


RESEARCH ARTICLE

Genetic variation among biparental Robusta coffee families and implications for variety development

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Abstract

Understanding the genetic variability, heritability and genetic advance (GA) of traits in any plant population is an important pre-requisite for variety development. The objectives of the study were to assess the level of genetic variability among vegetative growth traits and yield, assess the relationship among the growth traits and yield and predict GA for the most heritable traits among Robusta coffee full-sib families. The trial was established in June 2009 at the experimental fields of the Cocoa Research Institute of Ghana with 62 full-sib families planted in a randomized complete block design with six replications. Significant ($p < 0.05$) variation was observed among the full-sib families evaluated for all traits, except for span (canopy diameter). Span and number of laterals were genetically correlated ($p < 0.001$) with cumulative yield (2013–2017), with span being the vegetative growth trait most strongly related to cumulative yield ($r_g = 0.60$, $p < 0.001$). The most heritable vegetative growth and yield traits were, respectively, number of laterals ($H^2 = 0.59$) and cumulative yield ($H^2 = 0.41$). The top 10 families (BP40, BP41, BP9, BP36, BP34, BP28, BP37, BP14, BP4 and BP10) in terms of cumulative yield are proposed for multi-location evaluation and possible release as hybrids for coffee farmers in Ghana.

Keywords: *Coffea canephora*; Genetic variation; Heritability

Introduction

The genus *Coffea* of the family Rubiaceae consists of 124 species (Davis, 2011), of which two species, *Coffea arabica* L. and *Coffea canephora* Pierre ex. A. Froehner, make up the bulk of commercially traded coffee. The *C. canephora* also referred to as Robusta is a diploid species ($2n = 22$), characterized by higher productivity and caffeine content, better growth at lower altitude and tolerance to pests, diseases and drought than *C. arabica* (DaMatta et al., 2007). Robusta is the main type of coffee cultivated in Ghana.

The yield of coffee like many other tree crops in Ghana and West Africa at large has generally been considered very low. Production of coffee in Ghana has been generally low, ranging from a peak of 6700 tons in 1967/1968 to a low of 123 tons in 1983/1984 as a result of severe drought and bush fires of 1983. Production hereafter increased gradually, reaching a second peak of 5700 tons in 1999, and declining again thereafter (ICO, 2018). In Ghana, annual average yields of coffee were typically in the range of 0.1–0.2 t ha⁻¹ (Anonymous, 1996), though on-station trials have recorded dry bean yields in excess of 2 t ha⁻¹ (Akperley et al., 2018a; Anim-Kwapong et al., 2011). The use of unimproved or unselected planting materials coupled with poor adoption of recommended coffee farming practices has often been cited as some of the major causes of poor yields in the country. A recent effort by the government of Ghana through the Ghana Cocoa Board implemented a 4-year coffee Rehabilitation programme (CRP) in 2011 in order to promote the

production of the crop in the country. One of the key elements of the CRP was the distribution of improved planting materials to farmers across the coffee growing districts of Ghana.

National coffee production of 12650 tons was estimated at the end of the CRP in 2015 (ICO, 2018), from the hitherto national productivity of approximately 6000 tons. This increase in productivity may have been due to the use of improved planting materials as well as farmers' adoption of recommended husbandry practices for coffee farming among other things. This underscores the importance of improved planting materials in increasing coffee productivity in Ghana. Consequently, efforts to establish new coffee farms and re-establish most of the old coffee farms with improved coffee varieties have increased in recent times in Ghana. It is imperative that breeding efforts are geared towards the development of newer high-yielding coffee varieties in Ghana, to increase the genetic base of varieties that are currently deployed and also potentially increase the national coffee production.

Success in any breeding programme depends to a large extent on the knowledge and understanding of the genetic architecture and inheritance of characters of interest (Mistro *et al.*, 2004). Biparental mating is one of the simplest random mating designs available to effect recombination and breaking down undesirable linkages as pointed out by Comstock and Robinson (1952). To develop high-yielding genotypes coupled with good bean quality and tolerance to diseases and pests, a population with high variability serves as a prime source for effective selection. To obtain gains in the selection of superior genotypes, it is important to know both the genetic variability available in the species and the associations of traits to develop agronomically desirable genotypes (Oliveira *et al.*, 2010). In the genetic breeding of coffee and other plant species, the prediction of gains by a given selection strategy provides a more efficient orientation of breeding programmes and the choice of alternative and possibly more effective techniques. However, the selection of superior progenies is time-consuming, since the genetic basis of most important traits, mostly quantitative, is complex and strongly influenced by the environment (Cruz *et al.*, 2004). Notwithstanding, the assessment of progeny trials is a routine procedure in plant breeding programmes and through biometric procedures, the genetic variability of populations can be exploited more efficiently to facilitate assessment of genetic gains from selection.

