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Reciprocal recurrent selection applied to *Coffea canephora* Pierre. I. Characterization and evaluation of breeding populations and value of intergroup hybrids

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Summary

Two breeding populations have been identified with *Coffea canephora,* based on geographical and genetic differences: the Guinean group from West Africa and the Congolese group from central Africa. A reciprocal recurrent selection programme based on these groups was initiated in Côte d'Ivoire in 1984. Genotypes of both groups available in field collections are either of cultivated or wild origin.

Genotypic and phenotypic variability was evaluated within and between the groups for the following characteristics: isozyme patterns, architecture, drought tolerance and vigour, technological and organoleptic traits, pest and disease resistance. Variation between and within groups was found to be large. Based on isozyme analysis and phenotypic observations, two subgroups were identified within the Congolese group. Phenotypic values of parents and testers used in the first cycle of reciprocal recurrent selection are presented.

Results of two intergroup hybrid trials indicate high yield and vigour for these hybrids compared to intragroup hybrids, justifying the reciprocal selection approach. Furthermore, the variation observed indicates that recurrent selection would allow progress for selection traits for both populations and intergroup hybrids.

Introduction

Coffea canephora is the second important cultivated coffee crop, representing 20% of total world coffee consumption. It is a strictly allogamous perennial plant, cultivated in tropical lowlands with high rainfall patterns.

Early in the 20th century, the first coffee-tree plantations in West Africa were created with seeds imported from central Africa and also with local wild genotypes (Portères, 1937). Afterwards, farmers picked seedlings under productive trees for new plantations, some of those seedlings resulting from natural hybridizations between the two geographical origins. In the 1960's, imported clones and seeds from central Africa, especially from Zaire (Braudeau et al., 1962), and highly productive clones collected in local plantations were used as base material for *C. canephora* selection programs in Côte d'Ivoire. Interesting clones were gathered in a field collection while variety trials allowed the selection of seven commercial clones and six hybrids (Capot, 1977).

Since 1966, coffee surveys were carried out in several countries in central and western Africa (Berthaud, 1986). The material was planted in a large collection at Divo in Côte d'Ivoire which contains today more than 1,000 accessions of *C. canephora*. The wild *C. canephora* populations come from Côte d'Ivoire and Guinea (Berthaud, 1986; Le Pierres et al., 1989), from Cameroon (Anthony et al., 1985), from the Central African Republic (Berthaud & Guillaumet, 1978), and from the Congo (Namur et al., 1987).

In 1983, based on isozyme analyses, two different groups were identified within *C. canephora*: a 'Guinean' group from western Africa and a 'Congolese' group from the center of Africa (Berthaud, 1986). Allelic specificity for both groups were found for three loci.

Overall prevailing characteristics of the two groups are indicated below:

Guinean	Congolese
rust susceptibility	rust resistance
high caffeine content	medium caffeine content
low bean weight	high bean weight
drought tolerance	drought susceptibility
secondary branching	very little secondary branching
small internodes	large internodes
small elongated leaves	large broad leaves
small growth habit	tall growth habit
early harvest	late harvest

According to the analyses of Berthaud (1985), it was observed that the most productive selected clones and one productive hybrid in Côte d'Ivoire were hybrids between the two groups. Based on these observations, a reciprocal recurrent selection (RRS) programme (Comstock et al., 1949, Gallais, 1978) was proposed for *C. canephora* breeding (Berthaud, 1985). Such a programme was initiated in 1984 and is based on full-sib intergroup family selection through testers (Leroy & Charrier, 1989). Main selection criteria are productivity, vigour, architecture, technological and organoleptic qualities, and resistance to pests and diseases.

In the present article, the results obtained between 1983 and 1991 on characterization and evaluation of both breeding populations are given. Conclusions of the first hybrid trials which were set up to compare value of intergroup hybrids with intragroup hybrids are also presented. The consequences for the selection programme in terms of intergroup progeny testing and intragroup crossing are discussed.

Materials and methods

Materials

Genotypic and phenotypic diversity has been evaluated among the populations available in collection in Côte d'Ivoire. These populations were described by Montagnon et al. (1991) and include the following origins:

- seventeen wild populations from western and central Africa containing 9 to 99 genotypes: 12 from Côte d'Ivoire, 3 from Central African Republic, one from Cameroon and one from Guinea.
- twelve cultivated populations comprising 5 to 44 plants and selected in several African countries: four from Côte d'Ivoire, three from Zaire, and one of each of the following countries: Central African Republic, Uganda, Benin, Togo and Gabon. One hundred two individual plants selected in different Ivorian plantations were also evaluated.
- twenty one Guinean and 32 Congolese parents used in the first RRS cycle have been evaluated for agronomical characteristics in randomized single-tree plot clonal trials with 20 plants per clone planted in 1988.

