scientific reports

OPEN

Heterotic potential and combining ability of *Coffea arabica* L

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The use of hybrid vigor or heterosis in *Coffea arabica* L. cultivation has gradually been commercially explored worldwide since research has evolved in understanding this phenomenon and the vegetative propagation techniques or male-sterility making its use viable. Additionally, coffee producers adopting this technology have continuously increased. Therefore, we studied the existence and magnitude of heterosis and estimate the combining ability of parents in bi-parental crosses. The experiment was installed in 2019 using a randomized block design with three replications, with the experimental plot consisting of six plants. The experimental treatments consisted of 90 hybrids and 34 parental lines in which the grain yield in bags of processed coffee per hectare was evaluated according to the cumulative result of the first three harvests. Significant differences were observed between the 124 treatments, with the mean accumulated productivity values of the best hybrids surpassing those of the four most used commercial cultivars by more than 74 bags of coffee per hectare. The average yield mean heterosis was 64.2%, varying from − 26.1 to 184.4. Both the general combining ability (GCA) and the specific combining ability (SCA) were statistically significant, with the best-performing lines identified as potential parents being 'Acauã Novo', 'IAC 125 RN', 'MGS Liberdade', 'Catiguá MG2', and 'Sarchimor MG 8840'. Promising hybrids for commercial exploitation were identified with a productive advantage of 30% relative to the best commercial standard cultivar, reinforcing the potential of this technology for *C. arabica* L. cultivation future.

Keywords Yield, Productivity, Heterosis, General combining ability, Specific combining ability, Hybrid Vigor

Records of coffee cultivation began in the 16th century[1]. Since then, coffee production has expanded across the intertropical world, covering approximately 11 million hectares and involving around 25 million producers, establishing itself as the second most valuable global commodity and the second most consumed beverage worldwide[2]. The beneficial economic and social sector, provided by the crop, faces several challenges, primarily driven by climate change and its impacts on production and farmers' livelihoods. Rising temperatures, prolonged droughts, pest and disease outbreaks, labor shortages, and increasing production costs threaten the sustainability of coffee cultivation[3]. Additionally, there is an increasing demand for sustainability across the coffee supply chain. Addressing these challenges requires technological advancements to enhance the resilience of coffee production[4].

The development of improved coffee cultivars represents one of the most promising and sustainable strategies for addressing the challenges facing global coffee production. Advances in coffee breeding have resulted in cultivars with greater adaptability to climate change, resistance to pests and diseases, and improved yield stability. These cultivars reduce reliance on chemical inputs, enhance resource efficiency, and contribute to the long-term sustainability of coffee farming by maintaining consistent production under variable environmental conditions. Additionally, higher-yielding and high-quality cultivars can improve farmers' livelihoods by increasing productivity and meeting the evolving demands of global markets[5–7].

Hybrid vigor, or heterosis, has favored the agricultural success of different crops, meeting the needs of farmers in the search for more profitable businesses, driven mainly by increased productivity and increased efficiency. Hybrid plants can be combined into cultivars with a high level of productivity and complementary characteristics, such as resistance to diseases, pests, nematodes, and precocity. In addition to contributing to greater crop stability and productive adaptability, as they bring together the genetic constitution characteristics

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of parents that perform well in different environments, that is, plants that have a high proportion of favorable alleles[8].

In *C. arabica*, a self-pollinated plant with 2n = 4x = 44 chromosomes resulted from a natural hybridization between the *Coffea canephora* (Robusta coffee, subgenome CC (subCC)) and *Coffea eugenioides* (subgenome EE (subEE)) both with 2n = 2x = 22[9], the hybrid vigor in intraspecific crosses is studied since the beginning of 1950s. However, at that time the heterosis for grain yield did not gain breeders attention due to the low value and lack of viable propagation technique in large scale[10,11]. With technological evolution and broadened genetic basis, in 1980s promising results start to be published[12,13] and the first hybrid cultivar Ruiru 11 was developed in Kenia[14,15] and in 1990s the hybrid production intensified in Central America[5], Ethiopia[16], Kenia[17], Indonesia[18] and Colombia[19]. In Brazil, the study of hybrid vigor began in 1950[20]. To date, only two out of 124 available cultivars are propagated as clones, with an unknown level of heterozygosity[21]. According to the World Coffee Research (WCR) cultivar catalog, 10 of the 58 *C. arabica* cultivars are hybrids[22] and in Ethiopia 42 cultivars were released between 1977 and 2018, including 35 pure lines and seven hybrids[23].

Currently, most of the Arabica coffee sold worldwide comes from inbred cultivars due to the autogamy of the species and difficult in hybrid propagation by clones, although crossings could be carried out manually as in Ruiru 11 cultivar. The process to reach a homozygous cultivar, or pure line, has lasted approximately 25 years. In hybrid cultivar the development cycle can be reduced to 10 years[5]. The magnitude of heterosis, generally demonstrated in percentage, varies according to the phenotypic mean and diversity of the parents and the trait taking into consideration. As an example, according to the work of Bertrand et al.[24] heterosis values in *C. arabica* L. ranged from 20 to 50% in relation to those of the parents.

The same author and collaborators commented in 2011 that since 1997, coffee growers in Central America have had access to *C. arabica* L. F_1 hybrids propagated vegetatively, either by micropropagation or through somatic embryogenesis. The data presented in 2011 by the authors provide information from 2000 to 2006 for 15 locations in three Central American countries at different altitudes. They found that, in all altitude ranges, hybrids performed 52% better than cultivars did, ranging from 16 to 127% at low elevations (750 to 880 m) and 33%, considering mean values in higher lands (> 1,400 m), ranging from 8 to 95%[25].

An important information that could be extracted is the performance of parents in hybrid combination in a diallel design to through estimation of the combining ability. This genetic mean component could be divided into general (GCA) and specific (SCA). The main purpose is to choose parents capable of inheriting their desirable phenotype[26]. Both are essential to plant breeders to delineate the future crosses focus on the breeders' objectives, like developing a hybrid or homozygous cultivar, and could generate knowledge regarding the mode of genic action affecting the characteristics. Such information is of utmost importance because the one coffee plant could be of good performance but when used in crosses their merit could not be inherited. In *C. arabica* there is some information of combining ability of traits related to grain yield, morphological characters, beverage quality and root development, using parents with diverse genealogy and origin[16].