Information on genetic parameters of key selection traits, such as genetic variance and heritability, as well as on correlations among agronomic traits in coffee is of interest to guide and ensure that selection of superior genotypes in hybrid breeding programmes is optimized (Cilas *et al.*, 1998; Leroy *et al.*, 1994). Phenotypic correlations are related to genetic and environmental causes, but genetic correlations measure the degree to which different traits are controlled by the same gene(s) that are closely linked. It includes an association with heritability, which can thus be used for the indirect selection for traits that are difficult and complex to measure in a breeding programme (Cruz *et al.*, 2012). Additionally, such knowledge of genetic parameter estimates and associations is useful for coffee breeders to identify potential parents for developing improved cultivars (Reuben *et al.*, 2003) with broad genetic base as well as facilitate the breeding process through indirect selection.

Although there have been a number of studies on the significance of genetic parameters and genetic associations between vegetative traits and productivity traits in facilitating breeding of Robusta coffee, there exist some inconsistencies in the magnitude of genetic parameters of growth and yield traits to direct effective and efficient selection. Some of the studies conducted so far have, however, demonstrated variation among genotypes with regard to vegetative growth and yield traits (Akperley *et al.*, 2018a; Anim-Kwapong *et al.*, 2011; Cilas *et al.*, 2000, 2006; Leroy *et al.*, 1997; Montagnon *et al.*, 2003) that are worthy of note. The objectives of this study were to (i) evaluate the field performance of 62 full-sib families, (ii) assess the level of genetic variability for stem diameter, height, span, number of laterals and yield among the Robusta coffee full-sib families, (iii) determine the relationship among stem diameter, height, span, number of laterals and cumulative yield (yield from 2013 to 2017) and (iv) predict genetic advance (GA) for the most heritable growth and yield traits (i.e. number of laterals and cumulative yield).

Materials and Methods

Plant material

Sixty-two full-sib families developed through crossing of high-yielding, biotic and abiotic stress tolerant genotypes selected from previous hybrid and clonal trials at the Cocoa Research Institute of Ghana (CRIG) were used for the study.

Experimental design and field establishment procedures

The full-sib families were planted at the experimental fields of the CRIG, Tafo (latitude 06° 13' N, longitude 0° 22' W), which, situated in the eastern region of Ghana, is approximately 220 m above sea level. The soil at Tafo is sandy loam, classified as Haplic Luvisol, brown to yellowish red, well drained and developed in situ from weathered materials of hornblende granodiorite (Adu and Asiamah, 1992). Six-month-old seedlings of the 62 full-sib families were planted in the field in June 2009 using a randomized complete-block design with six replications. For each family, 10 plants were planted in each replicate block at a spacing of 2 m × 3 m. *Gliricidia sepium* was planted between rows at a spacing of 4 m × 6 m to provide a permanent shade which was pruned yearly. Weeds were removed manually every quarter within the year. The plants were allowed to grow on one or two stems during the period of the experiment.

Data collection and statistical analysis

Plant height (m) was measured, with a meter rule, from the soil surface to the apex of the plant. The diameter of the main stem (mm) was measured 10 cm above the soil surface with electronic calipers. Canopy diameter hereafter referred to as span (m) was taken as the width of the canopy, where tree canopy was the widest. The number of laterals per tree was counted at each recording time. Whenever there were multiple stems, stem diameter was calculated according to Stewart and Salazar (1992) and span was measured only on the biggest stem. Stem diameter, height, number of laterals and span were measured at yearly intervals from 2010 to 2013. Cherry weight (typically from October to January) was recorded for each tree for five productive years from 2013 to 2017, and transformation of cherry weight to clean coffee yield was done using a conversion factor of 0.22 (Coste, 1992).

An analysis of variance (ANOVA) was performed for each trait based on the following linear model:

$$Y_{ij} = \mu + g_i + b_j + e_{ij}$$

where Y_{ij} is the phenotypic measurement of the i th full-sib family in the j th block for trait Y , μ is the population mean, g_i is the effect of the i th family, b_j is the effect of the j th block and e_{ij} is the experimental error. Variance component estimates were used to estimate broad-sense heritability (H^2) as

$$H^2 = \frac{\sigma^2_g}{\sigma^2_p} = \frac{\sigma^2_g}{(\sigma^2_g + \sigma^2_e)}$$

where σ^2_g , σ^2_p and σ^2_e are the full-sib family, phenotypic and error variance components, respectively. The genetic correlations (r_g) between traits were estimated following Cooper et al. (1996) as

$$r_g = \frac{AM[\sigma g(jj')]}{AM[\sigma^2 g(j)\sigma^2 g(j')]}$$

where $AM[\sigma g(jj')]$ is the arithmetic mean of all pairwise genotypic co-variances between trait j and j' and $AM[\sigma^2 g(j)\sigma^2 g(j')]$ is the arithmetic average of all pairwise geometric means among the genotypic variance components of the traits. Pearson's correlation coefficients among the evaluated traits were also estimated.

