Gene action in diallel crosses among some Limmu coffee (*Coffea arabica* L.) genotypes in South Western Ethiopia

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Abstract

Knowledge of gene action enables breeders to design effective breeding strategies for the improvement of genotypes. Half diallel cross among limmu coffee (*Coffea arabica* L.) genotypes comprising 5 parents, $10F_1$ hybrids, and two checks carried out at agricultural research (Jimma, Agaro, and Gera centers) for the objective to determine nature of gene action and combining ability effects of diallel genotypes for yield and its components in 2017/18. Randomized complete block design (RCBD) with three replications used. Combined analysis of variance revealed significant (P<0.05) variation among 17 and 15 diallel genotypes for 24 traits indicating the presence of genetic variability for these traits. The mean square due to GCA and SCA was significant for 13 traits including yield, which implies both additive and non-additive gene actions involved for the expression of these traits. Additive gene action contributed a lot to nine traits including all fruit and bean traits than non-additive gene actions. However, non-additive gene action more contributed than additive gene action for 11 traits including yield (77.57%). GCA effect estimate showed the best general combiners were parent P_4 (L55/01) for yield, P_1 (L20/03) for all fruit and bean characters, and parent P_2 (L67/01) for three growth, leaf, and fruit traits. Based on the SCA effect, the best crosses were $P_4 \times P_5$ followed $P_1 \times P_5$ and $P_2 \times P_5$ for yield, $P_2 \times P_4$, and $P_3 \times P_4$ for six and five different traits, respectively. These hybrids could be used in variety development after testing for other desirable traits.

Keywords: Additive; Combining ability; Gene action; Non-additive.

1. Introduction

Arabica coffee (*Coffea arabica* L.) is a native cash crop to South-Western Ethiopia, is an allotetraploid (2n = 4x = 44) dicot which belongs to family *Rubiaceae* (Davis *et al*., 2006). It is an important crop which is produced in more than 80 countries including Ethiopia (Musoli *et al*., 2009). The global production of coffee in 2017/18 was 9.59 billion Kg, of which about 5.69 billion kg (59.3%) was Coffee arabica whereas; the remaining 3.9billion Kg Robusta type (FAS, 2018). In Ethiopia, the total area of production is estimated to be about 758,523.29 hectares (CSA, 2020). The estimated annual national production of clean coffee 482.56 tons and the national yield of coffee is 636.2 kg per hectare, which is quite low (CSA, 2020).

Arabica coffee is a predominantly self-pollinating crop, it is expected that the use of intra population selection methods (Fadelli and Sera, 2012) and important alternative for genetic breeding is hybridization which allow gene recombination and use of the existing variability to produce new cultivars adapted to different growing conditions (Fontes, 2001). Out crossing were also found in Arabica coffee through observations about 40 to 60% (Mayer, 1965) and mating system analysis about 76% (Berecha, 2014). With constant and concerted efforts, hybrid coffee varieties

through hybridization have been produced by Ethiopian Institute of Agricultural Research (EIAR), Jimma Agricultural Research Center (JARC). Over the last four decades (1977-2018), 42 coffee varieties *i.e.*, thirty-five pure lines and seven hybrids were released for various major coffee growing agro-ecologies of the country (Benti, 2017; JARC, 2018).

The genetic improvement of coffee's desired traits depends on the nature and magnitude of genetic variability and interactions involved in the inheritance of these traits. Different authors Kitila *et al.* (2011), Beksisa and Ayano (2016), Beksisa *et al.* (2017) and Weldemichael *et al.* (2017) reported the presence of the genetic diversity among Limmu Coffee germplasm accessions and the possibility of developing improved varieties through selection and/or hybridization.

Combining ability estimates provide useful information for selecting favorable parents and elucidate the nature of and magnitude of gene effects influencing quantitative traits (Fasahat *et al.*, 2016). Griffing (1956), diallel analysis for combining ability is the most widely used and provide information regarding to gene action. General combining ability (GCA) is associated with additive gene action that are additive in their effects, while specific combining ability (SCA) is associated with non-additive gene action caused by dominance and epistasis (Pederson *et al.*, 1998).

Some researchers found the importance of both additive and non-additive gene action for expression of coffee yield reported by Walyaro (1983), Belachew (2001), Mohammed (2004) and Ayano (2013), while others suggested that only non-additive gene action is important for coffee yield reported by Ameha and Belachew (1983). The present study was carried out with the objectives of analyzing the nature of gene action influencing yield and yield components, and to ascertain the relative performance regarding to combining ability effects (General and specific combining ability effect) for yield and its components among limmu coffee genotypes using diallel mating technique.

2. Materials and Methods

2.1. *Description of the study area*

The experiment was conducted in 3 representative sites of major coffee growing areas in southwestern Ethiopia (Table1). These were Jimma Agricultural Research Center (JARC), Gera Agricultural Research Sub-center (GARSC) and Agaro Agricultural Research Sub-Center (AARSC). The first 2 locations (Jimma and Agaro) represent mid altitude area whereas Gera represent highland area. JARC is located 352 km southwest of Addis Ababa. AARSC is located in Jimma zone, 397 km southwest of Addis Ababa and 45 km far from Jimma town. GARSC is located 421 km south west of Addis Ababa, 69 km far from Jimma town.

Table 1. Summary of ecological description of the study sites

Locations	Altitude (m.a.s.l)	Coordinate		Temperature (^{0}C)		Rainfall (mm)	RH (%)	Soil	
		Latitude	Longitude	Min.	Max.			Type	pH
Jimma	1753	7^{0}40'00"N	36^{0}47'00"E	11.6	26.3	1572	67	Reddish brown/ nitosols	5.20
Agaro	1650	7^{0}50'35"N	36^{0}35'30"E	12.4	28.4	1616	-	Mollicnito sols	6.20
Gera	1940	7^{0}7'0"N	36^{0}00'00"E	10.4	24.4	1878.9	75.03	Loam	-