Generally, for grain yield and their components GCA and SCA are statistically significant, with a predominance of SCA. Another important information is the possibility of interaction of combining abilities with environment (E) and the probability of lack of correlations between the parents phenotypic mean and the GCA and SCA magnitude[27]. So, crossing better parents and evaluating their descendants to obtain combining abilities could allow the cultivars evolution due to plants will always increase their performance trough plant breeding.

Since plant breeding is based on the accumulation of advantages, which must be used for the benefit of society. With this purpose, the Empresa de Pesquisa Agropecuária de Minas Gerais (EPAMIG) began crossing lineages in 2017, aiming to develop commercial hybrid combinations and generate information that optimizes the breeding program, thus helping to reduce the lack of information on the subject. Our hypothesis is based on two assumptions. First, heterosis could be reached by crossing correct parents. Second, combining ability of diverse *C. arabica* parental lines is present and some populations, generated by the crossings, would be more suitable to hybrid and others to pure lines cultivars development.

The results of increasing productivity are promising and can contribute to the sustainable development of Brazilian and global coffee farming through increased production efficiency, thus generating value for the entire chain. So, the purposes of this study were to verify the existence and quantify the heterosis for coffee grain yield, with a focus on exploring hybrid clonal cultivars and providing information to guide *C. arabica* plant breeding programs for generating variability to obtain cultivars through the estimation of combining abilities of the parents.

Materials and methods

The research was carried out at the Experimental Field of Patrocínio (CEPC), belonging to the Empresa de Pesquisa Agropecuária de Minas Gerais (EPAMIG) and located in the municipality of Patrocínio, Minas Gerais State, Brazil. The geographic coordinates of the experimental field are 18° 59' 31.9" south latitude and 46°59'15.2" west longitude, with an elevation of approximately 993 meters above sea level .

The climate of the region is considered tropical climate (Aw) according to the Köppen climate classification, with hot and rainy summers, cold and dry winters, average temperature of 21.7 °C and annual precipitation of 1124 mm[28]. The highest average monthly temperatures 24ºC occur in September and October. From May to July, the average monthly temperatures are around 19ºC. Annual precipitation is concentrated from October to March and in the months of June to August, normal climatological indicates accumulated volumes of less than 21 mm (Fig. 1).

The soil in the experimental area was classified as Oxisol typic Hapludox[29]. The chemical and physical characterization of this soil was determined after sample collection and laboratory analysis. In the collection of soil samples an auger was used. Simple samples were collected to form a composite sample from depths of 0-0.20, 0.20–0.40, 0.40–0.60 and 0.60–0.80 m (Supplemental Table S1).

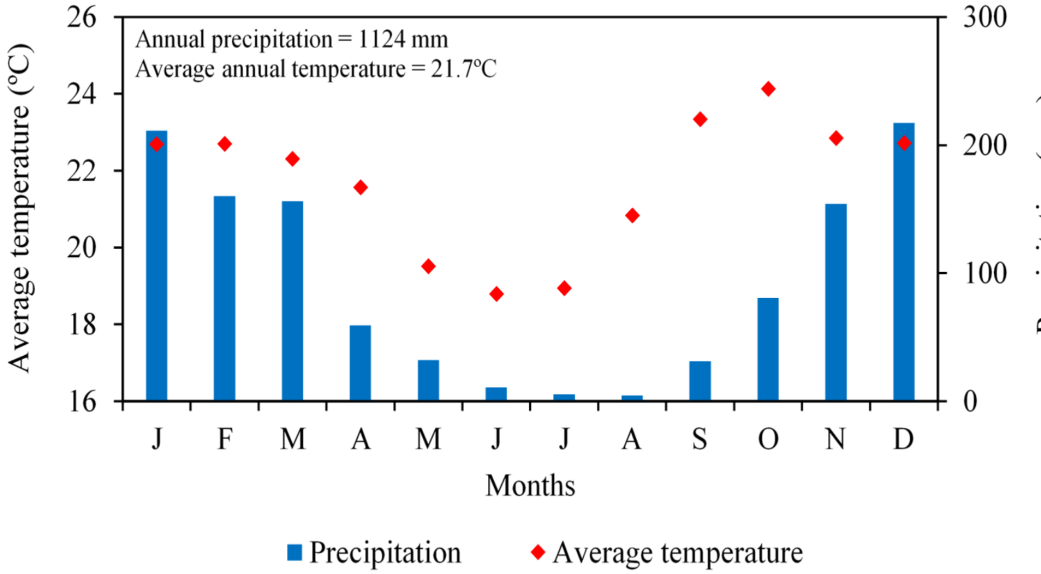

Fig. 1. Climatological normal for average temperature and precipitation for the Experimental Field of Patrocínio, Minas Gerais State, Brazil. J, January; F, February; M, March; A, April; M, May; J, June; J, July; A, August; S, September; O, October; N, November; D, December.

To obtain hybrid of *Coffea arabica* L., crosses were performed involving 56 parents represented by commercial cultivars and lines from the EPAMIG germplasm bank. These crosses were performed manually in 2017. After harvesting the fruits resulting from the crosses and producing the seedlings, planting was carried out in February 2019 in the full-sun conventional system. A spacing of 3.5 m × 1.0 m was used, three and a half meters between planting furrows and one meter between plants, resulting in 2,857 plants ha^{-1}.

The soil of the experimental area was prepared before planting and subjected to fertility analysis. Harrowing, limestone incorporation, opening of furrows and mineral and organic fertilization operations were carried out. Liming and fertilization were carried out following the recommendations[30] for the nutritional and acidity levels obtained in the soil analysis performed previously. Pest, disease and weed control practices followed a technological standard adopted by the experimental field, aiming to better understand the agronomic performance of *Coffea arabica* L. hybrids.

