

Analysis of Combining Ability in Western Ethiopian Origin Coffee (*Coffea arabica* L) for Morphological Characters

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Abstract: The choice of promising genotypes from diverse genetic bases and subsequent utilization of hybrids is one of the breeding strategies to improve productivity. Hence, the present experiment was conducted among elite coffee materials from Western Ethiopia. The data were recorded for five stem-, four branch- and three leaf- characteristics. The analysis of variance revealed highly significant ($P < 0.001$ and $P < 0.01$) differences among the 15 genotypes (5 parents and 10 F1s) for all traits except for total number of nodes, leaf area and number of nodes per primary branch. The combining ability analysis of variance showed significant general (GCA) and specific (SCA) combining ability mean squares for nine out of 12 characters measured, indicating the importance of both additive and non-additive gene actions. Parent P1 consistently exhibited positive GCA effects for nine characters, parent P2 for five characters and parent P4 for seven characters suggesting that these parents are good general combiners. Hybrids $P_2 \times P_5$, $P_2 \times P_4$, $P_2 \times P_3$, $P_3 \times P_4$ and $P_1 \times P_5$ were noted with High and positive SCA effects for each character. Therefore, it could be useful to include such potential hybrids in a breeding program and further evaluate their performance for yield and growth characteristics at full full-bearing stage.

Keywords: Coffee Arabica, Combining Ability, GCA and SCA

1. Introduction

Coffee (*Coffea arabica* L.) is a stimulant beverage crop and belongs to the family Rubiaceae and the genus Coffea. They are mostly grown in subtropical and tropical regions (Morris, 2018) and comprise 124 species [22, 26]. *Coffea canephora* Pierre and *Coffea arabica* L. are the only two economically important species widely cultivated worldwide. The two species' area coverage is estimated to be more than 10 million hectares worldwide [8]. Coffee Arabica is tetraploid and considered to be a 95% self-fertile i.e. only 5% cross-fertile species, meaning it can set fruit from its own pollen [21]. This makes Arabica coffee unique among diploid species of coffee under Genus coffea. The total land area coverage of Arabica coffee is estimated to be 700,474.69 ha with an annual average production of 469,091.1 tonnes in Ethiopia, out of which over half is consumed locally [10].

Ethiopia is endowed with the genetic diversity of Arabica coffee (12; 2). The agro-ecological diversity is also reported in Ethiopia [4]. For that reason, Ethiopian coffee is well-known for its very fine cup quality, unique aroma and flavor

across coffee-growing areas. Some of the famous coffee types that are acclaimed for having such unique and distinct characteristics include Sidamo, Yirgacheffe, Hararge, Ghimbi and Limu [24]. Western Ethiopian coffee mainly known as Wellega coffee is well known by the name of 'Gimbi Coffee' and 'Nekempte Coffee' on the world market and accounts for 33 % (31,844 tonnes/year) of the total coffee supply from the Oromiya regional state [10] and fetches a very high price on the world market.

Despite the existence of high genetic diversity that in turn provides immense opportunities for improvement programs, the shortage of improved varieties (pure line and hybrid varieties) is the major one. It is obvious that research work carried out so far on coffee genetics and breeding was not adequate to address these diverse agro-ecologies of the country. In any crop breeding program intended to address such problems as the ones mentioned above, combining ability studies is one of the basic breeding tools. Nevertheless, such studies on coffee are scanty at both national and international levels.

As mentioned earlier, the analysis of combining ability is

the other important tool which has presently become an integral part of a breeding program. It helps to identify the best-combining parent, to know the type of gene action involved in controlling the expression of a character, and to choose appropriate breeding methods [17, 20]. Indeed, diallel analysis for combining ability suggested by Griffing [16] is one of the powerful tools to provide the above information. In Arabica coffee, information in this regard is very scarce.

Even though some studies had been conducted in crosses of indigenous coffee materials originating from other parts of the country, there is no heterosis and combining ability studies that have been conducted specifically targeting coffee materials from Western Ethiopian origin, the area that accounts for 33% of coffee production from Oromiya Regional State as mentioned earlier. Consequently, the number of improved cultivars originating from the local landraces is limited to four pure lines. These cultivars by no means represent or adapt to the diverse agro-ecologies within Western Ethiopia/Wollega coffee growing region and are not adequate enough to represent all the different types of coffee in the area.

Therefore, the present combining ability study specifically targets crosses between variable parental lines originating western region of Ethiopia and contributes towards improving productivity and quality the objectives of 1. To determine the types of gene actions governing the expression of morphological traits in crosses of elite coffee materials from Western Ethiopia, 2. To assess the combining ability of the selected parental lines and identify the best combiners for use in future breeding programs aimed at developing heterotic F1 hybrids for morphological characters.

