Cocoa breeding must take into account the competitive value of cocoa trees

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ARTICLE INFO

ABSTRACT

Interactions between neighbouring plants in an ecosystem can lead to competition, even in single-species stands. Genetic selection of perennial plants based on the individual values of genotypes does not usually take into account interactions that develop over time. The purpose of this study was to ascertain whether the effects of competition might affect the performance of cacao genotypes tested over long periods, and at what point those effects begin.

Competition was studied on cacao trees (*Theobroma cacao* L) taking into account the diameter of the trees and their yields. The trial design set up in Côte d'Ivoire was a factorial mating design of the main cacao genetic improvement programme. The approach taken was a multivariate model based on 13 years of data gathering, including genetic, spatial and competition effects.

The results revealed a gradual onset of competition starting in the early years of production up to the 4th year, when its effect became significant. It first affected growth then, 2 years later, yields. Depending on the production years, the genetic effect and the spatial effect were the greatest. In years of strong competition, it could affect up to 10 % of the annual production variability, i.e. a quarter of the variability explained by genetics. The most vigorous trees always remained highly competitive and high-yielding. The competition effect will therefore always be substantial with selections of high-yielding individuals. "Group selection" of somewhat average, less competitive individuals would help to maximize yield gains through the combined performance of the group, rather than that of individual trees.

1. Introduction

Within a given ecosystem, relations between plants of the same species (within-species) or of different species (between-species) can lead to positive interactions (facilitation), neutral interactions, or negative interactions (competition) (Danet, 2017). In most single-species stands, such as the majority of cultivated ecosystems, the resources needed for growth and reproduction are typically limited, so the plants compete with each other to capture the maximum of resources. Morphological and physiological traits of varieties and crop densities can affect competition and thus influence production and growth dynamics between neighbouring plants.

Competition between plants is a subject that has been widely studied in natural ecosystems (Damgaard, 2011; Craine and Dybzinski, 2013), such as forest trees (Muir, 2005; Zhang et al., 2015), and in cultivated plants (Durban et al., 2001; Isaac et al., 2007; Montagnon et al., 2001). Several methods have been proposed for its quantitative evaluation (Weigelt and Jolliffe, 2003). A study on how planting density affects the functional characteristics of growth and biomass production in Chinese pine trees, based on the GreenLab model, evaluated the effect of competition and how trees react to such competition (Guo et al., 2012). Costa e Silva et al., 2017 studied the indirect genetic effect of neighbours on apparent total heritable variance, hence the response to selection, in *Eucalyptus globulus*. Some studies, such as the one by Lake et al., 2016 on chickpea, showed that the performance of competitive genotypes and non-competitive genotypes can be modified depending on the strength of the competition. York et al., 2015 showed in maize that selection for yields over the centuries has been accompanied by a change in root architecture and anatomy, so that new varieties have evolved towards phenotypes adapted to more intense competition for nitrogen. In the case of cotton, the yield per plant and the har-

vest index decreased exponentially with increasing plant density and thus the intensity of competition (Li et al., 2020).

With a view to broadening the genetic base and increasing genetic variability in the cacao tree (*Theobroma cacao* L.), some clones of the Upper Amazon populations (Pound, 1938) were introduced to the different genetic improvement programs around the world (Posnette, 1943; Mossu, 1985). In addition to becoming better established in the field than West African Amelonado populations (Toxopeus, 1970), these new genotypes proved to be more productive and more resistant to diseases (Knight and Rogers, 1955; Posnette, 1951). That selective advantage of the Upper Amazon cacao tree progenies led to the selection of others traits, such as vigour, without taking into account the competition effect they have on their neighbours (Wallace et al., 2018; Wilson, 1975). Several authors have highlighted the correlation between the strong vigour of the cacao tree and its high yields, on the one hand, and between the strong vigour of some cacao trees and the low yields of their neighbours on the other hand, due to competition between trees (Glendinning and Vernon, 1965; Martin and Lockwood, 1979). This phenomenon is often mentioned as one of the possible reasons for decreasing yields in plantations, hence in their working life span (Cilas et al., 2011; Tahi et al., 2019). Hence, for breeders, managing the competition effects of varieties that negatively affect the yields of their neighbours means incorporating competitive effects in the quantitative genetic models (Gallais, 1975).

Several models have been proposed to incorporate competitive effects in the quantitative genetic models. Glendinning and Vernon (1965) proposed that border trees data should not be included in the cocoa tree assessment trials. This technique eliminated the bias between high yields from border trees and lower yields from trees within the plot. Lachenaud and Oliver (1998) and Lockwood and Yin (1996) proposed to reduce planting densities for the most vigorous clones. The yield:vigour ratio (Paulin and Eskes, 1995) has been used as the main selection criterion, the aim being to enable the selection of high-yielding, compact genotypes. Lachenaud and Montagnon (2002) used the average of eight neighbours as a covariable for estimating values adjusted to the performance of individual cacao trees. In Côte d'Ivoire, the way in which competition affects the agronomic performance of new genotypes from the reciprocal recurrent selection program has never been considered. In order to select breeding parents of interest in that program, precise knowledge of such competition effects would be necessary to fit selection models to the optimum combinations of traits to be included in selection indices (Wallace et al., 2018). A few successful implementations of selection schemes accounting for competition effects have already been reported, notably for caged animals (Wade et al., 2010). As the selection of cocoa trees in this breeding program is multivariate, it is necessary to take into account all sources of co-variation for the study of the competition.

In this work, we set out to ascertain:

i) Whether there was competition between trees that affected their yield and their growth,
ii) Whether there existed any genetic effects in the expression of competition relations,
iii) The dynamics of those direct genetic and competition effects between trees.

To that end, we used a multivariate model including genetic, spatial and competition effects to study the dynamics of cacao tree fruit production (pods) and diameter growth. We based this analysis on regular monitoring of cacao trees derived from two genetic mixing cycles between Upper Amazon trees, over a period of 13 years, at Divo research station of the *Centre National de Recherche Agronomique* in Côte d'Ivoire.

