum vegetative vigor.
SC	Sprout color (young leaves) (score scale ranging from 1 to 4). 1, green; 2, light bronze; 3, bronze; 4, dark bronze.
RFC	Ripening fruit color (score scale ranging from 1 to 3). 1, Red; 2, Yellow; 3, Orange.
Y	Yield. Liters of fresh cherries harvested per plant.
MC	Maturation cycle (score scale ranging from 1 to 5). 1, early; 2, semi-early; 3, intermediate; 4, semi-late; 5, late cycle.
MU	Maturation uniformity (score scale ranging from 1 to 4). 1, uniform; 2, semi-uniform; 3, semi non-uniform; 4, non-uniform maturation.
RFS	Ripening fruit size (score scale ranging from 1 to 3). 1, small, 2, medium; 3, large fruits.
CLR	Coffee leaf rust incidence (score scale ranging from 1 to 5). 1, absence of pustules and hypersensitivity reactions; 2, few leaves with spore-free pustules ("flecks") and with hypersensitivity reactions; 3, few pustules per leaf with high spore production and poorly distributed; 4, average number of pustules per leaf, distributed in the plant with high spore production; 5, large number of pustules with high spore production and high defoliation of the plant. NOTE: Plants with score 1 or 2, resistant; 3–5, susceptible.
BES	Brown eye spot incidence (score scale ranging from 1 to 5). 1, no symptoms; 2–5, leaves with *C. coffeicola* (2, low incidence and 5, high incidence).
LM	Leaf miner infestation (score scale ranging from 1 to 5). 1, immune. leaves without any lesion; 2, leaves with few tapered lesions; 3, leaves with few and small lesions; 4, leaves with moderate infestation, typical lesions, and live larvae; 5, leaves with severe infestation, typical lesions and live larvae.

TABLE 5 | SSR primers used to amplify the genomic DNA.

N°	Name	bp[a]	Sequence[b]	Reference
1	CaEST-006	227	F: CAGAATTGTTGTGGAGGGAAC R: ATGAAGCCAAACCAGAGACA	Ferrão et al., 2015
2	CaEST-022	207	F: GCCATTTCACAATCTCACCTC R: AGACCCAGCAGACAACAACA	Ferrão et al., 2015
3	CaEST-029	199	F: AGGAGATGCCTGTGACGAAC R: GGACGGAAAGATTCTGGCTTT	Ferrão et al., 2015
4	CaEST-031	109	F: CGGAGCAAGTGAATTGAACAGA R: AAAGGGAAAGGAAGAAGGAG	Ferrão et al., 2015
5	CaEST-040	101	F: TGAGCTAACCAAGACCAGTTCC R: CAACAGGAAATCACCGCCTA	Ferrão et al., 2015
6	CaEST-045	259	F: GCATCCTACCGAGTACATACAA R: TCCATCAACAACAACCGAAG	Ferrão et al., 2015
7	CaEST-048	151	F: TGAGACAAGCTATGGAGGAGGA R: AACCAGATCAACAGGGTAGGG	Ferrão et al., 2015
8	CaEST-071	155	F: ATGGAGAGGAAGACGCAACA R: CCTTATTGAAGACGCCCAAA	Ferrão et al., 2015
9	CaEST-072	197	F: TTGCTTGCTCCGCATCCTAC R: ATCGCTTCCAAGAGGCTTTC	Ferrão et al., 2015
10	CaEST-089	152	F: GTGAACCTCCCTTTCCCTTG R: ACTGGTCTCTCGTCTGTGAA	Ferrão et al., 2015
11	SSR016	140	F: ACCCGAAAGAAAGAAGAACCAAG R: CCACACAACTCTCCTCATTC	Combes et al., 2000
12	SSR095	352	F: TAAGAAGCCACGTGACAAGTAAGG R: TATGGCCCTTCTCGCTTTAGTT	Moncada and McCouch, 2004

[a] *bp, size of the amplified fragment in base pairs.*
[b] *F, foward primer; R, reverse primer.*

hybrids. A network graph of the correlations was constructed as proposed previously (Rosado et al., 2017). The thickness of the lines represents the absolute score of the correlation. The width of the line was controlled by applying a cut-off score of 0.5, for easy graph visualization.

RESULTS

Genetic Diversity

Genetic diversity was analyzed based on the SSR marker data obtained by genotyping 76 *C. arabica* plants corresponding to 22 cultivars or elite accessions with potential use in the coffee breeding program. The markers were able to discriminate the cultivars and the molecular profiles revealed polymorphism within cultivars/accessions. Since the genotypes of the same cultivar/accession were segregated, two analyses were performed. The first analysis used 22 individuals, one for each cultivar/access, and presented the most frequent alleles for each SSR primer. This study aimed to verify the distance between cultivars and accessions. A total of 28 alleles were obtained from the selected plants. The number of alleles amplified by markers varied between two (CaEST-006, 029, 031, 071, 072, 045, 048, and SSR16) and three (CaEST-022, 040, 089, and SSR95), with an average of 2.3 alleles per locus.

The highest genetic distance estimates were observed between Catiguá MG2 and Acauã (0.750), Catiguá MG2 and Topázio MG 1190 (0.696), Catiguá MG2 and Arara (0.643), Catiguá MG2

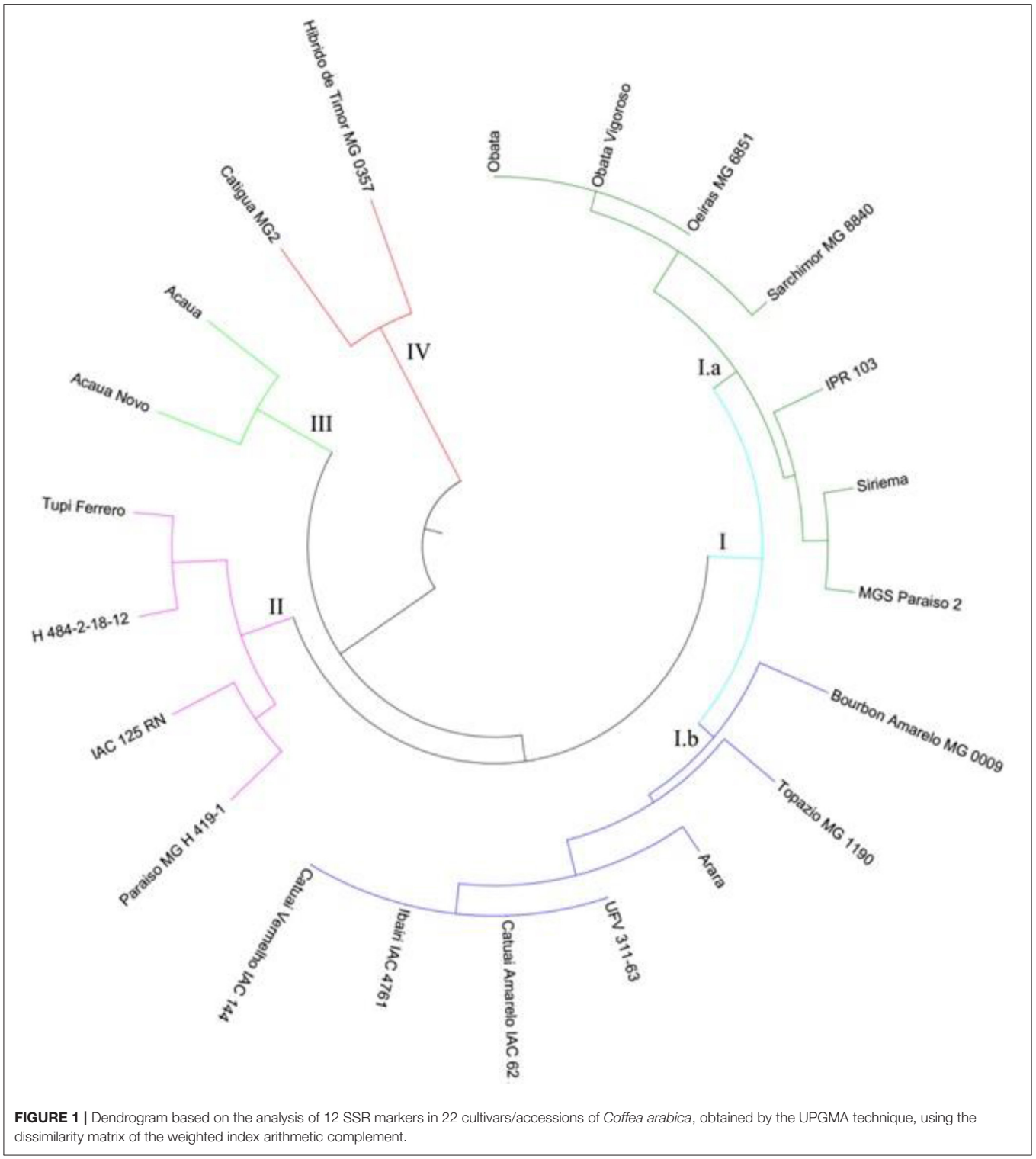


FIGURE 1 | Dendrogram based on the analysis of 12 SSR markers in 22 cultivars/accessions of *Coffea arabica*, obtained by the UPGMA technique, using the dissimilarity matrix of the weighted index arithmetic complement.

and Bourbon Amarelo MG 0009 (0.643), and Catiguá MG2 and Tupi Ferrero (0.643) (**Supplementary Table 1**). The clustering analysis of the 22 plants, based on the genetic distance matrix estimated between the pairs of individuals, using the 12 SSR markers, resulted in a dendrogram with four groups: I, II, III, and IV. Group I was subdivided into two subgroups: I.a and I.b (**Figure 1**).