2. Materials and Methods

2.1. Description of the Study Area

The study was conducted at Mugi research sub-stations of the Jimma Agricultural Research Center (JARC), which is located in the Kellem Wollega Zone. According to the Anfilo District Bureau of Agriculture (BOA), Mugi is located 34° 00' to the East, 8° 40' to the North, and 610km from Jimma at an altitude of 1570 masl. The minimum and maximum temperature of the area is 11.6 and 26.3°C, respectively with annual rainfall of 1655 mm/annum. Mugi is one of the major coffee-producing areas in western Ethiopia which is characterized by a wet humid sub-tropical climate.

2.2. Experimental Materials

Five pure line parents that were selected from the national coffee collection program based on yield, disease, insect pest resistance, and canopy class were crossed in a half-diallel fashion. The first parent, PX (P₁), was obtained from Southwestern national coffee collections trials but its specific accession number is unknown, hence designated as PX. The remaining four parental lines, W66/98(P₂), W78/84(P₃), W110/99(P₄) and W3/99(P₅) were screened from the Western region's national coffee collections established at Haru Sub-center. According to their canopy nature, P₁ is a very open type, P₂ is medium compact, P₃ is medium open, p₄ is intermediate and p₅ is open canopy classes. A detailed description of these parental lines is given in Table 1.

Table 1. Origin and description of parental lines.

Code No	Accession no	Origin	Altitude	Description
P1	PX	Mettu	1750	Very open, good stature, wide adaptation, spicy in quality. The accession number of this parent is not available
P2	W 66/98	West wollega	1800	Medium compact, CBD resistant, good stature, good survival rate in the field
P3	W 78/84	West wollega	1760	Medium open, high yield, fruity in quality
P4	W 110/99	West wollega	1600	Intermediate, good stature, good yield
P5	W 3/99	West wollega	1650	Open, vigorous, fruity in quality

Source: take out from JARC's Coffee Breeding and Genetics Research Division database.

The breeding materials i.e. the five parental lines and 10 F₁ hybrids evolved from all possible crosses among the five parents were established in a breeding trial field at Haru Agricultural Research Sub-Center in 2015, in an attempt to develop hybrid coffee varieties for the area that can produce higher yield compared to the released pure lines.

2.3. Experimental Design and Field Management

A total of 15 genotypes were planted out in the trial field in August 2016. The trial was planted in RCBD design with three replications. The spacing between plants was 2m x 2m and the number of plants per plot was six. Since the establishment of the trial, the field management practices have been regularly conducted as per the recommendation of JARC and these standard practices have continued throughout the experimental duration.

2.4. Data Collected

Data were collected for twelve morphological traits from the experimental plots from November 2017 to January 2018. Four very uniform coffee trees with no mechanical damage were carefully selected and tagged for each treatment. The marked trees were recorded for all the twelve characters considered as described below.

Stem Characters

Plant height (cm), Height up to first primary branch (cm), Total number of node (Counts), Inter-node length of the main stem (cm), Stem diameter (mm)

Branch Characters

Number of primary branches (Counts), length of primary branches (cm), Canopy diameter (cm), Number of nodes per primary branch (Count)

*Leaf characters*Leaf length (cm), Leaf width (cm), Leaf area (cm²)

checked by plant breeding tools software to confirm the accuracy of the computation.

2.5. Data Analysis

Analyses of variance were computed for all the morphological characteristics considered in this study using XLSTAT, Computer program and SAS (SAS, 2004) version 9.0 software to test for genotypic and block differences. Least Significant Difference (LSD at $P = 0.05$ and $P=0.01$) was employed to test the significance of differences among the genotypes (five parents and ten hybrids). Further genetic analyses were carried out only for those characters that showed significant differences among the genotypes. Computations of combining ability analysis were conducted using R software and also

3. Results**3.1. Analysis of Variance (ANOVA)**

The analysis of variance revealed highly significant ($P<0.01$) differences among the 15 genotypes (5 parents and 10 F₁s) for all the traits measured except for the total number of nodes, Leaf area and number of nodes per primary branch (Table 2). Similarly, mean squares due to hybrids alone indicated highly significant differences for all characters, except the total number of nodes, leaf area and number of nodes per primary branch.

Table 2. Mean squares due to Genotypes and crosses for 12 morphological traits from the analysis of variance (ANOVA).