2. Material and methods

2.1. Plant material and experimental design

The trial was set up at the Divo research centre in Côte d'Ivoire in a plot of the Reciprocal Recurrent Selection programme in June 2000 (Lachenaud et al., 2001). The trees came from 2 cycles of crosses between Upper Amazon cacao trees. The crosses were carried out using an incomplete factorial mating design of 40 parents (20 females and 20 males). Each female parent was crossed with four males, favouring crosses between half-sibs. In all, 75 crosses, called families, were each represented by 15 trees. There were three control crosses with 45 trees each. The 3 controls are high-yield hybrids distributed in Côte d'Ivoire. The first, family 203 is a high-yield cross identified in the first SRR cycle. The second, family 205 represents a control cross between Low Amazonian and Trinitario broodstock and the third, family 201 between High Amazonian broodstock. The field trial therefore comprised 1260 trees planted in a totally randomized design at a spacing of 2.5 m between trees and 3 m between rows, i.e. 0.96 ha. In all, 148 trees from various crossings outside factorial design were used to surround the trial and were not taken into account in the assessment. Banana trees were planted inside the trial and were used as temporary shade. This partial shade gradually disappeared as the cocoa trees grew. After 13 years of production, in 2015, 88 of the 1260 trees had died. Family 1 with 8 live plants had the lowest number of live plants in the trial.

2.2. Data gathering

Data were gathered tree-by-tree from 2002 to 2015, i.e. over 13 years of production. A production year consisted of the main harvests (September to January) and the secondary harvests of the following year (April to July, often August). Each tree was identified by its family (cross) number, the female parent, the male parent and its coordinates (its row number and tree number in the row). The data gathered in the field for each tree were the number of healthy pods produced during the production year and the number of damaged, rotten, and other pods, i.e. not reaching maturity, the total weight of healthy pods produced and the trunk circumference 20 cm from the ground (except in year 1 when the diameter was measured rather than the circumference). In the study, a year T corresponded to the production year number, i.e. T + 2 years after the trial was set up.

The variables used in the analyses were:

1) The trunk diameter (Diam), expressed in cm, was not available for production years 2, 9 and 10.
2) The growth was defined as the variation in diameter between two years. When the diameter was not available for the previous year, an average growth was calculated from the diameter of the last year available.
3) For each tree, the total number of pods (healthy, damaged, rotten, other) produced over the production year was calculated (Pod number). Podnumber (T, i) = healthy (T, i) + damaged (T, i) + rotten (T, i) + other (T, i) ; (T) between 1 and 13 represents the production year; (i) represents the tree.
4) For each tree, the number of pods produced since the first production year in 2002 was calculated (CumP). The cumulative data were only taken into account in the analysis from the third harvesting year onwards.
5) The average weight of a healthy pod (PWeight), expressed in kg, was determined from the ratio between the total weight of healthy pods produced and the number of healthy pods per production year. Pod weight was measured from the 6th to the 13th production year.

2.3. Statistical models

We fitted separate multi-trait models for each year using the available trait measurements for the corresponding year. A multi-trait model, although more complex, was chosen to reflect the multivariate focus of the selection program. Since the effects of competition were expected to change over time, terms of

interaction between genetics, competition and the effect of time would be required, making the model very complex. We therefore chose a single-year based on Cappa et al. (2015), but extended the model to multi-trait cases.

Let T be the number of measured traits and $y = (y_1', ..., y_T')'$ be the stacked vector of measurements of traits 1, ..., T for a given year. The model had a standard mixed-effects structure of the form $y = X\beta + Z_s u_s + Z_d u_d + Z_c u_c + \varepsilon$, where β is a vector of fixed effects with design matrix X, u_s, u_d and u_c are vectors of random effects accounting for the spatial, the additive-genetic direct and the additive-genetic competition (also known as *indirect*) effects respectively with corresponding incidence matrices Z_s, Z_d and Z_c, and ε is a vector of independent Gaussian residuals with variance σ_e^2.

Specifically, $\beta = (\mu_1, ..., \mu_T)$ contains the trait-specific *intercept* values, or trait means, and $\mathbf{X} = \oplus_{i=1}^{T} \mathbf{1}$, where $\mathbf{1}$ is a column vector of 1 s and $\oplus$ is the matrix direct sum, defined as the block matrix $A \oplus B = \begin{pmatrix} A & 0 \\ 0 & B \end{pmatrix}$ for any arbitrary matrices A and B, where $\mathbf{0}$ represents a zero-matrix.

The vector of spatial effects is structured by trait as $u_s = (s_1', ..., s_T')'$. The spatial effects s_t for trait t are modelled as individual-level bi-dimensional first-order auto-regressive processes. Their common covariance structure is given by the Kronecker product of first-order auto-regressive processes in the rows and the columns with trait-specific spatial variance parameters σ_{st}^2. Specifically, the full covariance matrix of the spatial random effect u_s is given by

$$\Sigma_g = S \otimes AR_1(\rho_r) \otimes AR_1(\rho_c)$$

Where $\mathbf{S} = \begin{pmatrix} \sigma_{S_1}^2 & \cdots & \sigma_{S_1 T} \\ \cdots & \cdots & \cdots \\ \sigma_{S_1 T} & \cdots & \sigma_{S_T}^2 \end{pmatrix}$ is the matrix of spatial variances and covariances, and $AR_1(\rho)$ is a matrix with entries $\frac{1}{1-\rho^2}\rho^{|1-j|}$. Note that the individual random effects are both spatially auto-correlated thanks to the auto-regressive structure, but also correlated across traits due to the matrix of covariance parameters $\mathbf{S}$.

The auto-correlation parameters for rows and columns ρ_r and ρ_c were fixed at 0.8 and 0.6, respectively for all traits. These values were selected from a grid of candidate values by minimizing the Average Information Criterion (AIC) (Akaike, 1973) in a preliminary evaluation (not shown).