The experimental plots were irrigated using a drip irrigation system. The amount of water applied was defined by the irrigation scheduling method based on evapotranspiration and soil water balance. The coffee crop evapotranspiration estimates were calculated according to Eq. 1. $ET_c = ET_o * K_c$ (1), where ET_c is the daily actual evapotranspiration (mm), K_c is the crop coefficient (dimensionless), and ET_o is the daily reference evapotranspiration (Penman-Monteith method) (mm). The adopted specific K_c values and the reference evapotranspiration (ET_o) in a daily step were obtained through recommendations by Allen et al.[31].

The experiment was performed in accordance with a randomized complete block design (RCBD) with three replications, with 90 hybrids of *C. arabica* L. and 34 lines out of the 56 lines that were used in the crosses (genotypes in advanced homozygosity). The evaluation was carried out by quantifying the fruits weight harvested from the six plants in the experimental plot.

The first harvest took place in 2021, followed by two additional harvests in the subsequent years, 2022 and 2023, when most of the plots had at least 50% of their fruits matured. The fruits harvested from the plots were weighed using a digital hand scale. Production data from the experimental plots for each harvest were adjusted to the ideal number of plants per plot using covariance, following the methodology outlined by Botelho et al.[32]. During the harvesting process, a four-liter sample from each plot was collected and weighed with a digital hand scale to estimate the conversion index between fruit and peeled coffee beans. The samples were then air-dried under sunlight for approximately 30 days. Once the samples reached a moisture level of around 12%, the beans were peeled and weighed using a digital desk scale. The moisture content was adjusted to 12%. Subsequently, the weight of peeled coffee beans per plot was calculated by multiplying the adjusted weight of the harvested fruit by the conversion index (kg of peeled coffee / kg of fruit). This weight was then converted into the variable grain yield of 60 kg bags per hectare (bags ha^{-1}) using a planting density of 2,857 plants per hectare and then accumulated grain yield (bags ha^{-1}) of 2021, 2022 and 2023 harvests were calculated to eliminate the annual effects of crop production fluctuations[33]. After checking the assumptions of variance analysis, statistical analysis was performed considering the RCBD of this variable using the GENES Version program. 1990.2021.132[34] and Scott and Knott mean test[35] was performed to set similar treatments groups. To calculate the GCA and SCA the Statistical Analysis SAS Software[36] program was used using accumulated hybrids grain yield flowing the Griffing[26] method 4 and fixed effect.

Results

Table 1 presents a summary of the variance analysis of the accumulated coffee yield of the 124 treatments (90 hybrids and 34 lines) harvested from 2021 to 2023. Significant differences between treatments were observed for the accumulated grain yield in bags ha^{-1}. The experimental coefficient of variation (CV%) observed was relatively high compared to that reported in commercial cultivar competition trials[37]. This is probably a reflection of the greater variability found between treatments since we are working with initial harvests of the crop and with different types of genotypes (hybrids and lines) in the same experimental trial.

The average yield values for treatments, parents and hybrids, in the first three harvests are shown in Table 2. The mean productive performance of the 90 hybrids was 66 bags ha^{-1} of processed coffee, which corresponds to 26.0 bags ha^{-1} of coffee more than the line mean and was 40.7 bags ha^{-1} of processed coffee in the accumulated harvests, highlighting the potential of these hybrid genotypes for commercial exploitation. The five best hybrid combinations, EPAMIG 37, EPAMIG 06, EPAMIG 36, EPAMIG 66, and EPAMIG 17, among the 90 evaluated, produced a mean of 120 bags ha^{-1} in the first three harvests. This value is well above the mean for most cultivated commercial standards, Catuaí and Mundo Novo. The mean grain yield for the hybrid combinations was 118 bags ha^{-1}, ranging from 11 bags in the worst combination to 130 bags ha^{-1} in the best combination. It is worth noting that the mean test used was efficient at differentiating the hybrids and their parents into four distinct groups and that 23 hybrids out of the 90 evaluated were positioned in the most productive group and no parent. In the second group of the mean grouping test out of 37 treatments, 28 were hybrids. In the third group formed by Scott and Knott test, 63% of the entries were hybrids. In the last group no hybrids were present, counting on two cultivars.

The same lowercase letters in the columns indicate groups formed by Scott and Knott test ($P \leq 0.05$).

The mean heterosis (MH%) considering 18 crosses (including both MH% and H%) was 64.2% (-26.11 to 184.4). In these same crosses, the heterosis rate in relation to that of the superior parent, heterobeltiosis (H%), was 40.8%, ranging from −42.9 to 196.7 (Table 3). In relation to heterosis, the highest values were obtained for the hybrid EPAMIG 30, and the highest heterobeltiosis was found for the hybrid EPAMIG 80. Despite the high mean heterosis values, some hybrids presented negative values, indicating that they are less productive than their parents are, revealing genetically close crosses. This fact is perfectly possible considering the narrow genetic base of the species *C. arabica* L.

The SH% values of the 90 combinations ranged from −74.4 to 181.2, with a 43.4% mean (Table 4). It is important to highlight that the yields of these 15 hybrids doubled in relation to the mean yield of the four cultivars most used for coffee growing (46.5 bags ha^{-1} in total), and the hybrids produced more than 97 bags ha^{-1} in total. The simple use of one of the three best hybrids for commercial crops would increase the accumulated yield of the first three years by more than 265%. Instead of producing 46.5 bags of processed coffee during the accumulation period, the producer would be producing 124 bags ha^{-1} of processed coffee.

Standards cultivars: Mundo Novo IAC 349 – 19, Catuaí Vermelho IAC 144, Catuaí Vermelho IAC 99, and Catuaí Amarelo IAC 62. Best cultivar: IPR 102.

Table 5 presents a summary of the diallel analysis considering the F_1 hybrids, highlighting the significance of the GCA and SCA effects, indicating that the additive GCA of the evaluated parents and SCA of hybrids are different. So, parents are different in their favorable allelic frequencies and some hybrids have better parent complementation than others as expected by their parents' average performance in crosses. The CGA accounted for 74% of the sum square of hybrids grain yield.