Characters	Mean squares					
	Parents and Hybrids			Hybrids alone		
	Genotype(14)	Block (2)	Error (28)	Cross (9)	Block (2)	Error (28)
Stem Characters:						
Plant Height (cm)	612.33***	1707.25***	137.14	849.04**	1045.43**	174.98
Total number of node	2.39 ^{ns}	6.098*	1.30	2.71 ^{ns}	3.71 ^{ns}	1.70
Stem Diameter	31.90***	58.49***	6.54	35.15**	31.01*	7.85
Height First Primary Branch	22.14**	1.40 ^{ns}	14.25	16.89**	41.13*	6.46
Inter-node Length	1.82***	4.42***	0.45	27.11**	7.16 ^{ns}	4.87
Branch Characters:						
Average Length Primary Branch	153.73**	85.78 ^{ns}	36.39	181.2**	34.76*	47.88
Canopy Diameter	1001.65***	2408.09***	161.66	1236.31***	1396.84**	191.96
Number of Primary Branch	14.25***	50.29*	5.11	16.89**	41.13*	6.46
No. of node per primary branch	3.19 ^{ns}	14.96***	1.69	3.90 ^{ns}	13.62**	2.15
Leaf Characters:						
Leaf Length	2.41**	5.068**	0.68	3.46**	3.96*	0.71
Leaf Width	0.69***	0.43*	0.11	0.962***	0.370 ^{ns}	0.122
Leaf area	72.36 ^{ns}	194.27 ^{ns}	48.22	92.45 ^{ns}	168.84 ^{ns}	52.21

1*** $P < 0.001$; ** $P > 0.001$ and $0.01 < p < 0.05$; $p > 0.05$ (non-significant); df = degree of freedom ();

Block differences were highly significant ($P<0.01$) for the characters' plant height, stem diameter, leaf length and inter-node length, while significant ($P<0.05$) for the characters' number of primary branches and leaf width.

3.2. Combining Ability Analysis

Combining ability analysis of variance for different growth

characters is shown in Table 3. The analysis revealed that the mean squares due to both general combining ability (GCA) and specific combining ability (SCA) effects were significant ($P < 0.05$) or highly significant ($P < 0.01$, $P < 0.001$) for all the characters measured except the GCA mean squares were not significant for the number of primary branches and height up to the first primary branch.

Table 3. Analysis of variance and components of genetic variance for morphological traits in 5 x 5 half diallel.

Traits	Mean squares			Variance component			
	GCA df (4)	SCA (10)	Error (28)	%GCA SS	%SCA SS	σ_e^2	$\sigma_{gca}^2/\sigma_{sca}^2$ Ratio
Stem Characters							
PH	155.77*	223.45***	45.71	21.80	78.20	45.71	0.09
SD	11.00**	10.49***	2.18	30.00	70.00	2.18	0.15
HFPB	4.99 ^{ns}	8.34**	1.99	19.33	80.67	1.99	0.07
IL	0.43*	0.68***	0.15	20.21	79.79	0.15	0.08
Branch characters							
ALPB	47.00*	53.00***	12.12	26.19	73.81	12.12	0.12
CD	352.80***	326.36***	53.98	30.00	70.00	53.98	0.16
NPB	3.55 ^{ns}	7.87**	1.80	32.18	67.82	1.80	0.48
Leaf Characters							

Traits	Mean squares			Variance component			
	GCA df (4)	SCA (10)	Error (28)	%GCA SS	%SCA SS	σ_e^2	$\sigma_{gca}^2/\sigma_{sca}^2$ Ratio
LL	0.80*	0.90**	0.22	29.00	71.00	0.22	0.14
LW	0.19**	0.26***	0.03	22.26	77.74	0.03	0.09

(σ_e^2) = error variance; $\sigma_{gca}^2/\sigma_{sca}^2$ SCA = ratio of GCA and SCA variances *, **, ns, Significant at 0.05 and 0.01 level of probability and non-significant, respectively, df = degree of freedom (), ALPB = Average length of primary branch (cm), CD = Canopy diameter (cm), HFPB = Height up to first primary branch (cm), IL = inter-node length (cm), LL = Leaf Length (cm), LW = leaf width (cm), NPB = number of primary branch, PH= Plant height (cm), SD = Stem diameter (mm)

Generally, the fact that the extent of mean squares of SCA was higher than that of GCA, indicated that the components of variances due to variance general combining ability and variance specific combining ability ratios were less than unity.

