Yield Stability Over Several Years in *Coffea canephora*: Definition of Synthetic Traits and Longitudinal Data Analyses

C. CILAS, C. MONTAGNON

CIRAD, TA A31/02, 34398, Montpellier, France

SUMMARY

The effectiveness of the perennial plants breeding is restricted by particular constraints linked to the crops lifespan. Moreover, acting of a production of fruits or seeds as to the coffee-tree, how many years of observation are necessary to define the trait of “production”? And how to integrate the variations of the trait in time with a breeding purpose in which stability and durability are often mentioned? To try to answer these questions, a trial comparing 20 clones of *Coffea canephora*, monitored over 9 years of production, was analyzed according to various methods. Two main methods were proposed: i) the first one proposed indexes definition – the indexes described precocity, alternation and intensity of inter-annual variations; ii) the second one proposed a modelization of the data by a longitudinal data analysis approach. It was found that the first cycle (first 4 years) are not always sufficient for predicting the yield capacity of the clones. The intensity of the relative differences between yields in successive years was a trait that was only heritable in the second production cycle. Low intensities for those differences were favorable to cumulative production. Strong alternations were not propitious to optimizing cumulative production. Several models were tested for longitudinal data analyses and *Compound Symetric’s* one with heterogeneous variances (CSH model) allowed to better describe data structure. Thus, correlations between yields of successive years were pretty stable that reveals an important trees’ effect among this clonal population. Variability was found for yield distribution over time. It is therefore possible to define “stability” traits and to select cultivars with lower annual yield variations, thereby ensuring regular income for coffee farmers.

INTRODUCTION

Cumulative production over several years of observations is often one of the only agronomic selection criteria used in fruit tree cultivation. However, different strategies exist that can culminate in identical cumulative yields, some varieties being early yielders, some being more stable over time; but that distribution of yields over time is only rarely taken into account in breeding. Yet, annual yield stability is of interest to growers, who count on regular income from their crops. Annual yield stability is therefore a trait that ought to be taken into account more, to enable genetic control of fruit load distribution over time.

For coffee producers, cumulative yields over a large number of years is the priority target trait for selection, but the “ways” of achieving the same accumulation are not equivalent: early-yielding cultivars that are stable over time are generally preferred. The first annual yields – when the bushes are young – have often been used to test their ability to predict cumulative yields over several years (Cilas et al., 1998; Montagnon, 2000), but few studies have been made of production stability over time with a view to improving yield distribution over time (Cilas et al., 2003). It is very important to study this stability trait because alternation phenomena are often reported (Coste, 1989; Amoah et al., 1997). Such alternation phenomena are a major drawback for growers. Apart from the applied aspect of such a study, it also proves important to gain a clearer understanding of production strategies in perennial fruit species, particularly with a view to finding out whether several strategies might exist within the same species. If genetic variability existed for those temporal characteristics, it could be used to select varieties that derive the most from certain cultivated ecosystems, depending on the cultural techniques adopted and farmers' cropping strategies – notably the pruning system.

Production stability between successive years was examined in a clonal trial involving the species *Coffea canephora* Pierre, monitored over 9 years of production: during the first 4-year cycle, then, after cutting back, for a cycle of 5 years after a year of vegetative growth without yields. The species *C. canephora* produces robusta coffee, which has less appreciated sensory qualities than arabica coffee (Coste, 1989), hence it is traded at a lower price. It nonetheless remains an essential product for the hot, humid tropics at low elevations, and some robusta varieties can achieve the qualities of certain arabica coffees when post-harvest processing is carried out properly. The coffee trees of this species are generally less susceptible to diseases and pests, and are often more productive, though sometimes with considerable irregularities.

MATERIAL AND METHODS

Planting material and experimental design

The planting material comprised 20 clones, selected on research stations from controlled crosses, or surveyed on smallholdings (Table 1). The genetic origin of clones was determined in compliance with the known genetic diversity of *C. canephora,* composed of two large genetic groups: Guinean and Congolese, whose hybrids display group heterosis (Berthaud et al., 1984; Leroy, 1993).