The direct and competition genetic effects are also structured by trait as

$(u_d = (d_1', ..., d_T')'$ and $u_c = (c_1', ..., c_T')')$. They are jointly modelled as zero-mean Gaussian distribution with covariance $\Sigma_g = G \otimes A$, where

$$\mathbf{G} = \begin{pmatrix} [\sigma_{d_i d_j}] & [\sigma_{d_i c_j}] \\ [\sigma_{c_i d_j}] & [\sigma_{c_i c_j}] \end{pmatrix}$$

Defined as a block-matrix where entries in row i and column j of the corresponding block are the variances of the direct and competition breeding values in the diagonal $\sigma_{d_i d_i}$ and $\sigma_{c_i c_i}$, the cross-trait covariances of the direct and competition effect $\sigma_{d_i d_j}$ and $\sigma_{c_i c_j}$, the within-trait direct competition covariances $\sigma_{d_i c_i}$ and the cross-trait direct competition covariance $\sigma_{d_i c_j}$ for trait i and j. Matrix $\mathbf{A}$ is the average numerator relationship matrix (Henderson, 1984), which accounts for genetic kinship.

The incidence matrices $\mathbf{Z_g}$ and $\mathbf{Z_d}$ are binary matrices with exactly one entry of 1 in each row that relates the individual observations with the corresponding random effect. This reduces to an identity matrix when the observations are properly sorted and there are no effects for non-observed individuals (e.g. missing or dead trees for the spatial effects or parent trees for the genetic effects). In general, they are square permutation matrices with some additional zero-columns at the positions of the random effects corresponding to non-observed individuals.

The incidence matrix $\mathbf{Z_c}$ brings into effect the hypotheses of the competition model. According to this hypothesis, an individual's com-

has all entries equal to zero except in the positions $\partial_i = j_1, \cdots\cdots j_{mi}$ corresponding to the m_i neighbours of the individual i, with values $f_{ij} > 0$, $j \varepsilon \partial_i$. These positive coefficients can be interpreted as the intensity of competition that each neighbour exerts over the phenotype of tree I, and were computed as

$$\mathbf{f_{ij}} = \frac{C_i}{d_{ij}^\alpha}, j \varepsilon \partial_i$$

Where α is the decay parameter that is fixed at 1 and $C_i = 1/\sum_{j\varepsilon\partial_i} 1/d_{ij}^{2\alpha}$ is a normalizing and variance-stabilising constant (Cappa and Cantet, 2008). Indeed, for a given trait, the effect of the competition over a focal tree i is the weighted average of its neighbouring breeding values.

$$\omega_i = \sum_{j\varepsilon\partial_i} \mathbf{f_{ij}} c_j$$

Where variance $\mathbf{Var}(\omega_i) = \sigma_c^2$, since $\sum_{j\varepsilon\partial_i} \mathbf{f}_{ij}^2 = \mathbf{1}$.

These models were implemented with the R-software breedR package (Munoz and Sanchez, 2018) and fitted in the R platform for statistical computing (R Core Team, 2019). The average genetic effects and competition for each family were calculated and plotted for annual production in years six and thirteen. The graphs were produced using the R-software ggplot2 package (Wickham, 2016).

3. Results

3.1. Growth and production dynamics

The trunk diameter increased rapidly at the outset (average trunk diameter growth of 2.7 cm per year from year 3), then diameter growth slowed in year 5, becoming even lower from year 7 onwards (Fig. 1A).

Over the 13 years, a cacao tree produced an average of 327 pods with individual variations between 1 and 1163 pods. Two production phases were seen over that cumulative period, the first with a steep slope up to year 6, then a second with a slightly gentler slope from years 7–13. Annual pod production per tree fell abruptly by half after the peak in year 6 and decreased up to year 13, with a few inter-annual variations (a peak in year 9, with an average of 29 pods per tree, followed by a trough in year 10, with an average of 12 pods per tree). Production was highly variable depending on the tree, with individual variations between 0 and 49 pods in year 1, and between 0 and 170 pods in year 6. The coefficient of variation for annual pod production was over 100 % in the first two production years, and then varied between 62 and 94 % (Fig. 1B).

The average weight of a pod was quite stable, at around 0.47 kg, with a slight increase in year 11 (0.52 kg). However, variations between individuals were lower than for the pod number, with a coefficient of variation varying between 20 and 29 % depending on the production year. During the production peak in year 6, the average weight of a pod was 0.44 kg, with individual variations of between 0.16 kg and 0.97 kg (Fig. 1A).

3.2. Extent of the different effects (spatial and genetic competition) in the model

The results of the multi-trait models are shown in Fig. 2. The total variance of the data was split between the variance explained by the direct genetic effect, the competition effect, the spatial effect, and the residuals.

