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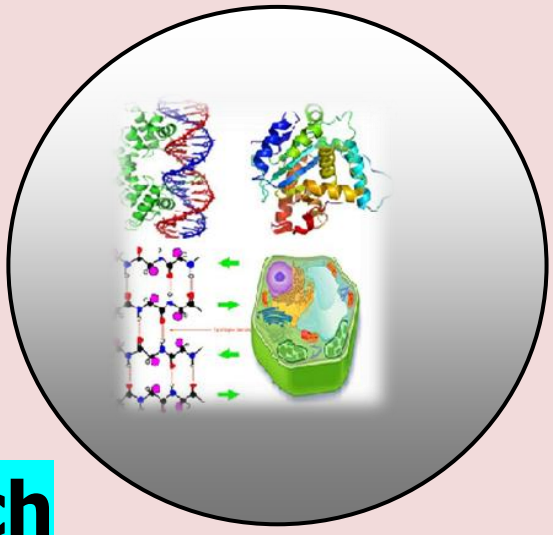
ISSN 2319-3077 Online/Electronic
ISSN 0970-4973 Print

UGC Approved Journal No. 62923
MCI Validated Journal
Index Copernicus International Value
IC Value of Journal 82.43 Poland, Europe (2016)
Journal Impact Factor: 4.275
Global Impact factor of Journal: 0.876
Scientific Journals Impact Factor: 3.285
InfoBase Impact Factor: 3.66

J. Biol. Chem. Research
Volume 36 (1) 2019 Pages No. 173-183



Journal of Biological and Chemical Research

An International Peer Reviewed / Referred Journal of Life Sciences and Chemistry

Indexed, Abstracted and Cited in various International and National Scientific Databases

Published by Society for Advancement of Sciences®

J. Biol. Chem. Research. Vol. 36, No. 1: 173-183, 2019
(An International Peer Reviewed / Refereed Journal of Life Sciences and Chemistry)
Ms 36/01/93/2019

ISSN 2319-3077 (Online/Electronic)
ISSN 0970-4973 (Print)

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RESEARCH PAPER

Received: 04/01/2019 Revised: 23/01/2019 Accepted: 24/01/2019

Genetic Variation, Heritability and Genotype X Environment Interaction of Yield and Various Agronomic Traits of Hybrid Coffee (*Coffea arabica* L.) Genotypes Grown under Highland Environments in South-Western Ethiopia

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ABSTRACT

An experiment to partition the component of variation in selected hybrid of Arabica coffee was conducted at two different sites around Gera district in South-western region of Ethiopia. Genetic variation, genotype × environment interaction of 15 quantitative morphological characters, was studied in ten Arabica coffee hybrids including two standard checks. The hybrids were evaluated at four environments (location-by-year combinations). The randomized complete block design was used in each environment. Data were collected on an individual tree basis for all traits except for yield, measured on a plot basis and converted to individual tree basis for statistical analysis. Results attained by this study showed that moderate to large genetic variation was detected for all agro-morphological traits of hybrid coffee genotypes, except for traits percent fruit bearing nodes per primary branch, number of primary branches per tree, number of primary branch nodes, number of berries per bearing node, percent fruit bearing primary branches per tree and number of main stem nodes. Some of the traits were under strong influence of environment than genetic as revealed by high range of variation across environments than genotypes. The traits that had a low ratio of σ^2ge/σ^2g also showed a high value for heritability, except for those traits (number of main stem nodes, percent fruit bearing primary branches and number of primary branch nodes) that had weak genetic component with much environmental variation. There were no or little evidence for re-ranking of hybrid coffee genotypes performance among four environments for all traits except for number of berries per bearing node indicating the stability of the former and the sensitivity of the latter trait or's by the fluctuations in the environment. For traits plant height, stem girth, canopy diameter, length of primary branches, internode length on the main stem and internode length of primary branches, with a low G x E interaction and high heritability, selection can be done at any of the environments within high land coffee agro-ecology in early breeding stages with high selection efficiency. Thus, these traits can be confirmed at the breeding site/research station.

Keywords Agronomic traits, Arabica coffee, Genotype x environment, Genetic variability and Heritability.

INTRODUCTION

Coffee is one of the world's most important agricultural commodities with more than 125 million people worldwide deriving their income directly or indirectly from its products (Lashermes, *et al.,* 2011). It is grown in about 80 countries spanning over 10.2 million hectares of land in the tropical and sub-tropical regions of the world especially in Africa, Asia and Latin America whereby the economies of these coffee growing countries depends heavily on the earnings from this crop (Mishra and Slater, 2012) including Ethiopia for which it is the main foreign currency earner.

