Considerations in breeding for improved yield and quality in arabica coffee (*Coffea arabica* L.)

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Abstract

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Variation for growth, yield and quality characters was studied in a diallel cross among 11 varieties of arabica coffee. The objective was to demonstrate the possible application of such information in breeding programmes for improved yield and coffee quality.

Growth characters especially girth, height, internode length on stem and primaries, and canopy radius had a high repeatability. Such characters are heritable, even with a single measurement taken on young coffee trees. For most yield characters, a good assessment can only be obtained if it is based on the mean of several years' records Regarding quality characters, single berry weight, % AA, %AB and %PB showed a high heritability.

Genetic variation for selected growth and yield characters was due to genes with additive and dominance effects. There was also evidence of epistatic effects among genes governing most of these characters, and especially so for yield. As a consequence many of the F_1 hybrids displayed considerable hybrid vigour varying between 10% to over 200% above the better parent. Variation for quality characters was chiefly due to the additive genetic effects, specific combining ability being relatively unimportant.

A detailed study of genotype-environment interactions revealed that it is possible to select for high yielding genotypes with the desired level of linear response to environments. Yield stability and compact growth are characters that could be selected for independently. Quality characters in general were relatively less influenced by effects of genotype-environment interactions.

Height and angle of primaries could be selected on basis of 1 year old seedlings in the nursery. It is also possible to base individual tree selection for yield on performance of fairly young coffee trees. This entails use of a preselection index comprising for instance, girth, canopy radius or internode length on primaries, bearing primaries or % bearing nodes, plus yield of the first 2—3 years of individual trees. For coffee quality, rapid improvement could be obtained by basing selection on %AA for bean size, and on the overall standard for liquor quality. The first year's assessment of these characters is already sufficient for selection purposes.

Implications of these results in breeding programmes are discussed. A breeding scheme is proposed aimed at developing compact high yielding coffee varieties with good quality which also combine resistance to the two main diseases of arabica coffee, coffee berry disease and coffee rust. The breeding scheme entails either development of hybrid varieties, or a programme of further selection to derive seed varieties. Important features of such a scheme are, 1) the use of information on genetic basis of variation for certain characters in planning hybridization programmes and, 2) a drastically reduced breeding cycle per generation as a result of basing selection, within each generation, on fairly young coffee trees.

Free descriptors: *Coffea arabica*, diallel cross, plant evaluation, repeatability, environmental stability, genetic variation, heritability, hybrid vigour, genotypic correlation, preselection index, coffee yield, compact growth, coffee quality, disease resistance, *Colletotrichum coffeanum*, *Hemileia vastatrix*, a breeding scheme.

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1. GENERAL INTRODUCTION

1.1. Background and objectives

Coffee is undoubtedly the most valued of the stimulant crops. In the recent past, it has been ranked after petroleum and it derivatives, as the most important product in international trade (Purseglove, 1968; Chouler, 1972).

Coffee growing can be considered as one of the most important agricultural occupations, upon which the economy of more than 50 developing countries depends (Rodrigues et al., 1975). In Kenya for example, coffee is by far the leading export commodity accounting on average for 30—40% of the country's export earnings. In addition, it is estimated that over 10% of the entire population of Kenya, derives their income directly from coffee. The total area under coffee production in Kenya by the end of 1979 was over 100,000 hectares. Estates account for about a quarter of the area while three quarters, is under small holdings (Anon, 1980). The total annual production by 1980 was about 87,000 tonnes of clean coffee.

Of the cultivated species of *Coffea*, arabica coffee *Coffea arabica* L., is by far the most important. It represents over 65% of the total area in the world used for coffee production. In Kenya, practically all the exported coffee is the arabica type.

Breeding work in arabica coffee started during the 1920's and 1930's in Brazil (Krug, 1935 & 1937). India (Srinivasan & Narasimhaswamy, 1940) Tanzania (Gilbert, 1938 & 1939) and Kenya (Melville, 1946; Thorold, 1947). Emphasis in selection was primarily for high yield, better bean size and liquor quality. In the recent past, improvement work has been dominated by breeding for disease resistance to two important diseases of arabica coffee, coffee rust or orange rust of coffee *Hemileia vastatrix* B. and Br. and coffee berry disease, *Colletotrichum coffeanum* Noak. (*Sensu* Hindorf).

These two diseases are the most serious obstacle to production of arabica coffee. Coffee rust, first recorded in 1861 around the shores of Lake Victoria in Kenya, had its first serious appearance in Ceylon (Sri Lanka) in 1868. Eventually arabica coffee plantations had to be abandoned and replaced by tea. Since then, it has spread to almost all coffee growing areas of the world, reaching Brazil in 1970 (Monaco, 1977). Coffee berry disease, an anthracnose of green and ripening berries, was first reported in Western Kenya in 1921. Though it has since spread to a number of countries, where it poses a serious threat to coffee production, it is still confined to Africa and only on arabica coffee. Control measures to both diseases arethrough intensive fungicide spray programmes which are prohibitively expensive especially to the small scale farmers. Breeding for disease resistance therefore appears to be the only alternative to the present control measures.

Breeding for resistance to both diseases has involved mainly programmes to incorporate major genes in new varieties (van der Vossen et al., 1976; Monaco, 1977; Carvalho et al., 1976). A large number of major genes conditioning resistance to specific pathotypes of *H. vastatrix* have been identified over years (d'Olveira, 1953; d'Olveira & Rodrigues, 1960; Rodrigues et al., 1975). The situation with respect to *C. coffeanum*, is not yet clear although recent genetic studies (van der Vossen & Walyaro, 1980), have shown that resistance is conditioned by a few major genes. Studies on selection methods for horizontal resistance to coffee rust are also in progress in Brazil (Eskes 1983; da Costa et al., 1978; Monaco, 1977). In Ethiopia, a mass selection programme within varieties of arabica coffee to accumulate resistance to CBD has been reported by Robinson (1974 & 1976) and van der Graaff (1978).

It is clear therefore, that further improvement in *C. arabica* will depend more on artificial hybridization among varieties that are genetically divergent, followed by selection within progenies of subsequent generations of selfing. Attention in selection will be devoted mainly to disease resistance plus of course yield and quality. Prospects for yield improvement are particularly good when consideration is given to development of compact and physiologically more efficient plant types which are better adapted to high density planting; substantial yield increases have in fact been reported from such high density plantings consisting of the present tall commercial cultivars (Mitchell, 1976; Browning & Fisher, 1976) and in other similar trials with arabica and robusta trees (Gaspar, 1977).

The current breeding programme in Kenya was initiated in 1971 with the main objective to develop new varieties of arabica coffee which combine resistance to coffee berry disease and coffee rust with high yield and good quality and eventually also compact growth (van der Vossen, 1973). The duration of such a breeding programme will largely depend on the efficiency of selection for yield and quality especially since methods of early selection for resistance to the two most important diseases of *C. arabica* are already available (Rodrigues & Bettencourt, 1965; van der Vossen et al., 1976a; Eskes, 1983). The present study was therefore primarily concerned with yield and quality aspects of this breeding programme. The objectives were, 1) to elucidate the genetic basis of variation and covariation for a number of important characters related to growth,yield and quality among some selected varieties of arabica coffee 2) to indicate how this information can be applied to arrive at optimal breeding procedures that are economic and result in maximum genetic gain and, 3) to examine against a background of information emerging from this study the implications of current breeding programmes in arabica coffee in relation to their ultimate goals.

1.2. Classification, origin and centres of high diversity of the *Coffea* species

The genus *Coffea* belongs to the family *Rubiaceae*, and consists of 90 to 100 species which have so far been identified. Only a few of these species however, are of economic importance. Chevalier (1942 & 1947) grouped the known species of *Coffea* into four sections: *Eucoffea* K Schum, *Argo-*

coffea Pierre, *Mascarocoffea* Chev., and *Paracoffea* Miq. The first three sections include coffees exclusively native to Africa. Whereas, representatives of *Paracoffea* are native to India, Indochina,Ceylon(Sri Lanka) and Malaya.

The cultivated species of *Coffea* belong to the Section *Eucoffea;* this section is in turn subdivided into the following subsections:

Section	Subsection	Species
Eucoffea	*Erythrocoffea*	*C. arabica* L. *C. canephora* Pierre *C. congensis* Froehner *C. eugenioides* Moore
	Pachycoffea	*C. liberica* Bull. *C. dewevrei* de Wild. *C. klainii Pierre* *C. abeokutae* Cramer *C. oyemensis* Chev.
	Nanocoffea	*C. humilis* Chev. *C. brevipes* Hiern and other species
	Melanocoffea	*C. carrisoi* Chev. *C. stenophyla* G. Dun and others
	Mozambicoffea	*C. ligustroides* Moore *C. racemoca* Lour. *C. salvatrix* Swyn. & Phil. and others

The basic chromosome number of *Coffea* x, is 11 (Bouharmont, 1963). *C. arabica*, is the only known natural allopolyploid in the genus with 2n= 4x=44, and is self compatible. The rest are diploids with 2n=2x=22 and are all allogamous and self incompatible.

The African Centre appears to be the origin of the *Coffea* species (Zeven and Zhukovsky, 1975). *C. arabica* has its primary centre of genetic diversity in the evergreen mountaineous region of the Kaffa, Illubabor and Gemu Gofa Provinces of South West Ethiopia, and the Boma Plateau of Sudan (Sylvain, 1953; Meyer, 1969). The intricate migrations of arabica coffee from the primary centre to Yemen, India, Sri Lanka, Indonesia, Europe,the Carribeans, South America and East Africa are summarised by Klinkowiski (1947)and Ukers (1948). Arabica coffee, apart from being the most widely cultivated species of *Coffea*, is also well known for its high quality coffee. Brazil and Columbia between them account for 40% of the world coffee exports. Kenya produces only about 2% (Anon, 1979).

Coffea canephora, Robusta coffee occupies 33% of the total world coffee growing area and gives coffee of lower quality than arabica coffee. It is indigenous to all lowland tropical forests of Western and Central Africa. The centre of greatest diversity is in the Congo basin, Zaire. It is mainly grown in Ivory Coast, Angola, Uganda, Cameroons and Indonesia. Because of self

incompatability, it is highly polymorphic as are other diploid species. *Coffea liberica* and *Coffea dewevrei* or *excelsa* are both indigenous to the dense forests of West Africa (Guinea, Liberia and Ivory Coast). Both become large trees and are considered to produce coffee of even lower quality. These are cultivated to a small extent in West Africa, Indonesia, French Guinea and Surinam. Account of geographic distribution of these and other species of *Coffea* are given by Chevalier (1942 & 1947) and Chouler (1972).

The evolutionary trend in *Coffea* as postulated by Charrier (1977) and Kammacher (1977), is as follows: The diploid *Coffea* species are thought to be descendants of common allogamous ancestors in Central Africa. These have achieved speciation by migrating in different directions where they gave rise to morphologically distinct populations. Thus, *Canephoroides* and *Liberio-excelsoides* differentiated westwards, whereas *Mozambicoffea* and *Mascarocoffea* differentiated south-westwards and *Coffea arabica* northwards. Each of these phylogenetic branches had a divergent evolution coupled with slight chromosome differentiation which however has not reached a stage of establishment of strong reproductive isolation barriers. The amphidiploid *C. arabica* has a common genome with one found in the diploid species. The origin of the second genome however, is still unknown (Charrier,1978a). The normal diploid behaviour of *C. arabica* is thought to be either due to strong preferential pairing or due to a genetic system that regulates synapsis of the *Triticum aestivum* type.

Breeding in coffee like in many other crop plants depends on utilisation of available germplasm. The present available collections however, represent only a small fraction of the natural diversity of the genus *Coffea* (Kammacher, 1977). On the other hand this genetic diversity is threatened because the forests in Africa and Madagscar which form the natural habitat of *Coffea* are vanishing rapidly due to timber extraction, and also to give way to agriculture including replanting with commercial varieties of coffee. It is because of this that conservation of coffee genetic resources has to be regarded as a matter of urgency, to save some of the genetic diversity. Two expeditions to explore and collect arabica coffee materials have been undertaken to Ethiopia in 1964 (FAO 1968) under the auspices of FAO, and in 1968 by the ORSTOM Mission (Charrier, 1978b). Other expeditions to collect diploid *Coffea* species have been undertaken by ORSTOM and IFCC in various African countries (Berthaud et al., 1977).

FAO/IBPGR in collaboration with ORSTOM are compiling an up to date inventory on existing coffee germplasm collections in Africa and elsewhere. Eventually, it is expected that FAO/IBPGR may provide assistance and collaboration for further exploration, introduction and exchange of materials and information between various coffee growing countries.

1.3. Growth habit, flower and fruit characteristics in arabica coffee

Detailed description of morphology and growth characteristics of arabica coffee is given by a number of authors for example Wellman (1961) and

Haarer (1962). *C. arabica* is a perennial woody shrub with a dimorphic growth characterisitic which essentially consists of distinct vertical (orthotropic) branches and horizontal (plagiotropic) branches.

Inflorescences develope from serial buds mainly on horizontal branches. Each inflorescence normally carries one to five flowers. The flowers have a short pedicel and a rudimentary calyx the petals are fused and form a corolla with five lobes. The pistil consists of an inferior ovary and a long style with two stigmatic lobes. The ovary is bilocular each with one anatropous ovule.

Flowering in arabica coffee is characterised by remarkable periodicity particularly in areas with distinct wet and dry seasons. In Kenya east of the Great Rift Valley the main flowerings occur at the onset of the rainy season in February — March and October — November. Flower initiation occurs after sufficient rainfall (at least 20 mm.) following a dry period. Techniques of artificial cross pollination in arabica coffee are fairly straight forward and have been described by Carvalho & Monaco (1969) and Walyaro & van der Vossen (1977). Coffee pollen loses viability rapidly under normal conditions. However, when stored under vaccum at $-18^{o}C$ the viability will be maintained for 3 or more years (Walyaro & van der Vossen, 1977).

In arabica coffee it takes 6 to 8 months from flowering to fruit ripening. The coffee fruit is a drupe usually containing two seeds. Ripe fruits have a thick fleshy pericarp (pulp) and a hard endocarp (parchment) in addition each seed is enveloped in a silver skin (testa) a remnant of the integument (Perisperm). The coffee bean consists of an endosperm and a small embryo embedded at the basal end of the seed. There is no seed dormancy in coffee; seed viability is normally lost within 3 to 6 months after harvesting. Coffee seed is recalcitrant as are most tropical fruits and nuts. It is possible to preserve the viability for up to 2½ years when coffee seed at moisture content of 41% is stored at a temperature of $15^{o}C$ (van der Vossen, 1979b).

It takes about 12 months from seed germination to a seedling ready for field planting. Under optimum conditions seedlings can start flowering within 12 months and the first good crop can be obtained within 2½ years after field planting.

1.4. Breeding in *Coffea* arabica

The introduction of arabica coffee into the main coffee producing areas was limited to only a small number of plants. As a consequence arabica cultivations in South East Asia, South and Central America and indeed to some extent in Kenya and Tanzania had a very narrow genetic base. The situation has since however improved due to introductions resulting from exchange programmes and from exploration missions to the primary centre of diversity. Nonetheless, selection work within arabica coffee has been pursued for a considerable length of time, initially in Brazil, India, Tanzania and Kenya and later on, in Columbia, Guatemala, Costa Rica and Mexico. The following is a brief account of breeding work in arabica coffee, intended to give a background to the present study.

Most of the basic genetic and cytological work in arabica coffee was carried on in Campinas Brazil. This has resulted in a considerable amount of information regarding genetic control of characters mainly showing simple, classical Mendelian, inheritance; indeed, a number of mutants studied are of practical value in breeding programmes. A detailed review of this work is

given by Krug & Carvalho (1951); Carvalho (1958 a & b) and Sybenga (1960).

Among the objectives of initial breeding programmes in most of the countries already mentioned, were selection for improved yield, good adaptation, regularity in bearing, better bean size and improved liquor quality. The selection method used was in most cases individual plant and line selection followed by progeny tests (Krug, 1945; Krug & Carvalho, 1941; Gilbert, 1938 & 1939; Melville, 1948; Ramanathan et al., 1950; Gowgill, 1951; Franco, 1947 & 1948; Machado, 1950). Artificial hybridisation was however used only to a limited extent. In Brazil, cultivar Bourbon Vermelho then Mundo Novo and eventually also Catuai Vermelho and Amerelo and Acaia were developed from such a programme. In Puerto Rico (Gomes & Esmoris, 1947) Columnaris was found to be the best variety. Cultivars N 39 and N 197 Bourbon types and H 66 and KP 423, Kents types were selections made from the breeding programme in Tanzania (Fernie, 1959&1961).

The now widely grown commercial cultivars in Kenya especially the SL selections were developed from early selection work carried out at the National (then Scott) Laboratories. Cultivar SL 28 was a single tree selection from a Bourbon type clone called Tanganyika Drought Resistant which was selected at Monduli Tanzania. SL 34 was also a single tree selection from French Mission trees growing at Loresho Estate Kabete just outside Nairobi (Jones, 1956). These cultivars are still outstanding as far as yield and quality are concerned and show remarkable adaptability.

With the advent of coffee rust in Ceylon and India efforts were directed towards identifying coffee genotypes resistant to this disease. One such variety was the Coorg cultivar which was found in India. It was eventually replaced by the Kent cultivar which was then resistant to coffee rust. This variety was introduced into several other countries. In the end however, it was also found to be susceptible to certain rust races. The first notable stage in coffee improvement for rust resistance was the programme of selection within natural interspecific hybrids of *C. arabica* and *C. Liberica* in India. This gave rise to selections of the S and B.A. series (Narasimhaswamy, 1960). From these selections and other combinations provided by CIFC a number of promising progenies have been obtained (Vishveshwara & Govindarajan, 1970).

In Tanzania, a breeding programme for rust resistance was initiated in 1952/53 when crosses were made between the Kent type commercial cultivars and Geisha and Amfillo (both introductions from Ethiopia). The performance of some of the Geisha VC 496 hybrids in terms of yield and rust resistance was very encouraging (Fernie, 1969; Millot, 1970). In Kenya, selection work within the Kent variety produced cultivars K7 and SL6 (Firman & Hanger, 1963). These cultivars, especially K7, are grown even at present on large scale at low altitudes.

The establishment of Centro de Investigacao das Ferrugens do Cofeeiro (CIFC) at Oeiras, Portugal was instrumental in fostering international collaboration to combat coffee rust through breeding for disease resistance (Rodrigues et al., 1975; Monaco, 1977). The Institute has since been evaluating numerous coffee collections and *H. vastatrix* samples from natural populations as well as from research centres.

In Brazil, breeding work on disease resistance was initiated already in 1950 with a programme of interspecific hybridization between tetraploid *C. canephora* and *C. arabica* (Monaco, 1977). Coffee varieties were also introduced from other countries including Ethiopia, India, Kenya and Tanzania. Screening of progenies of these materials was done by CIFC. Of most interest are populations of Icatu advanced generation of the interspecific hybridisation programme and those derived from crosses involving Hibrido de Timor with Brazilian varieties. Some progenies of Icatu have been re-reported to carry resistance to CBD in addition to coffee rust (Carvalho et al., 1976). As was mentioned earlier, selection for horizontal resistance to leaf rust is also in progress (Scali et al., 1974; Eskes et al., 1977; da Costa et al., 1978). Sources of resitance to rootknot nematode *Meloidogyne* and leaf miner *Perileucoptera coffeela* are also being sought (Fazuoli et al., 1977; Medina et al., 1977).

Since 1965 the Breeding Department of Cenicafe in Columbia in collaboration with CIFC has been also selecting for rust resistance (Castillo et al., 1972). The most promising results have been obtained from the programme involving crosses between Caturra and Hibrido de Timor. Selection within progenies of F3 and F4 generation of these crosses has yielded material so called CATIMOR which is homozygous for compact growth, resistant to most races of coffee rust and quite productive (Catillo & Moreno, 1980). The superior progenies from this programme will soon be released for commercial planting as the Columbia variety. Like in Brazil selection for horizontal resistance to leaf rust and evaluation of resistance to rootknot nematode *Meloidogyne* are also in progress (Gabriel & Pablo, 1980; Orozco, 1980, Baeza, 1980).

At the CIFC Oeiras between 1960 and 1979 work has been in progress involving screening for rust resistance and for other agronomic characters among progenies of crosses between various different coffee material (Betencourt et al., 1980). This programme was in collaboration with Angola and Brazil. Some outstanding selections with respect to rust resistance, productivity and compact growth have also been obtained from this programme.

In Eastern Africa, the rapid outbreaks of coffee berry disease CBD, in Kenya in 1960 and eventually in Tanzania in 1966 (Fernie, 1969) prompted further hybridisation programmes in Tanzania aimed at combining yield with resistance to CBD and coffee rust. Among progenitors for disease resistance were Hibrido de Timor, Rume Sudan, Kaffa and Geisha which were crossed to varieties N 39, KP 423 and H 66. Encouraging results regarding yield, quality and disease resistance were obtained from progenies of some of these crosses. Some of these progenies also formed the basis of multiple crosses proposed in 1970 by Visser (1970). In this programme emphasis in selection was to be on CBD and rust resistance plus fair yield and quality.

Because the widely grown commercial varieties in Kenya SL 28 and SL 34 are uniformly susceptible to both CBD and coffee rust the outbreaks of CBD during the 1960's put the Kenya Coffee Industry in a serious jeopardy. Crop losses of up to 50 percent can occur in years of severe CBD epidemics unless the disease is controlled by an intesive programme of fungicide sprays aimed

at continuously protecting the developing crop (Griffiths et al, 1971).

The breeding programme in progress at the Coffee Research Station Ruiru (also mentioned in section 1.1.) was initiated as a result of these two diseases. The general breeding programme at the CRS has been concerned with four main areas of research; hybridisation and selection programme, biometrical genetics studies, improvement of breeding techniques and vegetative propagation and nursery experiments (van der Vossen, 1973).

In the main breeding programme three different methods have been applied to achieve the objectives (i) the backcross method with a number of CBD and rust resistant varieties using the commercial cultivars and a few other varieties as the recurrent parents, (ii) the multiple way cross method to ensemble in one plant traits of more than two varieties eg. disease resistance, compact growth and erect branching, quality and yield followed by backcrossing to the commercial cultivars (iii) interspecific hybridisation of tetraploid *C. canephora* and *C. arabica*.

The first single crosses were made in 1966. Since then numerous crosses involving various combinations of different parental varieties have been made. Details of specific crosses, their pedigree and evaluation of progenies of these crosses are given by van der Vossen (1979a). In all cases selection within hybrids has included selection for seedling resistance by inoculation test on 6 week old seedlings according to the procedure of van der Vossen et al. (1976 a); field selection during the first two years in the field for general vigour and growth habit; selection for yield and quality for at least 3 years of production and selection for field resistance to CBD, leaf rust and other pests and diseases.

A number of promising selections with regard to CBD and leaf rust resistance, yield and quality have been obtained from this breeding programme. In addition, some outstanding progenies of CATIMOR material obtained from Columbia are undergoing evaluation at the CRS. It is expected that the new materials eventually released to the farmers may consist of outstanding hybrids selected among crosses between superior genotypes from the main breeding programme and those selected from the CATIMOR material.

Like many of the other coffee breeding centres the Coffee Breeding Unit at the CRS maintains a world collection of wild and cultivated varieties of arabica coffee and other species of *Coffea*. An important addition to this collection was the Ethiopian collection which represents 120 introductions of the 1964 FAO Mission. The Ethiopian collection has been enlarged by addition in 1980 of about 500 genotypes of the 1966 ORSTOM Ethiopian collection originally planted in Ivory Coast and about 21 genotypes of the 1964 FAO collection received from Brazil. The Ethiopian Collection undoubtedly, represents the most valuable germplasm collection on the Station for future breeding needs.

2. MATERIALS AND METHODS

2.1. Materials and experimental design

The parents chosen for this study were 11 varieties representing a number of introductions and cultivars of *Coffea arabica*. These varieties are diverse in many respects including growth habit, yield, quality and resistance to the 2 major diseases of arabica coffee. The varieties do not represent a random sample from any population. They are a selected sample and therefore constitute the entire population from which inferences were to be made. An important feature of this group of varieties was that it contained most of the progenitors of the main breeding programme at the CRS, Ruiru. The varieties were as follows:-

1. Caturra — introduced into Kenya in 1958 from Kivu, Zaire a dwarf and compact variety, originating from Brazil.

2. Pretoria — introduced from Guatemala to Lyamungu, Tanzania, and then to the CRS, Ruiru; a tall vigorous tree with very large leaves and beans resembling variety Maragogipe, highly resistant to CBD.

3. Erecta — a variety with erect branching characteristic, introduced from Puerto Rico to Lyamungu and eventually planted at the CRS, Ruiru.

4. SL28 — represents individual tree selection from the former Scott Laboratories, Nairobi (see section 1.4). It is one of the commercial cultivars in Kenya.

5. Mokka — of Arabian origin, a small conical shaped tree with small leaves, and small round beans of excellent liquor.

6. K7 — Kents type selection (see section 1.4), another commercial cultivar in Kenya. Has resistance to race II of *H. vastatrix* and shows partial resistance to CBD.

7. Hibrido de Timor — was introduced from the Rust Research Centre (CIFC) at Oeiras, Portugal in 1960. A tetraploid arabicoid hybrid which appeared spontaneously in the Portuguese Timor. It combines resistance to CBD with the R-type resistance, to most races of *H. vastatrix*

8. Padang — was imported initially from Guatemala, a very good yielder, shows partial resistance to CBD.

Table 1. The crossing plan of the incomplete diallel cross among 11 varieties of arabica coffee (1).

Parents	1	2	3	4	5	6	7	8	9	10	11
1. Caturra	1	2	4	7	11	16	22	29	37	46	56
2. Pretoria	—	3	5	8	12	17	23	30	38	47	57
3. Erecta	67	—	6	9	13	18	24	31	39	48	58
4. SL28	68	—	72	10	14	19	25	32	40	49	59
5. Mokka	69	—	73	76	15	20	26	33	41	50	60
6. K7	70	—	74	77	79	21	27	34	42	51	61
7. Hibrido de Timor	71	—	75	78	80	81	28	35	43	52	62
8. Padang								36	44	53	63
9. Laurina									45	54	64
10. Rume Sudan										55	65
11. SL34											66

(1) The crosses above the diagonal, plus the selfed parents (on the diagonal) constitute a complete half diallel among the 11 parents, whereas crosses among parents 1, 3, 4, 5, 6, 7, form a complete 6 x 6 full diallel. The numbers inside the table represent the family obtained from each cross; the same numbers are used consistently throughout the text

9. Laurina — a compact, conical shaped tree, with long fruits having a thick pericarp. It has a very low caffein content. Imported also from Guatemala.

10. Rume Sudan — was introduced into Kenya as seeds from wild coffee growing on the Boma Plateau in Sudan near Ethiopia. A fairly small and low yielding tree but our best progenitor for CBD resistance. This variety has been found to be fairly homozygous and homogeneous both for CBD resistance and for growth and yield characters.

11. SL34 — is another selection from the former Scott Laboratories (see also section 1.4). SL34 and SL28 are the main commercial cultivars in Kenya, and as was mentioned earlier, both are very high yielders and produce coffee of excellent quality.

The crossing scheme involving these parents gave an incomplete diallel consisting of 81 crosses. The incomplete diallel however, forms a complete half diallel between the 11 parents, 6 of the parents, also constitute of 6 x 6 full diallel. The crossing plan is given in Table 1. All crosses were completed between January and April 1973.

The experiment was planted out in May/June 1975, in a 9 x 9 partially balanced lattice square in 3 squares replicated twice. One replicate was planted at a density of 3,333 trees/ha and the other at 6,667 trees/ha. Each plot consisted of 8 trees, measurements being taken on the 4 central trees (see the plot structure in Figure 1).

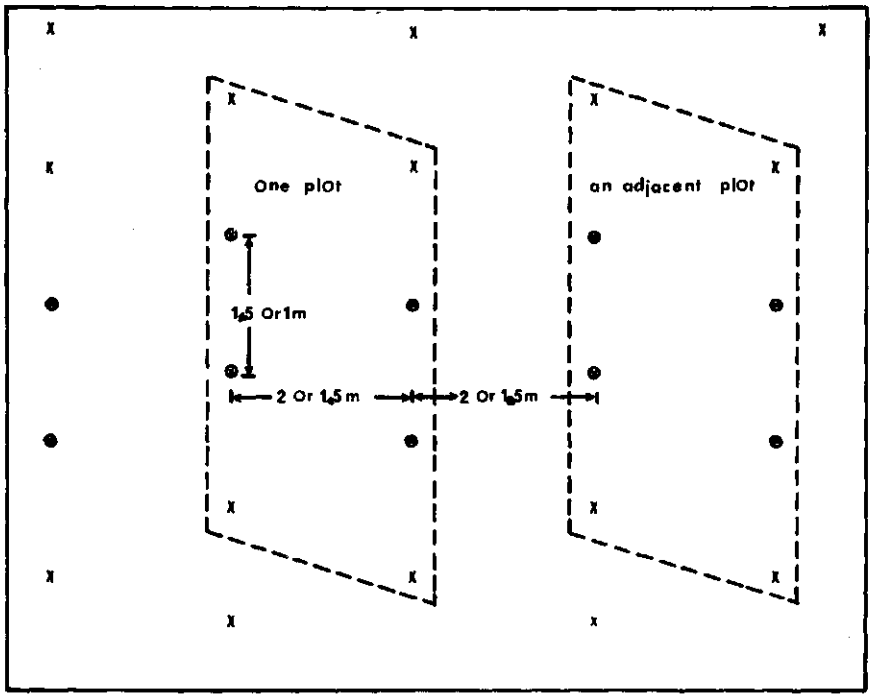


Fig. 1 Example of the plot structure
X represents guard trees.
● represents recorded trees.
Spacing of 2 by 1.5 m gives a density of 3333 trees ha^{-1}.
Spacing of 1.5 by 1 m gives a density of 6667 trees ha^{-1}.

The trees were maintained on single uncapped stem system with free growth except for pruning, in later stages, of the lowermost laterals where these were trailing on the ground. The full CBD and leaf rust control programme was applied to all blocks to prevent the bias arising from crop loss especially on disease susceptible varieties, and also to impart uniform tonic effect. Pest control measures however, were applied only whenever it became necessary. Fertilizer applications both ground and foliar, were according to the recommendations of the Chemistry Section of the CRS. These were based on results of soil and leaf analyses. Other cultural practices were according to the recommended practice in Kenya (Ombwara, 1968).

2.2. Characters recorded

Recording of this experiment was started in January 1976, i.e 6 months from the time of field planting, and was continued up to 48 months. The charaters which were measured were categorised as follows:

2.2.1. Growth characters

These were measured on each individual tree.

1. Girth of stem (G) — this was measured as the circumference of the stem in cm, taken about 5 cm from the ground level.

2. Height of the tree (H) — recorded as the length from the base to the tip of the tree, in cm.

3. Internode length (Int LS) — obtained for each tree (in cm) as the height of the tree divided by the number of nodes on the main stem.

4. Primaries (Pr) — the number of primaries counted per tree.

5. Radius of canopy (R) — this was obtained as the average length (in cm) of 4 primaries situated at the middle of the crown. On very young trees, it was the mean length of the 2 longest primaries.

6. Internode length (Int LPr) — this was estimated from 4 primaries per tree. For each primary, the length was divided by the number of nodes, and internode length was taken as the mean of these values (in cm) obtained from the 4 primaries.

7. Leaf area (Le) — ten leaves of comparable age were selected on each tree, the surface area of each leaf was then estimated as (length x width, at the broadest portion) x 0.88. The leaf area in cm^2 was then taken as the mean of these estimates for the 10 leaves.

8. Angle of primaries (Ang) — in degrees (^{o}); was measured as the angle of insertion of selected primaries on the main stem, then expressed as the mean of 4 primaries per tree.

9. Extension growth (E) — in cm, was measured as the mean increase in length on 4 primaries, initially tagged at 3 nodes from the tip, after a period of about 12 months.

10. Node production (No) — was obtained as the mean number of nodes per primary produced on the above primaries (no 9) over the same period of time.

2.2.2. Yield characters

These were also recorded on individual trees.

1. Bearing primaries (Pr b) — this was recorded as the number of primaries which were carrying berries, flowers or flower buds.

2. Bearing nodes (Nob) — for the first recording on young trees, the total number of nodes with berries flowers or flower buds were counted on the whole tree, and expressed as a percentage of the total number of nodes on

the same tree. The second recording however, was performed on the 4 selected primaries per tree.

3. Flowers per node (Fl no) — the number of flowers per node was calculated from marked segments of 4 selected primaries. This was during the main flowerings.

4. Fruit set (Frs) — was estimated as the percent of the above flowers which set fruit 4 months later.

5. Berries per node (be No) — was obtained as the mean number of berries per node on 4 selected primaries.

6. Yield of cherry — this was the weight of fresh fruits harvested per tree, expressed as Kg/tree.

7. Yield of clean coffee — the weight of sun dried coffee beans per tree, also expressed as Kg/tree.

2.2.3. Berry and bean characters

These were determined on coffee samples from 4 trees per plot.

1. Single berry weight (Sbr Wt) — obtained as the mean weight per berry in (g) from several samples each of 100 fresh berries.

2. Pulp — the weight of the fleshly pericarp (see section 1:3) expressed as a percentage of the fresh cherry weight.

3. Out turn — percent clean coffee over fresh cherry weight, (see section 2.2.2.)

4. PB — (Peaberries) were determined as the fraction of beans retained by a piano wire screen with 4.43 mm spaces. Peaberries result from abnormal fruit development (Carvalho & Monaco, 1969).

5. AA — the fraction of heavy beans retained by a no. 18 (7.15 mm) screen.

6. AB — the fraction of heavy beans retained by a no. 15 (5.95 mm) screen .

7. TT — light beans separated from AA and AB.

8. C — the fraction of beans retained by a piano wire screen with 2.90 mm spaces.

The bean fractions are expressed in terms of percentage by weight. A bean grader was used to determine the various fractions of bean sizes in each

sample i.e PB, AA, AB and C. Beans of Category AA and AB were then placed in a pneumatic separator and the percentage of light beans from AA and AB was then regarded as TT.

2.2.4. Liquor quality characters

Samples for assessment of liquor quality for each genotype were combined for each plant density rather than being treated on individual plots. This was because of the large number of genotypes included in this experiment. The assessment of liquor quality is organoleptic, and is based on a number of attributes; an explanation of these attributes is given by Devonshire (1956). The liquoring reports of the MCTA who assessed the quality of the material in this experiment included the following attributes:-

1. Quality of raw beans — the size and colour of raw beans with scores 0 — 7.

2. Quality of roast beans — the general appearance and centre cut of roast coffee with scores 0 — 5.

3. Liquor quality — assessed according to 'acidity', 'body' (both with scores of 0 — 4) and the 'flavour' (0 — 6) of the brewed coffee.

4. Overall standard — the overall evaluation of liquor quality on basis of the above attributes, with a score of 0 — 6.

In the above scoring system, O represents fine and 7 very poor. For this investigation, only liquor quality attributes (acidity, body and flavour) plus the overall standard were considered because quality, largely depends on these attributes.

2.3. Time Schedule for various recordings

Growth and yield characters mentioned in sections 2.2.1 and 2.2.2. were measured on trees at the time intervals given below:

	Characters:	Number of months from the time of field planting
growth characters	girth of stem	6, 18, 30, 48
	height of the tree	
	internode length on stem	
	primaries	
	radius of canopy	12, 24, 36, 48
	internode length (primaries)	
	leaf area	24, 48
	angle of primaries	12, 36
	extension growth	16 — 28, 30 — 42
	node production	
Yield characters	bearing primaries	12, 30, 36, 48
	bearing nodes	12, 36
	flowers per node	24, 36
	fruit set	28, 40
	berries per node	24, 36, 48
	yield	30, 42, 54

Table 2. Form of analysis of variance for a 9 x 9 lattice square

Source of variation	degrees of freedom [1]	degrees of freedom in this experiment	Mean squares
Replication	$(r-1)$	2	MS_R
Treatments	(k^2-1)	80	MS_T
Replications x Treatments	$(r-1)(k^2-1)$	160	E_T
Rows (adj)	$r(k-1)$	24	E_r
Columns (adj)	$r(k-1)$	24	E_C
Error	$(k-1)(rk-r-k-1)$	112	E_e
Total	(rk^2-1)	242	

[1] r = number of replications = 3, k = 9, giving number of treatments $k^2 = 81$

Regarding berry and bean characters, apart from single berry weight, which was determined immediately after each picking, the other characters were evaluated after processing and sundrying of the coffee samples. Liquor quality was assessed every year after processing of the samples for each of the three years of coffee harvests. Since samples were obtained from each plant density for each of the 3 years, the liquor quality determinations were regarded as 6 replications for the purpose of analysis of variance.

2.4. Analysis of the lattice square

The analysis of variance for the 9 x 9 partially balanced lattice square was according to the approach of Cochran and Cox (1957), for designs with (k + 1)/2 or fewer replications. The partitioning of this analysis of variance which was performed on values of plot means for each character is presented in Table 2.

The total sum of the squares and sums of squares for replications and for treatments were found in the usual manner. Sums of squares for rows within replications adjusted for treatments, and for columns eliminating treatments were obtained as the sums of squares of quantities L and M respectively. The remainder sum of squares, being the error. χ' and μ' were then obtained as,

$$\chi' = \frac{E_r - E_e}{k(r-1)E_r} \quad \text{and} \quad \mu' = \frac{E_c - E_e}{k(r-1)E_c}$$

For definition of E_r, E_c and E_e see Table 2. Where E_r or E_c was found to be less than E_e, the χ' or μ' was taken as zero, and if both were, then the experiment was analysed as if for randomised blocks.

The products of L's and χ', and M's μ' i.e δ's and ϵ's respectively, were used to adjust the corresponding treatment totals. The effective error mean square appropriate for testing adjusted treatment means was computed as,

$$E_e[(1 + \frac{rk}{k+1}(\lambda + \mu))]/r,$$

as is given in Table 2 (r =the number of replications = 3).

Data for most characters were initially analysed according to the lattice square. In cases where the lattice was clearly more efficient than the randomised blocks, adjusted treatments were computed. These were used for analysis of the diallel given later in sections 2.5.9 and 2.5.3.

2.5. The diallel cross

2.5.1 Introduction

The diallel mating design was chosen for this experiment because it has been shown to be a fairly efficient means of obtaining a rapid overall picture of the genetical control of various characters especially when applied to a group of inbred lines (Jinks, 1956). Crumpacker & Allard (1962) also concluded from a diallel analysis of heading date in wheat, that the results contained implications of predicting the outcome of selection, particularly the immediate effect of selection.. Kersey (1965) observed that the diallel cross was among the most informative of the mating schemes in terms of the large amount of information it provides about the genetic components of variation.

The theory and procedures for estimating various genetic parameters in the diallel cross, in terms of gene models have been discussed by Griffing (1955, 1956a, 1956b), Hayman (1954a, 1945b, 1957, 1958), Jinks & Hayman (1953), Jinks (1954, 1955), Dickinson & Jinks (1956) and Gardner & Eberhart (1966). Jinks (1956), Allard (1956a, 1956b) and Whitehouse at al. (1958) have used the diallel in early generation evaluation of parental materials in breeding programmes. Griffing (1956a, 1956b), Matzinger at al. (1959) and others have used the diallel in investigating general and specific combining ability. The application of the diallel in investigating genotype-environment interactions has been considered by Allard (1956a), Matzinger et al. (1959), Eberhart & Russell (1966, 1969), Dhillon & Singh (1977) and Cross (1977).

Analyses of the diallel cross have also been described for various types of experimental designs including those with or without parental varieties and reciprocal crosses (Hayman, 1954a; Griffing, 1956b; Jones, 1965), and differing relative degrees of replication of diagonal, parental, and off-diagonal, F_1, entries in the tables. There are also a number of alternative methods of deriving variance components according to whether maternal or reciprocal effects are assumed to be present or not in the model, and whether parental lines are a fixed sample or a random sample of a population of inbred lines (Griffing, 1956b; Wearden 1964; Hayman, 1960). Recently, methods have been given for analysis of combining ability for complete and incomplete diallels both for random and fixed models (Garretsen & Keuls, 1973; Keuls & Garretsen, 1977; Garretsen & Keuls, 1978).

For this experiment, the following alternative methods of analysis of the diallel were applied:

(1) the method of Eberhart and Russell (1966) in connection with genotype-environment interactions,
(2) the method of Griffing (1956b) modified for an incomplete cross by Garretsen & Keuls (1973, 1978),
(3) that of Jinks (1954) and Hayman (1954b) for analysis of genetic systems in terms of the diallel cross parameters.

A background and some outline of these procedures is given below.

2.5.2. Analysis of genotype-environment interactions in the diallel cross

Methods of predicting the performance of a variety over a range of environments, based on the average performance of a set of genotypes, have come to be considered as being most suitable for understanding effects of genotype-environment interactions. The method first proposed by Yates & Cochran (1938) was used by Finlay & Wilkinson (1963), who considered this approach in terms of plant breeding aspects in adaptation reactions of barley. Later on, Elberhart & Russell (1966) modified the method and applied it to maize yield trials.

Other methods which similarly consider genotype-environment as linear functions of the environment, but are based on different parameters to measure stability of genotypes have been proposed and applied to a number of situations (Perkins & Jinks, 1968; Freeman & Perkins, 1971; Perkins, 1972; Freeman, 1973; Grafius, 1969; Grafius & Thomas, 1971; Frey, 1972; Tai, 1979). The method of joint regression analysis of Eberhart & Russell (1966) has been most frequently used in a number of different crops.

As was mentioned in section 2.5.1., the study of genotype-environment interactions in this experiment was based on estimating stability parameters using a method similar to that of Eberhart & Russell (1966). The environments in this case referred to two plant densities (see section 2.1) as well as the several repeated measurements of each character recorded on trees at various stages of plant development as given in section 2.3. Environments were treated as random effects whereas the hybrids, as mentioned in section 2.1. were regarded as fixed effects.

Eberhart & Russell (1966) defined stability parameters according to the model,

$$Y_{ij} = \mu_i + \beta_i I_j + \delta_{ij}$$

Where Y_{ij} is the mean of the i^{th} genotype at the j^{th} environment ($i = 1, 2, ..., v$; $j = 1, 2 ..., n$), μ_i is the mean of the i^{th} genotype over all environments, β_i is the regression coefficient of the i^{th} genotype, δ_{ij} the deviation from regression of the same genotype at the j^{th} environment and I_j an environment index of the j^{th} environment.