The model only explained a small proportion of the trunk diameter growth variability observed. After the residuals effect, the largest effects were either the genetic effect or the spatial effect depending on the production year. The competition effect was the least important one in the model for this trait (between 1 and 5% of total variance). The model effectively explained the variability of the trunk diameter (over 70 % of total variability from year 5 onwards). The greatest effect in the model was the genetic effect. The spatial effect was very weak and the competition effect, although weak, appeared to rise over the production years, explaining from 5.5–6.5% of total variability from year 5 onwards.
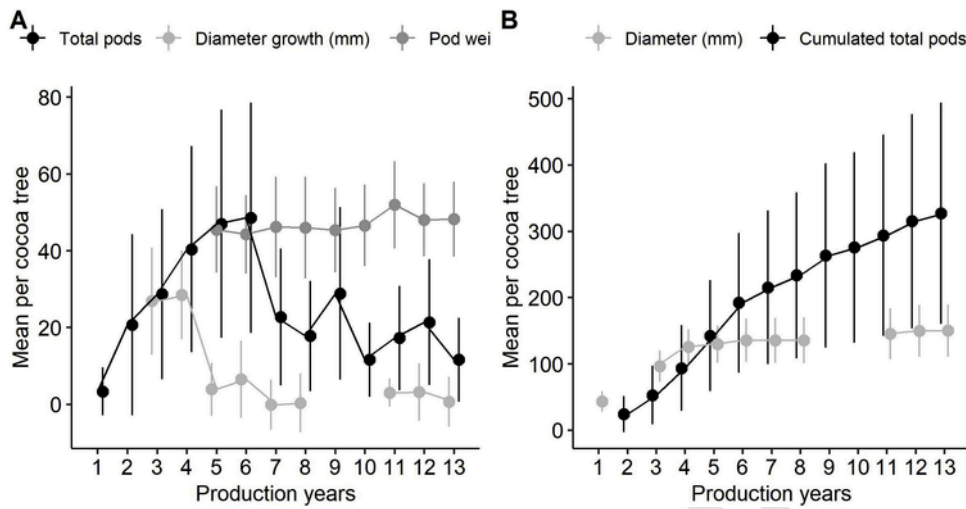
Fig. 1. Dynamics of the annual averages for the five studied variables on a minimum of 1172 cocoa trees. The dots represent the mean, the vertical bar, the standard deviation.(A) Average per tree of the total number of pods produced per year, annual diameter growth (unit, mm) and mean weight of one healthy pod (unit, g),(B) Diameter of cacao tree 20 cm from the ground (unit, mm), cumulative total pods per cacao tree.
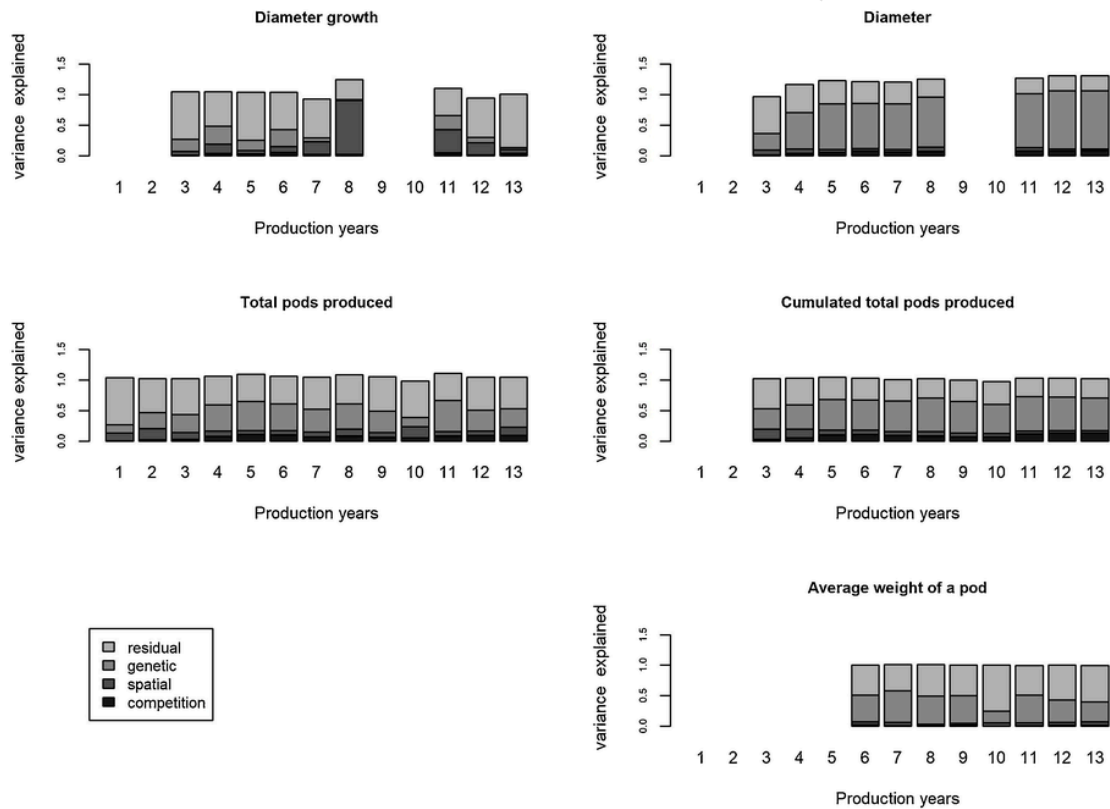

Fig. 2. Variance explained by the main effects of the separate multi-trait models for each year (genetic, spatial and competition) and residuals during the 13 years for the five variables studied.

The model explained between 40 and 60 % of the total variance of the annual production depending on the year, except for the first year, where it only explained 25 % (Fig. 2). The direct genetic effect was globally the greatest effect, even though it was weaker in some years (notably years 1 and 10). The spatial effect was strong in the first three years, as well as in year 10. As of year 3, a competition effect appeared. It accounted for between 5 and 10 % of total variance, i.e. 12–18% of the variance explained by the model. Competition became important in the 4th year. It reached highest level in the years 5 and 6, years of highest production. It fell in year 10, the year when the spatial effect was greatest. Cumulative production was explained better by the model, and the genetic effect was greater and more stable, which is expected for a cumula-

tive trait. However, as for annual production, a greater spatial effect was found in the first two years. It was not so strong in the following years. A competition effect appeared as early as the third year.

The model explained around 50 % of the total variance of the average weight of a pod, except in year 10. Only the genetic effect was strong. The spatial and competition effects were very weak.

3.3. Correlations of the genetic and competition effects

- Correlation between the genetic effect and competition effect of a variable

A negative correlation between the genetic effect and competition effect of a variable indicated that a tree of high genetic value for that variable negatively affected the same variable in neighbouring trees, irrespective of their own genetic value.

As early as the third year of measurement, a cacao tree with strong growth negatively impacted the growth of its neighbours (Fig. 3). That correlation became less strong and non-significant from the seventh year onwards, corresponding to the years in which trunk growth became very low. The correlation between the genetic effect and competition effect for trunk diameter was highly negative (< -0.7) throughout the period of study. A tree with a large diameter negatively impacted the diameter of its neighbours throughout the 13 years of measurement.

In the first two years of measurement, a cacao tree with a high yield did not impact the yield of its neighbours (correlation approaching 0). In the third year, a slight negative impact appeared (negative correlation of 0.5). From the fourth year onwards, the impact of high-yielding trees on the yield of their neighbours became highly negative (negative correlation of more than 0.7) and remained

substantial, except in years 10 and 13. For cumulative production, the effect observed for production in correlation lagged one year behind. The correlation between the genetic effect and competition effect became substantial as of year 5, and remained strong onwards.

For the average weight of a pod, the correlation between the genetic effect and competition effect was generally very weak (Fig. 3). There was therefore no relation between the average weight of the pods of a tree and that of the neighbouring trees.

• Correlation between the genetic effects of two variables

A positive correlation between the genetic effects of two variables indicated that a tree with a high genetic value for a variable also had a high genetic value for the other variable.