Arabica coffee (*Coffea arabica* L.) dominantly grows in South-western Ethiopia from where it is probably believed to be primarily originated (Davis, *et al*., 2006). Currently, commercial coffee farms are being expanding, in this region, at alarming rate with relatively increasing demand of responsive and high yielding hybrid varieties. The use of hybrid coffee is well known to contribute towards higher productivity and stability of performance under a wide range of environmental conditions (Bertrand, *et al*., 2010).

As the hybrid coffee gains commercial acceptance, the need for genetic information to assist in its improvement becomes more apparent. Many improved hybrid coffee genotypes have recently (Davis, *et al*., 2006; Behailu, *et al*., 2008) become available for breeding and production purposes. For instance, the current coffee breeding strategy in Ethiopia which considered bean quality in addition to increased yield and resistance to diseases is taken as new but complimentary strategies initiated in early 1980 had led identification of some elite hybrids derived from their Southwestern Ethiopian coffee parental origin (Behailu, *et al*., 2008). However, the magnitude of genetic variability for yield and its components has not yet been ascertained in these hybrids.

Genetic variability in Arabica coffee has been studied by several workers (e.g., Dharmaraj and Gopal, 1986; Yigzaw, 2005; Mistro, *et al*., 2008; Petek, *et al*., 2008; Olika, *et al*., 2011). Significant differences were observed among genotypes for all characters, and high phenotypic and genetic coefficients of variation for, plant height, and plant vigor were reported. Other characters, viz canopy diameter, internode length on primaries, stem girth and number of primary branch were reported to have high phenotypic and genetic coefficients of variation as well (Walyaro and Van der Vossen, 1979; Walyaro, 1983; Yonas and Tarekegn, 2015). Furthermore, same phenomenon was observed for number of berries per node (Walyaro and Van der Vossen, 1979), bearing primaries (Walyaro, 1983) and number of secondary branches per tree (Yigzaw 2005). Similarly, variation among coffee genotypes for percent coffee berry disease (CBD) incidence has been reported by Yonas and Tarekegn (2015). Considerable genetic and phenotypic variation observed in number of fruiting nodes per primary and secondary, number of berries per primary and in yield per plant was reported by Dharmaraj and Gopal (1986) in their investigation of growth and yield characters in some selections of coffee.

However, most of the above studies were run in a single environment and there is also little information on how those agronomic traits interact with the environment, e.g., genotype by environmental (G x E) interactions. Commonly, given resource requirement, the intensive evaluations activities will proceed in a single environment and possible modification of genetic potential by local growing environments (G x E interaction) are ignored. As such it is essential to determine the heritability estimates and magnitude of G x E interaction for Arabica coffee breeding program to be effective.

Heritability and the effect of G x E interaction estimates are also usually applicable only to a specific trait, population and a specific range of tested environments. Estimating genetic variance under only one environment may lead to biased genetic variance estimates (Dudley and Moll, 1969). Pooled analysis of variance over environments will determine the extent of G x E interaction as well as heritability estimates to predict average performance of a given genotype and genetic worth of a particular trait in a given set of environments (Comstock and Robinson, 1952; Comstock and Moll, 1963; Holland, *et al*., 2003), while further inclusion of the individual environment heritability estimate will aid possible comparisons to be made among environments and important for breeding decisions. Information concerning these parameters in Arabica coffee, especially in Ethiopia, is very scarce. Therefore, the objectives of this study were to: (1) determine the extent of variation in yield and other related characters in a group of ten hybrids coffee genotypes; (2) determine the heritable components of the overall variability with the help of suitable genetic parameters; and (3) determine the relative contribution/magnitude of G x E interaction to the variation in various agronomic traits of ten coffee genotypes across four highland local environments.

MATERIALS AND METHODS

Description of study sites and germplasm

The study was conducted in 2013/14 and 201415 production seasons at two different sites in Gera district of the south-western region of Ethiopia. The study sites represent the highland humid coffee growing agro ecology and are well known as hot spot for coffee berry disease (CBD). The sites were Gera Research Station and on-farm location around the station. The station is situated at $7^0$46'N latitude, $36^0$26'E longitude and an altitude of 1974 m above sea level (asl) with mean total annual rain fall of about 1880 mm. Average daily minimum and maximum temperatures are about 10.4 and 24.5^{o}c, respectively. The soil around Gera station is dominantly by Acrisols and Nitoso with P^H of 5-6 and medium to high exchangeable cation (Paulos and Tesfaye, 2000). The On-farm site shares most of the macro-environmental variables of the former site.