Table 1. Mean squares from analysis of variance for stem diameter (stem diam), height, span, number of laterals, yearly yields and cumulative yield (CY) among 62 full-sib families evaluated

Source of variation	d.f	Trait									
		Stem diam (mm)	Height (m)	Span (m)	No. of laterals	Yield					
						2013 (t ha ⁻¹)	2014 (t ha ⁻¹)	2015 (t ha ⁻¹)	2016 (t ha ⁻¹)	2017 (t ha ⁻¹)	CY (t ha ⁻¹)
Block	5	566.3	0.727**	3.549	1127.1***	0.186	40.50***	4.101**	0.879*	17.60***	41.78*
Family	61	996.7***	1.666***	6.343	926.3***	0.255**	18.84***	4.357***	0.757***	11.59***	86.26***
Residual	1697	410.2	0.187	4.894	84.54	0.159	4.038	1.361	0.373	3.292***	17.35

*, **, *** = significant at $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively
d.f. = degrees of freedom.

Genotypic coefficient of variation (GCV) and phenotypic coefficient of variation (PCV) were estimated following Burton (1952) as:

$$\text{GCV} = \frac{\sqrt{\sigma^2_g}}{M} \times 100, \text{ and } \text{PCV} = \frac{\sqrt{\sigma^2_p}}{M} \times 100, \text{ where } M \text{ is the trait mean.}$$

Expected GA under selection for the most heritable traits was calculated following Allard (1960) as:

$$\text{GA} = (k)(\sigma_p)(H^2)$$

where k is the selection differential which varies with selection intensity (values of k used were 2.42, 2.06, 1.76, 1.4 and 1.16 for selection intensities of 2, 5, 10, 20 and 30, respectively) and σ_p is the phenotypic standard deviation.

Vegetative growth data (stem diameter, height, span and number of laterals) used in the analyses included the mean trait measurements collected across a 4-year period (2010–2013), whereas the yield data spanned a 5-year period (2013–2017). The mean stem diameter, height, span, number of laterals, yearly yields and cumulative yield were subjected, separately, to ANOVA. Prior to ANOVA, normality of each dataset was checked by plotting residuals. Statistical analysis to obtain genetic parameter estimates was performed using META-R statistical software (Alvarado *et al.*, 2016). All other statistical analyses were performed using the GenStat statistical software, version 12 (VSN International Ltd, Hemel Hempstead, UK).

Results

Variation and field performance of Robusta coffee full-sib families for all traits assessed

There was a highly significant ($p < 0.01$) variation among the Robusta coffee families for all traits assessed, except for span (Table 1). Similarly, the effect of block was significant ($p < 0.05$) for all traits assessed, except for span and 2013 yield (Table 1). Also, in a combined ANOVA across years, there was a highly significant ($p < 0.001$) effect of family, year and family \times year interaction for yield (data not presented).

On average, the stem diameter varied from 23.0 mm in family BP59 to 39.1 mm in family BP58, with a mean of 33.4 mm for all families evaluated (Table 2). The tallest and shortest families were BP30 (2.0 m) and BP58 (0.8 m), respectively, with a mean of 1.4 m. Span ranged from 1.1 m (BP58) to 2.1 m (BP20), with a mean of 1.3 m. Number of laterals, on the other hand, ranged from 6.9 to 33.8 among the families evaluated (Table 2).

Yields were relatively lower in early years compared to later years. Yield recorded in 2013 ranged between 0.1 and 0.7 t ha⁻¹, with a mean of 0.3 t ha⁻¹ (Table 2). Yield in the second productive year (2014) was on average higher than yields recorded in the preceding year.

Table 2. Mean growth and yield trait measurements of 62 full-sib families evaluated