The genetic effect on trunk diameter was highly positively correlated with the genetic effect on annual production and a little less so for cumulative production (Fig. 4). In particular, a cacao tree with a larger diameter than the average tended also to produce more pods than average.
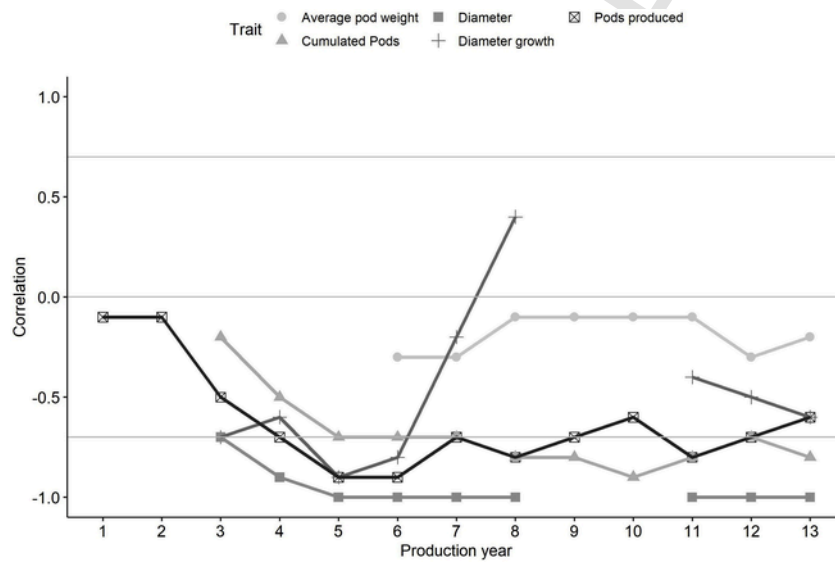

Fig. 3. Correlation between the individual genetic and competition values per variable (trait). These values were derived from the multivariate models by years. The threshold of 0.7 (grey lines) is represented only as a simple classification device for visual identification of the set of highest correlated effects.
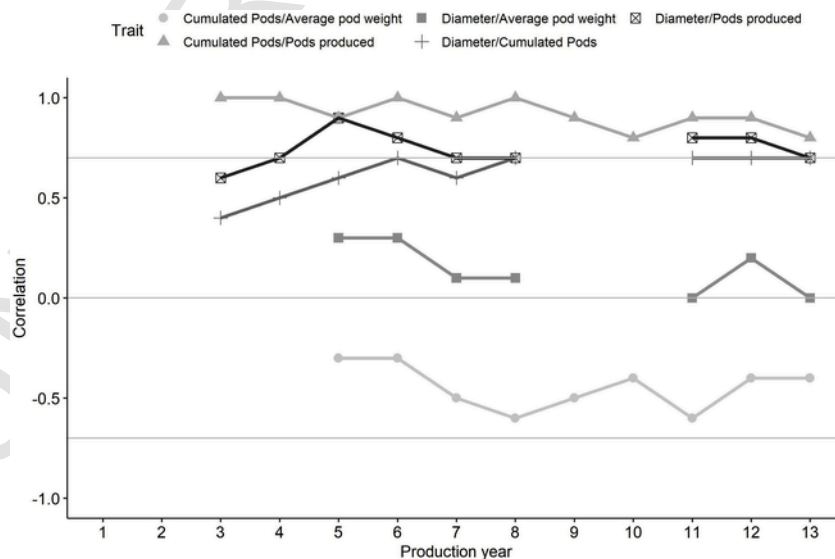

Fig. 4. Correlation between the individual genetic values of two variables (traits). These values were derived from the multivariate models by years. The threshold of 0.7 (grey lines) is represented only as a simple classification device for visual identification of the set of highest correlated effects.

The correlation between the genetic effect for the current year's production and the cumulative production was strong and positive. A cocoa tree that had high yields in previous years had also high yields in the current year. The correlation between the genetic effect for cumulative production and the average weight of a pod was always negative but was only below -0.5 in years 7, 8, 9 and 11. The trees producing the most pods therefore tended, after year 6 when production decreased, to produce lighter pods. There is no correlation between the diameter of the tree and the pod weight.

- Correlation between the genetic effect of one variable and the competition effect of another variable

A negative correlation between the genetic effect of one variable and the competition effect of another variable indicated that a tree with a high genetic value for one variable negatively impacted the other variable in the neighbouring trees, irrespective of their own genetic value.

The trees with a large diameter, which were also the ones with high production, negatively impacted the growth of their neighbours, right from the third year of measurement and up to the sixth year (Fig. 5). The trees with a large diameter and strong growth negatively impacted the annual and cumulative production of their neighbours right from the fourth year. Their impact on the av-

erage weight of a pod of their neighbours was also negative, but less so. It was only substantial in years 6 and 8.

The genetic effect for annual production was negatively correlated with the competition effects of the other variables, except for the average weight of a pod. This indicated that a tree with high production from year 4 onwards particularly impacted the growth of its neighbours, but not the weight of their pods. The genetic effect for cumulative production was negatively correlated with the competition effect for the trunk diameter from year 4 onwards, and strongly so from year 5. It was also negatively correlated, but less so, in years 8 and 9 with the genetic effect of competition on the average weight of a pod. This indicated that a high-yielding tree negatively impacted the diameter of its neighbours, but also to a lesser degree in some years, the weight of their pods.

- Correlation between the competition effects of two variables

A positive correlation between the competition effects of two variables indicated that a tree negatively impacting its neighbours for one variable will also impact its neighbours negatively for the other variable, irrespective of their own genetic value.

