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Full Length Research Paper

Genetic and environmental correlations between bean yield and agronomic traits in *Coffea canephora*

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Early identification and selection of genotypes with high yielding potential is a main breeding objective of *Coffea canephora*. Eighteen genotypes of *C. canephora* were assessed in three diverse environments over a 9-years period from 1996 to 2005. Genetic and environmental associations were assessed among 10 vegetative and five reproductive traits and yield. Genetic associations between yields over seven years and vegetative traits, except secondary branches per plant, were positive and significantly correlated with span (r_G = 0.65**), girth (r_G = 0.60**), diameter (r_G = 0.55*) and number of primary branches (r_G = 0.53*). The traits exhibited stronger genetic correlations with last 4 - 7 years yields (r_G =0.54* - 0.68**) than with first 1 - 3 years yields (r_G = 0.38 - 0.47*). Fruit-set observed in three fruiting seasons, when the trees were three, four and six years in the field, was consistently positive and significantly associated with yields over seven years (r_G = 0.60**; 0.63**; 0.66**). However, genetic associations between yields over seven years and flowers per node observed in the three fruiting seasons was consistently negative and significant for two seasons (r_G = -0.50*; -39; -0.62**). First 1 - 3 years yield was a better predictor (r^2_G = 0.79***) of yields over seven years, than first 1 - 2 years (r^2_G = 0.42**) and first year (r^2_G = 0.012) yield. Selection for potential high yielding genotypes should, therefore, be based on an index involving span, girth, diameter and number of primary branches, first three years yield, fruit-set, and flowers per node. High positive environmental correlations were observed between bean yields and fruit-set, number of fruits per node, number of flowering and fruiting nodes, girth and number of primary branches. However, environmental conditions that reduced yields also increased flowers per node and promoted vegetative growth by increasing secondary branching, span, length, diameter and number of nodes per primary branch. Efficient selection for yield based on vegetative traits should, therefore, be undertaken under optimum growing conditions where there is a better balance between vegetative growth and yield.

Key words: Vegetative traits, reproductive traits, *Coffea canephora*, genetic correlations, environmental correlations, yields, indirect selection.

INTRODUCTION

Coffee is one of the main agricultural commodities traded worldwide. Its cultivation is mainly by smallholder farmers who hardly breakeven due mainly to low yields, high production cost and low world market prices. Increasing productivity, while reducing the cost of production is a main breeding objective of most producing countries. To meet that objective, research programmes to select high yielding varieties have been initiated in Ghana. Yield improvement of Robusta coffee involves the modification of the genetic makeup and/or the modification of the growing environment of the crop. While methods for easy identification of genotypes with good morphological characteristics within the early years of cultivation and evaluation are available, identifying high yielding genotypes is often difficult to achieve and time consuming due to the long gestation period, biennial bearing and heterogeneous nature of Robusta coffee, in addition to large environmental component of variance for yield. A selection cycle is possible only after seven to eight years of cultivation. Hence, improving the yield of a population through recurrent selection takes a long time to achieve, while final testing of genotypes in multisite trials becomes

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Table 1. Planting material and their sources of origin.

Clones from Cote d` Ivoire†	Clones from Togo††
A129	197
A115	149
A101	126
B170	181
B96	375
B36	107
B191	
E174	
E138	
E139	
E90	
E152	

†Selection based on 10-years yields; ††Selection based on 3-years yields.

very expensive. Shortening the time required to obtain an accurate evaluation of yield potential would allow for faster release of new varieties at reduced cost, thus making the breeding programme more efficient. There have already been some reports of correlation studies among yield of coffee and juvenile and mature plant characteristics to address this problem (Ravohitarivo, 1980; Ameha, 1982; Bouharmont et al., 1986). However, most of these studies examined phenotypic correlations of total 5 - 10 years production with early yield and vegetative characteristics in *Coffea arabica*. The genetic correlation, which is the proportion of variance that two traits share due to genetic causes, is useful in studying the genetic relationships among traits under selection. Environmental correlations reveal associated changes in two traits caused by environmental and non-genetic factors (Falconer and Mackay, 1996). The few reports available on genetic correlations are mostly on Arabica coffee with genotypes planted at a single location (Walyaro and Van der Vossen, 1979; Walyaro, 1983; Leroy et al., 1994; Cilas et al., 1998, 2006). Generally, information on environmental associations among yield and agronomic traits are hardly used alongside yield data collected over locations and seasons to select high yielding genotypes. The magnitude and direction of these associations should be informative as a basis of indirect selection for yield and for environmentally modifying growing conditions. The objective of this study was, therefore, to estimate the magnitude and direction of genetic and environmental associations among yield and agronomic traits in Robusta coffee.

