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Combining Ability of Doubled Haploids in *Coffea canephora* P.

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With 2 figures and 6 tables

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Abstract

Fifty-five doubled haploids (DH) of *Coffea canephora* were crossed with either heterozygous genotypes or DH in order to study their combining ability. Three agronomic trials were established. Marked hybrid vigour was observed for all characters analyzed including yield. Large differences were evident among top-crosses involving different DH produced from the same parental clone reflecting the high level of heterozygosity of clones. Factorial mating design analysis indicated that all genetic variance was attributable to additive effects in estimates of yield as well as plant height and leaf characteristics. The general combining ability variance component was also predominant for stem girth and susceptibility to leaf rust, although effects due to interaction were detected. Some hybrid combinations had yield comparable to standard clonal varieties. The implications of such results for breeding of *Coffea canephora* are discussed. Particularly, the development of F_1 hybrid varieties is envisaged.

Key words: *Coffea canephora* — doubled haploid — combining ability — agronomic performance — hybrid — tree.

Coffea canephora Pierre is an allogamous diploid tropical tree species consisting of polymorphic populations and of strongly heterozygous individuals. Two gene pools corresponding to the two major geographical distribution groups i.e. Guinean (West Africa) and Congolese (Central Africa) were revealed by enzymatic polymorphism analysis, and intergroup hybrids showed important heterosis (BERTHAUD 1986). Current breeding programmes (CHARRIER and BERTHAUD 1988) are directed to the development of varieties distributed either through seed (synthetic and hybrid varieties) or after vegetative propagation (clones). Synthetic (hybrid) varieties can be produced at much lower cost, and are easier to distribute than the clonal varieties (DURIS 1985). However, the heterozygous nature of parents causes large variation in offspring, and interest in synthetic and hybrid varieties is therefore limited. Several studies in the Ivory Coast (CAPOT 1977, CHARMETANT et al. 1990) have clearly shown that the average production of synthetic and hybrid varieties is about 60 % that of standard clones.

Utilization of doubled haploids (DH) in plant breeding is steadily increasing. Large haploid breeding programs have been developed in a broad range of crop species including cereal, rapeseed and several *Solanaceae*, but no woody species (CHEN 1987, ZHANG et al. 1990). Therefore, the value of DH in tree breeding is still speculative and has to be explored. The ability to produce high numbers of DH from a wide range of genotypes in *C. canephora* (COUTURON 1982, LASHERMES et al. 1993a) affords a unique opportunity.

An earlier study indicated that DH of *C. canephora* can be used for genetical analysis although they are characterized by low vigour and reduced fertility (LASHERMES et al. 1993a). With regard to coffee breeding, a more significant consideration is the performance of DH in combination. In the present study we examine agronomic performances of hybrids involving different DH.

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Materials and Methods

The DH were produced according to the method previously described (COUTURON 1982) which is based on haploid plants occurring spontaneously in association with polyembryony. Details concerning the characteristics of DH are reported in LASHERMES et al. (1993 a). Fifty-five different DH were crossed with either heterozygous clones or DH. The DH used were produced from 8 different genotypes but in majority from the clones IF 200 and IF 160. Hybrid seeds were obtained using standard hybridization techniques, and sowed into prepared nursery beds. The seedlings were transplanted and grown in the nursery. After one year (first pair of lateral branches stage), the seedlings were transferred to the field. Standard varieties (clones IF 126, IF 202 and IF 461) were propagated by cuttings in the nursery and, after rooting, transplanted in the field with the seedlings.

Three separate trials, noted 1 to 3, were conducted at the coffee breeding station of Man, Ivory Coast. The trials included respectively 34 (trial 1), 13 (trial 2) and 44 (trial 3) hybrid combinations. IF 126, IF 202 and IF 461 were included as standard clonal varieties in trial 1 while only IF 126 and IF 461 were included in trials 2 and 3. By convention, DH genotypes are identified by the letters DH followed by two numbers; the first number indicating the clone of origin. For instance, DH 160-02 corresponds to the DH genotype number 2 produced from the clone IF 160. For all trials, the experimental design was a randomized complete block with either 20 (trials 1 and 2) or 19 (trial 3) individuals per entry (hybrid or clone). Trials 1 and 2 were planted in 1988 while trial 3 was planted in 1989. A high planting density of 2,666 trees per hectare (2.5 × 1.5 m spacing) was applied. Cultivation was performed without shade and fertilizer was applied three times a year [150 g urea and 100 g NPK (10 : 18 : 18)/tree/year]. Trees were trained to a three-stem growth system by pruning (COSTE 1989).