A second GD analysis was performed considering the genotypic data of 76 *C. arabica* plants, including one or more plants per cultivar/accession. The clustering analysis, based

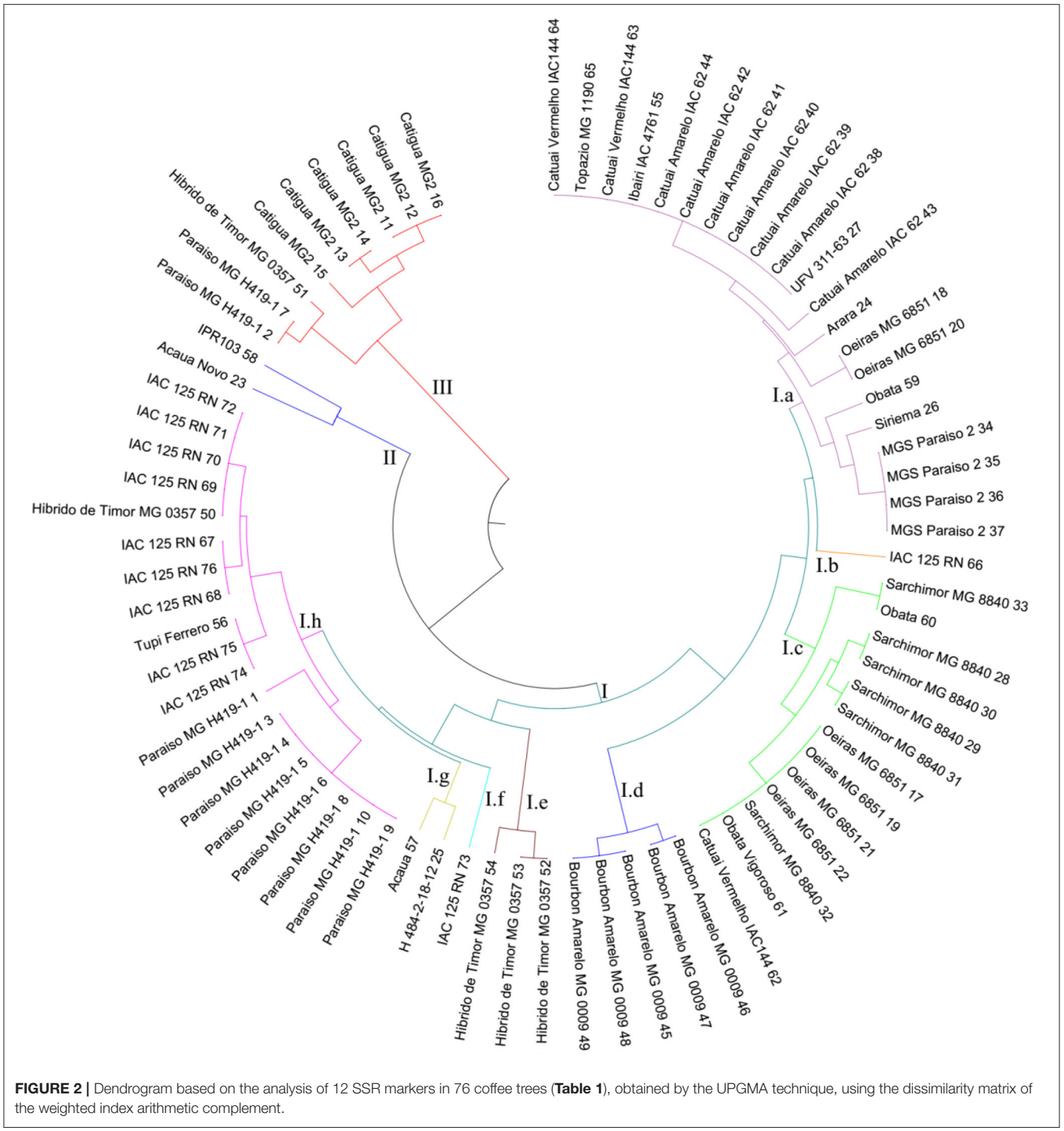


FIGURE 2 | Dendrogram based on the analysis of 12 SSR markers in 76 coffee trees (**Table 1**), obtained by the UPGMA technique, using the dissimilarity matrix of the weighted index arithmetic complement.

on the estimated genetic distance matrix between pairs of individuals, using 12 SSR markers, is shown in **Figure 2**. The dendrogram obtained consisted of three groups: groups I, II, and III. Group I was subdivided into eight subgroups: I.a, I.b, I.c, I.d, I.e, I.f, I.g, and I.h.

SSR marker analysis allowed us to observe polymorphisms within the nine cultivars/accessions: Catuaí Amarelo IAC 62, Sarchimor MG 8840, Oeiras MG 6851, Obatã IAC 1669-20, IAC 125 RN, Bourbon Amarelo MG 0009, Híbrido de Timor MG 0357, Catiguá MG2, and Paraíso MG H419-1. Some plants of the same cultivar/accession were allocated into different groups (plants of Paraíso MG H419-1, Híbrido de Timor MG 0357, Oeiras MG 6851, and IAC 125 RN cultivars). No polymorphism between individuals of Catuaí

TABLE 6 | Analysis of variance for 10 traits, evaluated in eight parents of arabica coffee and their hybrids obtained by a circulating diallel scheme.

		Mean square									
SV	**DF**	**VIG**	**SC**	**RFC**	**Y**	**MC**	**MU**	**RFS**	**CLR**	**BES**	**LM**
Treat	19	3.020**	0.098^{ns}	1.459**	5.168**	1.481**	0.379**	0.200^{ns}	0.150^{ns}	0.721**	0.134^{ns}
GCA	7	3.041**	0.099^{ns}	1.987**	5.802**	2.882**	0.614**	0.349^{ns}	0.313**	1.254**	0.061^{ns}
SCA	12	3.008**	0.097^{ns}	1.151**	4.797**	0.664**	0.241^{ns}	0.113^{ns}	0.056^{ns}	0.411^{ns}	0.177^{ns}
Error	57	0.542	0.071	0.267	1.669	0.332	0.200	0.167	0.114	0.299	0.125
Mean		6.652	1.191	1.865	3.743	3.396	2.842	2.217	1.840	2.733	1.235
CV(%)		11.064	22.303	27.735	34.516	16.960	15.740	18.422	18.371	19.990	28.678

SV, sources of variation; GSA, general combining ability; SCA, specific combining ability; CV, coefficient of variation; DF, degrees of freedom; Vig, vegetative vigor; SC, sprout color; RFC, ripening fruit color; Y, yield; MC, maturation cycle; MU, maturation uniformity; RFS, ripening fruit size; CLR, incidence of coffee leaf rust; BES, incidence of brown eye spot; LM, leaf miner infestation.

***significant by the F-test, at the level of 5%.*

^{ns}not significant.

Vermelho IAC 144 and MGS Paraíso 2 was observed (**Figure 2**).

Analysis of the Circulant Diallel

To assist the coffee breeding program, the most important *C. arabica* plants were selected for diallel analysis. The parental selection was based on the importance and complementarity of the agronomic traits (**Table 2**) and on the GD approach. The GD allowed the selection of coffee genotypes in all groups: Oeiras MG6851 and Siriema in group I.a; Arara and UFV 311-63 in group I.b; Paraíso MG H419-1 and H 484-2-18-12 in group II; Acauã Novo in group III; and Catiguá MG2 in group IV (**Figure 1**).