The environmental index was defined for each environment as the mean of all the v genotypes at that environment. The individual hybrid values within the diallel were then regressed against the environment index to give the regression coefficient which measures the response of the i^{th} genotype to varying environments. This second stability parameter, a function of squared deviations from linear regression S^2_{di} was computed by substracting the pooled error from the deviation mean squares.

Table 3. Form of analysis of variance where genotype x environment interactions are considered.

Source of variation	Degrees of freedom(1)	Sums of squares(2)
Environments	(n−1)	$V(SSI_j)$
Genotypes	(v−1)	$\frac{1}{n}(SSY_i)$
Genotypes x Env. (linear)	(v−1)	$\sum_{i=1}^{v}[(SPY_{ij}I_j)^2/SSI_j] - \frac{1}{v}(\sum_{i=1}^{v} SPY_{ij}I_j)^2/SSI_j$
Pooled deviations	(v−1)(n−2)	$\sum_{i=1}^{v}\sum_{j=1}^{n}\delta^2_{ij}$
Pooled error	m	

(1) n = number of environments; v = number of genotypes; m = pooled error degrees of freedom which were variable

(2) $I_j = \sum_{i=1}^{v} Y_{ij}/v$; $Y_i = \sum_{j=1}^{v} Y_{ij}$, $\sum_{j=1}^{n} \delta^2_{ij}$ = deviations sum of squares for each genotype

The generalised form of analysis of variance is given in Table 3, where the sums of squares due to genotype x environments are partitioned into genotype x environments (linear) and the deviations from regression model. The data used for this analysis, had to be first subjected to the analysis according to the lattice square as given in section 2.4.

2.5.3. Analysis of the Diallel according to general and specific combining ability

The general model for an incomplete diallel among a fixed group of lines following the approach of Garretsen & Keuls (1973, 1978) can be assumed to be:

$$Y_{ijk} = \mu + \lambda^*_i + \lambda^*_j + s^*_{ij} + r^*_{ij} + e_{ijk},$$

where, Y_{ijk} is the observation of the k^{th} replication of a cross between the i^{th} female and the j^{th} male, μ is the population mean, λ^*_i and λ^*_j, the g.c.a. effects, s^*_{ij} the s.c.a. effects such that $s^*_{ij} = s^*_{ji}$, r^*_{ij}, the reciprocal effects and, e_{ijk} the random error. The (*) denotes reduced parameters. The computations are performed in part, by inversion of a number of nested matrices according to the theory of least squares.

According to Garretsen & Keuls notation, Y is the data vector, N, A, B are matrices representing the general mean, g.c.a. and s.c.a. respectively. The total sum of squares is obtained as $(Y^2_C - Y^2_N)$, sum of squares of reciprocal differences as $(Y^2_C - Y^2_B)$, sum of squares (g.c.a. + s.c.a.) as $(Y^2_B - Y^2_N)$, and sums of squares of g.c.a. and s.c.a as, $(Y^2_A - Y^2_N)$ and $(Y^2_B - Y^2_A)$ respectively. Y^2_C is the raw total sum of squares, Y^2_N the correction term, and Y^2_B, the raw sum of squares of sums of reciprocals obtained as $\hat{s}^T(B^T y)$ where, $\hat{s} = (B^T B)^{-1}(B^T y)$. Y^2_A, the uncorrected sum of squares attributable to g.c.a., is derived as $\hat{\lambda}^T(A^T y)$, where $\hat{\lambda} = (A^T A)^{-1}(A^T y)$.

The estimates of GCA effects and SCA effects are then obtained as $\lambda^*_i = \hat{\lambda}_j - \frac{1}{2}\hat{\mu}$ and $s^*_{ij} = \hat{s}_{ij} - \hat{\lambda}_i - \hat{\lambda}_j$; and the variances as $\text{var}\,\lambda^*_i = \text{var}\,\hat{\lambda}_j - \frac{1}{4}\text{var}\,\mu_i$, and $\text{var}\,s^*_{ij} = \text{var}\,\hat{s}_{ij} + \text{var}(\hat{\lambda}_i + \hat{\lambda}_j)$. $\text{Var}\,\mu = \frac{1}{N}\sigma^2_e$, and $\text{var}\,\hat{\lambda}_i$, $\text{var}\,\hat{s}_{ij}$, are the product of the error variance σ^2_e, and the corresponding elements of the respective variance-covariance matrices.

This form of analysis of variance when applied to a fixed model will only give approximate F tests especially for SCA, if the diallel is incomplete, because of lack of orthogonality of some subspaces (Garretsen & Keuls, 1978). The above procedure was however regarded as satisfactory for the present experiment, since F — testing of the effects as such was not of central importance.

Repeated measurements of a number of growth, yield and quality characters (the data also initially analysed according to the lattice square) were subjected to this form of analysis mainly to get an impression of combining ability of parents and also to determine whether reciprocal effects are an important feature of the genetic variation for these characters.

2.5.4. Analysis of genetic systems in terms of the diallel cross parameters

The analysis used was given by Hayman (1954b) Jinks (1954) and Crumpacker & Allard (1962). An outline of the procedure is as follows:

The assumptions underlying the theory for analysis of the diallel cross are:

(1) no genotype-environment interaction within locations
(2) homozygous parents
(3) diploid segregation
(4) no reciprocal differences
(5) no non-allelic gene intercations
(6) no multiple alleles
(7) uncorrelated gene distribution among the parents

In this case, A - a is regarded as a single gene for which the n parental lines in the diallel differ. The midparent value is taken as zero and A allele adds $+ d_a$, and a, $-d_a$ while the heterozygote deviates by h_a from the midparent value; u_a and v_a $(= 1 - u_a)$ are frequencies of positive and negative alleles respectively in the parents. A number of first — and second — degree statistics, which have certain genetic expectations, can be derived from the contribution of this single gene difference to the families produced in the diallel cross. If the above assumptions are valid, the situation can be generalised over all independent genes, when certain of the statistics then become:

$$V_p = D + E$$

$$W_r = \tfrac{1}{2}D - \tfrac{1}{4}F_r + \frac{1}{n}E$$

$$\overline{W}_r = \tfrac{1}{2}D - \tfrac{1}{4}F + \frac{1}{n}E$$

$$V_r = \tfrac{1}{4}D - \tfrac{1}{4}F_r + \tfrac{1}{4}H_1 + E$$

$$\overline{V}_r = \tfrac{1}{4}D - \tfrac{1}{4}F + \tfrac{1}{4}H_1 + E$$

$$V_{\bar{r}} = \tfrac{1}{4}D - \tfrac{1}{4}F + \tfrac{1}{4}H_1 - \tfrac{1}{4}H_2 + \left(\frac{n-1}{n^2}\right)E$$

$$(ML_1 - ML_0)^2 = \tfrac{1}{2}h^2 + \left(\frac{n-1}{n^2}\right)E$$

where V_p is the variance of parents, W_r the parent-offspring covariance of the r^{th} array, $\overline{W}_r$ the mean covariance of arrays, V_r the variance of the r^{th} array, $\overline{V}_r$ the mean variance of arrays, $V_{\bar{r}}$, the variance of array means and, $ML_1 - ML_o$ the difference between progeny and parental means.

The diallel genetic components are defined, using Mather & Jinks (1971) notation, as follows: $D = S4uvd^2$, $H_1 = S4uvh^2$, $H_2 = S\ 16\ u^2v^2h^2$ and $F = (S\ F_r)/n = S\ 8\ uv(u - v)dh$. D measures the additive genetic variation, H_1 and H_2 both measure dominance effects whereas F, the covariance of dominance and additive effects, gives an indication of the relative frequencies of dominant to recessive alleles in the parents. E is an estimate of the environmental variance, obtained in this study as the replication x genotype mean squares (= E_T in Table 2), and n = number of parents.

Failure of any of the assumptions will invalidate the analysis of the diallel in some degree. The validity of some of the assumptions can be ascertained from available knowledge of *C. arabica* and to some extent, from information on the parents involved in the diallel. Regarding the other assumptions the judgement would depend on various other statistical tests to which the data for different characters were to be subjected during the analysis.

The amount of natural outcrossing in arabica coffee is fairly low usually less than 10% (Carvalho & Monaco, 1962). In addition, a number of varieties included in the diallel represent individual tree selections while the other varieties also show remarkable uniformity. From this, it could be concluded that most of the parents involved in the diallel are expected to be fairly homozygous. Regarding diploid segregation, the type of inheritance of tetraploid *C. arabica* is disomic and in meiosis only bivalents are formed (Carvalho & Monaco, 1969).

The absence of reciprocal effects will be confirmed from results of analysis of the form given in section 2.5.3. The assumption of absence of genotype-environment interactions within locations may not be strictly valid for some characters especially on basis of individual plants. This however, is not expected to introduce a serious bias into the genetic analysis especially when the analysis is based on plot means. Assumptions of no epistasis, no multiple alleles and uncorrelated gene distribution have to be tested from the actual analysis of the data.

One important relationship which is used to verify the validity of the assumptions of the diallel cross theory, is that between the variance V_r and covariance W_r of members of the same array. For a single gene case, it can be shown that substituting aa for AA will change both V_r and W_r by the same quantity $4\ u_a v_a d_a h_a$. In other words $W_r - V_r$ is constant over arrays. The same relation can be extended to any arbitrary number of independent genes i.e. the regression of W_r on V_r is expected to be a straight line of unit slope. The constancy of $W_r - V_r$ can also be tested by analysis of variance of $W_r - V_r$, a significant line effect indicating failure of the hypotheses. In addition, when the assumptions of the diallel are valid, the W_r intercept on the (W_r, V_r) graph indicates average level of dominance in the parents since when $V_r = 0$, $W_r = \frac{1}{4}(D - H_1)$.

This method of analysis of the diallel was performed on data obtained from a number of selected characters to determine the usefulness and applicability of this procedure in understanding the genetic basis of parental variation for these characters. The data used for this analysis were not adjusted according to the analysis of the lattice design, but were considered as for a randomised block design in three replications.

Apart from testing the validity of the diallel assumptions, this analysis was used to give estimates of the genetic components D, H_1, H_2, F and h^2. The following information was also derived from the analysis: average dominance estimated as $H_1/D(= Suvh^2/Suvd^2)$, the average degree of dominance, as $\sqrt{(H_1/D)}$ = $(\bar{h}/\bar{d})$ and the direction of dominance from the sign of $\bar{F} - \bar{P}$. The average frequency of negative versus positive alleles in the parents was obtained as $\frac{1}{4}H_2/H_1(= Su^2v^2h^2/Suvh^2 = \bar{u}\bar{v})$, and frequencies of dominant and recessive alleles, as indicated by the sign of F. Mather's Effective factor was estimated as $K = h^2/\frac{1}{4}H_2(= (Suvh)^2/Su^2v^2h^2$; the value will be underestimated unless the h effects of all genes are equal in size and sign, and the distribution of genes is uncorrelated. The above information regards only genes exhibiting dominance.

For each character, heritability in the narrow sense h^2_n and broad sense h^2_b was estimated, according to Mather & Jinks (1971), as,

$$h^2_n = \frac{\frac{1}{2}D_R}{\frac{1}{2}D_R + \frac{1}{4}H_R + E} = \frac{\frac{1}{2}D + \frac{1}{2}H_1 - \frac{1}{2}H_2 - \frac{1}{2}F}{\frac{1}{2}D + \frac{1}{2}H_1 - \frac{1}{4}H_2 - \frac{1}{2}F + E}$$

and

$$h^2_n = \frac{\frac{1}{2}D_R + \frac{1}{4}H_R}{\frac{1}{2}D_R + \frac{1}{4}H_R + E} = \frac{\frac{1}{2}D + \frac{1}{2}H_1 - \frac{1}{4}H_2 - F}{\frac{1}{2}D + \frac{1}{2}H_1 - \frac{1}{4}H_2 - \frac{1}{2}F + E}$$

The above estimates of heritability are on basis of plot means. Estimates appropriate for individual trees are identical in terms of genetic components except for the presence of linkage, residual heterozygosity in parents or correlated gene distribution. The error variance for individual trees however, will be *m* times the environmental component for plot means, E, where *m* (= 4) is the number of trees per plot.

3. VARIATION AMONG GENOTYPES FOR GROWTH AND YIELD CHARACTERS

3.1. Introduction

As is evident from section 1.4., improved yield is still one of the major goals of most breeding programmes in *C. arabica*. In a number of these breeding programmes attention is also being given to development of compact genotypes. Yield in coffee has been shown to depend in some degree on the vegetative vigour of the tree (Machado, 1952; Dhaliwal, 1968; Srinivasan, 1969). Compact growth on the other hand, is expected to be reflected in genotypes that are better adapted to high density planting. A combination of high yield of individual trees and compact growth, offers the best prospect for yield improvement in arabica coffee. It is important therefore, that growth and yield characters are also considered in evaluation of individual genotypes for productivity. In such evaluation programme, it is further necessary to identify among the various characters those which deserve most attention.

In a perennial tree crop like coffee, a number of successive measurements of a given character are often taken on the same tree during different stages of plant development. For some characters, it is useful to define the most suitable age of a tree when such characters can be measured most easily and with the utmost accurancy. For other characters however, a better indication of the genotypic value of an individual will be obtained from the mean values of successive measurements of each character taken over several seasons or years. In a breeding programme especially aimed at yield improvement, information on some of these aspects is of immediate practical value in enhancing efficiency of selection.

From yet another point of view, the behaviour of genotypes as measured on basis of growth and yield characters over several differing environments. is important in investigating the effects of genotype-environment interactions. Genotype–environment interactions are responsible for the failure of genotypes to have the same relative performance in different environments. As a consequence, overall progress from selection for superior types will often be reduced in the presence of large effects of genotype-environment interactions (Comstock & Moll, 1963).

In coffee like many other perennial crops, there is a marked tendency for yield fluctuations from year to year, as a result of successive vegetative-reproductive cycles, but also due to genotype-environment interactions. More specifically, genotype x locality interactions are a fairly common feature in coffee (Monaco & Carvalho, 1975; Monaco, 1977; Capot, 1978). However, inherent differences have been observed among certain coffee selections in their yield response to varying environments (Srinivasan & Vishveshwara, 1978). Furthermore, it may also be possible that some of the

growth and yield characters have an influence on yield stability in coffee as has been reported in a number of other crops (Zuber et al., 1960; Collins et al., 1965; Prior & Russell, 1975). An investigation of effects of genotype-environment interactions may provide information on whether it is possible in a breeding programme to select for genotypes which combine improved productivity with yield stability.

This chapter is concerned with a study of the above aspects among the genotypes of the diallel cross. Consideration is first given to the phenotypic variation of repeated measurements of growth and yield characters. Secondly, the method of Eberhart & Russell (1966) as given in section 2.5.2. is applied to the data, in conjunction with that of Griffing (1956) as modified by Garrestsen & Keuls (1973, 1978) (see section 1.5.3.): 1) to investigate the effects of genotype-environment interactions and the inheritance of stability parameters, for growth and yield characters, 2) to determine the value of parents in hybrid combinations in terms of their potential for producing high yielding stable hybrids and, 3) to examine the relationship between various growth and yield characters with yield stability.

3.2. Phenotypic variation for repeated measurements of growth and yield characters

Data obtained from a single measurement of each characters (see section 2.3.) in each plant density were analysed separately according to the lattice square (section 2.4.). In Table 5, the overall mean represents the mean of all genotypes for a particular measurement of a given character in each plant density. The standard errors are for the means of each genotype over the 3 replications, and the F values indicate the significance level of genotypic effects as tested against the appropriate error mean squares (see Table 2).

Repeatability in this context represents the proportion of the total phenotypic variance for several measurements of each character, which is due to genotypic differences. The form of analysis of variance for estimating the repeatability is given in Table 4.

Table 4. Form of analysis of variance for deriving repeatability(2) coefficients for growth and yield characters.

Source of variation	Degrees of freedom(1)	Expectations of mean squares
Environments	(e—1)	$\sigma^2_w + r\sigma^2_{gxe} + rg\sigma^2_e$
Genotypes	(g—1)	$\sigma^2_w + r\sigma^2_{gxe} + re\sigma^2_g$
Genotypes x env.	(g—1)(e—1)	$\sigma^2_w + r\sigma^2_{gxe}$
Pooled error	m	σ^2_w

(1) e = number of environments, g = number of genotypes, and m = error of df were variable for characters where all measurements were not adjusted, m = e(g—1)(r—1) where r = number of replications = 3.

(2) R (plot basis) = $\dfrac{\sigma^2_g}{\sigma^2_g + \sigma^2_{gxe} + \sigma^2_w}$

R (individual tree basis) = $\dfrac{\sigma^2_g}{\sigma^2_g + \sigma^2_{gxe} + n\sigma^2_w}$

where n = number of trees/plot = 4

In the same table the years and plant density effects are considered as the environments item. The variance due to environments was not pooled with that of the rest of the error items as is normal in estimating repeatability in the conventional sense. This was because, variation due to environments for most growth and yield characters is a result of enlargment of a tree or part of a tree with time and also of the changes in morphology of a tree brought about by plant competition. Such effects however, are not important as far as the performance, over several years and plant density, of a given genotype relative to other genotypes, is concerned. As can be seen in Table 4, though variation due to years and plant densities is disregarded, effects of interactions between genotypes and environments are taken into account in deriving the repeatability coefficients. These coefficients therefore still give some measure of the correlation between various repeated measurements of the same genotype.

Results in Table 5 indicate that the genotypes which were included in the diallel differed significantly with respect to each of the several repeated measurements of various growth and yield characters. The only exception in this respect was the number of flowers per node for the first measurement at the higher plant density.

Table 5. Phenotypic variation of repeated measurements of growth and yield characters in a diallel cross among 11 varieties of *C. arabica*. First line 3333 trees ha^{-1}; second line 6667 trees ha^{-1}.

Character	Overall means and standard errors of phenotypic means								F values and P(3)				repeatability	
	Year	1	2		3		4		1	2	3	4	$r^{(1)}$	$r^{(2)}$
1. grith	6.7,	0.22	14.1,	0.38	18.2,	0.44	22.3,	0.44	4.8***	13.6***	18.5***	25.7***	0.65	0.46
	7.0,	0.18	13.7,	0.31	17.5,	0.34	21.1,	0.40	9.4***	14.9***	22.5***	26.7***		
2. height	84.0,	2.27	150.6,	3.53	197.7,	5.34	265.3,	7.17	36.7***	33.0***	25.3***	27.7***	0.70	0.52
	87.3,	2.72	166.1,	4.41	233.3,	10.24	304.7,	8.60	24.5***	37.5***	8.9***	26.3***		
3. internode	4.4,	0.12	5.2,	0.12	4.9,	0.16	4.9,	0.16	37.8***	40.5***	22.9***	21.9***	0.80	0.63
	4.6,	0.12	5.5,	0.12	5.3,	0.24	5.4,	0.17	36.0***	53.9***	12.5***	24.6***		
4. primaries	25.8,	0.85	54.7,	1.24	76.7,	1.92	104.1,	2.73	6.7***	10.9***	6.2***	4.7***	0.46	0.21
	26.9,	1.00	58.3,	1.49	82.8,	2.15	108.1,	3.30	7.0***	9.8***	6.7***	3.9***		
5. radius of canopy	49.8,	1.74	87.9,	3.00	94.4,	3.00	102.7,	2.86	11.3***	11.3***	13.1***	7.9***	0.65	0.40
	49.8,	2.10	88.2,	3.10	93.8,	3.40	96.9,	3.20	11.8***	11.5***	9.4***	6.9***		
6. internode length (pr)	3.9,	0.12	3.1,	0.10,	3.0,	0.09	3.0,	0.09	17.8***	12.9***	14.6***	12.4***	0.75	0.40
	4.1,	0.13	3.4,	0.10	3.4,	0.12	3.5,	0.11	16.7***	12.9***	11.6***	13.8***		
7. leaf area			48.9,	2.63			57.0,	4.29		8.7***		12.1***	0.43	0.26
			49.8,	2.70			62.8,	5.21		24.8***		8.7***		
8. angle	51.5,	2.28			57.3,	2.23			6.7***		6.0***		0.61	0.30
	50.5,	2.10			56.8,	2.47			6.7***		6.1***			
9. extension growth			34.8,	1.57	30.1,	1.96				5.5***	5.0***		0.20	0.06
			37.7,	1.72	19.1,	2.59				8.5***	3.0***			
10. node production			14.3,	0.39	10.6,	0.62				5.8***	2.8***		0.26	0.10
			13.9,	0.42	6.4,	0.79				8.1***	3.4***			
11. bearing primaries	17.3,	1.14	46.6,	1.38	68.8,	2.56	91.3,	2.92	3.8***	8.8***	4.5***	4.0***	0.40	0.16
	18.8,	0.98,	49.3,	1.50	77.7,	2.70	93.3,	3.77	18.2***	9.0***	3.1***	3.5***		
12. bearing nodes	13.9,	2.21			54.8,	4.05			4.8***		1.2		0.25	0.08
	15.4,	2.63			58.1,	3.38			4.4***		2.1**			
13. flowers per node			9.1,	1.02	12.7,	0.79				2.8***	3.9***		0.10	0.03
			10.3,	1.44	11.1,	0.88				0.7	2.8***			
14. fruit set			56.3,	5.30,	54.5,	3.95				3.9***	2.6***		0.19	0.06
			50.0,	5.00	42.6,	3.98				2.5**	2.0***			
15. berries per node			6.2,	0.61	5.6,	0.64	5.6,	0.47		2.8***	2.5***	2.8***	0.22	0.07
			6.9,	0.83	5.7,	0.73	6.1,	0.60		2.7***	2.0**	2.1**		
16. yield of cherry			7.5,	0.82	3.5,	0.54	9.0,	0.98		5.1****	3.5***	4.2***	0.29	0.11
			4.9,	0.46	2.6,	0.41	2.8,	0.45		6.9****	4.4***	4.6***		
17. yield of clean coffee			1.1,	0.13	0.5,	0.08	1.4,	0.16		5.3**	3.9***	4.9***	0.31	0.12
			0.7,	0.09	0.4,	0.06	0.4,	0.08		3.6***	5.8***	4.7***		

The error Df were always equal to or more than 112, or equal to 160 for measurements where the lattice square was roughly equal in efficiency to the randomised block design.

(1) repeatability on plot mean basis.
(2) repeatability on individual tree basis.
(3) *** $P < 0.001$; ** $P > 0.001, < 0.010$; * $P > 0.010, < 0.050$; this notation applies to all other tables unless indicated otherwise

It is also evident (See F values and P in Table 5) that the amount of variation between genotypes for some growth characters (eg girth, height, radius of canopy, extension growth and node production) depended on the age of plant when measurements were taken. For other characters (internode length on primaries and berries per node) the variation among genotypes remained fairly constant regardless of the time of measurement. There are also other characters especially yield characters where this variation fluctuated considerably both between measurements and between plant densities. Repeatability for most growth characters was particularly high, especially on plot mean basis; the exceptions being extension growth and node production. In contrast most yield characters had in general rather low repeatability.

It can be concluded therefore, that a number of growth characters, in particular height, girth, internode length on the main stem and on primaries, are worth inclusion in evaluation programmes of various coffee materials. These characters, in addition to having high repeatability, already show maximum genotypic differences even when measured on fairly young coffee trees (See F values in Table 5). Most yield characters however, present considerable difficulty in measurement in terms of sampling, physical effort and time. Yield in particular requires many years of evaluation to get a good indication of the productivity of a particular genotype. Some yield characters are influenced even more by external environment than yield itself as a consequence, even multiple measurements repeated over time give little or no apparent gain in the accurancy of their assessment (see repeatabilities in Table 5). Such characters however are still important in studies related to components of yield, especially in physiological studies.

Regarding effects of plant density on growth and yield characters, it is evident from Table 5 that the overall means, at the higher plant density as compared to the lower density were consistently higher for most of the characters.. The exceptions in this case were later measurements of girth, angle of insertion of primaries, radius of canopy, extension growth and node production. Of most interest however, is that the yield of individual trees at the higher plant density was about half of that at the lower plant density. This can be accounted for partly by the fact that trees at the higher plant density tend to have fewer nodes on primaries. This difference becomes more pronounced as plant competition increases with time. It is clear from Table 5 that increased plant density restrict not only extension growth but also the number of new nodes formed on each young primary. In addition it was observed in the field, that at the higher plant density the crop on the trees was carried mainly on the upermost primaries, the rest of the tree being almost bare. This is due to poor light penetration through the canopy, which results in low flower bud initiation in the middle and lower sections of the tree. This eventually results in considerable reduction in yield per tree at the higher plant density. The magnitude of this yield reduction will vary according to genotypes, especially the way they interact with density. Such effects of interaction between genotypes and environments are considered in the next section.

3.3. Genotype-environment interactions

Results of analysis of variance involving genotype-environment interactions for various growth and yield characters are presented in Table 6. The number of environments is equivalent to the number of repeated measurements for each character multiplied by 2 (the number of plant densities). This number is given in brackets after each character in the Table. Differences due to genotypes, heterogeneity of their linear regression onto environments and pooled deviations were significant practically for all the traits studied. There was however, lack of significant variation for regressions among genotypes for angle of insertion and flowers per node, suggesting the absence of genetic variation for linear response with respect to these characters in the population. In addition, the pooled deviations item was not significant for node production and % bearing nodes but the linear component for same characters was significant, hence the variation among genotypes for these characters was mainly due to the linear component of GXE interactions rather than the non-linear fraction.

Table 6. Analysis of variance for growth and yield characters.

Source of variation	Df[1]	Mean squares and P			
		girth (8)[2]	height (8)	int. length (st.) (8)	primaries (8)
Genotypes (G)	80	14.50***	5176.52***	4.69***	119.92***
G x environ. (linear)	80	3.34***	870.32***	0.09***	16.58***
Pooled deviations	480	0.25***	92.47**	0.04*	7.54**
Pooled error		0.12 (992)	37.37 (1232)	0.03 (1232)	3.88 (944)
		canopy radius (8)	int. length (Pr.) (8)	bearing primaries (8)	
Genotypes (G)	80	518.30***	1.12***	114.94***	
G x environ. (linear)	80	35.40***	0.07***	19.43***	
Pooled deviations	480	17.70***	0.02**	8.51*	
Pooled error		6.95 (944)	0.01 (1040)	5.33 (1040)	
		leaf area (4)	angle (4)	extension growth (4)	node production (4)
Genotypes (G)	80	434.98***	113.78***	30.79***	2.97***
G x environ. (linear)	80	160.67***	7.74	24.95***	1.46***
Pooled deviations	160	45.53***	6.23	10.21***	0.56
Pooled error		14.95 (448)	5.21 (496)	3.99 (448)	0.34 (496)
		bearing nodes (4)	flowers/node (4)	fruit set (4)	
Genotypes (G)	80	53.31***	3.76**	106.51***	
G x environ. (linear)	80	21.32**	2.00	46.47**	
Pooled deviations	160	11.53	1.87	39.76***	
Pooled error		9.89 (448)	1.62 (496)	21.28 (448)	
		berries/node (6)	yield (cherry) (6)	yield (clean coffee) (6)	
Genotypes (G)	80	3.09***	5.88***	0.16***	
G x environ. (linear)	80	1.23***	2.36***	0.06***	
Pooled deviations	320	0.55*	0.89**	0.02**	
Pooled error		0.43 (720)	0.47 (768)	0.01 (816)	

[1] Pooled error Df in brackets after each pooled error mean squares.
[2] Number of environments in brackets.

Table 7. Analysis of variance for incomplete diallel for selected growth and yield characters.

Source of Variation	Df[1]	Mean squares and P			
		girth	height	int. length (St.)	canopy radius
GCA	10	12.25***	4376.35***	4.11***	418.86***
SCA	55	0.38***	144.86***	0.11***	21.21***
REC	15	0.09	7.43	0.01	5.86*
Error		0.09 (560)	25.45 (560)	0.01 (560)	3.00 (560)
		int. length (Pr.)	bearing primaries	flowers/ node	berries/ node
GCA	10	0.86***	75.53***	2.93***	1.72***
SCA	55	0.04***	6.69***	0.80**	0.40***
REC	15	0.01**	1.76	0.17	0.03
Error		0.003 (560)	1.26 (560)	0.48 (240)	0.11 (400)
		yield of cherry	yield of clean coffee		
GCA	10	3.45***	0.110***		
SCA	55	0.76***	0.020***		
REC	15	0.09	0.002		
Error		0.19 (400)	0.005 (400)		

[1] The error Df *of* in brackets

With regard to relative stability of different characters over environments, a comparison between genotypic mean squares and the corresponding pooled genotype deviation mean squares (in Table 6) shows that among growth characters internode length on the stem, girth, internode length on primaries, and height, were most stable in terms of their predictability in different environments. On the other hand, extension growth and node production were relatively most unstable. The number of bearing primaries, among yield characters, was most stable with yield of clean coffee being intermediate. In general, growth characters were more stable than yield characters. This confirms the result in section 3.2. Though many of the yield characters were measured over fewer environments, it is doubtful whether this would make much difference.

For many of the characters considered, the linear component represented a considerably large part of the total genotype-environment interactions. For instance, it accounted for over 69%, 61% and 40% of the total sum of squares due to genotype-environment interactions for girth, height and yield respectively.

3.4. Combining ability and stability of parental varieties and their hybrids

Both general combining ability (GCA) and specific combining ability (SCA) were highly significant for all the selected characters (Table 7) , GCA mean squares being larger than SCA mean squares. If however, the expectations of mean squaresof these components are taken into account, then the variance components due to GCA and SCA appear to be roughly of the same magnitude for most of these characters.

Reciprocal effects were not significant for most of the characters. They were significant however for canopy radius and internode length on primaries. Reciprocal differences for these two characters were mainly due to one particular cross between Hibrido de Timor and Erecta. Exclusion of this particular cross resulted in the overall reciprocal effects being less than the error mean squares. In addition, there existed already some uncertainty about the identity of this cross. It can be concluded therefore, that for most of the growth and yield characters considered, reciprocal differences were of trivial importance.

Table 8. Parental means ($\bar{x}$) general combining ability effects (GCAE), and stability parameters (b and s^2_d) for selected growth and yield characters.

Variety	$\bar{x}$	GCAE	b	s^2_d	$\bar{x}$	GCAE	b	s^2_d
	girth				height			
1.Caturra	12.02	−2.33***	0.71 ± 0.03	0.06	122.5	−46.5***	0.65 ± 0.03	−2.0
2. Pretoria	16.20	0.72***	1.11 ± 0.11	2.59***	210.9	12.9***	1.15 ± 0.03	−6.2
3. Erecta	15.63	0.32	1.06 ± 0.02	−0.05	195.2	6.7***	1.03 ± 0.02	−10.9
4. SL28	15.81	0.56***	1.05 ± 0.05	0.50***	198.5	6.1***	1.04 ± 0.04	39.2**
5. Mokka	13.49	−0.23	0.97 ± 0.03	0.17***	155.9	−3.9***	0.78 ± 0.04	45.0***
6. K7	16.07	0.70***	1.12 ± 0.05	0.51***	189.0	4.8***	1.07 ± 0.02	−10.2
7. H. de Timor	14.78	0.24**	1.06 ± 0.02	0.01	199.3	9.2***	1.10 ± 0.02	−19.7
8. Padang	14.71	0.12	0.98 ± 0.03	0.04	191.3	6.9***	1.01 ± 0.02	−18.2
9. Laurina	12.32	−0.47***	0.76 ± 0.06	0.73***	132.1	−2.5	0.68 ± 0.06	146.8***
10. R. Sudan	14.31	0.05	0.98 ± 0.04	0.24	171.0	1.7	0.81 ± 0.04	27.5***
11. SL34	15.79	0.34***	1.06 ± 0.02	−0.05	195.9	4.5***	1.07 ± 0.02	−14.4
	canopy radius				internode length (pr)			
1. Caturra	67.45	−9.56***	0.83 ± 0.05	−0.33	2.81	−0.39***	0.85 ± 0.09	0.002
2. Pretoria	85.10	3.89***	1.00 ± 0.10	24.23***	3.76	0.30***	0.83 ± 0.14	0.012**
3. Erecta	94.30	4.79***	1.19 ± 0.05	1.49	3.60	0.09***	1.13 ± 0.14	0.012**
4. SL28	89.66	4.04***	1.08 ± 0.05	0.13	3.72	0.19***	1.20 ± 0.17	0.014** *
5. Mokka	65.91	−3.11***	1.06 ± 0.08	14.43***	2.26	−0.30***	0.22 ± 0.12	0.006
6. K7	89.16	5.54***	1.17 ± 0.03	−3.42	3.56	0.14***	1.00 ± 0.10	0.009
7. H. de Timor	82.13	2.04***	1.05 ± 0.08	14.14***	3.72	0.18***	0.90 ± 0.06	−0.006
8. Padang	73.38	−2.40***	0.89 ± 0.05	1.38	3.18	−0.06***	0.84 ± 0.10	0.000
9. Laurina	54.12	−7.53***	0.69 ± 0.20	117.56***	1.95	−0.25***	0.17 ± 0.24	0.058***
10. R. Sudan	69.36	−1.20**	1.07 ± 0.13	41.33***	3.04	−0.03**	0.52 ± 0.11	0.004
11. SL34	85.65	3.56***	0.99 ± 0.05	−0.43	3.76	0.18***	1.18 ± 0.18	0.009
	bearing primaries				berries per node			
1. Caturra	53.53	0.36	0.91 ± 0.04	7.25***	5.72	− 0.04	2.12 ± 0.46	−0.15
2. Pretoria	51.97	−3.68	0.97 ± 0.02	−3.80	5.11	− 0.36***	1.91 ± 0.71	0.23
3. Erecta	56.88	0.99***	1.04 ± 0.03	−0.76	5.27	0.04	0.63 ± 0.70	0.21
4. SL28	53.99	−1.64***	0.91 ± 0.04	5.09	6.02	0.36***	0.14 ± 0.71	0.22
5. Mokka	46.93	0.25	0.93 ± 0.06	16.10***	3.66	−0.50***	−0.79 ± 0.50	−0.11
6. K7	58.96	0.02	1.11 ± 0.05	12.66***	5.56	−0.02	0.00 ± 0.28	−0.33
7. H. de Timor	55.41	0.51*	1.02 ± 0.04	6.65***	5.48	0.06	1.19 ± 0.14	−0.40
8. Padang	60.05	2.36***	1.06 ± 0.02	−2.50	5.49	0.13	1.64 ± 0.76	0.32
9. Laurina	68.82	4.89***	1.01 ± 0.08	30.99	4.01	0.23**	0.85 ± 0.63	0.09
10. R. Sudan	49.49	−2.81***	0.87 ± 0.04	4.23	3.71	−0.46***	0.72 ± 1.12	1.21***
11. SL34	55.83	−1.13***	0.99 ± 0.03	−0.48	7.12	0.62***	1.71 ± 0.43	−0.18
	yield of cherry				yield clean coffee			
1. Caturra	4.84	0.05	1.18 ± 0.21	1.01***	0.69	−0.00	1.19 ± 0.18	0.015***
2. Pretoria	4.23	−0.33***	0.76 ± 0.22	1.18***	0.64	−0.02	0.83 ± 0.23	0.033***
3. Erecta	4.39	−0.00	0.79 ± 0.12	0.02	0.59	−0.00	0.68 ± 0.11	−0.002
4. SL28	5.41	0.52***	1.29 ± 0.08	−0.25	0.79	0.08***	1.28 ± 0.08	−0.007
5. Mokka	1.43	−0.88***	0.41 ± 0.10	−0.12	0.20	−0.15***	0.29 ± 0.09	−0.005
6. K7	4.16	0.02	0.78 ± 0.21	0.98***	0.63	0.01	0.81 ± 0.24	0.036***
7. H. de Timor	3.77	−0.07	0.72 ± 0.14	0.21	0.57	−0.00	0.76 ± 0.13	0.001
8. Padang	5.86	0.76***	1.05 ± 0.09	−0.18	0.96	0.17	1.27 ± 0.14	0.006
9. Laurina	2.49	0.06	0.40 ± 0.12	0.07	0.26	0.01	0.34 ± 0.12	0.000
10. R. Sudan	1.55	−0.55***	0.26 ± 0.05	−0.40	0.20	−0.08***	0.21 ± 0.04	−0.010
11. SL34	5.64	0.48***	1.27 ± 0.21	1.03***	0.83	0.06***	1.20 ± 0.18	0.016***

Parental means, GCA effects and stability for a number of growth and yield characters are given in Table 8. Among the parents, Caturra had low mean performance ($\bar{x}$), below average linear response (b=1) and deviation mean squares not differentfrom zero ($S^2_d = 0$) for all the growth characters considered. In other words Caturra was the most suitable parent for compact growth habit since it was relatively less sensitive, on basis of these characters, to increased plant competition. In addition, it appeared to impart the compact habit and general stability to most of its F_1 hybrids.

It is also clear from this table, that the varietieties not only differed in their mean performance and GCA effects for these yield and growth characters, but also varied considerably in the expression of the same characters in different environments.

Table 9 gives the mean performance, SCA and stability of the 6 most productive hybrids. Compared to the average performance of all the F_1's these hybrids except for two, were more vigorous in their growth habit, and had more bearing primaries, except for one hybrid, as well as a higher number of berries per node. There was however, considerable variation in combining ability effects and in stability of these hybrids in different environments.

The relation between yield and stability of the parents is also shown in figures 2a (for yield of cherry) and 2b (for clean coffee). On basis of average standard deviation, all the parents with the exception of Padang (for cherry yield), had linear regression coefficients at least one standard deviation above or below the unit regression (b = 1). Hence for yield of cherry, Padang can be regarded as the most stable variety for it combines high yield with average linear response (b = 1) and minium deviation from regression (S^2_d = 0). The rest of the high yielders had either above average

Table 9. The means (x), specific combining ability effects (SCAE) and stability parameters (b, s^2_d), for selected growth and yield characters of the 6 highest yielding hybrids (on basis of clean coffee).

F_1	$\bar{x}$	SCAE	b	s^2_d	$\bar{x}$	SCAE	b	s^2_d
		girth				height		
1. Pad x SL34	15.59	0.01	1.03 ± 0.03	0.08	199.5	0.42	1.06 ± 0.02	-26.1
2. Pad x SL28	15.93	0.13	1.05 ± 0.02	−0.02	200.5	−0.13	1.03 ± 0.04	29.3
3. HdT x SL28	16.32	0.15	1.05 ± 0.03	0.07	205.4	0.82	1.07 ± 0.05	87.3***
4. Lau x K7	16.02	0.67**	1.06 ± 0.02	−0.01	204.0	12.04**	1.08 ± 0.03	1.6
5. Lau x HdT	15.04	0.16	1.01 ± 0.02	−0.04	206.8	12.40**	1.13 ± 0.04	47.5**
6. Lau x Pad	15.09	0.33	0.98 ± 0.03	0.09	198.3	6.19**	0.98 ± 0.05	62.9**
Mean of all F_1's	15.20				189.6			
		canopy radius				internode length (pr)		
1. Pad x SL34	84.5	0.76	1.02 ± 0.07	6.13	3.48	−0.05	1.05 ± 0.10	−0.000
2. Pad x SL28	86.3	2.08	1.02 ± 0.03	−4.74	3.50	−0.04	0.95 ± 0.12	0.006
3. HdT x SL28	87.4	−0.72	0.96 ± 0.05	1.67	3.90	0.11***	1.40 ± 0.15	0.014
4. Lau x K7	86.6	6.06***	1.07 ± 0.05	1.02	3.46	0.14***	1.14 ± 0.06	−0.007
5. Lau x HdT	79.3	2.25	1.00 ± 0.05	1.09	3.42	0.07	1.05 ± 0.13	0.010
6. Lau x Pad	72.5	−0.13	0.84 ± 0.07	10.29**	3.27	0.17***	0.99 ± 0.07	−0.004
Mean of all F_1's	83.5				3.46			
		bearing primaries				berries per node		
1. Pad x SL34	61.79	2.77**	1.08 ± 0.03	−0.49	6.40	−0.35	0.84 ± 0.68	0.18
2. Pad x SL28	59.19	0.68	1.03 ± 0.03	0.83	6.49	−0.00	1.69 ± 0.90	0.64**
3. HdT x SL28	56.21	−0.40	0.95 ± 0.04	4.86	7.06	0.40	−0.54 ± 0.89	0.60**
4. Lau x K7	61.20	−1.51	1.02 ± 0.03	0.88	6.69	0.48	0.76 ± 0.67	0.16
5. Lau x HdT	65.64	2.44*	1.11 ± 0.02	−2.51	7.33	1.02**	1.28 ± 0.50	−0.10
6. Lau x Pad	64.65	−0.39	1.09 ± 0.04	2.91	6.23	−0.14	0.83 ± 0.28	0.33
Mean of all F_1's	58.16				6.12			
		yield of cherry				yield clean coffee		
1. Pad x SL34	6.69	0.88	1.46 ± 0.11	−0.03	1.04	0.07	1.69 ± 0.10	−0.003
2. Pad x SL28	6.53	0.18	1.44 ± 0.12	0.05	1.00	0.02	1.41 ± 0.10	−0.003
3. HdT x SL28	6.76	0.89***	0.96 ± 0.18	0.64**	0.98	0.14**	1.02 ± 0.20	0.023**
4. Lau x K7	6.62	1.47***	1.16 ± 0.15	0.28	0.98	0.22***	1.17 ± 0.11	−0.001
5. Lau x HdT	6.48	1.38***	1.00 ± 0.11	−0.07	0.96	0.24***	1.07 ± 0.13	0.003
6. Lau x Pad	6.22	−0.15	1.10 ± 0.07	−0.31	0.98	0.06	1,15 b 0.08	−0.006
Mean of all F_1's	5.26				0.77			

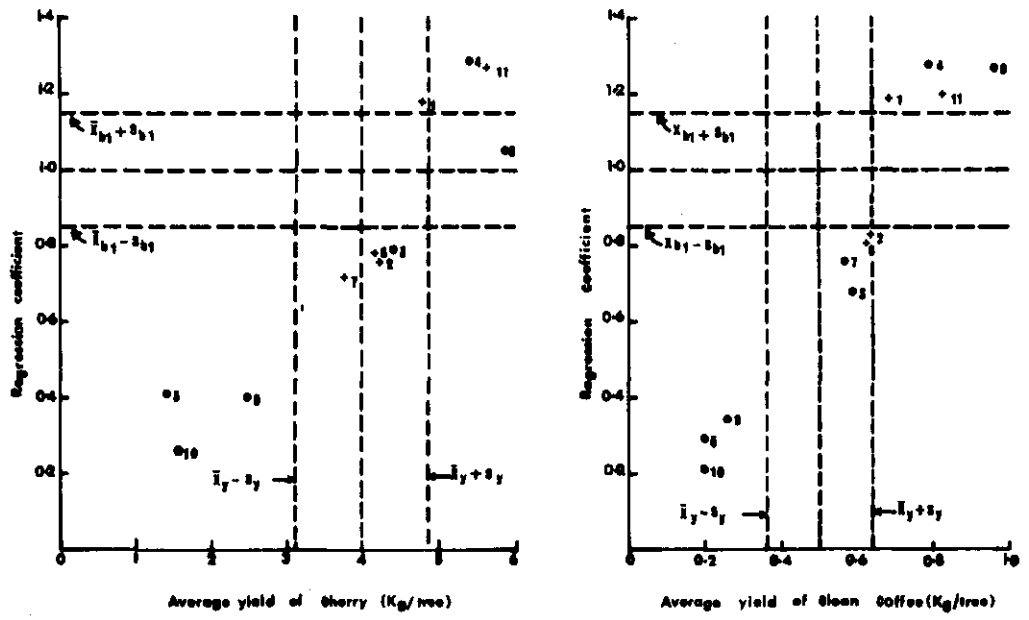


Fig. 2a The relation of yield of cherry and stability of parents. + s^2_d significant ($P < 0.05$); • s^2_d not significant.