3.2.1. Estimates of General Combining Ability (GCA)

Effects

Positive estimates of GCA effects from the differential analysis were revealed by parent P1 for all the morphological characters considered (Table 4). Similarly, Parent P4 exhibited fairly high and positive GCA effects for seven out of nine characters whereas the GCA effects for these remaining two characters viz. leaf width and first primary branch length were negative.

In contrast, parents P5 and P3 exhibited high or low but negative GCA effects for all the nine characters considered indicating the poor combining ability of these two parents as each is crossed with a series of other parental lines.

Parent P2 exhibited GCA effects which were positive for five and negative for four characters out of the nine total traits considered reflecting its fairly combining ability for some characters and poor combining ability for others. Detailed analysis for each stem, branch and leaf character are given below.

Stem characters

Three parents revealed significant and positive GCA effects for plant height. Out of these parents, P1 showed a significantly positive GCA effect of 4.528 and was the best general combiner for this trait. Parents P4 (4.07) and P2 (1.02) showed positive GCA effects but non-significant GCA effects and were equally important to be used in parental combination for plant height. Parent P5 showed a negative and significant GCA effect of (-6.304) similarly P3 also showed negative but non-significant GCA effect with the value of (-3.328). Both P5 and P3 were poor general combiners for plant height. Therefore, from the present study, P1, P4 and P2 could be utilized in coffee breeding programs intended to develop tall coffee plants while P5 and P3 could be useful in dwarf variety development programs.

Considering the remaining stem characters, P1 showed a highly significant ($P < 0.01$) GCA effect value of (2.00) for stem diameter and a significant ($P < 0.05$) GCA effect (0.282) for inter-node length. This parent, therefore, could be

considered as one of the favourable complementary parents in the improvement of these traits. Parent P5 showed significant and highly significant negative GCA effects (-1.128) for stem diameter and inter-node length (-0.347) similar to plant height. Parent P3 showed non-significant negative GCA effects for these two traits with values of -0.659 and -0.077 respectively. Considering the rest parents, P2 had non-significant negative GCA effects of -0.633 and -0.049 for stem diameter and inter-node length, whereas P4 had non-significant positive GCA effect of 0.423 and 0.190 for stem diameter and inter-node length, respectively.

On the other hand, parental line P2 showed highly significant GCA effects (1.40) for height up to first primary branch. This parent could be considered as the best general combiner for this trait and also parental line P1 showed non-significant positive GCA effect values of 0.15. The rest parents P3, P4 and P5 exhibited non-significant negative GCA effects of -0.4214, -0.7310 and -0.3976, respectively.

Branch characters

Parent P1 showed highly significant positive ($P < 0.01$) GCA effects for the average length of primary branch and canopy diameter with their respective values of 3.305 and 10.754. Similarly, P4 exhibited positive estimates of GCA effects of 1.280 and 1.207, for both characters, the average length of primary branches and canopy diameter, in that order. These results indicated that P1 and P4 could be useful materials in parental combination for the improvement of these traits. In contrast, P5 consistently exhibited significant negative GCA effect values of -3.642 and -7.941 for the average length of primary branches and canopy diameter, respectively. Parent P3 exhibited similar results of negative GCA effects of -1.00 and -4.102 for the average length of primary branch and canopy diameter, respectively. Following a similar analogy to the previous conclusion, negative GCA effects exhibited by P5 and P3, apparently suggested that these materials are poor general combiners for the two branch characters mentioned and may only be used if the breeding interest is for the reduced size of these traits. In conclusion, parent P5, P3 and P2 which showed negative GCA effects for canopy diameter (-0.959), could be useful materials in the development of hybrid variety having short and compact stature while P1 and P4 for open compact stature.

Table 4. Estimates of general combining ability (GCA) effects for some morphological characters in 5 x 5 half diallel cross in coffee.

Traits	Parents					SE(d) gi±	SE(d) gj±
	P1	P2	P3	P4	P5		
Stem Characters							
PH	4.52*	1.02	-3.32	4.08	-6.30**	2.29	3.61
SD	2.00**	-0.73	-0.65	0.42	-1.12*	0.49	0.79
HFPB	0.15	1.40**	-0.42	-0.83	-0.39	0.47	0.75

Traits	Parents					SE(d) gi±	SE(d) gi gj±
	P1	P2	P3	P4	P5		
IL	0.29*	-0.04	-0.07	0.19	-0.34**	0.13	0.20
Branch Characters							
ALPB	3.30**	0.05	-1.00	1.28	-3.64**	1.17	1.86
CD	10.75**	-0.95	-4.10	2.24	-7.94**	2.48	3.92
NPB	1.05*	-1.05*	-0.45	1.20*	-0.74	0.44	0.69
Leaf Characters							
LL	0.29	0.19	-0.26	0.22	-0.45**	0.16	0.25
LW	0.22**	0.10	-0.12	-0.04	-0.16**	0.06	0.10

