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Christophe Montagnon, Christian Cilas, Thierry Leroy, Antoine Yapo, Pierre Charmetant. Genotype-location interactions for *Coffea canephora* yield in the Ivory Coast. *Agronomie*, 2000, 20 (1), pp.101-109. 10.1051/agro:2000110 . hal-00885996

HAL Id: hal-00885996

<https://hal.science/hal-00885996>

Submitted on 1 Jan 2000

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Genotype-location interactions for *Coffea canephora* yield in the Ivory Coast

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(Received 20 October 1998; accepted 6 December 1999)

Abstract – A multi-site clonal trial comprising 16 clones and 9 locations in the Ivory Coast was used to study clone-location interactions for *Coffea canephora* yield. In addition to a two-way analysis of variance (ANOVA), ecovalences and linear regression of clones at selected sites and the Nassar and Hühn test were used. Certain interactions were detected, even though several clones proved to be stable. The methods used displayed complementarity. In particular, interactions with or without rank modification were identified. A multivariate analysis was used to describe interaction structuring and to group locations according to clonal response. The consequences for plant breeding are discussed.

Genotype × environment interaction / *Coffea canephora* / clonal selection / Ivory Coast

Interaction génotype-lieu pour le rendement de *Coffea canephora* en Côte d'Ivoire. Un essai multilocal comprenant 16 clones et 9 lieux en Côte d'Ivoire a permis d'étudier l'interaction clone-lieu pour le rendement de *Coffea canephora*. En plus de l'ANOVA à 2 facteurs, les écovalences, la régression linéaire des clones sur les lieux et le test de Nassar et Hühn ont été calculés. Une interaction a été détectée, bien que plusieurs clones se soient révélés stables. Les méthodes utilisées ont démontré leur complémentarité. En particulier des interactions avec ou sans modification du rang ont été mises en évidence. Une analyse multivariée a été réalisée pour décrire la structuration de l'interaction et pour regrouper les lieux en fonction de la réponse des clones. Les conséquences pour l'amélioration sont discutées.

interaction génotype-lieu / *Coffea canephora* / sélection clonale / Côte d'Ivoire

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1. Introduction

Since the early 1980s, *Coffea canephora* breeding in the Ivory Coast has been based on a reciprocal recurrent selection programme [13]. On-station research has shown the possibility of obtaining major genetic gains through clonal or hybrid selection [14]. However, an assessment of genotype-location interactions for *C. canephora* in the Ivory Coast is required before considering the extension of new varieties. Indeed, the pedoclimatic characteristics of the Ivorian coffee growing zone are not uniform [3, 18], especially as regards rainfall and the degree of soil saturation. The latter factor has already been taken into account in adapting the fertilizer formulas applied to coffee [24].

In the tropical tree crops studied on this subject, interactions between genotype and location have been found, though some stable varieties have been identified in all cases. This is the case for oil palm (*Eleais guineensis*) [4], cocoa (*Theobroma cacao*) [20] and *C. arabica* coffee trees [1, 2, 17, 25]. In most cases, the regression method described by Heberhart and Russel [10] was used. Only Montes et al. [17] and Agwanda et al. [2] also used the ecovalences described by Wricke [26].

No specific studies of genotype-location interactions are available for *C. canephora*. Multi-site clonal trials situated in different locations in the

Cameroon have been analysed in parallel, but without any overall study to quantify the interaction [7]. However, some preliminary work [8, 9, 23] has shown that interactions between varieties and sites may be found in the Ivory Coast.

At the end of the 1980s, a 16-clone confirmation trial was set up at 9 representative sites in the Ivorian coffee growing zone as the final step before extension. The design made it possible to study the overall interaction between clones and sites and to test the stability of each clone by different methods. An attempt was made to group sites according to clonal response.

2. Materials and methods

2.1. Description of the trial

The study sites (Tab. I) were at stations belonging to the Centre National de Recherche Agronomique de Côte d'Ivoire (CNRA) and observation points belonging to the Agence Nationale pour l'Appui au Développement Rural de Côte d'Ivoire (ANADER).

The plant material consisted of clones selected at research stations from controlled crosses, or taken from smallholding surveys (Tab. II). Their genetic origin was specified according to the known genetic diversity of *C. canephora*, which is

Table I. Main characteristics of the *C. canephora* multisite trial locations.

