



Effect of neighbouring perennials on cocoa tree pod production in complex agroforestry systems in Cameroon

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ABSTRACT

Agroforestry systems (AFS) are gaining major interest in cocoa producing countries. However, the analysis of competition effects in multispecific complex agricultural systems remains a key lock-in preventing both (i) a thorough understanding of resource partitioning, and (ii) the co-design of spatial patterns and management of cocoa AFS (cAFS) minimising competition. We sampled 48 cAFS 1000 m² plots in Central Cameroon and used an individual based approach to analyse the effect neighbouring tree community composition had on cocoa tree pod production. First, we determined the distance up to which each neighbouring tree influenced the production of a given cocoa tree and checked for the significance and the magnitude of this effect. We then explored the trade-offs between cocoa tree production and the abundance of associated trees. Our results first underline a significant intra-specific competition within the cocoa tree populations studied, which would need to be thinned down to 800–1100 individuals per ha. We also found a general negative effect of associated trees kept or grown for their fruits (e.g. mango, traditional species, citrus trees). Those effects were stronger when the trees were positioned between 6 and 11 m away from the cocoa trees. These trees clearly impaired pod production, especially for small diameter cocoa trees. Palm trees, however, had a positive effect on cocoa pod production, with suitable densities modelled ranging from 0 to 240 individuals per ha. Finally, we found both positive and negative effects of associated forest trees on cocoa pod production, which varied with the distance separating them from the cocoa trees and the size of the cocoa trees. Overall, our analyses show that cocoa production in complex cAFS is influenced both by intra- and inter-specific interactions while it remains difficult to distinguish between potential intertwined effects and resource limitations.

1. Introduction

Cocoa trees (*Theobroma cacao* L.) are a shade-tolerant species originating from the forests of the Amazonian basin. Today cocoa farming covers approximately 11 million hectares in the humid tropics. The Ivory Coast and Ghana are currently the main producers of cocoa beans; they produce approximately 60 % of the 5.5 million tons of beans marketed in 2020 (FAOSTAT, 2022). A large share of cocoa trees are cultivated in agroforestry systems (AFS) that support many ecosystem services and fulfil an array of local needs (Clough et al., 2009; Mortimer et al., 2018). While these multifunctional systems subsist only marginally in the two main producing countries (Asare et al., 2014; Gockowski

and Sonwa, 2011), they still prevail in Nigeria and Cameroon which together account for approximately 10 % of global production (Degrande et al., 2006; FAOSTAT, 2022; Jagoret et al., 2011; Laird et al., 2007; Oke and Odebiyi, 2007). Today, such cocoa agroforestry systems (cAFS) provide useful knowledge for the agroecological transition of cocoa farming in West Africa and other regions where monoculture prevails (Jagoret et al., 2019).

Yet, the functioning of complex cAFS is still difficult to grasp, in particular because of the numerous interactions that are at stake for the sharing of resources - both at the aboveground (e.g. radiation balance) and belowground levels (e.g. water, nutrients). However, since a couple of decades, a rising number of studies have shown that it is possible to

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explore complex cAFS functioning to help develop new and multifunctional biodiversity-based cocoa systems. In Cameroon for example, it has been demonstrated that cocoa yields can reach fairly high levels, which could be related to their aboveground structure (e.g. tree density, basal area, height) as well as to the functional groups of their associated tree community (e.g. succession guild, leaf life span) (Jagoret et al., 2017; Saj et al., 2017a). Indeed, even though the associated tree community creates competition with cocoa trees, it contributes concomitantly to the building of environmental conditions that sustain decades-long cultivation (Saj et al., 2017b). Such a result is obtained notably through the positive contribution of the associated tree community to nutrient/litter cycling, soil quality maintenance and the development of a specific microclimate (Nijmeijer et al., 2019; Saj et al., 2021). Although these examples shed new light on the functioning of cocoa stands in complex cAFS, there are still many interactions between associated tree communities and cocoa stands left to understand, notably with regard to trade-offs between ecosystem services (e.g. Andreotti et al., 2018) as well as to tree densities and spacing patterns. Besides, these issues need to be promptly addressed in the context of climate change (Lahive et al., 2019).

Few studies have investigated cocoa tree intra-specific competition to date. Most scientific publications on this topic are over 30 years old – except Salazar-Díaz and Tixier (2021) and Tosto et al. (2022) – and were achieved in pure stands and in the “optimal/experimental conditions” of that time, e.g. Armstrong (1979) or Mooleedhar and Lauckner (1990). Their conclusions cannot be transferred to complex cAFS, which are inherently managed very differently by farmers, be this in terms of cocoa tree stand densities or associated tree community densities and species. More recently, the design and tree density of bi-specific associations (cocoa associated with one species such as rubber, kola, citrus, avocado, coconut, etc.) were investigated with regard to their agronomic productivity and/or economic viability (Koko et al., 2013; Oladokun and Egbe, 1990; Osei-Bonsu et al., 2002; Snoeck et al., 2013). The results found for the investigated systems are unfortunately of little help to support the design of new cAFS containing more than two cultivated species or optimise existing ones, and in which inter-specific interactions to check for are inherently more numerous. To date, we have found only one study analysing the effects of different groups of associated trees on cocoa tree productivity (Notaro et al., 2021). This study was conducted in the Dominican Republic and it shows that some types of trees negatively affect cocoa production more likely than others.

While Saj et al. (2017b) and Jagoret et al. (2017) showed that cocoa yield can reach up to 750 kg ha⁻¹ year⁻¹ (or above) in Cameroonian cAFS on the very long-term, they also underlined the importance of the temporal evolution of cocoa and associated tree densities at the field scale. The characterisation of the spatial pattern within these systems may therefore provide a sufficient array of situations that could constitute the basis for an ad-hoc modelling. This is the hypothesis we tested in this study, which is based on the analysis of the production of cocoa trees from 48 farmer plots in Cameroon measured over three years. The studied plots cover the diversity of cAFS of the region especially in terms of trees associated to cocoa and the age of the fields. We used an individual based approach to analyse the effect of neighbouring tree composition on cocoa trees. Our analysis aimed at determining i) the distance up to which each species of tree influences the production of a given cocoa tree, and ii) the significance and the magnitude of this effect. We then used our statistical model to investigate which tree compositions in the neighbourhood of cocoa trees are likely to maximise cocoa production and which associated tree density works best. Our goal was to shed light on the different levels of inter- and intra-specific tree competitions and their impacts on cocoa production in complex cAFS. We also wanted to provide operational knowledge on the way to undertake such an analysis and how its results could be practically applied.