Table 1. Genetic origin of the 20 clones used.

Clones	Origin	Genetic group
503	Open pollination of Clone A1	Congolese
512, 513	410 x 411	Guinean x Congolese
526, 529	410 x 464	Guinean x Congolese
539	178 x A03	Congolese x Congolese
586, 587, 588, 594	181 x A03	Inter-group hybrid x Congolese
589	181 x 182	Inter-group hybrid x Congolese
609	A01 x 200	Congolese x Congolese
619, 621	392 x 200	Congolese x Congolese
119, 126, 305, 461	Selected in plantations	Inter-group hybrids
202, 392	Selected at INEAC (ex Zaire)	Congolese

The trial was set up at the Divo research station belonging to *Centre National de Recherches Agronomiques* (CNRA) in Ivory Coast, in a totally randomized single-tree plot design. There were 30 replicates per clone. The planting density was 1667 plants per hectare, i.e. a spacing of 3 m x 2 m. The coffee trees were grown from horticultural cuttings and were planted in 1987; they were grown freely on three stems. Mineral fertilization corresponded to the usual recommendations.

Yields were estimated annually and cumulative production was estimated over the first cycle (4 production years: from 1989 to 1992), over the second cycle (5 production years: from 1994 to 1998) and for the nine years as a whole. The yields were expressed in kilograms of green coffee per hectare (y_i being the yields in year No. i).

Construction of indexes, and statistical analyses

With tree crops, how can we process the information provided by several years of observations? When fruit or seed production is involved, the first trait that is generally used is the accumulation over all the years for which harvests are available. Annual yields may also be analysed. However, with *n* years of production available, one might imagine constructing *n* quantitative traits that possess a biological sense. The first analysis carried out was a Principal Components Analysis (PCA), which was used to summarize the information and recover the main components. The principal components were then interpreted and the heritability values for the newly constructed traits were estimated. The other avenue investigated was constructing synthetic traits linked to yield distribution over time. That approach was proposed by Monselise and Goldschmidt (1982) and has been used on mango (Reddy *et al.*, 2002), but it has never been used to define selection criteria. In addition, such indexes making it possible to determine yield distribution over time had never been used on coffee. It was therefore a matter of constructing indexes, or rather composite traits with a biological sense.

The first composite trait we used was an earliness index (EI):

$$EI = \frac{ny_1 + (n-1)y_2 + \ldots\ldots + 2y_{n-1} + y_n}{nY}$$

In our case, we constructed one earliness index for the first cycle, one for the second cycle, and an overall earliness index:

$$EI_1 = \frac{4y_1 + 3y_2 + 2y_3 + y_4}{4Y_{1-4}} \;\; ; \;\; EI_2 = \frac{5y_6 + 4y_7 + 3y_8 + 2y_9 + y_{10}}{5Y_{6-10}} \;\; ;$$

$$EI_g = \frac{9y_1 + 8y_2 + 7y_3 + 6y_4 + 5y_6 + 4y_7 + 3y_8 + 2y_9 + y_{10}}{9Y_{1-10}}$$

The overall index calculated over 10 years took 9 years of production into account, given that year 5 was a year without yields, as the trees were cut back after the harvest in year 4.

We then defined different two-yearly indexes. The first was an intensity index for the differences between successive years, *I,* for the first two cycles, and for both cycles together:

$$I_1 = \frac{1}{3}\left(\frac{|y_2 - y_1|}{y_2 + y_1} + \frac{|y_3 - y_2|}{y_3 + y_2} + \frac{|y_4 - y_3|}{y_4 + y_3}\right) \;\; ; \;\; I_2 = \frac{1}{4}\left(\frac{|y_7 - y_6|}{y_7 + y_6} + \frac{|y_8 - y_7|}{y_8 + y_7} + \frac{|y_9 - y_8|}{y_9 + y_8} + \frac{|y_{10} - y_9|}{y_{10} + y_9}\right)$$

$$I_g = \frac{1}{7}\left(\frac{|y_2 - y_1|}{y_2 + y_1} + \frac{|y_3 - y_2|}{y_3 + y_2} + \frac{|y_4 - y_3|}{y_4 + y_3} + \frac{|y_7 - y_6|}{y_7 + y_6} + \frac{|y_8 - y_7|}{y_8 + y_7} + \frac{|y_9 - y_8|}{y_9 + y_8} + \frac{|y_{10} - y_9|}{y_{10} + y_9}\right)$$