2b The relation of yield clean coffee and stability of parents. + s^2_d significant ($P < 0.05$); • s^2_d not significant.

linear response and, or significant deviations from regression. The lowest yielding parents in contrast, had below average linear response and deviation mean squares not different from zero.

Regarding the relation between yield and stability of F_1 hybrids (Figures 3a & 3b for cherry and clean coffee respectively), the striking feature in contrast to the relation between parental yield and stability (Figure 2a and 2b), is the cluster of more points around the regression coefficient 1. For yield of cherry and clean coffee respectively, 60 and 50% of all the F_1 regressions were within 1 standard deviation of unit regression coefficient. This indicates, that the F_1's were more homogeneous in their linear response than the parents, under these environments. Furthermore, this suggests that for yield of cherry and clean coffee, the F_1's were more stable than their parents in terms of linear response to varying environments. In addition, more parents recorded significant deviations from linear regression for yield of cherry and clean coffee (45 & 36% of the parents) than did the F_1's (25 & 27%). This again indicates that the hybrids were to some extent more stable in terms of specific sensitivity to environments, than the parents.

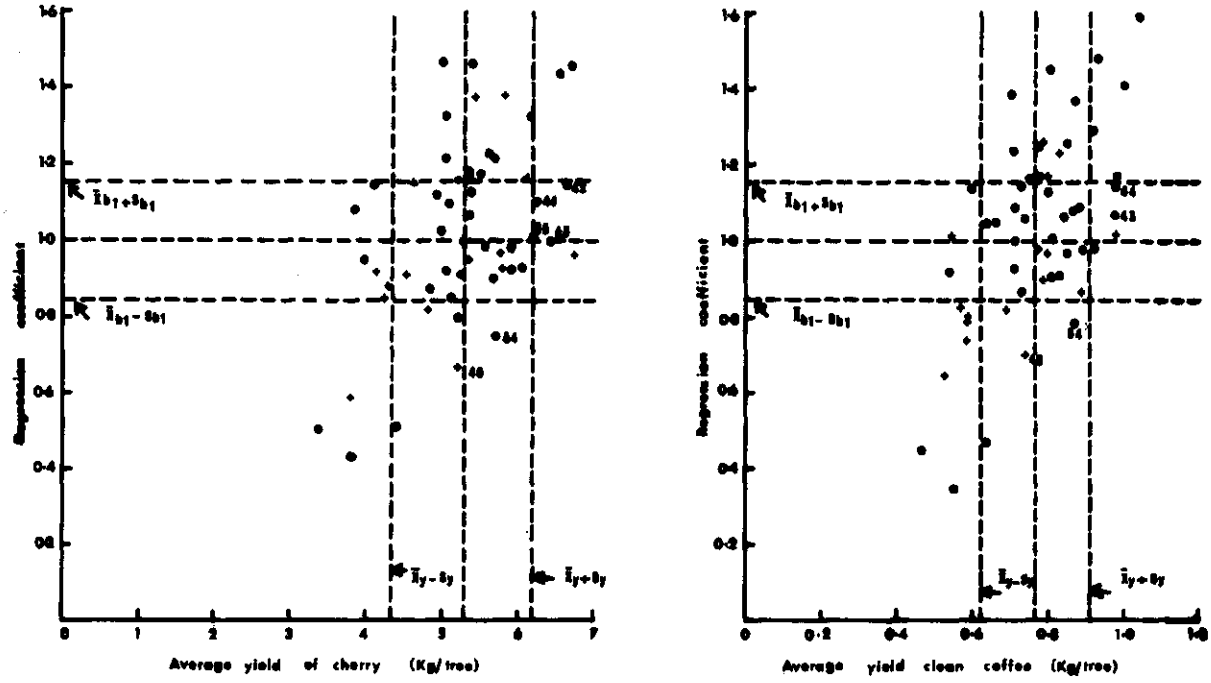


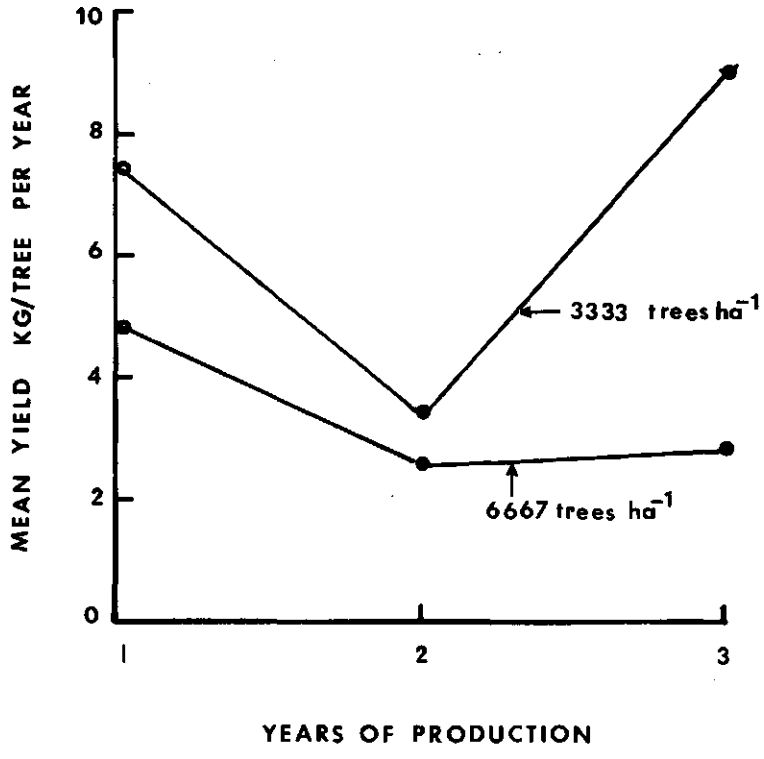
Fig. 3a The relation of yield of cherry and stability of F_1 hybrids. + s^2_d significant ($P < 0.05$); • s^2_d not significant.

3b The relation of yield clean coffee and stability of F_1 hybrids. + s^2_d significant ($P < 0.05$); • s^2_d not significant

Four F_1 hybrids representing crosses between Laurina and Hibrido de Timor (43), Laurina and Padang (44), Laurina and K7 (42), and Rume Sudan and SL 34 (65) (the last two crosses, in connection with yield of cherry only), had higher yields than the overall mean of all F_1's, average linear response ($b = 1$) and recorded no significant deviations from linear regression. These hybrids could be regarded as the most desirable owing to their overall superior performance. Of some interest also are two hybrids representing crosses between Rume Sudan and Laurina (54), and Rume Sudan and SL 28(49). These had average yields close to that of the F_1 overall mean but regression coefficients significantly smaller than 1, suggesting that these were the only hybrids with average or above average performance that were specifically adapted to unfavourable environments.

3.5. The behaviour of selected genotypes on basis of yield over 3 years of production at 2 plant densities.

Figure 4a demonstrates the yearly yield fluctuations that is typical in coffee. It is also evident that these fluctuations were less pronouced at



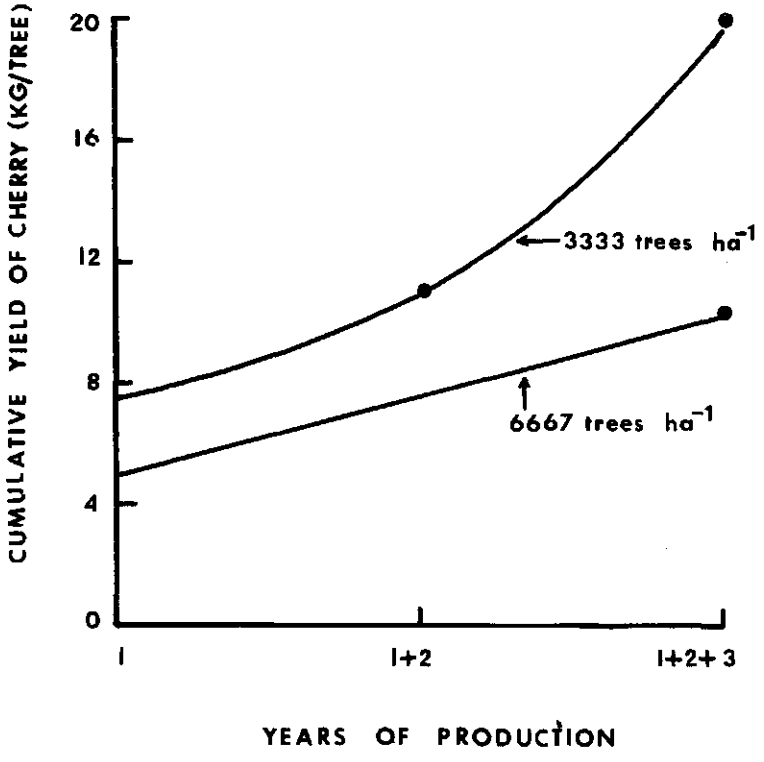


Fig. 4a Mean yield of cherry for all genotypes in each of the first 3 years production.

4b Cumulative yield of cherry for all genotypes for the first 3 years of production.

the higher plant density suggesting that such densities result in a better regulation on cropping over the years. It should be mentioned in this connection, that arabica coffee in the wild grows as an understorey shrub and hence it is a shade adopted species. Commercially however, it is grown under the open sun. The mutual shading offered by high density canopies is in some respect comparable to the shade conditions provided by over-storey plants. As a consequence, higher plant densities will result in increased leaf/crop ratio (Kumar, 1979). Under such conditions, very drastic yield fluctuations, at times resulting in overbearing as often happens with coffee growing at low densities, are most unlikely to occur.

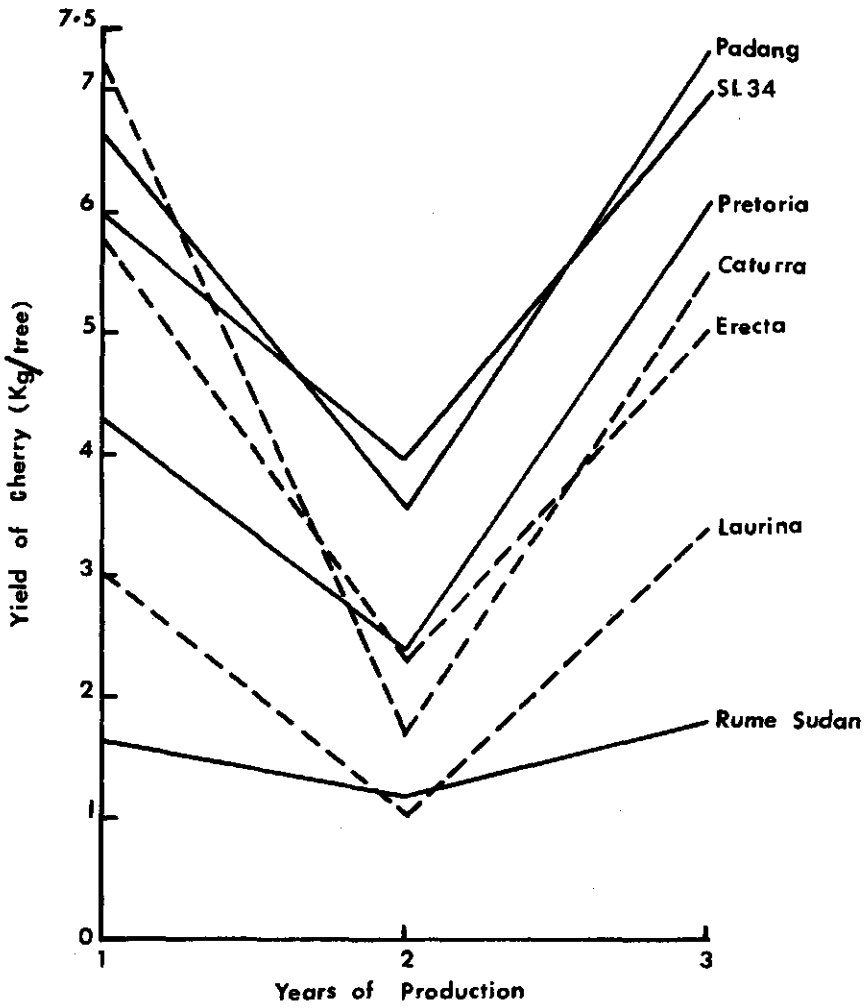


Fig. 5a Mean yield of selected parental varieties over the two plant densities for the first 3 years of production.

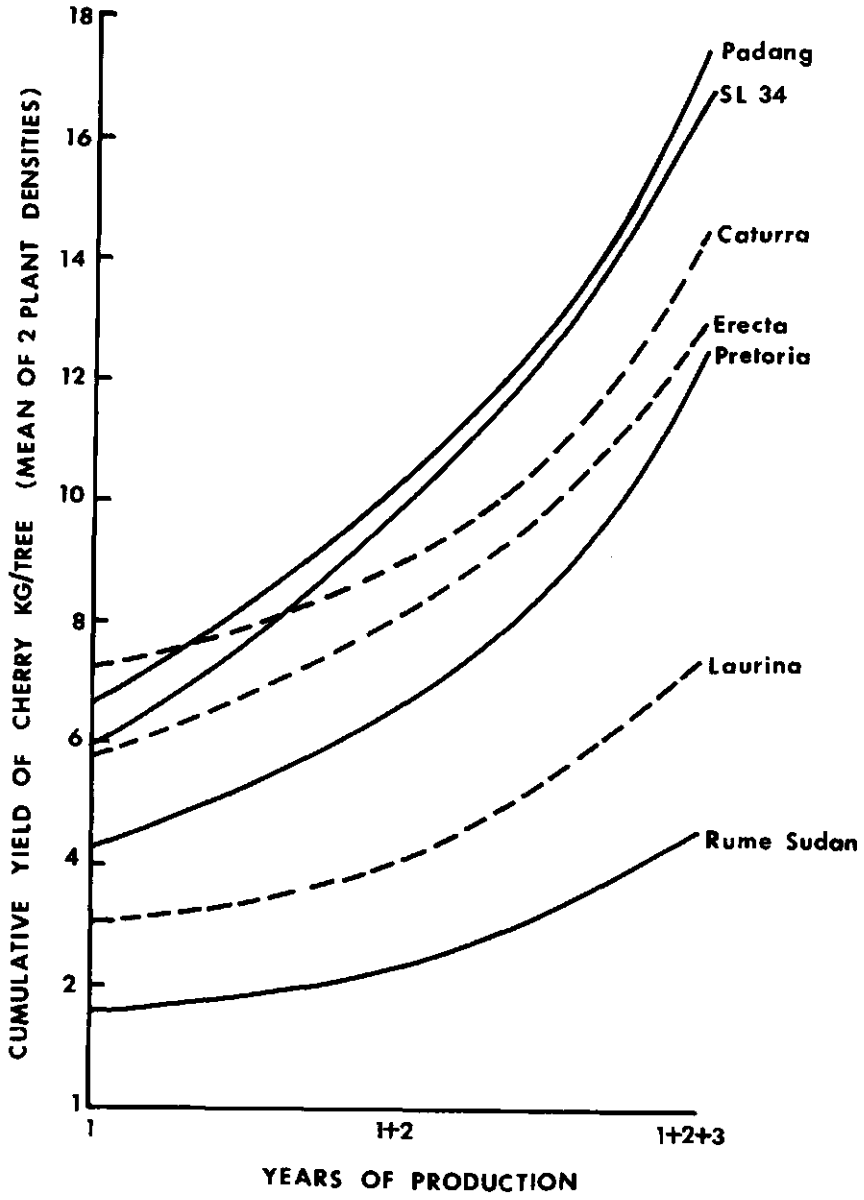


Fig. 5b Cumulative yield of selected parental varieties for the first 3 years of production over the 2 plant densities.

The increment in cumulative yield of individual trees over time (Fig 4b) was however, less at the higher plant density, and eventually is expected to level off earlier, than at the lower plant density. This is a result of more competition between plants, in terms of mutual shading, at the higher density relative to the lower density. This competition becomes much more pronounced at the higher plant density earlier than it does at the lower plant density.

Seven genotypes were selected to illustrate the effect on yield of two different plant densities over the first three years of production. The genotypes included varieties with compact growth (Caturra,Laurina and erecta), non-compact varieties (Pretoria, Padang, SL 34 and Rume Sudan).

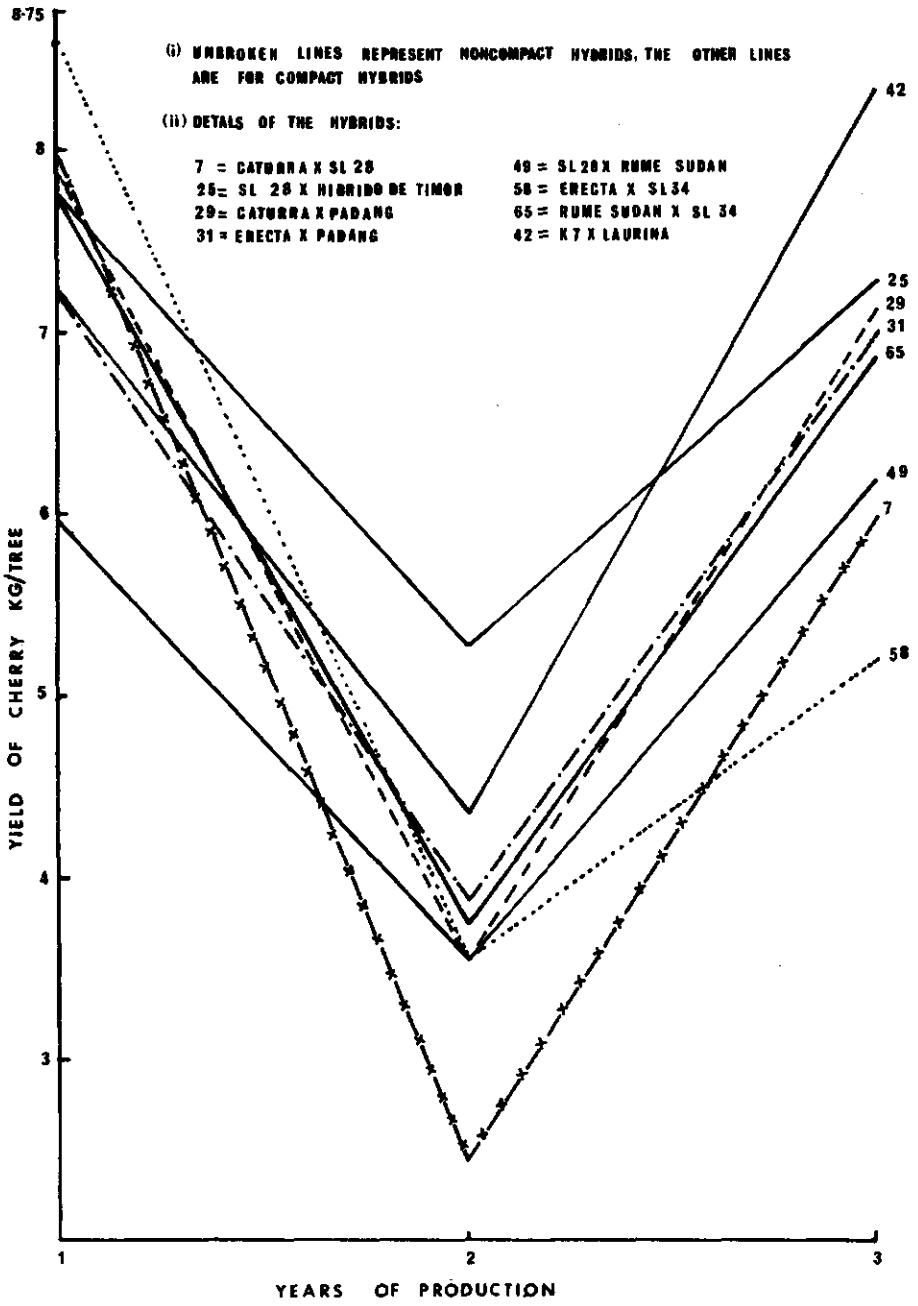


Fig. 6a Mean yield of selected F_1 hybrids over the two plant densities for the first 3 years of production.

It is clear from Figure 5a that these varieties differed not only with respect to yield for each of the 3 years, but also in terms of yield fluctuation over the 3 years of production. Furthermore, the compact varieties especially Caturra and Erecta showed even more pronounced yield fluctuation than some non-compact varieties. If the first year's yield is considered as some measure of precocity, then Caturra and to some extent Erecta can be regarded as being fairly precocious in addition to Padang and SL 34. Padang

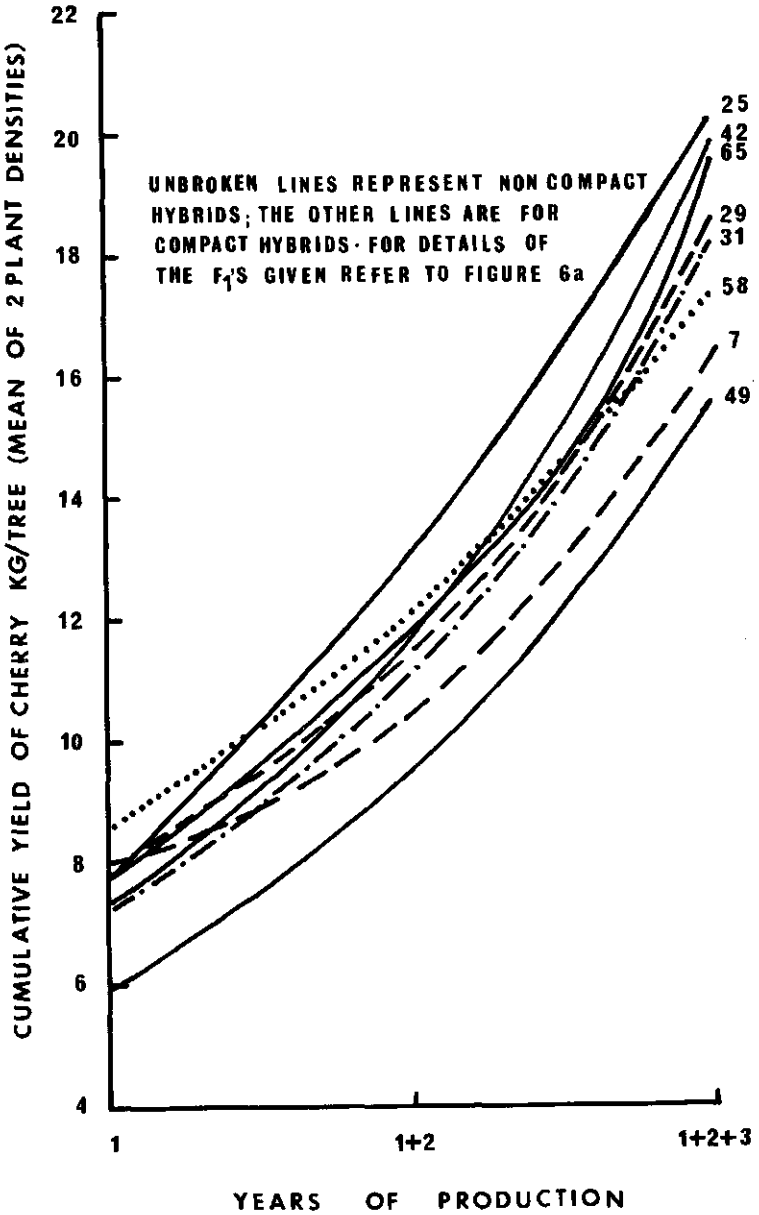


Fig. 6b Cumulative yield of selected F_1 hybrids for the first 3 years of production over 2 plant densities. Unbroken lines represent non-compact hybrids the other lines represent compact hybrids. for details of the F_1's refer Figure 6a.

and SL 34 were also the most outstanding varieties on basis of cumulative yield over the 3 years (see Figure 5b). On the other hand, the increase in cumulative yield for Caturra and Erecta tends to show more decline during later years of production when compared to some non-compact-varieties for instance, Pandang, SL 34.

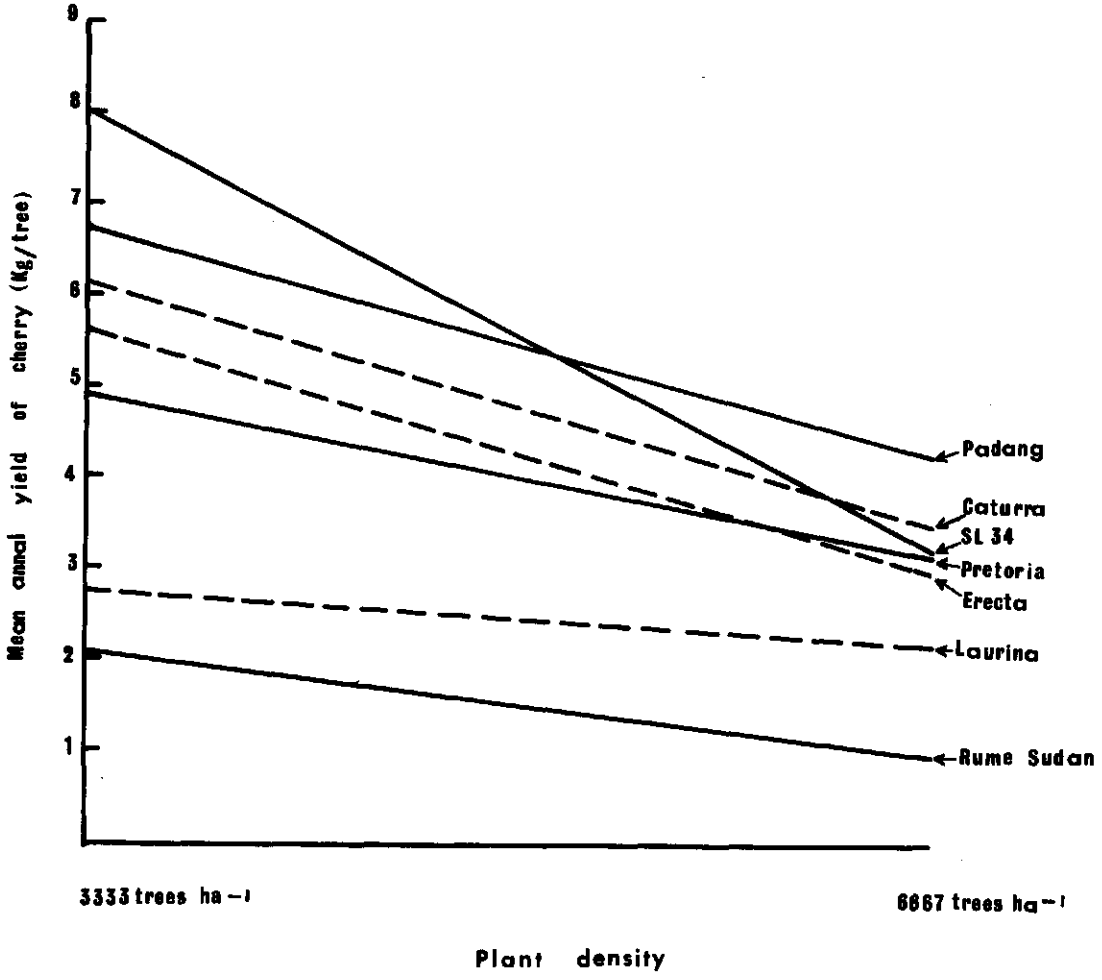


Fig. 7a Mean annual yield for the first 3 years of selected parental varieties at 2 plant densities.

Regarding eight F_1 hybrids (Figure 6a), it is evident that those with compact growth were not necessarily superior to the non-compact hybrids in terms of yearly yield fluctuation. It is true however that hybrids derived from crosses involving Caturra as one parent tended to be more precocious. As was with the parents, the hybrids of Caturra and Erecta, also tend to show a greater decline in cumulative yield over the years, when compared to some non-compact hybrids (Fig. 6b).

The effect of plant density on mean yield of the seven parental varieties, and the eight F_1 hybrids is depicted in Figures 7a and 7b respectively.

Increased plant density had the least effect on Laurina (Figure 7a), whereas the parent showing the greatest decline in yield at the higher plant density

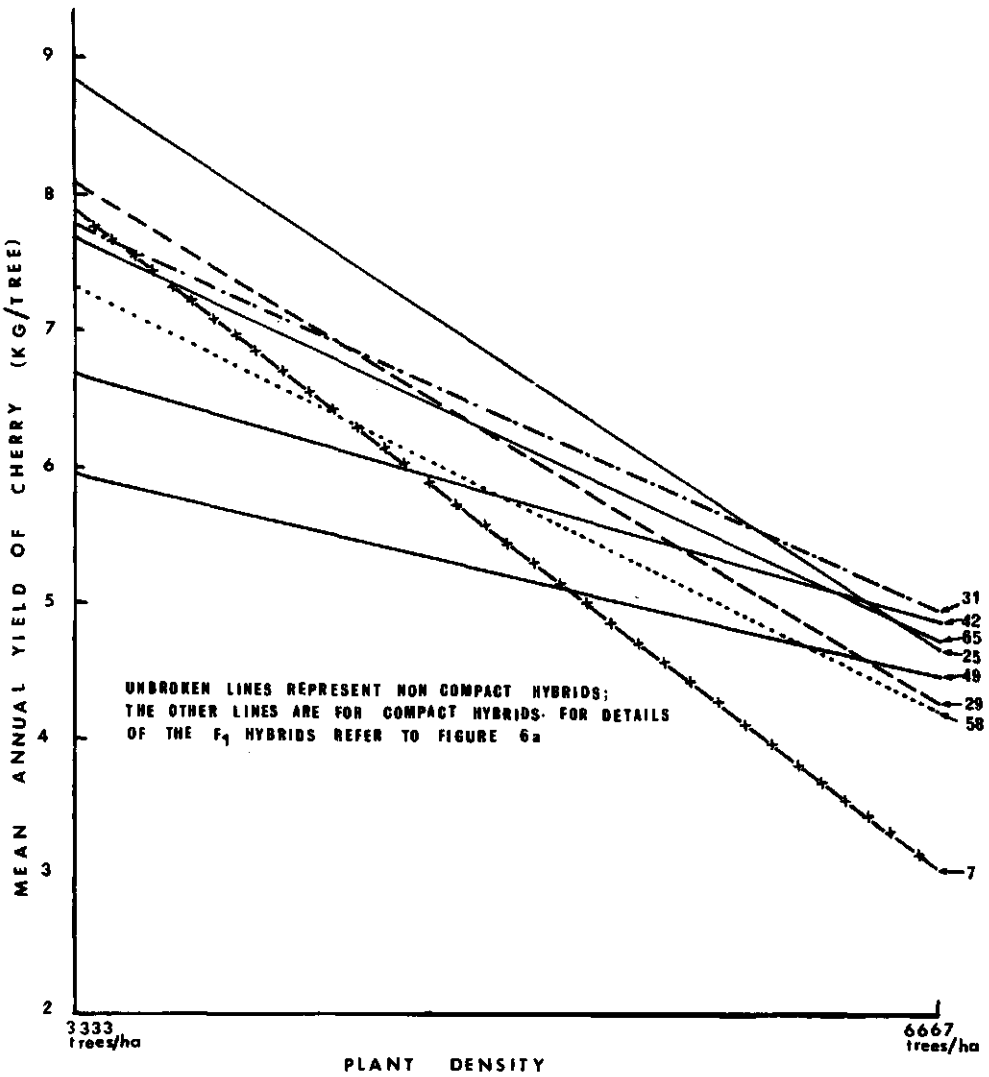


Fig. 7b Mean annual yield for the first 3 years of selected F_1 hybrids at 2 plant densities.

was SL 34. Padang and Pretoria both non-compact varieties appeared to be relatively less responsive to increasing plant density than even Caturra and Erecta. Two F_1 hybrids cross numbers 31 and 65 representing respectively progenies of crosses between Erecta and Padang, Rume Sudan and SL 28, were least sensitive to increased plant density (Fig. 7b). One compact hybrid derived from a cross between Caturra and SL 28 however recorded the greatest decline in yield at the higher plant density. It is however clear from Figures 7a and 7b that there are differences in sensitivity, in terms of yield response in different plant densities, both among compact genotypes as well as among non-compact genotypes.

From the foregoing, it could be concluded that compact growth does not always imply increased yield stability of such genotypes. Specifically, genotypes which are better adopted to increased plant density are not necessarily only those with compact growth habit. Compact growth however, is a fairly important character in coffee on basis of other considerations as will be discussed later. In the following section, the inheritance of the differences in sensitivity to varying environments among genotypes for yield as well as for other growth and yield characters is discussed.

3.6. Inheritance of stability parameters

Analysis of combining ability was performed on linear regression coefficients (b), and the functions of deviation mean squares (S^2_d), of the genotypes forming the half diallel. The relation between the offspring and midparent values for the same stability parameters was obtained as a joint regression calculated from 11 sets of offspring-midparent regressions. The 55 F_1's in the half diallel were grouped into 11 sets each containing 5 F_1's. The corresponding parental combinations within each set were chosen such that the midparent values were independent. In other words, a given parent occurred only once in each set, and as would be expected, each midparent combination had to be represented only once in all the 11 sets.

Results of analysis of combining ability for stability parameters of various growth and yield characters together with the estimates of half the regression coefficient of offspring on midparent, which is a measure of heritability, are given in Table 10. GCA effects were significant when tested against SCA mean squares for most characters. But this was only so for the linear component of genotype x environment interactions, suggesting that for most characters, linear response to different environments was largely governed by GCA. The variation among genotypes in the expression of deviations from linear response, could probably be ascribed mainly to SCA and/ or to other causes of non-genetic nature. This could not be confirmed from the analysis of combining ability alone due to the lack of an appropriate error.

The offspring-midparent regressions confirm that variation in linear response to environments may be under the influence of genes showing mainly additive and probably to some extent dominance effects. This is so because for a number of characters, linear response to environments was fairly heritable. On the other hand no meaningful estimates of offspring-midparent regressions were obtained for deviations from linear regression, for all characters considered. The estimates in most cases were not different from zero. Consideration of the two analyses would indicate that either the genetic control of this aspect of genotype-environment interactions is fairly complex, or that this aspect, for most characters, under these environments is not heritable.

3.7. The relation between yield stability and some growth and yield characters

Table 10. Mean squares of general and specific combining ability and estimates of half offspring-midparent regression (½*b* ō mp) for stability parameters of growth and yield characters

Source of variation	Df	*b*	s^2_d	*b*	s^2_d
		girth		height	
GCA	10	0.077***	0.253	0.088***	105885.22*
SCA	55	0.017	0.234	0.006	48926.77
½*b* ō mp	33	0.65 ± 0.10	0	0.30 ± 0.06	
		int. length (stem)		primaries	
GCA	10	0.291**	0.0046	0.0087**	0.00041
SCA	55	0.045	0.0033	0.0012	0.00024
½*b* ō mp	33	0.31 ± 0.06		0.20 ± 0.08	
		canopy radius		int. length (primaries)	
GCA	10	0.050***	686.75	0.229**	0.0002
SCA	55	0.004	478.77	0.36	0.0002
½*b* ō mp	33	0.30 ± 0.06		0.20 ± 0.04	
		leaf area		angle	
GCA	10	2.920***	6639.35	0.378*	22.780
SCA	55	0.20	4958.07	0.178	36.040
½*b* ō mp	33	0.48 ± 0.08		0.25 ± 0.09	
		extension growth		*node production*	
GCA	10	0.461**	251.93	0.083**	0.425
SCA	55	0.97	122.81	0.026	0.814
½*b* ō mp	33	0.22 ± 0.05		0.23 ± 0.08	
		bearing primaries		bearing nodes	
GCA	10	0.008**	61.830	0.027**	93.300
SCA	55	0.002	56.090	0.010	142.410
½*b* ō mp	33	0.10 ± 0.08		0.22 ± 0.10	
		flowers per node		fruit set	
GCA	10	0.674**	14.630	0.435**	3097.42
SCA	55	0.218	9.989	0.318	1657.78
½*b* ō mp	33	0.20 ± 0.07		0.12 ± 0.08	
		berries per node		yield of cherry	
GCA	10	0.723	0.141	0.205**	0.821
SCA	55	0.866	0.123	0.052	0.611
½*b* ō mp	33	0.04 ± 0.10		0.15 ± 0.07	
		yield of clean coffee			
GCA	10	0.264**	0.0002		
SCA	55	0.052	0.0003		
½*b* ō mp	33	0.20± 0.06			

The correlation coefficients between a number of selected growth and yield characters, and yield stability of parents as well that of F_1 array means are presented in Table 11. The F_1 array means were obtained as means of stability parameters of individual F_1's having a common parent. The growth and yield characters given in Tables 11 and 12, apart from yield, represent single measurements made mainly during the first and second year after field planting. Flowers per node however, were recorded on 3 year old plants. Yield was based on 3 years of production.

Parental yield was highly positively correlated with their linear response for yield over the environments (See table 11). There was however no such strong relationship between yield performance and the function of deviation mean squares (S^2_d) of parental varieties. A number of growth and yield characters were also positively correlated with parental linear regression for

Table 11. Correlations between parental performance for selected growth and yield characters, with parental yield stability and yield stability of F_1 array means.

Characters	Yield of cherry parental		F_1 array mean		Yield of clean coffee parental		F_1 array mean	
	b	s^2_d	b	s^2_d	b	s^2_d	b	s^2_d
1. girth	0.54	0.19	−0.22	0.35	0.52	0.28	−0.16	0.40
2. height	0.28	−0.07	−0.45	0.31	0.32	0.11	−0.34	0.33
3. canopy radius	0.64*	−0.35	−0.14	0.41	0.63*	0.37	−0.11	0.46
4. int. n. length (Pr)	0.63*	0.31	−0.25	0.31	0.64*	0.33	−0.18	0.38
5. bearing primaries	0.10	−0.00	0.25	−0.53*	0.14	0.02	0.41	−0.44
6. bearing nodes	0.49	0.39	0.31	−0.33	0.55*	0.59*	0.45	−0.23
7. flowers/node	0.87***	0.26	0.14	0.24	0.86***	0.16	0.24	0.34
8. berries/node	0.90***	0.60*	0.24	0.04	0.90***	0.48	0.39	0.15
9. yield of cherry								
9.1 parental yield	0.93***	0.36	0.36	0.02	0.96***	0.38	0.51	0.14
9.2 parental b		0.38	0.46	0.25	0.97***	0.28	0.56*	0.37
9.3 parental s^2_d			0.09	−0.14	0.37	0.90	0.20	−0.11
9.4 F_1 array mean b				0.03	0.45	0.11	0.94***	0.05
9.5 F_1 array mean s^2_d					0.12	−0.27	−0.10	0.99***
10. yield clean coffee								
10.1 parental yield					0.96***	0.40	0.49	0.14
10.2 parental b						0.34	0.59*	0.25
10.3 parental s^2_d							0.24	−0.25
10.4 F_1 array mean b								−0.05
10.5 F_1 array mean s^2_d								

yield. The number of berries per node and percent bearing nodes showed respectively, significant positive correlation with parental deviations for yield of cherry and yield of clean coffee. Regarding the relation between parental performance and average stability of F_1's sharing the same parent, parental growth characters tended to be negatively associated with the linear response of F_1 array means for yield, but positively associated with deviations from linear regression of the F_1 array means. The opposite was true for relations between yield stability of F_1 array means, and bearing primaries as well as percent bearing nodes of the parents. Parental yield and linear response for yield, tended to be positively correlated with both stability parameters of F_1 array means. Most of the correlations in this case however were not significant owing to the small number of entries.

The performance of F_1 hybrids in relation to their stability for yield (Table 12) showed in general that growth characters tended to be negatively correlated with linear response of the F_1's but positively correlated or not correlated at all with the deviations from regression. Some yield characters including yield itself were however, positively correlated with linear regressions of F_1's but negatively correlated with the F_1 deviations. This trend would suggest that vigorous F_1's on basis of some growth characters, tend to be less sensitive in their linear response to differing environments; on the other hand, F_1 hybrids with high performance, on basis of certain yield characters, tend to be relatively more sensitive in their linear response, but more stable in terms of deviations from linear response over environments. The same picture could be extended in some respects to the relation between the performance of parental varieties and average yield stability of their F_1 hybrids.

Table 12. Correlations between growth and yield characters and yield stability of F hybrids.

Character		Yield of cherry		Yield of clean coffee	
		b	s^2_d	b	s^2_d
1	girth	−0.19	0.16	−0.17	0.13
2	height	−0.30*	0.06	−0.25*	0.04
3	canopy radius	−0.13	0.24*	−0.08	0.22
4	int. n. length (pr)	−0.33*	0.16	−0.24	0.19
5	bearing primaries	0.40**	−0.04	0.34*	−0.09
6	bearing nodes	0.01	−0.31*	0.15	−0.27*
7	berries per node	0.26*	−0.07	0.36*	−0.03
8	yield of cherry				
8.1	x	0.48**	−0.23	0.58**	−0.19
8.2	b		−0.12	0.95***	−0.11
8.3	s^2_d			*−0.24**	*0.90***
9	yield of clean coffee				
9.1	x			0.57**	−0.24*
9.2	b				−0.21
9.3	s^2_d				

3.8. The significance of this study in relation to some aspects of arabica coffee breeding

When dealing with different genotypes of arabica coffee, there are certain characters that can be most useful for a rapid evaluation. Such characters in this study were mainly growth characters and include height of the tree, girth of the stem, internode length measured on primaries and on the main stem and radius of canopy. These characters require only a single measurement which can be performed even on young coffee trees, 1½ years after field planting. Yield characters, apart from number of bearing primaries, were in general not as suitable as the growth characters mentioned above.