2. Material and methods

2.1. Study sites and plot selection

We conducted the study in the Central Cameroon region, which is located between 2.1° and 5.8° N and 10.5–16.2° E, at 600–800 m a.s.l. The climate is hot and humid, with an average annual temperature of 25 °C (Santoir and Bopta, 1995). The precipitation regime is divided into two distinct wet and dry seasons, which durations increase from North to South (bimodal rainfall regime). Average total annual rainfall ranges between 1400 mm and 1800 mm. Local soils are ferrallitic, more or less desaturated. A vegetation gradient is also observed from North to South of this region, ranging from mosaics of forest galleries and herbaceous *Pennisetum purpureum* and *Imperata cylindrica* savannahs in the peri-forest zones in the North, to vegetation dominated by dense evergreen forest in forest zones in the South (Santoir and Bopta, 1995).

In 2007, we set up a network of 48 complex cocoa agroforests (cAFS) - established after partial forest clearing - in three different districts of Central Cameroon: Bokito, Ngomedzap and Obala (Jagoret et al., 2018a). In Central Cameroon, cAFS established after partial clearing are well described (Jagoret et al., 2011, 2017). When the plot ages cocoa stands are usually on average younger than the plot per se as cocoa trees are regularly rejuvenated or replaced. Besides, these systems contain associated trees kept from forest clearing, which therefore are older (and sometimes much older) than the cocoa stands. During the establishment phase, farmers also usually plant trees, notably exogenous or indigenous fruit trees. Therefore, their age corresponds approximately to the age of the plot. Later on, farmers can proceed to the elimination and/or replacement of some associated trees, be these first kept from forest clearing or those planted during the installation phase (Jagoret et al., 2018b).

The selection was discussed with the farmers and each cAFS was visited before any decision was made. Three main criteria guided the selection of the 48 cAFS and, within them, the 1000 m² (approx. 31.6 m x 31.6 m) to be sampled. First we chose cAFS that weren't in an installation/juvenile phase (cocoa yield increase) or in a declining phase (cocoa yield decrease). We also chose cAFS that were continuously managed since their establishment. Finally, each selected 1000 m² showed a stable composition and structure (no change within the 3 years before sampling i.e. no rejuvenation of cocoa trees, no debarking or planting of associated trees) and no change in this composition and structure was forecasted for the next three years. In the end, the 48 selected plots were on average 37.5 years old (with standard deviation of ≈ 22.5 years).

2.2. Data collection and observed variables

2.2.1. Cocoa tree stands and associated tree communities sampling

Within each 1000 m² plot, we located (X,Y ground level trunk coordinates) and inventoried all cocoa trees. The basal area of each cocoa tree was calculated from the diameter of its trunk measured at 0.5 m from the ground. In the case of multiple trunks, the basal area of all trunks were summed to obtain cocoa tree total basal area. The basal area reflects the vegetative vigour of the cocoa tree and appears closely linked to its productivity, particularly in experimental conditions (Lachenaud and Mossu, 1985) but also at the field level in cAFS (Saj et al., 2017b). The productivity of each cocoa tree was estimated by pod counts carried out over three years (2007–2008–2009) with three passages per year in June/July, August/September, and October/November. This frequency enabled us to account

for the gradual emergence of pods after the onset of the rainy season, while also taking into account the gap between the southern (forest zones) and northern (forest-savannah transition zone) parts of Central Cameroon (Jagoret et al., 2017). Since pods less than 10 cm long are susceptible to physiological wilt (Wood and Lass, 2001), only pods with a length > 10 cm were counted. Finally, we considered the total cocoa

tree productivity by summing the nine pod counts undertaken over three years in order to reduce inter-annual variations.

We located (X,Y ground level trunk coordinates) and inventoried all associated trees with a diameter above 10 cm. Associated tree species identification was based on their vernacular names (languages: Yambassa in Bokito, Eton in Zima and Ewondo in Ngomedzap). Correspondences with their scientific and common names were established using Vivien and Faure (2012). Latin names of these species are available in the Supplementary Material S1.

2.2.2. Associated trees groups

Associated trees were classified into five groups based on their use by the farmers, their occurrence within the studied cAFS and on characteristics likely to induce contrasting levels of interactions for water, light and nutrients within the studied systems (Jagoret et al., 2014; Saj et al., 2017a; Sauvadet et al., 2020; Vivien and Faure, 2012). Their position in the plot and their vernacular names were the sole information collected on the ground. These groups were as follows (Table 1):

i) “Forest trees”. This group included species such as *Terminalia superba*, *Ceiba pentandra* and *Milicia excelsa* which are generally preserved by farmers from clearing during cAFS establishment. These tall and large individuals constitute the cAFS upper stratum, their foliage and root development can develop strong and large-scale interactions with understory trees, including cocoa.

ii) “Palms”. This group included all the individuals from the Arecaceae family. The most representative species studied within the cAFS is *Elaeis guineensis* (oil palm). Once fully developed, palms generally occupy the cAFS intermediate stratum. Their foliage is different to that of other individuals and can cause damage to lower strata trees when leaves are shed. They can develop dense root systems within the upper soil horizon, which make them putative strong competitors for soil resources with their closest neighbours.

iii) “Mango trees”. The species *Mangifera indica* was considered a group as a whole since it regularly occurs in the studied cAFS and presents specific characteristics. It generally occupies, like palms trees, the intermediate stratum of the studied cAFS. Yet, the large development of its dark and permanent foliage provides a very dense shade inducing putative strong competition for light towards the lower stratum, and consequently cocoa trees.

iv) “Traditional fruit trees”. This group includes exotic and endemic species such as *Persea americana*, *Dacryodes edulis* and *Cola nitida*. They also occupy the intermediate stratum of the studied cAFS but provide less dense shade than mango trees and take less overall “3D-space” than trees from the “forest group”. This group would therefore induce a fortiori interactions at an intermediate scale (in terms of space and level) with cocoa trees.

v) “Citrus trees”. This group comprises of all species from the citrus genus (eg. *Citrus sinensis*, *Citrus reticulata*, *Citrus limon*). Citrus trees generally occupy the same stratum as cocoa trees and present a similar vegetative development in the studied cAFS. This group would therefore induce a fortiori interactions at a low scale (in terms of space) with cocoa trees.

Table 1
Density (number per ha) and characteristics of trees by group across the 48 studied plots.