The GCA assumed values between 69.3 to 'Bourbon Amarelo MG 009' to − 63.1 for 'Catiguá Amarelo'. However, both parents have participating of only one cross each. When we pick up the parents with more crosses, the 'Acauã Novo' was the best and 'MGS Catucaí Pioneira' the worst. The higher the GCA value, the higher the frequency of favorable alleles from the parents in relation to those used in the development of the 90 hybrids. Other high breeding value parents were 'IAC 125 RN', 'MGS Liberdade', 'Catiguá MG2', 'Sarchimor MG 8840', 'Gueisha' and 'IAC Obatã 4739'. Some of these good CGA parents are present in the phenotypic mean test (Table 2), with three of them ranking among the highest gain yield pure line parents. Furthermore, 'IPR 103' demonstrated notable grain yield and general combining ability (GCA), although it was involved in only one cross. On the other hand, 'IPR 102' had high grain yield and was one of the poorest GCA parent, probably indicating the presence of heterozygosis or negative heterosis with the parents crossed (Table 6).

The best ten SCA hybrids seven were classified in the first group of the mean test performed, one in the second and three in the third group. When considering the worst ten SCA hybrids, two were positioned in the second mean test group and the rest in the third group. The correlation between the mean phenotypic grain yield value and SCA was estimated in 0.49, a low value, indicating that the chosen of parents to make hybrids should

Sources of variation	df	Ms	F value
Replications	2	14151.47	
Treatments	123	2445.71	3.91 **
Residuals	246	624.49	
Mean		59.58	
CV (%)		41.94	

Table 1. Summary of analysis of variance for the yield of processed coffee in bags of 60 kg per hectare in the accumulated harvests carried out in 2021, 2022, and 2023. **Significant at 1%, according to the F test; CV (%) experimental coefficient of variation, df: degree of freedon; Ms: Mean Square.

Hybrids	bags ha^{-1}	Hybrids	bags ha^{-1}	Hybrids	bags ha^{-1}
EPAMIG 37	130 a	EPAMIG 46	70 b	EPAMIG 55	42 c
EPAMIG 06	124 a	EPAMIG 50	69 b	EPAMIG 18	41 c
EPAMIG 36	116 a	EPAMIG 49	68 b	EPAMIG 59	41 c
EPAMIG 66	114 a	IAC 125 RN	67 b	EPAMIG 65	40 c
EPAMIG 17	114 a	Icatu x Catimor H-29-1-8-5	67 b	EPAMIG 79	40 c
EPAMIG 84	113 a	EPAMIG 73	67 b	EPAMIG 42	39 c
EPAMIG 51	111 a	EPAMIG 08	66 b	Catucaí Amarelo 24–137	39 c
EPAMIG 02	108 a	EPAMIG 54	65 b	EPAMIG 62	39 c
EPAMIG 86	102 a	EPAMIG 19	65 b	EPAMIG 60	38 c
EPAMIG 53	101 a	Mundo Novo IAC 379 – 19	65 b	Topázio MG 1190	37 c
EPAMIG 29	100 a	EPAMIG 48	65 b	EPAMIG 16	36 c
EPAMIG 44	99 a	EPAMIG 10	64 b	Icatu x Catimor H 105-01-39	36 c
EPAMIG 21	98 a	EPAMIG 80	64 b	MG 0192 Caturra Vermelho	35 c
EPAMIG 33	97 a	EPAMIG 61	64 b	Catiguá Amarelo	34 c
EPAMIG 43	97 a	Acauã Novo	63 b	EPAMIG 71	34 c
EPAMIG 23	95 a	Guará	63 b	EPAMIG 03	34 c
EPAMIG 85	94 a	EPAMIG 13	61 b	Sumatra MG 0137	34 c
EPAMIG 27	94 a	EPAMIG 22	60 b	EPAMIG 05	32 c
EPAMIG 82	94 a	EPAMIG 15	59 c	Obatã IAC 4739	31 c
EPAMIG 58	93 a	EPAMIG 52	59 c	Gueisha	29 c
EPAMIG 01	92 a	EPAMIG 81	58 c	EPAMIG 76	28 c
EPAMIG 39	91 a	EPAMIG 20	57 c	EPAMIG 32	27 c
EPAMIG 09	89 a	EPAMIG 63	57 c	MG 0194 Caturra Amarelo	26 c
EPAMIG 30	86 b	EPAMIG 64	56 c	EPAMIG 34	26 c
EPAMIG 40	86 b	Azulão	55 c	MG 0176 Amphilo	25 c
IPR 102	84 b	EPAMIG 25	54 c	EPAMIG 57	23 c
EPAMIG 70	82 b	Catuaí Vermelho IAC 144	53 c	Icatú Precoce IAC 3282	23 c
IPR 103	80 b	EPAMIG 11	52 c	Catuaí Vermelho IAC 99	22 c
EPAMIG 31	79 b	EPAMIG 77	51 c	EPAMIG 89	22 c
EPAMIG 87	79 b	EPAMIG 88	50 c	Obatã IAC 1669-20	21 c
EPAMIG 24	79 b	EPAMIG 75	49 c	MG 0161 Maragogipe	20 c
EPAMIG 67	77 b	EPAMIG 74	49 c	EPAMIG 07	17 c
EPAMIG 78	77 b	EPAMIG 35	48 c	Híbrido Timor UFV 408 – 11	16 c
EPAMIG 28	76 b	MGS Aranãs	47 c	Típica Guatemala MG 003	15 c
EPAMIG 83	75 b	EPAMIG 68	47 c	EPAMIG 45	15 c
Sarchimor MG 8840	74 b	EPAMIG 38	45 c	Híbrido Timor UFV 376 – 52	15 c
IPR 100	74 b	EPAMIG 90	45 c	Pacas	15 c
EPAMIG 04	74 b	Catuaí Amarelo IAC 62	44 c	EPAMIG 12	11 c
EPAMIG 72	73 b	EPAMIG 47	44 c	Pacamara	10 d
EPAMIG 56	73 b	EPAMIG 69	44 c	Guatemalano	5 d
EPAMIG 41	71 b	Oeiras MG 6851	42 c	-	-
EPAMIG 14	70 b	EPAMIG 26	42 c	-	-

Table 2. Accumulated coffee grain yield values of F_1 hybrids and their parents of *Coffea arabica* L. in bags ha^{-1} during the 2021, 2022, and 2023 harvests.

not be based on phenotypic mean of the hybrids. Although EPAMIG 37 hybrid was the third in SCA and first rank in the phenotypic mean (Table 7).