Family	Stem diam* (mm)	Height (m)	Span (m)	NOL†	Yield‡					
					2013 (t ha ⁻¹)	2014 (t ha ⁻¹)	2015 (t ha ⁻¹)	2016 (t ha ⁻¹)	2017 (t ha ⁻¹)	CY (t ha ⁻¹)
BP40	35.9	1.6	1.4	31.5	0.5	4.8	2.3	0.9	3.4	11.4
BP41	35.2	1.4	1.3	25.7	0.5	4.2	2.3	0.3	3.8	10.9
BP9	36.1	1.6	1.4	31.4	0.3	4.5	1.9	0.3	3.0	9.5
BP36	37.4	1.7	1.4	31.7	0.7	4.4	2.2	0.5	3.0	9.3
BP34	34.3	1.5	1.3	31.5	0.4	3.4	2.2	0.7	2.9	9.3
BP28	33.3	1.5	1.3	31.4	0.7	3.4	2.8	0.3	2.8	9.2
BP37	35.1	1.5	1.3	28.2	0.7	3.8	1.6	0.8	2.8	9.2
BP14	33.0	1.5	1.3	25.8	0.3	3.7	1.8	0.5	3.0	8.9
BP4	34.3	1.6	1.3	28.6	0.5	3.8	2.4	0.4	2.8	8.7
BP10	37.8	1.5	1.3	29.7	0.3	3.6	1.9	0.4	2.7	8.7
BP47	35.8	1.6	1.3	33.2	0.4	3.8	1.5	0.7	2.6	8.1
BP53	35.6	1.6	1.4	29.9	0.2	3.8	1.4	0.4	2.7	8.1
BP56	27.1	1.0	1.2	17.9	0.5	4.1	1.3	0.3	3.2	8.0
BP30	33.6	2.0	1.3	27.3	0.2	3.7	1.6	0.3	2.8	7.9
BP32	33.9	1.5	1.3	28.9	0.4	3.6	1.7	0.3	2.3	7.8
BP51	37.1	1.6	1.4	31.5	0.4	3.9	1.5	0.6	2.0	7.6
BP29	33.5	1.5	1.3	28.9	0.3	3.2	2.1	0.3	2.2	7.5
BP54	36.2	1.5	1.3	33.8	0.6	2.9	1.7	0.5	2.6	7.4
BP2	30.9	1.3	1.3	28.0	0.3	3.0	1.6	0.5	2.5	7.3
BP52	37.8	1.6	1.4	33.8	0.3	4.5	1.6	0.3	2.4	7.2
BP35	35.9	1.4	1.3	30.0	0.4	2.9	1.7	0.4	2.3	7.1
BP5	35.0	1.5	1.3	24.9	0.4	3.6	1.6	0.4	2.5	7.1
BP42	33.3	1.5	1.3	29.7	0.5	2.7	1.6	0.3	2.6	6.9
BP33	33.6	1.4	1.3	29.3	0.5	2.7	1.5	0.4	2.1	6.8
BP44	33.4	1.4	1.3	25.8	0.6	3.4	1.4	0.3	2.1	6.7
BP1	33.9	1.3	1.3	24.2	0.1	3.4	1.4	0.3	2.2	6.7
BP17	32.3	1.5	1.3	25.8	0.2	2.9	1.6	0.6	2.4	6.7
BP6	33.0	1.5	1.3	26.8	0.3	2.0	1.6	0.4	2.6	6.6
BP11	33.1	1.5	1.3	25.6	0.3	2.9	1.2	0.4	2.6	6.6
BP20	33.3	1.4	2.1	25.0	0.1	3.6	1.0	0.4	2.1	6.5
BP25	34.7	1.1	1.2	19.8	0.3	2.7	1.1	0.3	2.7	6.4
BP16	35.0	1.6	1.3	29.4	0.4	2.5	2.3	0.3	2.1	6.4
BP43	30.9	1.3	1.3	27.2	0.4	2.2	1.2	0.5	2.4	6.3
BP15	35.0	1.5	1.3	26.1	0.3	3.5	1.8	0.4	1.7	6.3
BP3	34.3	1.6	1.3	24.2	0.3	3.0	1.8	0.3	2.3	6.2
BP19	34.2	1.6	1.3	29.0	0.4	2.9	1.2	0.4	2.2	6.2
BP8	35.0	1.5	1.3	26.8	0.2	3.0	1.3	0.3	2.0	6.1
BP22	34.3	1.6	1.3	30.5	0.2	2.6	1.3	0.3	2.4	6.1
BP24	32.3	1.2	1.2	17.1	0.2	3.2	1.4	0.3	1.7	6.1
BP49	34.7	1.5	1.3	25.5	0.2	3.0	1.6	0.3	2.1	6.0
BP13	30.9	1.4	1.3	21.0	0.1	2.6	0.9	0.7	2.6	6.0
BP58	39.1	0.8	1.1	17.3	0.1	1.8	1.5	0.3	2.3	5.7
BP46	25.2	1.1	1.2	16.8	0.3	2.4	1.4	0.4	2.3	5.6
BP12	35.3	1.5	1.3	25.8	0.4	2.5	1.4	0.3	1.9	5.6
BP38	35.1	1.6	1.3	31.7	0.4	2.8	1.4	0.3	1.6	5.5
BP27	30.9	1.3	1.3	22.5	0.2	2.3	1.3	0.4	2.1	5.4
BP60	26.8	1.1	1.2	15.5	0.1	3.2	0.8	0.2	2.4	5.4
BP7	34.2	1.4	1.3	23.0	0.1	2.5	1.4	0.3	1.9	5.4
BP26	34.2	1.2	1.2	18.8	0.2	2.4	1.2	0.3	2.2	5.3
BP57	25.6	1.0	1.2	17.1	0.2	2.8	1.2	0.2	1.9	5.2
BP55	35.3	1.5	1.3	29.4	0.4	1.8	1.3	0.3	2.0	5.0
BP48	34.4	1.5	1.3	30.0	0.3	1.9	1.3	0.3	2.2	4.9
BP50	35.6	1.5	1.3	29.8	0.3	1.7	1.2	0.3	2.1	4.9
BP21	33.5	1.7	1.3	27.0	0.3	1.7	1.2	0.3	1.9	4.8
BP39	32.0	1.3	1.3	22.6	0.3	2.4	1.3	0.3	1.5	4.6
BP62	24.2	0.9	1.2	10.0	0.2	1.0	1.0	0.4	2.5	4.4
BP59	23.0	0.9	1.2	15.4	0.1	1.3	1.4	0.2	2.0	4.2
BP23	33.6	1.5	1.3	27.8	0.3	1.9	1.0	0.3	1.8	4.2

(Continued)

Table 2. (Continued)