	Total count	Density per ha		Crown stratum	Shade type	Root foraging
		Mean (Std.dev.)				
(defined by observation and bibliography)						
Cocoa	6871	1431	(514)	Lower	Heavy	Shallow
Forest	631	139	(122)	Upper	Light	Deep and large
Mango	59	72	(52)	Intermediate	Heavy	Deep and large
Palm	179	37	(42)	Intermediate	Light	Shallow
Citrus	120	25	(50)	Lower	Heavy	Shallow
Traditional fruit	347	12	(18)	Intermediate	Intermediate	Unknown - diverse

2.3. Data analyses

2.3.1. Determination of the distance of influence of neighbouring trees on the production of each cocoa tree

We carried out an individual based analysis of the effect of tree composition in the neighbourhood of each cocoa tree. The analysis was conducted without any a priori on the distance of the effect of each tree group on cocoa production. We tested separately the effect of the density of the trees from each group at a given distance around each cocoa tree (i.e. the number of trees in a given radius around each cocoa tree) on their pod production (cumulated over 3 years). We used generalized linear mixed models (GLMM) with the number of pods of each cocoa tree as a response. The number of trees of a given group in a given radius and the basal area (root-squared-transformed) of each cocoa tree were used as predictors. In order to take into account the variability between sampled plots (village, soil, age of the field), we included plot identity as a random factor (Bolker et al., 2009). Since the response variable (total number of pods produced during three years) is a count variable, we used a “Poisson” link function that perfectly fitted the distribution of this variable. All GLMMs were built with the “glmer” function of the LME4 package (Bates et al., 2011). We explored how the radius in which the density of neighbouring trees around each cocoa tree altered the likelihood of the model (from 2 to 12 m with a step of 0.1 m). It was then possible to determine the radius (one or two optima) that exhibited the highest likelihood.

2.3.2. Construction of a complete model that predicts the production of each cocoa tree

The number of neighbouring trees within a radius of each cocoa tree (as defined corresponding to their distances of maximal effect, see §2.3.1) was then used together as a predictor in a complete model. The basal area of cocoa trees was also used as predictor and plot identity was a random factor. When more than one distance of maximal effect was observed for a given tree group (in our case there was a maximum of two peaks of likelihood), we considered the abundance of trees of this group between this distance and the next smaller distance of maximal effect (or zero if it is the smallest). We also included as predictors in the complete model the interaction between the abundance of each tree group and the basal area of cocoa trees. Then, we used a backward selection procedure to determine which predictors and interactions were significant in the complete model. The significance of each predictor was tested with a likelihood ratio test (LRT) and a Chi-squared test. Finally, the complete model with all significant predictors was used to predict individual cocoa tree pod production. The maximum likelihood of parameters of GLMMs was approximated by the Laplace method (Bolker et al., 2009). All statistical analyses were performed with R 4.0.4 (R Core Team, 2021) and with an alpha level of 0.05.

2.3.3. Exploration of the trade-off between cocoa tree production and abundance of associated trees

Finally, we used our model to predict the production of each cocoa tree from two different basal areas (differentiating small and large individuals 49 and 169 cm² respectively) for a wide range of combinations

of associated trees. In order to explore realistic associated trees patterns, we tested the existing combinations from our data set and these combinations in which we removed 1, 2 or 3 trees, from each given group of associated trees. We fixed the density of cocoa at 953 trees per ha to represent a realistic mature cocoa plot. We converted the number of trees in each radius determined in the previous step in density of trees per hectare (using the non-trivial procedure presented in [Supplementary Material S2](#)). We then selected the combinations that exhibited the best production (above 40 and 120 pods for small and large cocoa trees, respectively) while maintaining a minimal density of associated trees (we chose 250 associated trees per ha since it is just above the mean density of 230 in observed situations, eg. [Jagoret et al., 2018b](#)).

3. Results

As a whole, the 48 plots studied (corresponding to 4.8 ha) included 6871 cocoa trees and 1336 associated trees from at least 76 species ([Supplementary Material S1](#)). The average density of cocoa trees was 1431 ha^{-1} (see [Table 1](#) for details on all densities). Forest trees were the most abundant after cocoa trees. The spatial structure of the studied plots was particularly contrasted between those where few trees are associated with cocoa trees (e.g. plots 22 or 43, see [Supplementary Material S3](#)) and those with a complex structure where the density of associated trees is high (e.g. plots 11 and 16). A contrast was also observed between plots with a low diversity of species associated with cocoa trees (e.g. plot 19 where only mango and fruit trees are present) and those where the number of species is higher (e.g. plot 18 where