Regarding selection for superior genotypes in arabica coffee, particular attention has to be given to the effects of interactions between genotypes and environments. It has been demonstrated in this study (see section 3.3.) that variation among genotypes for most growth and yield characters is under considerable influence of genotype-environment interactions. A large proportion of these effects for many of the characters however, is due to the linear component of genotype environment interactions. Furthermore, genotypes included in this study differ for most characters, in their response to different environments. It is also apparent for some characters, that there are differences in the average response of parents as compared to the F_1 hybrids. In particular, for yield of cherry and clean coffee (see section 3.4.), the F_1's on average tend to show more stability than their parents suggesting in this case that heterozygosity appears to impart increased environmental stability.

To accomodate effects of genotype-environment interactions in a selection programme, environmental stability of individual genotypes has to be assessed. This will give some indication of the consistency in performance

over environments of a given genotype relative to the other genotypes. In describing a stable variety, Eberhart and Russell (1966) defined such a variety as one having unit regression ($b = 1$) and a minimum of deviation from regression ($S^2_d = 0$), in addition to high mean performance. For these stability parameters to be considered of practical value however; the mode of inheritance, and the magnitude of heritability of such parameters, has to be determined, and so is their reliability, based on repeatability of the same parameters at least over a number of environments that resemble those encountered within the normal range of growing conditions.

Finlay (1971), showed that linear response for yield in barley is a heritable trait. Fatunla & Frey (1976), on repeatability of regression stability index in oats, showed to the contrary that the trait was obviously not heritable. Finlay's (1971) results could be considered as representing situations where a single environmental factor or fairly similar combinations of different environmental factors are dominant in the range of environments under consideration. In random sets of combinations of diverse environmental factors, the situation may be quite different as was suggested by Knight (1971) and illustrated in the case of Oats (Fatunla & Frey, 1976). Indeed, it is to be expected that the overall effect of genes conditioning response to a given set of environments, may be quite different from that of other genes conditioning response to an entirely different set of environments.

It has been reported in a number of situations (Eberhart & Russell, 1966, 1969; Conolly & Jinks, 1975, Dhillon & Joginder Singh, 1977) that variation in linear response was governed mainly by general combining ability or additive and dominance genetic effects whereas the expression of non-linear fluctuations appeared to involve all types of gene action, including epistasis. This is in agreement with results obtained in the present study (see section 3.6). Heritability of stability parameters in this study suggests that whereas it may be possible to select for high yielding coffee genotypes with average linear response to environments, it may neither be feasible nor worthwhile to attempt selection for genotypes with lowered deviations from regression, at least in environments similar to those considered here. The environments in this study were characterised by 2 differing plant densities and yearly fluctuations under the same location. Under environments fairly similar to these ones, linear environmental response of the different genotypes may be reproduced in some degree. It is however most doubtful whether the same would be true for environmental fluctuations.

Of even more practical interest, is the relation between compact growth and yield stability. For genotypes considered in this study (see section 3.5.) compact growth appears to be fairly independent of yield stability both on basis of regularity in bearing, and on basis of adaptation to increased plant densities. It is possible, that because of the genetic background, environmental stability of such compact genotypes is expressed mainly in terms of growth habit, but not necessarily also in terms of yield stability. In other words even among compact genotypes, it is possible to select for improved yield stability.

Among parental varieties considered here, the high correlation between yield and linear regression (see section 3.7.) clearly indicates that selection for mean yield alone will save varieties that are superior at all yield levels.

This will always be so, if the region at which the regression lines converge on the environmental space is below the normal production environment range (Eagles et al., 1977). Regarding F_1 hybrids however, yield stability appears to depend in some degree on 1) the vegetative vigour, and 2) the performance, on basis of certain yield characters, of the F_1 hybrid or even of its parents.

Regarding yield of individual genotypes, it is clear from this investigation that many of the F_1 hybrids show pronouced hybrid vigour for yield. Yield of the outstanding F_1 hybrids in Table 9 for instance is well above that of their superior parents, as well as that of the most productive commercial cultivars (Table 8). Hybrid vigour, as will be discussed later, may have important consequences in breeding programmes in arabica coffee.

Finally, as regards yield stability in this study, Padang among parental varieties is the most outstanding (section 3.4.) whereas Laurina, is the ideal parent in hybrid combinations on basis of producing high yielding stable hybrids. Of some interest also, are two hybrids representing progenies of crosses involving Rume Sudan as one parent, which appear to combine average or above average yield with adaptability to unfourable environments.

4. THE INHERITANCE OF SELECTED GROWTH AND YIELD CHARACTERS

4.1. Introduction

Though extensive work has been done in the past in elucidating the genetic control of characters mostly showing simple, i.e. classical Mendelian, inheritance in *Coffea arabica* (section 1.4.), information on inheritance of quantitative characters from earlier work is scant and inconclusive. Yet characters of most economic importance in coffee, yield and quality as well as their components, all exhibit continuous variation and can be regarded as having quantitative/polygenic inheritance. The mode of gene action underlying the variation of such characters and the proportion of this variation that is genetic are of particular importance in breeding. This information is invaluable especially in planning and evaluation of hybridization programmes and can eventually be reflected in more rapid progress in improvement programmes not only for yield and quality in coffee, but also for certain desirable growth attributes.

Results from previous work (Stoffels, 1941 ; Gardner, 1950; Elguetta, 1950; Mendes et al., 1941; Castillo, 1957) have all suggested that heritability for most quantitative characters in arabica coffee, and in particular yield, is low. More recently however, Carvalho and Monaco (1972) cited by Monaco (1977) in evaluating heterogeneous germplasm consisting of Turrialba Collections, and populations of the 1964 FAO mission to Ethiopia, have concluded that a significant part of the total variation was due to the genetic component. Walyaro and van der Vossen (1979) also observed highly significant genotypic effects for most growth and yield characters in a number of arabica coffee varieties, and high to moderate heritabilities especially on plot mean basis, for yield as well as for some of the other quantitative characters. The most extensive work on quantitative characters done so far, was that undertaken by ORSTOM/IFCC in connection with a study of the structure and genetic variability of *C. arabica* populations collected from Ethiopia in 1966. These were evaluated in different environments characterised by low or high altitudes in Ivory Coast, Cameroon and Madagascar (Charrier, 1978b).

It is apparent from the more recent investigations that the low heritability previously observed for most quantitative characters in *C. arabica* was obviously a reflection of the very narrow genetic diversity the populations in question represented (see also section 1.4.).

In this Chapter, the genetic basis of variation for a number of important growth and yield characters is considered. The characters chosen for this study included the following: girth of stem, height, number of primaries

and bearing primaries. These represent measurements taken on plants between 1½ and 2½ years old in the field. Radius of canopy, internode length on primaries and angle of insertion, were taken on 1 year old plants, while the number of flowers per node, were taken on 3 year old plants in the field. Yield of cherry and clean coffee represents totals of 3 years of full production. The procedure of Hayman (1954b) and Jinks (1954) as given in section 2.5.4 was applied to the data for these characters. Apart from determining the usefulness of this procedure in elucidating the genetic control of these characters, results obtained from the analysis were expected to give some indications regarding the immediate outcome of selection for certain characters within the offspring generations of the diallel set of crosses.

4.2. Variation among the arrays for differences between array variances and covariances

As was mentioned in section 2.5.4, the constancy of $W_r - V_r$ over arrays is one important relationship used to verify the validity of assumptions underlying the diallel cross theory. Table 13 gives results obtained from the analysis of variance of $(W_r - V_r)$ values, partitioned according to plant density, array effects and their interaction. The values were not transformed initially according to Allard's suggestion (1956a). This was because the central interest was to test at the same time, using the same analysis of variance, the presence and constancy of additive x dominance, dominance x dominance as well as additive x additive gene interactions.

It is clear from Table 13 that out of the characters, six of them showed significant array differences in the magnitude of $(W_r - V_r)$. In particular, the heterogeneity of $(W_r - V_r)$ values was highly significant (P = 0.001 — 0.01) for height, yield of cherry and clean coffee yield, and significant (P = 0.01 — 0.02) for girth, radius of canopy and internode length on primaries. The arrays x density item for the same characters was not significant suggesting

Table 13. Analysis of variance of $W_r - V_r$ values for selected growth and yield characters.

Source	Df	Mean squares and P			
		girth	height	primaries	angle
Plant densities	1	1.22***	4495.25	21.59	0.02
Arrays	10	0.48*	14779.56***	78.09	75.08
Reps within plant densities	4	0.83***	878.77	135.32	1264.53***
Arrays x Plant densities	10	0.19	3320.63	46.18	84.87
Arrays x Reps within Pl. densities	40	0.19	2643.00	74.35	72.66
		radius canopy	int. Length (Pr)	bearing primaries	flowers/ node
Plant densities	1	78.26	0.026***	81.01	0.37
Arrays	10	507.14*	0.014*	46.42	1.82
Reps within Plant densities	4	489.52*	0.014*	349.80***	5.37***
Arrays x Plant densities	10	176.04	0.006	35.99	3.43*
Arrays x Reps within Pl. densities	40	198.05	0.006	53.80	1.68
		yield cherry	yield clean coffee	yield cherry (1)	yield clean coffee(1)
Plant densities	1	93.78***	0.038***	17.16***	0.0006
Arrays	10	26.30***	0.012***	4.58	0.0016
Reps within Plant densities	4	5.60	0.002	2.95	0.0008
Arrays x Plant densities	10	7.82	0.004	2.31	0.0005
Arrays x Reps within Pl. densities	40	5.56	0.003	2.76	0.0015

(1) After omission of 3 parental arrays, Df for Plant densities, Arrays, Arrays x Plant densities, and Arrays x Reps within Plant densities are respectively, 1, 7, 4 & 28.

that the heterogeneity of $(W_r - V_r)$ over arrays was fairly consistent over the two plant densities. Though the arrays item was not significant for number of flowers per node, the arrays x density item was, indicating heterogeneity of $(W_r - V_r)$ confined at least to one of the plant densities. Hence for all the above characters, one or a number of the diallel assumptions were obviously not valid. For the number of primaries, bearing primaries and angle of insertion however, $(W_r - V_r)$ values were homogeneous over arrays and across the plant densities. It can be concluded for the latter characters, that a simple additive-dominance model of independently distributed genes appears to provide adequate description of the diallel data.

Since yield of cherry and yield of clean coffee are the two most important characters, an attempt was made to trace the cause of the failure of the diallel assumptions in order to indentify, if possible, the parents responsible for the bulk of the disturbances. Omission of the progenies of at least 3 parental lines was necessary to restore the constancy of $(W_r - V_r)$ values over arrays in both plant densities (see Table 13). The parents removed were Hibrido de Timor, Laurina and Rume Sudan. Indeed Laurina and Rume Sudan had the largest $(W_r - V_r)$ values in both plant densities, but Hibrido de Timor was among this category only at the low plant density. In addition to the analysis of variance of $(W_r - V_r)$, the constancy of $(W_r - V_r)$ was also tested, as is given in section 2.5.4, by means of linear regression of W_r on V_r. The results, are given in the next section.

4.3. Genetic analysis by means of diallel cross graphs

Results of regression of W_r on V_r are summarised in Table 14, in terms of the value of W_r intercept a, uncorrected for the environmental component, the regression coefficient b and the standard error. The same results are depicted on graphs in figures 8 — 13 for height, number of primaries, yield of cherry and clean coffee.

From Table 14, it is clear that for girth of stem, height (see also Fig. 8b), radius of canopy and number of flowers per node, the regression line, at the higher plant density, deviated significantly both from zero and from one. A particularly poor fit was obtained for yield of cherry and clean coffee in both plant densities (see Table 14 and figures 10 and 11). However, as is shown in figures 12 and 13, omission of arrays 7, 9, and 10 representing the same parents mentioned in section 4.2, apparently restored the rectilinearity of W_r, V_r regression line for yield of cherry and clean coffee in both densities. Results obtained here in general, agree with those obtained from the analysis of variance given in section 4.2. in indicating the inadequacy of the simple additive dominance model for many of these characters. In this case also the number of primaries (see Figure 9), and number of bearing primaries appeared to conform to the diallel assumptions.

The means of individual progenies of the diallel cross were inspected to determine the occurance and direction of hybrid vigour in specific F_1 combinations for yield of cherry and clean coffee. Hybrid vigour in this study is defined as the amount by which the mean of an F_1 exceeds the better parent, i.e. it is that hybrid vigour which results in an F_1 falling outside the

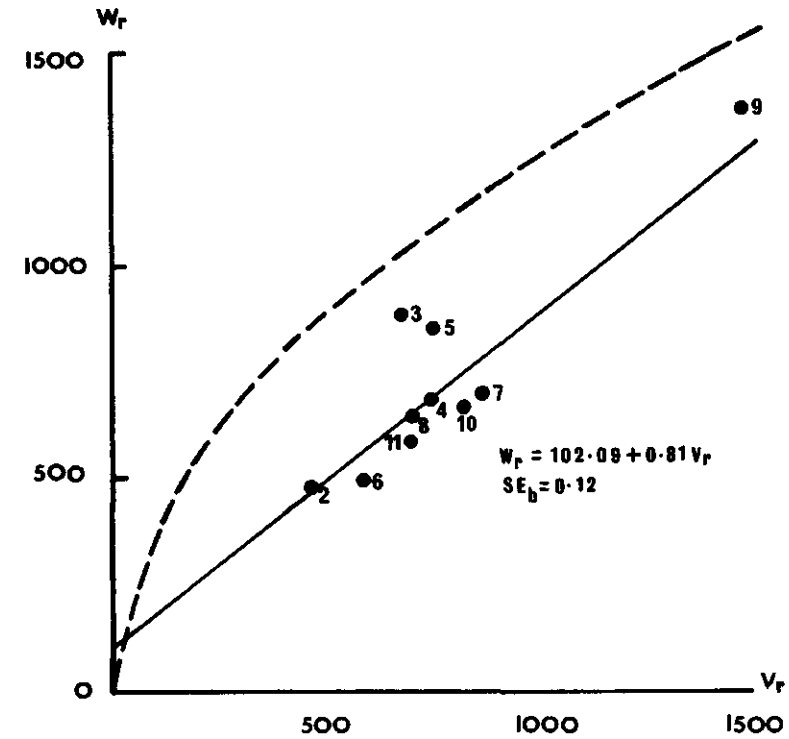
Table 14. Summary of results of regression of W_r on V_r

Character	Density	Intercept, *a*	*b*	SE_b
girth	1[(1)]	0.023	0.62	0.19
	2	0.320	0.59	0.11
height	1	102.090	0.81	0.21
	2	167.550	0.76	0.03
primaries	1	−5.600	1.07	0.20
	2	−1.790	1.02	0.19
radius of canopy	1	25.387	0.88	0.13
	2	45.570	0.79	0.08
Internode length (pr)	1	0.160	0.91	0.12
	2	0.263	0.92	0.09
bearing primaries	1	−10.400	1.19	0.22
	2	−2.330	1.10	0.10
flowers per node	1	−1.370	0.82	0.15
	2	1.130	0.43	0.13
yield cherry	1	2.560	0.38	0.19
	2	1.510	0.31	0.14
yield cherry (arrays 7, 9, 10 ommited)	1	0.466	0.97	0.20
	2	0.729	1.08	0.23
yield clean coffee	1	0.064	0.47	0.17
	2	0.026	0.37	0.11
yield clean coffee (arrays 7, 9, 10 omitted)	1	0.033	1.02	0.16
	2	0.041	0.74	0.24

(1) 1 = 3333 trees ha^{-1}
2 = 667 trees ha^{-1}

range of the parents with respect to some character. It includes heterozygosis and/or transgression resulting from effects of non-allelic interactions or gene dispersion. Hybrid vigour as used in this context, is the same as what is generally referred to as heterosis (Allard, 1960; Mather & Jinks, 1971).

In Tables 15 and 16, details are given of F_1 hybrids which recorded significant hybrid vigour respectively, for yield of cherry and clean coffee. The



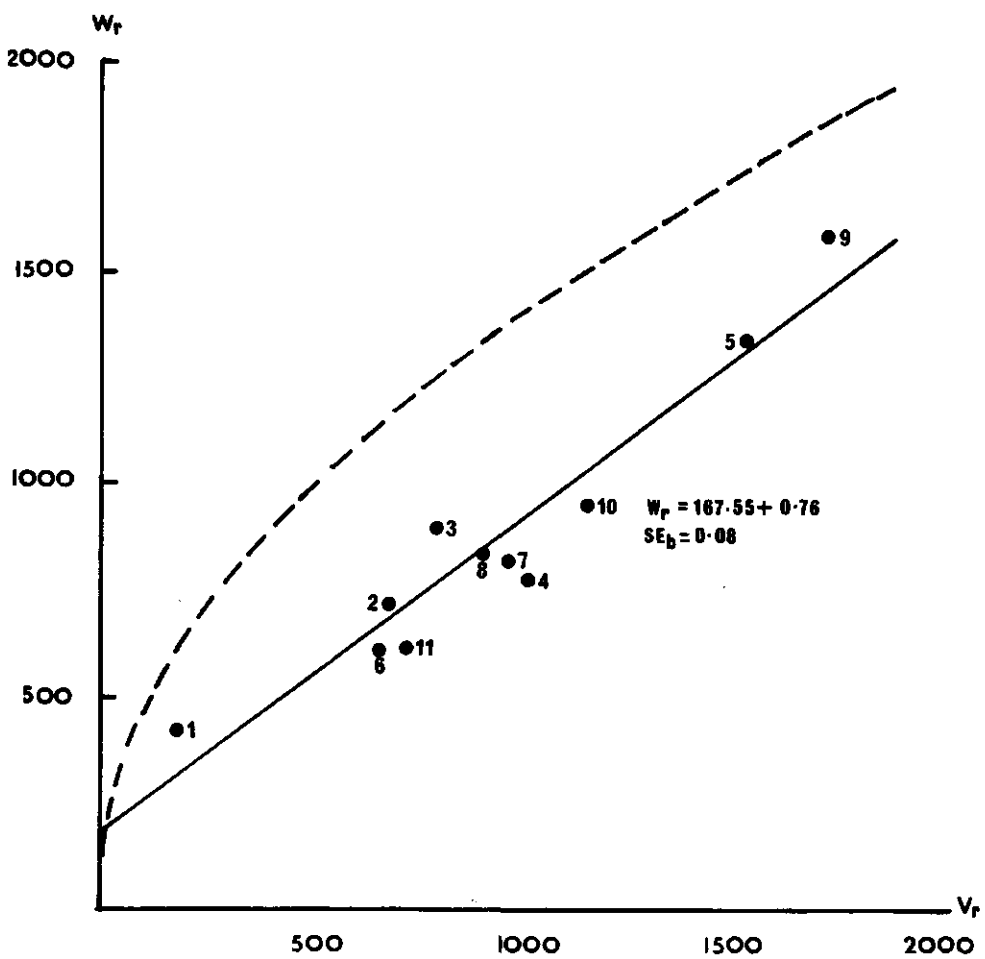


Fig. 8a Regression line of W_r on V_r and limiting parabola for height of the tree (cm) at the lower plant density.

8b Regression line of W_r on V_r and limiting parabola for height of the tree (cm) at the higher plant density.

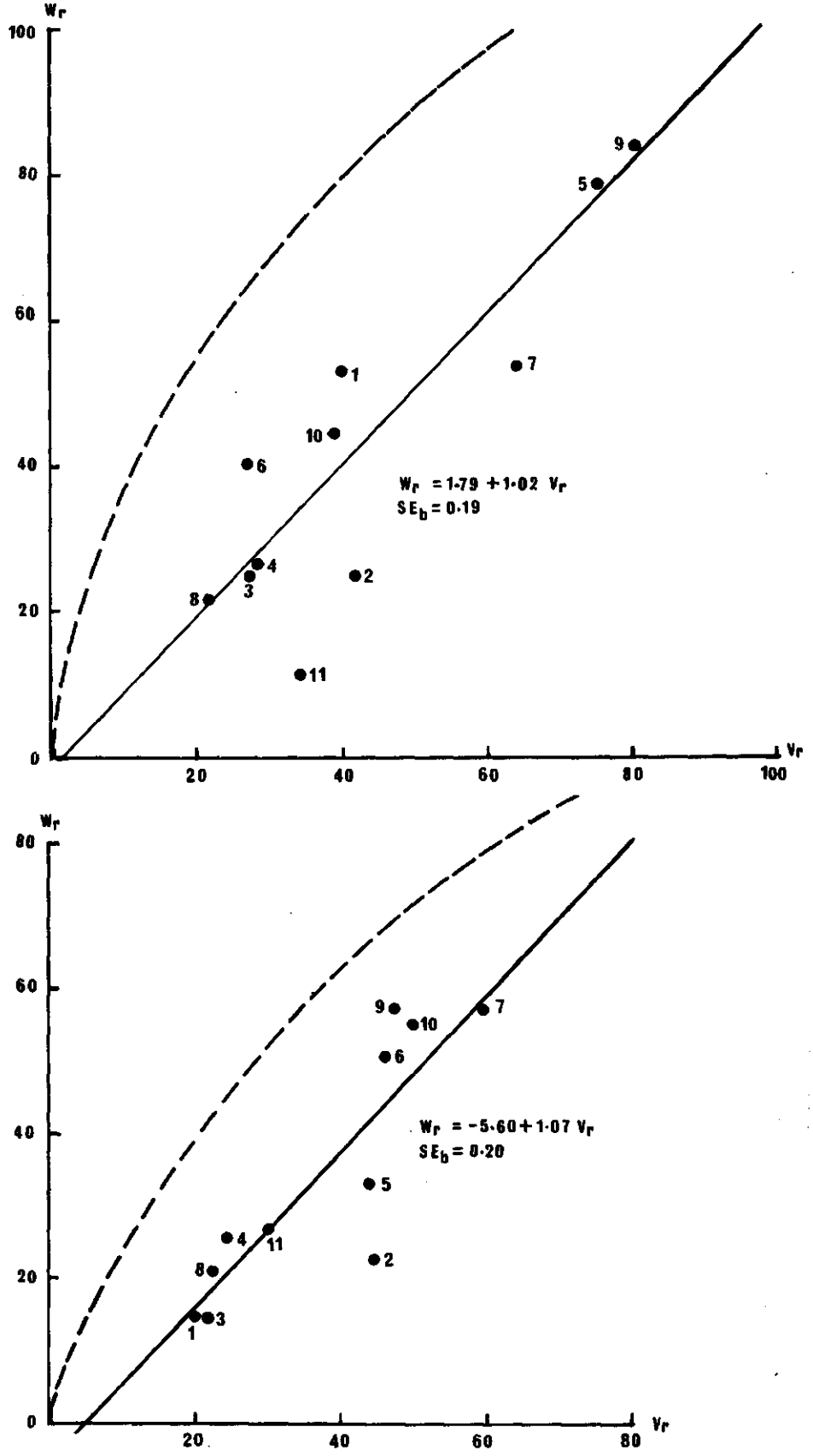
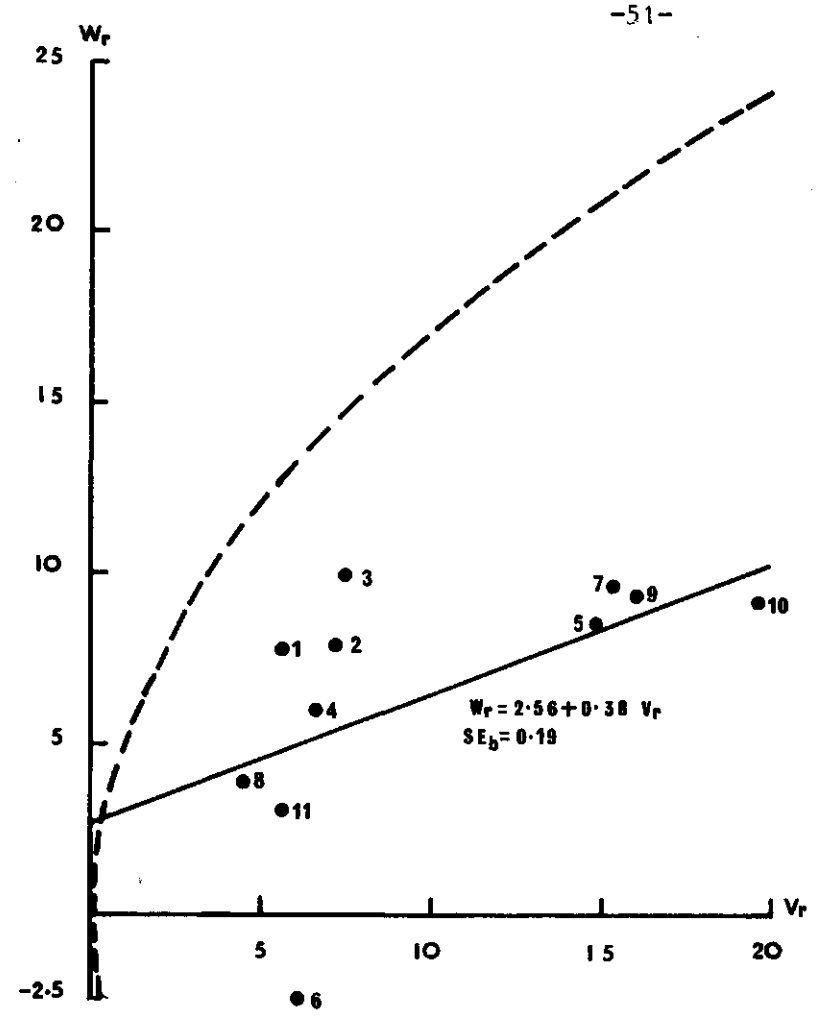


Fig. 9a Regression line of W_r on V_r and limiting parabola for number of primaries per tree (lower plant density).

9b Regression line of W_r on V_r and limiting parabola for number of primaries per tree (higher plant density).



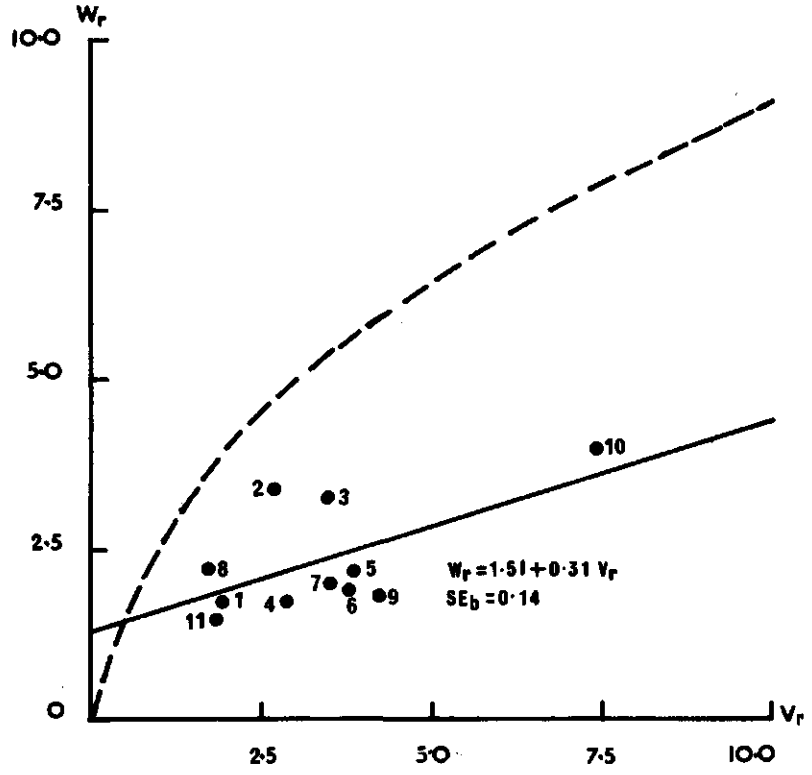


Fig. 10a Regression line of W_r on V_r and limiting parabola for yield of cherry (kg/tree) at the lower plant density.

10b Regression line of W_r on V_r and limiting parabola for yield of cherry (kg/tree) at the higher plant density.

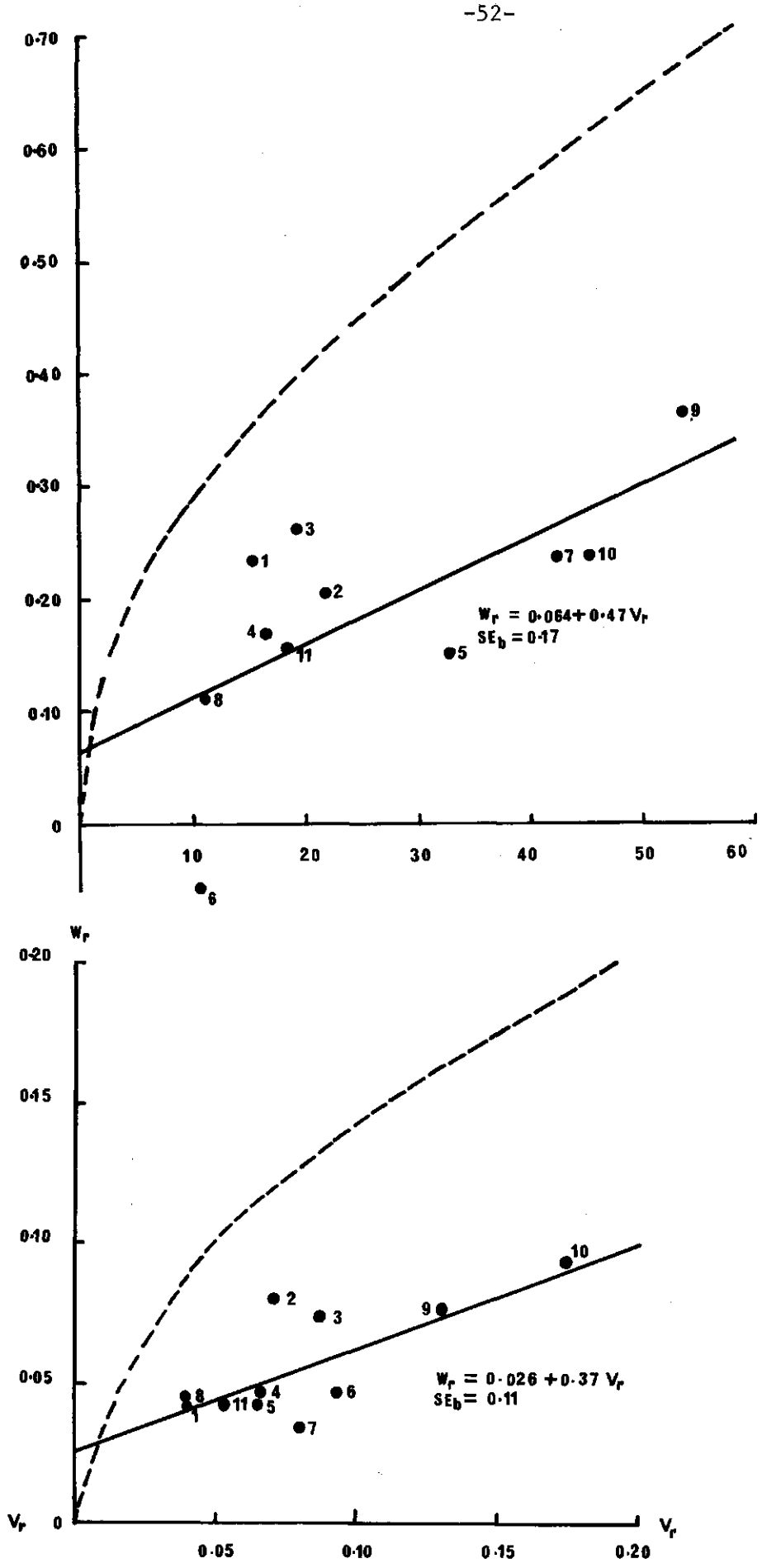
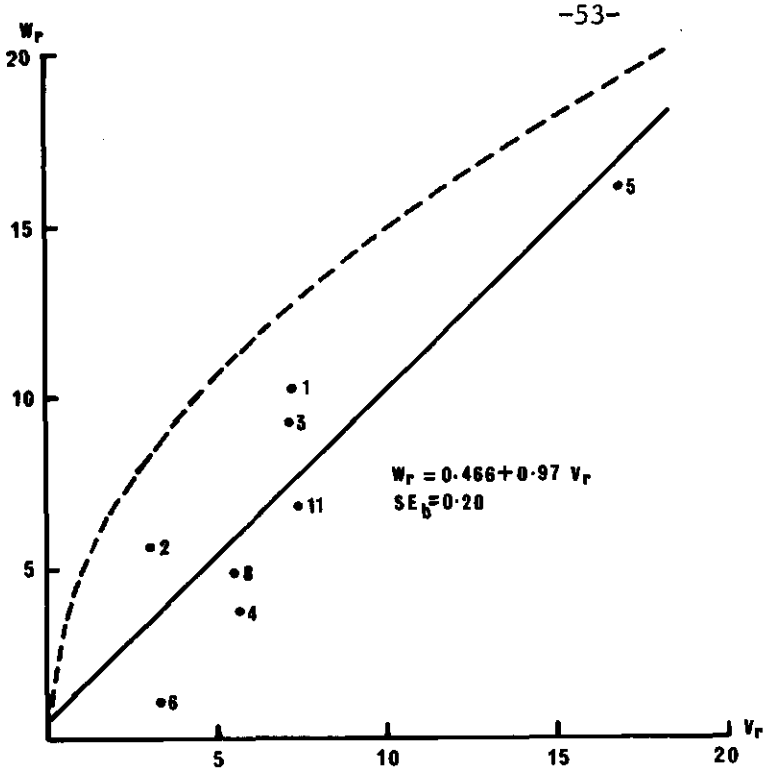


Fig. 11a Regression line of W_r on V_r and limiting parabola for yield clean coffee (kg/tree) at the lower plant density.

11b Regression line of W_r on V_r and limiting parabola for yield of clean coffee (kg/tree) at the higher plant density.



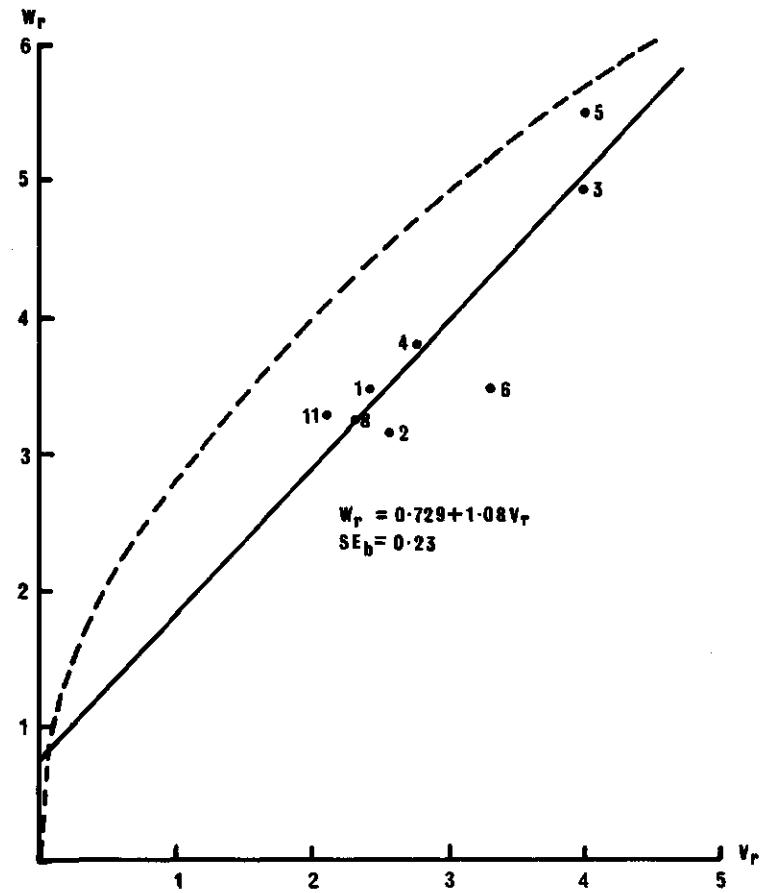
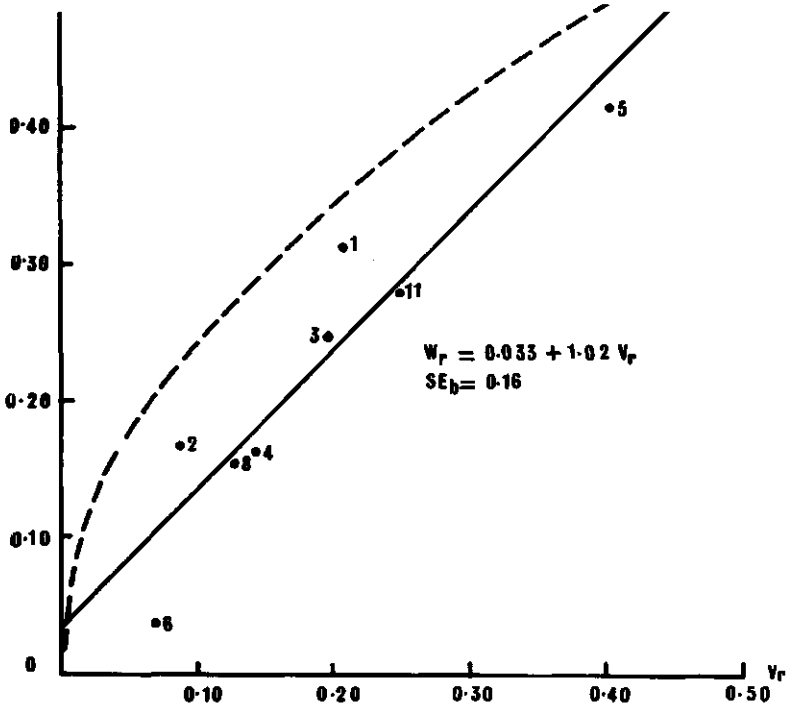


Fig. 12a Regression line of W_r on V_r for yield of cherry (kg/tree), omitting arrays 7, 9, 10 at the lower plant density.

12b Regression line of W_r on V_r for yield of cherry (kg/tree), omitting arrays 7, 9, 10 at the higher plant density.



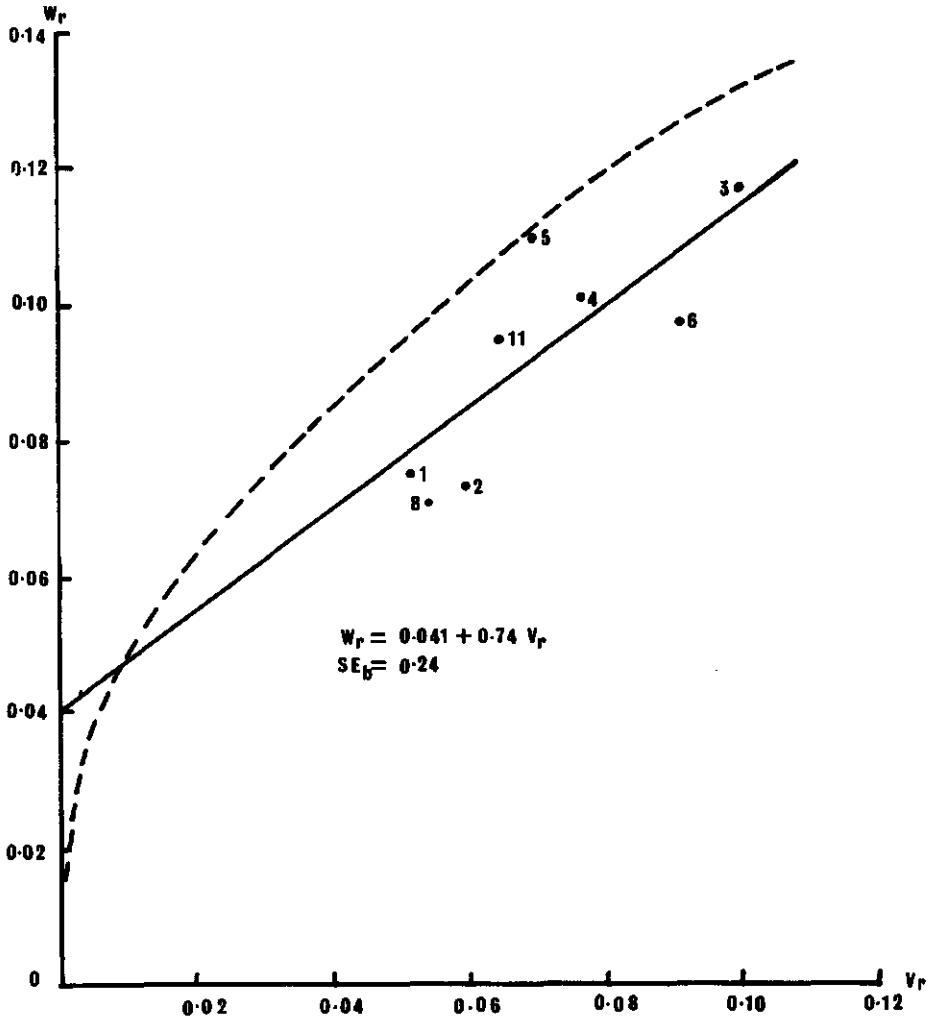


Fig. 13a Regression line of W_r on V_r for yield clean coffee kg/tree (omitting arrays 7, 9, 10) at the lower plant density.

13b Regression line of W_r on V_r for yield clean coffee kg/tree (omitting arrays 7, 9, 10) at the higher plant density.