Location	Region	Soil characteristics	Degree of saturation	Geology	Previous cover	Mean rainfall (mm / yr)
Abengourou ⁺	East	Red, clay, fine gravel	Saturated	Schists	Fallow	1300-1400
Bingerville ⁺	Middle-South	Beige, sand, draining	Unsaturated	Tertiary sands	Fallow	1900-2000
Divo ⁺	Middle	Red, clay, fine gravel	Saturated	Granite	Fallow	1300-1400
Guessabo ⁺⁺	Middle-West	Red, clay, fine gravel	Saturated	Granite	Forest	1500-1600
Maféré ⁺⁺	South-East	Beige, sand, draining	Unsaturated	Tertiary sands	Forest	1800-1900
San Pedro ⁺	South-West	Red, fine gravels	Unsaturated	Granite	Fallow	1450-1550
Soubre ⁺⁺	Middle-West	Red, some fine gravel	Saturated	Granite	Forest	1550-1650
Thyonle ⁺⁺	West	Red, some fine gravel	Saturated	Granite	Forest	1700-1800
Zagne ⁺	West	Beige, sand, draining	Unsaturated	Granite	Fallow	1600-1700

⁺: CNRA Stations

⁺⁺: ANADER Observation Sites

Table II. Genetic origin of the *C. canephora* multisite trial clones.

Clones	Origin	Genetic type (*)
	Clonal parents progenies	
503	A1 Open pollination	Congolese
512, 513	410 × 411	Guinean × Congolese
526, 529	410 × 464	Guinean × Congolese
539	178 × A03	Congolese × Congolese
586, 587, 588, 594	181 × A03	Intergroup × Congolese
589	181 × 182	Intergroup × Congolese
609	A01 × 200	Congolese × Congolese
	Survey in plantations	
119, 126, 305, 461		Intergroup

(*) Intergroup = genotype whose origin is an intergroup cross between a Congolese and a Guinean parent.

composed of two major genetic groups: Guinean and Congolese, the hybrid progenies of which display group heterosis [6, 13, 16].

At each location, the trials were planted in a totally randomised single-tree plot design. The number of replicates (= trees) per clone was 8 (Bingerville), 18 (Abengourou) and 30 (7 other locations). The planting density was 1,667 plants per hectare, i.e. a spacing of 3 m × 2 m. The cultivation method was free growth on three stems. Mineral fertilization corresponded to the extended recommendations.

Yield was estimated by cumulating the first four production years in each trial expressed in terms of kilogrammes of green coffee per hectare and per year.

2.2. Analysis methods

Statistically speaking, genotype-environment interaction is defined as the deviation from an additive model of performance for certain genotype-environment combinations. A two-way (locations and clones) ANOVA was therefore performed to study these interactions. The analysis revealed the effects of two main factors on variation in yield, along with the effect of interaction between

clones and locations. As the design was unbalanced, with variable numbers of replicates depending on the sites, the ANOVA model used was the Henderson 3 type of the generalized linear model [21]. The clone means were fitted to the location effects as a function of the imbalance in the overall design. Clone stability or interactivity was studied by 4 different methods:

- ecovalences [26] were used to estimate the relative contribution of each clone to the sum of the squares of the interaction effect. A clone with a low ecovalence was considered not to be very interactive;

- analysis joint regression of clone interaction on locations [5, 10];

- the Nassar and Hühn non-parametric test [19]. Genotype-environment interactions not resulting in significant changes in genotype ranking at the different locations were sometimes considered as “false interactions” [22]. The Nassar and Hühn test took into account genotype rank at the different locations. It is expressed by the following value S_i corresponding to each of the K clones ($i \in [1, K]$):

$$S_i = 2 \sum_{j=1}^{N-1} \sum_{j'=j+1}^N \frac{|r_{ij} - r_{ij'}|}{N(N-1)}$$

where N = number of locations

r_{ij} = rank of clone i in location j .

The expectation and variance of S_i are respectively:

$$E(S_i) = (K^2 - 1) / 3K$$

$$V(S_i) = (K^2 - 1)[(K^2 - 4)(N+3)+30]/45K^2 N(N-1).$$

Let Z_i and S be defined as:

$$Z_i = (S_i - E(S_i))^2 / V(S_i)$$

$$\text{and } S = \sum_i Z_i.$$

Given the hypothesis that all the genotypes were uniformly stable, S follows a chi-square law with K degrees of freedom. If the chi-square test is significant at the chosen risk level, a chi-square test with one degree of freedom on the Z_i values indicates which clones are significantly different from the others in terms of stability. It should be noted that such rank stability was different from the absolute performance stability for a variety in several locations (= homeostasis);

- a study of interactions for each clone-location pair: it was possible to establish a table with K rows and N columns, each box containing the value of the interaction between clone i in location j . The table was used to perform a multivariate analysis taking the clones (= rows) as individuals and the columns (= locations) as variables.

Table III. Result of the two-way (location and clone) analysis of variance for yield in the *C. canephora* multi-site trial.