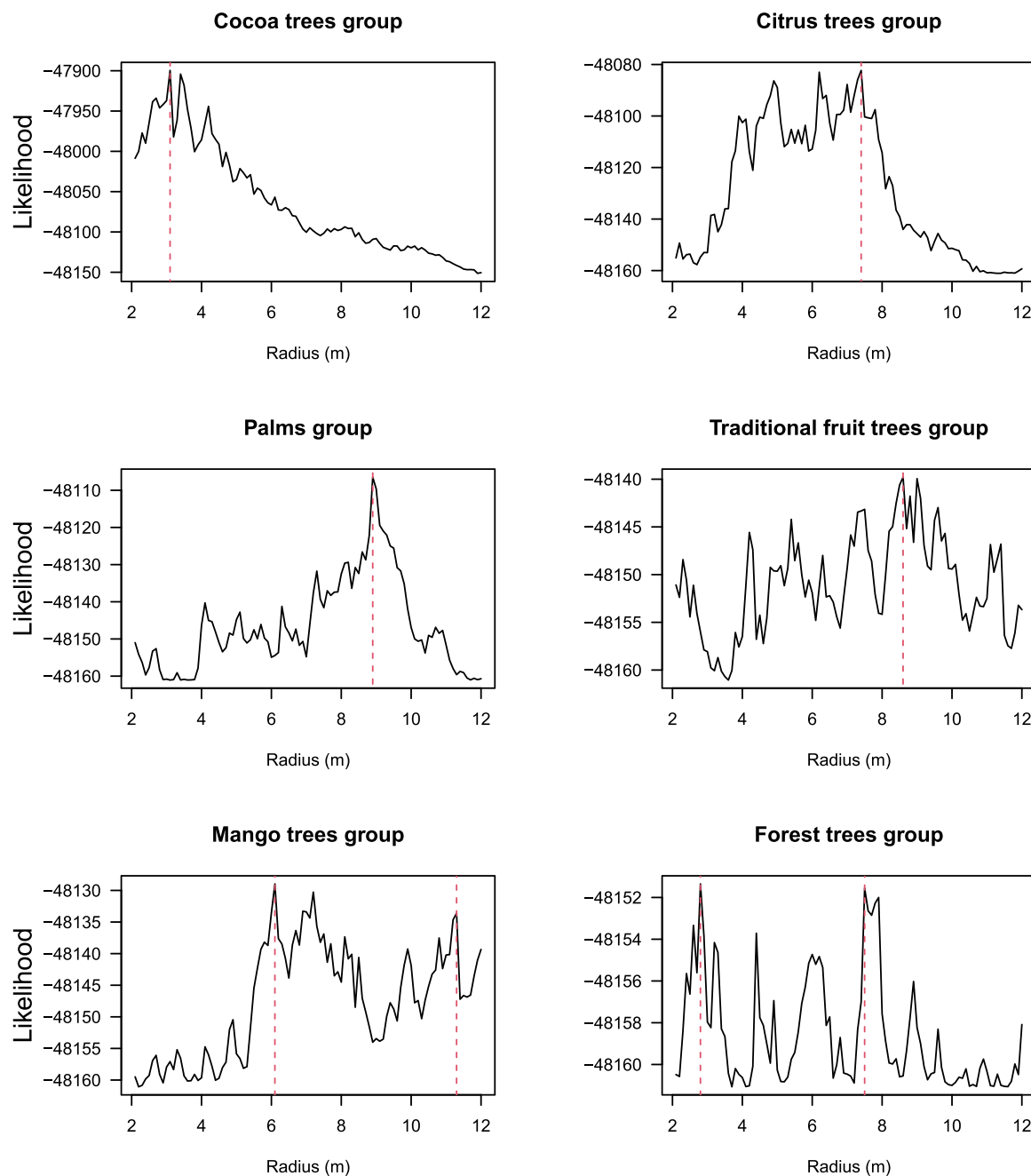


Fig. 1. Pods production likelihood of the prediction of with the abundance of the six groups of neighbouring trees according to the radius in which they are considered around each cacao tree. The vertical dashed lines are corresponding to the peaks of likelihood figuring out the distances at which the trees from the six groups altered most the cocoa production.

citrus, fruit trees, some forest trees and palms are present). Overall, we analysed the production of 4405 cocoa trees, as we excluded those located near plot borders.

3.1. Determination of the maximal distance of effect of each functional group on the production of each cocoa tree

The abundance of neighbouring cocoa trees showed a relatively simple effect pattern on cocoa production depending on the radius considered, with a very clear likelihood peak at 3.1 m (Fig. 1). For other groups of neighbours, there was a similar pattern of effect of their abundance on cocoa production according to the radius. The effect of citrus trees, traditional fruit trees and palms exhibited a single peak of likelihood at 7.4 m, 8.6 m and 8.9 m, respectively. Two peaks of likelihood were found for the two other groups: 6.1 m and 11.3 m for mango trees, and 2.8 m and 7.5 m for forest trees.

3.2. Analysis of the effect of neighbouring community on the production of each cocoa tree

All the selected predictors had a significant effect on the yield of cocoa trees (Table 2). As expected, the basal area of cocoa trees was a strong predictor of their production (Fig. 2). All interactions between abundance of associated trees and basal area were significant except for neighbouring citrus trees (data not shown). We verified graphically the normality of the residuals of our model (Supplementary material S4). Overall, there was a general trend for a negative effect of the abundance of associated trees on the cocoa yield (Fig. 3). The negative effect of neighbouring trees was stronger for cocoa trees and citrus trees neighbours than for other groups (Fig. 3.A&F). In the case of traditional fruit trees, this effect was almost neutral on the production of small basal area cocoa trees while it was much stronger for bigger cocoa trees (Fig. 3.B). There was a similar trend for mango trees regardless the distance (Fig. 3. C). Inversely, neighbouring palms had a positive effect on the cocoa production, regardless the size of the cocoa trees (Fig. 3.D). Interestingly, forest trees had opposite effects on cocoa production depending on the size of the cocoa trees, and with an inversed effect according to

Table 2

Results of the analysis of deviance on the effect of neighbouring plants, the squared-root basal are and their interactions (figured by “:”) on the production of pods of each cacao tree with a ‘Poisson’ GLMM (with the plot as a random factor on the intercept). For predictors corresponding to the abundance of trees in their optimal distance of effect, the numbers in subscripts after predictors are corresponding to the range of distance (m) around cocoa trees that was considered.

Predictors	Estimate	Df	deltaAIC	LRT	P
Intercept	2.482	1			<0.0001
BasalArea	0.1668	1	5136.2	5590.7	<0.0001
Cocoa 0-3.1	-0.0450	1	200.2	202.2	<0.0001
Forest 0-2.8	0.0881	1	20.9	22.9	<0.0001
Forest 2.8-7.5	-0.0961	1	253.3	255.3	<0.0001
Palm 0-8.9	0.0827	1	61.7	63.7	<0.0001
Citrus 0-7.4	-0.0566	1	115.3	117.3	<0.0001
Fruit 0-8.6	0.0339	1	24.3	26.3	<0.0001
Mango 0-6.1	0.1540	1	70.7	72.7	<0.0001
Mango 6.1-11.3	0.0968	1	29.3	31.3	<0.0001
Cocoa 0-3.1: Basal Area	0.0022	1	43.6	45.6	<0.0001
Forest 0-2.8: Basal Area	-0.0129	1	33.4	35.4	<0.0001
Forest 2.8-7.5: Basal Area	0.0101	1	257.2	259.2	<0.0001
Palm 0-8.9: Basal Area	-0.0053	1	23.4	25.4	<0.0001
Fruit 0-8.6: Basal Area	-0.0054	1	59.7	61.7	<0.0001
Mango 0-6.1: Basal Area	-0.0252	1	227.0	229.0	<0.0001
Mango 6.1-11.3: Basal Area	-0.0132	1	54.7	56.7	<0.0001

Df: degrees of freedom, deltaAIC: difference of Akaike information criterion between the complete model and the model without the predictor, LRT: Likelihood-ratio test, P: p-value of the Chi-square test.