For each individual tree, the following characters were recorded: (1) Girth of stem after 1 and 4 years of plantation, measured as the circumference in cm of the main stem taken about 5 cm from the ground level; (2) Height of the tree after 1 and 4 years of plantation, measured as the length in cm from the base to the tip of the tree; (3) Leaf area, mean in cm^2 (0.88 × length × width at the broadest portion, see WALYARO 1983) of five leaves of comparable age (penultimate leaves of secondary branches) after 4 years of plantation; (4) Leaf shape, mean ratio width to length; (5) Leaf rust (*Hemileia vastatrix*) susceptibility scored by repeatedly observing tree on a 1—5 scale with 1 = resistant, 5 = highly susceptible; (6) Yield estimated as the total weight (H_T) in kg of mature fresh cherries harvested per tree and per year; yield evaluation was carried out over two years, the first year of production being not taken account; (7) Earliness of maturation, fruit harvesting was accomplished in four surveys at three weeks interval with H_1, H_2, H_3 and H_4 representing the first, second, third and fourth harvest respectively; only red-ripe cherries were picked each time and a maturity index (M), reflecting the mean date of harvest, was calculated: $M = (1H_1 + 2H_2 + 3H_3 + 4H_4)/H_T$; (8) Peaberries determined as the percentage of berries containing only one round bean on a random sample of 300 berries. Hundred beans weight (9) calculated from the dry weight in g of a sample of 250 beans at 0 % humidity was estimated on four trees per entry.

Statistical analyses were performed using the NDMS (ORSTOM, France) computer package. Because the hybrid combinations included in each trial resulted from incomplete crossing schemes, subsets of the hybrids were considered for analysis. Based on a factorial mating design analysis, the general combining ability of parents was estimated according to SIMMONDS (1979). Spearman's rank correlation coefficients between characteristics of DH estimated on three plants per genotype (LASHERMES et al. 1993 a) and their respective top-crosses were obtained according to the procedure outlined in DAGNELIE (1970).

Table 1. Mean square values from variance analyses of hybrid combinations for yield (kg of cherries/tree/year)

Experiment	Source of variation	df	Mean square
Trial 1	Hybrid	33	140.45***
	Residual	636	7.00
Trial 2	Hybrid	12	113.43***
	Residual	246	11.60
Trial 3	Hybrid	43	16.79***
	Residual	720	2.66

*** Indicate significance at $P < 0.001$

Results

The different hybrids showed a large amount of variation for the different agronomic traits observed. Results of analysis of variance for yield are presented in Table 1. In the three trials, highly significant variations were detected among hybrid combinations. Yields of the standard clones varied across trials; Trial 3 was notably less productive than the other two. Proportion of hybrid combinations with yield equivalent to standard clonal varieties varied from 40 to 90 % depending on the trial (Fig. 1). This frequency was particularly high in trial 2 in which the hybrids are constituted by top-crosses involving the Guinean accession 02 200 as tester. The lowest yields were observed for hybrids constituted by related DH. No significant difference was observed between mean frequency of peaberries produced by the hybrid combinations and the standard clones; in trial 1 for instance, frequencies were respectively 15 % and 21 %.

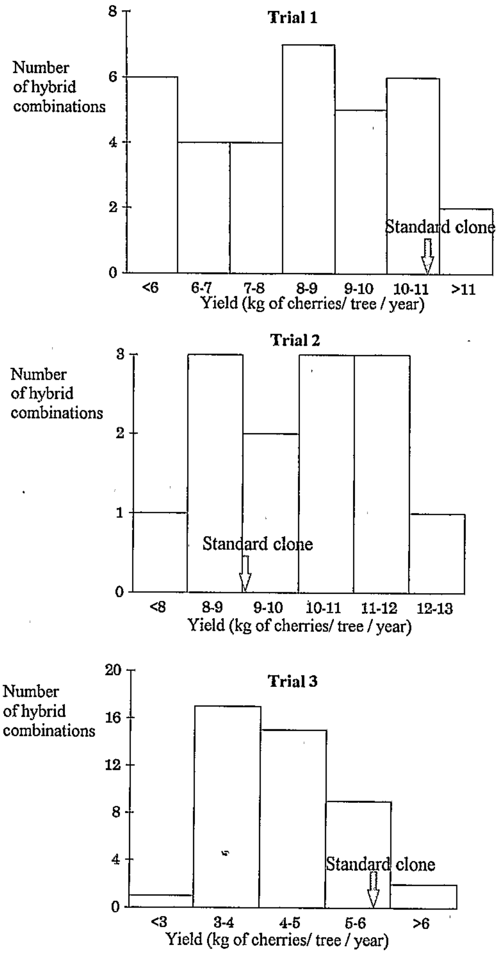

Fig. 1. Distributions of hybrid combinations for yield. Mean of standard clones included in each trial is indicated by arrow