MATERIALS AND METHODS

Twelve clones obtained by individual selection, based on yield, from a population of three half-sib family groups introduced from Cote d`Ivoire, together with six clones introduced from Togo, were used for the study (Table 1).

The study was conducted from 1996 to 2005 at three rain-fed sites (Tafo, Fumso and Bechem) within the forest zone of Ghana where coffee is grown, representing a range of soil types, fertility levels and climatic regimes (Table 2).

Single-node cuttings of the clones used were rooted in propagators and nursed in nursery bags for six months. Thirty-two plants of each genotype were randomly assigned to each of the three environments. At each location, the experimental design was a randomized complete block design with four replications. A single row of eight plants of each genotype were planted in each replication with plots measuring 2.44 x 19.51 m. Both inter-row and inter-plant spacings were 2.44 m giving a density of 1680 plants per hectare. Planting in the three environments was done in June 1996. No fertilizer was applied and crop management practices were similar for all locations. In order to assess genetic differences in number of stems produced, the plants were allowed to grow on one or two stems that had developed from the single-node cuttings. Stems were capped at 18 months from field planting by removal of the terminal bud and subsequently capped to 1.8 m and maintained at that height. The first capping resulted in each main stem developing into two branches at the point of capping.

Measurements of vegetative characteristics were taken three months after field planting on plant height, diameter of the main stem (girth) and number of primary branches and repeated each year after field planting until the plants were 48 months in the field, at the stage of maximum expansion. Vegetative measurements taken when the plants were 48 months in the field, was used for this study. Four random plants of each genotype in each plot were used. Traits assessed included girth(mm), taken at 10cm above the ground, crown diameter (span) in cm, taken as the length of the canopy measured at the widest portion of the tree canopy, number of stems, total number of primary branches counted per plant and per stem, and total number of secondary branches counted per plant. Length of primary branches (measured from the point of attachment to the main stem to the apex in cm), diameter of primary branches (10 cm from the main stem in mm) and number of nodes per primary branch were estimated as an average value of the six longest branches at the middle of the stem per plant. Internode length per branch was estimated as an average of length of primary branch divided by the number of nodes of primary branch for the six primary branches. Where there were more than one stem, stem diameter was calculated according to Stewart and Salazar (1992), and span was taken for only the biggest stem.

Table 2. Soil and climatic characteristics of experimental sites.

	Site of experiment		
Characteristic	**Tafo**	**Fumso**	**Bechem**
Soil type	Sandy loam	Coarse sandy to fine gravel	Humus fine sandy loam to fine clay
Altitude(above sea level)(m)	220	122	259
Latitude	6^o 13'N	6^o 6'N	7^o 5'
Longitude	0^o 22'W	1^o 27'W	2^o 2'
Mean total annual rainfall from 1996 - 2002 (mm)	1480	1320	1220
Mean monthly rainfall during flowering and fruit-setting period (Dec.- Feb.) from 1996 - 2002	44	29	17
Mean annual monthly raindays from 1996 - 2002	9.4	8.4	7.9
Mean monthly raindays during flowering and fruit-setting period (Dec.- Feb.) from 1996 - 2002	3.6	2.1	1.8
Mean annual average daily air temperature(^{o}C) from 1996 - 2002	26.8	27.0	26.2
Mean monthly average daily air temperature(^{o}C) (Dec.- to Feb.) from 1996 - 2002	27.1	27.2	26.2
Mean annual daily humidity at 1500 h (%) from 1996 - 2002	67.1	62.9	62.4
Mean daily humidity at 1500 h (%) (Dec.- to Feb.) from 1996 - 2002	56.7	56.0	48.3

Table 3. Form and generalized expectations of analysis of variance and covariance for two characters X and Y.