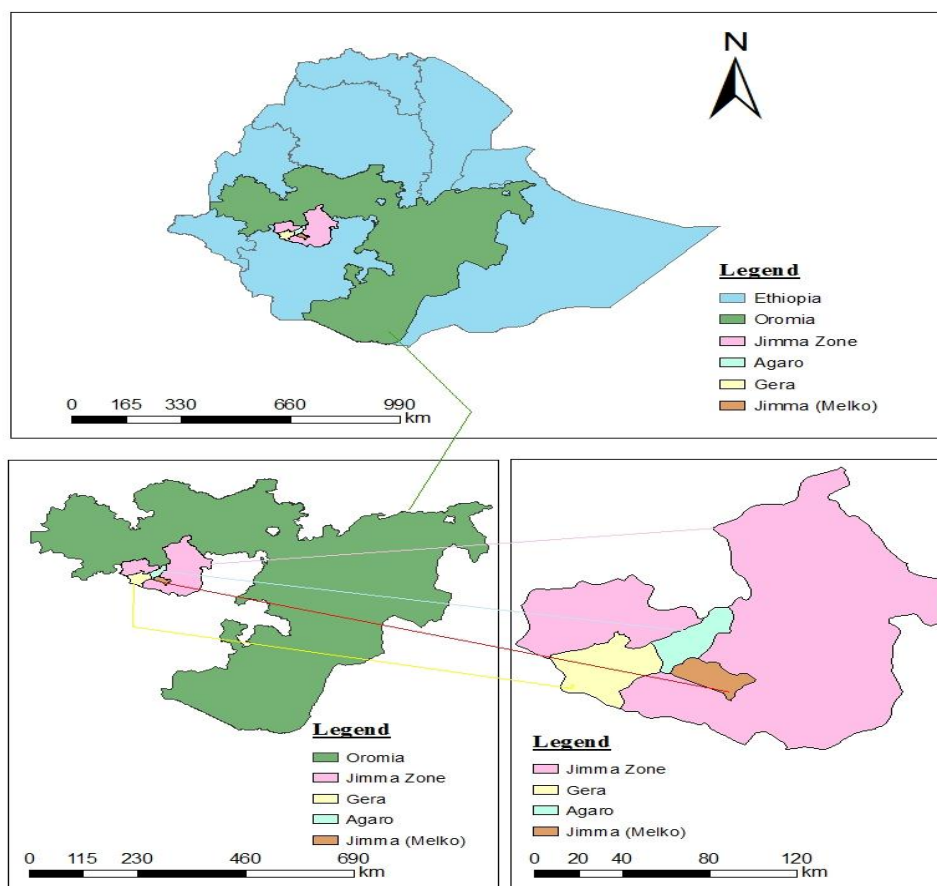Source: Jimma Agricultural Research center; (center profile)

Figure 1. Location of study area

2.2. Experimental materials, design and field management

The experimental materials consisted of seventeen entries described in Table 3. Limmu coffee genotypes were collected from Limmu kossa in 2001 and 2003 G.C. Five elite advanced pure lines promoted to verification trials were selected as parents from the collections based on 5-7 years mean yield, disease and insect pest resistance and overall growth performance. These parental lines were crossed in a half diallel fashion in 2014 and produced 10 hybrids by $\frac{p(p-1)}{2}$ formula, where p is number of parental lines (Griffing, 1956). Pure lines namely Dessu and 74110 was used as standard check at mid-altitude area (Jimma and Agaro) and highland area (Gera), respectively. One month after harvest, seeds of the parents and their respective F_1 hybrid

$\frac{p(p+1)}{2}$ = 15 entries were sown at nursery along with 2 checks in Dec 2014 G.C. Six months old seedlings were transplanted in the field in July, 2015, at Jimma Agricultural research center, Agaro and Gera research sub centers that represent the Limmu coffee growing area. One-row considered as plots consisting of 6 plants and a spacing of 2m x 2m were used area. The experiments were laid down in three replications of the randomized complete block design (RCBD). All agronomic management practices were uniformly applied to the plots following the recommendation from Jima Agricultural Research Centre (Taye *et al.*, 2008). This study was conducted on this established nursery. The characteristics of the 5 selected parental lines described in Table 2 and the whole experimental material (parents, their crosses and the checks) are summarized in Table 3.

Table 2. Parental lines selected for crossing and their morphological descriptions

Parents		Origin		Altitude (m.a.s.l)	Description/ characteristics
	Zone	Woreda	Collection place		
P1	L 20/03	Jimma	Limmukossa	Tenebo	1650	High yield, open canopy, vigorous, stiff stem, bold & oblong bean, deep green leaf, good survival
P2	L 67/01	Jimma	Limmukossa	Eyru	1600	High yield, many primary, secondary and tertiary fruit bearing branches, vigorous, intermediate canopy, open fruiting nodes, 100% survival, moderate resistance to CLR
P3	L 03/01	Jimma	Limmukossa	Weleke-Sombo	1550	Moderate resistance to CBD, strong branching, many primary, secondary and tertiary branches, good fruit setting (high yield), late maturing nature, compact canopy, 100% survival rate
P4	L 55/01	Jimma	Limmukossa	Cheraki	1500	Compact canopy, leafy (good leaf to stem ratio), vigorous stem, good resistance to CBD and CLR.
P5	L 45/01	Jimma	Limmukossa	Chime	1660	High yield (large number of fruits from top to bottom), 100% survival, vigorous, compact canopy, moderate resistance to CLR.

Source: Extracted from passport data existing in Jimma Agricultural Research Center (JARC) coffee breeding and genetics department

Table 3. List of experimental materials

S.No	Codes for parents, crosses and checks	designation
1	P_1	L20/03
2	P_2	L67/01
3	P_3	L03/01
4	P_4	L55/01
5	P_5	L45/01
6	$P_1 \times P_2$	L20/03 x L67/01
7	$P_1 \times P_3$	L20/03 x L03/01
8	$P_1 \times P_4$	L20/03 x L55/01
9	$P_1 \times P_5$	L20/03 x L45/01
10	$P_2 \times P_3$	L67/01 x L03/01
11	$P_2 \times P_4$	L67/01 x L55/01
12	$P_2 \times P_5$	L67/01 x L45/01
13	$P_3 \times P_4$	L03/01 x L55/01
14	$P_3 \times P_5$	L03/01 x L45/01
15	$P_4 \times P_5$	L55/01 x L45/01
16	hybrid check at Jimma and Agaro (Check1)	Ababuna
	hybrid check at Gera (Check1)	Gawe
17	pure line check at Jimma and Agaro (Check2)	Dessu
	Pure line check at Gera (Check2)	74110

2.3. Data collected

All data on growth characters were taken from the entire four plants of each entry. The quantitative traits were recorded as recommended by IPGRI (1996).