*, **, significant at 0.05 and 0.01 prob. Level, respectively. SE = Standard error, ALPB = Average length of primary branch (cm), CD = Canopy diameter (cm), HFPB = Height up to first primary branch (cm), IL = inter-node length (cm), LL = Leaf Length (cm), LW = leaf width (cm), NPB = number of primary branch, PH = Plant height (cm), SD = Stem diameter (mm)

Considering the number of primary branches characters, P1 and P4 exhibited positive GCA effects of 1.052 and 1.207, respectively. Contrarily P2, P3 and P5 showed negative GCA effects of -1.054, -0.459 and -0.745, respectively.

Leaf Characters

The parents P1 and P2 showed significant and non-significant positive GCA effects for leaf width, respectively. Contrarily, P3, P4 and P5 parents showed negative GCA effects for the same character but later parents had highly significant GCA effect. Considering leaf length, a highly significant GCA effect was recorded for the parent P5 (-0.458) followed by P3 (-0.262). The remaining three parents, P1, P2 and P4 had a positive GCA effect for this trait.

3.2.2. Estimates of Specific Combining Ability (SCA) Effects

The magnitude of SCA effects is of vital importance in selecting cross combinations with a higher probability of obtaining best-performing hybrids and transgressive segregates. In this study, the hybrids manifested considerable SCA effects variations for growth characters as given in Table 5.

Stem characters

Only two out of the ten hybrids studied manifested positive and significant SCA effects for plant height. The maximum SCA effect of 17.59 was recorded with P2 x P5 followed by P1 x P3 which exhibited 14.78. On the other hand, the lowest negatively significant SCA effect of -31.64 was observed with P3 x P5 while P1 x P2 and P1 x P5 also showed negative but no significant SCA effects of -9.00 and -5.91, respectively, for the same character. All the rest five hybrids exhibited positive but non-significant SCA effects.

Stem diameter is one of the most important growth parameters which is well associated with yield. Three of the ten hybrids studied manifested negative SCA effects and two of these hybrids, P1 x P2 and P1 x P5, exhibited non-significant negative SCA effects whereas the third cross, P3 x P5, revealed highly significant negative SCA effects. Except these three hybrids mentioned above, all the remaining seven exhibited positive SCA effects for the same character. Among those which showed positive SCA effects, hybrids P2 x P5, P2 x P3 and P1 x P3 showed significant or highly significant SCA effects of 3.69, 3.45 and 2.62, respectively. This indicated that these three hybrids, P2 x P3, P2 x P5 and

P1 x P3, are the best specific combinations for improved stem diameter and could be very useful materials for further breeding programs.

In the case of height up to the first primary branch, only one hybrid, P3 x P4, revealed a positive and significant SCA effect and was the best specific positive combiner. On the contrary, two hybrids, P3 x P5 and P4 x P5, revealed negative and significant SCA effect and hence were the poorest specific combinations for this trait. Among the remaining seven hybrids, two of them exhibited negative SCA effects and five hybrids showed positive but non-significant estimates of SCA effects for the same trait.

Considering the inter-node length of the main stem, hybrids P2 x P5 and P4 x P5 revealed positive and significant SCA effects with their respective values of 0.82 and 0.83. In contrast, hybrids P1 x P2 and P3 x P5 showed negative and significant SCA effects of -0.78 and -1.86, respectively. All the rest hybrids showed fairly high and positive SCA effects for this trait.

Branch character

Three hybrids P2 x P3, P2 x P5 and P4 x P5 consistently showed positive and significant SCA effects for the average length of primary branches and canopy diameter and were the best specific combiners in the improvement of the two important growth characters. In contrast, P3 x P5 exhibited highly significant negative estimates of SCA effects for the average length of primary branches (-15.11) and canopy diameter (-39.19) and was the poorest specific combination for these two traits. All the rest hybrids had non-significant positive SCA effects except P1 x P2 and P3 x P4 which exhibited non-significant negative SCA effects (-2.88 and -2.24, respectively) for the average length of the primary branch and significantly negative SCA effects (-9.86 and -3.00, respectively) for canopy diameter.

All hybrids showed positive and non-significant SCA effects except P1 x P4 and P3 x P5 for the number of nodes per primary branch. The hybrid, P1 x P4 showed negative SCA effects (-0.28), and P3 x P5 exhibited highly significant negative SCA effect (-4.15) for this trait. The hybrid P4 x P5 exhibited the highest positive SCA effect (2.18) among all hybrids and was the best specific combination for this particular trait.