Source of variation	Degrees of freedom	Mean square	Expectation of mean square	Expectation of mean cross-product
Replications/locations	(r-1)L			
Locations (L)	L-1	M_l	$\sigma^2_e+r\sigma^2_{gl} + rN(\sigma^2_E)$	$\sigma_{e(XY)}+r\sigma_{gl(XY)} + rN(\sigma_{E(XY)})$
Genotypes (G)	N-1	M_g	$\sigma^2_e+r\sigma^2_{gl} + rL(\sigma^2_g)$	$\sigma_{e(XY)}+r\sigma_{gl(XY)} + rL(\sigma_{g(XY)})$
G x L	(N-1) (L-1)	M_i	$\sigma^2_e+ r\sigma^2_{gl}$	$\sigma_{e(XY)}+ r\sigma_{gl(XY)}$
Error	(N-1) (r-1)L	M_e	σ^2_e	$\sigma_{e(XY)}$

r = number of replications = 4; L = number of locations = 3; N = number of genotypes = 18.

At flowering and fruiting time in December, 1998 to May, 1999, two plants from each plot, were randomly tagged. Three flowering primary branches at the middle of each plant were tagged for the determination of the number of flowering nodes per branch and number of flowers per node. Fruits that remained on the branches at six months from initial flowering were counted and used in estimating the number of fruiting nodes and fruits per node. Percent fruit-set (fruit-set) was estimated as the proportion of total flowers counted on the three flowering branches per tree that set fruit and remained on the branches at six months from flowering. To study genetic association among yields and reproductive traits as a factor of the age of the plants, the reproductive traits were further assessed in two more seasons: December, 1999 to May, 2000, and December, 2001 to May, 2002 using three trees per plot for each clone. The latter assessment was however at two locations, Tafo and Bechem.

Clean coffee yields were recorded on each tree for seven production years from October to January each year for the period 1998/1999 to 2004/2005. Transformation of cherry weight to clean coffee weight was done using the conversion factor 0.22 (Coste, 1992).

Analyses of variance and covariance were performed using MINITAB statistical software (MINITAB, 1997). The statistical model used for the combined analyses was:

$$Y_{ijk} = \mu + g_i + e_j + (ge)_{ij} + R_{jk} + \varepsilon_{ijk}$$

Where Y_{ijk} is the k^{th} observation of any variable in the r^{th} replications in environment j on genotype i; μ is the general mean; g_i and e_j represent the effects of the i^{th} genotype and the j^{th} environment; $(ge)_{ij}$ is the interaction effect between the genotypes and the environment; R_{jk} is the effect of the k-th replication within the j-th location, ε_{ijk} is the random error associated with the k^{th} observation on genotype i in environment j. i = 18; j = 3; r = 4. The effects g_i\`s, $e_j$\`s, $(ge)_{ij}$\`s and $\varepsilon_{ijk}$\`s are assumed independently and randomly distributed with zero means and variances σ^2_g, σ^2_l, σ^2_{gl} and σ^2_e, respectively.

The form of the analysis of variance and covariance with expectations of mean squares and cross products is presented in Table 3.

Genotypic correlations (r_G) and environmental (r_E) correlations between traits were computed as:

$$r_G = cov_{g(XY)} / \sqrt{\sigma^2_{g(X)} \ \sigma^2_{g(Y)}} \ ; \ r_E = cov_{E(XY)} / \sqrt{\sigma^2_{E(X)} \ \sigma^2_{E(Y)}}$$

Table 4. Genetic and environmental correlations between mean yields and vegetative traits (at 48 months) estimated in the combined analysis of variance and covariance for three locations in 18 Robusta coffee genotypes.

Trait	First three years yields	Last four to seven years yields	Yields over seven years
Girth	0.38	0.63**	0.60**
	0.26	0.67	0.49
Span	0.47*	0.68**	0.65**
	-0.98	-0.80	-0.91
Length of primary branches	0.25	0.47*	0.42
	-0.85	-0.53	-0.69
Diameter of primary branches	0.46*	0.54*	0.55*
	-0.99*	-0.89	-0.96
Number of nodes /primary branch	0.23	0.16	0.18
	-0.99*	-0.86	-0.95
Inter-node length / primary branch	0.01	0.26	0.20
	-0.56	-0.14	-0.34
Number of primary branches /plant	0.43	0.55*	0.53*
	0.56	0.87	0.75
Number of secondary branches /plant	-0.34	-0.25	-0.29
	-0.93	-0.99*	-0.99*
Number of stems / plant	0.24	0.41	0.38
	-0.97	-0.75	-0.87
Number of primary branches /stem	0.10	0.03	-0.07
	0.65	0.92	0.62

* = p ≤ 0.05, ** = p ≤ 0.01; genetic correlations (upper values); environmental correlations (lower values).