Family	Stem diam* (mm)	Height (m)	Span (m)	NOL [†]	Yield [‡]					
					2013 (t ha ⁻¹)	2014 (t ha ⁻¹)	2015 (t ha ⁻¹)	2016 (t ha ⁻¹)	2017 (t ha ⁻¹)	CY (t ha ⁻¹)
BP45	28.7	1.1	1.2	15.4	0.2	1.8	1.3	0.3	1.5	4.1
BP31	35.1	1.5	1.3	26.3	0.3	2.0	1.0	0.4	1.4	3.8
BP18	34.7	1.5	1.3	25.3	0.1	1.8	0.8	0.3	1.5	3.4
BP61	32.1	1.2	1.2	6.9	0.3	0.7	0.8	0.3	1.6	2.3
Mean	33.4	1.4	1.3	25.6	0.3	2.9	1.5	0.4	2.3	6.6
Min	23.0	0.8	1.1	6.9	0.1	0.7	0.8	0.2	1.4	2.3
Max	39.1	2.0	2.1	33.8	0.7	4.8	2.8	0.9	3.8	11.4
SED _{p < 0.05}	4.11	0.11	0.29	2.41	0.20	0.60	0.33	0.21	0.43	1.15

*Stem diameter.

[†]Number of laterals.[‡]CY = Cumulative yield from 2013 to 2017.**Table 3.** Genetic (below diagonal) and phenotypic correlations (above diagonal) between vegetative growth traits and yield of 62 full-sib families

Trait [†]	Stem diameter	Height	No. of laterals	Span	CY
Stem diameter (mm)	–	0.73***	0.75***	0.39**	0.38**
Height (m)	0.93***	–	0.81***	0.43***	0.39**
No. of laterals	0.95***	0.69***	–	0.46***	0.54***
Span (m)	0.86***	0.83***	0.61***	–	0.33**
CY (t ha ⁻¹)	0.38**	0.32*	0.46***	0.60***	–

[†]CY = Cumulative yield from 2013 to 2017.* $p < 0.05$.** $p < 0.01$.*** $p < 0.001$.

There was a high variation among the families evaluated for yield in 2014, with more than a six-fold difference between the highest (BP40) and lowest (BP61) yielding families (Table 2). A similar yield variation was observed for the yield recorded in 2015, with nearly a four-fold difference between the highest and lowest yielding families, with an average of 1.5 t ha⁻¹ (Table 2). Yields in 2016 were slightly lower than what was recorded in the preceding year. The average yield in 2016 among the families evaluated was only 0.4 t ha⁻¹ and ranged from 0.2 t ha⁻¹ in families BP57, BP59 and BP60 to 0.9 t ha⁻¹ in family BP40. Relatively high yields were recorded in 2017, ranging between 1.4 t ha⁻¹ (BP31) and 3.8 t ha⁻¹ (BP41) with an average of 2.3 t ha⁻¹ (Table 2).

There was a wide variation among the families for cumulative yield across the 5-year yield recording period with more than a four-fold difference between the highest (BP40) and lowest (BP61) yielding families (Table 2). There were no clear significant changes in family ranks in terms of yearly yields during the period of evaluation. In general, the top 10 families in terms of cumulative yield across the 5-year yield recording period were consistent among the highest-yielding families in terms of yearly yields (Table 2). This was also similar for the 10 lowest-yielding families which were consistent among the lowest-yielding families in terms of yearly yields (Table 2).

Relationship between vegetative growth and yield traits

The phenotypic (r) and genetic correlations (r_g) between vegetative traits (stem diameter, height, span and number of laterals) and cumulative yield produced estimates that were similar in direction but varied in magnitude (Table 3). Generally, all the phenotypic and genetic correlations were positive and significant ($p < 0.05$). In comparison, the genetic correlations were considerably higher than their corresponding phenotypic correlations in most cases for trait combinations (Table 3).

Table 4. Genetic parameter estimates of growth and yield traits of 62 full-sib families

Trait*	Genetic parameter [†]					
	σ^2g	σ^2p	H^2	GCV	PCV	σ^2e/σ^2g
Stem diameter (mm)	21.00 ± 6.40	91.21	0.23 ± 0.04	13.72	28.59	3.3
Height (m)	0.05 ± 0.01	0.09	0.56 ± 0.21	15.97	21.43	0.8
Span (m)	0.06 ± 0.04	1.28	0.05 ± 0.04	18.84	87.03	20.3
No. of laterals	36.83 ± 7.24	62.26	0.59 ± 0.11	23.71	30.82	0.7
Yield_13 (t ha ⁻¹)	0.01 ± 0.00	0.04	0.25 ± 0.09	33.33	66.67	3.0
Yield_14 (t ha ⁻¹)	0.58 ± 0.13	1.59	0.36 ± 0.04	26.26	43.48	1.7
Yield_15 (t ha ⁻¹)	0.12 ± 0.03	0.36	0.33 ± 0.05	23.09	40.00	2.0
Yield_16 (t ha ⁻¹)	0.04 ± 0.02	0.10	0.40 ± 0.14	51.56	81.52	1.5
Yield_17 (t ha ⁻¹)	0.33 ± 0.08	0.97	0.34 ± 0.04	24.98	42.82	1.9
CY (t ha ⁻¹)	2.51 ± 0.57	6.07	0.41 ± 0.04	24.00	37.33	1.4

*CY (t/ha⁻¹) = Cumulative yield from 2013 to 2017.