2.3.1. Stem characters
Plant height (PH) (cm), Height up to first primary branch (HuFPB) (cm) and Stem diameter (SD) (cm),

2.3.2. Branch characters
Length of the first single primary branch (LFSPB) (cm), Average length of primary branches (ALPB) (cm), Internode length on primary branches (ILPB) (cm), Number of primary branches (NPB) (no), Number of bearing primary branches (NBPB) (no), Number of secondary branches (NSB) (no) and Canopy diameter (CD) (cm).

2.3.3. Leaf characteristics
Leaf length (LL) (cm), Leaf width (LW) (cm), Leaf area (LA) (cm^2) and Leaf petiole length (LPL) (cm)

2.3.4. Fruit characteristics
Fruit length (FL) (mm), Fruit width (FW) (mm), Fruit thickness (FT) (mm)

2.3.5. Bean characteristics
Bean length (BL) (mm), Bean width (BW)(mm), Bean thickness (BT) (mm) and Hundred bean weight at 11% moisture (HBW) (g)

2.3.5.1. 100 bean weight at 11% moisture (HBW) (g)
An average of 100 matured beans was used to calculate 100 bean weights. Oven was used for drying of beans to make 0% moisture content and weight was recorded using sensitive balance by the following formula.

$$100 \text{ bean weight(g)} = \frac{\text{bean weight at 0\% MC}}{\text{Bean Number X 0.89}} \times 100$$

2.3.5.2. Yield (kg/ha)
Total fresh cherries were harvested per plot or from all trees during the first 2 years (2017 and 2018) bearing season and weighed in grams per plot basis and converted in to clean coffee (kg ha^{-1}).

2.4. Statistical analysis

The collected quantitative data from the experimental plots were subjected to SAS computer program version 9.3 Proc Mixed procedures (SAS, 2012). The statistical analysis contained treatments as a fixed factor while block and location as random factors. Analysis of variance was carried out according to the procedure recommended for Randomized Complete Block Design (RCBD) and the least significant difference (LSD) was used for mean separation. Combining ability (general and specific) analysis was done with Diallel SAS program for Griffing's diallel analyses (Zhang and Kang, 1997) based on the following linear model for combined location following method 2 model I (fixed effect) of Griffing (1956). The magnitude of GCA and SCA was evaluated using the ratio of their sum of squares to total sum of squares for diallel genotypes to determine the type of gene action as outlined by Machida *et al.* (2010).

$$Y_{ij} = \mu + g_i + g_j + s_{ij} + l_k + gl(ik) + gl(jk) + sl(ijk) + \frac{1}{bc}\sum_k\sum_l \varepsilon_{ijlk} \begin{cases} i,j = 1,2,3\dots,n \\ k = 1,2,3\dots,b \\ l = 1,2,3\dots,c \end{cases}$$

Where, Y_{ij} = the value of a character measured on cross of ith and jth parents, μ = overall mean, g_i, g_j = the general combining ability effect for the ith and j[th] parents, s_{ij}= the specific combining ability effect of the cross between the ith and j[th] parents such that s_{ij}= s_{ji}, l_k = environmental effect, gl(ik), gl(jk) = interaction effect of general combining ability effect of ith and j[th] parents with environments, sl(ijk)= interaction effect of specific combining ability effect of the cross from i[th] and j[th] parents with environments, $\frac{1}{bc}\sum_k\sum_l \varepsilon_{ijlk}$ = the experimental error due to environmental effect associated with the ijkl[th] observation. n, b and c = number of parents, blocks and sampled plants, respectively.

3. Results and discussion

3.1. Analysis of variance (ANOVA)

Combined analysis of variance (ANOVA) for growth, fruit and bean characters showed significant to highly significant difference among 17 genotypes (parents, their crosses and checks) for all traits except plant height up to first primary branch (HuFPB), internode length on main stem (ILMS), number of secondary branches (NSB), leaf width (LW), leaf area (LA) and leaf petiole length (LPL) Table 4 and 5. The difference between 17 Genotypes (checks included) and diallel genotype (when checks excluded) (GEI) by Environment interaction for bean yield was significant which indicates inconsistence performance of the genotypes across the three locations (Table 5 and 7). ANOVA at individual location showed that the presence non-significant difference among 17 genotypes and diallel genotypes at Agaro for bean yield. Due to this combining ability analysis at this location was removed from the analysis.

The difference between the diallel genotypes (only parents and their crosses) was significant for all traits except four traits; HUFPB, ILMS, NSB and LPL (Table 6). The diallel Genotype by Environment interaction (GEI), which was used as an error term to test genotypes, was large and significant for HUFPB, and may cause the effect of genotypes non-significant. These findings provided evidence for the presence of considerably high amount of genetic variability among the parental and their respective hybrids (F_1) of coffee genotypes, which may facilitate genetic improvement of yield and its components among limmu coffee genotypes and consistence of performance of the genotypes over the 3 locations for the majority of the traits. These results are in harmony with those previously reported by Belachew (2001), Mohammed (2004), Ayano (2013) and Getaneh (2017) who found significant difference between different diallel coffee genotypes for different traits.

3.2. Combining ability analysis

3.2.1. Growth characters

Combining ability analysis of combined data of growth characters for diallel genotypes indicated in Table 6. The detailed analysis of variance (ANOVA) for combining ability analysis revealed significant to highly significant mean square (MS) of both general combining ability (GCA) and specific combining ability (SCA) for height up to first primary branch (HUFPB), stem diameter (SD), average length of primary branch (ALPB), internode length on primary branch (ILPB), canopy diameter (CD), leaf length (LL), leaf width (LW) and leaf area (LA). However, only MS due to SCA was significant (p from 0.05 to less than 0.001) for plant height (PH), number of primary branch (NPB), number of bearing primary branch (NBPB) and length of first single primary branch (LFSPB) (Table 6). According to Griffing (1956) the GCA variance contains additive gene effect where as SCA variance contains non-additive gene effect. Hence, significant MS of both GCA and SCA suggesting that each additive and non-additive gene action was involved in controlling HUFPB, SD, ALPB, ILPB, CD, LL, LW and LA. These results were in agreement with Mesfin and Belachew (1983), Walyaro (1983), Belachew (2001), Mohammed (2004) and Ayano (2013) who reported importance of both additive and non-additive gene action for majority of these traits.