Table 15. F_1's showing hybrid vigour for mean annual yield of cherry to the extend that their performance significantly exceeds that of the better parent ($\bar{P}_1$)

Details of cross ($\bar{P}_1 \times \bar{P}_2$)	Yield kg/tree at 3333 trees ha^{-1}			Yield kg/tree at 6667 trees ha^{-1}		
	$\bar{P}_1$	$\bar{F}_1$	$\frac{\bar{F}_1 - \bar{P}_1}{\bar{P}_1} \times 100$	$\bar{F}_1$	$\bar{F}_1$	$\frac{\bar{F}_1 - \bar{P}_1}{\bar{P}_1} \times 100$
Caturra x Pretoria	6.2	6.8	10			
" x K7	6.2	7.6	23			
" x H. de Timor	6.2	7.8	26			
Padang x Caturra	7.3	8.2	12			
Caturra x Rume Sudan	6.2	7.0	13	3.3	3.8	15
Erecta x Pretoria	5.5	6.7	22	3.3	4.0	21
SL 28 x Pretoria				3.3	4.1	24
K7 x Pretoria	5.6	6.6	18			
Pretoria x Laurina	5.4	6.7	24	3.0	3.7	23
SL34 x Pretoria				3.5	4.0	14
SL28 x Erecta				3.3	3.8	15
K7 x Erecta	5.6	7.6	36	3.3	3.7	12
Padang x Erecta				4.3	5.0	16
Erecta x Laurina	5.5	6.8	24	3.3	3.6	10
" x Rume Sudan				3.3	4.0	21
SL34 x Erecta				3.5	3.9	11
SL28 x H. de Timor	7.6	8.8	16	3.3	4.7	42
" x Padang	7.6	8.7	15			
SL28 x Laurina				3.3	3.8	15
" x Rume Sudan				3.3	4.3	30
K7 x Mokka	5.6	6.5	16			
Laurina x Kokka	2.8	7.4	164	2.2	2.8	27
Mokka x Rume	2.3	7.1	209	1.1	3.7	236
K7 x H. de Timor				2.8	3.7	32
K7 x Laurina	5.6	8.4	50	2.8	4.8	71
" x Rume Sudan	5.6	7.0	25	2.8	3.3	18
H. de Timor x Laurina	5.5	8.3	51	2.5	4.5	80
SL34 x H. de Timor				3.5	3.9	11
Padang x Laurina	7.3	8.2	12			
SL34 x Padang	8.0	9.2	15			
Laurina x Rume Sudan	2.8	7.1	154	2.2	4.4	100
SL34 x K7				3.5	4.3	23
SL34 x Laurina				3.5	4.3	23
SL34 x Rume Sudan				3.5	4.5	29

performance of these hybrids was, on basis of yield of cherry, between 10% — 236%, and for clean coffee, between 8% — 300%, above the better parent. It is also clear from both Tables that hybrid vigour for some of the parental combinations was exhibited only in one of the plant densities, whereas for other parental combinations, hybrid vigour occurred irrespective of plant density. There is however, considerable variation in the level of hybrid vigour within parental combinations over the two plant densities, an indication of effects of genotype — environment interactions.

4.4. Validity of diallel assumptions

Regarding the characters considered in this study, the two analyses (given in sections 4.2. and 4.3.) have mutually established that for many of these characters, including characters of most interest, yield of cherry and clean coffee, a simple additive-dominance model is clearly inadequate in explaining the variation observed among parental varieties. Validity of assumptions of parental homozygosity, diploid segregation, and absence of genotype-environment interactions within locations (see section 3.4) are clearly not expected to introduce such a serious bias into the genetic analysis. The assumptions of no epistasis, uncorrelated gene distribution or multiple alleles are most likely to be responsible for most of the disturbances.

Table 16. F_1's showing a level of hybrids vigour, for mean annual yield of clean coffee which significantly exceeds the yield of the better parent ($\bar{P}_1$)

Details of the cross ($\bar{P}_1 \times \bar{P}_2$)	Yield kg/tree at 3333 ha^{-1}			Yield kg/tree at 6667 tree ha^{-1}		
	$\bar{P}_1$	$\bar{F}_1$	$\frac{\bar{F}_1-\bar{P}_1}{\bar{P}_1} \times 100$	$\bar{P}_1$	$\bar{F}_1$	$\frac{\bar{F}_1-\bar{P}_1}{\bar{P}_1} \times 100$
Caturra x Pretoria	0.90	1.00	11			
" x K7	0.90	1.06	18			
" x H. de Timor	0.90	1.09	21			
Padang x Caturra	1.20	1.30	8			
Caturra x Rume Sudan	0.90	0.99	11			
Pretoria x Erecta	0.84	1.01	20	0.47	0.60	28
SL28 x Pretoria				0.47	0.59	26
Pretoria x K7	0.84	0.98	17			
" x Laurina	0.84	1.08	29	0.47	0.57	21
SL34 x Pretoria				0.52	0.59	14
SL28 x Erecta				0.47	0.56	19
K7 x Erecta	0.83	1.09	31	0 47	0.52	11
Padang x Erecta				0.68	0.77	13
Erecta x Laurina	0.72	0.93	29	0.47	0.52	11
x Rume Sudan				0.47	0.60	28
SL28 x K7				0.47	0.55	17
" x H. de Timor	1.11	1.30	17			
Padang x SL28	1.20	1.30	8	0.47	0.56	19
SL28 x Laurina				0.47		
SL28 x Rume Sudan				0.47	0.62	32
K7 x Mokka	0.83	0.93	12			
Mokka x Laurina	0.28	1.03	268	0.24	0.37	54
" x Rume Sudan	0.28	0.96	243	0.14	0.50	257
K7 x H. de Timor				0.42	0.54	29
" x Laurina	0.83	1.24	50	0.42	0.70	67
" x Rume Sudan	0.83	0.98	18			
SL34 x K7				0.52	0.59	14
H. de Timor x Laurina	0.76	1.28	68	0.36	0.68	89
" " x Rume Sudan				0.36	0.48	33
Padang x Laurina	1.20	1.30	8			
Padang x SL 34	1.20	1.45	21			
Laurina x Rume Sudan	0.27	1.08	300	0.24	0.67	179
SL34 x Laurina				0.52	0.63	21
" x Rume Sudan				0.52	0.63	21

The curviture of W_r/V_r graphs especially for yield of cherry and clean coffee (see figures 10 and 11) is characteristic of effects of non allelic interactions or non-random distribution of genes among the parents. Complementary type of gene interactions or gene dispersion will both normally cause a deviation from unit slope and give a slope that is less than unity (Jinks, 1955). Gene dispersion however, will in general tend to cause less departure from unity (Mather & Jinks, 1971), because with more than two gene loci, there will be no mutually reinforcing systems of departure from rectilinearity of W_r/V_r as happens with gene association. Furthermore, by reducing the number of parents entering the diallel cross, effects of non-random distribution of genes among the parents of the remaining smaller diallel, are expected to cause even more serious disturbance of the W_r/V_r graphs. That satisfactory graphs were obtained for yield of cherry and clean coffee (see Figures 12 and 13) despite the reduction in the number of parents, suggests that non allelic interactions of the complementary type, rather than non-random distribution of genes, were the more common cause of disturbances of the W_r/V_r graphs. Indeed, it is most likely that for characters like girth and height (section 4.5), non-allelic interactions are probably the main cause of the disturbances of ($W_r - V_r$) relationships. There are a number of other characters, including yield of cherry and clean coffee (after omission of the 3 parents), where the diallel assumptions appear to conform. Of particular interest in connection with these assumptions is that such information also gives further evidence of the diploid inheritance especially of quantitative characters in *Coffea arabica*, which is supposed to

be an amphidiploid.

Further discussion regarding the practical implications of some of the diallel assumptions in breeding is considered in section 4.6. However for the present the interpretation of the diallel parameters, for the various characters, given in the next section is considered against a background of some of these limitations.

Table 17. Estimates of diallel components and proportional values.

Parameter/ratio	Density 1	Density 2	Density 1	Density 2
	girth		height	
D	2.33 ± 0.24	1.16 ± 0.17	511.19 ± 23.53	649.84 ± 26.78
F	1.86 ± 0.56	−0.07 ± 0.39	121.07 ± 53.78	145.44 ± 61.21
H_1	3.06 ± 0.50	1.68 ± 0.35	525.98 ± 48.48	653.27 ± 55.19
H_2	1.50 ± 0.42	0.91 ± 0.29	233.33 ± 40.76	265.83 ± 46.39
$(ML_1 - ML_o)^2$	3.05 ± 0.28	1.75 ± 0.20	257.46 ± 27.26	496.25 ± 31.03
$D - H_1$	−0.73 ± 0.42	−0.52 ± 0.29	−14.78 ± 40.36	−3.43 ± 45.94
$r_{pi/(Wr_i + Vr_i)}$	−0.46	−0.36	−0.15	−0.29
E	0.63 ± 0.07	0.39 ± 0.05	39.49 ± 6.79	60.77 ± 7.73
$(H_1/D)^{½}$	1.15	1.20 1.20	1.01	1.00
$H_2/4H_1$	0.12	0.14	0.11	0.10
K	2.04	1.92	1.10	1.87
h^2_n	0.50(0.26)	0.62(0.35)	0.77(0.61)	0.78(0.59)
h^2_b	0.69(0.36)	076(0.44)	0.91(0.72)	0.89(0.68)
	primaries		angle	
D	33.26 ± 1.96	53.08 ± 3.57	60.37 ± 5.76	45.56 ± 2.78
F	22.11 ± 4.49	45.62 ± 8.16	0.39 ± 13.16	−2.45 ± 6.34
H_1	32.63 ± 4.05	33.44 ± 7.53	6.40 ± 11.87	4.26 ± 5.72
H_2	18.42 ± 3.40	10.97 ± 6.18	11.86 ± 9.98	2.05 ± 4.81
$(ML_1 - ML_o)^2$	13.70 ± 2.28	21.34 ± 4.14	13.48 ± 6.67	0.81 ± 3.22
$D - H_1$	0.62 ± 3.37	19.64 ± 6.12	63.97 ± 9.98	41.30 ± 4.76
$r_{pi/(Wr_i + Vr_i)}$	0.18	0.27	—	—
E	4.52 ± 0.56	11.01 ± 1.03	—	14.56 ± 0.80
$(H_1/D)^{½}$	0.99	0.79	—	—
$H_2/4H_1$	0.14	0.08	—	—
K	0.74	1.95	—	—
h^2_n	0.58(0.36	0.52(0.24)	0.57(0.26)	0.63(0.30)
h^2_b	0.79(0.49)	0.62(0.29)	—	—
	canopy radius		internode length (pr)	
D	144.90 ± 5.22	136.93 ± 7.93	0.74 ± 0.03	0.88 ± 0.04
F	145.64 ± 11.93	116.03 ± 16.90	0.77 ± 0.06	0.76 ± 0.09
H_1	114.11 ± 10.75	82.19 ± 15.23	0.53 ± 0.06	0.49 ± 0.07
H_2	68.64 ± 9.04	48.53 ± 12.81	0.26 ± 0.05	0.22 ± 0.06
$(ML_1 - ML_o)^2$	151.10 ± 6.05	175.04 ± 8.57	0.60 ± 0.03	0.62 ± 0.04
$D - H_1$	30.79 ± 8.98	54.73 ± 12.68	0.21 ± 0.05	0.39 ± 0.06
$r_{pi/(Wr_i + Vr_i)}$	−0.74	−0.84	−0.76	−0.84
E	11.26 ± 1.51	15.45 ± 2.13	0.05 ± 0.01	0.06 ± 0.01
$(H_1/D)^{½}$	0.89	0.77	0.85	0.75
$H_2/4H_1$	0.15	0.15	0.12	0.11
K	2.20	3.61	2.29	2.85
h^2_n	0.44(0.26)	0.50(0.27)	0.51(0.31)	0.63(0.40)
h^2_b	0.78(0.47)	0.72(0.39)	0.79(0.47)	0.81(0.51)

	bearing primaries		flowers per node	
D_r	38.52 ± 3.49	62.23 ± 3.44	6.09 ± 0.49	4.75 ± 0.53
F	27.39 ± 7.98	67.23 ± 7.87	7.17 ± 1.12	4.36 ± 1.20
H_1	34.05 ± 7.19	48.18 ± 7.09	6.12 ± 1.01	3.44 b± 1.08
H_2	18.78 ± 6.05	15.80 ± 5.96	3.76 ± 0.85	2.53 ± 0.91
$(ML_1 - ML_o)^2$	17.37 ± 4.05	13.55 ± 3.99	8.72 ± 0.57	7.76 ± 0.61
$D - H_1$	4.48 ± 5.99	14.05 ± 5.90	−0.03 ± 0.84	1.31 ± 0.09
$r_{pi/(Wr_i + Vr_i)}$	0.12	−0.22	−0.79	−0.79
E	7.79 ± 1.01	7.99 ± 0.99	2.21 ± 0.14	2.41 ± 0.15
$H_1/D)^{½}$	0.94	0.88	1.00	0.85
$H_2/4H_1$	0.14	0.08	0.15	0.18
K	0.93	0.86	2.32	3.07
h^2_n	0.51(0.27)	0.54(0.28)	0.17(0.06)	0.18(0.06)
h^2_b	0.70(0.37)	0.69(0.36)	0.42(0.15)	0.35(0.12)
	yield (cherry)		yield (cherry) (arrays 7, 9, 10 omitted)	
D	9.57 ± 0.76	2.23 ± 0.19	6.76 ± 0.53	2.37 ± 0.12
F	10.85 ± 1.73	1.55 ± 0.43	3.66 ± 1.25	−0.21 ± 0.29
H_1	12.20 ± 1.56	3.08 ± 0.39	4.28 ± 1.21	0.73 ± 0.29
H_2	7.93 ± 1.31	2.28 ± 0.33	3.88 ± 1.05	0.75 ± 0.25
$(ML_1 - MLo)2$	17.68 ± 0.88	5.85 ± 0.22	6.96 ± 0.71	1.52 ± 0.17
$D - H_1$	−2.63 ± 1.30	−0.85 ± 0.32	2.48 ± 1.04	1.63 ± 0.25
$r_{pi/(Wr_i + Vr_i)}$	−0.72	−0.68	−0.61	−0.72
E	1.51 ± 0.22	0.69 ± 0.05	1.46 ± 0.18	0.53 ± 0.04
$(H_1/D)^{½}$	1.13	1.18	0.80	0.56
$H_2/4H_1$	0.16	0.18	0.23	0.25
K	2.23	2.57	1.80	2.03
h^2_n	0.30(0.16)	0.37(0.18)	0.42(0.20)	0.64(0.36)
h^2_b	0.70(0.37)	0.66(0.32)	0.65(0.32)	0.74(0.41)
	yield clean coffee		clean coffee (arrays 7, 9, 10 omitted)	
D	0.262 ± 0.018	0.053 ± 0.005	0.182 ± 0.011	0.050 ± 0.003
F	0.274 ± 0.040	0.035 ± 0.011	0.067 ± 0.026	−0.020 ± 0.008
H_1	0.312 ± 0.036	0.072 ± 0.010	0.083 ± 0.025	0.008 ± 0.008
H_2	0.196 ± 0.030	0.048 ± 0.009	0.078 ± 0.022	0.008 ± 0.007
$(ML_1 - ML_o)^2$	0.443 ± 0.020	0.115 ± 0.006	0.147 ± 0.015	0.019 ± 0.005
$D - H_1$	−0.050 ± 0.030	−0.018 ± 0.009	0.099 ± 0.022	0.043 ± 0.007
$r_{pi/(Wr_i + Vr_i)}$	−0.71	−0.61	−0.57	—
E	0.036 ± 0.051	0.018 ± 0.001	0.034 ± 0.004	0.014 ± 0.001
$(H_1/D)^{½}$	1.09	1.16	0.67	—
$H_2/4H_1$	0.16	0.17	0.24	—
K	2.23	2.40	1.88	—
h^2_n	0.38(0.21)	0.41(0.26)	0.53(0.28)	0.69(0.38)
h^2_b	0.74(0.41)	0.65(0.31)	0.70(0.37)	—

'Heritability ($h^2_n h^2_b$) is on plot mean basis and, in brackets; on individual tree basis.

4.5. Diallel cross parameters

Estimates of diallel cross parameters and proportional values are given in Table 17 for the 10 characters. The estimates of the additive gene effects (D) were significantly different from zero for all the characters. This was also true for the dominance effects (H_1 and H_2) except for angle of insertion where these effects were not significantly different from zero in both plant densities. Hence variation among the genotypes for angle of insertion could be ascribed to genes mainly with additive effects.

For the number of primaries and bearing primaries, the average dominance was complete at the lower plant density and partial, at the higher plant density as indicated by $(D - H_1)$ and $(H_1/D)^{½}$. For the same characters, the non-significant correlation coefficients between parental means and $(W_r + V_r)$ values, suggests that this dominance was ambidirectional. At loci exhibiting dominance, positive and negative alleles were unequally distributed among parents $((¼H_2/H_1) < 0.25)$, and there was an excess of dominant genes over all parents (F positive and significant). One or two effective factors were estimated for both of these characters, obviously underestimated due to cancellation of the h effects

Regarding yield of cherry and clean coffee there was significant apparent average overdominance for the diallel where all parents were included, see $(D - H_1)$ and $(H_1/D)^{½}$ in Table 17. The removal of the 3 parents however converts the situation from that of overdominance to average partial dominance. The distribution of the average frequencies of positive and negative alleles also changes from being unequal to a situation where $\bar{u} = \bar{v}$ i.e. the alleles are almost equally distributed among the parents. Whereas there was a drastic reduction in the magnitude of the estimates of dominance effects (H_1 and H_2) upon removal of these arrays, the additive effects in contrast were altered only to a small extent, at the lower plant density and not at all, at the higher plant density. The significant negative correlations between the performance of the common parent and the $(W_r + V_r)$ values indicated that the majority of the dominant alleles in the parents were acting in the direction of increased yield and the recessive alleles, in the direction of decreased yield. The values of K suggest approximately 3 effective factors controlling yield.

The picture regarding the remaining characters, is not as clear due to the reasons given earlier. Indeed no attempt was made to trace the sources of interactions for any of these characters as this was not considered within the scope of the present study. It could however be remarked that dominance effects for girth in particular, and height to some extent, bear some resemblance to those for yield. It is possible that the dominance effects may have

been overestimated due to the failure of one or a number of the diallel assumptions. For radius of canopy and internode length on primaries there was no evidence of overdominance. Indeed $(D - H_1)$ was positive and significant and $((H_1/D)^{1/2} < 1)$ indicating average partial dominance. Average dominance for number of flowers per node, at the lower plant density, was apparently complete. The number of effective factors K, for radius of canopy, internode length and number of flowers per node was estimated between 3 and 4.

4.6. Discussion

The results of analysis of the diallel performed on a number of selected growth and yield characters have indicated that for many of these characters, the assumptions underlying the diallel cross theory were not valid.It is a prerequisite however, that before any meaningful interpretation of the W_r, V_r graph in terms of certain genetic parameters is attempted, it must be shown that a simple additive-dominance model with independence of genes in action and distribution provides adequate description of the variation encountered in that particular diallel set of crosses. In dealing with a fixed population representing a number of genetically diverse parents, like the present population, gene interactions of one form or another are often to be expected, as the present results have shown. As a consequence, the interactions will invalidate genetic interpretation of such data on basis of a simple additive-dominance model. Similar problems are expected to be encountered elsewhere by nature of the populations most frequently used by breeders. In such situations the diallel assumptions as given may rarely be expected to conform. Indeed, these assumptions are most likely to be satisfied if the parents entering the diallel cross are related lines such as those which might have been produced by random mating of initial populations followed by non selective inbreeding. For obvious reasons breeders are hardly interested in such populations let alone the procedures used in developing them.

Viewed in this perspective, the technique of analysis of the diallel as proposed by Jinks (1954) and Hayman (1954b) has limited practical application. For indeed, the assumptions especially of absence of non allelic interactions and non-random distribution of genes are particularly difficult to satisfy. These shortcomings have been discussed by Kempthorne (1956), Nassar (1965), Feyt (1976) and Baker (1978). And they have been demonstrated in a number of cases considered among others by Jinks (1955), Allard (1956a), Kramer (1973) and Jana (1974). It is however worth pointing out that there are many documented cases where for some characters gene interactions are not an important feature of the genetic system, or are absent altogether, in certain fixed populations. Indeed such characters were also found in present study (see sections 4.2. and 4.3.).

The effects of the failures of some of these assumptions on the diallel graph have been investigated by Hayman (1957), Hill (1964), Nassar (1965), Mather (1967) and Coughtrey and Mather (1970). It has been shown that certain types of epistasis distort the W_r, V_r graph in certain characteristic ways and thus permit their detection (see also section 4.4.). Under favoura-

ble conditions where non allelic interactions are the sole cause of such disturbances the departure from, for instance, rectilinearity of W_r, V_r graph can be corrected by omitting arrays of offending epistatic parents. This has been demonstrated by Jana (1974), Kramer (1973) and others, as well as in this study for yield of cherry and clean coffee. This technique in such a situation is useful in that such information is of practical interest. It should however be realised that removal of certain arrays does not always work, particularly where drastic removal of parental arrays may introduce non random distribution of genes among the small number of parents, as was found by Jana (1974), or where epistasis is complicated by other disturbances such as correlated distribution of genes. Finally, it is also worth noting that in the F_1 diallel the W_r, V_r graph is comparatively less sensitive especially, to effects of duplicate gene interactions (Jinks, 1954, 1956). As a consequence, obtaining a proper fit does not imply in all cases that the assumptions conform. The genetic interpretation of the characters considered in the study, as was also mentioned in section 4.4, should be regarded with due consideration to some of these limitations of the theory of the diallel analysis.

An important observation from this study is that it represents the first case where substantial and widespread hybrid vigour for yield has been reported in *Coffea arabica* (see section 4.3.). Carvalho & Monaco (1969) stated that hybrid vigour in *C. arabica* had not been frequently found though isolated cases had been reported by Leon (1965) and Fernie (1965). Recently, Tostain and Pierres (1978) reported hybrids which were earlier and higher yielding than their parents. Carvalho et al. (1978) observed strong heterosis for yield in one cross between Bourbon Amarelo progenies but concluded that in general, cases of heterosis were rare. A considerable amount of hybrid vigour for yield was also reported by Netto & Pereira (1980) among a number of F_1 hybrids derived in crossing programme for leaf rust resistance. Results from this study and from other recent investigations indicate that hybrid vigour in *C. arabica* may be expected to occur fairly frequently, provided hybrids are derived from parental varieties that are more genetically diverse. Furthermore it was possible to establish in the present study (see section 4.4.) the possible causes of such hybrid vigour as being mainly the effect of complementary epistatic genes rather than overdominance at the heterozygous loci. The parents responsible for most of these interactions were Rume Sudan (10), Laurina (9) and Hibrido de Timor (7).

From distribution of parents on W_r, V_r graphs (Figures 12 and 13), Padang (8), SL 28 (4), K7 (6) (at the lower density) and SL 34 (11) (at the higher density), contain relatively most dominant genes for increased yields while Mokka (5) contains most recessive alleles acting mainly towards reduced yields. From these results, it is apparent that selection within progenies of crosses involving Padang with SL 28 or SL 34 or between these parents and those mainly responsible for non allelic interactions, i.e. Laurina, Hibrido de Timor and Rume Sudan, may give the greatest yield response, and depending on linkage of genes involved, homozygous transgressions

could be recovered which will be as good as the heterotic F_1's. However derivation of homozygous genotypes is a very long term process that would be most unsuitable for a perennial tree crop like coffee. On the other hand, the magnitude of hybrid vigour (see Tables 15 and 16) in some of the F_1 combinations may already, depending on other considerations, justify commercial production of F_1 hybrid varieties. This important aspect is a subject of further discussion in section 8.2.

Considering characters related to compact growth, Caturra is the most dominant parent for reduced height and infact appears to represent the limit to selection for reduced height, at least as far as this population is concerned (see Figure 8). In contrast, Laurina is the most recessive parent in this respect. For breeding purposes it should be easy to introgress the compact habit into new varieties by use of Caturra in crosses, since the character in this variety shows complete penetrance. Regarding angle of insertion, this study has shown that dominance effects are in fact not an important feature as far as variation among genotypes included in the diallel for this character is concerned. Examination of F_1 combinations involving Erecta as one of the parents revealed no single case of complete dominance for this character, except for a few hybrids showing partial dominance. Carvalho (1958) and Charrier (1978b) however, indicated that in their material the erect habit was completely dominant and the inheritance monofactorial.The disparities in these findings could probably be ascribed to differences in the expression of dominance in a different genetic background. It should be noted also that the above authors consider angle of insertion on basis of 3 classes (erect, semi erect and horizontal) and not as a continuous character, as was the case in this study.

In conclusion, it is evident from this study that many of the characters considered are fairly heritable (see Table 17) an indication that selection for these characters especially on the basis of plot means will yield rapid repose. It is however, worth noting that except for number of primaries, bearring primaries, angle of insertion of primaries, yield of cherry and clean coffee (after omission of three parents), estimates of narrow sense heritability for the other characters will be biased as a results of the presence of interactions among genes governing these particular characters (see section 4.4.). It is also worth noting that yield of cherry and clean coffee, based on three years of production, is heritable so long as it is considered on basis of plot means.

Broad sense heritability in this study, is of major interest especially for preselection purposes where the genotypic value of an individual rather than the breeding value only, is of central importance. This aspect is considered in the next chapter. Yield of cherry and clean coffee on plot mean basis, has such a high broad sense heritability (see Table 17), that it is already possible to distinguish with confidence among genotypes, those that are likely to be most productive.

5. CORRELATION AMONG GROWTH AND YIELD CHARACTERS

5.1. Introduction

Breeding programmes aimed at improved productivity in *C. arabica* have involved in the past straight selection for yield. This in many cases has had to require accumulated yield records taken over a considerable length of time (Antunes & Carvalho, 1957; Carvalho & Monaco, 1969; Monaco & Carvalho, 1969; Fernie, 1970). The significant phenotypic correlation observed in coffee between the first 2 — 3 years, and a total of 5 — 6 or more years of production (Stoffels, 1941; Krug & Carvalho, 1952; Dublin, 1967; Ferwerda, 1969), and between plant vigour and yield (see section 3.1.) however, suggest possibility of selecting for yield on young plants, on basis of plant vigour and/or a few years of yield. Walyaro and van der Vossen (1979) have indeed found that by applying an index based on yield of the first 2 — 3 years, measurements of girth of stem, and percent bearing primaries/or radius of canopy, the breeding cycle in coffee could be shortened to 5 years, representing a gain of 8 — 9 years, without much loss of selection efficiency. In that study however, girth measurements were recorded on mature trees whereas the other characters were recorded not on the original heads but on relatively young heads which had arisen as suckers from the original stems after change of cycle. Normally all such recordings would have been made during the first and second year of production.

The objectives of this Chapter therefore, were: 1) to provide additional information on genotypic and phenotypic correlation among various growth and yield characters, measured on fairly young coffee trees, 2) to demonstrate the usefulness of index selection with regard to yield improvement in *C. arabica*. and 3) to examine the relationship between performance of seedlings in the nursery, and the performance of the same plants in the field in order to verify whether this relationship can form a basis of preselection at the nursery stage.

5.2. Correlation between some morphological characters in the nursery and field performance of same plants

A number of growth characters were measured on about 1 year old seedlings of the diallel cross material while still in the nursery. Among the characters, the following were selected for this study: girth of stem, height of the seedling and mean length of 2 longest laterals (all the 3 characters were measured in cm), the number of laterals and number of leaves per seelding, area of a leaf (representing the mean of 10 leaves per seedling in cm^2) and angle of insertion of laterals on main stem (in ^{o}). Correlation coefficients

Table 18. Correlations between various morphological characters measured in the nursery, and compact growth characters and mean yield (cherry) of 3 years of the same genotypes measured in the field, on basis of progeny means.

Character (measured in nursery)	height	angle (measured in the field)	yield
1. girth	0.30*	0.09	0.08
2. height	0.91***	0.45***	0.12
3. no. of laterals	0.11	—0.23*	0.21*
4. length of longest lateral	0.68***	0.08	0.42***
5. no. of leaves	0.01	—0.25*	0.27*
6. leaf area	0.26*	0.65***	0.15
7. angle of laterals	0.16	0.77***	—0.02

of the form,

$$r = \frac{Cov_{xy}}{\sigma_x \sigma_y}$$

were computed on basis of means of the phenotypic values (≙genotypic values) between character x, measured in the nursery and character y, measured on the same genotype in the field. The characters considered in the field included, mean yield of the first 3 years of production in Kg/tree (only for the lower plant density), height, at 3 years after field planting (taken over both plant densities), and angle of insertion of primaries on the main stem (calculated over both plant densities and for the 2 repeated measurements at 12 and 36 months after field planting). The correlation coefficients betwen these characters are presented in Table 18.

Table 19. Form of analysis of variance and covariance and expectations of mean squares and mean products.

Source of variation	Degree of freedom(1)	Expectations of mean sqaures	Expectations of mean products
Replications	(r—1)	$\sigma^2_{wx} + g\sigma^2_{rx}$	$cov_{wxy} + g\ cov_{rxy}$
Genotypes	(g—1)	$\sigma^2_{wx} + r\sigma^2_{gx}$	$cov_{wxy} + r\ cov_{gxy}$
Genotypes x Reps	(g—1)(r—1)	σ^2_{wx}	cov_{wxy}

(1) r = number of replications = 3, g = number of genotypes = 66

Height of the seedling and angle of insertion of laterals on the main stem were highly positively correlated with the same characters measured on the trees in the field. Length of laterals per seedling showed significant, but low positive correlation with mean yield of the same genotype in the field.

5.3. Phenotypic and genotypic correlations among the various characters

Details of the characters used for the correlation study are given in sections 2.2.1. and 2.2.2. Among the repeated measurements of each character (see section 2.3.) only one measurement was selected. The selected measurements represent those taken between 1 year and 2½ years after field planting except for number of flowers per node which represents the measurement made 3 years after field planting, and yield of cherry which was based on 3 years of full production. The time of measurement of each of these characters is also given in Table 20.

To provide the estimates of variances and covariances, analysis of the form given in Table 19 was performed on data for these characters based on plot means. Included in the same table, are expectations of mean squares and mean products. From these analyses, genotypic and phenotypic correlations between characters x and y were estimated as,

$$\text{Genotypic correlation } (r_g) = \frac{\text{Cov}_{gxy}}{(\sigma^2_{gx}\ \sigma^2_{gy})^{½}}$$

and,

$$\text{Phenotypic correlation } (r_{ip}) = \frac{\text{Cov}_{gxy} + \text{Cov}_{wxy}}{[(\sigma^2_{gx} + \sigma^2_{wx})(\sigma^2_{gy} + \sigma^2_{wy})]^{½}}$$

where σ^2_{gx}, σ^2_{wx} and σ^2_{gy}, σ^2_{wy} are estimates of genotypic and environmental (on plot mean basis) variances of x and y respectively, and Cov_{gxy} and Cov_{wxy}, the genotypic and environmental covariances between characters x and y. These results are presented in Table 20.

The results indicate that genotypic correlations were in most cases higher than the phenotypic correlations and that there were some differences in the magnitude of both correlations for most characters, when estimated in each of the 2 plant densities. It can be concluded from this, that the inherent association between these characters is influenced to some extent by the external environment. Most growth characters were positively correlated with each other except for number of primaries, angle of primaries with the main stem and node production. The same positive relationship existed among yield characters the exception in this case being, the number of bearing primaries with flowers per node. Apart from percent fruit set,

Table 20. Genotypic (upper values) and phenotypic (lower values) correlations among growth and yield characters.

Character & age of plants in months	2.1[1]	2.2	3.1	3.2	4.1	4.2	5.1	5.2	6.1	6.2	7.1	7.2	8.1	8.2	9.1	9.2	10.1	10.2	11.1	11.2	12.1	12.2	13.1	13.2	14.1	14.2	15.1	15.2	16.1	16.2
1. G (18)	0.94	0.95	0.85	0.86	0.02	−0.03	0.79	0.70	0.80	0.72	0.40	0.26	−0.01	0.04	0.61	0.64	−0.48	−0.21	−0.01	−0.07	0.43	0.43	0.55	0.49	−0.02	−0.38	0.33	0.37	0.46	0.40
	0.83	0.85	0.69	0.73	0.10	0.04	0.73	0.60	0.74	0.60	0.38	0.23	−0.02	0.02	0.50	0.46	−0.24	−0.16	0.09	0.06	0.35	0.26	0.31	0.26	−0.06	−0.12	0.26	0.19	0.42	0.27
2. H (30)			0.89	0.92	0.03	−0.07	0.60	0.61	0.70	0.67	0.25	0.15	0.14	0.18	0.53	0.47	−0.55	−0.33	−0.06	−0.13	0.39	0.29	0.31	0.46	−0.05	−0.50	0.15	0.25	0.27	0.30
			0.85	0.86	0.08	0.03	0.56	0.51	0.65	0.64	0.25	0.12	0.10	0.14	0.47	0.43	−0.37	−0.22	0.02	0.02	0.28	0.17	0.19	0.25	−0.07	−0.22	0.11	0.19	0.27	0.24
3. Int L St (30)					−0.42	−0.44	0.70	0.72	0.80	0.79	0.52	0.43	0.31	0.29	0.68	0.51	−0.61	−0.46	−0.48	−0.45	0.21	0.23	0.32	0.60	−0.32	−0.72	0.40	0.17	0.13	0.25
					−0.37	−0.40	0.62	0.64	0.71	0.73	0.41	0.37	0.23	0.23	0.53	0.40	−0.45	−0.40	−0.38	−0.40	0.14	0.14	0.21	0.35	−0.17	−0.36	0.40	0.13	0.11	0.19
4. Pr (18)							−0.32	−0.44	−0.31	−0.42	−0.55	−0.57	−0.26	−0.23	−0.43	−0.23	0.10	−0.23	0.97	0.94	0.41	0.32	−0.13	−0.27	0.10	0.07	0.23	0.18	0.30	0.25
							−0.25	−0.34	−0.25	−0.37	−0.36	−0.44	−0.18	−0.13	−0.23	−0.07	0.12	0.26	0.88	0.87	0.19	0.09	−0.08	−0.15	0.01	0.06	0.11	0.06	0.29	0.10
5. R (12)									0.96	0.95	0.84	0.78	0.11	0.05	0.84	0.55	−0.30	−0.38	−0.25	0.32	0.32	0.37	0.79	0.72	−0.11	−0.40	0.48	0.43	0.57	0.46
									0.91	0.86	0.70	0.64	0.06	0.01	0.58	0.31	−0.22	−0.39	−0.14	0.28	0.30	0.27	0.49	0.42	−0.07	−0.13	0.39	0.24	0.50	0.35
6. Int L Pr (12)											0.84	0.75	0.28	0.11	0.83	0.50	−0.49	−0.57	−0.28	−0.32	0.38	0.37	0.72	0.69	−0.07	−0.51	0.46	0.42	0.58	0.52
											0.67	0.64	0.16	0.05	0.61	0.39	−0.32	−0.46	−0.17	−0.27	0.32	0.25	0.41	0.43	−0.03	−0.19	0.39	0.27	0.48	0.42
7. Le (24)													0.50	0.27	0.71	0.20	−0.35	−0.59	−0.43	−0.41	0.33	0.32	0.68	0.47	−0.02	−0.54	0.45	0.26	0.47	0.29
													0.32	0.12	0.54	0.12	−0.15	−0.46	−0.22	−0.30	0.26	0.21	0.36	0.29	−0.06	−0.20	0.31	0.06	0.35	0.26
8. Ang (12)															0.17	−0.47	−0.35	−0.58	−0.19	−0.13	0.28	0.40	0.20	−0.02	0.29	−0.48	0.01	−0.03	0.12	0.12
															0.14	−0.30	−0.18	−0.39	−0.13	−0.09	0.18	0.15	0.04	0.01	0.06	0.23	−0.02	−0.08	0.07	0.03
9. E (16–28)																	0.10	0.34	−0.42	−0.35	0.12	0.02	0.41	0.26	−0.22	−0.41	−0.23	−0.15	0.32	0.10
																	0.29	0.49	−0.17	−0.19	−0.00	−0.03	0.20	0.05	−0.22	−0.18	−0.08	−0.09	0.26	0.10
10. No (16.28)																			0.16	0.06	−0.37	−0.34	−0.20	−0.61	0.05	0.43	−0.01	−0.44	−0.12	−0.56
																			0.14	0.11	−0.33	−0.25	−0.13	−0.35	−0.06	0.13	−0.10	−0.23	−0.03	−0.44
11. B Pr (30)																					0.46	0.26	0.06	−0.12	0.64	0.76	0.41	0.38	0.40	0.30
																					0.31	0.16	−0.01	−0.07	0.32	0.41	0.29	0.22	0.37	0.17
12. B No$_1$ (12)																							0.41	0.32	0.74	0.20	0.45	0.49	0.62	0.60
																							0.19	0.09	0.35	0.11	0.34	0.29	0 50	0.41
13. Fl No (36)																									0.10	0.07	0.89	0.68	0.76	0.70
																									0.07	0.06	0.37	0.21	0.52	0.41
14. Fr S (30)																											0.46	0.55	0.56	0.30
																											0.17	0.25	0.31	0.16
15. Be No (24)																													0.93	0.90
																													0.55	0.43
16. Yield (mean of 3 years)																														

[1] Lower plant density and higher plant density are designated .1 and .2 respectively.

number of bearing primaries, angle of primaries and node production, most yield characters were in general, positively correlated with growth characters.

Of some interest however, is yield of cherry which was positively associated with most growth and yield characters except for internode length on main stem, angle of primaries, and node production. Among growth characters, internode length on primaries, canopy radius, girth and leaf area showed fairly high positive correlation with yield. Most yield characters on the other hand, and especially berries per node, flowers per node and percent bearing nodes, showed even higher positive correlation with yield.

The above results, are in fairly close agreement with those observed by Walyaro and van der Vossen (1979) and by Srivinasan (1980) using different materials of arabica coffee.

Apart from getting an impression of the overall interrelationship among the various characters, it is also important to investigate the possible application of such information in breeding and selection in *C. arabica*. The next section is devoted to this particular aspect.

5.4. Possibilities of selection for yield on young coffee trees

5.4.1. Definition and derivation of a selection index

Index selection in this context was regarded as an aid in early evaluation of yield potential achieved by incorporating information from a number of secondary or auxiliary characters, with early yield performance of the different genotypes under consideration. It therefore becomes obvious by definition that such index selection cannot be regarded in the conventional sense as a mass selection method. To make the distinction clear the index will be referred to as a preselection index.

Apart from yield of cherry for the first 2 years, the following characters were chosen to construct the various indices: girth of stem, radius of canopy, internode length on primaries, bearing primaries and percent bearing nodes. Among the criteria for selecting these characters were: 1) high genotypic correlation with yield of 3 years, 2) proportion of genotypic to phenotypic variation of character when measured on young coffee plants 3) relative ease of measurement and 4) the genotypic correlations among the secondary characters themselves. Regarding the last criterion, secondary characters which are highly correlated are most unsuitable when combined in the same index, reason why for instance, radius of canopy and internode length on primaries were never used together in constructing one particular index.

These characters were used to construct indices of the standard form,

$$I = \Sigma\, b_i\, x_i$$

where b_i are the relative weights in the index obtained from solution of multiple equations of phenotypic and genotypic variances and covariances, and x_i are the phenotypic values on individual tree basis of the correlated or secondary traits. This method is analogous to that which was proposed by

Table 21. Phenotypic variances (in brackets) and covariances for a number of selected Characters[1], and genotypic covariances for the same characters with yield of cherry (the last row and column), used to construct preselection indices in Tables 22 & 23. All variances and covariances are on individual tree basis. Values for the lower plant density and higher plant density are above and below the diagonal respectively.

	1	2	3	4	5	6	7	8
	(3.9368)	12.7290	0.8576	2.8389	5.7383	3.1859	4.6640	2.1904
	1	(92.9297)	5.4134	1.1445	27.7114	14.8087	24.5479	15.7593
		2	(0.4475)	−0.2121	1.7878	0.9465	1.5067	1.1079
1	(2.7105)		3	(52.6715	14.2861	10.6669	16.4600	6.5876
2	8.3782	(109.0705)		4	(94.4607	6.7440	14.4350	10.7786
3	0.5218	5.6128	(0.5410)		5	(17.0115)	21.3587	9.1071
4	1.2264	−16.6555	−1.0782	(51.9190)		6	(40.1198)	(16.990)
5	2.2036	23.3354	1.3275	6.2354	(119.4350)		7	(16.990)
6	1.0505	5.9670	0.5119	3.1859	7.3689	(8.9446)		8
7	1.0855	9.7877	0.8788	0.7111	12.0838	10.7573	(16.6534)	
8	0.9519	7.4017	0.6640	3.2291	6.5386	3.7981	(5.5634)	5.5634)

(1) 1 = girth of stem, 2 = canopy radius, 3 = internode length on primaries, 4 = bearing primaries, 5 = % bearing nodes, 6 = yield of 2 years, 7 and 8 = yield of 3 years (7 = phenotypic, covariances and variances, 8 = genotypic covariances and variances).

Robinson et al. (1951) and further discussed by Manning (1965)and Brim et al. (1959), and has been used in a number of investigations with different crops. The efficiency of various indices relative to direct evaluation on yield on basis of early yield alone was then estimated in this study as,

$$(b_i G_{iy})^{1/2} / (\sigma^2_{gy} / \sigma_{py}),$$

where $G_{iy's}$ are the genotypic covariances of the various auxiliary characters, with the desired character i.e. yield over 3 years, and σ^2_{gy} and σ_{py} are the genotypic variance and phenotypic standard deviation of yield (over 3 years) respectively. If the above genotypic variances and covariances depend only on additive effects, multiplying the above relation by selection intensity i would give the efficiency, in the familiar form of expected genetic advance from index selection relative to direct selection (Brim et al., 1959; Falconer, 1960).

Because the total variation among the genotypes of the diallel is being considered, the genotypic variances and covariances, respectively σ^2_{gx} and Cov_{gxy} (see Table 19), represent both additive and/or additive x additive effects of genetic variation and covariation, as well as the non additive genetic effects. It should be noted, that the error variance and covariance, σ^2_{wx} and Cov_{wxy} as derived in Table 19 and used for calculating phenotypic correlations in Table 20, are both based on plot means. The error appropriate for individual trees will be *m* times the error variance or covariance derived from Table 19, where m (= 4) is number of trees per plot (i.e. from which the mean was derived). The phenotypic variances and covariances given in Table 21 represent therefore ($\sigma^2_{gx} + m\,\sigma^2_{wx}$) and ($Cov_{gxy} + m\,Cov_{wxy}$) respectively, as these are calculated on individual tree basis.

5.4.2. Results

In Tables 22 and 23 are given, for the lower and higher plant densities, the expected improvement in yield, and the relative efficiency resulting from application of various preselection indices. Some of the indices con-

Table 22. Efficiency of various preselection indices relative to direct evaluation of yield potential on basis of early yield alone at the lower plant density.