Variation source	DF	Mean square	F	Probability
Location	8	126860	241	0.00
Clone	15	22189	42	0.00
Location *				
clone interaction	120	2153	4.1	0.00
Residual	3338	526		
Residual CV	46%			

3. Results

3.1. Study of clone-location interaction and clone stability

The two-way ANOVA revealed a highly significant effect for the location and clone factors and for variation between the two (Tab. III). There thus existed an interaction between clones and locations, even though the mean square for the interaction was relatively small compared to that for the locations and the clones. The general ranking of clones and locations has been provided for information (Tab. IV). Clone ranking for each location is given in Table V.

The analyses of interaction by ecovalences, regression slopes and the Nassar and Hühn test are summarized in Table VI.

Two clones showed clearly higher ecovalences than the others, i.e. clones 461 and 587.

Clones 119 and 126 displayed regression slopes that were significantly greater than 0. Their performance increased in line with the quality of general production conditions. Conversely, the regression slopes for clones 503 and 594 were significantly negative. They gave a harder performance.

The Nassar and Hühn test showed heterogeneity in the stability of clone ranks with respect to locations ($S = 45.79$ whereas the chi-square value for 16 degrees of freedom at 1% was 32). Taken individually, the rank of the 5 following clones appeared to be significantly more stable than that of the others: 588, 119, 503, 526 and 589.

The following observations can be made from this information and clone ranks per location (Tab. V):

- Clones 461 and 587 strongly interacted with the environment with major rank changes. Clone 461 came second at Abengourou, its best rank, and sixteenth and last at Maféré its worst rank. The best rank for clone 587 was third at San Pedro and the worst was sixteenth and last at Abengourou and Guessabo. This type of interaction was displayed

Table IV. Location and clone ranking after the analysis of variance for yield in the the *C. canephora* multisite trial.

Location	Yield*	Mean groups **	Clone	Yield*	Mean groups **
Guessabo	2617	A	588	2321	A
Soubré	2207	B	119	2130	B
Maféré	1964	C	503	2042	B C
San Pedro	1514	D	526	1917	C D
Thyonle	1364	E	461	1834	D E
Bingerville	1178	F	539	1691	E F
Divo	1164	F	594	1632	F G
Zagne	950	G	609	1627	F G
Abengourou	890	G	126	1587	F G
			512	1575	F G
			529	1530	F G H
			305	1448	G H
			513	1386	H I
			587	1224	I J
			589	1223	I J
			586	1129	J

* : Kilogrammes of green coffee per hectare and per year.

** : Means followed by the same letter are not significantly different at the 5% level according to Newman and Keuls' test.

Table V. Clone rank for yield in each *C. canephora* multisite trial location.

Clone	Abengourou	Bingerville	Divo	Guessabo	Maféré	San Pedro	Soubré	Thyonle	Zagne
119	3	3	3	2	2	4	2	3	9
126	13	12	11	7	7	15	8	7	11
305	9	16	10	9	14	10	12	14	6
461	2	13	4	3	16	8	9	2	3
503	1	1	1	5	8	1	3	5	5
512	6	11	9	6	10	6	11	9	14
513	12	9	15	11	5	16	14	8	16
526	10	8	5	4	4	5	5	4	7
529	11	6	13	8	6	14	10	11	15
539	7	7	7	13	3	11	6	12	2
586	15	4	16	15	11	12	16	15	12
587	16	10	12	16	9	3	15	13	8
588	8	2	2	1	1	2	1	1	4
589	14	15	14	12	15	13	13	16	13
594	5	5	6	14	13	7	4	10	1
609	4	14	8	10	12	9	7	6	10

by the ecovalence study, but also by the high value of parameter S_i in the Nassar and Hühn test;

• The four best clones in the study for overall yield (588, 119, 503 and 526) had significantly

more stable ranks than the others according to the Nassar and Hühn test. On the other hand, clone 119 seemed to be more dependent upon the environment for expressing its potential, whereas clone 503 was hardier, as shown by the respective regres-

Table VI. Genotype-environment interaction parameters for yield in the *C. canephora* multisite trial.

Clone	Rank Yield	Ecovalence (%)	Rank Ecovalence	Regression coefficient	Si Nassar (***)
588	1	5.99	8	ns	2.22 (*)
119	2	8.44	3	0.26 (*)	2.00 (**)
503	3	6.58	7	-0.49 (*)	2.89 (*)
526	4	2.65	11	ns	2.33 (*)
461	5	15.08	2	ns	5.89 ns
539	6	5.04	9	ns	4.50 ns
594	7	8.42	4	-0.37 (*)	5.06 ns
609	8	2.38	14	ns	3.67 ns
126	9	3.37	10	0.30 (*)	3.50 ns
512	10	2.37	15	ns	3.22 ns
529	11	1.91	16	ns	3.94 ns
305	12	2.65	11	ns	3.72 ns
513	13	7.80	6	ns	4.61 ns
587	14	16.79	1	ns	5.06 ns
589	15	2.50	13	ns	1.50 (**)
586	16	8.04	5	ns	4.00 ns

ns: Not significant

*: Significant at 5% level

**: Significant at 1% level

***: Expected value and variance of Si: 5.31 and 1.48

S = 45.79 significantly different from zero at the 1% level according to chi-square distribution with 16 degrees of freedom
i.e. the hypothesis of homogenous clonal rank stability is rejected.

sion slopes. This was a case of interaction without rank modification.