Table 4. Combined ANOVA of genotypes (parents, their crosses and checks) for stem, branch and leaf characters in 2017

		Mean square of stem characters						Mean square of branch characters		
SOV	Df	PH	PHuFPB	ILMS	NNMS	NIMS	SD	LFSPB	ALPB	ILPB
Genotype(G)	16	694.50^{***}	18.70^{ns}	0.6^{ns}	7.90^{*}	8.00^{**}	0.39^{***}	242.53^{***}	149.28^{***}	0.59^{**}
Environment	2	35473.28^{***}	125.99^{ns}	26.31^{*}	197.21^{***}	214.44^{***}	1.00^{ns}	2583.48^{***}	3834.63^{***}	2.30^{ns}
Rep (E)	6	429.20^{**}	27.50^{**}	2.3^{ns}	8.14^{ns}	5.81^{ns}	0.25^{*}	101.02^{ns}	64.57^{ns}	0.52^{ns}
G x E	32	169.00^{ns}	15.00^{***}	0.7^{***}	3.33^{ns}	3.16^{ns}	0.06^{ns}	59.57^{ns}	28.36^{ns}	0.22^{*}
Pooled Error	96	125.5	5.60	0.3	2.30	2.38	0.06	44.21	23.33	0.12
Total	152									
mean		158.72	27.17	7.17	19.27	18.36	3.31	83.88	73.02	4.76
CV%		7.06	8.7	7.73	7.87	8.4	7.57	7.93	6.61	7.37

Table 4. Continued

		Mean square of branch characters					Mean square of leaf characters			
SOV	Df	NPB	NBPB	PBPB	NSB	CD	LL	LW	LA	LPL
Genotype(G)	16	39.36^{**}	44.95^{***}	252.75^{**}	173.52^{ns}	678.42^{***}	1.49^{*}	0.33^{ns}	93.10^{ns}	0.01^{ns}
Environment(E)	2	1167.07^{***}	851.85^{**}	3508.81^{*}	1554.31^{ns}	15305.04^{***}	44.24^{**}	5.87^{**}	2231.31^{**}	0.58^{***}
Rep (E)	6	32.25^{ns}	81.47^{**}	471.65^{*}	583.39^{ns}	123.24^{ns}	3.16^{*}	0.47^{ns}	159.11^{ns}	0.01^{ns}
G x E	32	15.20^{ns}	12.81^{ns}	101.51^{ns}	302.35^{***}	176.20^{ns}	0.76^{*}	0.22^{***}	53.10^{***}	0.01^{ns}
Pooled Error	96	11.06	12.7	84.52	124.15	121.82	0.43	0.07	21.61	0.01
Total	152									
mean		33.45	13.24	38.56	43.93	156.72	13.97	5.68	53.46	0.86
CV%		9.94	26.91	23.85	25.36	7.04	4.67	4.65	8.7	11.19

Note: values with *, ** and *** showed Significant at 0.05, 0.01 and 0.001 probability level respectively, ns = non-significant, PH = Plant height (cm), PHuFPB= height up to first primary branch (cm), ILMS = internode length on main stem (cm), NNMS= number of nodes on main stem (no), NIMS = number of internode on main stem(no), SD = stem diameter(cm), LFSPB = length of 1st prim. Branch (cm), ALPB = average length of primary branch (cm), ILPB = internode length on primary branch(cm), NPB = No of primary Branch(no), NBPB = No of bearing primary branch(no), NSB = No of secondary branch(no), CD = canopy diameter(cm), LL= leaf length(cm), LW = leaf width(cm), LA= leaf area(cm^2), LPL = leaf petiole length(cm), CV = coefficient of variation

Table 5. Combined ANOVA of genotypes (parents, their crosses and checks) for fruit and bean characters

SOV	Df	Mean square fruit characters			Mean square of bean characters				
		FL	FW	FT	BL	BW	BT	HBW	Yield
Genotype(G)	16	3.19^{***}	1.21^{***}	0.47^{**}	2.86^{***}	0.27^{**}	0.30^{***}	27.19^{***}	227031.55^{***}
Environment	2	19.31^{**}	8.14^{**}	15.01^{***}	16.72^{*}	1.44^{***}	0.07^{ns}	48.93^{ns}	699479.05^{**}
Rep (E)	6	1.05^{**}	0.63^{*}	0.41^{*}	0.32^{ns}	0.01^{ns}	0.06^{ns}	10.71^{ns}	86919.74^{ns}
G x E	32	0.69^{ns}	0.23^{ns}	0.17^{ns}	0.21^{*}	0.03^{*}	0.02^{ns}	5.64^{*}	89680.75^{*}
Pooled Error	96	0.35	0.21	0.15	0.12	0.02	0.02	3.34	51089.17
Total	152								
mean		16.25	13.25	11.4	10.29	7.14	4.27	19.01	798.16
CV%		3.66	3.49	3.38	3.43	2.06	3.15	9.61	28.3

Note: values with *, ** and *** showed Significant at 0.05, 0.01 and 0.001 probability level respectively, ns = non-significant, SOV = source of variation, Df = degree of freedom, FL = fruit length(mm), FW = Fruit width(mm), FT = fruit thickness(mm), BL = bean length(mm), BW = bean width(mm), BT = bean thickness(mm), HBW = hundred bean weight(g), G x E = genotype by environment interaction, CV = coefficient of variation

Table 6 . Combining ability analysis of combined data for growth characters in 2017