The potential F_1 hybrids developed, using eight cultivars/accessions crossed in a partial diallel, were evaluated with SSR markers to determine whether the progenies were obtained from controlled crossbreeding or self-fertilization. All parents were genotyped with SSR primers, and polymorphic and informative markers were identified for each hybrid progeny. Informative markers have polymorphisms between the parents; in this case, each parent must amplify at least one different allele. Thus, hybrid progenies have alleles present in both parents (**Supplementary Figure 1**), whereas self-fertilized progenies have alleles present only in the female parent (**Supplementary Figure 2**). Based on molecular markers, *C. arabica* plants confirmed as true hybrids and originated from the parent used in the artificial hybridizations were used in the diallel study.

The circulant diallel scheme estimates the genetic parameters and selects the best parents and hybrids based on the GCA and SCA scores. Using this partial diallel approach, a sample of possible crosses was studied, and the potential of all hybrid combinations was predicted. Therefore, this analysis provided information about the parents using few crosses without any information loss, since all hybrids were estimated in the model.

The variance analysis for the 10 evaluated traits, as well as the means of the effects for GCA and SCA, are presented in **Table 6**. The treatment effects were significant for Vig, RFC, Y, MC, Fruit MU, and BES traits, showing a variability among the genotypes (parents and hybrids). General combining ability effects were significant for Vig, RFC, Y, MC, MU, CLR, and BES traits. These estimates provide information on gene concentration (favorable allele frequency) with additive effects in the parents. Specific combining ability effect was significant only for Vig, RFC, Y, and MC traits.

The GCA scores were estimated for each parent and the two best scores for Vig, Y, MU, CLR, and BES (significant for GCA using analysis of variance) are highlighted in bold in **Table 7**. Low GCA scores are desired for CLR and BES traits, since the lowest score is associated with plants resistant to these diseases. The same was considered for MU, as the lowest score indicates the highest uniformity. The estimates of the SCA effects for each hybrid and parent are shown in **Table 8**, and the best cross combination for Vig and Y, the most significant traits, are highlighted. The reliability of the CGA and SCA estimate were assessed from the confidence interval limits (**Supplementary Table 2**). In this analysis, if the range does not include the zero value, the estimate is statistically non-null. In addition, the confidence interval information is useful to assess whether there is a significant difference between the estimates in the case where the confidence intervals do not overlap.

Catiguá MG2 × UFV 311-63 and Catiguá MG2 × Acauã Novo were the best identified crosses for Vig. In this analysis, not only the best SCA effect, but also the cross involving at least one parent with a high GCA, were considered. Although both GCA and SCA effects were significant for RFC and MC traits, they were not highlighted in the table, as fruit color and MC did not affect the preference for the developed cultivar, but the information must be available for the grower.

The mean performance of the obtained hybrids and the predicted mean scores of the hybrid not obtained in the partial diallel design were estimated for each trait (**Table 9**). The hybrids from crosses Catiguá MG2 × UFV 311-63 and Paraíso MG H419-1 × Arara showed the highest mean scores for Vig (8.085 and 7.750, respectively). Hybrids from Catiguá MG2 × Acauã Novo and Paraíso MG H419-1 × UFV 311-63 had the highest mean scores for the Y trait (5.250 and 4.960, respectively). Of the 10 evaluated traits, Vig, RFC, Y, MC, and CLR showed significant

TABLE 7 | Estimated values for the general combining ability (GCA) effects of eight arabica coffee parents, based on the means of t10 agronomic traits.

	Estimates of the GCA Values									
Parent[a]	**Vig[b]**	**SC**	**RFC**	**Y**	**MC**	**MU**	**RFS**	**CLR**	**BES**	**LM**
1	−0.409	0.000	0.215	−0.204	0.013	0.222	−0.155	−0.056	0.215	0.003
2	**0.494**	0.074	0.236	**0.581**	0.116	−0.052	−0.164	−0.046	−0.131	−0.004
3	−0.537	−0.015	−0.143	−0.334	−0.270	**−0.179**	0.076	0.243	0.302	−0.031
4	−0.088	0.045	0.004	−0.308	0.423	−0.041	−0.036	0.088	**−0.178**	−0.034
5	0.045	0.085	−0.241	−0.650	−0.363	**−0.241**	0.147	**−0.070**	**−0.268**	0.110
6	**0.229**	−0.085	0.327	0.350	0.369	0.020	0.141	**−0.072**	−0.056	−0.021
7	0.172	−0.056	−0.477	**0.603**	0.119	0.211	−0.054	−0.069	0.238	0.009
8	0.093	−0.046	0.079	−0.036	−0.407	0.060	0.045	−0.018	−0.122	−0.032

[a] 1, Paraíso MG H419-1; 2, Catiguá MG2; 3, Oeiras MG 6851; 4, H484-2-18-12; 5, UFV 311-63; 6, Arara; 7, Acauã Novo; 8, Siriema.

[b] Vig, vegetative vigor; SC, sprout color; RFC, ripening fruit color; Y, yield; MC, maturation cycle; MU, maturation uniformity; RFS, ripening fruit size; CLR, incidence of coffee leaf rust; BES, incidence of brown eye spot; LM, leaf miner infestation. The two best scores for Vig, Y, MU, CLR, and BES (significant for GCA using analysis of variance) are highlighted in bold.

TABLE 8 | Estimated of the effects of specific combining ability (SCA) of 12 hybrids (in parentheses) and 8 parents based on the means of 10 evaluated agronomic traits.

	Estimates of S.C.A effects									
Cross[a]	**Vig[b]**	**SC**	**RFC**	**Y**	**MC**	**MU**	**RFS**	**CLR**	**BES**	**LM**
1 × 1	−1.377	0.017	−0.295	−1.777	−0.214	−0.078	0.094	−0.020	−0.163	−0.116
2 × 2	−0.434	0.162	−0.337	−0.467	−0.420	−0.238	0.112	0.044	−0.097	−0.060
3 × 3	−0.579	0.004	−0.578	−0.657	−0.106	−0.235	−0.036	0.171	−0.001	−0.174
4 × 4	−0.434	−0.030	0.128	−0.822	−0.118	−0.260	0.022	−0.015	0.040	−0.167
5 × 5	−0.909	0.138	−0.383	−1.400	−0.505	−0.028	0.240	0.051	−0.029	−0.038
6 × 6	−0.778	−0.021	−0.518	−0.402	−0.384	0.037	0.000	0.139	0.293	−0.111
7 × 7	−0.371	0.046	0.214	−0.573	−0.259	−0.222	0.140	0.048	−0.002	−0.252
8 × 8	−0.213	−0.099	−0.190	−0.295	−0.164	0.038	−0.057	0.070	0.093	0.079
(1 × 4)	0.262	−0.153	0.249	0.871	−0.332	0.392	−0.026	0.129	0.397	0.046
(1 × 5)	1.214	−0.026	0.746	2.072	0.202	0.012	−0.041	0.037	0.405	−0.016
(1 × 6)	1.278	0.145	−0.406	0.612	0.550	−0.248	−0.121	−0.127	−0.477	0.201
(2 × 5)	**0.894**	−0.185	−0.025	0.909	0.684	0.286	−0.281	−0.139	−0.169	0.241
(2 × 6)	−0.126	−0.180	0.490	−0.299	−0.046	0.108	0.139	0.028	0.038	0.037
(2 × 7)	0.099	0.042	0.209	**0.324**	0.202	0.081	−0.081	0.025	0.324	−0.158
(3 × 6)	0.403	0.077	0.952	0.492	0.258	0.067	−0.019	−0.179	−0.147	−0.016
(3 × 7)	0.213	−0.037	−0.245	0.361	−0.080	0.293	−0.157	−0.097	0.227	0.372
(3 × 8)	0.542	−0.047	0.450	0.460	0.034	0.109	0.248	−0.066	−0.078	−0.008
(4 × 7)	0.431	−0.970	−0.391	0.462	0.397	0.070	−0.043	−0.024	−0.546	0.290
(4 × 8)	0.175	0.310	−0.115	0.311	0.170	0.057	0.024	−0.075	0.069	−0.002
(5 × 8)	−0.290	−0.065	0.045	−0.181	0.124	−0.243	−0.158	0.001	−0.178	−0.149

[a] 1, Paraíso MG H419-1; 2, Catiguá MG2; 3, Oeiras MG 6851; 4, H484-2-18-12; 5, UFV 311-63; 6, Arara; 7, Acauã Novo; 8, Siriema.

[b] Vig, vegetative vigor; SC, sprout color; RFC, ripening fruit color; Y, yield; MC, maturation cycle; MU, maturation uniformity; RFS, ripening fruit size; CLR, incidence of coffee leaf rust; BES, incidence of brown eye spot; LM, leaf miner infestation. The best crosses estimated based on the SCA, involving at least one parent with high GCA, for the main significant traits (Vig and Y) are highlighted in bold.

differences between the means of treatments, according to the Tukey test at the 5% probability level (**Table 10**).