Index No.[1]	Content of preselection index (1)	Expected yield increase(2)	Efficiency %
	x_7	2.54	100
1.	$0.56x_1$	1.10	43
2.	$0.17x_2$	1.64	64
3.	$2.48x_3$	1.66	65
4.	$0.13x_4$	0.91	36
5.	$0.11x_5$	1.11	44
6.	$0.54x_6$	2.21	87
7.	$0.29x_1 + 0.20x_2$	1.94	76
8.	$0.20x_1 + 0.61x_7$	3.20	126
9.	$0.10x_2 + 0.84x_6$	3.05	120
10.	$0.08x_2 + 0.58x_7$	3.27	129
11.	$3.56x_3 + 0.22x_4$	2.33	91
12.	$1.69x_3 + 0.84x_6$	3.08	121
13.	$1.52x_3 + 0.58x_7$	3.31	130
14.	$0.14x_4 + 0.23x_5$	1.86	73
15.	$0.17x_5 + 0.57x_7$	3.32	131
16.	$-0.06x_1 + 0.09x_2 + 0.59x_7$	3.23	129
17.	$-0.05x_1 + 3.63x_3 + 0.22x_4$	2.33	92
18.	$-0.17x_1 + 1.82x_3 + 0.59x_7$	3.33	131
19.	$0.09x_2 + 0.03x_4 + 0.57x_7$	3.27	129
20.	$0.05x_2 + 0.18x_5 + 0.81x$	3.19	126
21.	$0.04x_2 + 0.16x_5 + 0.55x_7^6$	3.35	132
22.	$1.60x_3 + 0.04x_4 + 0.56x_7$	3.32	131
23.	$1.03x_3 + 0.15x_5 + 0.54x_7$	3.39	133
24.	$-0.09x_1 + 0.10x_2 + 0.03x_4 + 0.57x_7$	3.28	129
25.	$-0.41x_1 + 1.74x_3 + 0.19x_5 + 0.84x_6$	3.27	129
26.	$0.04x_2 - 0.01x_4 + 0.16x_5 + 0.55x_7$	3.35	132
27.	$1.03x_3 - 0.02_{x4} + 0.15x_5 + 0.54x_7$	3.38	133
28.	$-0.18x_1 + 0.07x_2 - 0.01x_4 + 0.16x_5 + 0.57x_7$	3.37	132
29.	$-0.33x_1 + 1.64x_3 + 0.02x_4 + 0.16x_5 + 0.55x_7$	3.42	135
30.	x_8	3.42	135

(1) x_1 = girth of stem, x_2 = radius of canopy, x_3 = internode length on primaries, x_4 = bearing primaries, x_5 = % bearing nodes, x_6 = yield (cherry) of 2 years, x_7 = yield of cherry of 3 years (individual tree), x_8 = yield of cherry of 3 years (on plot mean basis).

(2) This was calculated for yield of 3 years as $\sigma^2_{gy}/\sigma_{py}$, but for other indices as $\Sigma(b_i G_{iy})^{1/2}$; the definition of these quantities is given in the text.

structed included also yield of 3 years as a secondary character. The inclusion of 3 years yield was deliberate and the reason for doing so will become obvious later on. Another character X_8, represents also yield of 3 years but gives the relative efficiency of basing selection on the mean yield of a number of trees per genotype rather than on individual tree performance.

It is clear from the 2 tables the many of the preselection indices, especially those including yield of the first 2 or 3 years of production, were much more efficient than direct selection based on 3 years yield performance of individual trees. Furthermore, a number of these indices are already as efficient as straight selection for yield potential based on mean yield of a number of trees per genotype (index number 30). As is mentioned in section 4.6. mean yield on basis of plot means for 3 years of production has such a high broad sense heritability that it is justified to regard it as the ultimate desired character.

Table 23. Efficiency of various preselection indices relative to direct evaluation of yield potential on basis of early yield alone, at the higher plant density.

Index No.	Content of preselection index (1)	Expected yield increase(2)	Efficiency (%)
	x_7	1.36	100
1.	$0.35x_1$	0.58	43
2.	$0.07x_2$	0.71	52
3.	$1.23x_3$	0.90	66
4.	$0.06x_4$	0.45	33
5.	$0.05x_5$	0.60	44
6.	$0.42x_6$	1.27	93
7.	$0.29x_1 + 0.08x_2$	0.93	68
8.	$0.31x_1 + 0.56x_7$	1.84	135
9.	$0.06x_2 + 0.71x_6$	1.78	131
10.	$0.05x_2 + 0.55x_7$	1.85	136
11.	$1.94x_3 + 0.14x_4$	1.32	97
12.	$1.00x_3 + 0.70x_6$	1.82	134
13.	$0.46x_3 + 0.55x_7$	1.83	134
14.	$0.08x_4 + 0.13x_5$	1.05	77
15.	$0.08x_5 + 0.52x_7$	1.85	136
16.	$0.20x_1 + 0.04x_2 + 0.54x_7$	1.87	137
17.	$0.13x_1 + 1.81x_3 + 0.13x_4$	1.33	97
18.	$0.28x_1 + 0.19x_3 + 0.55x_7$	1.85	136
19.	$0.07x_2 + 0.12x_4 + 0.53x_7$	1.97	144
20.	$0.05x_2 + 0.08x_5 + 0.65x_6$	1.84	135
21.	$0.04x_2 + 0.07x_5 + 0.50x_7$	1.89	139
22.	$0.73x_3 + 0.11x_4 + 0.52x_7$	1.93	142
23	$0.38x_3 + 0.08x_5 + 0.49x_7$	1.87	137
24.	$0.07x_1 + 0.79x_3 + 0.08x_5 + 0.63x_6$	1.88	138
25.	$0.06x_1 + 0.07x_2 + 0.11x_4 + 0.53x_7$	1.97	144
26.	$0.06x_2 + 0.11x_4 + 0.06x_5 + 0.49x_7$	1.99	146
27.	$0.63x_3 + 0.10x_4 + 0.07x_5 + 0.48x_7$	1.96	144
28.	$0.07x_1 + 0.06x_2 + 0.10x_4 + 0.06x_5 + 0.49x_7$	1.99	146
29.	$0.16x_1 + 0.46x_3 + 0.09x_4 + 0.07x_5 + 0.48x_7$	1.97	144
30.	x_8	1.93	141

(1) x_1 = girth of stem, x_2 = radius of canopy, x_3 = internode length on primaries, x_4 = bearing primaries, x_5 = % bearing nodes, x_6 = yield (cherry) of 2 years, x_7 = yield (cherry) of 3 years (on individual tree basis), x_8 = yield of cherry of 3 years (on plot mean basis).

(2) See footnote in Table 22.

5.5. Discussion

5.5.1. Causes of correlation among characters

It is often useful to consider possible causes of correlation between characters because such information may have important practical consequences on the effect of correlated characters in improvement of a given character. Genetic causes of correlation between metric characters have been ascribed chiefly to pleiotropy, but in some cases to close linkage between genes regulating the two characters (Falconer, 1960). Though pleio-

tropy is a common property of major genes, there is little evidence of pleiotropic gene action of polygenes as major causes of correlation between characters (Mather & Jinks, 1971). Janssens (1979) in discussing relations between coheritability, correlated response, linkage and pleiotropy in cases of polygenic inheritance, concluded according to his hypothesis, that cases of pure polygenic pleiotropic inheritance were probably exceptions. For the characters which he considered, pleiotropy was shown to be relatively unimportant compared to linkage as a cause of association between characters. Genetic correlations among multiple traits however, can also be physiological or due to allometry of development (Grafius, 1978).

In the present study, the correlations observed among growth and yield characters are probably a result of linkage and/or physiological and developmental relationships among these characters. Of particular significance however, are the positive correlations between yield and most of the other characters (section 5.3.) indicating that it is possible to manipulate some of these characters in yield improvement programmes. On the other hand, the fairly low correlation between yield and height or internode length of the stem, imply that it is possible to select for compact plant types in this population with little or no effect on productivity.

5.5.2. Selection on nursery plants

The high positive correlation between height of the seedlings and that recorded on mature trees in the field, and between angle of insertion of laterals on the main stem of seedlings and the angle of laterals of field trees (Table 18 indicate that effective slection for these characters can already be performed on seedlings in the nursery. Carvalho & Monaco (1969) have also indicated that genetic studies of some morphological characters for instance, branching system, leaf shape and colour, can be carried out on seedlings in the nursery. Regarding yield however, nursery selection is clearly not feasible. Length of the longest lateral is the character most correlated with yield; though the correlation coefficient ($r = 0.42$) is highly significant, it accounts for about only 20 percent (r^2) of the variability observed among genotypes for yield. Though the very poor performing seedlings can already be discarded in the nursery, as indeed is the normal practice, effective selection for yield will have to depend on growth and yield characters as measured in the field, in addition to early yield performance

5.5.3. Selection for yield in arabica coffee

Accumulated yield of the first few years of production is of considerable practical value especially as concerns selection for yield potential in coffee (Krug & Carvalho, 1952; Monaco and Carvalho, 1969; Ferwerda et al., 1969). Furthermore, the efficiency of selection for yield can be considerably enhanced by incorporating information from certain growth and yield characters with early yield (Walyaro & van der Vossen, 1979). The result would be a substantial saving on the length of the breeding cycle in coffee.

This in general however, is only true so long as selection is based on progeny means, or on the means of a number of trees representing each genotype, as opposed to within progeny or individual tree selection.

In breeding programmes involving a perennial tree crop like coffee, it would be most economical if selection for yield were to be based on performance of individual trees in their early years of production. This, in the first instance, would avoid the problem of basing selection on progeny tests and secondly, it would enable selection for yield to be practised on individual trees even in early segregating generations. It would therefore be no longer necessary to retain most of the genotypes in breeders population in order to practice selection in fairly advanced generations of inbreeding. Clearly this particular aspect is crucial as it implies more effective and efficient breeding procedures in coffee. Early generation evaluation however, requires that the characters in question have high heritability to enable selection to be performed at the individual plant level. In coffee, on the other hand, yield of individual trees even when considered over several successive years, is not a very heritable trait. It cannot therefore be expected to form an efficient basis for early evaluation of yield potential of individual trees. Indeed Fazuoli & Carvalho (1979), found that selection of the best individual plants needed to be based on the first 10 - 12 years of production in order to include the year of maximum production.

Results obtained in the present study (section 5.4.2.) however indicate that selection based on a number of indices (Tables 22 & 23) involving various growth and yield characters plus yield of the first 2 or 3 years of individual trees, will be more efficient than that based on the first 3 years yield of individual trees alone, and is just as efficient as that which is based on mean yield of a number of trees per genotype. In other words application of such preselection indices will allow evaluation for yield potential to be performed on individual trees during their early years of production, thus making it possible to select and retain already in the segregating generations only superior individual genotypes that are most likely to be high yielding even in later years of production.

As was mentioned in section 5.4.1., such indices as given here are for preselection purposes and can only be applied to the population for which they have been constructed. For subsequent generations derived from the same population, or for other different populations, indices based on similar characters but with different genetic content will have to be constructed, again using information obtained from that respective population. This is so because genetic correlations among characters, depending on the causes of such correlations, may differ in different populations or even in different environments. Furthermore, even if the genes affecting the correlated characters were pleiotropic, continued selection for these characters in later generations of the same population, may eventually result in these genes being rapidly brought to fixation and thereafter no correlated response will be observed (Falconer, 1960). Nonetheless, evaluation of a given population of coffee, may reveal other characters or different combinations of such characters as were found in this study, which are responsible for some or most of the variation observed among genotypes for yield. Such characters

would then be selected for inclusion in a preselection index.

Of even more concern, is that this expression of the best genotypes on basis of early yield alone may not always be true with all populations of arabica coffee. Indeed this was observed in Brazil in connection with alien germplasm from Ethiopia, and prompted Monaco (1977) to conclude that for heterogeneous germplasm, a minimum of 12 years is required before selection is made on basis of productivity. These results may have been due to large effects of genotype-environment interactions masking the true performance of genotypes (see also section 3.8.). In this case, additional use of information on certain growth and yield characters, rather than early yield alone, may have provided a better indication of the actual yield of the different genotypes. As was indicated also in section 3.8., yield response of genotypes to different environments depends in some degree on the vegetative vigour and the performance in terms of certain yield characters of a given genotype. It is also possible that some of the collections in the Ethiopian material may have been late yielding genotypes. These late yielders however, may not be of any particular significance, unless of course they are outstanding for other traits of economic importance, in which case they would have to be considered in a different perspective. Otherwise, to the coffee growers, such genotypes are already highly unsuitable. In a breeding programme aimed specifically at yield improvement therefore, the precocious genotypes are the ones to be given most consideration.

6. VARIATION FOR COFFEE QUALITY CHARACTERS

6.1. Introduction

Coffee quality is the single important factor that determines the relative price of a given quantity of coffee. The Kenyan arabica coffee, is always sold at a premium price on international coffee markets because of its distinctive fine quality and is always used for blending with other inferior coffees in order to upgrade them. The Kenya coffee industry, including the farmer, is very much aware of this and always strives to maintain or even improve the quality of the Kenyan coffee. Indeed, in the breeding programme at the CRS (Ruiru), assessment of coffee quality is regarded as important as productivity and disease resistance (van der Vossen, 1973).

Coffee quality depends on bean size and liquor quality. The growing conditions of a coffee tree in the field have considerable influence on bean size, and so is the stage of harvesting of cherries and the mode of processing on the final assessment of liquor quality. Apart from these factors, it is also true that certain of the quality characteristics are inherent to a varying degree (Fernie, 1965; Carvalho & Monaco, 1969). On basis of repeatability, van der Vossen and Walyaro (1977) concluded that the proportion of genetic variation to total phenotypic variation was high for most berry and bean characters. They also reported significant differences among 8 varieties of arabica coffee for various liquor quality attributes. Precise information on how consistent especially the liquor quality characteristics are for a given genotype is however lacking. Unlike berry and bean characters, liquor quality is assessed organoleptically, which is regarded as being subjective (Wootton, 1967; Kulaba, 1979) and therefore not very reliable. It would indeed be of considerable advantage if scientific procedures were developed which relate quality to specific content of compounds found in the bean. However, no such satisfactory method has so far been developed.

This Chapter is concerned with variability observed among 11 coffee varieties (see section 2.1.) and their hybrids for various quality characters (see sections 2.2.3. and 2.2.4.) over three years at two plant densities, with the aim of providing information on how consistent and heritable the berry and bean characters are, and whether the present method of liquor quality evaluation can be considered for breeding purposes as a basis of selection for liquor quality. The mode of genetic variation and combining ability of the various parental varieties for these quality attributes are also considered.

6.2. Phenotypic variation and repeatability of coffee quality characters

Results given in Table 25 for berry and bean characters were derived in a similar manner to those in Chapter 3, Table 5, where analyses for a given character, were performed separately for each successive measurement and

each plant density. The analyses were of the form given in section 2.3. For most berry and bean characters, unlike growth and yield characters, the lattice square was found not to be that superior to the randomised block design. It was therefore not necessary to adjust the values of genotypes, for all of these characters, according to the lattice square. Like in Table 5, the overall means given in Table 25 represent at one particular measurement in each plant density, the means of all the genotypes, and the standard errors are for the means of each genotype over 3 replications. The F values give significance level of genotypic effects as tested against genotypes x replications mean square (= E_T in Table 2). As was mentioned in section 2.3., liquor quality characteristics were determined 6 times for each genotype (one determination for each density every year, for 3 years). Hence only one analysis of variance was performed for each characteristic. For these liquor quality characteristics, analysis according to the lattice square could not be performed because these were assessed on plant density basis rather than on replication basis. In the same Table 25b, the range, the standard error of phenotypic means and the coefficient of variation are given, in addition to the overall mean, F values and repeatability, in this case on basis of each determination per plant density.

Repeatability coefficients given in Table 25, were calculated differently from those in Chapter 3, Table 5. These were derived according to Table 24, where the overall analysis of variance contained as sources of variation, between genotypes mean squares and error mean squares which include the mean square components of years and density effects together with their interactions with genotypes, plus the pooled error mean squares.

Genotypic effects for most quality characters (Table 25) were highly significant except for the last measurement of percent outturn, at the higher plant density, and for body, which was significant, but only at P(= 0.05). From the F values, it can be concluded that variation among genotypes for berry and bean characters is in general greater than for liquor quality attributes. Genotypes at the higher plant density, on average, in relation to the

Table 24. Form of analysis of variance for deriving repeatability(2) coefficients for quality characters.

Source of variation	Degrees of freedom(1)	Expectations of mean squares	
		plot mean basis	Plant density basis
Genotypes	(g−1)	$\sigma^2_w + r\sigma^2_e + re\sigma^2_g$	$\sigma^2_w + e\sigma^2_g$
Environments/genotypes x environ.	g(e−1)	$\sigma^2_w + r\sigma^2_e$	σ^2_w
Pooled error	e(g−1)(r−1)	σ^2_w	

(1) e = number of environments, g = number of genotypes, r = number of reps.

(2) R (plot basis) = $\frac{\sigma^2_g}{\sigma^2_g + \sigma^2_e + \sigma^2_w}$ or $\frac{\sigma^2_g}{\sigma^2_g + r\sigma^2_w}$ (for characters estimated on plant plant density basis)

R (individual tree basis) = $\frac{\sigma^2_g}{\sigma^2_g + \sigma^2_e + n\sigma^2_w}$

where n = number of trees/plot = 4

Table 25. Phenotypic variability of repeated measurements of berry, bean and liquor quality characteristics in a diallel cross among 11 varieties of *C. arabica*. First line, 3333 trees ha^{-1}, second line 6667 trees ha^{-1}.

a. berry and bean characteristics

Character	Overall means and standard errors of phenotypic means			F values and P(3)			Repeatability	
	Year			Year			$r^{(1)}$	$r^{(2)}$
	1	2	3	1	2	3		
1. Single berry weight (g)	2.1, 0.12	2.3, 0.10	2.1, 0.08	7.5***	17.3***	26.9***		
	2.2, 0.10	2.5, 0.12	2.3, 0.11	15.1***	16.6***	19.1***	0.74	0.49
2. Pulp (%)	70.7, 1.25	70.8, 1.45	68.9, 0.87	2.7***	2.5***	5.9***		
	70.2, 1.02	70.9, 1.27	69.5, 1.04	3.9***	2.4***	3.1***	0.32	0.12
3. Outturn (%)	13.9, 0.63	13.4, 0.46	15.2, 0.57	2.8***	4.7***	3.3***		
	14.5, 0.53	13.2, 0.56	14.9, 0.75	2.6***	2.3***	1.4	0.20	0.08
4. PB %	21.3, 2.82	22.8, 2.28	18.5, 1.70	7.1***	11.3***	25.2***		
	26.5, 2.67	23.2, 2.72	21.5, 2.75	15.1***	8.3***	10.3***	0.66	0.40
5. AA (%)	21.8, 3.75	26.3, 3.96	28.5, 3.35	9.3**	7.4***	18.5***		
	31.5, 3.11	28.6, 4.27	29.9, 3.92	18.2***	7.6***	11.4***	0.70	0.41
6. AB (%)	26.6, 4.47	21.3, 3.59	26.3, 3.14	5.1***	7.6***	15.6***		
	24.9, 3.90	20.6, 4.65	23.5, 4.16	13.2***	5.7***	7.7**	0.64	0.35
7. TT (%)	19.5, 3.26	20.9, 3.83	19.2, 3.36	2.8***	3.7***	4.1***		
	10.0, 2.15	20.3, 5.08	17.0, 2.43	2.3**	2.2**	4.8**	0.22	0.09
8. C (%)	7.2, 2.04	5.4, 1.27	4.8, 0.89	10.3***	34.0***	47.7***		
	4.2, 0.80	3.7, 1.12	4.4, 1.40	33.3***	4.7***	14.2***	0.71	0.49

b. Liquor quality

Character	Phenotypic means		Overall mean	C/V (%)	F value and P(4)	Repeatability (r)
	range	S.e				
1. acidity	0.92 – 2.25	0.17	1.68	25	2.03***	0.15
2. body	0.92 – 2.17	0.20	1.53	31	1.6*	0.08
3. flavour	2.22 – 3.97	0.20	3.26	15	3.1***	0.23
4. standard	2.25 – 4.20	0.16	3.36	11	7.0***	0.48

(1) Repeatability on plot mean basis (i.e. 4 trees)

(2) Repeatability on individual tree basis

(3) Error Df was 160

(4) Error Df was 325

lower plant density tended to have higher single berry weight, a higher percentage of PB, and AA but a lower proportion of AB, TT, and C beans (see overall means, Table 25). Again from the F values and P in the same table, it is evident that variation observed among genotypes for each character over successive measurements does not necessarily vary according to the age of plants on which the characters were assessed. This is unlike what was observed for some growth characters in section 3.2.

Repeatability was high for most berry and bean characters, especially for single berry weight, percent PB, AA, AB and C, but low for liquor quality characteristics with the exception of overall standard, which had fairly high repeatability. The coefficient of variation (Table 25b) was fairly low for overall standard in particular, and flavour, and could be regarded as being within the range of variation that is encountered in many experiments.

6.3. Effect of genotype-environment interactions on quality characters

Analysis of genotype-environment interactions for quality characters was performed as given in section 2.5.2. Whereas differences due to genotypes were highly significant for practically all the quality characters (Table 26), differences due to linear regression or to pooled deviations from linear regression, in this case for berry and bean characters only, were not as highly significant and in some cases were not significant at all. There were indeed significant differences among genotypes, in linear response to environments for single berry weight, percent PB, AA, C and the overall standard, and also for deviations from linear regression for %PB, %AA, %AB and %C. On the other hand, even for those characters where one or both of the genotype x environment interactions were significant, their magnitude in terms of mean squares compared to mean squares for the overall genotypic effects, or compared to the pooled error mean squares, indicate that these interactions are in general not an important source of variation among genotypes, at least in the environments considered here.

Furthermore if for example, a comparison is made between mean squares (in Tables 6 and 26) for pooled genotype x environment interactions (σ^2_{gxe}) and the mean squares for the genotypic component (σ^2_g) for the same character, derived from expectations of mean squares, the ratio ($\sigma^2_{gxe}/\sigma^2_g$) is found to be 0.40, 0.33 and 1.51 for girth, height and yield of cherry respectively, whereas for the quality characters, single berry weight,%PB and %AA the same ratio is only 0.10, 0.18 and 0.16. It is because of such considerations that a detailed study of genotype-environment as given in Chapter 3, for growth and yield characters was found unnecessary for these quality characters.

6.4. Genetic variation for quality characters

6.4.1. Analysis of combining ability

The analysis for berry and bean characters is according to the method of Gerretsen and Keuls (1973, 1978) given in section 2.5.2. For liquor quality

Table 26. Analysis of variance for berry bean and liquor quality characteristics.

Source of variation	Df	Mean Squares and P			
		S. berry Wt. (g)	Pulp (%)	Outturn (%)	PB %
Genotypes (G)	80	0.94***	16.77***	3.50***	376.26***
G x environ (linear)	80	0.02**	1.61	0.49	15.84**
Pooled deviations	320	0.01	1.77	0.46	10.32*
Pooled error	960	0.01	1.36	0.35	6.35
		AA (%)	AB (%)	TT (%)	C (%)
Genotypes (G)	80	827.60***	685.29***	132.99***	161.89***
G x environs (linear)	80	31.96**	19.82	17.83	11.32***
Pooled deviations	320	21.37*	26.41***	18.32***	4.28***
Pooled error	960	14.05	16.03	12.93	1.74
		acidity	body	flavour	standard
Genotypes (G)	65	0.36***	0.36**	0.76***	0.95***
G x environs (linear)	65	0.14	0.19	0.27	0.19**
Pooled deviations	260	0.18	0.24	0.25	0.13

Table 27. Expectations of mean squares in terms of genetic effects and environmental variation in an incomplete and complete diallel among 11 varieties of arabica coffee, repeated over a number of environments.

Source of variation	df[1]	Incomplete diallel[2]	complete half diallel[3]
GCA	(n−1)	$\sigma^2_w + r\sigma^2_{gxe} + 16.12re\sigma^2_g$	$\sigma^2_w + 13e\sigma^2_g$
SCA	½n(n−1)	$\sigma^2_w + r\sigma^2_{gxe} + 1.45re\sigma^2_s$	$\sigma^2_w + e\sigma^2_s$
REC	½n*(n*−1)	$\sigma^2_w + r\sigma^2_{gxe} + re\sigma^2_{rec}$	
Genotypes x environments	(g−1)(e−1)	$\sigma^2_w + r\sigma^2_{gxe}$	σ^2_w
Within error	e(g−1)(r−1)	σ^2_w	

(1) n = 11, number of parents in the incomplete diallel; n* = 6, number of parents involved in reciprocal crosses; g = 81, or 66, number of genotypes in the incomplete or complete diallel respectively; e = 6, number of environments; r = 3, number of replications per each plant density.

(2) Coefficients of σ^2_g and σ^2_s i.e 16.12 and 1.45 are derived using the method of Garretsen & Keuls (1973, 1977).

(3) Coefficients of σ^2_g and σ^2_s are according to Griffing (1956), Model 1. for both incomplete and complete half diallels, σ^2_g and σ^2_s represent respectively general combining ability effects $\frac{1}{(p-1)}\Sigma g^2_i$ and specific combining ability effects $\frac{1}{p(p-1)}\Sigma\Sigma s_{ij}$ using the notation of Griffing (1956) for fixed effects.

attributes, the data were analysed as for a complete half diallel using the method of Griffing (1956). The resutls are presented in Table 27. General combining ability (GCA) and specific combining ability (SCA) were both highly significant for the berry and bean characters considered, as well as for overall standard. There were also significant differences among genotypes with regard to acidity, body and flavour for GCA but not for SCA. The variance component due to GCA, taking into account expectations of mean squares, was always greater than that for SCA. Reciprocal effects were highly significant for all berry and bean characters given in Table 27.

Table 28 gives the expectations of mean squares of analysis of variance for incomplete and complete half diallel assuming the parents are a fixed sample. The coefficient (1.45) for SCA effects σ^2_s for the incomplete diallel is

Table 28. Analysis of variance for incomplete diallel for berry and bean characters, and for a complete half diallel for liquor characteristics; and proportions of genetic effects to total phenotypic variation for the same characters.

Source of	Df	Mean squares and P			
		S. berry wt (g)	PB (%)	AA (%)	AB (%)
GCA	10	1.11***	378.22***	823.88***	770.46***
SCA	55	0.02***	21.10***	46.37***	21.81***
REC	15	0.01***	6.65***	16.41***	15.57***
G x E	400	0.003*	1.90*	3.92*	4.18*
Within error	960	0.002	1.06	2.34	2.67
T_n		0.70(−0.02, + 0.01)	0.53(−0.03, + 0.02)	0.53(−0.03, + 0.02)	0.54(−0.01, + 0.02)
T_b		0.81(+ 0.01, −0.01)	0.73(+ 0.02, −0.02)	0.74(+ 0.02, −0.01)	0.68(+0.01, −0.01)
		acidity	body	flavour	standard
GCA	10	0.20***	0.19***	0.55***	0.86***
SCA	55	0.03	0.04	0.05	0.04***
Error	325	0.03	0.04	0.04	0.02
T_n		0.15	0.09	0.23	0.44
T_n		–	–	–	0.51

approximate. It is however possible to place limits to this coefficient by considering the case as if it were for a complete half diallel with a coefficient of 1, or a complete full diallel with a coefficient of 2. The differences in magnitude of ratios T_n and T_b estimated thus are given, in brackets, in Table 27. It appears, in this case, that the approximation is fairly satisfactory for the purpose of estimating these ratios. The ratio of GCA effects, to total phenotypic variation, T_n, and that of total genotypic effects including GCA effects, SCA effects and reciprocal effects, to total phenotypic variation, T_b were both estimated, on plot mean basis, or on density basis, for liquor quality characters, as

$$T_n = \frac{2\sigma^2_g}{2\sigma^2_g + \sigma^2_s + \sigma^2_{rec} + \sigma^2_e}$$

and

$$T_b = \frac{2\sigma^2_g + \sigma^2_s + \sigma^2_{rec}}{2\sigma^2_g + \sigma^2_s + \sigma^2_{rec} + \sigma^2_e}$$

σ^2_g, σ^2_s and σ^2_{rec} are defined in Table 28. σ^2_e is the environmental variance derived, for berry and bean characters as $\sigma^2_{gxe} + \sigma^2_w$; for liquor quality characters, $\sigma^2_e = \sigma^2_w$.

Estimates of T_n and T_b for the various quality characters are given in Table 27. The variance components were calculated from results given in Table 27 except the mean squares in this Table had to be adjusted by multiplying with certain factors. This is so because the mean squares in Table 27 are based on the mean phenotypic values over 3 years and 2 densities while the ratios T_n and T_b are calculated on plot basis, or density basis (for liquor quality characters). For single berry weight, %PB, %AA and %AB, the mean squares in Table 27 are adjusted by multiplying each by 18, the number of observations from which each phenotypic mean was derived, i.e. 3 years x 2 plant densities x 3 replications. For liquor quality characters, the mean squares are first multiplied by 6, the number of determinations per genotype. In addition where SCA mean squares were not significant, these were pooled with the error mean squares, especially for liquor quality characters.

It is clear from Table 27, that the proportion of total phenotypic variation that is genetic was high for berry and bean characters given here, and for the overall standard but fairly low for the rest of the liquor quality attributes, confirming results on repeatability in Table 26. The ratio of total genotypic effects to total phenotypic variation, T_b was particularly very high for single berry weight, %PB and %AA.

6.4.2. Combining ability of individual genotypes

The following parents, SL34, SL28, K7 and Hibrido de Timor were characterised by high single berry weight and high proportions of AA beans but low proportions of AB beans (See Table 29). These parents also showed high GCA for single berry weight and %AA but had significantly negative GCA for % AB, except for SL34. Pretoria also had high single berry weight and good combining ability for this character. In contrast, Mokka and Rume

Table 29. Parental means (x̄) and general combining ability effects (GCAE) for berry bean and liquor quality characteristics.

Variety	x̄	GCAE	x̄	GCAE	x̄	GCAE	x̄	GCAE
	single berry Wt. (g)			PB (%)		AA (%)		AB (%)
1. Caturra	2.17	−0.03***	12.51	−2.02***	20.02	−2.45***	27.66	−1.57***
2. Pretoria	3.24	0.69***	28.28	8.42***	28.68	1.70***	6.42	−13.95***
3. Erecta	1.82	−0.20***	7.67	−5.87***	3.28	−11.60***	41.75	12.80***
4. SL 28	2.57	0.15***	20.06	0.14	38.30	7.13***	22.56	1.48***
5. Mokka	1.18	−0.31***	7.16	−4.28***	1.03	−4.66**	32.80	7.73***
6. K7	2.28	0.03***	15.05	−1.70***	38.49	6.16***	18.41	−3.64***
7. H. de Timor	2.43	0.03***	23.00	3.53***	36.88	5.18***	17.85	−5.59***
8. Padang	2.01	−0.11***	13.11	−3.24***	32.68	4.77***	25.94	0.61
9. Laurina	1.96	−0.02***	3.59	−4.27***	3.21	1.71***	22.10	−2.87***
10. R. Sudan	1.60	−0.31***	32.98	−9.52***	1.91	−14.20***	23.31	5.27***
11. SL34	2.68	0.15***	21.44	−0.17	40.86	6.30***	18.01	−0.49
		acidity		body		flavour		standard
1. Caturra	2.08	0.22***	2.00	0.11***	3.75	0.26***	3.47	0.12***
2. Pretoria	1.92	0.10***	1.42	−0.21**	3.39	0.26***	3.94	0.60***
3. Erecta	1.75	0.03	1.59	0.05	3.25	−0.01	3.28	−0.05
4. SL28	1.50	−0.17***	1.42	−0.03	2.95	−0.19***	2.92	−0.24***
5. Mokka	1.50	−0.08*	1.67	0.06	3.05	−0.07*	3.22	−0.10***
6. K7	2.00	0.10***	1.50	−0.01	3.77	0.17***	3.66	0.14***
7. H. de Timor	1.50	0.12***	1.75	0.22**	3.33	0.22***	3.44	0.20***
8.Padang	1.67	0.07*	1.67	0.03	2.89	0.03.	3.11	−0.10***
9. Laurina	1.59	−0.06	1.67	−0.03	3.25	−0.13***	3.56	−0.06**
10. R. Sudan	1.83	−0.01	1.25	−0.01	2.84	−0.10***	2.73	−0.18***
11. SL34	1.25	−0.17***	1.17	−0.18***	2.36	−0.38***	2.56	−0.34***

Table 30. Means (first line) and specific combining ability effects (second line) for %AA and overall standard.

a. %AA

Parents	2	3	4	5	6	7	8	9	10	11
1	27.70	11.63	31.89	22.60	30.53	30.17	30.54	33.90	8.92	35.34
	0.69	−2.07	−0.54	1.95	−0.94	−0.32	0.46	6.88***	−2.18	3.73**
	2	31.42	30.98	36.37	30.06	27.61	36.68	27.52	20.28	29.36
		13.55***	−5.61**	11.57***	−5.56**	−7.03**	2.44	−3.65**	5.02**	−6.40**
		3	20.23	11.63	19.07	25.54	20.55	15.97	3.36	20.58
			−3.06**	0.13	−3.25**	4.18**	−0.38	−1.90	1.40	−1.88
			4	29.92	(45.41)	(41.37)	(43.29)	(45.01)	16.87	(42.75)
				−0.31	4.34**	1.28	3.62	8.40**	−3.82**	1.55
				5	32.39	27.33	27.21	33.56	11.33	34.29
					3.12**	−0.95	−0.65	8.75**	2.43	4.89***
					6	38.81	(40.55)	(45.67)	15.23	35.73
						−0.30	1.85	10.03***	−4.49**	−4.49**
						7	38.73	39.37	16.25	37.85
							1.01	4.70**	−2.49	−1.39
							8	39.04	12.28	(41.00)
								4.79**	−6.04**	2.16
								9	26.39	(42.67)
									11.11***	6.89**
									10	13.88
										−5.98**

b. Overall standard

Parents	2	3	4	5	6	7	8	9	10	11
1	4.11	3.41	3.33	3.22	3.83	3.95	3.06	3.36	3.47	3.14
	0.04	−0.02	0.10	−0.16	0.22	0.28**	−0.32**	−0.05	0.17	0.00
	2	3.61	3.98	4.06	4.20	4.45	3.94	3.94	3.95	3.92
		−0.30**	0.27*	0.20	0.11	0.30**	0.08	0.05	0.18	0.30*
		3	3.44	3.30	3.39	3.53	3.33	3.14	3.14	(2.89)
			0.37**	0.08	−0.06	0.02	0.11	−0.11	0.00	−0.09
			4	3.00	3.28	3.28	3.03	(2.78)	(2.89)	(2.25)
				−0.01	0.03	−0.03	0.01	−0.27*	−0.04	−0.53***
				5	3.36	3.50	3.28	3.19	(2.83)	(2.81)
					−0.04	0.05	0.12	−0.01	−0.25	−0.11
					6	3.56	3.28	3.14	3.28	3.44
						−0.13	−0.12	−0.29**	−0.04	0.28**
						7	3.39	3.39	3.44	3.45
							−0.07	−0.10	0.07	0.23
							8	3.14	3.22	3.14
								−0.06	0.14	0.21
								9	3.39	(2.89)
									0.27	−0.07
									10	(2.86)
										0.02

Enclosed in brackets, are hybrids with bean size or liquor quality very similar to the best parental variety SL34. Details regarding the parents are given in Table 29.

Sudan, and to a lesser extent, Erecta and Laurina had low single berry weight and %AA in addition to having poor GCA for single berry weight and %AA, except for Laurina which had fairly good general combining ability for %AA. Pretoria, Rume Sudan and Hibrido de Timor had the highest %PB and appeared to impart this characteristic to most of their hybrids. SL34 and SL28 were clearly the best parental varieties to be used in improvement programme for bean size.

Pretoria, Caturra, K7 and Hibrido de Timor appear to give in general liquor of inferior quality and in most cases also appear to transmit this poor quality to most of their hybrids. Pretoria however had liquor with full body and had good GCA for this character. But from the liquoring reports, it also imparts a characteristic "Maragogipe" flavour, which is undesirable, in all its hybrids. SL34 was the best variety in terms of each one of the liquor quality characteristics, and also with regard to combining ability for these characteristics. It was followed by Rume Sudan which had liquor with excellent body and flavour but lacking in acidity, it had also good combining ability for flavour and overall standard. SL28 had quite good liquor quality and good combining ability for acidity, flavour and overall standard. Padang and Mokka had liquor of fair quality but lacking in one or a number of the liquor attributes.

A number of F_1 hybrids recorded significant positive SCA for %AA (Table 30a), indicating that these crosses had a much higher proportion of %AA than would be expected on the average cross performance of the parental array. Regaring overall standard (Table 30b) a number of F_1 hybrids showed significant negative SCA, in this case also implying that such hybrids had much lower scores (hence better liquor quality) for overall standard, than the average of all other hybrids of the same parental array. As was mentioned in section 2.5.3. statistical significance of these effects is not of primary interest in this study, rather it is the actual performance of the F_1 hybrids that deserves most attention. Of some interest are three hybrids derived from crosses among varieties SL28, K7 and Laurina (see Table 30a) which had over 45% of their beans in category AA which is already better than the parent with the highest %AA SL34 (see Table 29), i.e. 40.9. Several other hybrids had percent AA ranging between 41 and 45. As for liquor quality, F_1 hybrids representing the following crosses: SL28 x Laurina, SL28 x Rume Sudan, Erecta x SL34, Mokka x SL34, Laurina x SL34 and Rume Sudan x SL34, had liquor of very similar quality to that of SL34 and were by far superior to K7, which is fairly widely grown in Kenya as one of the commercial cultivars. Incidentally, the hybrid derived from a cross between SL28 and SL34, had the best liquor quality which even excelled that of SL34.

6.4.3. The nature of reciprocal effects observed for %AA

As was indicated in section 6.4.1., reciprocal effects were a consistent feature of the variation observed among genotypes for berry and bean characters. It is because of the presence and the magnitude of these effects that a genetic analysis according to the method of Jinks (1954) and Hayman (1954b) was not applied to the data of berry and bean characters in form of a half diallel. It was obvious for these characters, that the dominance effects upon which most conclusions are based, when applying this method, would

Table 31. Analysis of variance of a complete 6 x 6 subdiallel for % AA, and variation in magnitude of reciprocal effects over years.

a. Analysis of variance

Source of variation	Df	Ms	F value and P
Female parents	5	454.29	115.89***
Male parents	5	374.99	95.66***
Interaction	25	19.43	4.96***
Average maternal effects	5	35.77	9.13***
Specific reciprocal effects	10	6.68	1.70
Ave. maternal effects x years	10	3.04	0.70
Specific rec. effects x years	20	2.52	0.64
Error(1)	400	3.92	

b. Variation in magnitude of reciprocal effects with years.

Source of variation	Df	Mean squares and P		
		1977	1978	1979
Average maternal effects	5	26.61***	47.04***	51.89***
Specific reciprocal effects	10	8.67	12.92	13.56
Error(2)	320	5.94	8.48	6.65

(1) Estimated from Genotypes x Environments (years and densities Ms, see Table 28.

(2) Represents Genotypes x Reps within densities Ms.

be seriously biased as a result of these reciprocal differences. Nevertheless, it is still important for practical purposes to have some insight regarding the nature of these effects. For this purpose, the factorial analysis of Jinks and Broadhurst (1963), also given by Mather and Jinks (1977), together with the method of Hayman (1954a) were applied to the data derived from a full subdiallel consisting of 6 parents (see section 2.1., Table 1). Only %AA was considered, as it is regarded as one of the more important characters related to bean size, and in addition, it happened to have the largest reciprocal effects (according to F values, see Table 28).

As can be seen from Table 31a, there was more variation among parents used as females than among the same parents used as males, an indication that female mean squares were being inflated by maternal effects. The interaction mean squares, which in this case measures only the dominance effects, was also highly significant as was the case in Table 28. In the second part of Table 31, reciprocal effects were partitioned according to those originating purely from average maternal effects and those arising from various other forms of interaction. For example, interactions between genes in the progeny genotype, or genes conditioning maternal effects, all these fall under the category of specific reciprocal effects. The table is further subdivided into items representing interactions between average maternal effects and years, and specific reciprocal effects and years. Results

from the Table indicated that practically all reciprocal effects observed for %AA could be ascribed to average maternal effects rather than specific reciprocal effects. Furthermore, there were no interactions between the average maternal effects and the years. That average maternal effects were fairly consistent over the year, can also be confirmed from the magnitude of the mean squares for these effects in different years (Table 31b). It could therefore be inferred from these results, that these effects appear to be of a permanent nature, otherwise if they were temporary, then with time, the magnitude of reciprocal differences is expected to decline, which of course was not apparent here.

6.5. Discussion

6.5.1. Phenotypic variation and genotype-environment interactions

Coffee quality is of such importance that it has often to be considered in breeding programmes of arabica coffee. The relative emphasis placed on it however, varies according to the coffee standards various producing countries regard as satisfactory. Certain characters related to bean size are thought to be fairly heritable. Information on the relative influence of different environments on these characters is of interest, especially as compared to some growth and yield characters. In addition, as was indicated in section 6.1., there is some uncertainty with regard to the liquor quality aspect mainly because of the present method of evaluation; yet, selection for cup quality in breeding programmes has to depend on results of this organoleptic assessment.

The present investigation has confirmed that there are large inherent differences among genotypes not only for most berry and bean characters, but also for some of the liquor quality characteristics (section 6.2.). Furthermore, most characters related to bean size have such high repeatability that genotypes can easily be categorised for these characters by basing assessment on only a few environments. The consistency of berry and bean characters over different environments is further confirmed by results in section 6.3. which indicate that genotype x environment interactions compared to genotypic variation were relatively unimportant. In other words, unlike most growth and yield characters, these berry and bean characters tend to be less influenced by different environments. It is worth remarking here however, that environments included in this study, i.e. 3 years and 2 plant densities are rather restricted. The conclusions therefore may or may not strictly apply to such widely varying environments characterised for instance by differences in location and altitude.

Regarding liquor quality most of the attributes in contrast to berry and bean characters tend to show less marked variation between genotypes, an exception being the overall standard. However, the procedure of organoleptic evaluation of liquor quality, as was performed on these samples, by the same MCTA liquorer, was found to be fairly consistent and accurate especially regarding the overall standard and flavour (see section 6.2.). Procedures based on chemical analysis when developed, will be useful in

complementing the present method. It is doubtful however, if they can be used as a substitute to the present method of coffee tasting. After all, organoleptic evaluation can be considered more akin to the consumers preferance, as it is the consumer in the end who finally judges cup quality. It can be further concluded from this study that the present method of determination of cup quality, is sufficiently reliable to be used as a basis of selection in quality improvement programmes.

6.5.2. Genetic variation for quality characters

For all quality characters considered, GCA was more important than SCA (section 6.4.1.) in contrast to growth and yield characters where these effects were equally as important (section 3.4.), indicating that for quality characters most of the variation may have been due to additive genetic effects. As a consequence, it could be expected that cases of pronounced genic interactions may not be as prevalent for these characters as they were for most growth and yield characters (Chapter 4).