Discussion

The use of hybrid cultivars to explore heterosis has been established in other species[38]. In *C. arabica*, this technology is gradually being adopted by coffee growers, especially in Brazil. If field conditions replicate the heterosis observed in experiments over the past seven decades, adopting hybrid cultivars could significantly boost grain yield with a simple and cost-effective change. Our hypothesis that heterosis could be reached by crossing complementing parents and combining ability of diverse *C. arabica* parental lines is present were confirmed by the results. The findings here encourage further development of hybrid cultivars and provide valuable information for parent selection, which is crucial for progress in plant breeding[39].

Hybrids	H%	MH%	Hybrids	H%	MH%	Hybrids	H%	MH%
EPAMIG 01	43.9	–	EPAMIG 31	173.0	–	EPAMIG 61	0.9	30.4
EPAMIG 02	95.5	–	EPAMIG 32	−4.8	–	EPAMIG 62	12.0	–
EPAMIG 03	–	–	EPAMIG 33	30.4	87.6	EPAMIG 63	115.0	–
EPAMIG 04	–	–	EPAMIG 34	−38.2	–	EPAMIG 64	20.0	–
EPAMIG 05	–	–	EPAMIG 35	–	–	EPAMIG 65	−14.2	–
EPAMIG 06	66.7	–	EPAMIG 36	71.0	76.5	EPAMIG 66	141.9	–
EPAMIG 07	–	–	EPAMIG 37	92.6	96.4	EPAMIG 67	14.7	35.0
EPAMIG 08	3.4	–	EPAMIG 38	–	–	EPAMIG 68	−0.2	–
EPAMIG 09	–	–	EPAMIG 39	35.7	84.5	EPAMIG 69	−7.0	–
EPAMIG 10	–	–	EPAMIG 40	130.8	–	EPAMIG 70	29.6	28.0
EPAMIG 11	−22.5	–	EPAMIG 41	−3.9	–	EPAMIG 71	−47.2	–
EPAMIG 12	–	–	EPAMIG 42	−46.3	–	EPAMIG 72	55.6	30.9
EPAMIG 13	–	–	EPAMIG 43	31.2	–	EPAMIG 73	3.0	–
EPAMIG 14	–	–	EPAMIG 44	33.4	–	EPAMIG 74	–	–
EPAMIG 15	−19.5	–	EPAMIG 45	–	–	EPAMIG 75	−23.9	–
EPAMIG 16	−42.9	−26.1	EPAMIG 46	−17.3	–	EPAMIG 76	−11.7	–
EPAMIG 17	78.6	110.8	EPAMIG 47	−47.8	–	EPAMIG 77	238.6	–
EPAMIG 18	−5.9	–	EPAMIG 48	−23.2	–	EPAMIG 78	114.1	–
EPAMIG 19	47.2	–	EPAMIG 49	−19.4	–	EPAMIG 79	291.0	–
EPAMIG 20	29.7	–	EPAMIG 50	−6.7	−12.5	EPAMIG 80	328.1	–
EPAMIG 21	122.6	–	EPAMIG 51	38.9	99.2	EPAMIG 81	82.9	–
EPAMIG 22	−19.0	1.7	EPAMIG 52	–	–	EPAMIG 82	25.5	34.1
EPAMIG 23	78.6	–	EPAMIG 53	59.1	–	EPAMIG 83	40.9	–
EPAMIG 24	23.9	–	EPAMIG 54	–	–	EPAMIG 84	624.7	–
EPAMIG 25	139.4	–	EPAMIG 55	–	–	EPAMIG 85	25.8	108.0
EPAMIG 26	6.7	–	EPAMIG 56	254.9	–	EPAMIG 86	61.0	77.2
EPAMIG 27	135.7	–	EPAMIG 57	–	–	EPAMIG 87	–	–
EPAMIG 28	90.8	–	EPAMIG 58	46.1	108.9	EPAMIG 88	34.6	–
EPAMIG 29	243.1	–	EPAMIG 59	61.5	–	EPAMIG 89	−39.8	–
EPAMIG 30	196.7	184.4	EPAMIG 60	52.1	–	EPAMIG 90	–	–

Table 3. Heterosis (MH%) and heterobeltiosis (H%) of F1 hybrids of *Coffea arabica* L. for the processed coffee yield in the accumulated harvests of 2021, 2022, and 2023.

After identifying the best hybrid combinations, a selection of genotypes was carried out among the individuals with the best combinations. Although *C. arabica* L. is a segmental allopolyploid species with a disomic inheritance and regular meiotic behavior[40], phenotypic variability is observed between plants resulting from the same hybrid combination. This fact allows the best individuals to be explored within the best combinations, further expanding the genetic gain from selection. Aiming to quantify the gain from selection within the combinations, this was estimated for the best selected cross, EPAMIG 37, considering that this combination mean in the third harvest was 83.4 bags ha^{-1} and that four genotypes were selected within this combination, with a mean of 100.6 bags ha^{-1}. Considering a heritability of 0.7 for yield, the gain with selection was estimated to be 14.6% (12 bags ha^{-1}) by selecting within the best hybrid combination. These selected genotypes, along with others, are being cloned and will be evaluated again in the final stages of the EPAMIG breeding program.

Among the different ways of verifying the superiority of hybrids, crossing heterosis calculations are widely used in plant breeding. Normally, this heterosis can be expressed as a function of hybrid combination superiority in relation to the mean performance of the parents involved in the crossing or their superiority in relation to the best parent (heterobeltiosis). In this experiment, both were calculated for a small number of crosses in which both parents were present in the test.

From a practical view, the most important thing is to offer the producer superior cultivars. This superiority may be related to the best cultivars commercially used, which could be called heterosis in relation to commercial standards. It is known that national coffee production is based on a few cultivars, with the Mundo Novo and Catuaí cultivars (and their derivations/lines) serving as the basis of 80% of national plantations[37]. The hybrid combination superiority in relation to the standard mean (standard heterosis – SH%) for the 90 combinations was calculated using the standard of the cultivars Mundo Novo IAC 379/19, Catuaí Vermelho IAC 144, Catuaí Vermelho IAC 99, and Catuaí Amarelo IAC 62; thus, we could infer the gain in possible yield by using *C. arabica* L. hybrids.