An alternation index was then defined. This was a matter of characterizing the property of certain coffee trees in which a year of high yields was followed by a year of low yields, and a year of low yields was followed by a year of high yields. These yields in peaks and troughs were characterized by differences between successive production years that changed sign between successive differences. Alternation index *A* was therefore the sum of an indicative variable *B* (0,1).

If $y_{i+1} - y_i$ was of the same sign as $y_{i+2} - y_{i+1}$, or if one of the two differences was nil then B_i=0;

If $y_{i+1} - y_i$ was of the opposite sign to $y_{i+2} - y_{i+1}$, and if none of the differences was nil then B_i=1;

We therefore defined an alternation index for the first cycle, an index for the second cycle and an index for both cycles together:

$$A_1 = \sum_{i=1}^{4} B_i \ ; \ A_2 = \sum_{i=6}^{10} B_i \ ; \ A_g = A_1 + A_2$$

We also used an index of maximum intensity for the differences between successive years:

$$MI = \frac{\max(|y_{i+1} - y_i|)}{Y_{1-10}}$$

The broad sense heritability for these different traits was estimated, along with the associated confidence intervals. The confidence intervals were estimated by the Wald method (Agresti and Coull, 1998). We also estimated the genetic and environmental correlations between some of the traits.

Another avenue investigated was to describe relationships between successive years by longitudinal data analyses with mixed models (Verbeke and Molenberghs, 2000). Repeated data analyses allowed to precise autocorrelation structures of individual data on time. Several models were investigated: a first-order autoregressive model, with homogenous variances (AR), with heterogeneous variances (ARH), a *Compound Symetric* model (i.e. with constant correlation between years) with homogenous variances (CS), with heterogeneous variances (CSH) and the unstructured model (UN) where correlations between different years are independent as well as variances of the different years. Models can be written as:

$$Y_{ijkl} = \mu + C_i + A_j + (CA)_{ij} + b_k + E_{ijkl}$$

with: μ : mean
C_i : clone i effect
A_j : year j effect
$(CA)_{ij}$: clone x year interaction
b_k : bloc k effect
E_{ijkl} : residual of tree l belonging to clone i bloc k for the year j
Y_{ijkl}: yield of tree l belonging to clone i bloc k for the year j

and :

1- in the first-order autoregressive model:

$$V(E_{ijk}) = \sigma^2 \quad \text{if the variances are homogenous between years (AR1)}$$
$$= \sigma_j^2 \quad \text{otherwise (ARH1)}$$
$$\text{and} \quad \mathrm{Corr}(E_{ijkl}, E_{i'j'k'l'}) = \begin{cases} \rho^{|j-j'|} & \text{if } i=i',\ k=k',\ l=l' \\ 0 & \text{otherwise} \end{cases}$$

2- in the Compound Symetry model:

$V(E_{ijkl}) = \sigma^2$ if the variances are homogenous between years (CS)

$= \sigma_j^2$ otherwise (CSH)

and Corr $(E_{ijkl}, E_{i'j'k'l'}) = \rho$ if $i=i'$, $k=k'$, $l=l'$

0 otherwise

3- in the unstructured model:

$V(E_{ijkl}) = \sigma_j^2$

and Corr $(E_{ijkl}, E_{i'j'k'l'}) = \rho_{jj'}$ if $i=i'$, $k=k'$, $l=l'$

0 otherwise

To choose the most suitable model, several criteria exist: log of likelyhood, Akaike criteria (AIC) or Schwartz criteria (BIC); lower these criteria are better the model is. When two models are nested, the comparison of their likelyhood allows to choose the best one without ambiguity (Verbeke and Molenberg, 2000).

Table 2. Means, broad sense heritabilities and confidence intervals for the broad sense heritabilities relative to yield traits.