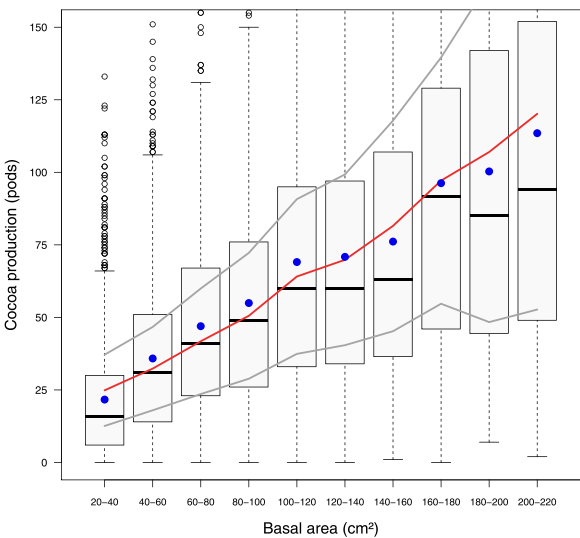


Fig. 2. Effect of the basal area (rounded classes) on the coca production (in pods) cumulated over 3 years. The boxplot represents the data and the blue dots the mean value measured per range of basal area. The red and grey lines show the average prediction and its standard deviation calculated with the complete model, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

their distance to cocoa trees (Fig. 3.E). On the one hand, the closer forest trees had a neutral effect on the production of small cocoa trees but their effect was very strongly negative on big cocoa trees. On the other hand, the farther forest trees had a negative effect on the production of small cocoa trees while their effect was strongly positive for big cocoa trees.

3.3. Exploration of the relationship between cocoa production and the abundance of associated trees

Overall, there was a general significant negative correlation (estimate=-0.012, $p < 0.001$) between the density of associated trees and the production of small cocoa trees (Fig. 4). Inversely, this correlation was significantly positive for larger cocoa trees (estimate=0.018, $p < 0.001$). According to the complete model presented in Table 2, it was possible to select optimal combinations of associated trees that maximize cocoa production while keeping a minimal density of associated trees (blue and red points in Fig. 4). For small cocoa trees, these optimal combinations led to densities of neighbouring trees between 255 and 524 trees per hectare, while it ranged between 460 and 1043 trees per hectare for big cocoa trees. For small cocoa trees, there was an optimum for associated tree densities in the middle of the tested range. For large cocoa trees the selected combinations were in the upper half of the tested densities of associated trees.

The tree composition of the selected combinations of neighbourhood were contrasted between small and large cocoa trees (Fig. 5). Our results suggest that the production of small cocoa trees is optimal when associated with less than 300 forest trees per ha, while larger cocoa trees could be in optimal conditions when associated with 337–900 forest trees per ha. Inversely, our results also suggest that small cocoa trees may produce optimally with 120–240 associated palm trees per ha, while larger cocoa trees may be in optimal conditions of production with less than 120 palm trees per ha. Only a reduced density of citrus and mango trees were selected for both small and large cocoa trees. In the selected combinations, there was up to 171 and 86 traditional fruit trees per ha for small and large cocoa trees, respectively.

4. Discussion

Our results underline the multifaceted effects of neighbouring trees

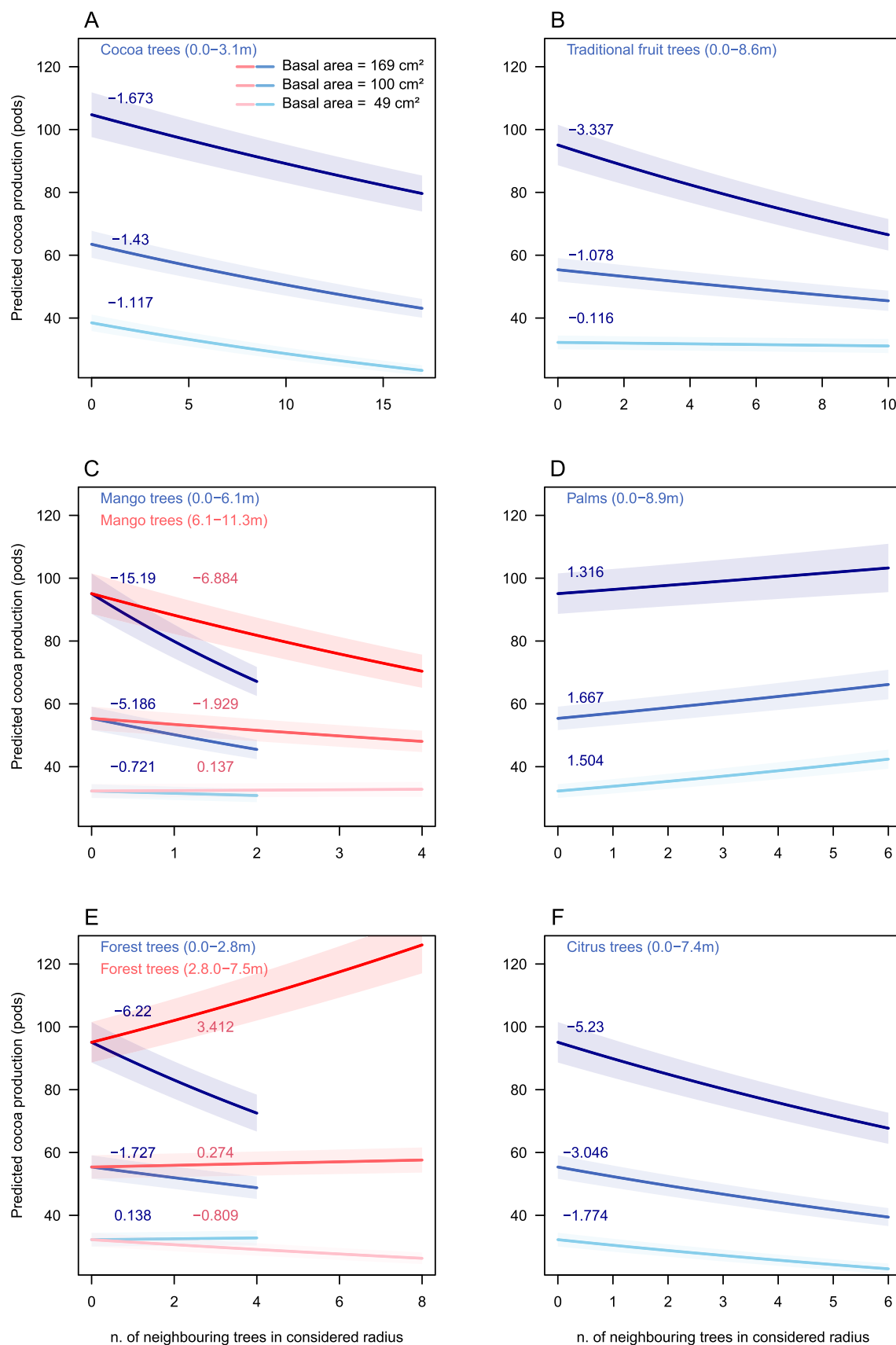


Fig. 3. Cocoa production (number of pods cumulated over 3 years) predicted with the complete model (see Table 2) in the variation range of each predictor for three values of basal area of cocoa trees (in cm²). The curves show the mean response and the areas show the standard error interval predicted by the model.