Two hybrid trials were planted in 1985 and 1988 in order to confirm the value of intergroup hybrids, compared with intra-Guinean (GUI), intra-Congolese (CON) hybrids and commercial clones. In the trial planted in 1985, 4 randomly chosen intergroup hybrids (GUI × CON) with 5 intra-Congolese hybrids and 3 commmercial clones are compared. Seventy four to 100 plants were tested for each progeny and placed in a fully randomized design with single-tree plots. In the trial planted in 1988, 6 intra-Guinean, 3 intra-Congolese and 12 intergroup hybrids in a partial diallel design with seven parents (4 Guinean and 3 Congolese), with 29 single-tree replications fully randomized are compared. In both hybrid trials, vigour, architectural traits, quality and yield (4 and 2 harvests, respectively) were observed.

Characterization of breeding populations

Isozyme analyses were carried out for six isozyme systems involving 9 different loci, as described by Berthou & Trouslot (1977).

Phenotypic observations

Eight agronomical and plant characteristics have been evaluated:
- drought susceptibility estimated at the end of the dry season of 1990 by a visual note (1 to 5 scale) for degree of wilting;
- tree height and longest primary branch length recorded two years after plantation;
- total number of internodes of the main stem and for the longest primary branch recorded two years after plantation;
- average internode length for stem and branches;
- total number of internodes estimated as a multiplication of the number of internodes on the main stem by the number of internodes on the longest branch;
- stem diameter at 30 months.

Architectural characteristics are of interest for selection related to high density planting and to avoid lodging of heavy bearing plants. These traits were observed for the Guinean and Congolese parents in the clonal trials. The global diversity is described from Principal Components Analysis with standardized variables (Greenacre, 1984). This analysis permits the data to be summarized as a reduced number of independant factors.

Twelve traits were observed in the hybrid trials (Table 6). Data from these trials were treated by analysis of variance, and the means were compared with Newman & Keuls test at 5% probability of unequal numbers of replications (Kramer, 1956). Diallel trial was analysed with the CSDIAL program, elaborated by CIRAD for diallel using Griffing model.

Technological and organoleptic qualities

Two technological traits have been evaluated: bean weight and caffeine content. Dry bean weight is expressed in grams of 100 dry beans prepared from samples of 500 to 1000 fresh berries. In the cultivated collections, samples were harvested in 1985, 1986 and 1990. In the collections of wild genotypes, most samples were collected in 1987 and 1990.

Caffeine content, in percentage of dry matter, was measured in green coffee samples prepared from 100 to 200 fresh berries. Presented results are based on samples analyzed between 1969 and 1987.

Ten genotypes (4 Congolese, 3 Guinean and 3 hybrid clones) were evaluated for cup quality. Four samples per genotype, each of 1,5 kg, were harvested between September and November 1989. After hulling, the fresh berries were plunged in water for one night and then washed before drying in the open air. They were tested in the CIRAD/CP laboratories at Montpellier, France, for the following roasting and organoleptic characteristics: bean weight loss and increase of bean volume; bitterness, body and acidity (intensity noted on a 1 to 3 scale). Roasting traits are important for freeze-drying, widely applied to *C. canephora* coffee processing. A note for overall cup quality was attributed to each sample. The drinking panel consisted of 7 to 10 experienced tasters. Each cup-quality evaluation consisted of four randomly chosen samples, each clone was tested with four replications.

Diseases and pests

Resistance to coffee leaf rust (*Hemileia vastatrix*) and the coffee twig-borer (*Xylosandrus compactus*), were annually estimated in the field since 1983. Susceptibility to coffee leaf rust induces leaf fall and decreases yield of susceptible clones of *C. canephora,* as has been observed at Divo, Côte d'Ivoire (Montagnon et al., 1993). Branches attacked by the borer die, thus affecting directly productivity.

A 1 to 5 point scale for reaction type was used for evaluation of coffee rust susceptibility (Eskes & Toma-Braghini, 1981). Plants were considered as resistant if no sporulation was observed. The highest