Trait	Mean	h^2	Confidence interval at 95%
y1	25.33	0.286	[0.140, 0.432]
y2	5.49	0.001	[0, 0.007]
y3	95.21	0.450	[0.278, 0.622]
y4	7.15	0.383	[0.223, 0.543]
y1-4	133.18	0.452	[0.282, 0.623]
y6	11.86	0.466	[0.298, 0.633]
y7	23.27	0.405	[0.241, 0.569]
y8	43.77	0.523	[0.358, 0.688]
y9	84.14	0.482	[0.313, 0.650]
y10	30.95	0.464	[0.297, 0.630]
y6-10	193.99	0.615	[0.459, 0.771]
y1-10	327.17	0.607	[0.449, 0.765]
PC1		0.629	[0.475, 0.783]
PC2		-0.002	[-0.025, 0.021]
PC3		0.266	[0.129, 0.403]

Where PC1, PC2 and PC3 are the first 3 principal components of the PCA.

RESULTS

Annual yields and cumulative yields

The broad sense heritabilities for the annual and cumulative yield traits are shown, as are the associated confidence intervals (Table 2); the means for those traits for the trial as a whole are also shown. Alternation was found for mean yields for the first cycle: over 4 years, a year of high yields was followed by a year of low yields. That was no longer the case in the second cycle, during which average yields increased over the first four years and decreased in the 5th year. After initial cutting back, a more developed root system probably limited competition between fruit production and vegetative growth. Cumulative yields over several years had higher heritabilities than annual yields. It was thus necessary to take several years into account for the productive ability of the genotypes to be expressed. The lowest heritability, which was not significantly different from 0, concerned the lowest annual yields for the trial as a whole. Unfavourable environmental conditions may therefore have masked the genetic potential of the coffee trees.

Principal components analysis

The Principal Components Analysis was used to represent linkages between yields in the different years (Figure 1). For instance, annual yields were closely linked, except for the yields in 1990, which were very low and atypical. The first principal component was linked to cumulative production, whereas the second was linked to the yields in 1990. These first two axes accounted for 55.5% of total variability (44.1% for the first component and 11.4% for the second). The 3rd component accounted for no more than 8.7% of total variability and could be used to separate yields in the first cycle from those in the second cycle. The heritabilities for the components were estimated at the same time as those for annual and cumulative yields (Table 2).