When checking whether combinations can be commercially exploited based on their productive performance, it is essential to calculate their superiority in comparison to the mean performance of the most productive commercial cultivar (SHS). In this specific case, seven hybrids demonstrated a productive performance greater

Hybrids	SH %	SHS%	Hybrids	SH %	SHS%	Hybrids	SH %	SHS%
EPAMIG 01	97.7	8.4	EPAMIG 31	71.6	− 5.9	EPAMIG 61	38.6	− 24.0
EPAMIG 02	132.6	27.5	EPAMIG 32	− 40.2	− 67.2	EPAMIG 62	− 15.8	− 53.8
EPAMIG 03	− 26.6	− 59.7	EPAMIG 33	110.0	15.1	EPAMIG 63	22.6	− 32.8
EPAMIG 04	59.1	− 12.8	EPAMIG 34	− 43.3	− 68.9	EPAMIG 64	22.3	− 33.0
EPAMIG 05	− 30.6	− 61.9	EPAMIG 35	4.6	− 42.7	EPAMIG 65	− 12.5	− 52.1
EPAMIG 06	166.4	46.0	EPAMIG 36	149.6	36.8	EPAMIG 66	146.6	35.2
EPAMIG 07	− 62.9	− 79.7	EPAMIG 37	181.2	54.1	EPAMIG 67	67.4	− 8.2
EPAMIG 08	42.0	− 22.1	EPAMIG 38	− 2.4	− 46.5	EPAMIG 68	1.7	− 44.2
EPAMIG 09	93.1	5.9	EPAMIG 39	96.7	7.9	EPAMIG 69	− 5.2	− 48.1
EPAMIG 10	39.4	− 23.6	EPAMIG 40	86.0	2.0	EPAMIG 70	77.4	− 2.8
EPAMIG 11	13.1	− 38.0	EPAMIG 41	53.6	− 15.8	EPAMIG 71	− 25.9	− 59.4
EPAMIG 12	− 74.4	− 85.9	EPAMIG 42	− 14.2	− 52.9	EPAMIG 72	58.6	− 13.1
EPAMIG 13	31.2	− 28.1	EPAMIG 43	109.6	14.9	EPAMIG 73	44.6	− 20.7
EPAMIG 14	51.9	− 16.7	EPAMIG 44	113.2	16.9	EPAMIG 74	5.5	− 42.2
EPAMIG 15	28.7	− 29.4	EPAMIG 45	− 67.4	− 82.1	EPAMIG 75	6.8	− 41.5
EPAMIG 16	− 21.6	− 57.0	EPAMIG 46	50.8	− 17.3	EPAMIG 76	− 39.7	− 66.9
EPAMIG 17	145.4	34.5	EPAMIG 47	− 4.7	− 47.8	EPAMIG 77	9.6	− 39.9
EPAMIG 18	− 10.2	− 50.8	EPAMIG 48	40.1	− 23.2	EPAMIG 78	66.5	− 8.7
EPAMIG 19	40.4	− 23.0	EPAMIG 49	47.1	− 19.4	EPAMIG 79	− 13.4	− 52.5
EPAMIG 20	23.7	− 32.2	EPAMIG 50	50.2	− 17.6	EPAMIG 80	39.4	− 23.6
EPAMIG 21	112.4	16.5	EPAMIG 51	140.6	31.9	EPAMIG 81	25.0	− 31.5
EPAMIG 22	30.4	− 28.5	EPAMIG 52	27.5	− 30.1	EPAMIG 82	102.1	10.8
EPAMIG 23	106.1	13.0	EPAMIG 53	118.6	19.8	EPAMIG 83	62.6	− 10.9
EPAMIG 24	70.2	− 6.7	EPAMIG 54	40.8	− 22.8	EPAMIG 84	144.4	34.0
EPAMIG 25	17.0	− 35.9	EPAMIG 55	− 8.6	− 49.9	EPAMIG 85	102.5	11.0
EPAMIG 26	− 8.5	− 49.8	EPAMIG 56	58.3	− 13.2	EPAMIG 86	121.2	21.3
EPAMIG 27	102.1	10.8	EPAMIG 57	− 49.7	− 72.5	EPAMIG 87	71.4	− 6.0
EPAMIG 28	63.6	− 10.3	EPAMIG 58	100.8	10.1	EPAMIG 88	8.5	− 40.5
EPAMIG 29	115.6	18.2	EPAMIG 59	− 11.5	− 51.5	EPAMIG 89	− 51.5	− 73.4
EPAMIG 30	86.5	2.2	EPAMIG 60	− 16.6	− 54.3	EPAMIG 90	− 2.8	− 46.7

Table 4. Grain yield superiority in the accumulated harvests of 2021, 2022, and 2023 of *Coffea arabica L.* F_1 hybrids in relation to the mean performance of the standards cultivars (SH%) and in relation to the best cultivar evaluated in the trial (SHS%) for the processed coffee yield.

Sources of variation	df	Ms	Probability
GCA	55	2558.16	0.000
SCA	34	1491.50	0.000
Residuals	178	238.43	

Table 5. Summary of the analysis of variance and the general (GCA) and specific ability (SCA) of combining the parents and hybrids of *Coffea arabica* L. for processing cumulative coffee grain yield in bags of 60 kg per hectare during 2021, 2022, and 2023 harvests. df: degree of freedon; Ms: Mean Square; Probability: p-value.

than 30% (25 bags ha^{-1} more) in relation to the best commercial cultivar present in the trial. Considering this fact and given that the superiority of most cultivated coffee cultivars today is greater than 75 bags ha^{-1}, we can infer that cultivar renewal must be intensified, which will allow coffee growers to achieve greater profitability on their property in a short period of time. As demonstrated, the grain yield of hybrids must pre priority rather than magnitude of heterosis[16].