SOV	DF	PH	HUFPB	SD	LFSPB	ALPB	ILPB	NPB
Site (E)	2	30023.74^{***}	129.92^{*}	1.00^{ns}	2152.18^{***}	3087.97^{***}	0.97^{ns}	1219.12^{***}
Rep (E)	6	325.60^{*}	23.80^{**}	0.22^{**}	99.78^{ns}	55.05^{ns}	0.48^{**}	32.98^{*}
Genotypes (DG)	14	606.36^{***}	18.82^{ns}	0.41^{***}	233.44^{***}	131.59^{***}	0.54^{***}	29.77^{*}
G × E	28	163.58^{ns}	10.60^{**}	0.06^{ns}	53.76^{ns}	22.40^{ns}	0.13^{ns}	11.52^{ns}
GCA	4	62.460^{ns}	36.149^{*}	0.456^{**}	109.166^{ns}	84.537^{*}	1.234^{**}	19.173^{ns}
SCA	10	823.916^{***}	11.881^{*}	0.386^{***}	283.149^{***}	150.408^{***}	0.268^{*}	34.008^{**}
GCA × E	8	198.052^{ns}	9.962^{ns}	0.058^{ns}	53.989^{ns}	20.574^{ns}	0.196^{ns}	19.083^{ns}
SCA × E	20	149.793^{ns}	10.849^{*}	0.065^{ns}	53.669^{ns}	23.127^{ns}	0.097^{ns}	8.491^{ns}
Residual	84	130.959	5.172	0.069	45.828	6.839	0.135	11.908
RCGCA		2.94	54.89	32.08	13.36	18.36	64.79	18.40
RCSCA		97.06	45.11	67.92	86.64	81.64	35.21	81.60

Table 6. Cont'd

SOV	DF	NBPB	NSB	CD	LL	LW	LA
Site (E)	2	795.42^{**}	2184.23^{ns}	12037.14^{***}	33.05^{**}	3.49^{**}	1493.65^{**}
Rep (E)	6	67.26^{**}	500.14^{ns}	107.54^{ns}	3.09^{**}	0.43^{***}	149.60^{***}
Genotypes (G)	14	40.91^{**}	128.59^{ns}	690.09^{***}	1.42^{*}	0.32^{**}	89.81^{**}
G ×E	28	14.04^{ns}	159.65^{ns}	145.45^{ns}	0.60^{ns}	0.10^{ns}	30.91^{ns}
GCA	4	23.069^{ns}	-	374.486^{*}	2.579^{*}	0.529^{*}	152.277^{*}
SCA	10	48.048^{***}	-	816.333^{***}	0.954^{*}	0.236^{**}	64.817^{**}
GCA × E	8	14.214^{ns}	-	70.498^{ns}	0.594^{ns}	0.133^{ns}	33.596^{ns}
SCA × E	20	13.976^{ns}	-	175.433^{ns}	0.602^{ns}	0.089^{ns}	29.837^{ns}
Residual	84	13.368	24.78	126.198	0.456	0.076	23.111
RCGCA		16.11		15.50	51.96	47.29	48.45
RCSCA		83.89		84.50	48.04	52.71	51.55

Note: values with *, ** and *** showed Significant at 0.05, 0.01 and 0.001 probability level respectively, ns = non-significant, PH = plant height, HuFPB = height up to first primary branch(cm), SD = stem diameter (cm), LFSPB =Length of first single primary branch(cm), ALPB = Average length of primary branch(cm), ILPB = internode length on primary branch(cm), NPB = Number of primary branch(no), NBPB = number of bearing primary branch (no), , NSB = number of secondary branch(no), CD= Canopy diameter(cm), LL = leaf length(cm), LW = leaf width(cm), LA = leaf area(cm^2) GCA= general combining ability, SCA= Specific combining ability , GCA x E = general combining ability interaction with environment(site), SCAxE=Specific combining ability interaction with environment(site),RCGCA = Relative contribution of general combining ability, RCSCA = Relative contribution of specific combining ability.

In contrary to this, Mohammed (2004) and Getaneh (2017) reported only additive gene action involved for expression of CD and SD, respectively during their studies. Though, only MS due to SCA indicating that non-additive gene action alone is responsible for PH, NPB and NBPB through limmu coffee genotypes. Ayano *et al*. (2014) reported in their findings non-additive gene action contributed more (87.8%) than additive gene action for PH. In contrary to this, Belachew (2001) and Getaneh (2017) reported the importance of both additive and non-additive gene action for the expression of PH.

3.2.2. *Yield, fruit and bean characters*

Combining ability analysis of variance across the 2 locations for yield depicted in Table 7. The MS due to GCA and SCA were highly significant across 2 locations revealing both additive and non-additive gene actions are responsible for yield expression among limmu coffee genotypes. The relative contribution of SCA was as high as 77.57% for yield which indicated the preponderance of non-additive gene action for this trait. An interaction of both GCA and SCA with environment (GCA x E and SCA) MS was significant for bean yield which indicates the inconsistent contribution of gene actions across the 2 locations. This

result is in agreement with Walyaro (1983), Belachew (2001), Wassu *et al*. (2009) and Ayano (2013) who reported the importance of both additive and non-additive gene action for expression of yield coffee, different from Mesfin and Belachew (1983) who found only the SCA MS was significant for yield of coffee.

The GCA and SCA MS of fruit and bean characters indicated in Table 8. The results showed that both general (GCA) and specific (SCA) combining ability MS were highly significant for fruit width (FW), fruit thickness (FT), bean length (BL) and bean width (BW). These results indicated that both additive and non-additive type of gene effects were involved in the inheritance of these traits. However, only MS due to GCA was highly significant (P ≤ 0.01) for fruit length (FL), bean thickness (BT) and 100 bean weight (HBW) indicating the contribution of additive gene action alone for the inheritance of these characters across the 3 locations. The relative contribution of GCA was higher than SCA for all fruit and bean traits studied except FT suggesting the more contribution of additive gene action for those traits. This is in line with Ayano (2013) who reported more contribution of additive gene action for those fruit and bean characters in his study.