[†] σ^2g = genotypic variance; σ^2e = error variance; σ^2p = phenotypic variance; H^2 = broad sense heritability; GCV = genotypic coefficient of variation; PCV = phenotypic coefficient of variation.

Genetic correlations indicated that selection for increased stem diameter could increase height ($r_g = 0.93, p < 0.001$), number of laterals ($r_g = 0.95, p < 0.001$), span ($r_g = 0.86, p < 0.001$) and cumulative yield ($r_g = 0.38, p < 0.01$) (Table 3). Similarly, selection for increased height could lead to increased number of laterals ($r_g = 0.69, p < 0.001$), span ($r_g = 0.83, p < 0.001$) and a moderate increase in cumulative yield ($r_g = 0.32, p < 0.05$) (Table 3). Number of laterals was highly correlated with span ($r_g = 0.61, p < 0.001$) but moderately correlated with cumulative yield ($r_g = 0.46, p < 0.001$). Span on the other hand was strongly correlated with cumulative yield ($r_g = 0.60, p < 0.001$).

Variance components and genetic parameter estimates for traits assessed

The variance component estimates, the broad sense heritability (H^2) and GCV and PCV for all traits studied are presented in Table 4. For all traits investigated, except for height and number of laterals, the genetic variance components were smaller than their respective environmental variance components (Table 4), leading to a positive and greater than 1 environmental variance to genetic variance ratio. Thus, these traits were influenced by environmental factors more than genetic factors. This was more pronounced in span measurements which had the highest (20.3) ratio of environmental to genetic variance. Number of laterals was least influenced by the environment as it recorded the lowest (0.7) environmental to genetic variance ratio in the current study (Table 4).

The relatively high environmental influence on most of the traits assessed led to moderate heritability estimates, except for number of laterals which recorded the highest heritability of 0.59 and span which recorded the lowest heritability of 0.05. Also, a high heritability estimate of 0.56 was observed for height. The high heritability observed for number of laterals was not surprising as it was the trait least affected by the environment as judged by the low ratio of environmental to genetic variance estimates (Table 4). Of the yield traits assessed, the highest heritability estimate was observed for cumulative yield (Table 4). The PCV was higher than the GCV for all traits studied (Table 4). Yield in 2016 recorded the highest GCV of 51.6% and stem diameter recorded the lowest GCV of 13.7% (Table 4). The PCV for all the traits evaluated followed a similar trend with span and height recording the highest (87.0%) and lowest (21.4%) PCVs, respectively (Table 4).

Expected genetic advance

Expected GA under selection with varying selection intensities (2, 5, 10, 20 and 30%) was estimated only for number of laterals (Figure 1a, b) and cumulative yield (Figure 1c, d) which recorded broad sense heritability of 0.59 and 0.41, respectively. The reason for this is that we

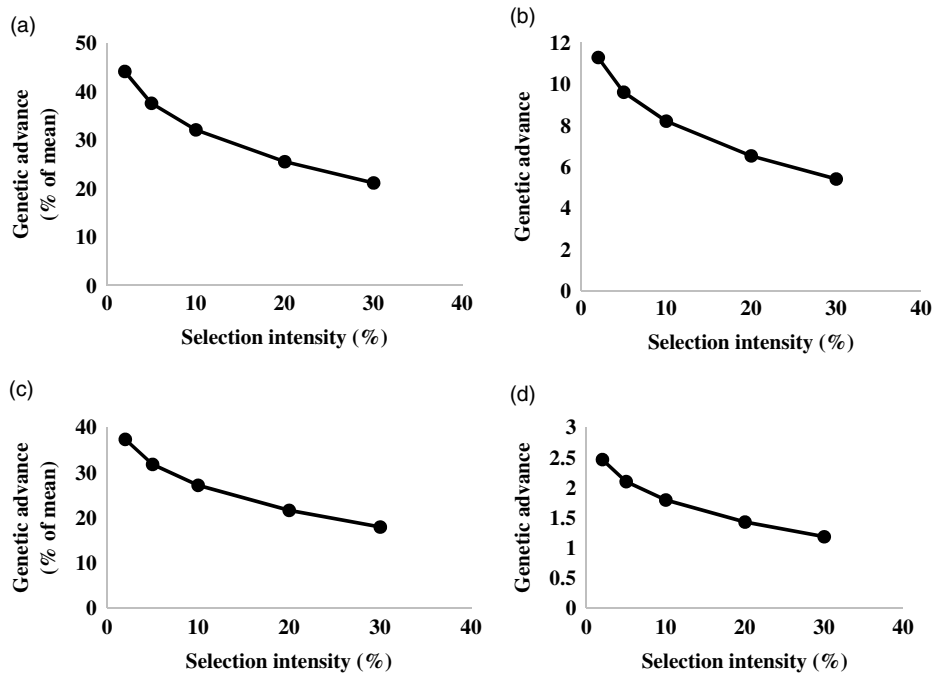


Figure 1. Expected genetic advance as percentage of trait mean (a) and expected genetic advance (b) under varying selection intensities for number of laterals of 62 full-sib families. Expected genetic advance as percentage of trait mean (c) and expected genetic advance (d) under varying selection intensities for cumulative yield of 62 full-sib families.