Results on evaluation of twenty-four top-crosses (Trial 3) involving different DH derived from IF 200 and DH 160-02 as common parent tester, are presented in Table 2. Highly significant variations were observed among the top-crosses for girth, height, susceptibility to leaf rust, leaf characteristics, yield and cherry maturity. No significant difference was observed between the mean value of top-crosses involving the 24 DH and the performance of the combination DH 160-02 × IF 200 for any of the characters examined (Table 3).

The performances of a subset of hybrids included in trial 1 were analyzed as a factorial mating design involving DH 160-02, DH 160-04, DH 160-05 as female parent and DH 200-16, DH 200-20, DH 200-25, DH 200-30 as male parent. The analysis (Table 4) revealed a highly significant effect of the parent (female or male) on girth, height, leaf area, leaf shape, rust susceptibility, yield and maturity; indicating the importance of genetic factors. In the case of girth and height, genetic effects were detected only by the evaluation after four years from planting. Interactions between male and female parent were significant for the characters girth, rust susceptibility and maturity. However, these interactions accounted for a small part of the total variance. For percentage of peaberries, only effects due to interaction were detected. A high correlation coefficient was shown (Fig. 2) between observed yields of hybrid combinations and yields predicted from parental general combining ability (GCA), indicating that GCA accounted for a large proportion of the difference between hybrid combinations.

The analysis of variance (Table 5) for yield of eight top-crosses involving two genetically distant testers (DH 200-30 and 02 0200) and four DH derived from IF 160 indicated a highly significant difference between the DH derived from IF 160. No interaction effect was detected.

Table 2. Mean square values from variance analyses of top-crosses (DH 160-02 parent tester), involving 24 different DH derived from IF 200 (Trial 3), for different agronomic traits

Traits	Source of variation	df	Mean square
Girth 4	Top-cross	23	24.58***
	Residual	432	3.26
Height 4	Top-cross	23	1706.70***
	Residual	432	144.55
Leaf rust susceptibility	Top-cross	23	3.87***
	Residual	432	0.28
Leaf area	Top-cross	23	3820.06***
	Residual	432	544.60
Leaf shape	Top-cross	23	0.00421***
	Residual	432	0.00028
Yield	Top-cross	23	18.07***
	Residual	432	2.72
Maturity	Top-cross	23	1.438***
	Residual	432	0.065

*** Indicate significance at $P < 0.001$

Rank correlation coefficients were calculated between characteristics of 21 DH derived from IF 200 and their respective top-crosses to DH 160-02 (Table 6). No significant correlations were observed between vigour or yield of DH, and height, girth and yield of top-crosses. On the other hand, significant rank correlation coefficients were observed between values of DH and their respective top-crosses for leaf shape and leaf area.

Table 3. Comparison of mean values for different characters between top-crosses (DH 160-02 parent tester) involving either the clone IF 200 or 24 different DH derived from IF 200 (Trial 3)

Character	Male parent of top-crosses[1]			Student t-test	Rank sum test (Mann-Whitney)
	IF 200	DH derived from IF 200			
	Mean of 19 trees	Mean of 24 top-crosses	Range		
Height 4 (cm)	205	206	185—225	ns	ns
Girth 4 (cm)	23.7	24.5	22.4—26.2	ns	ns
Leaf rust susceptibility (score)	4.1	4.0	3.1—4.8	ns	ns
Leaf area (cm^2)	169	168	141—201	ns	ns
Leaf shape (w/l)	0.42	0.41	0.37—0.43	ns	ns
Yield (kg/tree/year)	4.7	4.6	3.3—7.1	ns	ns
Maturity (index)	1.84	1.94	1.42—2.58	ns	ns
Hundred beans weight (g)	14.1	14.0	11.5—16.8	ns	ns
Peaberries (%)	9.5	11.7	5.6—39.6	ns	ns

ns Indicates no significant difference.
[1] For each top-cross, 19 trees were observed.