Table 7. Combining ability analysis of combined data for bean yield across 2 locations

SOV	DF	SS	MS	Pr>F
Site (E)	1	575984.00	575984.00	0.0003
Rep (E)	4	415158.81	103789.70	0.0411
Diallel Genotypes (DG)	14	3652885.25	260920.37	<.0001
DG ×E	14	1280097.84	1280097.84	0.0120
GCA	4	645542.38	161385.59	0.0051
SCA	10	3007342.87	300734.29	<.0001
GCA × E	4	443683.53	110920.88	0.0316
SCA × E	10	836414.32	83641.43	0.0346
Residual	56	2173013.75	38803.82	
RCGCA			22.43	
RCSCA			77.57	

DF= degree of freedom, SS= Sum square, MS = Mean square, GCA= general combining ability, SCA= Specific combining ability, GCA x E = general combining ability interaction with environment, SCA x E = Specific combining ability interaction with environment, RCGCA = Relative contribution of general combining ability, RCSCA = Relative contribution of specific combining ability

Table 8 . Combining ability analysis of combined data for fruit and bean characters in 2017

SOV	DF	FL	FW	FT	BL	BW	BT	HBW
Site (E)	2	14.951**	6.717**	13.032**	14.128***	1.126***	0.070 ns	43.793 ns
Rep (E)	6	1.147 ns	0.546 ns	0.462 ns	0.332*	0.009 ns	0.057**	11.164**
Diallel Genotypes (DG)	14	4.218***	1.831***	0.819**	2.664***	0.312***	0.252***	24.857***
G × E	28	0.807 ns	0.270 ns	0.241 ns	0.161 ns	0.025 ns	0.020 ns	6.288*
GCA	4	11.854**	4.211***	1.380*	8.678***	0.900***	0.857***	77.894**
SCA	10	1.164 ns	0.878*	0.594*	0.258*	0.076**	0.010 ns	3.643 ns
GCA × E	8	1.363*	0.261 ns	0.265 ns	0.152 ns	0.032 ns	0.029 ns	9.367*
SCA × E	20	0.585 ns	0.274 ns	0.231 ns	0.164 ns	0.022 ns	0.017 ns	5.057 ns
Residual	84	0.626	0.357	0.238	0.123	0.023	0.018	3.553
RCGCA		80.29	65.73	48.16	93.08	82.48	97.28	89.53
RCSCA		19.71	34.27	51.84	6.92	17.52	2.72	10.47

Note: values with *, ** and *** showed Significant at 0.05, 0.01 and 0.001 probability level respectively, ns = non-significant, FL(mm) = fruit length(mm), FW = fruit width(mm), FT = fruit thickness(mm), BL=bean length, BW=bean width(mm), BT= bean thickness(mm), HBW = 100 bean weight(g), DF= degree of freedom, GCA= general combining ability, SCA= Specific combining ability, GCA x E = general combining ability interaction with environment, SCA x E = Specific combining ability interaction with environment, RCGCA = Relative contribution of general combining ability, RCSCA = Relative contribution of specific combining ability

3.3. Combining ability effect

3.3.1. General combining ability (GCA) effect

3.3.1.1. Growth characters

The estimate of GCA effects of parental lines for growth characters across locations presented in Table 9. Among parental lines, P_2 exhibited positive and significant to highly significant GCA effect for height up to 1st primary branch (HUFPB), stem diameter (SD) and leaf width (LW). Parent P_4 showed negative and highly significant GCA effects for height up to 1st primary branch (HUFPB), average length of primary branch (ALPB), internode length on primary branch (ILPB), canopy diameter (CD), leaf length (LL), leaf width (LW) and leaf area (LA). In contrary to P_4, parent (P_3) revealed positive and highly significant for all leaf characters. Several authors reported parents, which exhibited positive and negative GCA effects for stem diameter at various time (Mesfin, 1982; Belachew, 2001; Mohammed, 2004; Ayano *et al.*, 2014; Getaneh, 2017). Likewise, this result in line with Belachew, (2001) and Mohammed, (2004) who reported that parents

which exhibited positive and/or negative GCA effects for ALPB, and Mohammed (2004) and Ayano (2013) who reported some parents which had negative and highly significant GCA effect for CD. Similar finding was reported by Ayano *et al.* (2014) and Getaneh (2017) who reported parents exhibited either positive and/ or negative GCA effect for all leaf characters and leaf area, respectively. A parent exhibiting significantly positive and negative GCA effects for a particular character is assumed to have high degree of favorable and unfavorable alleles, respectively (Stangland *et al.*, 1983). Hence, P_2 had positive and significant GCA effects for HUFPB, SD and LW, and P_3 for LL, LW and LA suggests these lines may have favorable allele to improve these traits. Similarly, P_4 had negative and highly significant GCA effect for HUFPB, ALPB, ILPB, CD, LL, LW and LA suggest this line has unfavorable alleles to for these traits. The consistent negative and significant to highly significant GCA effect of P_4 for ALPB, ILPB and CD suggested the tendency of the line to reduce these traits simultaneously. This may originated from the compact growth habit/canopy stature of the line. Parental Lines with negative and

significant GCA effects for these traits may be desirable when the objective is to develop manageable size of hybrid for intercropping purpose and planting larger densities of population per a given area. From management point of view, it is attractive, training is unnecessary and pruning is restricted to removing lowest branch which touch the ground and relatively easy for picking time.

Table 9. Estimation of GCA effects of parental lines for growth characters across locations in 2017

Parents	Stem characters		Branch characters			Leaf characters		
	HUFPB	SD	ALPB	ILPB	CD	LL	LW	LA
P_1	0.3270	-0.0363	0.2235	0.0629	-0.2085	0.014	-0.0723[*]	-0.607
P_2	0.6444[*]	0.1430[***]	0.7540	0.0628	2.6778[*]	0.03067	0.08267[**]	0.8295
P_3	0.1153	0.0016	0.2421	0.1603[**]	1.0508	0.3067[***]	0.11034[***]	2.2457[***]
P_4	-1.3079[***]	-0.0282	-2.0146[**]	-0.1871[***]	-3.9122[**]	-0.2333[**]	-0.0926[**]	-1.7456[**]
P_5	0.2212	-0.080[**]	0.7950	-0.0988[*]	0.3921	-0.11806	-0.0281	-0.7227
SE(gi)	0.2563	0.0296	0.5641	0.0413	1.2659	0.0761	0.03102	0.5417

Note value with *, ** and *** showed significant at probability level of 0.05, 0.01 and 0.001 respectively, SE(gi) = Standard error of general combining ability effects HUFPB = height up to first primary branch , SD = stem diameter, ALPB = average length of primary branch, ILPB = internode length on primary branch, CD = canopy diameter, LL = leaf length, LW = leaf width, LA = leaf area

3.3.1.2. *Yield, fruit and bean characters*

Estimation of GCA effects of parental lines for yield, fruit and bean characters depicted in Table 10. The highest positive and highly significant GCA effect for bean yield (across 2 environments) was recorded for parental line P_4 (L55/01). The lowest value GCA effect for bean yield was observed in line P_2 (L67/01). Parental line P_4 (L55/01) may be a desirable line or good general combiner for bean yield which had mostly positive GCA effects than the others at individual and across locations. Different authors such as Walyaro (1983), Mesfin and Belachew (1983), Belachew (2001), Mohammed (2004) and Ayano (2013) reported parental lines which had higher GCA effect for yield of coffee.