To access the occurrence and degree of heterosis, graphs were drawn considering the mean of the parentals and hybrids based on seven traits (**Figure 3**). SC, RFC, and MC were not analyzed as these traits did not affect the cultivar preference. Higher levels of heterosis were found for Vig and Y. The data allow us to select hybrids that surpassed the average of their parents in some traits. Hybrid H15 showed high heterosis for Vig and Y, but low for other traits, including negative heterosis for RFS. H16 also showed high heterosis for Vig and Y and lower diseases incidence, but negative heterosis for MU and RFS. The performance of the hybrids is related to the combining ability of the parents for traits of interest. Thus, to reach heterosis for Y and Vig the best crosses are Paraíso MG H419-1 with UFV 311-63, H484-2-18-12, and Arara as well as Catiguá MG2 × UFV 311-63. However, the hybrids showed lower MU and RFS and higher incidence of BES and LM than one of

TABLE 9 | Hybrid means (in parentheses) and predicted mean values of the hybrid not included in the circulating diallel analysis for 10 agronomic traits.

Parent[a]	1	2	3	4	5	6	7	8
VIG[b]								
1	–	6.738	5.707	(6.418)	(7.503)	(**7.750**)	6.415	6.335
2		–	6.610	7.059	(**8.085**)	(7.250)	(7.418)	7.240
3			–	6.028	6.160	(6.748)	(6.500)	(6.750)
4				–	6.609	6.793	(7.168)	(6.833)
5					–	6.926	6.869	(6.500)
6						–	7.053	6.974
7							–	6.917
8								–
SC								
1	–	1.264	1.176	(1.083)	(1.250)	(1.250)	1.134	1.145
2		–	1.250	1.309	(1.165)	(1.000)	(1.250)	1.219
3			–	1.221	1.261	(1.168)	(1.083)	(1.083)
4				–	1.321	1.151	(1.083)	(1.500)
5					–	1.191	1.220	(1.165)
6						–	1.050	1.060
7							–	1.089
8								–
RFC								
1	–	2.316	1.936	(2.333)	(2.585)	(2.000)	1.603	2.159
2		–	1.958	2.104	(1.835)	(2.918)	(1.833)	2.180
3			–	1.725	1.481	(3.000)	(1.000)	(2.250)
4				–	1.627	2.195	(1.000)	(1.833)
5					–	1.950	1.147	(1.748)
6						–	1.715	2.270
7							–	1.467
8								–
8								–
Y								
1	–	4.120	3.204	(4.103)	(**4.960**)	(4.500)	4.142	3.502
2		–	3.989	4.016	(4.583)	(4.375)	(**5.250**)	4.287
3			–	3.101	2.758	(4.250)	(4.373)	(3.833)
4				–	2.785	3.785	(4.500)	(3.710)
5					–	3.442	3.695	(2.875)
6						–	4.695	4.056
7							–	4.309
MC								
1	–	3.524	3.138	(3.500)	(3.248)	(4.335)	3.528	3.001
2		–	3.242	3.935	(3.833)	(3.835)	(3.833)	3.105
3			–	3.549	2.763	(3.753)	(3.165)	(2.753)
4				–	3.456	4.188	(4.335)	(3.583)
5					–	3.402	3.152	(2.750)
6						–	3.884	3.358
7							–	3.108
8								–

(Continued)

TABLE 9 | Continued

Parent[a]	1	2	3	4	5	6	7	8
MU								
1	–	3.012	2.885	(3.415)	(2.835)	(2.835)	3.275	3.124
2		–	2.611	2.749	(2.835)	(2.918)	(3.083)	2.850
3			–	2.622	2.422	(2.750)	(3.168)	(2.833)
4				–	2.560	2.820	(3.083)	(2.918)
5					–	2.621	2.812	(2.418)
6						–	3.073	2.921
7							–	3.113
8								–
RFS								
1		1.897	2.137	(2.000)	(2.168)	(2.083)	2.008	2.107
2			2.128	2.017	(1.918)	(2.333)	(1.918)	2.097
3				2.257	2.439	(2.415)	(2.083)	(2.585)
4					2.328	2.322	(2.085)	(2.250)
5						2.505	2.310	(2.250)
6							2.330	2.403
7								2.208
8								
CLR								
1	–	1.738	2.027	(2.000)	(1.750)	(1.585)	1.715	1.766
2		–	2.038	1.882	(1.585)	(1.750)	(1.750)	1.777
3			–	2.171	2.013	(1.833)	(1.918)	(2.000)
4				–	1.857	1.856	(1.835)	(1.835)
5					–	1.698	1.701	(1.753)
6						–	1.699	1.750
7							–	1.753
8								–
BES								
1	–	2.817	3.249	(3.168)	(3.085)	(2.415)	3.186	2.826
2		–	2.904	2.425	(2.165)	(2.585)	(3.165)	2.480
3			–	2.857	2.766	(2.833)	(3.500)	(2.835)
4				–	2.287	2.500	(2.248)	(2.503)
5					–	2.409	2.703	(2.165)
6						–	2.916	2.556
7							–	2.850
8								–
LM								
1		1.234	1.207	(1.250)	(1.333)	(1.418)	1.246	1.206
2			1.201	1.197	(1.583)	(1.248)	(1.083)	1.199
3				1.171	1.315	(1.168)	(1.585)	(1.165)
4					1.312	1.180	(1.500)	(1.182)
5						1.325	1.354	(1.165)
6							1.223	1.182
7								1.212
8								

[a] *1, Paraíso MG H419-1; 2, Catiguá MG2; 3, Oeiras MG 6851; 4, H484-2-18-12; 5, UFV 311-63; 6, Arara; 7, Acauã Novo; 8, Siriema.*

[b] *Vig, vegetative vigor; SC, sprout color; RFC, ripening fruit color; Y, yield; MC, maturation cycle; MU, maturation uniformity; RFS, ripening fruit size; CLR, incidence of coffee leaf rust; BES, incidence of brown eye spot; LM, leaf miner infestation. The highest means for the main traits that were statistically significant are highlighted in bold.*

TABLE 10 | Means of five agronomic traits, evaluated in F_1 hybrids (H1–H12) obtained in a circulating diallel scheme and the respective parents of arabica coffee trees, in Viçosa, state of Minas Gerais, Brazil.

Genotype	Vig[b]		SC		Y		MC		CLR	
H1[a]	6.418	abc[c]	2.333	ab	4.103	abc	3.500	abcd	2.000	ab
H2	7.503	ab	2.585	b	4.960	a	3.248	abcd	1.750	ab
H3	7.750	ab	2.000	ab	4.500	ab	4.335	a	1.585	b
H4	8.085	a	1.835	ab	4.583	ab	3.833	abc	1.585	b
H5	7.250	ab	2.918	a	4.375	abc	3.835	abc	1.750	ab
H6	7.418	ab	1.833	ab	5.250	a	3.833	abc	1.750	ab
H7	6.748	abc	3.000	a	4.250	abc	3.753	abc	1.833	ab
H8	6.500	abc	1.000	b	4.373	abc	3.165	abcd	1.918	ab
H9	6.750	abc	2.250	ab	3.833	abc	2.753	acd	2.000	ab
H10	7.168	ab	1.000	b	4.500	ab	4.335	a	1.835	ab
H11	6.833	abc	1.833	ab	3.710	abc	3.583	abcd	1.835	ab
H12	6.500	abc	1.748	ab	2.875	abc	2.750	bcd	1.753	ab
Mean[c]	7.077		2.028		4.276		3.577		1.800	
Paraíso MGH419-1	4.458	d	2.000	ab	1.558	bc	3.208	abcd	1.708	ab
Catiguá MG2	7.208	ab	2.000	ab	4.438	ab	3.208	abcd	1.793	ab
Oeiras MG 6851	5.000	cd	1.000	b	2.418	abc	2.750	bcd	2.498	a
H484-2-18-12	6.043	bcd	2.000	ab	2.305	abc	4.125	ab	2.000	ab
UFV 311-63	5.833	bcd	1.000	b	1.043	c	2.165	d	1.750	ab
Arara	6.333	abcd	2.000	ab	4.040	abc	3.750	abc	1.835	ab
Acauã Novo	6.625	abc	1.125	b	4.375	abc	3.375	abcd	1.750	ab
Siriema	6.625	abc	1.833	ab	3.375	abc	2.418	cd	1.875	ab
Mean	6.016		1.620		2.944		3.125		1.901	

[a]*H1, Paraíso MG H419-1 × H484-2-18-12; H2, Paraíso MG H419-1 × UFV 311-63; H3, Paraíso MGH419-1 × Arara; H4, Catiguá MG2 × UFV 311-63; H5, Catiguá MG2 × Arara; H6, Catiguá MG2 × Acauã Novo; H7, Oeiras MG 6851 × Arara; H8, Oeiras MG 6851 × Acauã Novo; H9, Oeiras MG 6851 × Siriema; H10, H484-2-18-12 × Acauã Novo; H11, H484-2-18-12 × Siriema; H12, UFV 311-63 × Siriema.*

[b]*Vig, vegetative vigor; SC, sprout color; RFC, ripening fruit color; Y, yield; MC, maturation cycle; CLR, incidence of coffee leaf rust.*

[c]*Means followed by the same letter in the column do not differ statistically by the Tukey test, at 5.0% probability.*

their parents. Hybrids with better MU than both parents were obtaining with the crosses Paraíso MG H419-1 × H484-2-18-12 and Oeiras MG 6851 × Acauã Novo. Higher fruit size was found only with the hybrid from Oeiras MG 6851 × Siriema. In general, the incidence of disease (CLR and BES) and infestation of LM were higher in the hybrids comparing with one of their parents.