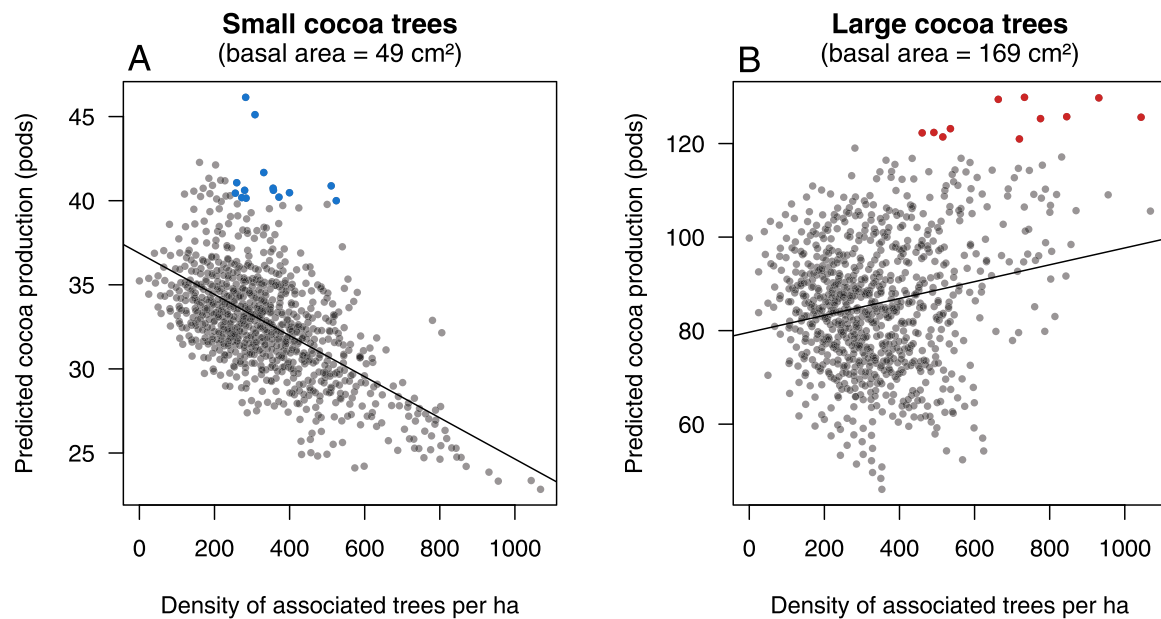


Fig. 4. Relationship between the cocoa production predicted for a given tree by the model and the density of associated trees per ha for small and large cocoa trees (basal area = 49 and 169 cm² respectively for A and B). Each dot represents a combination of neighbouring context. The red and blue dots show the selected combinations that optimise production (≥ 40 pods and ≥ 120 for small and large cocoa trees, respectively) while keeping density of neighbouring trees ≥ 250 per ha. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

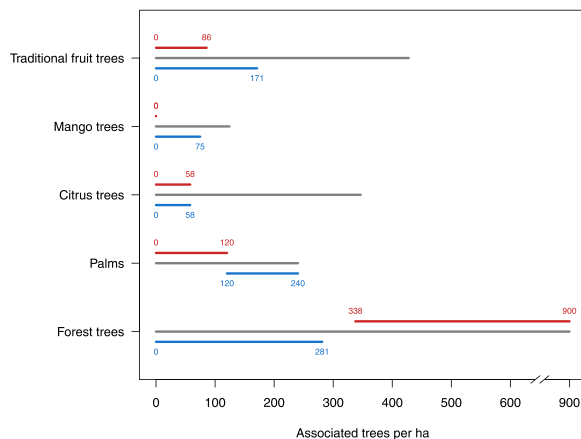


Fig. 5. Composition of the selected combinations of neighbourhood that optimise production (above 40 and 120 pods per tree for small and large cocoa trees, respectively) while keeping the density of associated trees ≥ 250 per ha (see Fig. 4). Blue and red lines show the cases of the production of small and large cocoa trees (basal area = 49 and 169 cm² respectively for A and B). The grey lines show the range of variation of this density in the whole dataset. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

on cocoa tree pod production in the studied cAFS, and show that these effects seem to depend on the basal area of a cocoa tree as well as on its distance to its neighbours. They also putatively point at different resource limitations. The relationship between the predicted production of pods and the abundance of associated trees for each combination of neighbouring context was found globally negative (especially for small cocoa trees). Yet, our results also underline that – based on our complete model – monocultures do not maximize pod production. Hence, they back Cameroonian farmers' choice to use agroforestry systems to cultivate cocoa. However, they also show that both densities of cocoa and associated trees are far from being optimised with regard to cocoa production.

In Fig. 6 we offer some management recommendations based on our

results and some of the references discussed hereafter. These recommendations are more precise for the cocoa tree stand (where we look for an improved yield within the studied complex cAFS) than for the associated tree community. Indeed, we were limited by data available in our study for the different groups of associated species (notably their basal area and height). Besides, as the composition of associated tree communities depends on farmers' targets, these targets should first be discussed before any recommendation is made.

4.1. Cocoa pod production and intraspecific interactions

4.1.1. Cocoa trees intraspecific interactions

Cocoa trees' intraspecific interactions were clearly negative regardless of their basal area, which underlines their sensitivity to competition with their closest peers. In our sample, cocoa stand mean density was close to 1500 ha⁻¹. Such a density corresponds to a distance of ca. 2.6 m between a cocoa tree and its four closest peers and ca. 3.65 m with its four second closest peers – if planted regularly (i.e. same distances between trees on a row and between tree rows). With maximal effect at a distance of 3.1 m, our results show that most cocoa trees clearly underwent intraspecific competition.