wanted to focus on traits with the highest heritability estimates from which the most gains could be made in our breeding programme. There was a decline in expected GA with increasing selection intensity for all traits (data not presented). For both number of laterals and cumulative yield, GA as the percentage of trait mean at 2% selection intensity was about twice that at 30% selection intensity and intermediate at 10% selection intensity. Among all the traits assessed, there was a superior GA for number of laterals, regardless of the selection intensity (Figure 1a, b).

Discussion

Genetic variability and estimation of genetic parameters of key productivity traits are of significant importance to guide selection in a hybrid breeding programme. Though the gene pool of Robusta coffee in Ghana based on morphological characters has been determined to be narrow (Akperterey *et al.*, 2018b), the results from the present study indicated the presence of variation among the families for most vegetative growth traits and all yield traits, based on which significant improvement could be made in the breeding of the crop in the country. The presence of the significant variation may be attributed to the larger number of families included in the study. The significant variation observed in this study is consistent with previous studies where high genetic variation for yield (Cilas *et al.*, 2006; Mistro *et al.*, 2004) and yield components (Petiard *et al.*, 2004) were observed in Robusta and Arabica coffee (Cilas *et al.*, 1998).

Other authors also found significant differences among coffee progenies from crosses of commercial cultivars with Timor hybrid accessions, in bean yield assessment experiments (Carvalho *et al.*, 2008). Similarly, Walyaro and Van der Vossen (1979), working on Arabica coffee, showed the prevalence of highly significant genetic variation for berry yield during single year, first 2 years, and cumulative 10 years yield. They also observed highly significant genetic variation for vegetative traits including height, stem diameter, number of primary branches and span.

Information on genetic correlations is a prerequisite in developing selection criteria for a population and hybrid development. According to Cruz et al. (2012), simultaneous selection of traits targeting direct effects whose magnitudes are high may result in gains in the main variable. Generally, the vegetative growth traits were more genetically correlated with cumulative yield than yearly yields (data not presented), which may indicate that the vegetative growth traits predict the yield capacity of trees better than they do for yield in 1 year as shown by Cilas et al. (2006). From the current study, the direct effect of number of laterals on cumulative yield was 0.46 ($p < 0.001$). This correlation was lower compared to Cilas et al. (1998) who found high significant genetic correlation between number of primary branches and 4-year cumulative yield in Arabica coffee. The disparity in findings could be attributable to differences in plant species and test environments in both studies.

From our study, span was the vegetative trait most significantly correlated with cumulative yield ($r_g = 0.60$, $p < 0.001$). This may be an indication that there was less competition between trees in our study as shown in one of the trials of Leroy et al. (1994). These results indicate that direct selection of families with greater number of laterals or larger span could increase the yield. Therefore, vegetative growth characters like number of laterals and span could be utilized in breeding programmes to select varieties for higher yield. Similar to the findings in this study, Silvarolla et al. (1997) showed significant correlations between vegetative characters and yield. There was a significant genetic relationship between stem diameter and cumulative yield as well as between height and cumulative yield. This agrees with the findings of Carvalho et al. (2010) who reported a significant positive correlation between plant height and yield, but contrary to the findings of Cilas et al. (1998) who found a negative genetic correlation between 4-year cumulative yield and height in Arabica coffee. Since the correlation was moderate in our study and contrary to findings in other studies, further studies may be required to better inform on the relationship of both traits in selection.

For all the traits evaluated in this study, except height and number of laterals, the environmental variance was larger than the genetic variance, suggesting that families with better yield or trait measurements may not have the same response in each season or year, making it difficult to maintain predictability. The heritability estimates for most traits assessed were generally low to moderate. This, coupled with the high variation index (ratio of environmental variance to genetic variance), most above unity, indicates the predominance of environmental to the detriment of genetic components. This was also confirmed with the estimates of PCV which were higher than those estimated for the GCV for all traits. On the contrary, high broad sense heritability estimates were observed for two vegetative traits: height and number of laterals, and a moderate heritability estimate was observed for 2016 yield and cumulative yield. Similarly, Leroy et al. (1994) found high broad sense heritability estimate for 4-year cumulative yield in a recurrent selection study in Robusta coffee. The high heritability estimates for height and number of laterals and the moderate heritability estimates observed for yield in 2016 and cumulative yield coupled with the relatively low environmental to genetic variance component estimates for these traits reflect a positive outlook for selection in the improvement of the aforementioned traits.