A tree impacting the annual production of its neighbours for the current year also impacted, in the same way (correlation > 0.7), their cumulative pro-
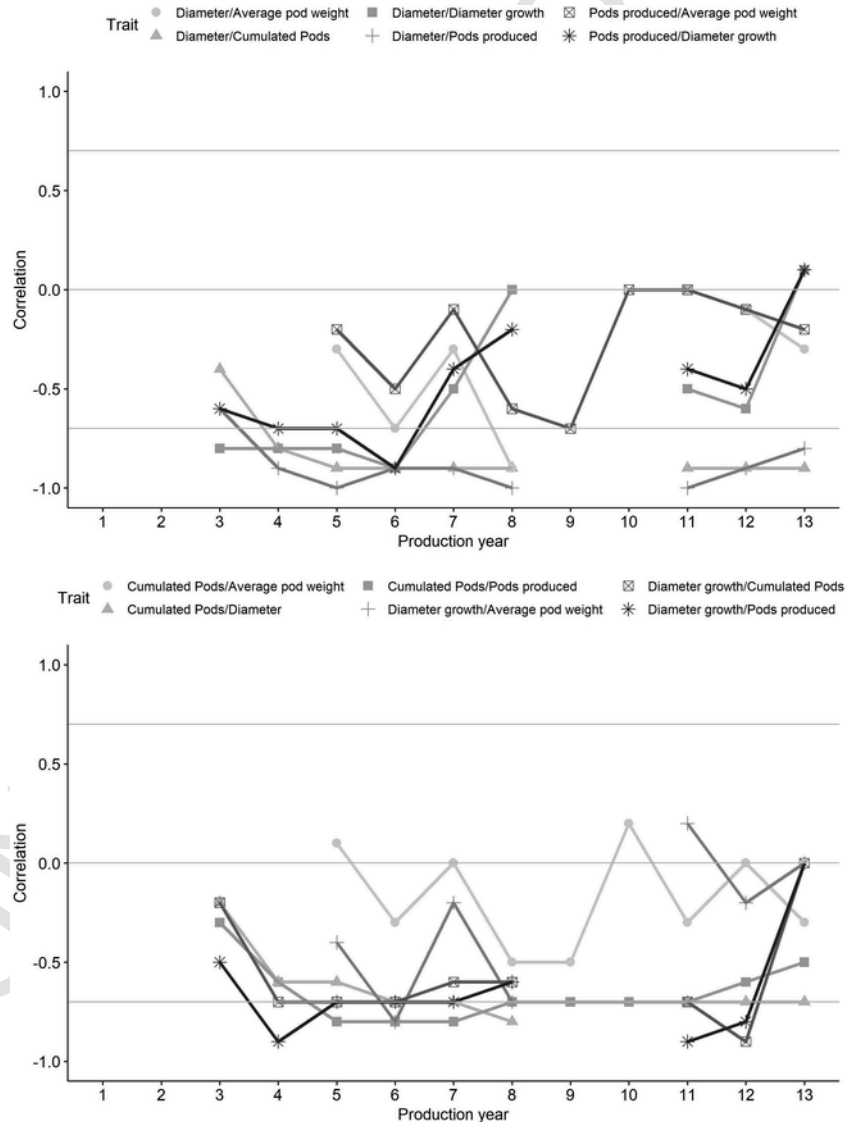

Fig. 5. Correlation between the individual genetic and competition values for two different variables (traits). These values were derived from the multivariate models by years. The threshold of 0.7 (grey lines) is represented only as a simple classification device for visual identification of the set of highest correlated effects.

duction and their diameter (Fig. 6), i.e. their growth and production, right from the beginning of the study.

A tree impacting the average weight of a pod of its neighbours also impacted their growth in years 5, 6 and 7 (correlation > 0.7), and their yields in the same way up to year 9, more or less strongly depending on the years (strongly in 6, 8 and 9).

- Classification of families according to their genetic and competition characteristics for production

The 78 families (75 selected families and 3 controls) were distributed according to their average genetic and competition effects for production in year 6 and the cumulative yield over 13 years (Fig. 7). There were few high-yielders. The strong antagonistic correlation between competition and direct effects determined that the producers with a strong direct effect were also highly competitive. Nevertheless, four families of high-yielding cacao trees could be considered as moderately competitive, with competition effects closer to zero. Of those four families, two had the same female parent (parent 26). They were families 30_51 (E4/1-16 x BL9/2), 26_63 (E4/1-15 x C2/1-3), 27_57 (E4/3-2 x IFC705) and 26_60 (E4/1-15 x E4/1-6). Among the families with high production, there is also some room to select less vigorous candidates without generally affecting production (Fig. 8A and B).

4. Discussion

4.1. Variation in competition over time

Two phases were found for competition expression (Fig. 1). The first phase extended from the first year to year 4, when the effect of competition was weak (Fig. 2). Over that period, the diameter, diameter growth and production increased rapidly. There did not appear any significant competition effect on any of these three traits. From the fourth year, a second phase began, marked by a slowdown in diameter growth, while production growth remained the same until it peaked two years later. The slowdown in diameter growth coincided with the time when competition between the cacao trees became important for both production and diameter (Fig. 2). This staggering of the growth rate trend and the production peak was in line with the observations of Glendinning (1966, 1960). There are several possible explanations for this phenomenon. Under the conditions of our study one hypothesis could be that, as the previous plant cover in the plot was a cacao seed garden, the soil may have been impoverished for certain nutrients needed by the cacao trees. Another nonexclusive explanation could be a competition for water related to longer dry periods due to climate change over the studied period. Those deficiencies would have heightened strong and early root competition (Casper and Jackson, 1997; Schenk,
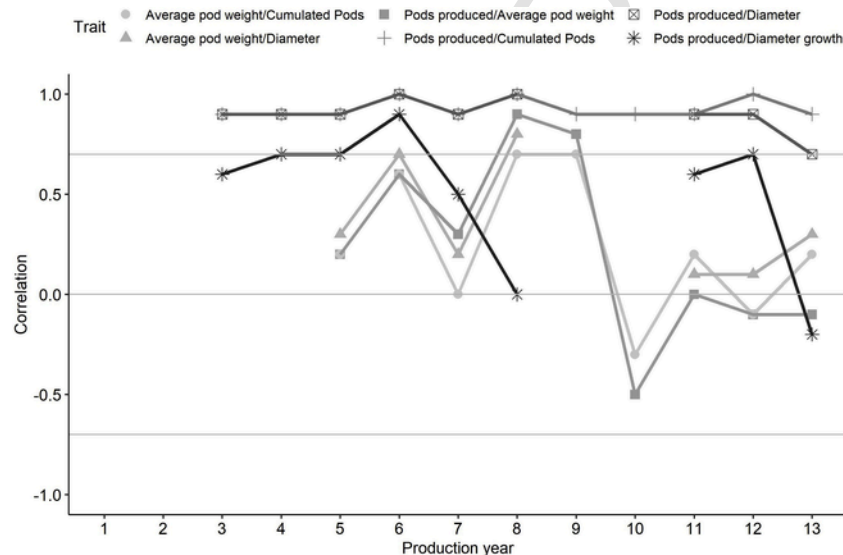