Correlation Analysis

Correlation analysis allowed us to verify the relationship between the performance mean of the hybrids analyzed in the diallel model, considering each of the 10 morpho-agronomic traits and the parental SCA, PD, and GD (based on molecular markers).

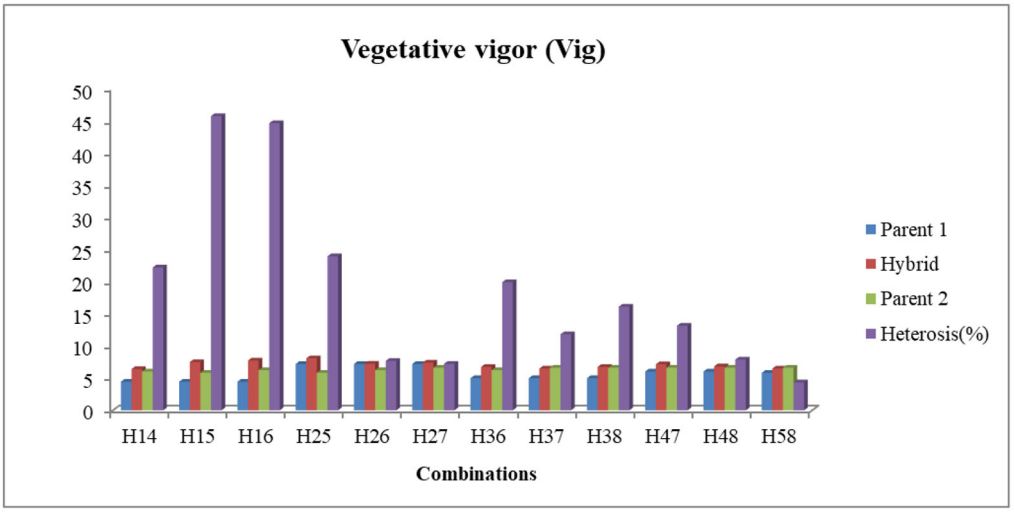
The maximum score obtained from the correlation index was 0.93 (**Figure 4**). In general, PD was not correlated linearly with GD. Phenotypic diversity was also poorly correlated with SCA and the mean performance of the hybrids. The average score of the traits displayed a higher correlation with GD than with PD. Specific combining ability and the means of the hybrids for Vig and Y traits displayed the highest positive correlations with GD. In addition, the CLR trait was highly negatively correlated with Vig trait.

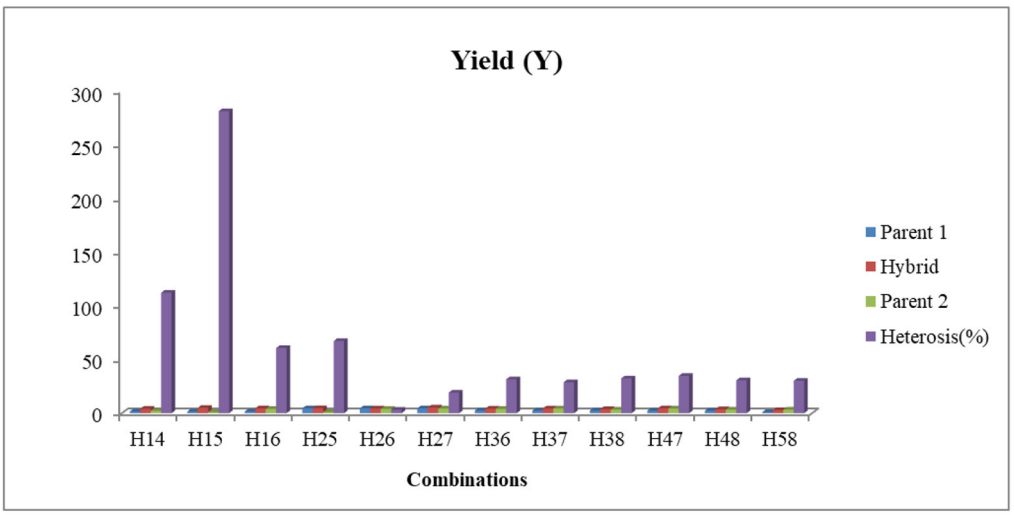
DISCUSSION

Genetic Diversity

The success of crop breeding programs lies in the efficient identification and incorporation of GD, while preserving the important economic traits of an individual plant (Swarup et al., 2020). To achieve this goal, breeders usually use cross-cultivated genotypes to avoid the linkage drag of wild genetic material, but they need to maintain diversity to address the producer and consumer demands. In addition, higher GD in plants allows them to adapt to sudden environmental changes (Raza et al., 2019).

In this study, the DNA of 22 coffee cultivars and accession, with the potential to be used in breeding, showed low diversity (mean: 2.3 bands/primer). The narrow genetic base of *C. arabica* has been reported worldwide, which is explained by the recent origin of the species with a single polyploidization event, autogamous reproduction system, and poor initial global distribution (Missio et al., 2011; Sousa et al., 2017a; da Silva et al., 2019; Jingade et al., 2019; Merot-L'anthoene et al., 2019; Sánchez et al., 2020; Scalabrin et al., 2020). Moreover, its genetic resources have been conserved in the field and, therefore, may be quickly eroded due to local hazards and global climatic change, worsening the genetic variability reduction (Legesse, 2020). For Brazilian cultivars analyzed in this study, the limitation of low