The GCA effect expresses the mean performance of the parent in combination with other parents, and the SCA evaluates the part of the combination not explained by the GCA for each parent involved. In genetic terms, the GCA estimate is associated with genes with predominantly additive effects, in addition to dominance effects and some epistatic interactions of the additive × additive type. The SCA estimate, in turn, basically depends on dominance effects and other epistatic interactions that are usually of small magnitude and, therefore, neglected[41]. Several studies have documented the significance of both GCA and SCA effects and most of them argued that SCA effects are proportionally higher than GCA[16,42]. In our study, the GCA was proportionally higher than SCA. However, this discussion in not valid in practice due to the allelic frequency at each locus is probably

Parents	*n*	GCA	Parents	*n*	GCA
Bourbon Amarelo MG 009	1	69.3	Catucaí Amarelo 24–137	3	– 2.2
MGS EPAMIG 1194	1	42.8	Catuaí Amarelo IAC 62	6	– 2.9
IPR 103	1	36.7	Obatã IAC 1669-20	2	– 3.4
Acauã Novo	9	33.2	Obatã IAC 4739	2	– 4.6
IAC 125 RN	4	25.3	Topázio MG 1190	4	– 4.6
MGS Liberdade	9	24.7	Bourbon Vermelho MG 0035	1	– 6.2
Rouxinol	1	20.8	MG 0151 Icatu Precoce IAC 3282	3	– 7.1
Guará	2	19.9	H-419-6-2-7-1-1	5	– 7.7
Catiguá MG 2	5	19.6	MG 0308 H. Timor 475 – 55	1	– 8.1
Típica Guatemala MG 003	2	18.3	Bourbon Vermelho MG 0055	7	– 8.6
Azulão	1	17.2	MGS Ametista	12	– 9.4
Icatu x Catimor H-29-1-8-5	1	16.3	Icatu x Catimor H 105-01-39	1	– 9.5
MG 0161 Maragogipe	1	15.0	Catuaí Vermelho IAC 99	2	– 11.5
Sarchimor MG 8840	6	13.9	IPR 100	7	– 11.7
Híbrido Timor UFV 376 – 52	1	12.5	Oeiras MG 6851	1	– 12.1
Gueisha	5	11.6	Bourbon Amarelo MG 0038	3	– 12.9
Híbrido Timor UFV 408 – 11	1	10.2	IPR 102	5	– 13.5
IAC Obatã 4739	3	8.8	IPR 106	2	– 17.7
MG 0194 Caturra Amarelo	1	8.4	IPR 105	1	– 21.2
Icatú Precoce IAC 3282	1	6.9	Villa Sarchi MG 0210	1	– 24.1
Catiguá MG 3	1	6.2	MG 0176 Amphilo	3	– 24.7
Sumatra MG 0137	1	6.2	Pacas	1	– 26.2
Bourbon Vermelho MG 0083	1	5.2	MG 0192 Caturra Vermelho	2	– 26.4
MGS Paraiso 2	6	4.9	MGS Catucaí Pioneira	12	– 27.9
Catuaí Vermelho IAC 144	1	4.8	MG 0165 Maragogipe Amarelo	1	– 33.5
H-516-2-1-1-7-1	9	3.1	Pacamara	1	– 45.7
Mundo Novo IAC 379 – 19	7	0.8	MG 0282 H. Timor UFV 376 – 12	1	– 45.9
MGS Aranãs	7	– 1.4	Catiguá Amarelo	1	– 63.1

Table 6. Values of the general combining ability (GCA) of *Coffea arabica* L. parents for the variable processed coffee yield in the accumulated harvests of 2021, 2022, and 2023 and (n) number of crosses.

different from 0.5, at least this assumption could not be made. In this situation de GCA does not contain only additive effect and the SCA contains lesser dominance effects. Thus, the degree of dominance or any index of ratio between these estimates are ineffective[43].

In the process of obtaining hybrids, we tried to fully exploit the effects of GCA and SCA. Since the "per se" performance of parents is extremely important and can be observed in parents who have good GCA, it is expected that in programs aimed at obtaining hybrids, at least one of the parents has good GCA and that in crosses, they express the maximum SCA[39,44,45]. Our results of GCA identified the cultivars Acauã Novo and Catigua MG 2 as good parents, as were reported by Medeiros et al.[39]. It is important to remember the importance of evaluating the merit of parents based on their cross performance due to possible lack of correlations between the phenotypic mean and combining abilities[27].

Two of drawbacks of our work are early evaluations and lack of environmental interaction estimates of heterosis and combining abilities. The evaluations of accumulated three harvests are sufficient to reach above 80% of accuracy[46]. However, there could be a reduction in heterosis as the plants become old. In Fontes et al.[45] the authors reported a 7% heterosis reduction from the fourth to the sixth harvest. If the decline in heterosis over successive harvests is a general phenomenon when comparing hybrids and their parents, the observed rate of decrease was 3.5% per harvest. Therefore, if this rate remains constant, heterosis will no longer be present after five harvests, beginning with the sixth. Even under this scenario, hybrids would remain economically viable, as they would provide a faster return on investment for producers, thereby reducing financial risks. Another important aspect to consider is the potential for productive heterosis following pruning, which is an essential practice in modern coffee cultivation. Given that heterosis is highest during the early developmental stages of coffee plants, when root and vegetative growth rates are elevated, it is reasonable that maximum heterosis could be restored after pruning. This is due to the accelerated vegetative and root growth triggered by branch removal and partial root system senescence. The single environmental experiment led to absence of estimates of the heterosis and combining abilities interaction with environment. Some authors have reported the presence of significative GCA and SCA interaction[16,42]. So, it will depend on GCA and SCA of each location and parents[26].