Table 5. Estimates of specific combining ability (SCA) effects for growth characters in 5 x 5 parent half-diallel crosses in coffee.

Hybrids	Stem Characters		Branch Characters			Leaf Characters			
	PH	SD	HFPB	IL	ALPB	CD	NPB	LL	LW
P ₁ x P ₂	-9.00	-1.49	0.17	-0.78*	-2.88	-9.86	0.23	-0.40	-0.16
P ₁ x P ₃	14.78*	2.62*	1.32	0.47	1.34	7.91	1.55	0.17	0.22
P ₁ x P ₄	3.12	0.38	-0.54	0.28	1.68	8.85	-0.28	0.52	0.02
P ₁ x P ₅	-5.91	-0.85	-4.29	0.40	2.73	6.50	1.09	-0.11	-0.27
P ₂ x P ₃	11.19	3.45**	1.90	0.42	6.39*	15.25*	0.08	0.76	0.32
P ₂ x P ₄	4.37	1.14	1.30	0.06	5.14	8.44	0.41	-0.63	0.03
P ₂ x P ₅	17.59**	3.69**	2.13	0.82*	6.42*	18.63*	1.44	0.88*	0.56**
P ₃ x P ₄	5.56	0.37	2.45*	0.10	-2.24	-3.00	1.06	-0.41	-0.05
P ₃ x P ₅	-31.64**	-6.70**	-3.46**	-1.86**	-15.11**	-39.19**	-4.15**	-2.10**	-1.22**
P ₄ x P ₅	9.96	2.48	-2.57*	0.83*	7.13*	13.84*	2.18	0.60	0.08
SE(d)Sij ±	5.90	1.29	1.23	0.34	3.04	6.41	1.14	0.41	0.17
SE(d)Sij-Sik	8.85	1.93	1.85	0.51	4.56	9.61	1.71	0.62	0.26
SE(d)Sij-Skl	8.08	1.77	1.69	0.46	4.16	8.77	1.56	0.57	0.23

*, **, significant at 0.05 and 0.01 prob. Level., respectively, SE = Standard error, ALPB = Average length of primary branch (cm), CD = Canopy diameter (cm), HFPB = Height up to first primary branch (cm), IL = inter-node length (cm), LL = Leaf Length (cm), LW = leaf width (cm), NPB = number of primary branch, PH= Plant height (cm), SD = Stem diameter (mm)

Leaf characters

Similar to stem and branch characters, the SCA effects of the hybrids tested were largely positive but non-significant. It was only P₂ x P₅ that revealed positive and highly significant and significant SCA effects for leaf width (0.88) and leaf length (0.56), respectively. In contrast, P₃ x P₅ showed a highly significant negative SCA effect for both leaf length and leaf width characters with values of - 2.10 and -1.22, respectively.

4. Discussions

4.1. Analysis of Variance (ANOVA)

Mean squares due to genotypes of both Parents and hybrids and hybrids alone indicated highly significant differences for all characters, except the total number of nodes, leaf area and number of nodes per primary branch characters. Similarly, the reports of previous studies showed significant differences among genotypes for morphological traits in different sets of crosses studied in Arabica coffee [5, 23, 1]. Thus, the present study showed a large proportion of the variations observed between the genotypes could be attributed to genetic variation that existed between the genotypes because this experiment was conducted at one location. Therefore, it was justifiable to conduct a detailed genetic analysis and estimate the amount of heterosis and GCA and SCA effects for those traits significant differences were manifested among the genotypes.

Block differences were highly significant ($P < 0.01$) and significant ($P < 0.05$) for most of the characters measured. This result was as expected since the experimental field was a gentle slope in nature and soil variation was expected within the field between the top, middle and bottom parts. Indeed, the blocking was carefully designed and the replications were laid out against the slope to maintain uniformity within block or replication.

4.2. Combining Ability Analysis

The analysis revealed that the mean squares due to both

general combining ability (GCA) and specific combining ability (SCA) effects were significant ($P < 0.05$) or highly significant ($P < 0.01$, $P < 0.001$) for all the characters measured except that the GCA mean squares were not significant for the number of primary branches and height up to the first primary branch. This result indicates the existence of genetic variability among the parental lines included in the present study and the involvement of both additive and non-additive gene actions in the inheritance of all the traits except the effects of additive gene action is inconsiderable in controlling the expression of the number of primary branches and height up to the first primary branch.