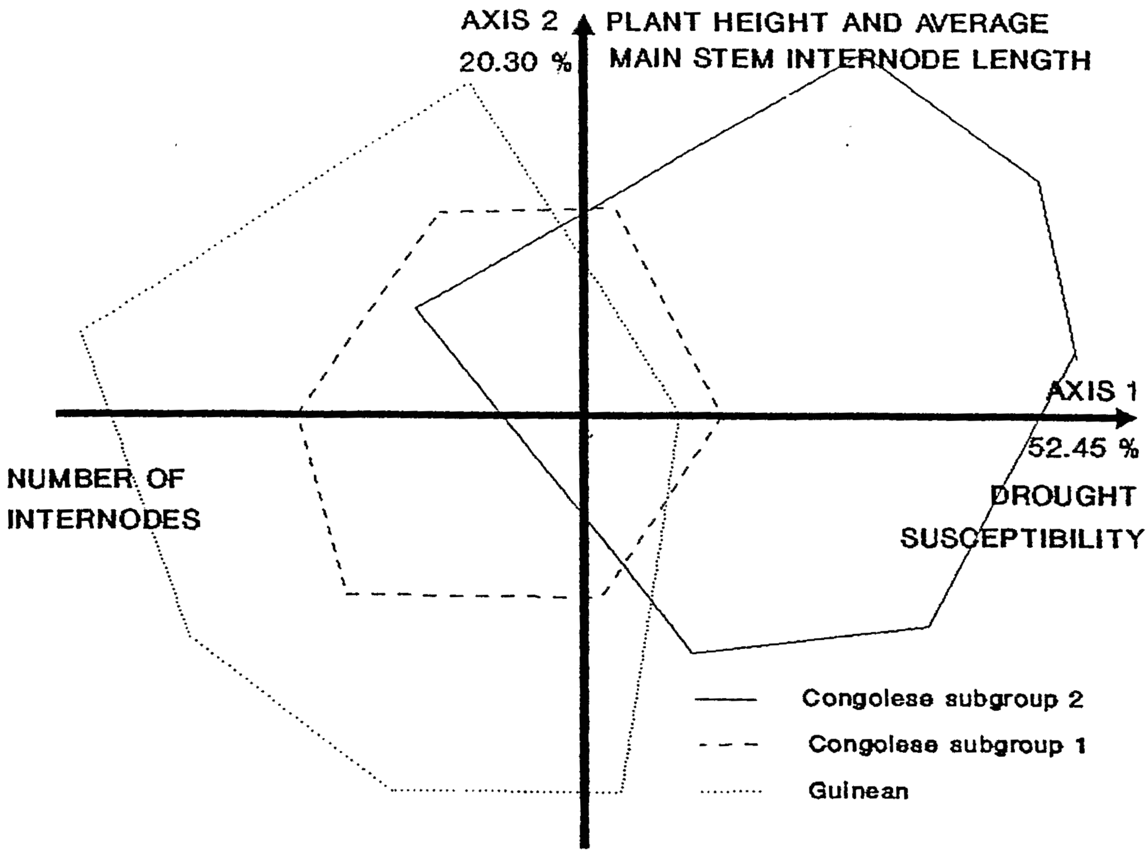

Fig. 1. Principal Components Analysis on some phenotypical characteristics for Guinean and Congolese parents.

observed score for each genotype over several years was taken into account for the analyses.

An intensity scale from 1 to 5 was applied on individual plants for scoring coffee twig-borer resistance. Genotypes with average notes less than 3 were considered as resistant.

Results and discussion

Characterization and evaluation of breeding populations

Characterization by isozyme studies

The analyses of isozymic alleles frequencies include earlier reported results (Berthaud, 1986; Montagnon et al., 1991) as well as new results from 34 Guinean and 51 Congolese genotypes. Those analyses confirm the division of the Congolese group into two subgroups (Montagnon et al., 1991), of which alleles of the esterase system are different. As will be shown later, these subgroups have also distinct phenotypical features.

Based on isozyme analyses, the wild and cultivated populations were classified as follows:

- Guinean wild populations identified as 'Kouin', 'Gbapleu', 'Logbonou', 'Fouroug', 'Maraoue', 'Bossematie', 'Ira 1', 'Ira 2', 'Bafingdala', 'Gbapleu 2', 'Pelezi' and 'Gonate' from Côte d'Ivoire, and the Piné population from Guinea as well as 39 genotypes from plantations' surveys realized in Côte d'Ivoire;
- Congolese subgroup 2: wild populations from central Africa and the Congo basin ('Cameroun', 'Doungba', 'Libengue', 'Ndongue') and the following cultivated origins: 'INEAC 2 and 7', 'Lula', 'Boukoko', 'Uganda', 'C10 Man';
- Congolese subgroup 1: cultivated populations originated from coastal areas between east Côte d'Ivoire and Gabon: 'Ebobo', 'Aboisso', 'Robus-