Reciprocal effects however, were also a fairly important cause of variation among genotypes for berry and bean characters. For %AA (section 6.4.3.), these effects appear to be largely due to average maternal effects, and because they were persistent over several years, it can be concluded that these effects are cytoplasmic rather than those arising from common maternal environment.

Varieties SL34 and SL28 were outstanding both for bean size and liquor quality together with Rume Sudan which had excellent liquor quality but rather small bean size. There are also a number of F_1 hybrids which had very good bean size and remarkably good liquor quality similar to that of SL34 (see section 6.4.2.). It can be observed from results in section 6.4.2., that in general, F_1 hybrids derived from parents with good coffee quality attributes, also tend to give coffee of good quality. This is expected when, as was observed for these characters, SCA is of less importance.

On the whole it would seem that improvement of bean size and liquor quality in arabica coffee is an objective that can easily be attained. In the first instance most quality characters are highly heritable, especially bean size characters and the overall standard (see section 6.4.1.). Furthermore, it is even possible as has been indicated to derive F_1 hybrids from certain parental combinations, that can give coffee of as excellent quality as that obtained from the best Kenyan commercial varieties. Due consideration however, should be given to reciprocal differences especially as regards bean size. For instance use of a variety like Mokka as the female parent will tend to give F_1 hybrids with lower %AA, than if the same parent is used as the male parent. SL28 and Caturra, appear to behave in the opposite way.

7. CORRELATION BETWEEN COFFEE QUALITY CHARACTERS

7.1. Introduction

The relationship between the various quality characters is expected to indicate how selection when applied to one of these characters, will influence simultaneous changes in the other characters. In particular, for characters related to bean size, it may be desired to improve a number of these simultaneously, for instance %AA and %AB. The ease with which both characters can be improved will obviously depend on the extent to which they are correlated, and whether the correlation is positive or negative.

Since most berry and bean characters plus the overall standard of the liquor were shown to be quite heritable (Chapter 6), a further aspect of considerable relevance is the indication which can be obtained about the actual quality of a given genotype, when only the first assessment of these quality characters is considered.

This chapter deals mainly with these two aspects of coffee quality.

7.2. Results

Genotypic and phenotypic correlations between these characters are presented in Table 32. The calculation of these correlations was as given in section 5.3. Berry and bean characters, were based on mean values in each replication obtained from 3 years of assessment of each character, while liquor quality characters were based on each single determination per plant density.

Table 32. Genotypic (upper values) and phenotypic (lower values) correlations between coffee quality characters.

a. berry and bean characters.

Character	(2.1)[1]	2.2	(3.1)	(3.2)	(4.1)	(4.2)	(5.1)	(5.2)	(6.1)	(6.2)	(7.1)	(7.2)	(8.1)	(8.2)
1. S. berry Wt.	−0.43	−0.48	0.69	0.16	0.32	0.52	0.62	0.41	−0.75	−0.82	−0.26	0.43	−0.46	−0.42
	−0.20	−0.37	0.42	0.14	0.30	0.49	0.58	0.41	−0.70	−0.75	−0.22	−0.37	−0.44	−0.44
2. Pulp			−0.51	−0.94	−0.67	−0.23	−0.54	−0.38	0.55	0.50	0.38	0.23	0.45	0.46
			−0.28	−0.74	−0.19	−0.17	−0.22	−0.34	0.17	0.38	0.13	0.20	0.30	0.41
3. Outturn					0.41	0.11	0.68	0.40	−0.43	−0.31	−0.40	−0.14	−0.78	−0.54
					0.26	0.08	0.46	0.35	−0.26	−0.21	−0.26	−0.20	−0.51	−0.44
4. PB							0.04	0.05	−0.38	−0.50	−0.57	−0.71	−.033	−0.38
							0.05	0.02	−0.38	−0.49	−0.48	−0.56	−0.33	−0.35
5. AA									−0.57	−0.66	−0.47	−0.45	−0.60	−0.60
									−0.54	−0.63	−0.45	−0.44	−0.58	−0.58
6. AB											0.24	0.51	0.07	0.36
											0.13	0.31	0.06	0.29
7. TT													0.34	0.61
													0 30	0.53
8. C														

b. liquor quality characters

Character	(2)	(3)	(4)
1. Acidity	0.35	0.87	0.61
	0.36	0.63	0.48
2. Body		0.32	0.04
		0.40	0.22
3. Flavour			0.90
			0.74
4. Standard			

[1] In Table 25a, lower plant density and higher plant density are designated (.1) and (.2) respectively.

Table 33. Correlation betwen first year determination of %AA and the overall standard with the mean of 3 years determination of the same character.

	correlation coefficient	
Character	lower plant density	higher plant density
%AA	0.98***	0.94***
Overall Standard	0.87***	0.86***

Of particular interest is the relationship between single berry weight, % PB and % AA on one hand, and % AB, % TT and % C on the other hand. Single berry weight was positively correlated with % AA and % PB as was % TT with % C, and at the higher plant density, % AB with % TT. However single berry weight, % AA and % PB were all mostly highly negatively correlated with % AB , % TT and % C. No correlation appeared to exist between % PB and % AA. It is also clear from Table 32a, that differences in plant densities, appear to have an influence on the degree of correlation among some of these characters.

Most of the liquor quality characters in Table 32b, were positively correlated, with acidity and flavour, flavour and overall standard being particularly very highly correlated. There appears however to be no strong association between body and overall standard indicating that body is relatively unimportant for the assessment of liquor quality in arabica coffee in Kenya. On the other hand, the overall standard appears to depend very much on the flavour while flavour and acidity appear to be inherently associated.

Table 33 gives the correlation between first years assessment of % AA and the overall standard, with that of 3 years determination of the same characters. The calculations were based on mean values of each plant density.

7.3. Discussion

From the results obtained in this study, it is evident that genotypes with high single berry weight also tend to have high proportions of AA and PB beans but low proportions of AB and C bean grades. The high negative correlation between % AA and %AB deserves particular attention especially in a programme aimed at improvement of bean size. Normally, the objective of such a programme would be to have a high proportion of both AA and AB, since both categories of beans are highly valued, though AA is regarded somewhat better than AB. The strong negative association, implies that these two characters are complementary and therefore simultaneous selection for increased % AA and % AB may not be expected to give a high response, despite both characters being highly heritable. As a consequence, better response will be realised only if selection is practiced for one of the characters while ignoring the other character. In the case of selection for increased % AA, the immediate consequence would be a correlated increase

in single berry weight accompanied by a decrease in % AB, % TT and % C. The proportion of PB would probably remain unaffected. It is clear therefore that selection for % AA at the expense of % AB would eventually result in a better overall bean size.

Regarding liquor quality, selection specifically on basis of overall standard already implies improvement in some or most of the constituent attributes. Consideration of each of these constituent characteristics however, may reveal possibilities of further improvement of the overall standard by hybridization say between genotypes with similar liquor quality in terms of overall standard, but each one of them lacking in one different aspect but outstanding in others.

As was shown in Chapter 4, individual plant selection for yield on fairly young coffee trees may be possible through some form of preselection index. For quality characters application of such a procedure would serve no useful purpose. If % AA and overall standard are regarded as the most important quality characters, it is clear from the previous Chapter that these characters are already quite heritable. As a result, selection applied on the same characters is expected to be fairly effective. It is therefore most doubtful whether incorporating information from the other characters would improve on the selection efficiency for % AA or the overall standard. On the other hand, in terms of time, it may be crucial to base evaluation of quality say on only one or two assessments of the quality characters. This is true especially in situations involving a programme of progeny tests or test crosses where obtaining information on quality of certain parental genotypes within the shortest possible time will greatly enhance the speed of further progress of the programme. Results in Table 33 indicate that the first years assessment of % AA and the overall standard already gives a good impression of the actual coffee quality of a given genotype on basis of 3 years of successive determination of these two characters. This suggests that it may even be possible to select genotypes with outstanding coffee quality immediately after the first year of full production.

8. CONSIDERATIONS IN BREEDING AND SELECTION FOR CERTAIN IMPORTANT CHARACTERS IN ARABICA COFFEE

8.1. Introduction

Arabica coffee being a perennial tree crop has a relatively long juvenile period. Breeding programmes in such a crop are of necessity long term. Because the species is autogamous, the present commercial cultivars, having been derived as single tree selections, show a high degree of true breeding and are therefore propagated mostly by seed. Asexual propagation by means of grafting or by rooting softwood cuttings is possible (van der Vossen & Op de Laak, 1976; van der Vossen et al., 1977) and can be especially useful for breeding purposes. Among the main goals of most current breeding programmes, including the one in progress at the CRS (Ruiru) are: improved yield coupled with compact growth, quality and disease resistance.

In order to achieve these goals, breeding procedures have to involve hybridization among different varieties selected for certain desirable attributes which they carry. Planning of such a programme, and indications of immediate consequences of selection is best understood against a background of information relating to the mode of inheritance, and the amount of genetic variation among the available genotypes, for the character in question.

For instance, regarding the performance of F_1 hybrids, intense hybrid vigour may have, especially in a perennial crop, important consequences as far as breeding and selection for the given character is concerned. On the other hand, when considering an F_2 population, not only the number of genes or groups of tightly linked genes segregating but also the effects of these genes, will have a great influence on the effect of selection applied to a certain character. With 1 gene segregating for example, selection of 25% of F_2 individuals at either end of the scale will lead to immediate fixation of homozygous types in the next generation. With 5 independent genes segregating however, only one individual in a population of 1,024 will be homozygous for each of the extreme genotypes. The probability of fixation of such a genotype in the next generation is very small and especially so, if the gene effects are also masked by the external environment. Therefore, with characters controlled by a small number of gene loci, each with fairly large effects, the segregation pattern in the F_2 is often clear enough to allow genotypes to be categorised according to the combination of genes they carry. The distribution of phenotypes will of course vary depending on the presence of dominance and/or epistatic effects as well as linkage between genes controlling the character.

Aids in selection in form of special techniques applied in judging the actual genetic worth of individual plants have to be given more attention, as these are extremely useful in early generation evaluation. Their development also depends on having detailed information on the genetic control of a character as well as the interrelationship between the character in question and other characters. Such aids in selection have been emphasised throughout this study, and no doubt, are essential if reasonable progress has to be made in a breeding programme of perennial crop with a long juvenile period, where time is an extremely important element.

In this Chapter, information derived mainly from the present study, will

form the basis for considering some of the above aspects in breeding and selection programmes for each of the characters given below.

8.2. Yield improvement

Selection of parental genotypes may depend on making crosses between all or most of the selected parental varieties, which will also include the best varieties currently in use. This type of crossing scheme has two main advantages:

1) it will enable evaluation of combining ability of the different genotypes not only for yield, but also for other equally important attributes which the different genotypes may carry (e.g. quality, growth habit and disease resistance) all at the same time,
2) it can be used for studying the genetic control of the various characters in that population.

It is often useful to realise that crosses between high yielding genotypes may not always give rise to progenies that are superior to both parents, unless the parents differ considerably with respect to certain growth and yield characters. In this study for example, such outstanding hybrids are those of crosses involving Padang and SL28 or Padang and SL34 (see Table 34). It is even possible also, for some very unproductive variety when crossed with a high yielding variety, to give rise to an F_1 hybrid that is superior to the more productive variety. For example Laurina with Padang and Laurina with K7 in the same table. Laurina in this case, is outstanding for the number of bearing primaries but has also very short internodes. It is possible that recombinations of these and other characters when Laurina is crossed to the better performing parents, are responsible for the superiority of the F_1 hybrids. As was indicated in section 4.6. and is clear from Table 34, hybrid vigour or heterosis in general, is most likely to occur where crosses are made between varieties that are genetically diverse. As was also mentioned in Chapter 4, and is evident in this Table, the performance of some of these hybrids on basis of yield can justify their immediate use as commercial varieties. This will be possible, only if they combine the high yield with good quality and disease resistance.

Table 34. Some growth and yield characters for selected parents together with cherry yield of the same parents and their F_1 hybrids.

Character[1]	Parents					
	Laurina	Padang	H.d. Timor	K7	SL28	SL34
Girth (cm)	11.09	13.31	13.21	14.33	14.72	14.61
C. radius (cm)	15.05	43.86	47.79	50.11	53.56	52.53
Int. L. Pr (cm)	1.68	3.74	4.24	4.10	4.45	4.40
B. Primaries (nr)	61.94	50.00	46.59	46.37	46.05	45.53
B. Nodes (%)	13.56	16.01	8.91	21.93	14.16	14.23
Be/node (nr)	4.24	6.52	6.17	5.63	6.11	7.88
Yield	Laurina	Padang	H.d. Timor	K7	SL28	SL34
Laurina	2.49	6.22	6.43	6.62	5.65	5.89
Padang		5.86	5.58	5.24	6.53	6.69
H.d. Timor			3.77	4.83	6.76	5.67
K7				4.16	5.49	5.21
SL28					5.41	5.19
SL34						5.64

(1) Girth, Bearing Primaries, Bearing nodes and Berries per node (Be/node) were taken during the second year after field planting; canopy radius, Internode length on primaries, on plants 1½ years after field planting. Yield, is the mean yield per tree over three years of production. All measurements are means for two plant densities.

In general, if hybrid vigour results mainly from overdominance at the heterozygous loci governing a character (i.e. intrallelic interactions), then there will be no justification in carrying on selection in further generations. Rather, the F_1 hybrids themselves can be used for commercial production. If, on the other hand, heterosis is due either to the accumulated action of favourable dominant or semidominant genes dispersed amongst the parents, or to complementary interaction of additive, dominant or recessive genes at different loci (non allelic interactions), then it is worth remembering in principle, that homozygous lines can be derived as good as the F_1's showing the hybrid vigour. Regarding yield in this study, hybrid vigour observed could be ascribed mainly to complementary epistatic genes (section 4.4.).

As was mentioned in section 4.6. the process of continued selfing in subsequent generations to derive homozygous lines for a tree crop like coffee is prohibitive both in terms of time and expense. However, if high yielding seed varieties have to be produced, then it would be necessary to carry out successive cycles of selection in the F_2 and F_3 generations of selfing. In the F_2 generation, selection would be on individual plant basis with only the high yielding trees being retained. In the F_3 generation, line differences will become apparent and also the level of heterozygosity within each line. Selection would then be for outstanding individual trees in the superior lines and preferably in those lines showing least variation among individual trees. It may be possible for seed obtained from such selected F_3 trees to be used for commercial production, though this material will still have some degree of residual heterozygosity. The average performance of this fourth generation however, may be comparable to that of the heterotic F_1's and will be well above the average performance of the F_2 generation. This is so because, though the number of heterozygous loci will decrease with inbreeding and so is the hybrid vigour, these will be compensated for by accumulation of favourable genes, which might even result in transgression. For such a scheme to be applicable especially in the Kenyan situation, not only have the genotypes released to the farmer to be high yielding, they must also be uniform in growth habit, and must carry CBD resistance genes at least on 2 loci or preferably 3 loci in a homozygous state. In addition, they should be resistant to coffee rust.

The advantage of hybrid varieties in arabica coffee is that development of such varieties is much more rapid and such hybrids will normally show remarkable uniformity with respect to various characters. Furthermore, such hybrids may show hybrid vigour caused by intra — or inter — allelic interactions. In the breeding programme at the CRS (Ruiru), use of hybrid varieties may be preferred as it will offer a quicker solution to the farmer's problem.

8.3. Breeding for improved coffee quality

Normally yield improvement is considered concurrently with coffee quality. Unlike yield however, variation among genotypes for quality characters, as was found in the present study (section 6.5.2.), is mainly due to additive effects of genes. As a consequence, progenies derived from single or multiple crosses involving parents with good quality characteristics, will also be expected by and large to give coffee of good quality. Very often however, it becomes necessary to make crosses where one of the parents is lacking in some quality characters. For instance, Rume Sudan (with very small bean size) or Pretoria (with inferior liquor quality). In such a case, it may be necessary to improve the resultant hybrid by making a number of backcrosses to a recurrent parent with better coffee quality, or crossing the hybrid to a different parent having both better coffee quality and possibly other desirables attributes.

In the case of a backcross scheme, it is advisable for the number of backcrosses to be restricted to 1 or 2, otherwise in a perennial crop with a long juvenile period, it can be time consuming. In any case, because of the high heritability of the quality characters, selection in later generations derived from such backcrosses will still give opportunity for further improvement. Evaluation of quality in each generation can be done during the first one or two years of production (see section 7.3.) and will be based on coffee samples derived normally from a number of trees per progeny. In improvement of bean size and liquor quality, selection should be restricted to genotypes having a high % AA (disregarding %AB), and a good overall standard (section 7.3.).

In making crosses between various parents, it is also worth noting that reciprocal differences especially for bean characters may occur (see section 6.4.3.). Because of this, it is advisable in general to use genotypes with better bean size as the female parents, rather than vice versa.

There were a number of F_1 hybrids in this study with good bean size, and satisfactory liquor quality which also happened to be very productive. Among such hybrids for example are those derived from crosses of Padang and SL34, Padang and SL28, and Laurina and K7 (see Tables 15, 16, 31 and 34). Clearly such hybrids would be most suitable for the programme of hybrid variety production discused in section 8.2. Unfortunately none of these hybrids show a satisfactory level of disease resistance. In other words, these F_1 hybrids have to undergo further hybridization with desease resistant varieties before they can be considered suitable for commercial use.

8.4. Compact growth characters

For requirements of modern agriculture compact plant types are often preferred because in general, they tend to be more suitable for planting at higher densities. As a consequence, not only is production per unit area of land increased but also if desired the total area under a certain crop may be reduced to release extra land for production of alternative crops, which may be of equal value to the farmer. This aspect is especially relevant to Kenya where the majority of the coffee is produced in the high potential areas which happen also to be ideal for production of food crops. Becuase there is an increasing demand for food production due to the high population growth, coffee in this respect, is in direct competition with food crops (van der Vossen & Walyaro, 1981).

In arabica coffee, genes confering compact growth can be found in varieties with reduced plant size, like Caturra, San Bernardo, Turrialba Compact, Laurina and Mokka, or in varieties with lateral branches which are more or less orthotropic, for instance Erecta and Semi erecta. In Caturra, Turrialba Compact and San Bernardo, the character displays for practical purposes almost complete dominace whereas in Laurina and Mokka, it is semi-recessive or recessive. In addition, Mokka and Laurina are highly unproductive probably because of having extremely short internodes on the laterals. These two varieties seem to be of little use in breeding programmes for compact growth. Laurina however is a valuable parent due to its good combining ability for yield and quality.

The compact growth character as occurs in Caturra is extremely useful in breeding programmes. Apart from being dominant and showing complete penetrance, the character is probably monofactorial (Carvalho, 1958a) and hence easy to manipulate. It can be used for instance, in deriving homogeneous compact plant types even though the genotypes may be heterozygous at loci controlling other characters. In production of hybrid varieties,

use of plants homozygous for the Caturra gene as one parent, automatically ensures that all hybrids will be uniformly compact. Caturra in this study (section 3.4.) also appears to impart remarkable stability for compact growth habit to most of its F_1 hybrids in environments of increased plant density.

One drawback with Caturra in this study is that most of its F_1 hybrids were not that outstanding in yield performance, especially in their response to high plant density. Some of these compact genotypes appeared to be even more sensitive to increased plant competition than some of the tall genotypes (section 3.5.). As a consequence, most progenies of crosses involving Caturra as one parent did not display marked hybrid vigour to the extent of that observed in a number of other parental combinations at the higher density. The use of Caturra in single hybrids therefore may not produce anything better in terms of yield than the present commercial varieties, especially when planted at higher densities. It is expected on the other hand, that the new compact varieties to be eventually developed should represent plant types that are at least more productive at higher plant densities than the varieties presently grown commercially. Nonetheless, Caturra can still be improved through hybridization and further selection. For example the material like Catimor, selected F_3 or F_4 genotypes from a cross between Caturra and Hibrido de Timor (see section 1.4.), is in many respects superior to Caturra or even its F_1 hybrids.

Aside from individual tree yield of compact genotypes, their growth habit from the farm management point of view is very attractive. Training (capping) of such trees is unnecessary and pruning is restricted to removing the lowest branches which touch the ground. Furthermore, picking on such genotypes will be relatively easy, and cases of breakages of the main heads, as often occurs with tall varieties carrying a heavy crop or during picking, will be considerably lessened. The only obstacle in such densely planted coffee is that it will be much more difficult to control CBD and rust unless such genotypes also carry resistance to these two diseases. This aspect is discussed in the next section.

Combining compact growth of the type of Caturra with new improved genotypes is an easy procedure. Selection for compact types is even more facilitated in that it can be performed on seedlings about 1 year old in the nursery (see section 5.2.). This also helps the breeder to cut down on the number of plants eventually to be planted in the field.

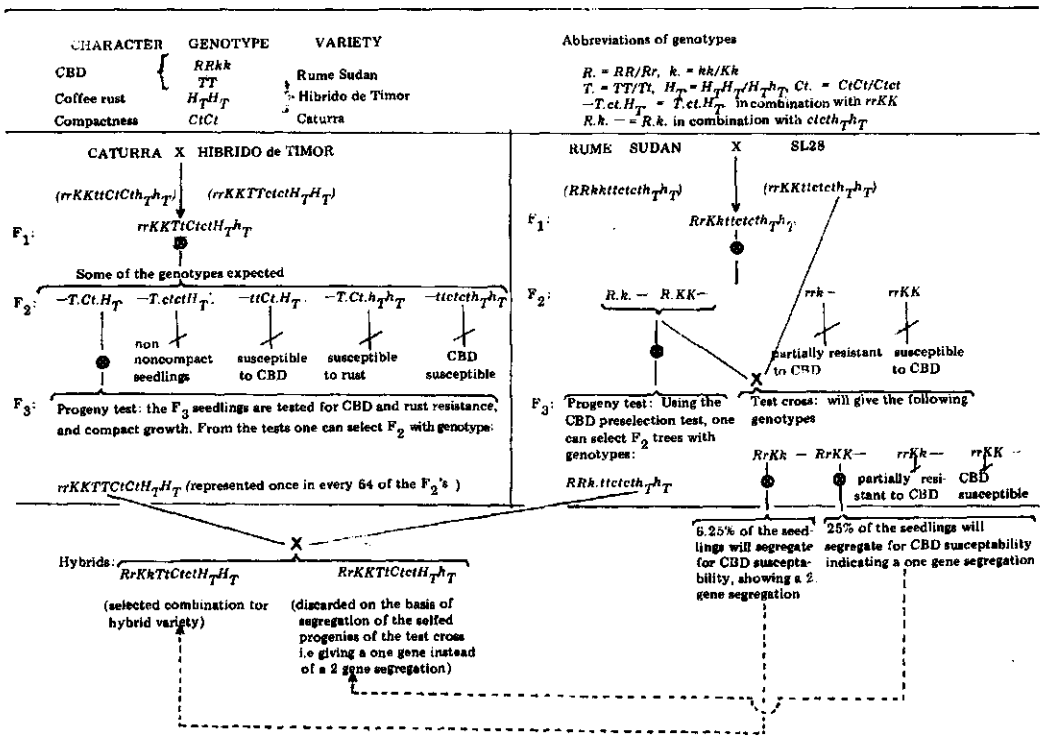
Regarding breeding for genotypes with more erect branching pattern, evaluation for this character can also be done on seedlings in the nursery. The performance of F_1 hybrids derived from Erecta as one parent, in this study (section 3.5.) was in many cases also rather disappointing especially for yield. A few hybrids however, showed good yield stability. This character at the present moment does not seem to merit such serious attention in breeding programmes as compared to other more important characters like disease resistance, yield and quality. It could however be considered in later stages of such breeding programmes.

8.5. Disease resistance

In the breeding programme at the CRS, Ruiru, and in many other breeding institutions for arabica coffee, disease resistance receives more attention than any of the characters that have so far been considered. As is mentioned in Chapter 1, resistance in arabica coffee is sought to 2 main diseases, coffee berry disease, and coffee rust. No detailed treatment of this subject will be given here, all that is considered is a simplified scheme on how disease resistance can be combined with compact growth, yield and quality in a breeding programme.

Breeding for resistance to coffee rust involves programmes to transfer vertical resistance genes, and/or horizontal resistance governed by polygenes, to new varieties being developed. For a detailed review of this subject, see Rodrigues et al. (1975) and Monaco (1977). Regarding coffee berry disease, the programme at the CRS Ruiru, aims at introducing resistance by also making use of a number of major genes (van der Vossen et al, 1976; van der Vossen & Walyaro, 1981). Though there is circumstantial evidence that such resistance to CBD may be of a stable nature (Masaba, 1981), it is thought however, more advisable to accumulate in one genotype as many resistance genes as possible to enhance the stability. The CBD resistance genes have been designated (van der Vossen & Walyaro 1981) as: the dominant *R*— and the recessive *k*— both found in variety Rume Sudan, the *k* — gene also occurs in variety K7. Hibrido de Timor carries one resistance gene on the *T*— locus, with intermediate action. In addition as was mentioned earlier (section 2.1.), this variety is also resistant to most physiologic races of coffee rust. Such a gene or a complex of genes will be designated H_T, for illustrative purposes. The breeding scheme is aimed at developing compact varieties with at least 3 resistance genes to CBD plus resistance genes to coffee rust.

For the purpose of illustration 4 varieties are used, Rume Sudan, SL28, Hibrido de Timor and Caturra. Two alternative schemes are also given in Figure 14 and 15 respectively, for a programme of hybrid variety production, and one suitable for production of seed varieties. The scheme starts with making crosses between Caturra and Hibrido de Timor, to combine the CBD *T*— gene, Leaf rust resistance, with the compact *Ct* gene of Caturra. Rume Sudan is crossed to SL28 to introduce the *R*— and *k*— genes into the other F_1 hybrid. As can be seen in Fig 14, it is fairly easy to select from the F_2 generation a genotype homozygous especially for the *T*—, *Ct* - and H_T— genes on basis of the progeny test performed on seedlings obtained from the selfed F_2 generation. Because such a genotype is represented only once out of 64 invididuals it is advisable to raise large number of F_2 seedlings. However, F_2 seedlings susceptible to CBD can already be discarded on basis of the preselection test for CBD resistance (van der Vossen et al, 1976), and non-compact seedlings can also be discarded while still in the nursery (see section



8.4.). Eventually only about 40% of the F_2's will be planted in the field, and on screening for leaf rust resistance on young plants in the field, using the leaf disc inoculation test (Eskes et al., 1977), about only 30% of the initial number of F_2's raised will remain to be selfed for progeny tests.

Regarding fixing of the *R*— and *k*— genes in the other hybrid this will depend mainly on the preselection test for CBD resistance. As indicated in Fig 14, it will be necessary also to perform a test cross in order to distinguish F_2 individuals carrying the 2 genes in a homozygous state from those carrying only one gene. The resistant F_2 individuals are crossed to a susceptible variety e.g. SL28 and SL34 and the seedlings raised are preselected for CBD resistance. From these results it is possible to distinguish immediately F_2 plants homozygous for the *k*— gene but heterozygous for the *R*— gene, because the *k*— gene is partially recessive. To discover F_2 genotypes carrying the *R*— gene in a homozygous state, will require seedlings raised from the testcross to be planted out in the field and eventually on flowering, to be selfed. It is on basis of results obtained from the CBD preselection of these seedlings that F_2 individuals homozygous for one *R*— gene can be distinguished from those with 2 resistance genes *(RRkk)*.

However from results of CBD preselection performed on seedlings obtained from selfed resistant F_2 plants it is already possible to select those F_2's carrying *RRK*— or *RRkk*. Such plants when crossed to genotypes homozygous for the H_T—, C_t— and *T*— genes, will give hybrids having CBD resistance on 2 or 3 loci. Combining ability of the individual trees selected in each of these two groups in terms of other characters e.g. yield and quality can then be evaluated in trials, involving these hybrids. When the final results of CBD preselection on progenies of the test crosses eventually become available, it is then possible to discard the F_2 trees in this group with genotypes *RRKK* or *RRKk*. The remaining best combining F_2 trees with genotypes *RRkk*—, in one group, and —*TTCtCt*$H_T H_T$, in another group, will then be used for production of hybrid varieties through artificial cross pollination.

An alternative scheme involves making four way crosses i.e. (Caturra x Hibrido de Timor) x (Rume Sudan X SL28). The progenies of such a cross will be preselected for CBD resistance discarding susceptible seedlings i.e. carrying *rrKktt*—, *rrKKtt*—, and of the remaining seedlings, those having non-compact growth *(—ctct)* as observed in the nursery. While in the field, they will also be screened for leaf rust resistance. The remaining selected plants will be selfed and the progeny will again undergo these screening tests. On basis of segregation of these progenies for CBD resistance, it will be possible to distinguish individuals of the initial four-way cross carrying at least 3 CBD resistance genes. Such genotypes, carrying the genes *RrKkTt* in combination with *Ctct* $H_T h_T$ will occur only once in every 32 non-discarded F_1 individuals. The selfed progenies of these F_1 individuals will form the F_2 generation, and those selected in this generation for disease resistance and compact growth will in turn also be selfed to form the F_3 generation.

After discarding susceptible and non compact F_3 seedlings, the remaining seedlings will be planted in the field again to be screened for coffee rust. On flowering, the selected F_3 individuals will be selfed and also testcrossed to a susceptible variety. Progenies of selfed F_3 individuals will be screened for CBD resistance, compact growth and eventually also, rust resistance. On

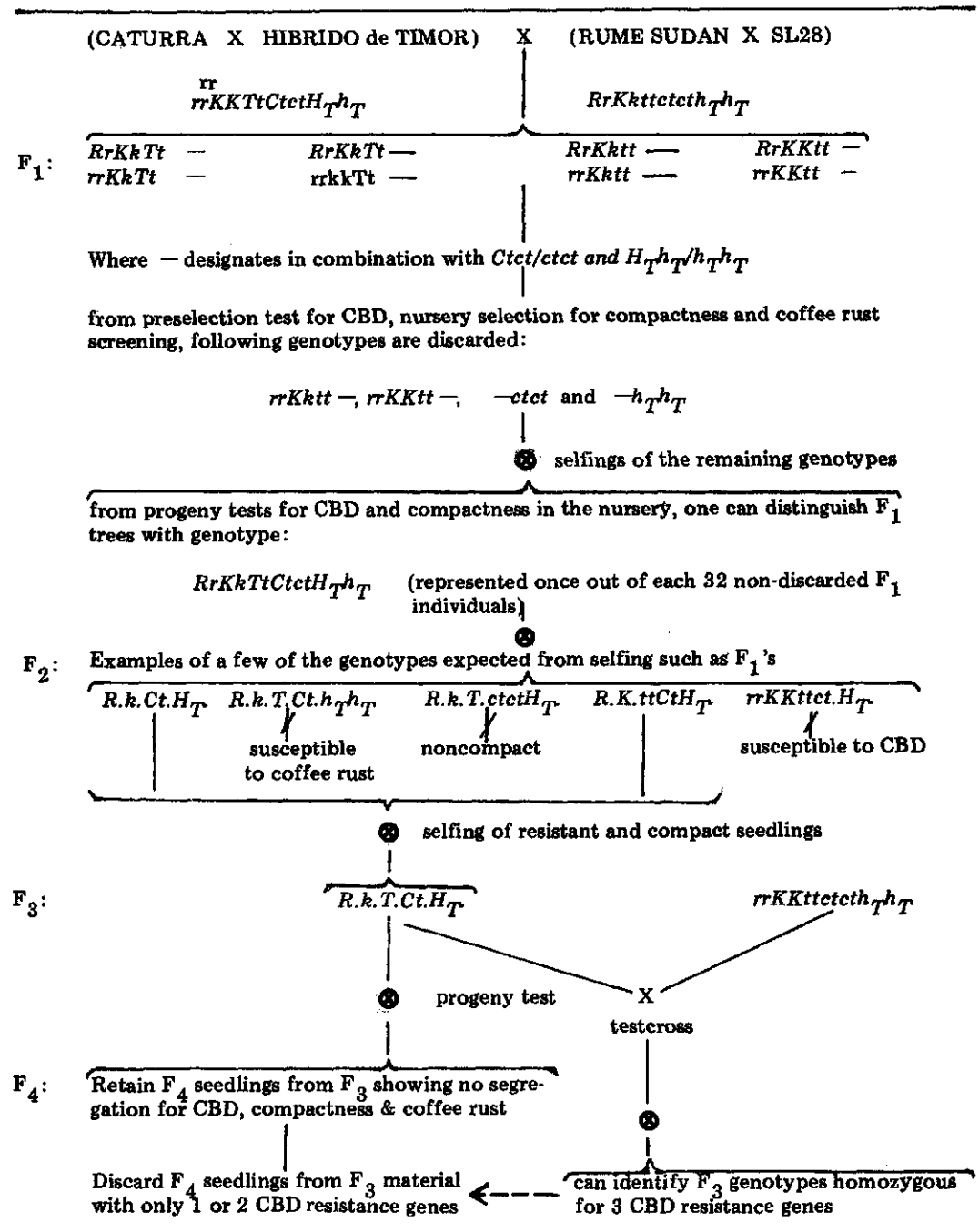


Fig. 15 Alternative scheme for deriving disease resistant and compact seed varieties.

basis of these results, only F_3 individuals whose selfed progenies show no segregation with respect to all the above characters will be selected. Regarding seedlings of the testcross, these will first be screened for CBD, in order to distinguish F_3 individuals carrying the $k-$ gene alone in homozygous state. The resistant seedlings of the test cross will be planted in the field and

on first flowering will be selfed. On basis of segregation during the CBD preselection of the seedlings of the selfed plants from the testcrosses, individuals in the F_3 generation carrying 1 or 2 CBD resistance genes can be discarded together with their F_4 progenies.

Seed varieties can then be selected among remaining F_3 or F_4 material, homozygous for the 3 CBD resistance genes and for rust resistance as well as homozygous for *Ct*— gene for compact growth. As would be expected, the scheme aimed at producing seed variety (see Fig 15) takes a considerably longer time, than that for producing hybrid varieties (see Fig 14) though in the end multiplication of seed for the farmers is a lot easier.

In the above scheme, apart from progeny tests, test crosses have had to be used. This is so because, whereas it is easy to distinguish through progeny tests a genotype with two CBD resistance genes e.g. *RrKk* from that with only one resistance gene *RrKK*, it is not easy to differentiate the genotype *RRKK* from *RRKk* by the same procedure. As indicated earlier, the *R*— gene is dominant and imparts a high level of CBD resistance whereas the *k*— gene is partially recessive imparting a relatively low level of resistance. If the last two genotypes were progeny tested, *RRKK* would reproduce itself and all progenies would be resistant. *RRKk* would give *RRKK*, *RRKk* and *RRkk* and these progenies, on average would have a relatively higher level of resistance compared to those with the genotype *RRKK*. In practice however, the difference in the level of resistance between these two sets of progenies may be so marginal that there may be difficulties in distinguishing which of the original genotypes had two resistance genes. If on the other hand, the two genotypes were testcrossed thus: *RRKK* x *rrKK* to give *RrKK*, and *RRKk* x *rrKK* to give *RrKK*, *RrKk* followed by selfing these progenies i.e. *RrKK* and *(RrKK, RrKk)*, the proportions of true susceptible seedlings would be the best indicator of the number of resistance genes carried in the original genotypes. A similar situation would also arise for example in the case of genotypes *RRKk* and *RRkk*.

Finally it is worth mentioning that resistance to coffee rust in Hibrido de Timor was regarded for ease of presentation in this scheme, as a single factor. Some evidence suggest that this resistance may be conditioned by a number of genes. In view of limited information available about the nature of each specific gene, in selection, rust resistance of the Hibrido de Timor type, can still be regarded for practical purposes as one complex factor. In any case, provisions are contained in the proposed Scheme for progeny testing the immediate parental genotypes before their progenies can be recommended for use by the farmers.

Breeding for stable resistance to coffee rust would entail including also sources of horizontal resistance in such a programme. This is possible if one of the varieties included in the programme also shows some horizontal resistance. In this case for example Rume Sudan. Leaf disc inoculation test is able to distinguish to some extent, reaction due to horizontal resistance (a long latent period after infection) from that due to vertical resistance (showing complete absence of infection). Using such a technique it is possible to select initially, in the progeny of one set of crosses, genotypes with a high level of horizontal resistance and cross these eventually to those selected for vertical resistance. Hybrid seed from such crosses would give genotypes carrying genes both for vertical and horizontal resistance. For a seed variety breeding programme, further selection for horizontal resistance within later generations of selfing may be complicated in the presence of vertical resistance genes. When practicing selection however, instead of discarding genotypes showing horizontal resistance, they should be retained so as to end up eventually with a population of genotypes having vertical resistance but also with some level of horizontal resistance.

9. PRACTICAL IMPLICATIONS OF RESULTS OF THIS RESEARCH IN BREEDING OF ARABICA COFFEE

9.1. Introduction

Results of research on genetic basis of variation among a number of varieties of arabica coffee, for growth, yield and quality characters, have been described. The effects of genotype-environment interaction, and the relationships among the various characters, have also been considered. On basis of this information, some of the main objectives of breeding programmes, and considerations to be taken into account in order to achieve such objectives, have been discussed.

It is worth noting in the first instance, that the materials used in this investigation were assumed to constitute the population of our interest (section 2.1.). In view of this, the conclusions drawn from this study apply strictly to this particular population and only approximately so, to other populations of a fairly similar genetic constitution. Moreover, the environments considered here, i.e. two plant densities and three or four years of repeated measurements, were too few to generalize these conclusions. Ideally the experiment should have been repeated not only in time, but also at different locations.

Notwithstanding these limitations, a number of the points emerging from this study may have important bearing on other breeding programmes connected with arabica coffee. The conclusions however, are especially relevant to the breeding programme at the CRS Ruiru. In the next section, 9.2., some of the main conclusions from this study are given, after which a breeding scheme for arabica coffee is discussed in detail (section 9.3.)

9.2. A summary of the main conclusions

1) Owing to their high repeatability and ease of measurement the following characters can be regarded as most suitable for rapid evaluation of different materials of arabica coffee (section 3.2.): girth of stem, height, internode length on main stem and on primaries and canopy radius.

2) When selection is practiced for growth and yield characters, particular attention should be given to effects of genotype-environment interaction. In this study, (section 3.3.) a large proportion of these effects was due to the linear component of genotype-environment interaction, which for most characters was found to be fairly heritable (section 3.6.). Under such circumstances, it is possible to select not only for high yielding genotypes, but also in combination with the desired level of linear response.

3) As regards especially yield (section 3.4.), F_1 hybrids on average tend to be more stable than their homozygous parental varieties. The linear response of different parental varieties depends largely on their mean yield, but also

to some extent on growth and yield characters of the variety. For F_1 hybrids, yield stability depends on their vegetative vigour and on the performance of the same hybrids or even their parents, for certain yield characters (section 3.7.).

4) Compact growth and yield stability are fairly independent (section 3.5.). It may be possible therefore to select for compact genotypes which combine high yield and improved yield stability.

5) Apart from the additive and dominance effects of genes, there is evidence of epistasis among the genes governing many of the growth and yield characters investigated. This epistasis is mainly responsible for disturbances of (W_r, V_r) relationships (section 4.4. & 4.6.). Otherwise for a number of other characters, including yield (after omission of 3 parents) the diallel assumptions appear to conform. Of some practical interest with regard to these assumptions of the diallel cross theory, is that this especially also confirms the diploid nature of *Coffea arabica*, which is considered to be an amphidiploid.

6) In arabica coffee, hybrid vigour may occur fairly frequently where hybrids are derived from parents that are more genetically diverse (section 4.6.). In the present study, hybrid vigour for yield was found to be due mainly to effects of complementary epistatic genes.

7) A number of growth characters (see sub 1) plus bearing primaries, among yield characters, had a high narrow sense heritability. Yield however, was heritable but only when considered on basis of plot means for 3 successive years of production.

8) Among characters that can be selected on seedlings in the nursery stage (section 5.5.2.) are reduced height and angle of primaries with the main stem.

9) Yield of cherry is positively correlated with a number of growth characters, and highly correlated with some yield characters, espeically % bearing nodes, flowers per node and number of berries per node (section 5.3.).

10) Preselection indices based for example on girth, canopy radius or internode length on primaries, bearing primaries or % bearing nodes, plus yield of the first 2 or 3 years of production of individual trees, are just as efficient as straight selection based on yield performance for 3 years of progeny means or means of a number of trees per genotype (section 5.5.3.).

11) Variation for quality characters (section 6.5.5.), is largely due to additive genetic effects. In addition, berry and bean characters show reciprocal differences which for % AA appear to arise from cytoplasmic effects.

12) Quality characters are less influenced by effects of genotype-environment interaction (section 6.5.1.). As a consequence, most bean size characters are highly heritable. Among liquor quality characters, the overall standard is most heritable. A number of F_1 hybrids in this study, have coffee quality remarkably similar to that of the present best commercial cultivars in Kenya, SL34 and SL28.

13) There is a strong negative association between the proportions of AA

and that of AB bean grades (section 7.3.), implying that these characters are complementary. Selection should therefore be restricted to only one of them, in this case % AA. Liquor characters especially acidity and flavour, flavour and the overall standard, are highly correlated. For selection however, only the overall standard need be considered.

14) The first years evaluation of % AA and the overall standard is already sufficient for selection purposes (see section 7.3.).

9.3. A breeding scheme for arabica coffee

On basis of some of the conclusions derived from this study consideration will now be given to some generalized but refined approach to breeding for certain important characters in arabica coffee. A schematic presentation of such a programme, and the estimated duration of the entire programme as well as that of each of its various phases, are respectively depicted in Figure 16 and 17. The goal of the scheme is to develop new varieties which combine improved yield and quality, with compact growth and disease resitance. The various steps of the proposed breeding scheme are as follows:

1) The initial stage involves selecting a number of varieties to be used as possible progenitors of the breeding programme. At this stage some kind of a diallel cross will be useful because it will give information on genetic control and heritability of the various characters in the population, as well as the combining ability of the different parents. In Figure 16, this stage represents generation A and is evaluated for 3 years (see Figure 17).

2) Depending on the information obtained from evaluation of generation A, the second stage, giving rise to generation B (Figure 16), may involve making further crosses between selected F_1 hybrids to a different parent resulting in a three way cross hybrids, or backcrossing them, or even making four way cross hybrids. This often is necessary to incorporate more characters, or to improve the initial single cross hybrids, since not all characters for which improvement is necessary will be represented to an acceptable level in any one single cross hybrid.

As shown in Figure 16, it is also advisable to divide the crosses into say, two separate groups on basis of certain characters. If a large number of characters are being considered as often is the case, it is easier to maintain them using a relatively small number of individuals per family by selecting for the desired level of expression of such characters in separate lines. This overcomes the risk of losing some of the favourable genes which often occurs when dealing with a large number of different genes confined in one small population. In particular, to keep track of several different genes responsible for resistance to some disease (e.g. CBD) it is most helpful, if they are kept in different populations in the initial breeding stages, see also section 8.5. It is also possible in this connection for example, to include in one population, compact plant types.