Despite the limitations, our work has the benefit of crossed a broad genetic diversity present in *C. arabica*, such as landraces and cultivars derived from "Typica", "Bourbon", Timor Hybrid, and introgression of *C. canephora* and *Coffea liberica*. In the literature reviewed of heterosis and combining ability in *C. arabica*, it is not found one work dealing with this number of crossed parents. Additionally, the parents represent the elite high-performance

Hybrids	SCA	Hybrids	SCA	Hybrids	SCA
EPAMIG 66	46.68	EPAMIG 47	0.83	EPAMIG 19	− 1.21
EPAMIG 09	39.75	EPAMIG 02	0.00	EPAMIG 88	− 1.82
EPAMIG 37	38.29	EPAMIG 06	0.00	EPAMIG 46	− 2.31
EPAMIG 77	24.29	EPAMIG 07	0.00	EPAMIG 41	− 2.82
EPAMIG 44	19.80	EPAMIG 12	0.00	EPAMIG 31	− 2.92
EPAMIG 29	19.28	EPAMIG 15	0.00	EPAMIG 85	− 4.34
EPAMIG 58	18.54	EPAMIG 16	0.00	EPAMIG 70	− 4.57
EPAMIG 17	17.54	EPAMIG 23	0.00	EPAMIG 73	− 4.78
EPAMIG 04	15.64	EPAMIG 30	0.00	EPAMIG 42	− 5.38
EPAMIG 74	14.08	EPAMIG 34	0.00	EPAMIG 61	− 8.68
EPAMIG 82	12.92	EPAMIG 35	0.00	EPAMIG 24	− 8.93
EPAMIG 13	12.63	EPAMIG 38	0.00	EPAMIG 55	− 9.16
EPAMIG 49	10.74	EPAMIG 39	0.00	EPAMIG 01	− 10.65
EPAMIG 21	10.67	EPAMIG 40	0.00	EPAMIG 89	− 11.24
EPAMIG 53	9.16	EPAMIG 43	0.00	EPAMIG 45	− 11.60
EPAMIG 59	8.99	EPAMIG 51	0.00	EPAMIG 26	− 12.16
EPAMIG 25	8.93	EPAMIG 52	0.00	EPAMIG 67	− 12.36
EPAMIG 62	8.68	EPAMIG 54	0.00	EPAMIG 48	− 12.39
EPAMIG 72	8.00	EPAMIG 56	0.00	EPAMIG 18	− 13.99
EPAMIG 86	7.93	EPAMIG 57	0.00	EPAMIG 75	− 14.08
EPAMIG 28	7.04	EPAMIG 63	0.00	EPAMIG 65	− 16.60
EPAMIG 05	6.72	EPAMIG 64	0.00	EPAMIG 22	− 16.61
EPAMIG 33	5.88	EPAMIG 68	0.00	EPAMIG 32	− 22.24
EPAMIG 87	5.13	EPAMIG 78	0.00	EPAMIG 03	− 22.36
EPAMIG 27	5.12	EPAMIG 79	0.00	EPAMIG 76	− 24.29
EPAMIG 36	4.57	EPAMIG 80	0.00	EPAMIG 08	− 24.92
EPAMIG 84	4.34	EPAMIG 81	0.00	EPAMIG 69	− 25.72
EPAMIG 10	4.03	EPAMIG 83	0.00	EPAMIG 60	− 27.53
EPAMIG 20	3.59	EPAMIG 90	0.00	EPAMIG 11	− 30.51
EPAMIG 50	3.13	EPAMIG 14	− 0.98	EPAMIG 71	− 35.78

Table 7. Values of the specific combining ability (SCA) of *Coffea arabica* L. F_1 hybrids for the processed coffee yield at the 2021, 2022, and 2023 cumulative harvests.

cultivars in Brazilian agriculture and so, with accumulation of favorable alleles gathering across many years of plant breeding process. It is evident that the parents should be with high grain yield and GCA and divergent, regardless of the molecular concepts of heterosis[47].

As already mentioned, knowledge about the genetic potential of *C. arabica* L. genotypes in crosses is not abundant in literature as in cereal crops. However, this information is highly important for directing breeding programs. Plant breeding is based on the accumulation of advantages, in short, the accumulation of favorable alleles for different characteristics. Therefore, it is plausible that those genotypes that present better GCA are the most suitable for cultivation conditions, given that the final reflection of this adaptive capacity is the high productivity of their hybrid combinations. Thus, combining a single combination of characteristics of parents who present high GCA and who still manifest SCA heterosis would be ideal. These combinations could be used directly in commercial management if propagated vegetatively by any currently known technique, whether minicutting, somatic embryogenesis, or both[48,49].

In 1985, Ameha and Belachew emphasized that "heterosis needs to be exploited as quickly as possible, and any delay could jeopardize the coffee industry in a short period of time"[13]. While the coffee chain could have potentially advanced further, the data indicates significant improvements in most key indicators. Hybrid cultivars have been adopted by farmers, and the benefits of heterosis, along with other advantages, have been successfully transferred into field conditions. According to coffee growers, hybrid cultivars offer some benefits, including higher yields, faster fruiting, rapid plant growth, excellent cup quality, and increased resistance to pests and diseases. Additionally, hybrids demonstrate greater productivity over time, provide faster profitability in the initial harvests, and require simpler farming practices. However, access to hybrid seedlings remains a shortcoming[50].

Conclusions

There was heterosis for productivity in the first three accumulated harvests of the studied hybrids.

Hybrids mean heterosis was 64.2%, and the heterobeltiosis was 40.8%.

The general and specific combining ability is present in parents and their crossed progenies. The best parents are cultivars Acauã Novo, IAC 125 RN, MGS Liberdade, Catiguá MG2, Sarchimor MG 8840 and these should be preferentially explored in new hybrid combinations.

Data availability

The data set generated during and/or analyzed during the current study are available from the corresponding author upon reasonable request.

Received: 3 October 2024; Accepted: 18 February 2025
Published online: 07 March 2025

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Acknowledgements
The authors thank Fundação de Amparo a Pesquisa do Estado de Minas Gerais (FAPEMIG), Conselho Nacional de Desenvolvimento Científico e Tecnológico - CNPQ, Instituto Nacional de Ciência e Tecnologia - INCT-Café, Consórcio Pesquisa Café - CBP&D/Café.

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Funding
This work was supported by the Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG, grant number PPE00103-22 and the Consórcio Pesquisa Café (CBP&D/Café, grant number 10.24.22.026.00). The authors Vinícius Teixeira Andrade and Jéfferson de Oliveira Costa received research support from FAPEMIG. Authors Gladyston Rodrigues Carvalho and Cesar Elias Botelho received research support from Conselho Nacional de Desenvolvimento Científico e Tecnológico CNPq.

Declarations

Competing interests
The authors declare no competing interests.

Additional information
Supplementary Information The online version contains supplementary material available at https://doi.org/10.1038/s41598-025-91149-y.

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