Fig. 6. Correlation between the individual competition values for two different variables (traits). These values were derived from the multivariate models by years. The threshold of 0.7 (grey lines) is represented only as a simple classification device for visual identification of the set of highest correlated effects.
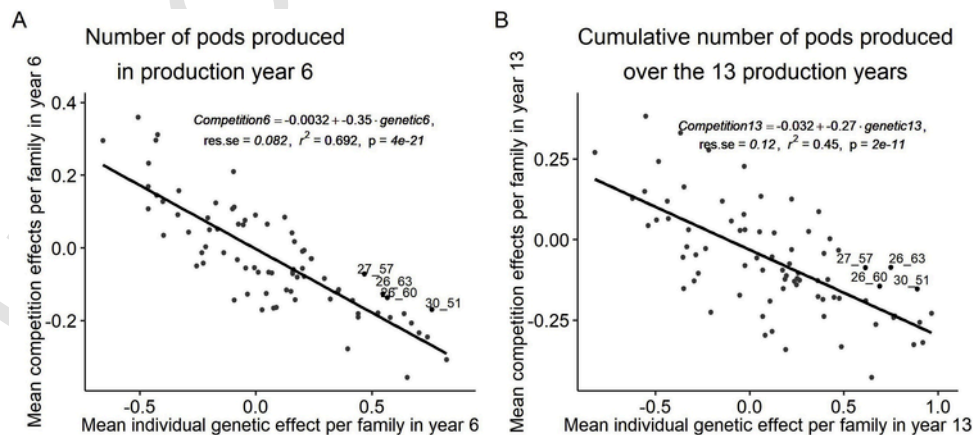

Fig. 7. Relationship between mean genetic and competition effects per family for the number of pods produced in year 6 (A) and for the cumulative number of pods produced in year 13 (B). Families are indicated by points, linear regression by a line. The names of the four families that were high-yielding and less competitive than the other families in year 6 are displayed (A). The same families are plotted in year 13 (B). For each regression, statistics are given (parameters, residual standard error res.se, R-squared, probability of F-statistic p).
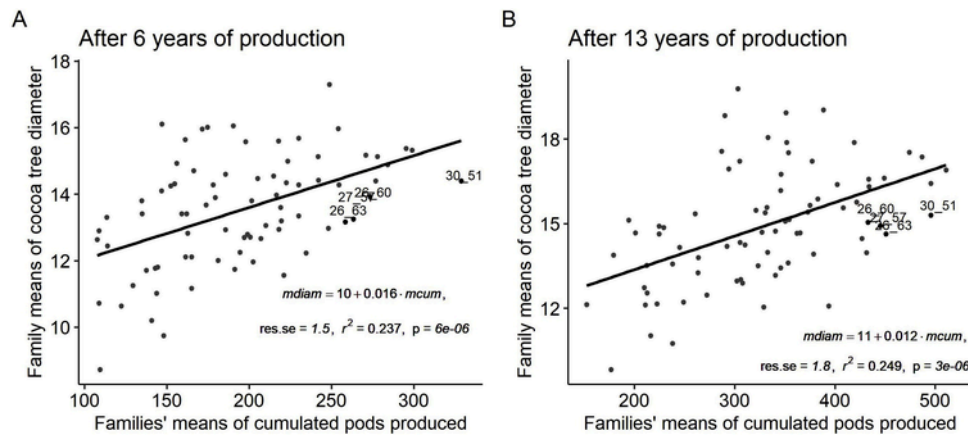
Fig. 8. Observed relationship between the number of pods produced and the average diameter of the cacao tree per family in year 6 (A) and year 13 (B). Families are indicated by points, linear regression by a line. The names of the four families that were high-yielding and less competitive than the other families, identified in Fig. 7 (A), are displayed. For each regression, statistics are given (parameters, residual standard error res.se, R-squared, probability of F-statistic p).

2006), hence the importance of the spatial effect in the early years (Fig. 2). Despite of that, the impact of this potential nutrient scarcity on the main physiological requirements, namely vegetative growth measured here by the change in diameter, and generative growth (production), was not detectable up to year 4. Between years 4 and 6, the drop in nutrient resources could have led to within-tree competition, followed by a mobilization of the available resources for pod production to the detriment of tree growth, which slowed down. This kind of situations could be reflected by trade-offs between the replacing lost biomass (roots, pods and leaves) and developing the organs of the plant (Zuidema et al., 2005). Also, canopies increase in size and join up, with the subsequent competition for light (Gao et al., 2013; Yapp and Hadley, 1991). Over time, that competition for light could also play a role in the increase of differences between trees for biomass production. That difference, in a high-density context, could increase competition between trees. If competition for light was the key factor, one would have expected a steady increase in competition with time and tree growth. But in our case, the competition stagnates rapidly, showing that competition for light is not the only factor. The 2 out of 4 row thinning method recommended by Lachenaud and Oliver (1998) and Lachenaud and Montagnon (2002) could make it possible to reduce the effect of light-related competition and thus restore the plot's productive potential.

When nutrient resources in the soil decrease, production falls. Virtually all the resources of plants are assigned to its maintenance. This drop in production around 10 years has also been shown by several authors such as Ryan et al. 2009, Owusu, 1980 and Ahenkorah et al. (1974). In this case, fertilizer is recommended to reduce the disparities in plot fertility and consequently minimize competition for resources between trees. This fertilizer application according to Snoek et al. (2016) should take into account the nutrient levels in the soil to correct it but also focus on the nutrients used for growth and pod production.

The competition within and between trees therefore occurred gradually. It was amplified over time as demand for resources increased, leading to an increase in antagonistic interactions between neighbouring plants.