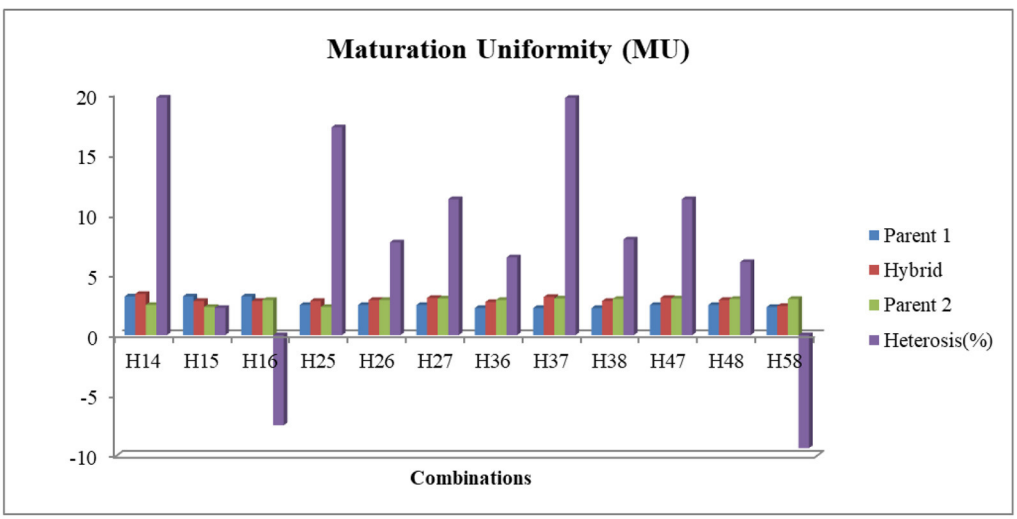
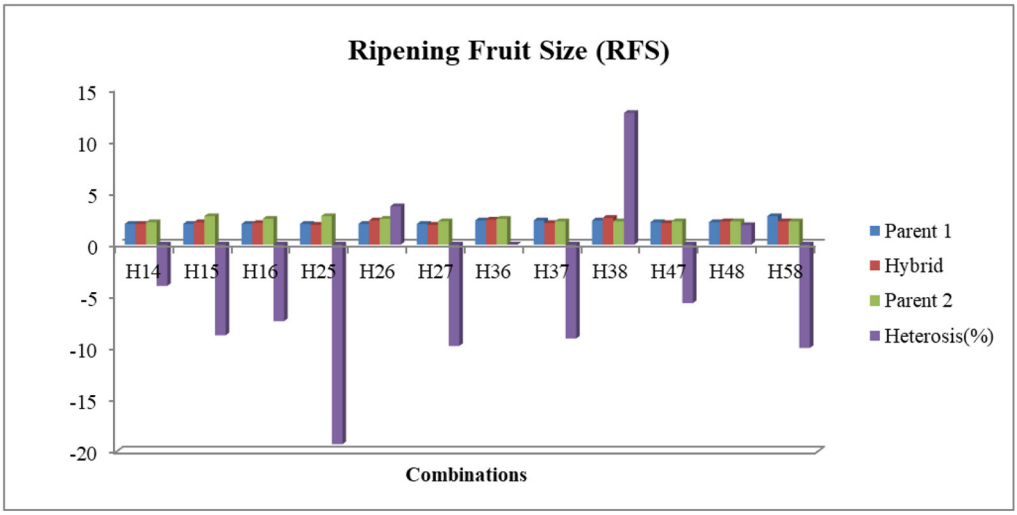
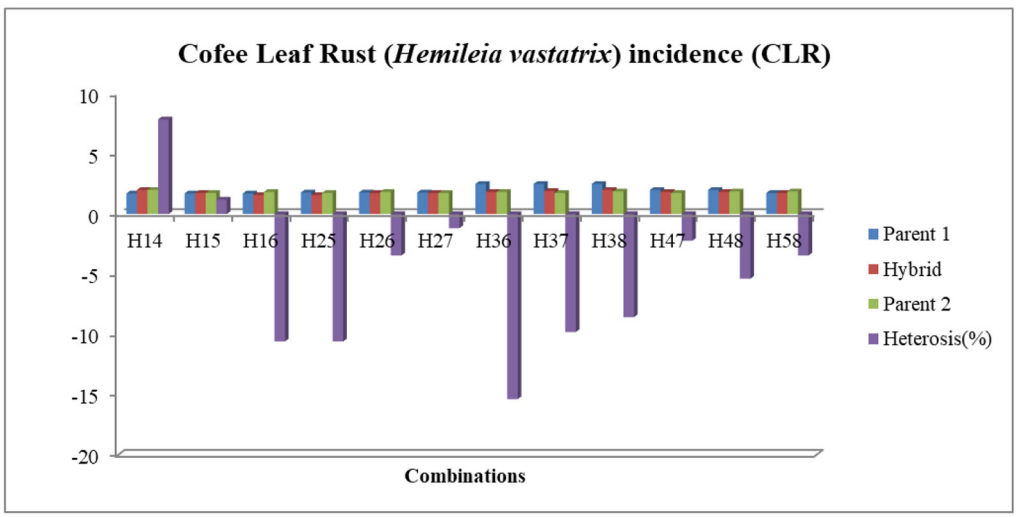


FIGURE 3 | Continued





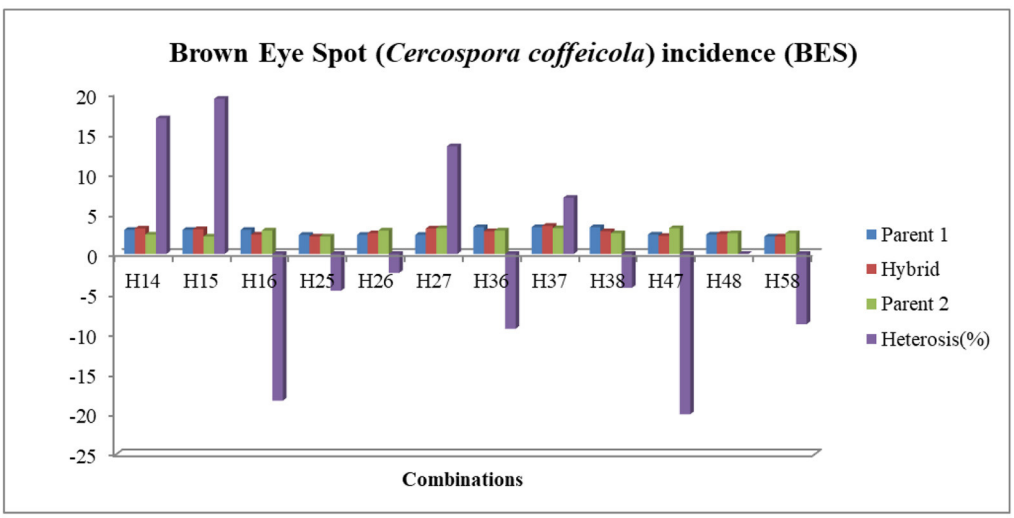


FIGURE 3 | Continued

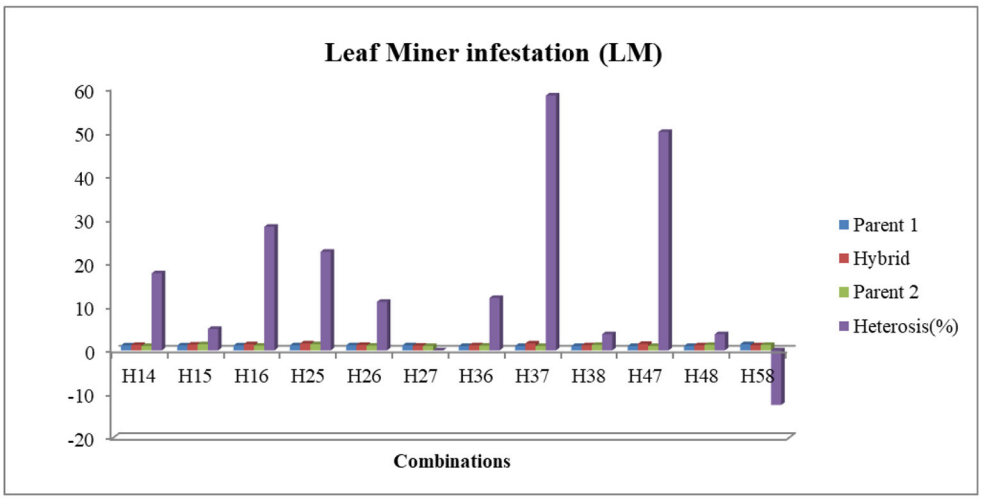


FIGURE 3 | Estimated means of parents and hybrids and values for the heterosis of 12 F_1 hybrids (H14 to H58—**Table 3**) obtained in a circulating diallel scheme, based on the means of agronomic traits.

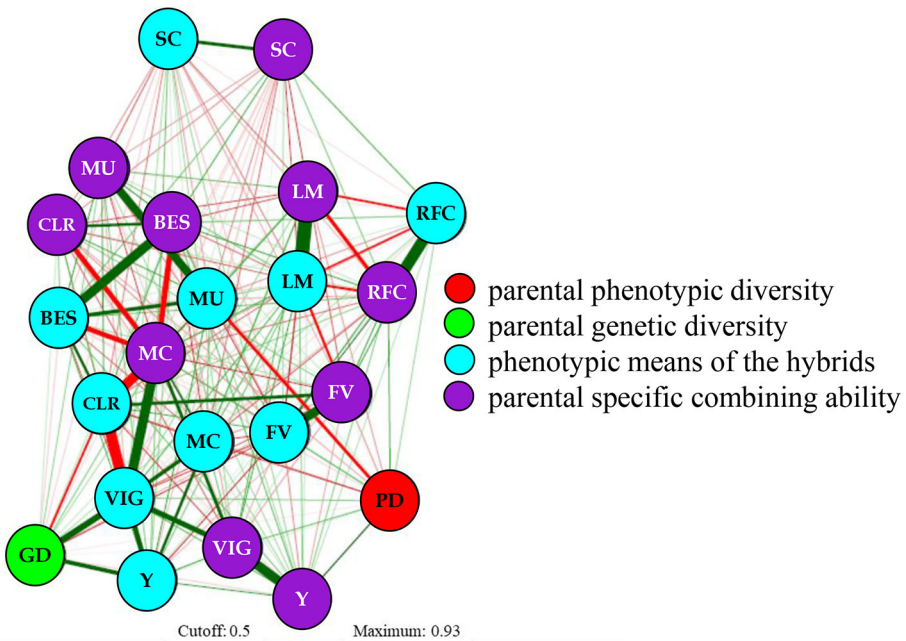


FIGURE 4 | Network correlation showing the relationship among the phenotypic diversity (PD) of the diallel parents, the genetic diversity (GD) of the parents based on SSR markers, the mean performance of the hybrids for each trait, and the specific combining ability. Evaluated traits: vegetative vigor (Vig), sprout color (SC), ripening fruit color (RFC), yield (Y), maturation cycle (MC), maturation uniformity (MU), ripening fruit size (RFS), incidence of coffee leaf rust (CLR), incidence of brown eye spot (BES), and leaf miner infestation (LM). The green lines correspond to the positive correlations and the red lines to the negative correlations. The width of the line is proportional to the intensity of the correlation.

variability has been aggravated by the low number of plants introduced in the country and used in genetic breeding. It has been demonstrated that Brazilian *C. arabica* cultivars originate from a few parents (Setotaw et al., 2013). The genetic base of 121 cultivars released in Brazil between 1939 and 2009 was defined by 13 ancestors, among which seven ancestors contributed 97.55% genetic base. Low genetic variability of the 34 main *C. arabica* cultivars planted in Brazil has been confirmed in another study (Sousa et al., 2017b).