Falconer, [13] suggested that when non-additive gene action is predominant in the expression of a trait, selection will not be effective in improving the character and the character in question. The present findings thus may suggest the limited efficiency of the selection method to improve the characters considered and the need to consider other breeding methods such as hybridization which enables to exploitation of the advantage of dominant gene effects.

The previous genetic studies in crosses among indigenous Arabica lines were similar to the present results. Thus different scholars reported the importance of additive and non-additive gene actions for growth characters viz stem diameter, number of nodes, number of primary branches, length of first primary branch, and number of secondary branches [18].

Likewise, Bayetta [5] studied indigenous coffee crosses at the nursery stage and reported the importance of both additive and non-additive gene action in shoot characters such as stem diameter, plant height, number of nodes, inter-nodes length, shoot fresh weight, shoot dry weight, and shoot volume. Wassu [23] also indicated the importance of both additive and no-additive gene actions for stem diameter, plant height and number of primary branches. On the other hand, the preponderance of additive gene effects was reported by Ayano [1] for many growth traits except plant height which was predominantly controlled by non-additive gene action.

4.3. Estimates of General Combining Ability Effects

In the present study, all the parental lines exhibited variable GCA effects for different growth characters except P1. Parent P1 consistently exhibited the best general combining ability as it is crossed with a series of other parental lines for all the morphological characters studied probably contributing genes with positive additive effects to their progeny. Therefore, this parent could be used fully for inclusion in coffee breeding programs aimed at increasing vigour in coffee. Gardener, [14] suggested that the parent exhibiting significantly positive and negative GCA effects for a particular character is assumed to have a high degree of favourable and un-favourable alleles, respectively. Therefore, this result clearly shows that parent p1 has favourable alleles since the parent exhibited a significantly positive GCA effect. These results reveal a close agreement between per se mean performance and the GCA effect for all characters studied. Thus, crossing p1 with the complementary parent and selection from the transgressive segregating generations is expected to lead to substantial genetic improvement for all growth characters studied.

Parent P2 also showed a positive non-significant GCA effect for characters namely plant height, the average length of the primary branch, leaf length and leaf width, while a highly significant positive GCA effect for characters' Height up to the first Primary branch. This parent, according to this study, was the best general combiner next to P1 for these traits and could also be useful for improving them along with P1. Parent P4 also showed a positively significant GCA effect for all measured characters except leaf width and height up to the first primary branch while it showed a significant GCA effect for the character number of nodes per primary branch. This parent also appeared to be important for use in parental combination or hybridization programs for improving those characteristics. These results indicate that the two open-type parents, P1 and P4, are good general combiners and have the ability to transfer their vigorous character to their offspring in parental combination. Therefore, it could be very useful to consider these two parental lines in a hybrid development program intended to improve the growth performance of coffee varieties.

Bayeta, [6] reported that the parent showing good GCA for many desirable traits would be more useful in any breeding program since it's not practically possible to breed for individual growth characters. In this regard, the parent P1 that exhibited maximum GCA effect for all stem, branch and leaf characters must be useful followed by P2 and P4 for use in breeding programs for the simultaneous improvement of multiple traits. In addition, these parents could be used in hybrid variety development more effectively and also they may contribute favourable alleles for the development of vigorous hybrids. The present results are similar to those of [1, 6, 23], who reported greater positive GCA effects in most of the parents for morphological characters.

On the contrary, Parents P5 followed by P3 consistently showed negative GCA effects and were poor general

combiners for all stem, branch and leaf characters and were, therefore, not very useful for the improvement of the characters considered in this study. Hence, probably these parents could be useful in a breeding program designed to develop hybrids with reduced growth characteristics, i.e. compact growth habit.

Parent P2, which is known for its compact growth, also showed a negative GCA effect for characters such as stem diameter, canopy diameter, number of node-per primary branch, and inter-node length. As indicated earlier, this result shown by the compact parent, was expected and suggested the usefulness of this parental line in breeding for reduced plant size. These results revealed a close agreement between per se mean performance and GCA effect for this parent.

4.4. Estimates of Specific Combining Ability Effects

The results clearly indicated that P2 x P5 and P1 x P3 were the best specific combinations for plant height and this result is very similar to their mean performances shown in Table 5 for the same trait. Hence, these hybrids could be selected for their specific combining ability and subsequent transgressive segregation breeding for plant height improvement even though tallness is not a desirable trait in coffee due to its inconveniency for harvesting or picking. On the other hand, some other hybrids showed negative SCA effects which may suggest the possibility of obtaining cross combinations/hybrids of shorter plant stature.