The broad sense heritability reported here does not differ much from those published elsewhere, especially for yield in both *C. canephora* (Srinivasan et al., 1979) and *C. arabica* (Cilas et al., 1998; Walyaro and Van der Vossen, 1979). Cilas et al. (1998) and Cilas et al. (2006), working on Arabica and Robusta coffee, respectively, found broad sense heritability for height similar to the findings in the current study (0.49 vs 0.56). However, some conflicting broad sense heritability values have been observed for number of laterals and height in other studies in comparison to this study. Akpertey et al. (2018a) reported relatively low broad sense heritability values of 0.10 and 0.20 for number of laterals and height, respectively, in comparison to what was observed in the current study. Similarly, Anim-Kwapong and Anim-Kwapong (2012) reported a low broad sense heritability (0.25) for number of laterals as opposed to a heritability value of 0.59 observed for the same trait in this study. Additionally, Leroy et al. (1994) reported broad sense heritability

estimate of approximately 1.0 for height and stem diameter in Robusta coffee. As heritability is a property of the population being sampled, the reason for these differences may lie in the type and structure of the populations used to estimate the components of variance, as gene frequencies differ from one population to the other and the history of the population.

Heritability for yield varied for the five yearly harvests from 2013 through 2017, reflecting a biennial pattern where a low heritability estimate in one year was followed by a high heritability estimate for yield in the subsequent year. As reported by Mistro *et al.* (2007), the prediction of genetic parameters of a population is of paramount importance in the breeding programme. However, for certain traits such as yield, the estimation of a parameter may be variable due to the genetic variability in a population and to environmental conditions. With regard to coffee productivity, the different heritability estimates for the five harvests and cumulative yield are probably a result of differential gene expression during plant growth and development, differences in size, vigour and initial seedling development shortly after planting in the field and of environmental conditions in the harvest year. Therefore, the estimates of heritability coefficients must be interpreted with caution. One must be aware of the bias of these estimates since the broad sense heritability is the ratio of the genetic variance between families to the phenotypic variance in experiments.

Of all the yield traits, broad sense heritability was lowest and the ratio of environmental variance to the genetic variance component was highest for the first harvest in 2013. The high ratio of environmental variance to the genetic variance component that led to a relatively low heritability estimate for yield in 2013 can be attributed to the differences in vigour and early growth of seedlings in the nursery and field. These differences in seedling vigour and early growth lead to very disparate yields in the first or early harvests. However, these differences tend to even out from the second harvest onwards when the plant growth and development are more intense on both shoot and root systems leading to less plot-to-plot variation. It is therefore very important that the heritability for yield should be estimated after the first harvest.

The highest heritability estimates for yield traits in the current study were observed for cumulative yield. The influence of the environment on the expression of cumulative yield was relatively low as evidenced by the relatively low (1.4) ratio of environmental variance to genetic variance component. However, there was a highly significant family \times year interaction for yield in the combined ANOVA. Therefore, selection for yield in a high-yielding year may not be the same as in a low-yielding year. Selection for cumulative yield should therefore be based on the cumulative performance of families and not on high- or low-yielding year's yield performance.

Despite the influence of the environment in the expression of most traits assessed in this study, moderate to high significant gains from selection were observed for the two most heritable traits (number of laterals and cumulative yield). The estimate of GA as a percent of mean (GAM) for number of laterals was relatively high and ranged from 21 to 44% for 30 and 2% selection intensities, respectively, which are comparable to the findings of Atinafu *et al.* (2017) who reported an estimated GAM of 25.6% for number of laterals at a 5% selection intensity. Similarly, the expected GAM for cumulative yield ranged between 17 and 37% for 30 and 2% selection intensities, respectively. These findings are much lower compared to the report of Abdi (2009) who reported a much higher (111.4%) GAM for bean yield per plant for Arabica coffee at a 5% selection intensity. This significant disparity in GAM estimates between both studies could be attributed to the difference in species and environments. The relatively high heritability estimates observed for number of laterals and cumulative yield combined with the relatively high GAM estimates would lead to significant improvement of both traits in our breeding programme through selection as the combined use of heritability and GA has been shown to be vital for the effective improvement of a particular trait in a population (Yigzaw, 2005). A combined consideration of GCV, broad sense heritability estimates and GA is important as selection criteria, and hence, number of laterals and cumulative yield that combined moderate to high heritability estimates with high GA indicate the control of additive genes, and selection may be effective in improving both characters in a breeding programme.

In conclusion, results from the study revealed significant genetic variation for vegetative growth traits and yield, except for span. This implied the availability of variation for genetic improvement of key traits in our breeding programme. Heritability estimates, excluding those for stem diameter, span and first yield recording (2013), were moderate to high, suggesting that even though trait expression was influenced by the environment, they were also influenced by genes, and parental performance could be used in selecting superior families. Reasonably high expected GA values obtained under selection intensities of 2 to 30% for the two most heritable growth (number of laterals) and yield traits (cumulative yield) suggested that an appreciable progress could be made in improving these traits through selection. The direct selection for number of laterals and cumulative yield provides genetic gains and would increase the frequency of favourable alleles in the population. The top 10 families (BP40, BP41, BP9, BP36, BP34, BP28, BP37, BP14, BP4 and BP10) in terms of cumulative yield combined with high early vegetative growth are proposed for multi-location evaluation and possible release as hybrids in Ghana.

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