Table 4. Mean squares from analyses of variance of hybrids derived from a factorial mating design (Trial 1) involving DH 160-02, DH 160-04, DH 160-05 as female parents and DH 200-16, DH 200-20, DH 200-25, DH 200-30 as male parents[1]

Source of variation	df	Character									
		Girth 1	Girth 4	Height 1	Height 4	Leaf area	Leaf shape	Leaf rust susceptibility	Yield	Maturity	Peaberries
Female parent (F)	2	26.7	360.1**	135	15178***	14949***	0.0137***	21.02**	64.8*	1.68	59.4
Male parent (M)	3	26.4	244.3**	408	9799***	638	0.0161***	2.66	87.6**	10.20**	44.3
Interaction F × M	6	7.3	21.6***	277*	340	280	0.0004	1.41***	9.7	0.51***	71.8**
Residual	228	4.3	4.5	108	356	386	0.0003	0.12	6.4	0.07	20.3

*, **, *** Indicate significance at $P < 0.05$, $P < 0.01$ and $P < 0.001$ respectively.
[1] Female parent and male parent were treated as random effects.

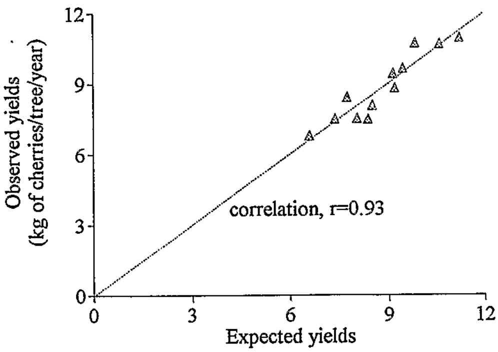

Fig. 2. Observed yields of 12 hybrid combinations, resulting from a factorial mating design, plotted against yields predicted from parental general combining ability

Discussion

The potential value of DH in genetic research and plant breeding have been widely reviewed (CHOO 1983, BAENZIGER et al. 1984, GALLAIS 1989). Only via haploidy can homozygous genotypes be developed in a strictly allogamous species with a long juvenile period such as *C. canephora*. Applications of DH in breeding depend on biological characteristics of the species concerned and in *C. canephora* the combining ability of the DH is of paramount importance.

Strong hybrid vigour was observed for most hybrid combinations evaluated in this study and the reduced fertility which characterized the DH (LASHERMES et al. 1993a) was not observed in the hybrids. Because most DH had to be grafted onto a heterozygous clone to survive in the field, heterosis (or inbreeding depression) cannot be precisely quantified but it is considerable.

The large variation for agronomic characters observed among top-crosses involving different DH produced from IF 200 and a homozygous tester, reflects the high level of heterozygosity of the parental clone. Cultivated clones of *C. canephora* are only a few generations removed from their wild ancestors, and heterozygosity is maintained by a self-incompatibility system (BERTHAUD 1980).

The average value, in terms of combining ability, of a random group of 24 DH derived from the clone IF 200 did not differ from the

Table 5. Analysis of variance for yield (kg of charries/tree/year) of top-crosses involving two different tester parents, DH 200-30 (Trial 1) or 02 0200 (Trial 2), and four DH's derived from IF 160 (DH 160-01, DH 160-02, DH 160-05 and DH 160-06)

Source of variation[1]	df	Mean square value	F-test
Tester + trial (T)	1	13.6	8.40
DH derived from IF 160 (DH)	3	78.2	6.39***
Interaction T × DH	3	1.6	0.13
Residual	152	12.2	

[1] "Tester" and "trial" effects are confounded and were treated as fixed effects. DH derived from IF 160 was treated as random effect.
*** $P < 0.001$.

Table 6. Rank correlation coefficients between characteristics of 21 doubled haploid genotypes derived from IF 200 and their respective top-crosses (DH 160-02 used as the common parent female)

	Character doubled haploid			
Character top-cross	Leaf area	Leaf shape	Plant vigour	Yield
Height	0.10	−0.28	−0.06	0.19
Girth	−0.25	−0.01	0.19	0.06
Leaf area	0.60**	−0.01	−0.41	0.38
Leaf shape	0.01	0.65**	0.10	−0.33
Yield	−0.33	0.01	0.09	−0.07

** $P < 0.01$.

value of the parental clone suggesting that the DH produced are an unbiased sample of the parental gametes when considering the agronomic traits analyzed. Another possibility could be a comparable selection during the DH production and the sexual reproduction. Similar results were observed for the clone IF 160 (data not shown). It is obvious from this study that DH can be produced which present better combining ability than their parental clone for important agronomic characters such as resistance to leaf rust, yield and bean size.

As expected from the large genetic distance between the Congolese and Guinean gene pools (Berthaud 1986), productive combinations were intergroup hybrids between the Guinean accession 02 200 and different DH produced from clones belonging or related to the Congolese pool. High yield was also observed for hybrids between two DH derived from the Congolese pool. Such result can be related to the important genetic diversity observed within the Congolese pool and subgroups proposed by Berthaud (1986) and Montagnon et al. (1992).