The study used eight experimental coffee hybrids that were originally developed by crossing among germplasm primarily collected for their resistance to CBD (Table 1). The hybrids were and selected from previous screening trials for showing better resistance to CBD, desirable cup quality and high yielding potential (Behailu, *et al*., 2008). Two commercial checks Ababuna (Hybrid check) selected from long-term hybridization program and 74110 (Variety check) originating from individual tree selection were included in the trial for comparison.

Table 1. Description of the hybrids and commercial checks included in this study.

Code- name	Germplasm Composition*	Cross categories†
HC¶1	SW X SW	CBD res +Q x CBD res +Q
HC2	SW X SW	CBD res +Q x CBD res +Q
HC3	SW X SW	CBD res +Q x CBD res +Q
HC4	SW X SW	CBD res +Q x CBD res +Q
HC5	SW X SW	CBD res +Q x CBD res +Q
HC6	SW X SW	CBD res +Q x CBD res +Q
HC7	SW X SW	CBD res +Q x CBD res +Q
HC8	SW X SW	CBD res +Q x CBD res +Q
Ababuna (Hybrid check)	SW X SW	CBD res x high yielder
74110 (Variety check)	SW	CBD res

*SW=South-western Ethiopian ; † CBD res= CBD resistant; Q =quality; HY=high yielder;
¶HC =Hybrid coffee **Experimental design and field management**

The hybrids were established using a Randomized Complete Block Design (RCBD) with three replications at each site in July, 2008. Each plot comprised of sixteen coffee trees planted in two rows for each genotype. The spacing between rows and trees within the rows were 2 m by 2 m. Each experiment was surrounded by one row of border trees to provide competition to peripheral plots and at the same time to protect the plots from wind and wild life damage. Fertilizer and crop management practices were was uniformly applied at both sites throughout the trial periods as to the recommendation (Endale, *et al*., 2008). At each sites, one Susbania susban shade tree was established to provide shade for every four coffee trees, however at early growth stages the coffee seedlings were uniformly protected from direct sun light by small grass shelters up until the shade trees have come to provide the appropriate shading level. All the coffee trees were maintained in single stem pruning system to maintain uniformity within as well as among plots.

Trait observed

In this study a number of important vegetative growths, stress parameter (CBD incidence), yield and its related traits were observed. These traits were measured for two consecutive years at third and fourth full bearing stages of the coffee trees using eight central trees in each plot. The traits measured included plant height (PH; cm), measured from ground level to tip of the tree; stem girth (GIRTH; cm), taken at 5cm above the ground; number of primary branches produced (NPB), obtained by direct counting the branches; percent fruit bearing primary branches (BP; %), obtained by the ratio between the number primary branches produced and the number of fruiting branches per tree;

canopy diameter (CD; cm), measured as an average value of the length of each tree in east-west and north-south direction; number of main stem nodes (SNN), obtained by direct counting of the tree; internode length on the main stem (ILS; cm), obtained by the ratio between the total height of above the first primary and their respective total number of nodes minus one per tree; number of branch nodes (BNN), obtained by direct counting in the selected branches; percent fruit bearing nodes (BN; %), estimated as the percent of the number of nodes with berries on four selected primaries per tree; internode length of primary branches (ILB; cm), obtained by the ratio between the length of the branches and the number of nodes of the selected primary branches; length of primary branches (LPB; cm), measured in four selected branches per tree from middle part of the tree; number of secondary branches (SB), obtained by direct counting in four selected branches; number of berries per bearing node (BeNo), counted after six months of flowering and obtained by direct counting the number of fruits from two heavily bearing nodes per branches in four selected branches; percent coffee berry disease incidence (CBD; %), assessed visually in the field on individual tree basis following the procedure of Vander Graaf (1981); berry yield (YLD; kg tree^{-1}), recorded as the weight of fresh cherries harvested from sixteen trees in plot basis and converted to berry yield per tree. Data averaged across plots for each seasons across locations were used for statistical analysis.