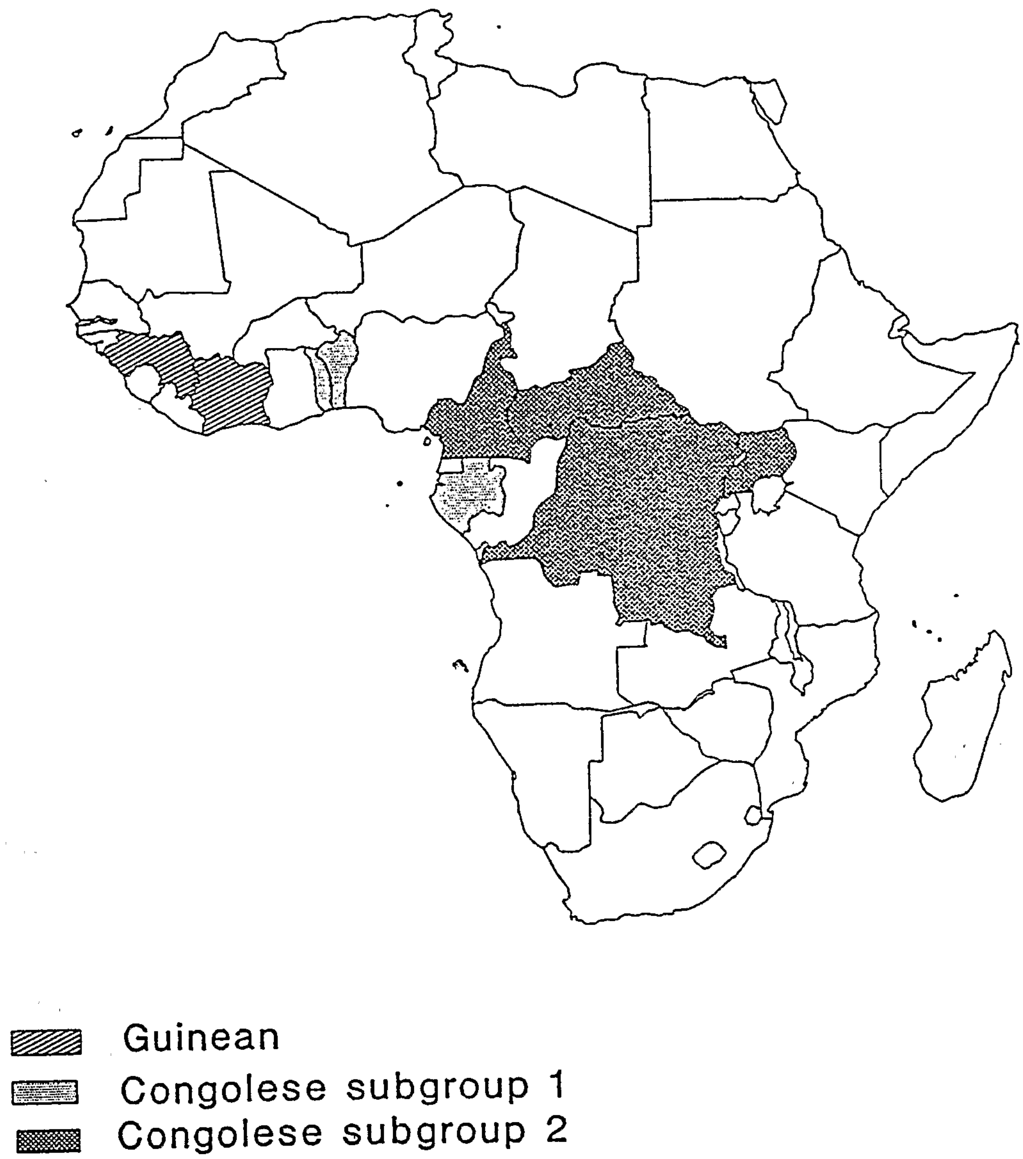

Fig. 2. Geographical origin of studied populations.

ta A1', 'Niaouli', 'Togo' and 'Kouilou'. The Kouilou population consists of clones selected in Madagascar.

The geographical origin of studied populations is presented in Fig. 2.

Concerning the choice of the parents used in the first cycle of RRS between 1984 and 1991, the main criterium has been isozyme pattern regarding the main groups (Guinean and Congolese). As a second criterium, the choice took into account the different geographic origins of the populations, as well as the presence of typical alleles for subgroups 1 and 2 of the Congolese main group, in order to maintain the natural genetic variability.

Variation for selection criteria

Agronomical and plant characteristics

A Principal Components Analysis was carried out for all individual tree data except stem diameter.

Table 1. Vigour of parental populations measured as stem diameter at 30 months in two clonal trials (expressed as % of the commercial control clone 461)

Group		No	Average	Minimum	Maximum	C.V. (%)
Guinean	Wild	17	78.2	55.8	103.5	16
	Cultivated	4	75.7	73.4	78.2	3
Congolese subgroup 2	Wild	6	67.0	56.9	80.4	15
	Cultivated	16	71.7	58.3	87.2	10
Congolese subgroup 1	Cultivated	7	87.6	83.1	90.7	3

The two genetic subgroups within Congolese genotypes are considered separately. Axes 1 and 2, presented in Fig. 1, explain 72% of total variation. The first axis separates drought susceptible genotypes from genotypes with a high number of internodes. Congolese genotypes from subgroup 2 are more susceptible to drought and present a smaller number of internodes than Guinean or Congolese subgroup 1 genotypes. Axis 2 is related to height of trees and average internode length on the stem. Variation on this axis is higher for the Congolese subgroup 2 and Guinean than for Congolese subgroup 1. Guinean genotypes are smaller plants with shorter internodes than Congolese genotypes. For the characteristics evaluated, the Congolese subgroup 1 resembles the Guinean group: this subgroup has similar adaptation characteristics (drought resistance and architecture) to the Guinean genotypes.