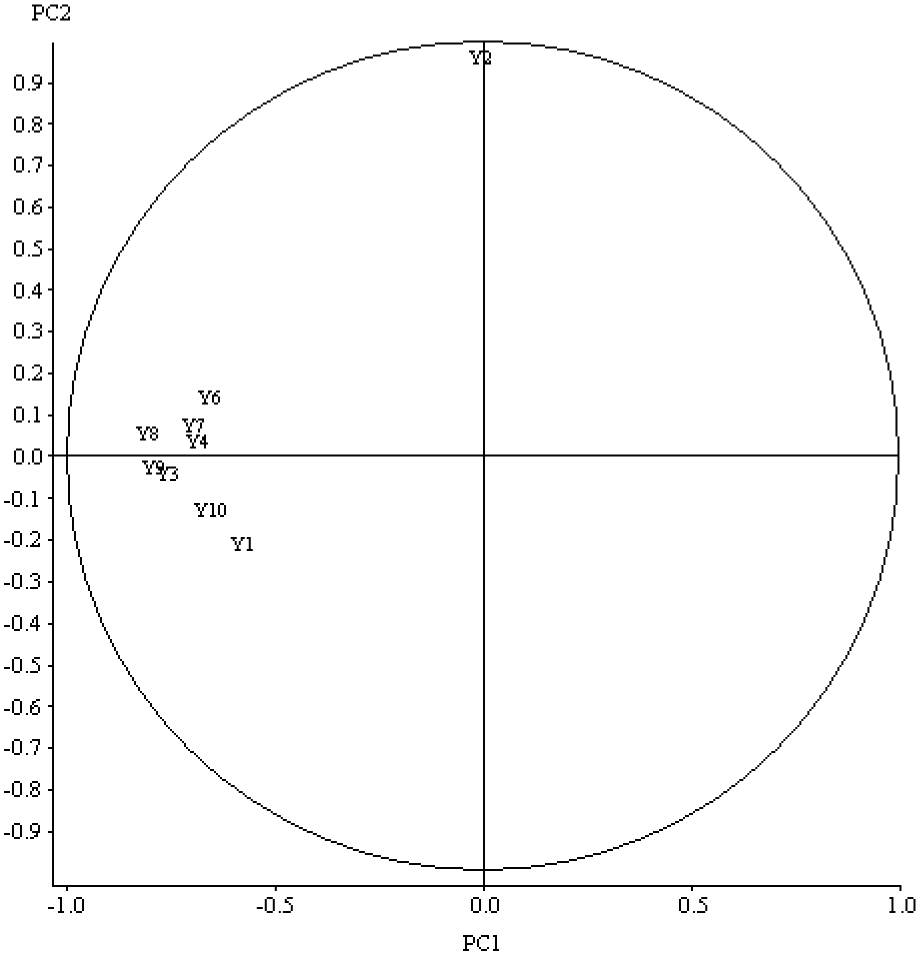

Figure 1. Principal Components Analysis. Circle of correlations between annual yields.

Synthetic traits

The same parameters – heritabilities and associated confidence intervals – were estimated for the synthetic traits described earlier (Table 3). The earliness traits were heritable irrespective of the cycle considered. The intensity of differences between yields in successive years was only heritable for the second cycle and for the 2 cycles together. The alternation traits had low, but significant, heritability.

Table 3. Means, broad sense heritabilities and confidence intervals for the broad sense heritabilities relative to the synthetic traits defined.

Trait	Mean	h^2	Confidence interval at 95%
EI_1	0.596	0.307	[0.150, 0.464]
EI_2	0.497	0.258	[0.122, 0.395]
EI_g	0.501	0.211	[0.089, 0.333]
I_1	0.867	0.026	[0, 0.068]
I_2	0.448	0.378	[0.218, 0.538]
I_g	0.628	0.267	[0.128, 0.406]
A_1	1.83	0.088	[0.006, 0.169]
A_2	0.516	0.096	[0.020, 0.172]
A_g	0.675	0.061	[0.001, 0.121]
MI	0.334	0.286	[0.143, 0.428]

Clone classification and correlations

In order to gain a clearer picture of the linkages between these traits, we classed the clones for the most heritable traits (Tables 4 and 5). Genetic correlations between the traits were then estimated (Table 6).

The classification for annual yields evolved over time (Table 4). The most productive clones appeared to be those which had lower alternation intensities (Table 5), with lower I_g and *MI* values. The earliness of the first cycle did not seem to be a trait that was favourable for cumulative yields (Table 5).

The genetic and environmental correlations between yields in successive years provided a clearer understanding of production trends (Table 6). The genetic correlations were relatively stable, between 0.418 and 0.916, and the correlations were not higher for years close to each other. The environmental correlations were more variable and tended to decrease the further the years were apart.
The correlations between cumulative production and the synthetic traits defined earlier were used to identify those characteristics that were conducive to good overall production (table 7). First cycle earliness was not a favourable criterion for cumulative production. In addition, the more intense the differences between successive years, the lower were the cumulative yields (*Ig* and *MI* correlated negatively with *Y1-10*). The most stable clones were therefore also the most productive over the 2 production cycles.

Table 4. Comparison of the clones for yield traits: Newman-Keuls multiple comparison of means test at 5%.