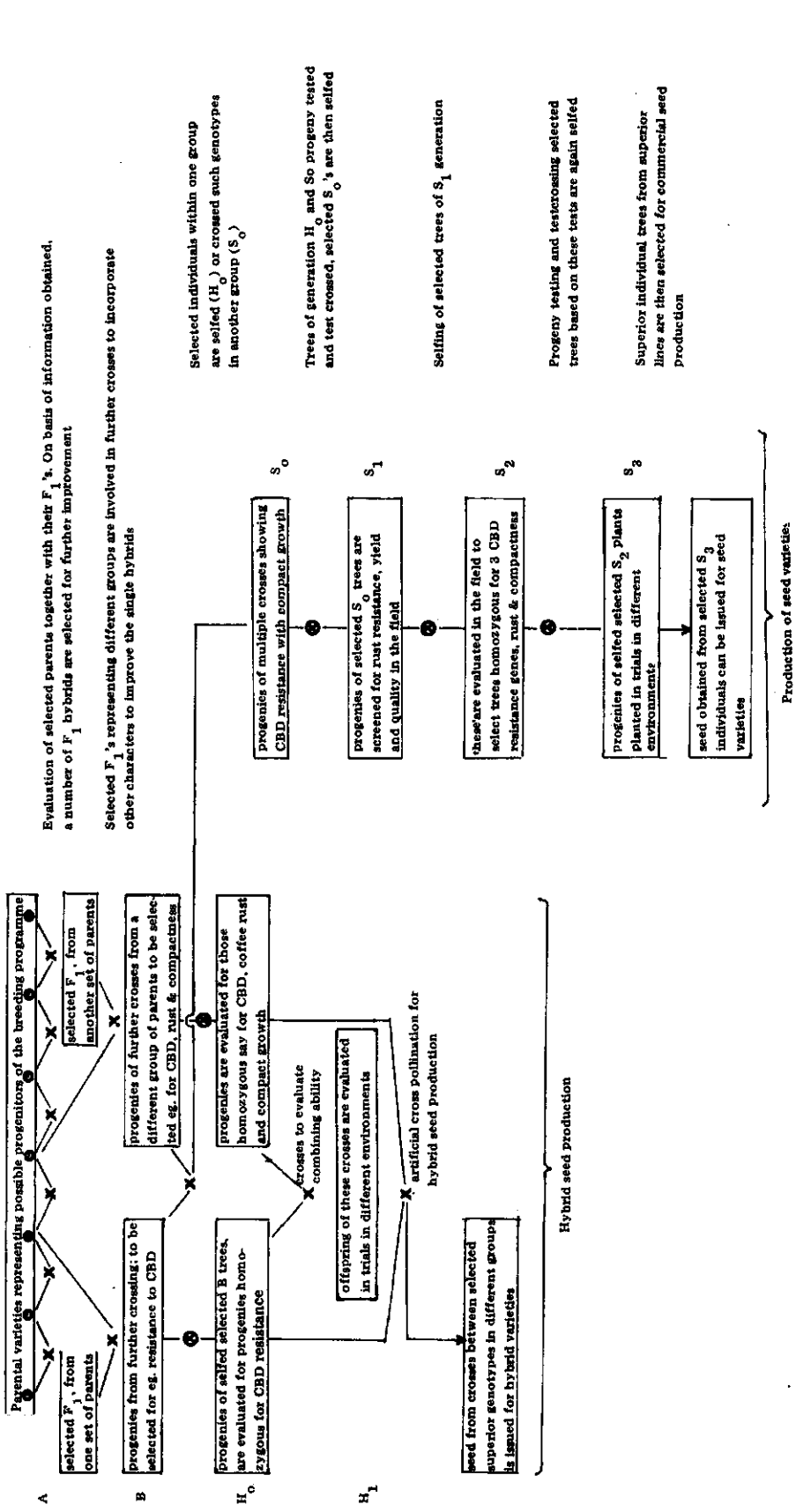


Fig. 16 A scheme of a breeding programme for arabica coffee.

In addition, crosses made within each group should give a population with progenies that are productive and which have good coffee quality. However, when such selected progenies from different populations are eventually crossed, it should also be possible to obtain from such crosses genotypes that are even more productive than their immediate parental populations. Information of this kind should have been obtained during evaluation of generation A. As a rough guide (see also sections 4.6. and 8.2.), the probability of obtaining eventually superior genotypes will be much higher if one population is derived from parents that are genetically different from those that give rise to the other population.

Using some of the parents in this study for illustration, one could consider the following three-way crosses: (Rume Sudan x Laurina) x SL28 or SL34, as one group, and (Hibrido de Timor x Caturra) x Padang, as another group. In the first group, Rume Sudan carrying 2 CBD resistance genes (see section 8.3.) is crossed to Laurina to improve yield and bean size. The resulting F_1, with CBD resistance and satisfactory bean size and yield, is crossed to SL28 and SL34 to improve further on bean size,liquor quality and yield. In the second group, Hibrido de Timor with coffee rust resistance, plus one other CBD resistance gene, is crossed to Caturra to combine disease resistance with compact growth (see also section 8.3.). This F_1 is then crossed to Padang to improve on yield. Considering information obtained in this study, it is evident that genotypes derived from a cross between progenies of the above three-way crosses are most likely to be much more productive, with better bean size and liquor quality. Other similar groups of crosses that could be considered in this study would be: Pretoria, K7, SL28/SL34 versus Hibrido de Timor, Caturra, Laurina; or Rume Sudan, Erecta, SL34 versus Caturra, Hibrido de Timor and Laurina or Padang. Pretoria carries CBD resistance genes on 2 loci, i.e R_2R_2 and kk. K7, as given in section 8.5., carries the kk genotype for CBD resistance and Erecta, is used for the erect branching character.

Such progenies representing generation B will segregate for some of these characters for instance disease resistance and compact growth (see also Figure 15). This offers the chance 1) to discard seedlings that are susceptible to CBD when applying the preselection test, 2) to eliminate non-compact genotypes in the nursery in the populations where compact types are included and, 3) to discard in the field plants susceptible to coffee rust in certain populations only. The supperior phenotypes on basis of yield and quality, among the remaining individual trees within each family (derived from each set, for instance, of three-way cross hybrids) will be selected for the next stage of the breeding programme. As indicated in Figure 17, evaluation of generation B take up to 4½ years from the time of field planting.

3) Two alternative approaches are possible in the next stage of the breeding programme. These are designated in Figure 16 as H and S generations representing schemes for hybrid seed production and for production of seed varieties, respectively. As was indicated in section 8.5. and will become apparent later on, the programme of producing seed varieties suffers two major drawbacks, 1) it is much more time consuming and, 2) it requires larger population. It is therefore not appropriate if there is an urgent need for improved varieties.

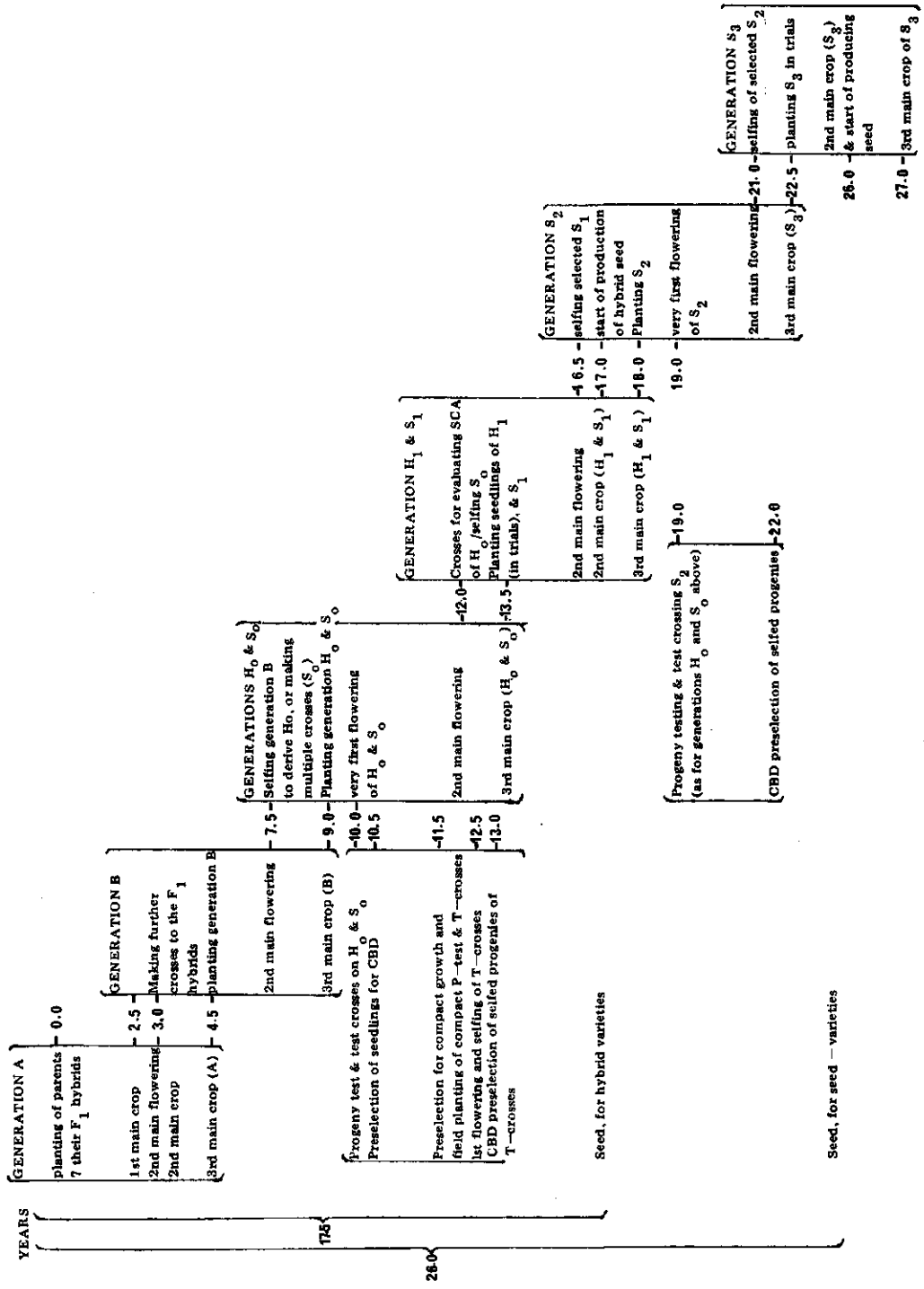


Fig. 17 The duration in years of the various phases of the breeding scheme given in Figure 16.

Development of hybrid varieties requires that genotypes selected from the two populations should be homozygous for certain of the characters they carry. The following stages would be necessary in this scheme for eventual production of such varieties:

(i) Selected genotypes of generation B are selfed. This can already be done when these trees are having their second main flowering (see Figure 17). The progenies of these selfings, generation H_o (Figure 16) will in turn be evaluated to select genotypes in both populations homozygous for disease resistance genes they carry and in one population for compact growth. To identify such genotypes, during the very first flowering which occurs within 12 months after field planting (see section 1.3.), trees of generation H_o will be selfed for progeny tests for disease resistance and compact growth. In addition as shown in Figure 15, and explained in section 8.5., it is necessary to test cross trees in the population carrying the *R*— and *K*— genes to distinguish those genotypes homozygous for the two genes.

Since disease resistance and compact growth can be evaluated during the seedling stage, by the time further crosses are made to evaluate combining ability (for generation H_1), information on progeny tests will already be available. Furthermore, as shown in Figure 17, evaluation of the selfed progenies of test crosses can be completed, just before the seedlings of generation H_1 are planted out in the field. Seedlings for progeny tests or testcrosses to determine disease resistance in parental genotypes need only be planted in small plots with a few trees representing each of the selected genotypes of H_o generation.

(ii) Generation H_1 (figure 16), represents progenies of crosses made between outstanding individuals from one population to similar selected individuals in the other population. The crosses are for determining H_o genotypes in the two populations with high specific combining ability especially for yield and quality. As is evident from selection applied within each population in the previous generations (see also section 8.5.), progenies of these crosses are expected to be compact, *Ctct*, and to carry at least 3 genes for CBD resistance i.e. *RrKkTt* plus resistance for coffee rust $H_T h_T$. These progenies can be planted out in trials in different locations and probably at different densities, to get an impression of yield performance,quality and the level of disease resistance in the field. These will be evaluated at least for the first 2 years of full production, before the best combining genotypes of H_o generation, on basis of performance of these crosses, can be selected for hybrid seed production. Evaluation of these trials as given in Figure 17 however, will still continue until the third main crop.

(iii) The final stage in production of hybrid seed involves artificial cross pollination. Practical problems connected with such a programme of large scale emasculation and artificial cross pollination will soon be investigated. The perennial nature of the plant, already excludes use of genetic or cytoplasmic male sterility. Possibilities of inducing temporary male sterility by chemical means may however be worth investigating. Nonetheless, it can be expected that the advantages of hybrid varieties in a perennial crop which happens also to be highly valued economically, are much more, compared to the problems to be encountered in artificial cross pollination.

Regarding the programme of developing seed varieties, the aim will be to combine most of the desired characters in single individual genotypes. The resultant genotypes should be homozygous especially for disease resistance genes and for compact growth. Such a programme would proceed as follows:

(i) Instead of selfing outstanding individuals of generation B as was done for production of hybrid varieties, such genotypes from one population are crossed to outstanding genotypes in the other population (see Figure 16). The progenies of these crosses will form the S_o generation of the seed variety programme. These multiple crosses will also show clear segregation for disease resistance and compact growth (see Figure 15). Only those seedlings resistant to CBD and with compact growth need be planted. After discarding plants susceptible to coffee rust in the field, the remaining S_o genotypes will be selfed during the very first flowering. One year after field planting (see Figure 17). The selfings are for progeny testing to determine S_o genotypes which carry in heterozygous form the 3 CBD resistance genes, *RrKkTt* (see also Figure 15).

On basis of information from the progeny tests, which will be obtained within 2 years after planting S_o generation (see Figure 17), the main selfing programme can be carried out on selected S_o gentoypes to give rise to progenies of generation S_1. This will be done during the second main flowering, 3 years after planting of S_o generation.

(ii) These progenies in S_1 generation, after screening for CBD resistance in the laboratory, and compact growth in the nursery, can be planted out in the field to be screened initially for rust resistance. Eventually, they will be evaluated for yield and quality. Selected individuals in this generation will in turn be selfed (See Figure 17) to give rise to S_2 generation (Figure 16).

(iii) S_2 genotypes will also be screened both for disease resistance and compact growth as in (ii). During their very first flowering, one year after field planting (Figure 17), the remaining selected genotypes will be selfed and testcrossed, as was done for generation H_o. The selfings are aimed at progeny testing for disease resistance and compact growth, while testcrosses are for distinguishing S_2 genotypes homozygous for 3 CBD resistance genes, *RRkkTT* (see section 8.5. and Figure 15). As is evident in Figure 17, before the selfed progenies of selected S_2 individuals are ready to be planted in the field as S_3 generation (Figure 16), the relevant information from progeny tests as well as from the selfed progenies of the testcrosses, will have become available.

(iv) The S_3 generation planted out eventually, is therefore expected to represent genotypes not only homozygous for the 3 CBD resistance genes as well as for compact growth, but also resistant to coffee rust; S_3 plants grouped according to their S_2 parents, can be planted out at different densities and locations as was the case for genotypes of H_1 (generation for hybrid seed production). The best yielding S_3 genotypes with good coffee quality, selected from superior S_2 lines, are expected to give rise to progenies with good overall performance for the same characters (see sections 8.2. and 8.3.). After the second main crop (Figure 17), such selected outstanding genotypes can be used for production of seed for commercial varieties.

It is evident from Figure 17, that the duration of the selection cycle in each generation in the proposed scheme, about 4½ — 5 years, is much shorter than that in many coffee breeding programmes. This is a result of basing selection on the performance of fairly young coffee trees. In fact crosses

or selfings for the next generation of the breeding scheme, are made mainly during the second main flowering. It is worth mentioning again, that the very first flowering in arabica coffee will occur within 1 year after field planting, the first main flowering to give the first full crop however, occurs about two years after field planting (see also section 1.4.). The first evaluation of genotypes in this scheme depends on early vegetative vigour and precocity as measured on basis of the first year of full production. Quality assessment will be accomplished using the first years crop (see section 7.3.). Evaluation of coffee rust and CBD resistance can be done before this period. As mentioned earlier (sections 5.5.2. and 8.5.) selection for CBD resistance and compact growth is always done beforehand on seedlings in the laboratory and in the nursery, whereas for coffee rust, evaluation is done on young trees in the field, but using the leaf disc inoculation test (see section 8.5.).

Evaluation of each generation however, is continued up to three years of full production (Figure 17). This serves mainly to confirm results of the first evaluation, so that — if necessary — further crosses can be made involving promising genotypes which might have been overlooked. It is also possible on basis of such continued evaluation, to discard genotypes of an entire pedigree if its members in the end, for some reason, prove to be unsuitable. This, in any case, can be done before the progenies giving rise to the next generation are planted out in the field.

As was mentioned in section 8.1., vegetative propagation in arabica coffee is possible and practicable. It could indeed be considered as one important way of cutting down drastically the duration of a breeding programme since, even in a heterozygous state, it is possible to fix all the desirable traits of a selected superior genotype if it is asexually propagated. However, use of conventional methods of vegetative propagation for multiplication of selected materials to release them eventually to the growers, still faces a number of practical problems. It would also entail drastic changes in the present techniques of management of commercial varieties. Nonetheless, vegetative propagation is useful in some stages of breeding. It can be used in the proposed breeding scheme for instance, in multiplication of selected H_o genotypes, which form the parents of hybrid varieties, or of selected S_3 genotypes (Figure 16), in order to get enough trees for production of seed. In either case, multiplication can be achieved by grafting scions of selected genotypes on seedling rootstocks, or by topworking these on trees already growing in the field.

In conclusion, as regards the alternative approaches given in the breeding scheme, development of hybrid varieties as opposed to seed varieties is to be preferred in most situations. It entails on enormous saving on breeding time, a gain of at least 8 years (Figure 17). In addition, it is more economical in terms of size of populations the breeder has to handle. It's major shortcoming i.e. large scale artificial cross pollinated is indeed labour demanding but not a complicated operation. As a consequence, seed for hybrid varieties maybe more expensive than seed for seed varieties. Nonetheless, the cost of hybrid seed will still represent a negligible fraction of the total establishment costs of a coffee farm. Yet in the end, hybrid varieties may perform even better than seed varieties on basis of yield (section 4.6.) and yield stability (section 3.4.) and can give as good quality coffee as the best of the present commercial cultivars (section 6.5.2.).

SUMMARY

Apart from coffee being the source of one of the most popular non-alcoholic beverages, its production is the mainstay of the economy of many developing countries. Arabica coffee, *Coffea arabica* L., is by far the most important of the cultivated species of *Coffea*. Its production however, faces a serious threat as a result of two devastating diseases, coffee rust *Hemileia vastatrix* B. & Br., and coffee berry disease *Colletotrichum coffeanum* Noak (Sensu Hindorf). In Kenya for instance, the breeding work in progress is aimed at developing new varieties of arabica coffee which combine resistance to both of these diseases, with high yield, good quality and also compact growth.

The duration of such a breeding programme, will largely depend on the efficiency of selection for yield and quality, especially since methods of early selection for resistance to the two most important diseases of *C. arabica* are already available (Rodrigues & Betterncourt, 1965; van der Vossen et al., 1976; Eskes, 1983). The objective of the present study has been to provide a better insight into the genetic basis of variation and covariation for growth, yield and quality characters among selected varieties of arabica coffee, and to indicate how such information can be used to improve the efficiency of selection for yield and quality.

The study is based on results from a diallel cross among 11 varieties of arabica coffee many of which are also progenitors of the main breeding programme at the CRS, Ruiru. The experiment was planted in 1975 at 2 plant densities i.e. 3,333 trees ha^{-1} and 6,667 trees ha^{-1} and was evaluated for 4 years. Details of materials, experimental design and methods of analysis are given in Chapter 2.

The general introduction (Chapter 1) includes also the taxonomy and evolution of *Coffea* species, together with an account of growth habit, flower and fruit characteristics of *C. arabica*. To provide some background to this study, a brief account is also given of the previous and current breeding work in arabica coffee.

Chapter 3 deals first with variation among the diallel material for repeated measurements of growth and yield characters. Girth of main stem, height, internode length on stem and primaries, and canopy radius have the highest repeatability and are also fairly easy to measure. They can be regarded therefore, as being most suitable for rapid evaluation of materials like those in the present study. Furthermore, these characters already give a good indication of the actual value of a genotype even when measured on coffee trees 1½ to 2½ years after field planting. To get a good impression of yield characters of a given genotype however, requires that assessment of such characters, based on the means of several individuals, is taken over a number of successive years.

The effect of genotype-environment interactions on the various characters, and the combining ability of different parents for these characters are also considered in this Chapter. It is demonstrated in the study, that variation among genotypes for these characters is under considerable influence of genotype-environment interactions. A large proportion of these effects is however, due to the linear component of genotype-environment interactions, which, for most characters, is fairly heritable. It can be concluded therefore, that it is possible to select for high yield but also in combination with desired

level of linear response to environments. Though yield stability depends in some degree on certain yield characters as well as on vegetative vigour, it is fairly independent of compact growth. This indicates, that even among compact gentoypes, it may be possible to select both for productivity and for yield stability. As regards especially yield in this study, F_1 hybrids on average tend to show more stability, compared to the parents, in different environments.

In Chapter 4, the genetic basis of variation for some of the characters selected on basis of results from Chapter 3, is considered by applying the diallel analysis procedure of Hayman (1954) and Jinks (1954). Apart from the additive and dominance effects of genes there is evidence of epistasis for many of the characters, which is mainly responsible for disturbances in the (W_r, V_r) relationships. For a number of other characters for instance, number of primaries, bearing primaries and yield of cherry and clean coffee (after omission of three parents), the diallel assumptions appear to conform. Of some practical interest in connection with these assumptions is that such information also gives further evidence of the diploid inheritance especially of quantitative characters in *C. arabica* (= amphidiploid).

Many F_1 hybrids in this study displayed intense hybrid vigour particularly for yield, varying between 10% to over 200% above the better parent. This hybrid vigour is mainly due to effects of complementary epistatic genes. It is also concluded from this and other recent studies, that such hybrid vigour in *C. arabica* may occur fairly frequently where hybrids are derived from parental varieties that are more genetically diverse. Furthermore, it can be exploited in breeding programmes immediately by producing hybrid varieties but also eventually by further selection in later generations of inbreeding.

The following values of narrow sense heritability, h^2_n, of these characters: girth 0.50—0.61, height 0.77—0.78, primaries 0.58—0.52, angle 0.56—0.62, canopy radius 0.44—0.50 internode length on primaries 0.51—0.63, bearing primaries 0.51—0.53 and flowers per node 0.17—0.18. Yield of cherry and clean coffee however, were heritable (h^2_n = 0.42—0.64, 0.53—0.68) but only when the yield was based on plot means for 3 successive years of production.

The relationship among growth and yield characters is considered in Chapter 5. The genotypic correlation r_g, between height of the seedling and that of the mature plant (0.91) and that of the angle of laterals of seedlings, and of mature plants (0.77) suggests that these characters can already be selected on basis of 1 year old seedlings in the nursery. Yield of cherry is positively correlated with a number of growth characters for instance, girth, canopy radius and internode length on primaries, and highly correlated with some yield characters especially % bearing nodes, flowers per node and number of berries per node. As a consequence, use of preselection indices based for example on girth, canopy radius or internode length on primaries, bearing primaries or % bearing nodes, plus yield of the first 2 to 3 years of production of individual trees, will be just as efficient as straight selection based on yield performance for 3 years of progeny means or means of a number of trees per genotype. It is therefore possible in arabica coffee using such a procedure, to base individual tree selection for yield on the performance of fairly young trees.

Apart from yield, coffee quality is another equally important aspect to be considered in an improvement programme. This is especially true for the Kenyan coffee which is renown for its distinctively fine quality. In this study, berry, bean and liquor quality characters were assessed among the diallel material at the 2 plant densities for three years (Chapter 6). Variation for these characters was chiefly due to the additive genetic effects. Progenies derived from crosses between parents with good coffee quality attributes, also tend to give in general, coffee of good quality. This is to be expected when specific combining ability is of less importance as it was for these characters.

In addition, unlike growth and yield characters, quality characters in general are less influenced by effects of genotype-environment interactions. Berry and bean characters especially single berry weight, % AA, % PB and % AB are highly heritable with estimates of h^2_n varying from 0.50 to 0.70. Regarding liquor quality overall standard was the most heritable character (h^2_n = 0.44).

The best commercial varieties SL34 and SL28 are also indeed the most outstanding among the parental varieties for both bean size and liquor quality. But there are among the hybrids, a number of these with coffee quality remarkably similar to that of the two commercial varieites.

Chapter 7 deals with correlation between these various quality characters. Of some interest is the strong negative association (r_g = —0.56, —0.65 at lower and higher plant densities) between % AA and % AB both of which are highly valued. This implies that such characters are complementary and hence for improvement purposes only one of them should be considered, in this case % AA. Liquor quality characters on the other hand, are all positively correlated especially acidity and flavour (r_g = 0.76), and flavour and overall standard (r_g = 0.84). For selection, however, only the overall standard need be considered. Furthermore, the first year's assessment of % AA and overall standard of liquor is already sufficient for selection purposes.

On the basis of information obtained in this study, various aspects of breeding for yield quality and compact growth in arabica coffee are discussed (Chapter 8). Attention is also given to incorporating into such a programme resistance to coffee berry disease and coffee rust. Finally in Chapter 9 a breeding scheme is proposed aimed at developing new varieties of arabica coffee combining all the above attributes. The scheme entails either production of hybrid varieties, or a programme of further selection within progenies of subsequent generations of selfing to derive seed varieties. Notable features of this scheme include, the use of information as that derived in this study for better planning of hybridisation programmes. Secondly, because selection within each generation is based mainly on the performance of fairly young coffee trees, the breeding cycle can be drastically reduced to an average of 4½ to 5 years.

SAMENVATTING

Koffie is de basis van één van de populairste niet-alcoholische dranken. De economie van veel ontwikkelingslanden drijft voor een goed deel op de koffieteelt. Arabica koffie, *Coffea arabica* L., is verreweg de belangrijkste van de in cultuur gebrachte soorten van *Coffea*. De produktie wordt helaas ernstig bedreigd door twee rampzalige ziekten: koffieroest, *Hemileia vastatrix* B. & Br., en koffiebessenziekte, *Colletotrichum coffeanum* Noak (sensu Hindorf). Onder andere in Kenya is veredelingswerk gaande met als doelstelling de ontwikkeling van nieuwe rassen van arabica koffie waarin resistentie tegen beide ziekten gecombineerd is met hoge opbrengst, goede kwaliteit en compacte groei.

De duur van zo'n veredelingsprogramma zal sterk bepaald worden door de doeltreffendheid van selectie op opbrengst en kwaliteit. Dit is vooral het geval omdat voor vroege selectie op resistentie tegen de twee belangrijkste ziekten van *Coffea arabica* al methoden voorhanden zijn (Rodrigues & Betterncourt, 1965; Van der Vossen *et al.*, 1976; Eskes, 1983). Het doel van het onderhavige onderzoek was een beter inzicht te verschaffen in de genetische basis voor variatie en covariatie (voor groei, opbrengst en kwaliteitskenmerken) tussen geselecteerde rassen van arabica koffie en voorts aan te geven hoe zulke informatie gebruikt kan worden om de doeltreffendheid van selectie op opbrengst en kwaliteit te verbeteren.

Het onderzoek is gebaseerd op de resultaten van een diallele kruising tussen 11 rassen van arabica koffie. Veel van die rassen worden als geniteur gebruikt bij het veredelingsprogramma van het Coffee Research Station (CRS) in Ruiru, Kenya. Het experiment werd in 1975 bij 2 plantdichtheden geplant, nml. 3333 bomen per ha en 6667 bomen per ha. Het werd gedurende 4 jaar waargenomen. Bijzonderheden omtrent het materiaal, het proefschema en de analysemethoden zijn te vinden in hoofdstuk 2.

De algemene inleiding (hoofdstuk 1) bevat tevens de taxonomie en de evolutie van *Coffea* soorten, alsmede een verhandeling over habitus en bloem- en vruchtkenmerken van *C. arabica*. Als achtergrondsinformatie wordt in kort bestek het oude en het nieuwe veredelingswerk beschreven.

In hoofdstuk 3 komt eerst de variatie binnen het diallele materiaal aan de orde, voorzover blijkend uit herhaalde waarnemingen aan groei- en opbrengstkenmerken. Omvang van de hoofdstam, lengte, internodiumlengte langs de stam en langs de primaire zijtakken en straal van de kruin hebben de hoogste herhaalbaarheid. Deze kenmerken zijn tevens tamelijk gemakkelijk meetbaar. Ze kunnen daarom beschouwd worden als het meest geschikt voor een snelle evaluatie van het onderzochte materiaal. Deze kenmerken geven voorts een goede indicatie van de feitelijke waarde van een genotype, zelfs wanneer die wordt vastgesteld aan de hand van waarnemingen bij koffiebomen die pas 1½ tot 2½ jaar te velde staan. Voor een goede indruk van opbrengstkenmerken van een bepaald genotype is het echter nodig dat de waarnemingen voor die kenmerken, uitgedrukt als het gemiddelde over een aantal bomen, gedurende enige opeenvolgende jaren worden verricht.

Het effect van genotype x milieu interactie op de diverse eigenschappen en de combinatie-geschiktheid van verschillende ouders voor die eigenschappen worden eveneens in dit hoofdstuk in beschouwing genomen. Uit het onderzoek bleek dat er een aanzienlijke invloed is van genotype x milieu interactie op de variatie, tussen genotypen, voor deze eigenschappen. Een belangrijk deel van deze effecten is evenwel toe te schrijven aan de lineaire component van genotype x milieu interactie, welke, voor de meeste kenmerken, in tamelijke hoge mate genetisch bepaald wordt. Er kon daarom worden geconcludeerd dat het mogelijk is te selecteren op hoge opbrengst in combinatie met het gewenste niveau van lineaire responsie op milieu's. Hoewel stabiliteit voor

opbrengst enigszins bepaald wordt door zowel bepaalde opbrengstkenmerken als door vegetatieve groeikracht is dat aspect tamelijk onafhankelijk van compacte groei. Dit geeft aan dat het mogelijk kan zijn te selecteren op zowel productiviteit als stabiliteit; zelfs bij compact groeiende genotypen. Uit dit onderzoek bleek dat F_1 hybriden gemiddeld genomen stabieler zijn over verschillende milieu's dan hun ouders; in het bijzonder wat de opbrengst betreft.

In hoofdstuk 4 wordt de genetische basis voor de variatie in beschouwing genomen door toepassing van de diallele analyse volgens Hayman (1954) en Jinks (1954). Dit gebeurt voor een paar eigenschappen, welke uitgekozen zijn op grond van de resultaten die in hoofdstuk 3 vermeld staan. Behalve voor additieve en dominante geneffecten zijn er voor veel van de eigenschappen ook aanwijzingen voor epistasie. Deze epistasie is voornamelijk verantwoordelijk voor storingen in de (W_r, V_r) relaties. Voor een aantal eigenschappen bleken de veronderstellingen voor de diallele analyse wel op te gaan; b.v. voor aantal primaire zijstengels, aantal vruchtdragende zijstengels en opbrengst aan bessen en schone bonen (na weglating van 3 ouders). Het is ten aanzien van die veronderstellingen van practisch belang dat deze informatie op aanvullende wijze blijk geeft van diploide overerving bij *C. arabica* (een amphidiploid); vooral voor kwantitatieve eigenschappen.

Veel van de F_1 hybriden in dit onderzoek manifesteerden een sterke bastaardgroeikracht, in het bijzonder voor opbrengst (tussen 10% en 200% beter dan de beste ouder). Deze bastaardgroeikracht berust voornamelijk op effecten van complementaire epistasie. Uit dit onderzoek werd, evenals uit ander recent onderzoek geconcludeerd dat zulke bastaardgroeikracht in *C. arabica* tamelijk algemeen kan optreden indien de hybriden verkregen worden uit ouderlijke rassen die in genetisch opzich nogal verschillen. De bastaardgroeikracht kan in de veredeling onmiddellijk benut worden door de produktie van hybride rassen, maar bepaalde bestanddelen ervan ook op de lange duur door voortgezette selectie in latere inteeltgeneraties.

De volgende schattingen werden verkregen voor de erfelijkheidsgraad in engere zin (h^2_n): stamomvang: 0,50-0,61; lengte: 0,77-0,78; aantal primaire zijstengels: 0,58-0,52; hoek: 0,56-0,62; straal van de kruin: 0,44-0,50; internodiumlengte bij primaire zijstengels: 0,51-0,63; aantal vruchtdragende primaire zijstengels: 0,51-0,53 en aantal bloemen per oksel: 0,17-0,18. De opbrengst aan bessen en aan schone bonen bleek alleen erfelijk bepaald (h^2_n = 0,42-0,64; 0,53-0,68) wanneer de opbrengst gebaseerd was op veldjesgemiddelden over 3 opeenvolgende produktiejaren.

De samenhang tussen groei- en opbrengstkenmerken wordt in hoofdstuk 5 in beschouwing genomen. De genotypische correlatie, r_g, tussen lengte van de kiemplant en van de volwassen boom (0,91) en die van de hoek die de zijstengels maken bij jonge planten en bij de volwassen bomen (0,77) duiden erop dat deze eigenschappen al beselecteerd kunnen worden bij zaailingen in de kweektuin. Besopbrengst is positief gecorreleerd met een aantal groeikenmerken, bijvoorbeeld stamomvang, straal van de kruin, internodiumlengte bij de primaire zijstengels. Besopbrengst is ook sterk gecorreleerd met een aantal opbrengstkenmerken, in het bijzonder: het percentage vruchtdragende oksels, het aantal bloemen per oksel en het aantal bessen per oksel. Gebruik van selectie-indices voor vroege selectie, waarin bijvoorbeeld zijn opgenomen: stamomvang, straal van de kruin of internodiumlengte langs de primaire zijstengels, aantal vruchtdragende zijstengels of percentage vruchtdragende oksels, plus opbrengst in de eerste 2 of 3 produktiejaren van individuele bomen, zal even doeltreffend zijn als directe selectie gebaseerd op gemiddelde opbrengst, gedurende 3 jaar, van nakomelingschappen, of gemiddelde opbrengst van een aantal bomen per genotype. Het is dus mogelijk om bij arabica koffie op deze wijze reeds bij vrij jonge bomen op opbrengst te selecteren.

Koffiekwaliteit is een aspect dat even belangrijk is in een veredelingsprogramma als de opbrengst. Dit is in het bijzonder het geval voor koffie uit Kenya, welke befaamd is om zijn uitzonderlijk goede kwaliteit. In dit onderzoek werden bes-, boon- en drankkwaliteitskenmerken van het diallele materiaal beoordeeld voor de 2 plantdichtheden gedurende 3 jaar (hoofdstuk 6). Variatie voor deze eigenschappen berustte voornamelijk op additieve genotypische effecten. Nakomelingschappen, verkregen uit kruisingen tussen ouders met goede koffie kwaliteitsmerken, vertoonden in het algemeen de tendens tot koffie met een goede kwaliteit. Dat is ook te verwachten omdat specifieke combinatie-geschiktheid voor de betrokken eigenschappen van minder belang is. In tegenstelling tot de groei- en opbrengstkenmerken werden de kwaliteitskenmerken in het algemeen minder beïnvloed door genotype x milieu interactie. Bes- en booneigenschappen worden in hoge mate erfelijk bepaald, in het bijzonder individueel boongewicht, percentage AA, percentage PB, en percentage AB (met schattingen voor h^2_n variërend van 0,50 tot 0,70). Voor de criteria voor drankkwaliteit was de totaalindruk het duidelijkst erfelijk bepaald ($h^2_n = 0,44$).

Van de commerciële rassen waren SL 34 en SL 28 inderdaad de beste geniteurs, zowel voor boongrootte als voor drankkwaliteit. Sommige hybriden hadden een koffiekwaliteit die opmerkelijk goed overeenkwam met die van de twee commerciële rassen.

Hoofdstuk 7 handelt over correlaties tussen diverse kwaliteitskenmerken. De sterke negatieve samenhang (r_g = -0,56 en -0,65 bij lage, resp. hoge plantdichtheid) tussen percentage AA en percentage AB is niet zonder belang. Deze klassen worden beide hoog gewaardeerd. Dit betekent dat deze kenmerken complementair zijn. Voor verbetering kan dus slechts één klasse in aanmerking komen; in dit geval percentage AA. Aan de andere kant waren drank kwaliteitskenmerken allemaal positief gecorreleerd, zoals zuurgraad en aroma (r_g = 0,76) en aroma en totaal indruk (r_g = 0,84). Voor selectie behoeft alleen de totaal indruk te worden beschouwd. Voorts is het voor selectie voldoende de eerstejaars beoordeling van percentage AA en totaalindruk te kennen.

Op grond van de in dit onderzoek verkregen informatie worden verschillende aspecten van veredeling met betrekking tot opbrengst, kwaliteit en compacte groei van arabica koffie besproken (hoofdstuk 8). Er wordt ook aandacht gegeven aan het opnemen, in zo'n programma, van resistentie tegen koffiebessenziekte en koffieroest. Tenslotte wordt in hoofdstuk 9 een veredelingsschema voorgesteld dat als doel heeft de ontwikkeling van nieuwe rassen van arabica koffie, waarin alle hiervoor genoemde eigenschappen gecombineerd zijn. Het schema behelst hetzij de produktie van hybride rassen, hetzij voortgezette selectie, binnen nakomelingschappen van opeenvolgende, uit zelfbevruchting te verkrijgen generaties, teneinde een generatief reproduceerbaar ras te ontwikkelen. Opmerkelijke kenmerken van dit schema zijn ten eerste het gebruik van informatie, zoals verkregen in het onderhavige onderzoek, voor een betere opzet van kruisingsprogramma's. Ten tweede: omdat de selectie binnen elke generatie voornamelijk gebaseerd is op de prestaties van tamelijk jonge koffiebomen kan de duur van de veredelingscyclus drastisch beperkt worden; tot gemiddeld 4½ tot 5 jaar.

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Curriculum vitae

The author was born in Kakamega in the Republic of Kenya, on 6 September 1946, being the second son of Mr and Mrs Mutsotso. From 1963 to 1969 he did his secondary school education at Kakamega High School and Kenyatta College Nairobi. He graduated in 1972 with BSc. 1st class honours in Agriculture (Crop Production) from Makerere University Kampala Uganda. He took up postgraduate studies at the University of Birmingham England, in the Department of Genetics, where he obtained an MSc. degree in Applied Genetics in 1974. He has since been involved in the Coffee Breeding Project at the Coffee Research Station, Ruiru Kenya. The project is under the terms of a bilateral technical aid agreement between the Netherlands and Kenya Governments. At present, the author is the project leader.

THEOREMS (STELLINGEN)

1. That a compact coffee variety like Caturra is more sensitive in terms of productivity, to increased plant competition than even some of the tall varieties, may be due to its canopy structure but more important, it may be a reflection of its relatively poor below ground competition.

2. Though heritability of a character is an important concept in breeding, it suffers two main drawbacks, 1) it is a property not just of a character but also of the population and environment 2) its predictive value depends on the frequency of the dominant allelles in the population and on the breeding method.

3. Gale is probably right to conclude that conditions under which neutral gene theory would work are rather restricted and that the evidence available so far strongly suggests that natural selection is the prime mover of the process of evolution.

   J.S. Gale, 1980. Population Genetics. Blackie, 189 p.

4. Notwithstanding the claim by Carvalho and Monaco that commercial production of hybrid seed in *C. arabica* is not economically feasible unless heterotic F_1's are propagated vegetatively, it may be easier in practice and even more economical to produce hybrid seed by ar tifical cross pollination even if a system of male sterility is absent altogether.

   A. Carvalho & L.C. Monaco, 1969. Outlines of Perennial Crop Breeding in the tropics. Misc. Paper 4 Landbouwh. Wageningen 198–216.

5. Because of falling earnings in the coffee producing countries, research in coffee should be directed more towards aspects that will reduce production costs of the farmers than towards recommending new and effective but more expensive inputs.

6. International collaboration is indespensible if faster progress has to be achieved in breeding programmes especially of perennial crops. Breeding for coffee berry disease and coffee rust are clear examples of such collaboration.

   C.J. Rodrigues J., 1977. Int. Scient. Coll. Coffee ASIC (Abidjan 28 Nov. – 3 Dec. 1977); 537 – 538.
   A. Carvalho, L.C. Monaco & H.A.M. van der Vossen, 1976. Bragantia 35 (28): 343 – 347.
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7. Failure of many technical aid programmes stems from numerous factors among them perhaps the most important are 1) lack of proper feasibility studies particularly in terms of the national priorities of the project, and 2) failure by the donor countries to monitor closely the progress of such projects and especially, local manpower development.

8. If stabilizing selection as a general phenomenon in crop pathosystems does not exist as suggested by Parlevliet, to such an extent that it can be regarded as an empty concept, then the merits claimed by van der

Plank of using multilines instead of pyramiding vertical resistance genes are clearly questionable.

J.E. Parlevliet 1981. Euphytica 30: 259 – 269.
J.E. van der Plank, 1968. Disease Resistance in Plants. Academic Press 206 p.

9. The most important contribution breeding can make to developing countries is what was suggested by Swaminathan et al., to improve yield and yield stability in order to cushion the small farmer from undue risk resulting especially from pest epidemics and weather aberrations.

M.S. Swaminathan, J. Sneep & A.J.T. Hendriksen, 1979. Plant Breeding Perspectives D.J. van der Have, PUDOC: 396 – 429.

10. It may be worth reassessing the strategies in animal improvement programmes in the tropics which depend on direct introduction of European or American breeds, or crossing these breeds with indigeneous cattle; indeed Maule has claimed that tropical breeds are small because that's the best shape for survival, they eat less, are better at converting what they eat and produce calves more successfully than do larger breeds.

J. Maule, 1981. Int. Agric. Development 1 (9): 37.

11. Apart from making some developing countries become once more credit worthy in the eyes of international lending institutions, it remains to be seen whether devaluation measures in such countries will be the answer to their present ailing economies.

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