Even with the recognized narrow genetic base of *C. arabica* plants available to be used in the breeding programs, informative data on GD was obtained through molecular markers, genetic distance matrix analysis, and dendrograms in this study. Bourbon Amarelo MG 0009, Topázio MG 1190, Catuaí Amarelo IAC

62, Ibairi IAC 4761, and Catuaí Vermelho IAC 144 were allocated to subgroup I.b (**Figure 1**). This can be explained by the fact that these cultivars/accessions are susceptible to CLR (Legesse, 2020) and do not have the introgression of genes from other coffee species. Genes that confer resistance to CLR and other diseases and pests have been introgressed into *C. arabica* cultivars through interspecific hybrids. The chromosomal section responsible for resistance introgressed in the cultivar and is responsible for increasing the GD (Setotaw et al., 2013, 2020), which explains the separation of cultivars with no interspecific genome. The exception was observed for the cultivar Arara and accession UFV 311-63, which were allocated in subgroup I.b, but they are considered rust-resistant. Arara originated from the spontaneous hybridization between Obatã IAC 1669-20 and Catuaí Amarelo. Obatã IAC 1669-20 itself probably originated from the spontaneous hybridization between Sarchimor and Catuaí (Pereira and Oliveira, 2015). Successive backcrosses with cv. Catuaí may explain the genetic similarity to susceptible coffee trees.

The remaining cultivars/accessions were rust-resistant and distributed in the other groups of the dendrogram, except for the cultivar Arara and accession UFV 311-63, which were allocated in subgroup I.b, the group of rust-susceptible cultivars. Rust-resistant *C. arabica* cultivars are generally derived from the HdT or Icatu interspecific hybrids between *C. arabica* and *C. canephora* (Del Grossi et al., 2013). These germplasms carry genes from the *C. canephora* species, which facilitates *C. canephora* genome introgression in *C. arabica* (Sousa et al., 2017a; Setotaw et al., 2020). These results demonstrate the potential of HdT and Icatu to expand the genetic base of *C. arabica*.

The high dissimilarities in scores between Catiguá MG2 and Acauã cultivars (0.750), and Catiguá MG2 and Topázio MG 1190 cultivars (0.696) can be explained by the parents of these cultivars, which are genetically distant. Catiguá MG2 was originated by crossing Catuaí Amarelo IAC 86 and HdT UFV 440-10, while Acauã originated from the cross between Mundo Novo IAC 388-17 and Sarchimor IAC 1668 (Carvalho, 2008). Topázio MG 1190 originated from the cross between Catuaí Amarelo and Mundo Novo, and therefore does not present *C. canephora* introgression in the genome (Legesse, 2020). Catiguá MG2 showed relatively high genetic distance score (>0.464) with all cultivars/accessions analyzed, except Híbrido de Timor MG 0357 (0.214). This HdT corresponds to the seed obtained from accession HdT UFV-441, which has a high genetic similarity with HdT UFV-440, the progenitor of the cultivar Catiguá MG2 (Silva et al., 2018; Setotaw et al., 2020).

The polymorphism observed in the 76 *C. arabica* plants evaluated in our study, including the polymorphism within cultivar, must be considered for parent selection for the *C. arabica* breeding programs. This information can be used to choose cultivars and individuals within cultivars to be crossed to explore the existing genetic variability and complementarity. For example, if a cross between IAC 125 RN and HdT MG 0357 is the choice due to the complementarity of interest traits, the HdT MG 0357 plant n° 51 should not be selected, as it has been allocated to some IAC 125 RN plants. In contrast, plant n° 51 of HdT MG 0357 can be used, as they were allocated to different groups. These results demonstrate the high efficiency of SSR markers in assisting the selection of the best plants within each cultivar/accession, avoiding the selection of genetically similar plants.

Hybrid Identification by Molecular Markers

Coffea arabica plants were crossed considering their diversity and complementary traits and potential F_1 hybrids were obtained for *C. arabica* breeding. Before advancing to the next breeding generation, the true hybrids were identified. Confirmation of cross success and discrimination between parent genotypes and hybrids is essential for genetic breeding. During breeding, the obtained hybrids are prone to contamination by out-crossing with foreign pollen or physical admixtures (Carvalho, 2008; Krishna et al., 2020). In autogamous species, such as *C. arabica*, self-pollination is common before controlled out-crossing, preventing the transfer of desired traits in progenies. Therefore, cross certification and genetic purity testing of hybrids is a routine and essential approach to an efficient breeding program. Early hybrid identification is a limitation for coffee breeding (Sánchez et al., 2020), and molecular marker analysis can facilitate this process.

In this study, SSR markers were used to certify artificial crossing in a diallel scheme, and the desired crosses were detected in most analyzed hybrids. These results show the informative power of SSR markers in crossbreeding certification. This certification is of great importance in breeding programs, particularly of perennial species, such as *C. arabica*, as it eliminates unwanted genotypes and self-fertilized progenies early, thus saving time, financial resource, and labor.

Although the hybridizations were artificially made by hand, self-fertilized progenies were identified. Hybridization in autogamous plants generally consists of emasculating the flowers and removing the anthers few days before pollination (Georget et al., 2019). In *C. arabica*, the flowers are hermaphrodite and autogamy occurs due to the phenomenon of cleistogamy, which occurs before the flower opens. In this case, emasculation must be performed before the flower opens and before it has been self-pollinated; however, the stigma must already be ripe. Thus, emasculation or crossing was probably performed after self-pollination in the self-fertilized F_1 progenies.

Diallel Analysis

To efficiently select the best crosses for coffee breeding, a diallel analysis was performed in addition to testing the parent diversity, with eight coffee cultivars/accession. The diallel results also revealed the gene action involved in important agronomic characteristics. The variance analysis carried out for 10 morpho-agronomic traits showed additive and non-additive genetic variability, which were statistically significant for both GCA and SCA. For all evaluated traits, the GCA was higher than the SCA, indicating high contribution of the additive gene action in controlling the traits. The additive genes affect the proportion of phenotypic variation transmitted to successive generations and are therefore responsible for the performance of the genotypes in the progeny at when homozygosity is reached (Silva et al., 2013). In autogamous breeding programs, plant selection is practiced in advanced generations of self-fertilization, maximizing genetic progress through the additive effects of genes (Hallauer et al., 2010). Classical *C. arabica* breeding is composed of genealogy and

backcross breeding methods, and the mating system is applied for effective pure-line selection from selfing and elite genotype testing (Fanelli Carvalho et al., 2020). Thus, in autogamous species, such as *C. arabica*, GCA is important for breeders because it depends on additive variance, while SCA depends on the variance due to deviations in dominance.

Low positive or negative GCA estimate indicates that the parental GCA does not differ from the general average. However, when these estimates are high, the parent is superior to the other parents of the diallel. Thus, to develop the hybrid, the best combination should be those with high SCA estimates, whose parents have a high GCA estimate (Kaushik and Dhaliwal, 2018). In this study, Catiguá MG2 and Arara had high GCA estimates for Vig trait (0.494 and 0.299, respectively), indicating that these genotypes are the most recommended for developing a base population for breeding aimed at enhancing Vig. However, the cross between these two parents produced a hybrid with a negative SCA score. Thus, crossing Catiguá MG2 and UFV 311-63 should be prioritized for Vig improvement, as both parents presented positive GCA estimates and high SCA effect. The diallel analysis also showed that the combination of Paraíso MG H 419-1 and Arara has potential for Vig breeding as it presented a high SCA effect score (1.278) and involves one of the parents with high GCA estimate (Arara). Vig is an important trait for coffee, as it is positively correlated with Y (Severino et al., 2008; Pedro et al., 2011) and genotype adaptation, reflecting less depleted plants (Nadaleti et al., 2018).