Growth traits (PH, GIRTH, NPB, SNN, CD, internode length on the main stem, LPB, BNN, ILB and SB) evaluated after the end of each harvest year ensuring the recovery of trees and before the start of flush re-growth (February /March, in this case). Yield related traits (BP, BN and BeNo) evaluated after six months of main flowering of each year per site (July/ August, in this case). The stress parameter, percent coffee berry disease incidence (CBD) assessment was carried out during August; the peak months of disease build up, for two production years per site. Yield (YLD) recorded as the weight of fresh cherries harvested per tree on plot basis for two production years from October to January each year per site for the period of 2013/14 to 2014/15.

Data analysis

Preliminary analysis of the data using GLM with the MIXED procedures of SAS (SAS, 2008) was conducted per location using year × genotype as fixed factors and repeated with year and genotype as random effects to confirm if there were any significant differences between the years. Significant differences were observed for all traits except two traits (internode length on the main stem and coffee berry disease incidence) at research station site and two traits (berry yield and coffee berry disease incidence) at on-farm site between two years (2013/14 and 2014/15) measurements, though year × genotype interactions effects were non-significant, the two locations henceforth were treated as four environments for possible comparisons to be made across individual environments.

All data were tested for the homogeneity of trial variance errors using Bartlett's test before statistical analysis was proceeded. In cases of non-homogeneity, data were transformed to meet requirements of significant test. Accordingly, CBD incidence by square root (√ + 0.5). Analysis of variance was performed by Proc GLM with the MIXED procedure of SAS (SAS, 2008). For purpose of testing the significance of variation due to genotypes, genotype x environment, genotypes were considered fixed effects. Environment and replications within environments were considered random effects. The components of variance were estimated for each trait separately with the restricted maximum likelihood (REML) method of SAS PROC MIXED (Littell, *et al*., 1996; SAS Institute Inc., 2008) considering all effects except the overall random mean.

Heritability on plot-basis and its approximate standard error at each environment and across environments were estimated for each trait using SAS Proc MIXED model of SAS after Holland et al. (2003). Data were being balanced in present study for which the REML based variance component estimates were comparable with ANOVA (Shaw, 1987), for this reason the genotypic mean, phenotypic and genetic variances from REML analysis were used to estimate phenotypic and genotypic coefficient of variation according to the formula given by Burton (1952).

The magnitude of the G x E interaction relative to the genetic variance was determined from REML variance component estimates of each trait using the ratio σ^2ge/σ^2g.

RESULT AND DISCUSSIONS

Phenotypic variation

There were significant difference ($P<0.05$ to $P<0.01$) between two year (2013/14 and 2014/15) measurements at both locations for most of agro-morphological traits at both sites.

Though year × genotype interactions effects were non-significant, the two locations henceforth were treated as four environments for possible comparisons of the genotypic value (heritability) of each environment with their average value across environments.

Relatively low range of variability ranges were observed across genotypes (1.92 % for percent fruit bearing primary branches to 45.8% for coffee berry disease incidence) than across environments (5.62% for canopy diameter to 48.39% for coffee berry disease incidence) (Table 2). Higher ranges occurred across environments than cultivars for most of traits, especially high ranges recorded for coffee berry disease incidence (45.39%), number of secondary branches (47.83), percent of fruit bearing nodes (32.75), number of berries per bearing node (29.98) and percent of fruit bearing primary branches (16.14). However, ranges in some growth characters (canopy diameter, internode length on the main stem and length of primary branches) and berry yield per tree were relatively larger across genotypes than across environments. These moderate to high variability for some characters could be attributed to the diversity of the hybrids used in this study.

There was significant phenotypic difference among the genotypes in every character, except for number of main stem nodes (Table 3), confirming the existence of considerable variability among the genotypes for these significant characters offering a better scope for further improvement of the crop.

There was also significant to highly significant differences ($P < 0.05$ to $P < 0.01$) among environments for all agronomic and yield characters (Table 3). This is attributable to microclimate differences (like shade) might occurred between two sites, especially at early growth stages of the coffee trees, apart from this, these repeatedly measured growth and yield characters were also subjected to the time related environment differences that cause changes in their size. Similarly, large environmental influences on growth and yield traits have been reported by various authors (Walyaro, 1983; Yonas and Tarekegn, 2015).

However, a non-significant interaction effect of genotype with environment was observed for all traits, except for number of berries per bearing node (Table 3). This non-significant interaction indicates that hybrids performed uniformly across environments. Gichimu, *et al*. (2010) has reported similar result and described as positive observation for the new lines indicating that the lines were stable as is required for all varieties.