3.2. Multivariate analysis of interaction

The first two axes of the multivariate analysis carried out on the interaction values for each clone-location pair explained 33% and 25% respectively of the total variation observed. Representation of the individuals in the plane defined by these two axes (Fig. 1) confirmed the originality of clones 461 and 587. Clone 586 displayed a performance which was relatively similar to that of clone 587. No clear relationship was found between the genetic origin (Tab. II) and graphic distribution of the clones. It can be seen that only clones 586 and 587, which had the same original performance, belonged to the same family.

On the other hand, four groups of locations can be seen as corresponding to similarities in pedoclimatic characteristics (Tab. I):

- Soubré, Guessabo, Thyonlé: saturated soils with previous forest cover.
- Divo, Abengourou: saturated soils with previous fallow cover and rainfall of less than 1,400 mm/year.
- Zagné, San Pedro: desaturated soils with moderate rainfall.
- Bingerville, Maféré: desaturated soils with rainfall over 1,800 mm/year.

A certain structuring of clone-location interaction was thus defined. The main factor in the structuring would appear to be the degree of soil saturation, with the previous crop cover and rainfall as secondary factors.

Figure 1. Representation of locations (top) and clones (bottom) in plane 1-2 of the multivariate analysis carried out on the interaction values for each clone-location pair.

4. Discussions - conclusions

The existence of genotype-environment interactions in *C. canephora* has been clearly established for the first time. Given the diversity of the methods used, their relative merits were compared and a certain number of important conclusions were made regarding plant breeding.

4.1. Comparison of analytical methods used

Ecovalences clearly indicated the two most interactive clones with a change of rank, but not those clones that were most stable for rank or that were interactive without rank modification. The

latter were revealed by studying regression slopes, which, however, did not show interactive clones with rank modification. The non-parametric Nassar and Hühn method identified the most stable clones in terms of rank in each location.

The multivariate analysis carried out on the interaction values for each location-clone pair provided essential information on interaction structuring. Each method provided different but complementary data, thereby making them all useful.

4.2. Structuring of clone-location interaction

Strong geographical structuring of clone-location interaction was detected. It was mainly linked to the degree of soil saturation. This confirmed the

observations carried out in determining mineral fertilizer formulas adapted to different soil types in the Ivory Coast [24]. The classical distinction within the Ivorian coffee zone was found, between the zone west of the river Bandama and the coastal strip in the South, where the soils are relatively desaturated on the one hand, and the rest of the zone where the soils are relatively saturated. The multivariate analysis incorporated Thyonlé in those locations with saturated soils, whereas that site is in a region with desaturated soil (West). However, analysis of soil in this particular plot confirmed more than 70% saturation. Thyonlé is therefore apparently not representative of its geographical region.

The previous plant cover and rainfall also play an important role. These two factors are paramount. Indeed, the previous plant cover, which was mostly forest in the distant past, has evolved towards fallow and the dry seasons seem to be increasingly severe [15].

A practical consequence of this geographical structuring is the possibility of choosing four locations rather than nine when setting up future multi-site trials. The CNRA stations cover the entire range of variability encountered, apart from the group of saturated soils after forest with moderate rainfall.

These genotype-environment interactions would be worth elucidating. Indeed, they are linked either to tolerance to biotic or abiotic stress, or to plasticity phenomena [11]. Some regions of the genome involved in such phenomena have been identified in several species [12].

4.3. Choice of clones

This study concentrated on yield. The final choice of clones will also take into account tree architecture, technological and organoleptic qualities, and resistance to different diseases and insects.

Despite the existence of certain interactions, our results show that the four most productive clones at all sites (119, 503, 526 and 588) were stable as

regards the Nassar and Hühn test: irrespective of the location, they always ranked among the highest yielders. Analysis of the regression slope revealed interaction without rank modification for clones 119 and 503. Such interaction is not a problem for breeders. These four clones are therefore serious candidates for extension throughout the coffee growing zone. Among the interactive clones with rank modification, hence specifically adapted to a pedoclimatic type, only clone 461 could be extended in the zones with saturated soils.

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