Vigour, measured by stem diameter, was observed in 1991 in clonal trials (Table 1). The dry period of 1990 was very severe, therefore, bad scores of Congolese subgroup 2 genotypes may be due to its high susceptibility to drought rather than to low vegetative vigour. Cultivated Congolese subgroup 1 shows the best scores, due to good vegetative vigour and drought resistance. For average stem diameter, slight differences were found between cultivated and wild genotypes for both groups. Great variation was observed within groups, specially for the wild Guinean group. All parents are less vigorous than the commercial intergroup hybrid clone 461.

In accordance with previous studies on phenotypic characteristics of *C. canephora* populations, the Congolese subgroups 2 and 1 correspond to the morphological description of 'Robusta' and 'Kouilou', respectively (Portères, 1939, 1959; Cramer, 1957).

Table 2. Average bean weight (grams per 100 beans) for the parental and base populations (between brackets) of Guinean and Congolese groups of wild or cultivated origin

Group		No	Bean size			C.V. (%)
			Average	Minimum	Maximum	
Guinean	Wild	60	9.0	6.4	11.8	15
		(135)	(9.0)	(5.0)	(18.0)	(21)
	Cultivated	11	11.0	9.1	14.7	15
		(39)	(10.0)	(7.5)	(14.7)	(17)
Congolese subgroup 2	Wild	38	9.7	6.0	16.2	22
		(91)	(9.5)	(4.8)	(19.0)	(25)
	Cultivated	31	15.5	8.1	19.9	18
		(105)	(15.4)	(8.1)	(20.6)	(15)
Congolese subgroup 1	Cultivated	13	16.8	13.0	24.3	16
		(84)	(14.2)	(9.1)	(24.3)	(22)

Table 3. Caffeine content (in percentage of dry beans) for the parental and base populations (between brackets) belonging to the Guinean and Congolese groups

Group		No	Caffeine content			C.V. (%)
			Average	Minimum	Maximum	
Guinean	Wild	9	2.6	2.2	3.0	14
		4	2.9	2.5	3.1	10
	Cultivated	(26)	(2.9)	(2.5)	(3.4)	(9)
Congolese subgroup 2	Wild	32	2.5	1.5	3.2	17
		(179)	(2.3)	(1.5)	(3.5)	(16)
	Cultivated	31	2.1	1.6	2.8	14
		(106)	(2.3)	(1.6)	(3.1)	(18)
Congolese subgroup 1	Cultivated	13	2.6	2.0	3.0	12
		(80)	(2.7)	(1.7)	(3.6)	(14)

Technological and quality characteristics
Within Guinean and Congolese subgroup 2, cultivated and wild genotypes were considered separately. Only cultivated genotypes of Congolese subgroup 1 are present in our studies.

Bean weight. At present, commercial clones have an average bean weight of 12.5 gram per 100 beans, ranging from 10 to 20 grams.

Average bean weight based on a variable number of measurements are presented in Table 2. Guinean parents have smaller beans than the Congolese ones, and wild genotypes have also smaller beans than cultivated genotypes, reflecting the effect of previous selection carried out in the 1960's.

The average bean weight is highest for parents from cultivated subgroup 2 (15.5) and subgroup 1 (16.8). Compared to values observed for the total populations, the effect of parental selection for this trait in cultivated genotypes is pointed out. Due to the generally low values of Guinean genotypes, the

Table 4. Average values and range for three coffee types for roasting characteristics (percentage of loss of bean weight -LBW-, and increase in bean volume -IBV-) and cup quality (bitterness, acidity, body and general note)

Characteristic	Average values (Minimum–Maximum)		
	Guinean (3)**	Congolese (4)	Hybrids (3)
LBW	14.9 A*	13.0 B	12.8 B
	(13.5–16.0)	(11.9–13.9)	(12.0–14.0)
IBV	101.4 A	82.8 C	90.0 B
	(94.5–114.5)	(79.7–87.4)	(84.6–98.1)
Bitterness	2.16	1.67	1.62
	(2–2.5)	(1.25–2)	(1.25–2)
Acidity	1.0	1.1	1.1
	(1–1)	(1–1.25)	(1–1.25)
Body	2.33	1.87	1.83
	(2.25–2.5)	(1.75–2)	(1.25–2.25)
General note	4.59 A	5.02 A	4.96 A
	(4.3–5.1)	(4.7–5.4)	(4.1–5.8)

* Different letters indicate significant differences according to Newman and Keuls test at 5% probability level.
** Number of clones tested per group.

average bean weight for parents of this group remains rather low.