Table 2. Variability ranges of genotypes and environment mean values for yield and agronomic traits of ten coffee hybrids and checks evaluated at Gera environments.

Traits		Ranges			Mean	CV%
	Genotype n=10	CV%	Environment n=4	CV%	n=40	
Growth traits						
PH	235.14-311.24	7.67	244.86-297.59	8.56	268.23	10.73
GIRTH	4.96-6.39	8.39	5.19-6.38	8.48	5.77	11.14
NPB	76.04-84.28	4.10	72.65-89.49	8.73	80.89	9.05
SNN	41.40-43.86	2.17	40.66-46.46	6.38	42.62	6.47
CD	161.50-211.46	7.43	175.22-198.17	5.62	183.07	8.89
ILS	5.13-6.96	8.92	5.43-6.29	7.05	5.83	10.98
LPB	70.98-103.26	10.12	75.45-94.18	9.56	83.44	13.13
BNN	20.75-22.96	3.33	18.82-24.13	12.02	21.68	11.30
ILB	3.42-4.57	8.02	3.48-4.27	8.69	3.88	11.16
SB	4.16-6.63	14.95	3.21-8.59	47.83	5.37	45.40
Yield and yield related traits						
BP	79.96-85.59	1.92	68.55-94.83	16.14	82.58	14.42
BN	38.25-46.11	5.13	29.99-56.44	32.75	43.17	29.66
BeNo	20.32-23.30	4.55	14.63-29.67	29.98	21.63	27.42
YLD	3.31-5.82	17.31	3.78-5.44	14.91	4.82	25.87
Stress parameter						
CBD	0.92-3.35	45.87	0.92-2.43	48.39	1.62	67.21
	(0.35-10.72)		(0.35-5.40)		(2.12)	

Figures in parenthesis indicate original value

PH, plant height (cm); GIRTH, stem girth (cm); NPB, number of primary branches per tree; SNN, number of main stem nodes; CD, canopy diameter (cm); ILS, internode length on the main stem (cm); LPB, length of primary branches (cm); BNN, number of primary branch nodes; ILB, internode length of primary branches (cm); SB, number of secondary branches per primary branch; BP, percent fruit bearing primary branches per tree (%); BN, percent fruit bearing nodes per primary branch (%); BeNo, number of berries per bearing node; YLD, berry yield (kg tree^{-1}) ; CBD, percent coffee berry disease incidence (%)

Genetic variation and heritability

The magnitude of phenotypic variation does not reveal the relative amount of genetic and non-genetic components of variation. These were ascertained with the help of genetic parameters such as genotypic coefficient of variation and heritability estimates. The relatively higher magnitudes of GCV were recorded for berry yield, number of secondary branches, length of primary branches, internode length on the main stem, stem girth, internode length of primary branches, plant height and canopy diameter (Table 4). Other studies have obtained similar results (Walyaro and Van der Vossen, 1979; Walyaro, 1983; Yigzaw, 2005; Mistro, *et al*., 2008). Moreover, these traits other than berry yield and number of secondary branches also showed higher GCV than environmental coefficient of variation (CV %) emphasizing the dominant genetic over environmental control of these traits in coffee in our experiment while percent fruit bearing nodes, number of primary branches, number of primary branch nodes, number of berries per bearing node, percent of fruit bearing primary branches and number of main stem nodes exhibited least GCV. The low GCV of these traits corroborated with higher range values across environments than cultivars in Table 2. The result was partly contradictory to Dharmaraj and Gopal (1986) who reported that high GCV for percent of fruit bearing nodes and number of berries per bearing node. Percent coffee berry disease incidence had highest genotypic coefficient of variation (GCV), though correspondingly largest environmentally determined variation (CV %) was observed. On an average, the higher magnitude of GCV was recorded for coffee berry disease incidence (43.03) berry yield (14.82), number of secondary branches (13.71), length of primary branches (9.95) and stem girth (8.31) suggesting sufficient variability is available and thus exhibited scope for genetic improvement through selection for all these traits.

Table 3. Mean Square value of yield and agronomic traits ten Arabica coffee genotypes over four environments.