Besides, this mean stand density was close to the recommendations for intensive cocoa cropping systems, i.e. 1330 to 1660 cocoa trees ha⁻¹ (Wood and Lass, 2001) and was the result of the systematic replacement of dead or dying cocoa trees by farmers (Jagoret et al., 2011, 2017) to comply with these recommendations. Our results confirm the limit of this practice above a given threshold cocoa tree stand density (see § 4.1.2). Indeed, if Moolledhar and Lauckner (1990) showed that the higher cocoa yields obtained in young cocoa stands was due to the high densities, Lachenaud and Oliver (1998) and Lachenaud and Montagnon (2002) demonstrated that the densities recommended for cocoa monocultures induced intraspecific competition after a few years of cropping. In Indonesia, Bastide et al. (2008) showed that a 33 % decrease in density on a 21-years period did not result in cocoa yield decrease, thus confirming that mortality of cocoa trees had been offset by an increase in the productivity of living trees due to their vegetative development and gradual appropriation of the space left by missing individuals. In the Ivory Coast, Lachenaud and Oliver (1998) showed the benefits of

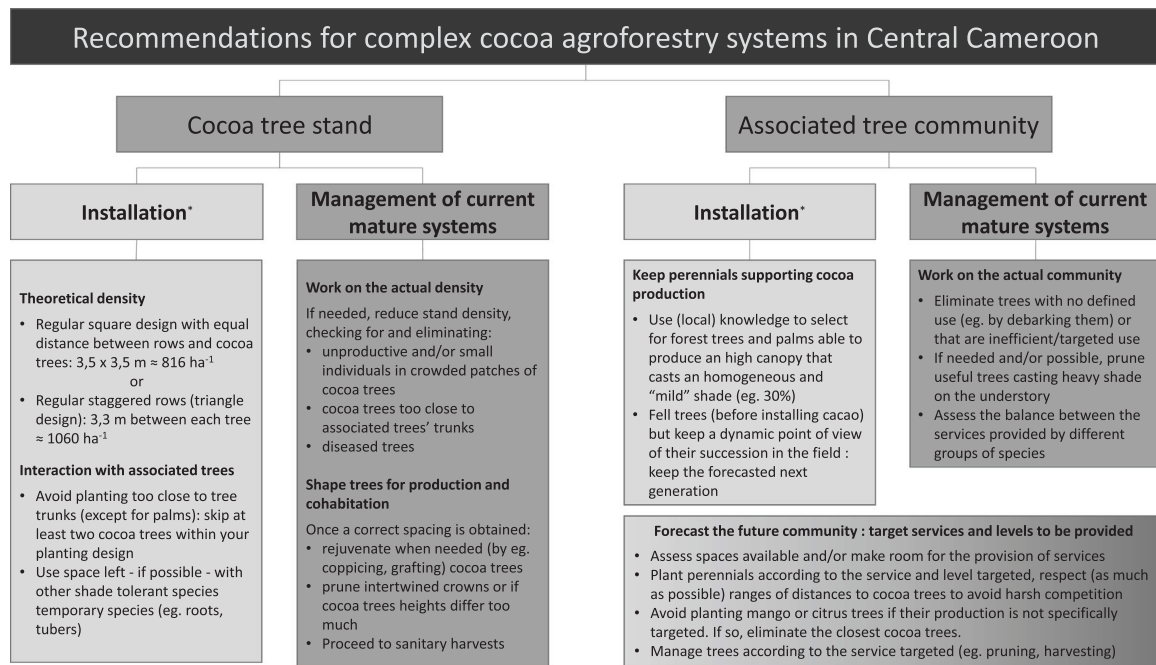


Fig. 6. Management recommendations for local complex cocoa agroforestry systems, focusing on the results from this study on the effects of cocoa tree intra- and inter-specific interactions.

removing progressively up to half of cocoa trees during early development stages (4–10 years), which led to a yield increase of 35–65 %.

The regeneration of old cocoa trees carried out by farmers (Jagoret et al., 2011, 2018b), which results in the multiplication of trunks on cocoa trees certainly accentuate cocoa trees *in planta* competition. Moreover, even if farmers do prune cocoa tree suckers regularly (Jagoret et al., 2018c) they idiosyncratically prune upper-order branches favouring crown growth in height. Consequently, cocoa trees in these systems can be fairly tall and reach mean heights above 4 m (Saj et al., 2017a) favouring self-shading and inter-individual shading. The same reasoning can be applied belowground, favouring competition for soil resources.

4.1.2. Consequences in terms cocoa stand management (Fig. 6)

In order to reduce intra-specific competition and optimise individual cocoa yields in existing systems we would suggest (i) to significantly reduce cocoa tree densities, for instance to 800–1000 trees ha^{-1} , as in many other producing countries (ICCO, 2022). This reduction of cocoa tree density could be based on the elimination of the least vigorous cocoa trees that are generally unproductive. This type of cocoa trees can reach 30 % of cocoa stands in Central Cameroun (Jagoret et al., 2017). Such a reduction would help farmers to better use their time on the field to (i) undertake cocoa trees pruning (Tosto et al., 2022) and (ii) and make the maintenance and phytosanitary protection of their cocoa orchards more profitable, as this is generally divided equally between the least and most productive cocoa trees (Wibaux et al., 2017). For the setting up of new cAFS, we would suggest the following: if the farmers are willing to reach a cocoa stand density of ca. 1100 ha^{-1} , they would need to place them in staggered rows in order to obtain a spacing of ca. 3.3 m between the closest neighbours. For a regular planting pattern, a distance between trees and rows of 3.5 m would ensure a fair lowering of intraspecific competition ($816 \text{ trees ha}^{-1}$). Whatever the options chosen, an important extension work is to be done to practically apply these new recommendations on the field.

4.2. Cocoa pod production and associated tree interspecific interactions

4.2.1. Associated trees interactions

Forest trees were the most abundant group associated to cocoa and had a complex effect on pod production that varied according to the distance to - and basal area of - cocoa trees. At short distances (0–0.28 m), we found a neutral effect on small cocoa trees and a negative effect on bigger ones. There may be several reasons for such a result at this neighbouring range. Cocoa trees may have been disadvantaged by a lower access to water. The rainwater may not homogeneously be distributed on the soil surface and preferentially streams along large branches and trunks (Bellot et al., 1999; Parker, 1983), which can prevent water access for cocoa trees close to the trunk and carpenter branches. Besides, at that distance, access and quality to light may be much lower than farther from the trunk (Blaser-Hart et al., 2021). For small cocoa trees, we can hypothesise that their development was impaired by a low access to light (which generally results in tapered architecture and low basal area) and consequently their ability to produce the necessary vegetative material to support pod production. At a larger distance range from the forest trees, the positive effects on big cocoa trees may be due to a better access to light as well as to nutrients from the forest tree litter decomposition and nutrient-enriched rainwater throughfall (Khan, 1999; Nijmeijer et al., 2019). Besides, some of the forest trees are oxalic and may raise soil pH locally, which could ease nutrient uptake in the studied Cameroonian poor ferrallitic soils (Sauvadet et al., 2020). Yet, this positive effect clearly depended on the cocoa tree's basal area. Small cocoa trees seemed not able to benefit from these putative benefits, which may underline a "biomass" threshold under which competition still prevail for cocoa trees.