4.2. Degree of competition

After the onset of competition between trees, its level remained stable for the diameter (between 5.5 and 6.5 % of total variability) and for cumulative production (Fig. 2). Some of that stability was probably due to the smoothing effect of cumulation. However, for its part, the competition effect on production remained variable. Competition could substantially affect annual production, up to 10 % of variability, i.e. almost a quarter of the variability explained by genetics (Fig. 2). Depending on the year, the model explained a more or less large share of variability (Fig. 2). Climate change in Côte d'Ivoire has led to more frequent and longer drought periods (Brou et al., 2005; Ehounou et al., 2019; Kassin et al., 2008). This climatic variability between years may explain

the variations of the model. Overall, competition explained a smaller share of the model, but its relative share compared to genetics remained high (between 16 and 33 %). Consequently, between-tree competition phenomena cannot be overlooked.

The competitive value of a tree was negatively correlated with its genetic value, be it for growth or production, which were two highly genetically correlated traits (Fig. 3). Vigorous and productive trees were therefore strongly competitive and altered the vigour and production of their neighbours. Conversely, trees with low vigour and production were not competitive. No families of high-yielders were found that were less competitive than the others (Fig. 7). These families were stable over time and corresponded to families with a rather strong production to vigour relation (Fig. 8). This seemed to back the use of the "production to vigour" indicator as a selection criterion by certain breeders to identify high-yielding and less vigorous trees (Paulin and Eskes, 1995). However, such selection is probably not optimum when considering the plot scale. Indeed, the production achieved, i.e. the production to be optimized, corresponds to the mean genetic production corrected by the competition effect, which can reach a quarter of that genetic production. The competition effect on production in a monoclonal plantation therefore needs to be taken into account to carry out optimum selection. Moreover, using the "production to vigour" ratio does not correct the negative influence of highly competitive trees over their neighbours, which might be prevented from expressing their potential right from the early years. One solution would be to carry out selection in monoclonal plots that incorporates the competition component in the genetic assessment, but this considerably increases the means required for trials. Another solution would be to use a selection model integrating "group selection". According to (Griffing, 1967), such selection scheme would integrate interaction components between conspecifics as well as the direct effects. Muir (2005) proposed an up to date formulation in the framework of mixed models. Following the evaluation model we used here, this would mean to combine direct and competition effects for the set of traits affected by competition in a similar way as for a classical index selection, in its base form or with weightings. In the study by Muir (2005), examples for caged animals involving long-term artificial selection are shown suggesting a substantial advantage for the index accounting for competition effects. Many other successful examples exist in animals (Wade et al., 2010). The principle is that eventual losses by selecting less than optimal producers would be compensated for by less unfavourably interacting trees in the plantation, giving overall a greater group performance (Wallace et al., 2018). Such schemes, however, are not being implemented in perennials yet, probably due to the fact of the relative novelty of competition models for these species. It is for plants, and notably for perennials, that competition is probably of greater importance than for livestock, given the lack of escape options for the former when it comes to circumvent adverse interactions.

4.3. Relation between growth and production

Our study of the correlations between the different effects (genetic, competition and spatial) explained by the model confirmed that the production of a tree was strongly and positively linked to its trunk diameter throughout the production period (Fig. 3). The trees that were most vigorous right from the early years were the ones with the highest cumulative production over the 13 years.

However, there was within-tree competition between the cumulative production of a tree and the average weight of its pods from year 7, a year where production declined (Figs. 1 and 4). These trade-offs taking place on a tree scale were linked to interactions between individuals. The characteristics of the neighbours of a tree determined its access to resources. A tree under limiting growth conditions due to its neighbours made trade-offs between growth and the number and weight of its pods. Whilst the average weight of a pod remained stable on a plot scale, the differentiation between low- and high-yielding trees, associated with the drop in production, might confirm the hypothesis of resource exhaustion. According to (Niklas and Enquist, 2002; Zuidema et al., 2005), the energy produced by a plant is first used to maintain it. Then, the first energy reserves (carbohydrates) are assigned to the replacement of lost organs, such as leaves and harvested fruits, and for root renewal. Lastly, the second set of reserves is assigned to organ growth. The drop in production and loss of fruit weight a year after full production might be explained by exhaustion of the carbohydrate reserves needed for organ replacement and growth.

The effects of competition on production and growth were found to be highly correlated, as were the genetic effects. It was the same trees that competed with their neighbours in terms of diameter and production. On the other hand, competition between trees did not appear to change the average pod weight, which was more affected by within-tree competition (Figs. 3 and 5).

5. Conclusion

We showed that competition between trees occurs right from the early years in cacao plantations and its effects quickly become substantial under the conditions in Côte d'Ivoire. Such competition is probably linked to soil exhaustion or to water shortage, so fertilization or irrigation is recommended to reduce production losses in plots.

The degree of competition confirms the urgent need to take it into account in breeding programmes, especially in randomized trials. It seems impossible to select trees with high yields but low competitiveness, but it is possible to find trees that are a little less competitive than other high-yielders. Models integrating a competition effect make it possible to approach analytically the production achieved. The development of "Group Selection" would need to be developed to improve overall selection efficiency.

Changes in competition over time justify research to optimize selection criteria and selection periods, in order to select individuals with low competitiveness. Pre-selection in the first five years after planting, then again just before the drop in yields, i.e. in the eighth year, could be considered. Identifying molecular markers associated with less competitive types of trees could help to identify those that are highly competitive right from the nursery stage, to enable better management of planting densities.

CRediT authorship contribution statement

Caudou Inago Trebissou: Investigation, Conceptualization, Writing - original draft, Writing - review & editing. **Mathias Gnion Tahi:** Investigation, Resources, Writing - review & editing. **Facundo Munoz:** Methodology, Formal analysis, Writing - review & editing. **Leopoldo Sanchez:** Methodology, Writing - review & editing. **Simon-Pierre Assanvo N'Guetta:** Writing - review & editing. **Christian Cilas:** Conceptualization, Writing - original draft, Writing - review & editing. **Fabienne Ribeyre:** Visualization, Conceptualization, Formal analysis, Writing - review & editing.

Declaration of Competing Interest

The authors report no declarations of interest.

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