Caffeine content. At present, commercial clones in Côte d'Ivoire have a high average caffeine content of 2.7%, which may have negative effects on consumption (Kozlowski, 1976). Low caffeine content is therefore one of the main objectives in our selection programme. Variation for this trait is important in relation with location, date of harvesting, and year of evaluation (Charrier & Berthaud, 1975).

As shown in Table 3, caffeine content variation is large among the genotypes from all groups. Guinean genotypes present higher caffeine contents than Congolese ones. Genotypes of any group with high values (more than 3%) were eliminated for parental selection. Parents of the cultivated Congolese were most selected for this trait and show therefore lower caffeine contents.

According to previous results, the inheritance for bean size and caffeine content is mostly additive (Bouharmont et al., 1986; Charrier & Berthaud, 1988; Le Pierres, 1987; Ravohitrarivo, 1980). Recurrent selection for these traits may therefore be efficient.

Roasting characteristics and cup quality. Results for roasting characteristics are presented in Table 4. The best scores for bean volume increase were obtained with the Guinean genotypes, intergroup hybrids are intermediate. Guinean genotypes have higher values for body and bitterness, whereas Congolese and intergroup hybrids have similar values for these traits. No differences were observed for acidity. The average values for general cup quality did not differ significantly between groups, however individual genotypes showed significant differences. The best genotypes for general cup quality are found among the hybrid and Congolese groups. The lower cup quality of most Guinean genotypes appeared to be related to high levels of bitterness and strong body detected in the coffee samples. The results suggest that selection for cup quality can be efficient within intergroup hybrids.

Coffee rust and branch borer resistance

As infection conditions for coffee rust vary from year to year, the maximum scores over the 3 years of evaluation were considered. Results, in term of percentage of resistant plants, for all the genotypes of the five groups, are presented in Table 5.

A high percentage of wild and cultivated Guinean genotypes is susceptible to rust, as previously observed (Berthaud & Lourd, 1982). For parental selection, susceptible genotypes with low vigour were not used, but vigorous ones or those known to be good parents were used even if susceptible. Congolese genotypes present a high level of resistance to rust. The few susceptible Congolese clones were rejected as parents for intergroup hybrids. In the hybrid progenies, selection for resistance to coffee leaf rust is always possible, if a Congolese resistant parent is used (Charrier & Berthaud, 1988).

The overall level of susceptibility to the coffee twig-borer is low and only slight differences were

Table 5. Number and percentage of resistant genotypes for coffee leaf rust and branch borer

Group		Coffee leaf rust		Branch borer	
		Number of clones No.	Resistant clones %	Number of clones No.	Resistant clones %
Guinean	Wild	249	28	181	77
	Cultivated	39	31	25	88
Congolese subgroup 2					
	Wild	170	97	128	50
	Cultivated	130	84	128	73
Congolese subgroup 1					
	Cultivated	79	73	79	94

observed between the groups (Table 5). Susceptible genotypes were eliminated as parents.

Value of intergroup hybrids

Hybrid trial

Vigour and cumulated yield of four harvests were analyzed in the first hybrid trial planted in 1985. The four intergroup hybrids were as vigorous as the three clonal controls and significantly more vigorous than the four intragroup hybrids. The three commercial clones are significantly higher yielding (cumulated four years yield of 16.7 kg of fresh cherries per tree) than the hybrids. The intergroup hybrids (12.3 kg) are significantly higher yielding than intra-Congolese hybrids (9.5 kg). High productivity of clonal controls is partly due to their precocity as cuttings come one year earlier into full production than seedlings.

Results on bean weight shows superiority of intra-Congolese hybrids (16.5 g for 100 beans) in relation to intergroup hybrids (13.1 g). However, large variation was observed within intergroup hybrids, which allows for efficient selection. No differences were observed for the percentage of peaberries. In this trial, the 17 highest-yielding trees, with resistance to rust and branch borer and producing coffee with good bean weight, have been identified for clonal selection. Twelve of them belong to the intergroup hybrids and only 5 to the intra-Congolese hybrids. This confirms the value of intergroup hybrids

Table 6. Comparison after analysis of variance between three types of hybrids: intra-Guinean (GUI), intra-Congolese (CON) and intergroup hybrids (HYB) tested in a diallel trial. Average values for selection traits and significant differences according to Newman & Keuls test at 5% probability are indicated