Mango trees showed a steady negative effect on pod production for large- and medium-sized cocoa trees, this effect being stronger for the farther range of distances tested (6.1–11.3 m). The dark foliage and large crown expansion of mango trees provide a heavy shade and may explain the difference observed with forest trees, making light the very first limiting resource. Litterfall from evergreen mango trees may also play a role, since the material shed (leaf litter) could be recalcitrant to decomposition (Isaac and Nair, 2006; Musvoto et al., 2000). Also, the stronger negative effect on pod production at farther distances could be

explained by the extensive (fine) root systems developed by this species (Shah et al., 2010).

The traditional fruit trees group had similar effects to those of mango trees within the range of distances tested (0–8.6 m). Since this group comprised of a number of evergreen species occurring in the same strata as mango trees (Supplementary Material S1; Saj et al., 2017a), its litter could also be recalcitrant to decomposition. However, the lighter crowns of many trees from this group in comparison to mango trees should theoretically allow a better access to light. Such an effect may have been balanced by another type of resource limitation. For instance, most individuals from the traditional fruit group were non-pioneer-light-demanders or shade-tolerant species (Saj et al., 2017a). These succession guilds can be fierce competitors for soil resources during the later stages of secondary forest regeneration (Vroh and Yao, 2018), which may be the case in the studied cAFS where associated trees can be decades-old.

The citrus trees group had a slightly different effect, but similar to the cocoa group within a larger range of distances (0–7.4 m). Such a result underlines a competition effect for all cocoa trees regardless of their basal area. In the studied cAFS, citrus trees roughly occupied the same space and volume as cocoa trees, probably making them direct competitors for crown development. Besides, as for mango trees, the shedding of their dark and dense evergreen recalcitrant foliage putatively induced larger root foraging (Castle, 1978). Being pioneers whilst cocoa trees are shade tolerant, they have the potential to outcompete cocoa roots in that matter.

Finally, palms showed a positive effect on pod production within the distance range tested (0–8.9 m), independently from cocoa basal areas. Hence, it appeared that even if palm leaf shedding may damage cocoa trees, it did not impair cocoa access to resources. Palm trees, with their shallow and short distance foraging roots (Jourdan and Rey, 1997), may not induce sharp competition for water and nutrients. Besides, the light shade cast by the palms may not impair cocoa trees' access to light.

4.2.2. Consequences in terms associated tree community management (Fig. 6)

The positive effects found for palm trees show that their current density (c.a. 35–40 ha⁻¹) seemed suitable in the cAFS studied. Hence, all other things being equal, they may be introduced / eliminated / managed within this range. If the cocoa stands are thinned to reach the densities < 1000 individuals per ha much more palms may be introduced. These choices depend on each farmer's choice to produce more or less oil or wine depending on market prices and how much they value them (Jagoret et al., 2014).

The results obtained on forest trees showed opposite effects on pod production, depending on the distance range between them and cocoa trees. The negative effect found close to trunks shows that farmers should avoid planting cocoa trees too close to forest trees i.e. at less than 3 m, which is currently the case for a fair number of individuals (see Supplementary Material S4). The positive effect found underlines the need to maximise the number of cocoa trees under forest trees canopy, which underneath soil is putatively well covered by a layer of branches and leaves. It is however difficult to suggest from our data optimal densities and design, while our simulations revealed the possibility to keep a fair amount of forest trees. A young cocoa stand (which may be represented here by small diameter trees) would clearly benefit from a less crowded environment than a mature one. In this case, one may hypothesise that it would be possible to increase forest tree density once the cocoa trees reach a certain biomass/basal area. That said, crown height and shape, basal area, leaf-life span as well as litter recalcitrance are probably the major factors to look at in order to maximise the positive effects of forest trees and propose ad-hoc forest trees selection taking into account the long-term evolution of the canopy cover. Besides, forest tree density should be carefully managed also because of the many ecosystem services provided by these trees (Nijmeijer et al., 2019; Sauvadet et al., 2020).

The other associated tree groups showed a consistent negative effect on pod production and underline the trade-offs farmers' undertake when growing them in their cAFS (Jagoret et al., 2014; Saj et al., 2017a). This is especially the case for exogenous mango and citrus trees. Hence, our results point to the need to avoid/eliminate these species within cAFS to support cocoa yields. Yet, these issues need to be tackled at larger levels (farms, village etc...) with local farmers and stakeholders in order to improve both cocoa production levels, local markets and support to food security of cAFS side-products (Notaro et al., 2020). Finally, if the lowering of cocoa stand density proposed in the previous paragraph becomes effective, resource availability and distribution may change within the systems. In this case a reassessment of inter-specific competition would be needed and used to think over a renewed management of the associated community.

5. Conclusions

In this paper we developed an original method to study tree crowding effects on individual cocoa tree production in complex agroforestry systems. Our results underline the significant competition between cocoa trees occurring in the cAFS tested and the need to thin stands. Furthermore, while our results underline the general negative effects of associated trees kept or grown for their fruits, especially mango and citrus trees, they also point out at the positive effect of palms. Finally, we found both negative and positive effects to forest trees, which varied with the distance separating them from - and the size of - the cocoa trees. Such results underline both (i) the need to think dynamically the management of forest trees in relation with the development of the cocoa stand, (ii) the fact that forest trees can support pod production in complex cAFS. Overall, it has been difficult to distinguish between resource limitations which are at play in cocoa production. To go further, we suggest applying the same analytical method now using/measuring functional indicators of trees, which could be better related to their resource use.

CRedit authorship contribution statement

Stephane Saj: Writing – original draft, Writing – review & editing, Conceptualization, Visualization, Supervision. **Patrick Jagoret:** Investigation, Conceptualization, Resources, Supervision. **Hervé Todem Ngnogue:** Investigation, Resources. **Philippe Tixier:** Writing – original draft, Methodology, Data curation, Validation, Visualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.eja.2023.126810](https://doi.org/10.1016/j.eja.2023.126810).

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