Where $cov_{g(xy)}$ was the estimated genotypic covariance component for traits X and Y, $\sigma^2_{g(X)}$ and $\sigma^2_{g(Y)}$ the genotypic variance component for traits X and Y respectively; $cov_{E(xy)}$ was the estimated macro-environmental (location) covariance component for traits X and Y , $\sigma^2_{E(X)}$ and $\sigma^2_{E(Y)}$ the macro-environmental variance component for traits X and Y respectively (Falconer and Mackay, 1996). Significance test for the correlations was by standard procedure (Steel et al., 1997).

RESULTS

Genetic correlations

Genetic correlation coefficients between yield and vegetative traits from the combined data across the three locations are shown in Table 4. Bean yields over seven years showed significant positive genetic correlation (r_G =0.53*- 0.65**) with girth, span, diameter and number of primary branches. These traits exhibited stronger correlation with last 4 - 7 years yields (r_G =0.54* - 0.68**) than with first 1 - 3 years yields (r_G =0.38 - 0.47*). An inverse relationship between yields and number of secondary branches was observed. Associations among the vegetative traits showed significant (r_G =0.67**- 0.77***) genetic correlations among span, girth and diameter of primary branches (Table 5). Number of secondary branches per plant was inversely associated with traits that showed significant genetic correlations with yield namely: girth, span, diameter and number of primary branches. However, only the association with span was significant (r_G = -0.48*).

Genetic correlations between yields and the reproductive traits show that in 1998/1999 alone, when the trees were only two and half to three and half years old, genetic correlations between first two years yields and fruit-set and fruits per node had already coefficients of 0.66 and 0.68 respectively (not shown). Genetic correlation coefficients between bean yield and the reproductive traits in 1998/1999, 1999/2000 and 2001/ 2002 fruiting seasons from the combined data across the three locations are shown in Table 6. All associations in 1998/1999 were positive, except with flowers per node. Fruit-set was significantly (r_G = 0.59**- 0.65**) associated with first 1-3 year yields, last 4-7 year yields and yields over seven years. Number of fruits per node and fruiting nodes, however, significantly (r_G = 0.48* - 0.49*) correlate positively with early yields but significant correlations with late yields

Table 5. Genetic and environmental correlations among vegetative traits (at 48 months) estimated in the combined analysis of variance and covariance for three locations in 18 genotypes of Robusta coffee.

Trait	1	2	3	4	5	6	7	8	9
1. Girth	-								
2. Span	0.67**	-							
	-0.08								
3. Length of primary branches	0.32	0.78***	-						
	0.29	0.93							
4. Diameter of primary branches	0.70***	0.77***	0.38	-					
	-0.24	0.98	0.86						
5. Number of nodes /primary branch	-0.05	0.35	0.39	0.24	-				
	-0.17	0.99*	0.89	0.92					
6. Internode length / primary branch	0.32	0.39	0.56*	0.13	-0.55*	-			
	0.81	0.70	0.91	0.78	0.62				
7. Number of primary branches per plant	0.39	0.13	0.11	0.02	-0.10	0.16	-		
	0.95	-0.40	-0.04	-0.54	-0.49	0.37			
8. Number of secondary branches / plant	-0.32	-0.48*	-0.39	-0.30	-0.43	0.04	-0.02	-	
	-0.59	0.85	0.60	0.93	0.90	0.22	-0.82		
9. Number of stems/ plant	0.36	0.00	-0.11	0.08	-0.41	0.26	0.67**	0.18	-
	0.00	1.00***	0.96	1.00***	1.00***	0.86	-0.36	0.81	
10. Number of primary branches / stem	-0.05	0.05	0.17	-0.15	0.28	-0.11	0.22	0.12	-0.55*
	0.90	-0.50	-0.15	-0.63	-0.58	0.27	0.99*	-0.88	-0.43

* = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$; genetic correlations (upper values); environmental correlations (lower values).

and yields over seven years were not observed. Significant inverse associations were observed between number of flowers per node and late yield as well as yields over seven years (r_G = -0.54* and -0.50* respectively). Similar trend were observed between the traits recorded in 1999/2000 and 2001/2002 fruiting seasons (Table 6). Genetic correlations among the reproductive traits in two seasons (Table 7) showed significant genetic association between fruit-set and fruits per node (r_G = 0.70*** - 0.77***) and between fruiting and flowering nodes (r_G = 0.76*** - 0.85***).