Trait	Average values and significance of differences			F Anova values and level of significance
Yield (2 harvests) in kg of fresh cherries per tree	GUI = 3.4	CON < 3.7	HYB 7.2	80***
Stem diameter at 30 months (mm)	GUI = 69	CON < 72	HYB 77	48***
Height of trees at 24 months (cm)	GUI < 143	CON < 155	HYB 160	50***
Length of longest branch at 24 months (cm)	CON < 80	GUI < 94	HYB 104	81***
Number of stem internodes (NSI) at 24 months	CON < 22.7	HYB < 24.0	GUI 25.9	36***
Number of internodes on the longest branch at 24 months (NIB)	CON < 14.5	HYB < 20.1	GUI 22.3	137***
Total number of internodes (NSI x NIB) at 24 months	CON < 330	HYB < 489	GUI 584	114***
Bean size (1991 harvest) in grams per 100 beans	GUI = 9.3	CON < 9.7	HYB 11.3	45***
Peaberries (%)	GUI < 23	CON < 28	HYB 38	57***
Conversion to green coffee (%)	CON < 15	HYB = 19	GUI 20	26***
Time of harvesting (1 to 4 point scale, 1 = early, 4 = late)	GUI < 1.5	HYB < 2.2	CON 2.9	241***
Degree of grouped harvesting (% of total yield during main harvest)	CON = 73	GUI < 77	HYB 80	5**

*** : significant at 0.1% level of probability.
** : significant at 1% level of probability.

for clonal selection. Later on, it was shown that among the 12 intergroup selected trees, four possess a caffeine content below 2% and only two over 2.5%, which is too high for selection. In conclusion, selection for lower caffeine content could also be efficient in intergroup hybrids.

Diallel trial

Table 6 presents the significance of differences observed for 12 traits between the three types of hybrids: intra-Guinean, intra-Congolese and intergroup. Table 7 presents the variation within groups for yield, stem diameter and bean weight. Heterosis is observed for yield and the three vegetative vigour traits: the intergroup hybrids show higher values than the intra-group hybrids. Variation for yield and vigour is also much higher among the intergroup hybrids than among the other types of hybrids (Table 7). These results confirm once more the value of intergroup hybrids for selection (clonal or hybrid). Among vegetative traits, the height of the trees and the length of the longest branch are best correlated with the first two harvests ($r = 0.49$ and $r = 0.53$ respectively), and intergroup hybrids are superior for these traits. Intergroup hybrids present intermediate to high values for number of internodes, which, together with high vigour, is apparently favorable for obtaining good yields.

Technological characteristics were studied in 1991. Bean weight was found to be higher in intergroup hybrids than in intra-Congolese hybrids, which was unexpected and in contrast to the results of the first hybrid trial (see above). This result may be explained by the low rainfall in July/August 1991, which could have affected more the bean weight of drought susceptible plants (intra-Congolese hybrids). The variation observed among intergroup hybrids, presented in Table 7, would allow for selection of hybrids and clones with average 100 bean weight over 13 grams. Percentage of peaberries is significantly higher in intergroup hybrids. Possibly, high values for this trait indicate some degree of ovary sterility, which may result from the genetic distance between Guinean and Congolese (Berthaud, 1985). The results on conversion of ripe cherry weight to green coffee weight shows no significant differences between averages for intra-Congolese and intergroup hybrids. However, intra-Congolese hybrids show a significantly lower value for this trait.

Time of harvesting is, as expected, intermediate for intergroup hybrids (Table 6). Degree of grouped harvesting, an important characteristic related to cost of coffee production, is higher for intergroup hybrids. Therefore, this trait might be improved by selection among intergroup hybrids.

Only preliminary results are available for caffeine content. Variation within the groups is found to be higher than between the groups. Twenty three percent of the intergroup hybrids trees evaluated so far present caffeine contents below 2.5%, these figures being 7% for intra-Congolese hybrids, and 6% for intra-Guinean hybrids. Therefore, selection of

Table 7. Yield, average bean weight and vigour of individual hybrids, between and within different groups, compared in a diallel trial. Significant differences according to Newman & Keuls test at 5% probability are indicated by different letters

Crosses	Yield (2 harvests) in kg of fresh berries per tree	Average 100 bean weight (grams)	Vigour (stem diameter at 30 months in mm)
Guinean			
155 × 410	5.8 cdefg	9.1 def	71 abcdef
410 × 414	3.8 fgh	9.6 cdef	64 f
410 × 416	3.4 fgh	9.1 ef	71 abcdef
155 × 416	2.5 gh	9.1 def	68 cdef
155 × 414	2.2 h	10.5 cde	67 def
414 × 416	1.9 h	8.1 f	66 ef
Congolese			
444 × 464	4.3 efgh	10.1 cde	75 abcde
69 × 464	3.4 fgh	9.6 cdef	72 abcdef
69 × 444	2.9 gh	9.3 def	69 bcdef
Intergroup hybrids			
155 × 444	11.2 a	12.9 a	81 a
410 × 444	9.7 ab	12.4 ab	81 a
410 × 69	8.1 bc	10.4 cde	77 abcd
410 × 464	7.8 bcd	11.2 bc	71 abcd
155 × 69	7.7 bcd	10.9 cd	75 abcdef
155 × 464	7.3 bcde	10.5 cde	79 abcde
416 × 444	6.5 cdef	11.0 cd	80 ab
414 × 444	5.3 cdefgh	12.4 ab	79 ab
414 × 69	4.9 defgh	10.1 cde	74 abcdef
416 × 464	4.7 efgh	10.3 cde	77 abc
414 × 464	4.6 efgh	10.6 cde	74 abcdef
416 × 69	4.3 efgh	11.0 cd	73 abcdef