Traits		Source of variation				CV (%)
	Environment (E)	Reps(E)	Genotypes (G)	G x E	Error	
Growth traits						
PH	15797.64*	2262.74**	5078.29**	140.10	384.11	7.31
Girth	7.19**	0.20	2.82**	0.05	0.10	5.60
NPB	1487.34**	105.69**	132.07**	21.90	28.92	6.64
SNN	221.57**	22.62**	10.27	4.91	5.98	5.74
CD	3170.74**	266.95**	2217.73**	56.87	62.86	4.34
ILS	5.06**	0.44*	3.24**	0.13	0.18	7.26
LPB	1909.22**	66.85*	855.16**	23.01	30.90	6.67
BNN	203.63*	35.36**	6.27**	1.31	2.31	7.02
ILB	3.41*	0.32**	1.16**	0.04	0.08	7.20
SB	197.52**	2.05	7.72**	1.18	1.09	19.47
Yield and yield related traits						
BP	5332.07**	85.42**	30.18*	12.00	11.17	4.05
BN	59963.00**	117.02**	58.82*	24.72	15.93	9.24
BeNo	261.08**	23.33**	11.64*	8.38*	3.83	9.05
YLD	15.50*	3.52*	8.35**	2.23	1.50	25.43
Stress parameters						
CBD	18.4**	0.67	6.61**	0.88	0.66	50.30
DF	3	8	9	27	72	

* and ** Significant at the 0.05 and 0.01 probability levels, respectively

PH, plant height (cm); GIRTH, stem girth (cm); NPB, number of primary branches per tree;

SNN, number of main stem nodes; CD, canopy diameter (cm); ILS, internode length on the main stem (cm); LPB, length of primary branches (cm); BNN, number of primary branch nodes;
ILB, internode length of primary branches (cm); SB, number of secondary branches per primary branch;
BP, percent fruit bearing primary branches per tree (%); BN, percent fruit bearing nodes per primary branch (%); BeNo, number of berries per bearing node; YLD, berry yield (kg tree^{-1}); CBD, percent coffee berry disease incidence (%)

Table 4. Estimates of genotypic (σ^2G), genotype-environment interaction (σ^2GE), and error (σ^2e) variance components and broad sense heritabilities on a plot (with SE), phenotypic coefficient of variation (PCV %), genotypic coefficient of variation (GCV%) and ratio of genotype*environment interaction variance to genetic variance for all yield and agronomic traits .

Traits	σ^2G	σ^2GE	σ^2e	PCV(%)	GCV(%)	σ^2ge/σ^2g
Growth traits						
PH[1]	396.73	0.00	317.6	9.38	7.43	0.00
GIRTH	0.23	0.13	0.09	11.63	8.31	0.57
NPB[1]	8.76	0.00	27.00	7.15	3.66	0.00
SNN[1]	0.38	0.00	5.69	5.61	1.45	0.00
CD[1]	179.71	0.00	61.23	8.44	7.32	0.00
ILS[1]	0.03	0.00	0.17	10.98	8.75	0.00
LPB[1]	68.86	0.00	28.75	11.68	9.95	0.00
BNN[1]	0.35	0.00	2.04	6.62	2.73	0.00
ILB[1]	0.09	0.00	0.07	9.98	7.73	0.00
SB	0.54	0.03	1.09	24.04	13.71	0.06
Yield and yield related traits						
BP	1.51	0.28	11.17	4.36	1.49	0.19
BN	2.84	2.93	15.93	10.79	3.90	1.03
BeNo	0.27	1.52	3.83	10.96	2.40	5.63
YLD	0.51	0.24	1.50	31.12	14.82	0.47
Stress parameter						
CBD	0.48	0.07	0.66	68.44	43.03	0.15

PH, plant height (cm); GIRTH, stem girth (cm); NPB, number of primary branches per tree; SNN,
number of main stem nodes; CD, canopy diameter (cm); ILS, internode length on the main stem (cm);
LPB, length of primary branches (cm); BNN, number of primary branch nodes; ILB,
internode length of primary branches (cm); SB, number of secondary branches per primary branch;
BP, percent fruit bearing primary branches per tree (%); BN, percent fruit bearing nodes per primary branch (%); BeNo, number of berries per bearing node; YLD, berry yield (kg tree^{-1});CBD, percent coffee berry disease incidence (%)