Genetic correlation coefficients between overall seven year yields and the first year, first 1 - 2, 1 - 3, and last 4 - 7 years yields were positive and highly significant (r_G = 0.89*** - 0.99***) with first 1 - 3 years and last 4 - 7 years yields (Table 8).

Environmental correlations

Environmental correlations between coffee bean yields and the vegetative traits observed (Table 4) showed that, environmental conditions contributing towards low coffee berry yields favoured span, length and inter-node length of primary branches, and number of stems per plant and significantly (r_E = 0.99*) increased diameter and number of nodes and the formation of more secondary branches. Environmental correlations among the vegetative traits (Table 5) were mostly positive. However, inverse associations were observed between number of primary branches per plant/ per stem and the traits span, length and diameter of primary branches, number of nodes per primary branch and number of secondary branches; and between girth and span, diameter of primary branches, number of nodes per primary branch and number of secondary branches. Significant positive environmental associations (r_E = 1.00***) were observed between number of stems per plant and the traits span, diameter of primary branches and number of nodes per primary branch.

Environmental conditions which favored fruit-set, number of fruits per node, fruiting and flowering nodes in 1998/1999 and 1999/2000 fruiting seasons had positive effects on all the yield traits (Table 6). However, environmental conditions that promoted the formation of more flowers per node in both fruiting seasons resulted in low yields. Environmental correlations among the traits (Table 7) showed that, fruit-set, fruits per node, fruiting and flowering nodes were environmentally positively associated but negatively associated with flowers per node.

Environmental associations among the yield traits (Table 8) were all positive. However, only environmental conditions that determined first two years yields significantly (r_E = 0.1***) determined overall seven year yields. Good environmental growing conditions must therefore be maintained at the early growth stages of the plants to promote early bearing and subsequent higher yields at the matured plant stage.

DISCUSSION

Knowledge of correlations among characters is useful in

Table 6. Genetic and environmental correlations between mean yields and reproductive traits (in three production seasons) estimated in the combined analysis of variance and covariance for three locations in 18 Robusta coffee genotypes.

Trait	Year	First three years yields	Last four to seven years yields	Yields over seven years
Fruit-set	1998/1999	0.65^{**}	0.59^{**}	0.63^{**}
		0.97	0.97	0.99^{*}
Number of fruits/node		0.48^{*}	0.21	0.30
		0.92	0.61	0.80
Number of fruiting nodes		0.49^{*}	0.17	0.23
		0.99^{*}	0.91	0.99^{*}
Number of flowers/node		-0.29	-0.54^{*}	-0.50^{*}
		-0.70	-0.96	-0.85
Number of flowering nodes		0.19	-0.04	-0.02
		0.99^{*}	0.83	0.95
Fruit-set	1999/2000	0.75^{***}	0.46^{*}	0.60^{**}
		0.99^{*}	0.96	0.99^{*}
Number of fruits/node		0.56^{*}	0.15	0.29
		0.99^{*}	0.92	0.97
Number of fruiting nodes		0.51^{*}	0.17	0.29
		0.99^{*}	0.89	0.95
Number of flowers/node		-0.20	-0.42	-0.39
		-0.96	-0.99^{*}	-0.99^{*}
Number of flowering nodes		0.02	-0.05	-0.05
		0.60	0.26	0.42
Fruit-set	2001/2002	0.30	0.73^{***}	0.66^{**}
Number of fruits/node		0.10	0.37	0.29
Number of flowers /node		-0.27	-0.63^{**}	-0.62^{**}

* = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$; genetic correlations (upper values); environmental correlations (lower values). Values in 2001/2002 represent genetic correlations at Tafo and Bechem only.