Like other crops, one of the main objectives of coffee breeding programs is to increase productivity (De Paiva Barbosa et al., 2019a). Therefore, based on diallel data, Acauã Novo and Catiguá MG2 had the highest GCA scores for Y (0.603 and 0.581, respectively). The hybrid from the cross between these two parents showed an estimated SCA score of 0.324. Thus, as the estimated SCA score for this hybrid was high and positive and involved the two parents with the highest GCA scores, the cross between Catiguá MG2 and Acauã Novo is recommended for this trait. Another potential cross would be between the Catiguá MG2 and UFV 311-63, since the hybrid resulting from this cross had the highest estimated SCA score (0.909) and involved one of the parents with high estimated GCA score.

UFV 311-63 and Oeiras MG 6851 displayed the best GCA scores for fruit MU (−0.241 and −0.179, respectively) and no significant difference in the SCA scores. The lowest negative scores are desirable for MU, since the lowest scores indicate the highest fruit ripening uniformity. MU is related to coffee beverage quality, and in the recent years, there has been an increasing demand for the best quality coffees (De Paiva Barbosa et al., 2019a); moreover, MU contributes to labor reduction during harvest.

In addition to yield and quality, coffee breeding focuses on biotic stress resistance. In this study, we evaluated the parental resistance to CLR, BES, and leaf miner. Phenotypic evaluation was based on the incidence and infestation of these biotrophic agents. Thus, the plants that received the lowest score were the most resistant, implying that low GCA and SCA scores are desired. Arara and UFV 311-63 displayed the best GCA scores for CLR (−0.072 and −0.070, respectively), and no significant difference in the SCA scores. Thus, crosses involving UFV 311-63 and Arara have the greatest potential for resistance to CLR. UFV 311-63 and H 484-2-18-12 displayed the best GCA scores for BES (−0.268 and −0.178, respectively), and no significant difference in the SCA scores was obtained. Crosses involving at least one of these parents are recommended. Leaf miner infestation was similar in all parents studied.

The hybrids with the highest scores of phenotypic mean for Vig and Y traits were obtained from the recommended crosses based on GCA and SCA evaluation (Catiguá MG2 × UFV311-63 for Vig and Catiguá MG2 × Acauã Novo for Y). Moreover, the mean yield of these hybrids was higher than that of their parents. This result shows that the combining ability evaluation-based hybrid prediction is an effective technique and can be particularly useful for breeding programs, since cross selection in the diallel scheme was based on genetic parameters.

In general, crosses involving Catiguá MG2, UFV 311-63, and Arara were the most promising. Hybrids originating from Catiguá MG2 were recommended for Vig and Y traits, and this cultivar also showed the highest genetic distance from almost all other *C. arabica* progenies analyzed according to the GD study (**Figures 1**, **2**). These results show a potential relationship between GD, phenotypic mean, and combining ability. In addition, Catiguá MG2 has been used as a source to enhance cup quality and obtain specialty coffee (Alex et al., 2016; De Paiva Barbosa et al., 2019b). This cultivar has also been highlighted for its high resistance to CLR (Del Grossi et al., 2013) and moderate resistance to bacteriosis caused by *Pseudomonas syringae* (Fernandes et al., 2020).

As the crosses were made between fairly inbred parents, the heterosis was also evaluated for the different traits. Hybrid vigor or heterosis represents the average superiority of a crossbred individual in relation to the average performance of their parents. Heterosis also depends on genetic differences between the parents being crossed. In our work, hybrids that surpassed the average of their parents in some traits were identified. Other studies showed the advantages of exploiting heterosis in *C. arabica* hybrids, with significant yield gains, when compared to the average of the parents and the best parent (Bertrand et al., 2005, 2011). However, no hybrid in our work showed superiority for all evaluated agronomic characteristics. A higher level of heterosis was found for Vig and Y and, in general, the cultivar Paraíso MG H419-1 was used as one of the hybrids parentals.

Correlation Analysis

In breeding programs, genetically contrasting cultivars/accessions containing relevant agronomic traits are mostly crossed. Thus, through gene recombination, it is possible to obtain genetic gains that enable the success of breeding programs. Nevertheless, the ideal situation is the involvement of genetically diverse parents with good proven performance in crosses, whenever possible (Ramalho et al., 2013). To assist this strategy, it is important to evaluate cultivars and elite accessions and test the relationship among their GD (obtained here by molecular markers), PD, phenotypic mean of their hybrids, and combining ability. Thus, if these parameters are somehow correlated, a complex parameter should be estimated using a simple and low-cost analysis. For example, for Vig and yield (Y), the cross between Catiguá MG2 and UFV 311-63

has recommended based on the scores of general and specific combining abilities obtained through diallel analysis. Genetic distance matrix analysis indicated that these two genotypes had a high genetic dissimilarity score (distance = 0.589).

The joint analysis of molecular and phenotypic data was especially important in our work. Diallel analysis were performed based on phenotypic data from a single year, the first year with significant yield (3.4 years after planting). Since some evaluated traits are quantitative, data from additional years would be required to confirm the performance of hybrids and parentals. However, the high correlation between GD and phenotypic data allowed the early selection of genetic materials, which is essential for coffee, a perennial crop with a long reproductive cycle.

Network correlation indicated that PD was not linearly correlated with GD in the eight *C. arabica* plants evaluated using circulating diallel (**Figure 4**). Phenotypic diversity was also poorly correlated with specific combining abilities and mean performance of hybrids in all evaluated traits. However, hybrid performance and parent-specific combing ability were closely correlated with GD. These results corroborate those obtained for corn (Makumbi et al., 2011) and sunflower (Reif et al., 2013). The correlation between molecular marker-based GD and combining ability was evaluated in genetically related and unrelated groups of sunflowers *(Helianthus annus L.)* (Reif et al., 2013). A strong correlation was observed for related genotypes, but not for unrelated genotypes. For tropical test lines of corn *(Zea mays L.)*, a high correlation was also observed when related genetic materials within the same heterotic group were crossed.

Previous studies have demonstrated a high correlation between the combination ability estimated using diallel crosses and genetic distance estimated using molecular markers, when genetically related genotypes are crossed. *Coffea arabica* plants are genetically related due to their narrow genetic base and, therefore, reduced genetic variability (Sousa et al., 2017a), which can maximize the correlation between these parameters. The correlation among molecular GD, hybrid performance, and SCA can help in cultivar selection for the genetic improvement of *C. arabica*. The use of molecular GD allows the early selection of *C. arabica* plants in the breeding program, which is particularly important for perennial and long-cycle species (Sousa et al., 2019).

Vig and Y traits were the most positively correlated with GD. In addition, CLR incidence trait was highly negatively correlated with Vig trait. These traits have been the focus of most coffee breeding programs. The 12 SSR markers used to assess GD were pre-selected in other studies (Pestana et al., 2015; Sousa et al., 2017b) because they are highly polymorphic, assuming high importance in this species due to their narrow genetic basis. Thus, it can be inferred that GD evaluation-based parent selection for the genetic improvement of *C. arabica* is a useful technique, since the molecular distance was highly correlated with the phenotypic means of the hybrids and parent combining ability.

CONCLUSIONS

Molecular marker-based GD analysis allows a detailed assessment of the genetic distance between and within coffee cultivars/accessions. Using molecular markers is an efficient approach to assist parent selection and true hybrid identification to develop a segregating *C. arabica* population for breeding and therefore efficiently increase GD in *C. arabica* cultivars. Circulating diallel cross is an effective technique for the genetic improvement of *C. arabica*, and selecting crosses based on general and specific combining abilities can be very useful for obtaining promising breeding population.

Coffea arabica breeders can increase GD through strategic molecular marker integration, crossbreeding certification, and diallel approach, while preserving the economically important traits of individual crops. Using this strategy, elite genetic resource can be included in breeding programs and new cultivars may be developed in response to rapid shifts in global coffee cultivation conditions and resources due to climate change and new demand from coffee producers and consumers.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

EC and AO: conceptualization. AM, TS, and CC: methodology. CC: software. EC, AO, LZ, and AP: validation. AM and EC: formal analysis and investigation. AO and AP: resources. AM, EC, TS, and VS: writing—original draft preparation and review and editing, EC: supervision. EC, AO, LZ, and AP: funding acquisition. All authors have read and agreed to the published version of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fsufs.2021.705278/full#supplementary-material

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