[1]Negative variance component estimates set equal to zero

The heritability value derived from a genotypes evaluated over number of environment would increase the accuracy of the estimates of each trait (Falconer and Mackay, 1996). Heritability estimates among the traits ranged from 0.00 for number of main stem nodes and number of primary branch nodes in GRS2, number of main stem nodes and number of berries per bearing node in GOF2 to 0.78 for canopy diameter in GOF1 (Table 5). Across all the environments the heritability estimates ranged from 0.05 for number of berries per bearing node to 0.75 for canopy diameter. The plant vigor traits plant height, stem girth and canopy diameter had high broad sense heritabilities with a range from 0.32 to 0.78. Canopy diameter had the highest observed heritability in all the environments with a range of 0.70 to 0.78. The traits length of primary branches and internode length on the main stem also had high broad sense heritability with a range from 0.50 to 0.76. The same magnitudes of high heritability (>0.50) for above traits were reported by various investigators (Walyaro, 1983; Yigzaw, 2005; Petek, *et al*., 2008; Yonas and Tarekegn, 2015). Olika, *et al*. (2011) reported similar result for plant height and internode length on the main stem but lower heritability estimates for canopy diameter, stem girth and length of primary branches. Traits with high heritability should be responsive for selection.

The traits berry yield, number of secondary branches and coffee berry disease incidence had heritability estimates with a range from 0.16 to 0.53, 0.26 to 0.47 and 0.25 to 0.56 with 0.23, 0.33 and 0.39 average estimates across environments, respectively. Yonas and Tarekegn (2015) reported similar result for berry yield (0.26) but for coffee berry disease incidence lower (0.12) in magnitude than the present finding. This suggests that heritability estimates are influenced in part by the environment and population under study. The traits percent fruit bearing nodes and number of berries per bearing node had moderate heritability estimates with a range from 0.29 to 0.51 at two and three of four environments, respectively while at the other the remaining respective environments they exhibited very low estimates (0.00 to 0.16) indicating the need of separate selection strategies to be followed for the two groups of environments. The traits number of main stem nodes, percent of fruit bearing primary branches and number of primary branch nodes had low heritability in each environment compared to the other traits with a range from 0.00 to 0.23. These traits exhibited zero heritability in some environments due to the registered low or negative σ^2G estimates a relative to σ^2e in those environments. Across all the environments traits number of main stem nodes, percent of fruit bearing primary branches and number of primary branch nodes still had the lowest heritability. Thus, selection based on these traits would not be effective. Heritabilities, in most of the cases decrease with tree age at both sites. This may have been due the variation observed among phenotypes being decreasingly influenced by additive genetic effects, or simply as result of increased environmental determined variances modified over time.

Table 5. Heritabilities on plot mean basis (and their standard error) for yield and agronomic traits at each environment and across environments.

Traits	Environment †				
	GRS1 ‡‡	GOF1	GRS2 ‡‡‡	GOF2	across
Growth traits					
PH	0.55(0.18)	0.56(0.18)	0.32(0.21)	0.40(0.21)	0.55(0.13)
GIRTH	0.70(0.14)	0.66(0.15)	0.61(0.17)	0.74(0.12)	0.71(0.10)
NPB	0.23(0.21)	0.32(0.21)	0.16(0.21)	0.11(0.21)	0.24(0.11)
SNN[1]	0.07(0.20)	0.23(0.22)	0.00	0.00	0.06(0.06)
CD	0.70(0.14)	0.78(0.11)	0.71(0.13)	0.77(0.11)	0.75(0.10)
ILS	0.50(0.19)	0.68(0.14)	0.54(0.18)	0.61(0.17)	0.61(0.12)
LPB	0.62(0.16)	0.76(0.12)	0.73(0.13)	0.61(0.17)	0.70(0.11)
BNN[1]	0.06(0.20)	0.19(0.21)	0.00	0.05(0.20)	0.15(0.09)
ILB	0.65(0.16)	0.70(0.13)	0.16(0.21)	0.62(0.16)	0.57(0.13)
SB	0.26(0.22)	0.29(0.21)	0.36(0.21)	0.47(0.20)	0.33(0.13)
Yield and yield related traits					
BP	0.09(0.21)	0.01(0.19)	0.20(0.21)	0.05(0.20)	0.12(0.09)
BN	0.38(0.21)	0.51(0.19)	0.03(0.20)	0.16(0.21)	0.13(0.10)
YLD	0.16(0.21)	0.53(0.18)	0.34(0.21)	0.30(0.12)	0.23(0.12)
BeNo[1]	0.51(0.19)	0.45(0.20)	0.29(0.22)	0.00	0.05(0.09)
Stress parameter					
CBD	0.56(0.18)	0.53(0.19)	0.43(0.20)	0.25(0.22)	0.39(0.14)