Clones	*y1-10*	*y1-4*	*y6-10*	*Y1*	*y2*	*y3*	*y4*	*y6*	*y 7*	*y8*	*y 9*	*y10*
503	558 **a**	215 **a**	343 **a**	38 **ab**	6	151 **ab**	21 **a**	26 **a**	49 **a**	107 **a**	122 **ab**	38 **bcde**
526	514 **ab**	178 **ab**	337 **a**	37 **ab**	5	121 **bcd**	15 **b**	21 **ab**	35 **bc**	82 **b**	134 **a**	66 **a**
119	480 **abc**	188 **ab**	292 **a**	35 **ab**	5	126 **bc**	22 **a**	19 **bc**	36 **bc**	49 **cd**	139 **a**	49 **b**
588	449 **bcd**	215 **a**	234 **b**	35 **ab**	5	167 **a**	8 **bcde**	13 **cde**	23 **cde**	46 **cde**	90 **bcde**	62 **a**
461	414 **cde**	179 **ab**	235 **b**	48 **a**	8	110 **cde**	13 **bc**	9 **ef**	23 **cde**	52 **cd**	104 **bc**	47 **bc**
594	382 **def**	151 **bc**	231 **b**	29 **bc**	4	114 **cde**	5 **cde**	23 **ab**	24 **cd**	49 **cd**	99 **bcd**	35 **bcdef**
539	360 **defg**	139 **bcd**	221 **bc**	27 **bcd**	5	101 **cdef**	6 **cde**	18 **bcd**	29 **bc**	53 **cd**	90 **bcde**	31 **cdefg**
126	350 **efg**	120 **cde**	230 **b**	20 **bcd**	6	89 **cdef**	5 **cde**	6 **ef**	41 **ab**	56 **c**	98 **bcd**	29 **defgh**
529	331 **efg**	114 **cde**	217 **bc**	22 **bcd**	8	81 **def**	3 **de**	7 **ef**	24 **cd**	44 **cde**	98 **bcd**	44 **bcd**
512	317 **efg**	124 **cde**	192 **bcd**	19 **bcd**	1	93 **cdef**	11 **bcd**	7 **ef**	24 **cde**	39 **cde**	95 **bcd**	27 **defgh**
305	308 **gh**	121 **cde**	186 **bcd**	30 **abc**	6	82 **def**	3 **de**	9 **ef**	35 **bc**	33 **def**	99 **bcd**	11 **h**
619	266 **gh**	128 **cde**	138 **def**	36 **ab**	6	84 **cdef**	2 **e**	8 **ef**	23 **cde**	27 **ef**	66 **defg**	14 **gh**
609	266 **gh**	126 **cde**	140 **def**	12 **cd**	6	99 **cdef**	9 **bcde**	17 **bcd**	11 **def**	33 **def**	59 **efg**	21 **efgh**
513	259 **gh**	95 **cdef**	165 **cde**	11 **cd**	8	70 **efg**	5 **cde**	5 **ef**	23 **cde**	38 **cde**	81 **cdef**	18 **fgh**
621	202 **hi**	82 **def**	120 **efg**	35 **ab**	5	41 **gh**	1 **e**	2 **f**	12 **def**	23 **ef**	61 **efg**	22 **efgh**
589	201 **hi**	98 **cdef**	103 **efg**	25 **bcd**	4	70 **efg**	0.1 **e**	1 **f**	8 **ef**	26 **ef**	41 **gh**	27 **defgh**
587	201 **hi**	114 **cde**	87 **fg**	12 **cd**	5	97 **cd**	0.2 **e**	12 **de**	2 **f**	26 **ef**	34 **gh**	13 **gh**
202	179 **hi**	76 **efg**	103 **efg**	11 **cd**	5	59 **fg**	0.3 **e**	3 **f**	8 **def**	24 **ef**	56 **fg**	12 **gh**
586	122 **i**	52 **fg**	70 **g**	7 **d**	5	39 **gh**	1 **e**	11 **ed**	6 **f**	12 **f**	24 **h**	15 **gh**
392	110 **i**	35 **g**	76 **fg**	7 **d**	10	16 **h**	1 **e**	2 **f**	9 **def**	12 **f**	40 **gh**	12 **gh**

Table 5. Comparison of the clones for synthetic traits: Newman-Keuls multiple comparison of means test at 5%.