productive clones with lower caffeine content will be possible in intergroup hybrids.

General discussion and conclusions

Characterization and evaluation of base populations

The *C. canephora* collections available in Côte d'Ivoire represent more than 800 genotypes, 450 collected from the wild and about 350 of cultivated origin. It should be noted that even the cultivated genotypes in these collections have been mass selected for only one or two generations. The Côte d'Ivoire collection is the most representative collection of *C. canephora* worldwide.

The main genetic groups of *C. canephora*, Guinean and Congolese, were defined by Berthaud (1986) and based on the analysis of three major discriminating isozyme loci, tested with 471 genotypes from the Côte d'Ivoire collections. The present results refer to about 300 genotypes and complete Berthaud's studies on the isozyme characterization of these collections.

The great majority of the cultivated canephora populations in the world appear to consist of Congolese genotypes. The Guinean group is limited to Côte d'Ivoire and Guinea (wild or cultivated). Based on the analysis of other isozyme loci, a better understanding of the genetic variation within the main groups has been obtained. Two subgroups were identified within the Congolese group, which were named subgroups 1 and 2, based on presence of a specific allele of the esterase system. The distinction of the two subgroups appeared further justified by phenotypic characterization and the geographic origin. Subgroup 2 is of cultivated or wild central African origin, whereas subgroup 1 is of cultivated origin, from coastal areas from east Côte d'Ivoire to Gabon.

Phenotypic evaluation of Guinean and Congolese genotypes has been conducted between 1984 and 1992. The results confirm the contrasting and complementary characteristics of the two main groups. Congolese subgroup 1 presents phenotypic adaptative characteristics similar to Guinean genotypes (drought resistance, secondary branching, size of internodes). Based on the distinction of subgroups 1 and 2, genotypes belonging to these groups have been mixed separately after the first cycle of RRS scheme and a separate set of hybrids between genotypes of subgroups 1 and 2 was created in 1992.

Choice of parents and testers from base populations

The choice of parents in the first cycle of selection was based on isozyme allelic conformity for the three main alleles, representative value according to inter and intrapopulation geographic origin, variability for minor isozyme alleles and phenotypic characteristics. Negative selection regarding the phenotypic traits has been generally weakly applied, except for rust resistance, bean size and caffeine content.

For the first cycle of RRS, the parents chosen between 1984 and 1991 for crosses with testers are the following: 11 cultivated and 90 wild Guinean genotypes; 45 wild Congolese subgroup 2 and 44 cultivated Congolese genotypes (31 of subgroup 2 and 13 of subgroup 1), and four Congolese genotypes from plantations' surveys (subgroup unknown).

Three Congolese (two subgroup 2 and one subgroup 1) and two Guinean genotypes, all of cultivated origin, were chosen as testers in the RRS program. The use of testers is justified by practical purposes and predominance of general combining ability observed for the main selection criteria (Charrier & Berthaud, 1988; Leroy, unpublished data). The testers have been selected for their good general combining ability for vigour, architectural traits, and technological quality (Capot, 1977).

Confirmation of intergroup hybrid value

In 1984, when the RRS program started, the supposed intergroup hybrid value was mainly based on the evidence that five out of seven commercial clones selected in Côte d'Ivoire were natural intergroup hybrids. Results presented here show that, in hybrid trials, average vigour and yield of intergroup hybrids is significantly superior to intragroup hybrids, suggesting the existence of heterosis for these traits. Great variation was observed between intergroup hybrids, therefore selection within and between intergroup hybrids families for these traits should be successful. Other important traits are technological and organoleptic quality traits. Bean weight of intergroup hybrids is highly variable, therefore selection should be effective. Organoleptic quality data presented here relate to a limited number of clones. Although, the best clone (number 126) is of intergroup hybrid origin, more data will be needed to confirm that selection for this trait can be effective.

In conclusion, the results confirm that RRS can be favorably applied to *C. canephora* for improving varieties and breeding populations. Further results on genetic parameters and selection progress obtained will be presented in forthcoming publications.

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