Table 7. Genetic and environmental correlations among reproductive traits (in two production seasons) estimated in the combined analysis of variance and covariance for three locations in 18 Robusta coffee genotypes.

Trait	1	2	3	4	5
1. Fruit-set		0.70^{***}	0.35	-0.44	0.12
		0.80	0.99^{*}	-0.86	0.95
2. Number of fruits/ node	0.75^{***}		0.10	0.33	-0.38
	0.99^{*}		0.89	-0.37	0.95
3. Number of fruiting nodes	0.58^{**}	0.54^{*}		-0.36	0.85^{***}
	0.98	0.99^{*}		-0.76	0.99^{*}
4. Number of flowers/node	-0.25	0.41	-0.08		-0.36
	-0.98	-0.95	-0.92		-0.65
5.Number of flowering nodes	0.13	0.21	0.76^{***}	-0.07	
	0.53	0.45	0.67	-0.33	

* = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$; 1998/1999 correlations (upper triangle); 1999/2000 correlations (lower triangle); genetic correlations (upper values); environmental correlations (lower values).

determining the success of indirect selection of one trait for the other in an improvement programme for any crop (Falconer and Mackay, 1996). Indirect selection of one trait for the other depends on many factors. Selection for yield in a perennial crop like coffee should be advantageous with traits that are determined at the juvenile or

Table 8. Genetic and environmental correlations among yield traits estimated in the combined analysis of variance and covariance for three locations in 18 Robusta coffee genotypes.

Trait	1	2	3	4	5
1. Yields over seven years	-				
2. Last four to seven years yield	0.99***	-			
	0.98				
3. First year yield	0.11	0.03	-		
	0.92	0.97			
4. First two years yield	0.65**	0.75***	0.43	-	
	1.00***	0.98	0.94		
5. First three years yield	0.89***	0.81***	0.31	0.79***	-
	0.97	0.90	0.83	0.98	

** = p ≤ 0.01, *** = p ≤ 0.001; genetic correlations (upper values); environmental correlations (lower values).

early reproductive stages of the plant. The significant positive genetic associations between bean yields and girth, span, diameter and number of primary branches, as well as the significant genetic associations observed among span, girth and diameter of primary branches suggest the possibility of increasing yields at both the juvenile and adult plant stages through the selection of vigorous young plants with thick and strong main stems and primary branches as well as wider span, characteristic of genotypes with erect primary branches. The significant associations observed in this study agrees with previous findings that, Robusta coffee yields (Bouharmont et al., 1986; Leroy et al., 1994; Cilas et al., 2006), as well as Arabica coffee yields (Walyaro and Van der Vossen, 1979; Walyaro, 1983; Cilas et al., 1998) are positively correlated with young plant vigour. Coffee trees were four years old and in their second fruiting season when the traits were observed. It is likely that the positive effects of good vegetative growth of stems on yields are due to the availability of reserves in such stems which provide yield enhancing assimilates. Stem reserves have been shown to play an important role as source of assimilate for fruit and grain yields in other plant studies (Blum et al., 1997; Ehdaie and Waines, 2006).

The positive genetic correlations and negative environmental associations between yields and span, length, diameter, nodes and inter-node length of primaries and number of stems per plant, show that environmental conditions that resulted in low yields contributed towards increased vegetative growth. Indirect selection of vegetative traits for yield in any breeding programme should, therefore, be undertaken under optimum conditions where there is a better balance between vegetative growth and yield.

The production of more secondary branches could be expected to result in more flowering and fruiting nodes and more fruits. However, the inverse genetic association between secondary branching and yields as well as the vegetative traits associated with yields (span, girth, diameter and number of primaries) and the significant inverse environmental association between secondary branching and yields clearly indicate that secondary branching in coffee does not translate into high yields. Selecting plants with low secondary branching should therefore be advantageous for yields in coffee. Reducing secondary growth by pruning could also improve coffee yields significantly.