Clones	EI_1	EI_2	I_2	I_g	A_g	*MI*
503	0.572 **ef**	0.541 **ab**	0.377 **ef**	0.576 **de**	0.653 **ab**	0.266 **def**
526	0.587 **def**	0.490 **bcdef**	0.351 **f**	0.555 **e**	0.680 **ab**	0.242 **e**
119	0.567 **ef**	0.487 **bcdef**	0.391 **ef**	0.586 **cde**	0.690 **ab**	0.289 **cdef**
588	0.574 **ef**	0.459 **def**	0.325 **f**	0.566 **e**	0.648 **ab**	0.372 **bcd**
461	0.626 **cde**	0.466 **cdef**	0.414 **def**	0.600 **bcde**	0.593 **ab**	0.258 **ef**
594	0.594 **def**	0.518 **abcd**	0.354 **f**	0.592 **bcde**	0.759 **a**	0.308 **cdef**
539	0.593 **def**	0.521 **abcd**	0.374 **ef**	0.581 **bcde**	0.693 **ab**	0.281 **cdef**
126	0.587 **def**	0.508 **bcde**	0.454 **cdef**	0.619 **bcde**	0.690 **ab**	0.277 **def**
529	0.609 **cdef**	0.463 **cdef**	0.410 **ef**	0.602 **cde**	0.640 **ab**	0.275 **def**
512	0.550 **ef**	0.470 **cdef**	0.452 **cdef**	0.645 **bcde**	0.680 **ab**	0.355 **bcde**
305	0.630 **cd**	0.520 **abcd**	0.560 **bc**	0.701 **b**	0.752 **a**	0.384 **bc**
619	0.672 **bc**	0.529 **abc**	0.493 **bcde**	0.660 **bcde**	0.717 **ab**	0.362 **bcde**
609	0.542 **f**	0.522 **abcd**	0.401 **ef**	0.598 **bcde**	0.733 **a**	0.370 **bcd**
513	0.576 **ef**	0.491 **bcdef**	0.492 **bcde**	0.646 **bcde**	0.607 **ab**	0.348 **bcde**
621	0.735 **a**	0.446 **ef**	0.540 **bcd**	0.688 **bcd**	0.655 **ab**	0.324 **cdef**
589	0.628 **cde**	0.428 **f**	0.443 **cdef**	0.658 **bcde**	0.593 **ab**	0.388 **bc**
587	0.565 **ef**	0.569 **a**	0.729 **a**	0.817 **a**	0.752 **a**	0.493 **a**
202	0.692 **def**	0.467 **cdef**	0.565 **bc**	0.693 **bc**	0.621 **ab**	0.384 **bc**
586	0.577 **ef**	0.539 **ab**	0.449 **cdef**	0.604 **bcde**	0.683 **ab**	0.354 **bcde**
392	0.713 **ab**	0.452 **ef**	0.602 **b**	0.657 **bcde**	0.580 **b**	0.440 **ab**

Table 6. Correlations between annual yields and cumulative yields (genetic, lower triangle; environmental, upper triangle) .

	y1	*y3*	*y4*	*y6*	*y7*	*y8*	*y9*	*y10*	*y1-10*
y1	-	0.347	0.207	0.157	0.196	0.261	0.158	0.109	0.481
y3	0.672	-	0.248	0.325	0.266	0.333	0.401	0.256	0.778
y4	0.594	0.753	-	0.158	0.225	0.302	0.213	0.140	0.410
y6	0.418	0.767	0.712	-	0.295	0.265	0.374	0.213	0.505
y7	0.623	0.642	0.717	0.565	-	0.360	0.286	0.110	0.514
y8	0.614	0.773	0.790	0.733	0.846	-	0.341	0.261	0.633
y9	0.737	0.739	0.844	0.618	0.916	0.831	-	0.354	0.729
y10	0.688	0.769	0.695	0.541	0.529	0.688	0.747	-	0.494
y1-10	0.783	0.904	0.876	0.757	0.855	0.915	0.938	0.838	-

Table 7. Correlations between synthetic traits and cumulative yields (genetic, lower triangle; environmental, upper triangle).