GCA effects among parental lines across locations was significant to highly significant for 3 fruit characters namely fruit length (FL), fruit width (FW) and fruit thickness (FT) and four bean characters namely bean length (BL), width (BW), thickness (BT) and 100 bean weight (HBW). Among parental lines, Parent P_1 line displayed positive and highly significant GCA effects consistently for all fruit and bean characters. In contrary to P_1, parental line P_4 showed highly significant and negative GCA effects for all bean characters. Parent P_5 exhibited negative and highly significant GCA effects for bean length and thickness, but positive and non-significant for bean width.

In general, parent P_1 is considered as good general combiner for all fruit and bean characters, and it may contribute favorable allele that can improve bean characters in its progenies. This may have originated from boldness and big fruit and bean size character of P_1 line as compared to other lines. P_2 may have favorable allele for fruit width and thickness improvement. Parental line P_4 is poor general combiner and had unfavorable allele which reduce all bean and fruit characters. Similarly, P_5 is poor general combiner for all bean and fruit characters except bean width. Poor combining ability of these parental lines may have originated from smaller size of P_4 followed by P_5 for these traits. Similar result was reported by Ayano *et al*. (2014) who conducted research on South-western coffee hybrid that parent which had bold bean and fruit size showed larger GCA effect than smaller size.

Table 10. Estimation of GCA effects of parental lines for fruit and bean (in 2017) and yield (in combined 2017 and 2018) characters across locations

| Parents | Fruit characters | | | Bean characters | | | | Yield | | |
	FL	FW	FT	BL	BW	BT	HBW	Jimma	Gera	Across
P_1	0.6978***	0.3009***	0.1362*	0.61333***	0.163365***	0.19025***	1.9387***	29.991	-103.434*	-36.722
P_2	-0.0137	0.1864**	0.1565**	-0.17587***	0.002571	0.02517	-0.5516*	-75.876	-27.263	-51.569
P_3	0.0003	0.0314	0.0042	0.04349	-0.00632	-0.03784*	-0.4517*	-38.506	-17.436	-27.970
P_4	-0.4673***	-0.2020**	-0.1647**	-0.35349***	-0.1733***	-0.09816***	-0.8150**	36.391	167.294***	101.842***
P_5	-0.2171*	-0.3167***	-0.1322*	-0.12746**	0.013683	-0.07943***	-0.1204	48.000	-19.161	14.419
SE(gi)	0.0892	0.0673	0.0550	0.0394	0.0171	0.0152	0.2124	39.395	37.477	27.186

Note value with *, ** and *** showed significant at probability level of 0.05, 0.01 and 0.001 respectively, SE(gi) = Standard error of general combining ability effects, FL= fruit length, FW=fruit width, FT= fruit thickness, BL=bean length, BT= bean thickness, HBW=hundred bean weight

3.3.2. Specific combining ability (SCA) effect

3.3.2.1. Growth characters

Specific combining ability (SCA) effect of Limmu coffee hybrid lines for Growth characters across locations is presented in Table 11. Among hybrids, more than half of the hybrids had positive SCA effect for plant height (PH) and stem diameter (SD). Two hybrid combinations P_2 x P_4 and P_3 xP_4 had highly significant positive SCA effects for SD. Similarly, these hybrids displayed significant positive SCA effect for CD. Hybrid combinations showed positive and significant to highly significant SCA effect for SD and may be useful for improvement of stem vigour through hybridization program. Similar finding was reported by Belachew (2001); Mohammed (2004) and Ayano *et al. (*2014) that more than half of hybrids showed positive SCA effects for stem diameter. Likewise, hybrid line P_2 x P_4 showed highly significant positive SCA effect for ALPB, NBPB, LW and LA. Hybrid P_4 x P_5 showed significant to highly significant SCA effect for SD, LFSPB, LW and LA alone. Hybrid combination having positive SCA effects for ALPB and CD might be an important genotype developed for wider/open canopy structure while hybrid having negative and significant SCA effect might be desirable for compact canopy structure. This result is in line with Belachew (2001) and Ayano (2013) who reported hybrids which had either negative or / and positive SCAE for these traits. Mohammed (2004) reported, 2 hybrids showed positive and significant SCA effect for ALPB in his study, among 10 F_1 hybrids.

3.3.2.2. Yield, fruit and bean characters

Estimates of SCA effect for yield, some fruit and bean characters are indicated in Table 11. The result indicated that hybrid combination P_1 x P_2 and P_4 x P_5 displayed highest positive and highly significant SCA effect for yield at Jimma. Similarly, at Gera, P_2 x P_5 followed by P_4 x P_5 and P_3 x P_4 had positive SCA effect followed for yield. The SCA effects for bean yield were significant to highly significant and positive for the hybrid P_4 x P_5, P_2 x P_5 and P_1 x P_2 across environments. Estimates of the GCA effects of 5 parents in this study revealed that parent (P_4) had good general combining ability for yield the environments. Higher SCA effect of hybrids P_4 x P_5 may resulted from either of both lines exhibited large GCA effect for bean yield. This result is in line with Mesfin (1982), Belachew (2001), Mohammed (2004) and Ayano (2013) who reported highest hybrid combination among the lines that exhibited large and negative GCA effect for bean yield.

Highest positive and significant SCA effect was exhibited by P_3 x P_4 for both fruit width and fruit thickness. Higher SCA effect was manifested by P_1 x P_2 followed by P_3 x P_5 for bean length. Three hybrid combinations P_1 x P_2, P_1 x P_4 and P_2 x P_3 displayed positive and significant SCA effects for bean width. This result agrees with Ayano *et al*. (2014) who reported either positive or negative and significant SCA effects for fruit thickness, bean length, bean thickness, positive and significant to highly significant for bean width and 100 bean weights in their study.