Having established that fruit-set and fruits per node of coffee trees were associated with yields, genetic associations further studied in 1999/2000 and 2001/2002 production seasons (when the second and fourth yields were recorded) established that fruit-set was in fact the most important reproductive trait that determined coffee yields at both the early and late reproductive stages of the coffee plant. Studies on genetic correlations of Robusta and Arabica coffee yields and agronomic traits have been undertaken before (Walyaro and Van der Vossen, 1979; Leroy et al., 1994; Cilas et al., 1998, 2006). In these previous reports, however, association between reproductive characters and yields were not matched with data on variation in age of plants. In associations examined in the present study, the influence of the age of the plants on how fruits per node, fruit-set and flowers per node affected yield was thus isolated.

The inverse genetic associations between number of flowers per node and fruit-set and yields imply that, comparatively more flowers were produced at the nodes by low yielding plants than by high yielding ones. Walyaro and Van der Vossen (1979), working on Arabica coffee observed similar negative genetic association of number of flowers per node with fruit-set and yields. Environmental conditions that promoted the production of more flowers per node also resulted in poor fruit-set and low yields as observed with secondary branching. In coffee flower buds borne in the axils of leaves on primary branches have the potential of either developing into new shoots or inflorescence. According to Wrigley (1988), more of the buds would produce shoots depending on the strength of the stimuli to vegetative growth. It is therefore likely that, any genetic or environmental condition that leads to the initiation of more auxiliary buds will also result in the formation of more flowers and/or secondary branches. For coffee, drought was observed to be an important stimulus for flower bud initiation as well as flowering (DaMatta and Ramalho, 2006). Evidence from comparative studies has shown that, drought-sensitive plants maintain lower internal water status than drought-tolerant ones under water-deficit conditions (Meinzer et al., 1990; Pinheiro et al., 2005). Drought-sensitive plants are, therefore, more likely to have higher stimulus for flower bud initiation, hence, maintaining higher flowering and secondary branching than drought-tolerant plants. It also implies that, flower bud initiation and therefore flowering and secondary branching would be higher in drier environments than under optimum conditions, hence, the genetic and environmental associations observed in this study between number of flowers per node, number of secondary branches per tree, fruit-set and yields.

The significant positive environmental associations between yields and fruit-set and fruiting nodes confirm these observations and highlight the importance of the environment in determining yields. The three environments used for the study range from high to low rainfall areas, varying seasonally in rainfall amount and distribution, most especially, during the flowering and fruit setting periods. Precipitation during fruit-set and fruit development was found to affect yields in coffee (Barros et al., 1999). Fruit-set and fruiting nodes on primary branches and hence yields were higher in Tafo, a high rainfall environment, than at Bechem, a low rainfall environment (data not shown). It is therefore important that coffee is grown in areas where there is enough rainfall during the fruit-setting and fruit expansion periods. In areas where rainfall is below optimum, coffee plants could benefit from irrigation, especially, during the fruit setting period. Cannell (1973) observed that the number of flowering and fruiting nodes on which flowers and fruits are borne increased by the application of fertilizers, especially nitrogen, as well as by mulching and irrigation. Adequate nitrogen supply had also been suggested for improved tolerance to drought (Ramalho et al., 1999, 2000). Fruit-set, fruits per node and hence yields should therefore improve with the application of fertilizers. The optimum environment for Robusta coffee cultivation must therefore be where rainfall is well distributed without a prolonged dryness, especially, after flowering to facilitate fruit setting; coupled with regular pruning to reduce secondary branches, and observance of good cultural practices for soil fertility improvement.

Conclusion

The high genetic correlations among fruit-set, first three years yields, and yields over seven years and between yields and the vegetative traits indicate that, selection for high yielding genotypes is feasible when coffee plants are five years in the field based on fruit-set, first three years yields, span, girth, diameter and number of primary branches.

The main vegetative trait that affected yield environmentally, namely, secondary branching, was determined at the juvenile or early fruiting stages of the plant. Four reproductive traits, namely number of flowering nodes, flowers per node, fruiting nodes and fruit-set that affected yield environmentally were also determined at the early fruiting stages. With the environmental associations observed, it is possible to increase yield through simple agronomic practices. Such practices must reduce secondary branching and increase the diameter of the main stems, the number of primary branches, the number of flowering and fruiting nodes, fruits per node and fruit-set.

In this study, the genotypic and environmental variances and covariances of the traits were estimated from a population of 18 preselected genotypes and could be specific to the studied population. Nonetheless, these results should form an important basis for a pre-selection index for high yielding plants and for environmentally modifying growing conditions for increased coffee productivity.

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