The success of obtaining the desired transgressive segregants depends on obtaining genetic recombination between both linked and unlike alleles [7]. On the other hand, observed frequencies of transgressive segregants were found to be more frequent in the F2 generation than others. Hence, in view of the importance of transgressive segregants, further investigation should continue in the F2 generation. According to Ysdav, [25], a comparison of the combining ability of parents and hybrids was observed and predicted frequencies of transgressive segregants in wheat hybrids indicated that the potential hybrids for transgressive segregants for traits that had high SCA effects and involved high and low general combiners. The hybrids involving low general combiners irrespective of their SCA effects showed poor performance with respect to transgressive segregation. Therefore, for the search of transgressive segregants, it would be more effective to advance those superior specific hybrids that evolved from crosses between parents having high and low GCA effects.

Hybrids, P3 x P5, exhibited highly significant negative SCA effects for the average length of primary branches and canopy diameter was the poorest specific combination for these two traits. All the rest crosses had non-significant positive SCA effects except P1 x P2 and P3 x P4 which exhibited non-significant negative SCA effects for the average length of primary branch and significant negative SCA effects for the canopy diameter. In contrast Hybrids, P2 x P3, P2 x P5 and P4 x P5 consistently showed positive and significant SCA effects for average length of primary branch and canopy diameter. These results clearly suggested that

those hybrids that revealed significantly positive SCA effects tended to favor open-type growth habit while those hybrids with highly significant negative SCA effects did encourage the development of compact growth habit which is favourable for closer spacing.

The overall SCA effects analysis generally indicated that more than half of the hybrids studied exhibited positive SCA effects for each of the morphological traits considered. Hybrids P1 x P3, P2 x P3 and P2 x P5, consistently showed positive SCA effect for all the nine morphological traits measured where the SCA effects were significant or highly significant for some of these characters.

Hybrid P2 x P3 exhibited a significant positive SCA effect for three characters, viz. stem diameter, the average length of primary branch and canopy diameter out of nine characters measured. Hybrid P4 x P5 also exhibited significant positive SCA effect for three out of nine traits which includes average length of primary branch, canopy diameter and inter-node length. This hybrid exhibited a negative SCA effect for height up to the first primary branch, but a positive SCA effect for all the rest traits. Hybrid P1 x P3 exhibited a significant positive SCA effect for plant height and stem diameter and a positive SCA effect for all the rest traits.

Considering overall growth performance, hybrids P1 x P3, P2 x P3 and P2 x P5 exhibited positive SCA effects for all the nine morphological characters and hybrids P1 x P4, P2 x P4 and x P5 that also manifested positive SCA effects for eight out of nine characters could be considered good specific combinations for their growth performance and need to be further studied to select the best few hybrids for commercial use or further use in advanced generation breeding program.

Most of the hybrids identified as desirable, on the basis of their SCA effects for these traits, had at least one of the parents involved as a good general combiner for the traits as the poorest specific combinations (e.g. P3 x P5) were largely observed from crosses between very poor combining parents. Therefore, in any hybrid breeding program aimed at the development of vigorous hybrids with acceptable out-turn, it is of paramount importance to understand the general combining ability of parents to be employed in a breeding program.

5. Conclusion

For many Ethiopian farmers, coffee is their single most important source of income. Thus, improvement of production and productivity is of paramount importance to assist the coffee growers. The analysis of variance revealed highly significant ($P < 0.001$ and $P < 0.01$) differences among the 15 genotypes (5 parents and 10 F_1 s) for all the traits considered except for total number of node, leaf area and number of nodes per primary branch. This clearly showed the presence of inherent variations among the genotypes for most of the characters studied. The results of combining ability analysis, on the other hand, showed that variations due to both the general (GCA) and specific (SCA) combining ability mean squares were significant for nine out of 12 characters

measured indicating the importance of both additive and non additive gene actions in determining the expression of these characters. However, the fact that the degree of mean squares due to SCA were higher than that of GCA and the components of variances ratios were less than unity, the non-additive gene actions were probably of primary importance in the inheritance of all the morphological traits studied. Parent P1 consistently exhibited high and positive GCA effects for all the nine morphological characters studied implying that this parent had contributed positive additive effect to its progenies and was the best general combiner followed by Parent P4. When we consider SCA, Hybrids P₂ x P₅, P₂ x P₄, P₂ x P₃, P₃ x P₄ and P₁ x P₅ were noted with High and positive SCA effects for each character.

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Conflicts of Interest

The authors declare no conflicts of interest.

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