Table 11. Estimation of SCA effects of hybrid lines for yield, fruit and bean characters across locations in 2017

Crosses	Stem characters			Branch characters					Leaf characters			
	PH	HUFPB	SD	LFSPB	ALPB	ILPB	NPB	NBPB	CD	LL	LW	LA
P_1 x P_2	4.321	1.0459	-0.0086	3.8192	1.8898	0.0108	-0.1093	0.0494	-0.3884	-0.1924	-0.1132	-1.8930
P_1 x P_3	2.0194	-0.7584	0.0296	-1.0750	-0.5335	-0.0576	-0.0697	-0.5882	-1.7429	0.1566	0.0951	1.5314
P_1 x P_4	-1.732	0.1093	-0.0346	-2.1226	-0.4250	0.0649	0.8311	-0.3051	2.4052	0.4540*	0.1747*	3.4310*
P_1 x P_5	4.0547	0.7584	0.1248	3.3236	2.9449*	0.1733	0.8541	1.5776	5.9506	-0.1392	0.0013	-0.5182
P_2 x P_3	4.5591	-0.8536	0.0126	0.3563	-0.3047	-0.1192	-0.3488	0.4356	2.7041	-0.1737	-0.0062	-0.7890
P_2 x P_4	5.8818	-0.0600	0.2579**	2.3827	4.5445**	0.1193	1.1631	2.9594**	7.4819*	0.3033	0.2060*	3.1956*
P_2 x P_5	-3.586	0.3616	-0.0512	-2.1049	-3.7297*	-0.0388	-0.1129	-1.1843	-2.8748	0.0394	-0.0585	-0.3799
P_3 x P_4	4.1358	0.7284	0.2212**	8.8959***	1.9731	0.0753	1.2213	-0.0855	7.0534*	0.0127	0.0702	0.5144
P_3 x P_5	-2.861	0.3192	-0.0819	-2.4727	1.4634	0.0880	0.9784	1.6993	-0.5216	0.1979	-0.0063	0.7650
P_4 x P_5	-1.448	-0.0035	-0.2033**	-4.1526*	-2.3408	-0.0998	-1.2081	-0.7015	-4.8642	-0.2989	-0.2313**	-3.3644*
SE(ij)	3.3296	0.6617	0.0764	1.9697	1.4564	0.1068	1.0041	1.064	3.2686	0.1964	0.0801	1.3987

Table 11. Continued

crosses	Yield			Fruit and Bean characters			
	Jimma	Gera	Combined	FW	FT	BL	BW
P_1 x P_2	348.558**	45.205	196.881*	-0.0214	0.1397	0.1845	0.1013*
P_1 x P_3	-78.033	-41.758	-59.895	0.1698	0.0689	-0.1895	-0.0441
P_1 x P_4	-163.645	121.073	-21.286	0.1975	0.1081	0.0844	0.0922*
P_1 x P_5	85.5092	16.977	51.243	-0.1080	-0.1097	0.1061	-0.0519
P_2 x P_3	30.846	92.601	61.723	-0.2819	-0.3132*	-0.0373	0.0920*
P_2 x P_4	110.958	-180.463	-34.751	0.2329	0.2291	0.0325	-0.1059*
P_2 x P_5	-266.677*	132.745	148.728*	0.1505	0.0155	-0.1918	-0.0587
P_3 x P_4	-71.706	122.112	25.201	0.3697*	0.3616*	0.0470	0.0794
P_3x P_5	61.979	30.080	91.897	-0.0558	-0.0100	0.1446	-0.0507
P_4 x P_5	278.126**	123.119	200.623**	-0.2894	-0.2703	-0.0544	0.0121
SE(ij)	101.72	96.76	70.195	0.1738	0.1419	0.1018	0.0441

Note: value with *, ** showed significant at probability level of 0.05 and 0.01 respectively, SE(sij) = Standard error specific combining ability effects, PH = plant height, HuFPB = height up to first primary branch, SD = stem diameter, LFSPB = length of first single primary branch, ALPB = average length of primary branch, ILPB = internode length on primary branch, NPB = number of primary branch, NBPB = number of bearing primary branch, CD = canopy diameter, LL= leaf length, LW = leaf width, LA = leaf area, FW = fruit width, FT = fruit thickness, BL = bean length, BW = bean width

4. Conclusion

An experiment to study the gene action and combining ability effect of yield and its components in limmu coffee genotypes using diallel analysis was undertaken at Jimma, Agaro and Gera agricultural research centers during 2017/18. In the 5 × 5 diallel crosses of elite limmu coffee genotypes; there was significant difference between genotypes for all traits considered except number of secondary branch (NSB) across locations. The diallel analysis identified the importance of both additive and non-additive gene action for height up to 1st primary branch (HUFPB), stem diameter (SD), average length of primary branch (ALPB), internode length on primary branch (ILPB), canopy diameter (CD), leaf length (LL), leaf width (LW), leaf area (LA), fruit width (FW), fruit thickness (FT), bean length (BL), bean width (BW) and yield. For fruit length (FL), bean thickness (BT) and 100 bean weight (HBW), only MS due to GCA was significant indicating the contribution of additive gene action alone for the inheritance of these characters across locations. Only MS due to SCA was significant (p from 0.05 to $\leq$ 0.001) for plant height (PH), number of primary branch (NPB), number of bearing primary branch (NBPB) and length of 1st single primary branch (LFSPB). The result of the current study showed that based on GCA effects parent P_1 (L20/03) considered as good general combiner for all fruit and bean characters. Parent P_4 (L55/01) had negative and highly significant GCA effect for majority of growth characters (14), and positive and significant for bean yield. Hence, this line might be good general combiner for bean yield and desirable to develop manageable size of hybrid because this line may have the tendency to reduce HuFPB, ALPB, ILPB and CD simultaneously. Based on SCA effects, hybrid line P_4 x P_5 and P_1 x P_5 for bean yield, P_3 x P_4 followed by P_2 x P_4 for FW, FT, SD, LFSPB and CD could be considered as best combination for these traits.

Generally, among parental lines P_1 (L20/03) and P_4 (L55/01) could be considered as good parent for future hybridization program and hybrid combination P_4 x P_5, P_1 x P_2, P_3 x P_4 and P_2 x P_4 could be considered as best combinations and promoted to next breeding program after further testing for other desired traits (quality, disease and insect pest tolerant).

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