The factorial mating design analyses indicated that all genetic variance was attributable to additive effects in estimates of yield as well as height, leaf area and leaf shape. The general combining ability variance was also predominant for girth, maturity and rust susceptibility although effects due to interaction were detected. Comparable results were obtained for hundred beans weight (data not shown). Only, occurrence of peaberries appeared to be controlled by non-additive genetic factors. Similar importance of the general combining ability has been observed by Bouharmont et al. (1986) in analyzing incomplete diallel designs involving clones. These results may appear in contradiction to the lack of significant rank correlation observed between values of DH and their respective top-crosses for yield, height and girth. If only additive effects were involved, a rank correlation between DH and top-crosses would be expected. A possible explanation is that the evaluation of DH is distorted since the homozygosity of DH leads to the expression of deleterious alleles. In the absence of such negative effects, a relationship between DH and top-cross evaluations might be more likely. It is noticeable that the characters for which we found (LASHERMES et al. 1993a) a relatively low inbreeding depression, leaf area and leaf shape, are these showing rank correlations between DH and top-crosses. Such a situation where an important general combining effect coexists with a strong inbreeding depression has frequently been reported for allogamous species (GALLAIS 1989) including trees species (LANAUD 1987, NAMKONG and KANG 1990).

Evidence from this study indicates that DH not only provide unique and useful information on the genetics of *C. canephora,* but can be successfully used as homozygous parents in the production of homogeneous F_1 hybrids. This new type of variety could combine several advantages: low cost, full benefit from heterosis, homogeneity; and could have a considerable impact on coffee growing. However, it may raise several difficulties. 1) Inbreeding masks the real potential of DH and, for several characters including yield, no prediction of their value as progenitors seems to be possible before test crossing. The number of DH that can be tested for combining ability is technically and economically limited. Results in this study indicate that the mean combining ability of a group of DH can be anticipated from the value of their parental clone. So, a partial solution could be to focus the production of DH on clones showing the best combining ability. Furthermore, development of molecular marker technology and gene mapping (TANKSLEY et al. 1989, LASHERMES 1993b) may offer the possibility of marker-assisted selections among DH. 2) Another difficulty in developing F_1 hybrid varieties is the seed production. Yield of most DH is limited, and both parents of a hybrid should be compatible and have synchronized flowering. A preliminary selection among DH could be made on the characters directly related to the production of seeds; the selected trees being subsequently tested for combining ability. Nevertheless, seed production technology will require further attention. The development of three-way cross varieties could be an interesting approach to reduce seed production difficulty. In addition, three-way cross varieties would be heterogeneous for the self-incompatibility genes and could avoid the necessity to mix varieties in the plantations to insure cross-pollination.

Relating to the reciprocal recurrent selection program (COMSTOCK et al. 1949) developed in *C. canephora* (LEROY et al. 1993), selected DH genotypes could be used as tester. Since the general combining ability is predominant, improvement of populations would not be affected. Absence of genetic variability attributable to the parent tester in the testing progeny should lead to a higher selection efficiency.

Zusammenfassung

Kombinationseignung von Doppelhaploiden bei *Coffea canephora* P.

Zur Bestimmung der Kombinationseignung wurden 55 Doppelhaploide (DH) von *Coffea canephora* mit heterozygoten Klonen und mit DH gekreuzt. Es wurden drei Feldversuche angelegt. Bei allen untersuchten Merkmalen einschließlich dem Ertrag wurde eine deutliche Hybridwüchsigkeit beobachtet. Zwischen den Topcross-Nachkommenschaften, in die verschiedene, von denselben elterlichen Klonen stammende DH einbezogen waren, gab es große Unterschiede — ein Hinweis auf das starke Ausmaß der Heterozygotie der Klone. Die Analyse des faktoriellen Kreuzungsplans machte deutlich, daß die gesamte genetische Varianz der Schätzwerte sowohl für den Ertrag als auch für Pflanzenhöhe und Blattmerkmale von additiven Effekten verursacht wurde. Ebenso war die Varianzkomponente für die allgemeine Kombinationseignung bei Stammumfang und Anfälligkeit gegenüber Blattrost die wichtigste, obwohl auch Wechselwirkungseffekte beobachtet wurden. Einige Hybridkombinationen hatten Erträge, die dem Standard der Klonsorten entsprachen. Es wird die Bedeutung der Befunde für die Züchtung von *Coffea canaphora* diskutiert, wobei insbesondere die Entwicklung von F_1-Hybridsorten hervorgehoben wird.

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