GRS† = Gera research station, GOF = Gera On-farm

‡‡Year 1 and ‡‡Year 2

PH, plant height (cm); GIRTH, stem girth (cm); NPB, number of primary branches per tree; SNN, number of main stem nodes; CD, canopy diameter (cm); ILS, internode length on the main stem (cm); LPB, length of primary branches (cm); BNN, number of primary branch nodes; ILB, internode length of primary branches (cm); SB, number of secondary branches per primary branch; BP, percent fruit bearing primary branches per tree (%); BN, percent fruit bearing nodes per primary branch (%); BeNo, number of berries per bearing node; YLD, berry yield (kg tree^{-1}) ; CBD, percent coffee berry disease incidence (%);

[1]Unable to calculate h^2_{bs} due to negative variance components and thus set equal to zero

Genotype by environment interaction

Analysis of variance (Table 3) indicated that all the characters studied were less influenced by changes in the environment, except for number of berries per bearing node. The σ^2 ge/σ^2g ratio also confirmed that the G x E interaction effects was negligible or low for all traits except for number of berries per bearing node and percent of fruit bearing nodes (Table 4). The estimate of σ^2GE was low or negative for most traits and thus the negative estimates are considered as equal to zero. The traits that had a low ratio of σ^2 ge/σ^2g also showed a high value for heritability, except for those traits (number of main stem nodes, percent of fruit bearing primary branches and number of primary branch nodes) that had weak genetic component (Table 4) with much environmental variation (Table 2 and Table 3). The trait number of fruits per bearing node (BeNo) with the lowest heritability (0.05) also had the highest σ^2ge/σ^2g ratio of 5.63. Lack of G x E interaction effects for almost all traits, in present study, is explained by small number of test materials and the uniformity of the test environments (located in the same agro-ecological zone). Large materials and diverse environments need to be analyzed in order to better estimate genetic parameters and G x E for agro-morphological traits in Arabica coffee.

Generally, for plant vigor traits (plant height, stem girth and canopy diameter), length of primary branches, internode length on the main stem and internode length of primary branches with low G x E interaction and high heritability 0.55 for plant height to 0.75 for canopy diameter, selection can be done at any environments within highland coffee agro-ecology in early breeding stages with high selection efficiency. Thus these traits can be confirmed at the breeding site/research station. Besides having high heritability, these six morphological traits can be directly measured and selected in the field. Therefore, it would be gainful to select for high yielding genotypes indirectly through these traits. This would be possible, since we observed (data do not shown) strong genetic correlation between these six traits and berry yield apart from having high heritabilities.

CONCLUSION

A breeder, in most of the case often desire to understand how the traits of interest of his crop are inherited and how they respond to the different environments to be able and make a more designed breeding program. Fourteen traits that constitute the basic structure of the coffee plant with one stress parameter and determine the productive ability of a given genotype were chosen to study their response to the change of environment. The traits had a high GCV with high heritability thus enabling the breeder to actively breed for or against these traits. It was also important to understand how the environment would affect these traits.

Results attained by this study showed that moderate to large genetic variation was detected for all agro-morphological traits for hybrid coffee genotypes, except for percent fruit bearing nodes per primary branch, number of primary branches, number of primary branch nodes, number of berries per bearing node, percent of fruit bearing primary branches and number of main stem nodes. Heritabilities were generally high for plant vigor traits (plant height, stem girth and canopy diameter), length of primary branches, internode length on the main stem and internode length of primary branches, moderate for coffee berry disease incidence and number of secondary branches and low for percent of fruit bearing nodes per primary branch, number of primary branches, number of primary branch nodes, number of berries per bearing node, percent of fruit bearing primary branches and number of main stem nodes including yield. There were no or little evidence for re-ranking of hybrid coffee genotypes performance among four environments (two location and two year combinations) for all traits except for number of berries per bearing node indicating the stability of the former and the sensitivity of the latter trait or ‘s by the fluctuations in the environment. Moreover, for traits plant height, stem girth , canopy diameter, length of primary branches length, internode length on the main stem and internode length of primary branches, with a low G x E interaction and high heritability, selection can be done at any of the environments within high land coffee agro-ecology in early breeding stages with high selection efficiency . Thus these traits can be confirmed at the breeding site/research station.

ACKNOWLEDGEMENTS

This work was co-financed by Ethiopian Institute of Agricultural Research (EIAR) and Jima University (JU). Thanks due to Jima Agricultural Research Center (JARC) for providing me experimental materials, and Gera coffee breeding section for the management of experimental sites.

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