	EI_1	EI_2	I_2	I_g	A_g	MI	$y1\text{-}10$
EI_1	-	0.028	-0.051	-0.059	-0.127	-0.136	-0.068
EI_2	-0.461	-	-0.189	-0.157	0.059	-0.071	0.065
I_2	0.376	0.204	-	0.726	0.122	0.247	-0.136
I_g	0.307	0.212	0.988	-	0.303	0.228	-0.111
A_g	-0.378	0.963	0.110	0.162	-	-0.029	0.068
MI	0.147	0.119	0.792	0.844	0.226	-	0.262
$y1\text{-}10$	-0.433	0.129	-0.719	-0.690	0.148	-0.747	-

Longitudinal data analyses

Among the tested models, the ARH1 model allowed a better adjustment than the AR1 model and the CSH model allowed a better adjustment than the CS model (table 8). The CSH model gave an AIC and a BIC similar to those of the UN model. With the UN model, we have to estimate 45 parameters, but only 10 with the CSH model. The UN model took into account the irregularities of the correlations' values between the yields of the different years; these correlations, estimated with the UN model, are the environmental correlations between the yields of the different years (Table 6). With the ARH1 model, the correlation between the yields of two successive years was $r = 0.22$ and between the yields of two years (y and $y + i$) the correlation was $r_i = (0.22)^i$. With the CS model, the correlations between two years (y and $y + i$) was, for all i, $r = 0.178$ whereas with the CSH model $r = 0.204$. The CS model, like the AR1 model, needed only 2 estimated parameters; however these two models were removed on the basis of the adjustment's criteria (AIC, BIC) values (table 8). The best adjustment of the CSH model indicated that a tree effect existed within each clone. This effect means that either strong micro-environmental effects on yield expression existed, or individual tree effects, linked to tree life or tree origin, existed within clonal effects; and this effect persists on time. With this autcorrelations' control in the model, a significant interaction "clone x year" remained ($F_{152, 4104} = 12.70$, with $p < 0.0001$).

Table 8. Choice criteria of longitudinal data analysis model for annual yield.

Model	**-2 Log Vrais.**	**AIC**	**BIC**
AR1	42309	42313	42322
ARH1	39772	39792	39835
CS	42078	42082	42091
CSH	39540	39560	39603
UN	39321	39411	39603

DISCUSSION AND CONCLUSION

Different methods were thus used to judge the production stability of clones over successive production years. The Principal Components Analysis did not bring out any traits indicating yield distribution over time. That analysis indicated that annual yields per tree were generally positively correlated. When we considered mean plot yields, we found alternating production in the first cycle, but that was no longer the case in the second cycle, during which average yields rose in the first 4 years, then decreased in the 5th year. Alternation phenomena, which have often been reported in coffee, appeared primarily to exist in the first production cycle, when the root systems of the trees had not developed much. The heritabilities for annual yields were generally higher for second cycle yields than for first cycle yields, and the highest heritabilities were for cumulative yields.

The intensity of relative differences between yields in successive years was a trait that was only heritable in the second production cycle. The low intensities found for those differences were favourable for cumulative yields. First cycle earliness was genetically and negatively correlated with cumulative yields. The productive clones were therefore more regular over time and high annual yields penalized their production capacity less in the following years.

Longitudinal data analyses supplied complementary points of view. These analyses allowed to define the correlations' structure between the individual tree yields of the different years. A first-order autoregressive model with heterogeneous variances fitted well data. However, the *Compound Symetric* model with heterogeneous variances (CSH) was the best one. This model indicated that correlations were constant between individual yields of the different years. This good adjustment revealed an important tree effect within the tested clones. A significant interaction "clone x year" remained and this interaction was mainly due to the clones with extreme yields – high or low. The « clone x environment » interaction was a *contrario* lower for the high yields clones (Montagnon *et al*, 2000). Thus, different years cannot be considered as different sites probably because of the positive autocorrelations at tree scale.

Annual yields are therefore not a stable trait in the *C. canephora* coffee tree. There is greater alternation in the first cycle when trees have yet to be subject to pruning. It is likely that competition between vegetative growth and fruit production is less once the root systems are more developed. Variability was found for yield distribution over time within the planting material studied. It is therefore possible to select cultivars with lower annual yield variations, thereby ensuring regular income for coffee farmers.

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