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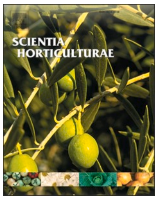

The effect of pruning on yield of cocoa trees is mediated by tree size and tree competition

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ABSTRACT

In cocoa cultivation pruning is considered an essential yield-enhancing practice but its effects on cocoa tree growth and yield, and how these are mediated by tree size and competition are poorly understood.

Here, we evaluate the impact of experimental pruning on: light interception, leaf flushing and the number of flowers and of developing, wilted and harvested pods. The pruning treatment removed an average 26.4% of cocoa tree aboveground biomass and was aimed to create an open cup-shaped crown. Stem basal area and sum of neighbor tree basal area were used as proxies for tree size and tree competition, respectively. All response variables were analysed at tree level as a function of pruning, tree size and tree competition using generalized linear mixed effect models.

After one year, pruned trees recovered initial losses in whole-canopy light interception but maintained a more uniform distribution of light in the canopy. Pruning directly increased flushing activity, while the effect on the other variables was mediated by the interaction with tree size and competition. Pruning increased the positive effect of tree size and competition on flower number and similar effects were found for small pod number. The latter effect was counterbalanced by an increase of pod wilting in pruned trees under high competition, resulting in similar numbers of large and harvested pods on the stem in pruned and unpruned trees. For pods in the canopy, pruning did enhance the positive effect of tree size and strongly reduced the negative effect of competition on pod number. As canopy pods made up 60% of the total, similar pruning effects were found for the total number of harvested pods. The predicted net effect of pruning on the number of harvested pods varied greatly with tree size and competition, ranging from -58% for small trees under low competition, to +150% for large trees under high competition. This large variability stresses the importance of individual-level analysis to quantify pruning effects and calls for more attention to individual tree characteristics in training and practice of cocoa pruning. The pruning-induced reduction of negative competition effects suggests that pruning can contribute to realizing high-density cocoa stands.

1. Introduction

Cocoa (*Theobroma cacao* L.) is one of the world's most important commodity crops and is grown by 5–6 million mostly small-holder farmers for whom it often is the main source of cash income (Fairtrade Foundation, 2016). About 70% of cocoa is grown in West Africa where yield at small-scale farms are low (Asante et al., 2021). In Ghana for example average farmer yield varies from 210 to 1000 kg ha^{-1} (depending on the growing region), and it is estimated to be 50–70% lower than attainable yield (Abdulai et al., 2020). Closing the yield gap would substantially benefit farmer livelihood (van Vliet et al., 2021) and contribute to reducing the pressure on remaining forested area (Hoffmann et al., 2020). Several factors have been identified to explain the current low yields, including impacts of pests and diseases, low fertilizer input, farm ageing, erratic rainfall pattern, low planting density and inadequate maintenance practice (Anim-Kwapong and Frimpong, 2004; Dormon et al., 2004; Asante et al., 2021). In addition to these, pruning - defined here as the removal of part of a plant for horticultural purposes (Ferree and Schupp, 2003) - is considered an important practice to increase the efficacy of fertilization, assist in pest and disease control and

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directly enhance productivity. Yet, pruning instruction manuals, and extension services provide rather general and standardized instructions that often fail to address the specificity of farm contexts, contributing to the low adoption rate of this practice (Obeng Adomaa et al., 2022). Pruning recommendations also lack solid scientific support. So far, the cocoa pruning literature has reported inconsistent effects of pruning on yield. Overall effects have been found to be either positive (Bahaudin et al., 1986; Balasimha, 2007), selectively positive only for medium or light pruning intensity (Govindaraj and Jancirani, 2017; Leiva-Rojas et al., 2019), neutral (Ampofo, 1986) or negative (Thomas and Balasimha, 1992). But effects have also been found to depend on crop development. For instance, in a six-year trial pruning had a negative effect on yield during the first four years while effects were neutral to positive in the final two years (KAU, 1992). Another long-term experiment (Bonaparte, 1966) reported a reversed pattern: small positive pruning effects on yield in young trees, which became negative after 10 years. Comparisons across studies and generalization of pruning effects are hampered by the wide variety of pruning methods and site conditions, as well as the qualitative nature of pruning studies.

Pruning studies have predominantly focused on the effect on yield (but see Leiva-Rojas et al., 2019; Thomas and Balasimha, 1992) thus providing limited insights in tree functional responses to pruning and in the underlying mechanisms of yield responses. Just like other forms of biomass removal such as herbivory or physical damage, pruning has profound effects on plant functioning (Persello et al., 2019). It entails direct losses of biomass and resources (e.g. nutrients), reduction of leaf area, and thus whole-plant photosynthesis. But plants can mitigate these negative effects through a suite of compensatory mechanisms including activation of dormant meristems, increased photosynthetic activity due to enhanced water and nutrients availability for leaf area, and mobilization of reserves (Anten et al., 2003; Van Staalduinen and Anten, 2005). Pruning also reduces self-shading, thus potentially increasing photosynthesis in certain parts of the crown (Ferree and Schupp, 2003). Depending on the phenological stage of the tree however this increase in vegetative growth can go at the expense of flower and fruit production (Martínez-Ramos et al., 2009; Wilkie et al., 2008). The net effect of pruning on yield will therefore be determined by the magnitude of its negative and positive effects on growth, allocation and pod production.

The net effect of pruning in cocoa plantations likely also depends on the size of trees. Substantial variation in tree sizes exists within even-aged cocoa fields and part of this variation may be induced by mixing different cocoa hybrids in the same field, a common practice in West Africa (Trebissou et al., 2021). Differences in growth rates between hybrids, or micro-environmental variation, may create asymmetric competition among neighboring trees, (i.e., faster-growing larger plants gaining disproportionately large shares of available resources, Schwinning and Weiner, 1998) that may result in a large variation in tree size, and production within the same field (Trebissou et al., 2021). Pruning treatments in stands with trees differing in size may change competitive interactions. The modifying role of tree size and competitive interactions on pruning effects has never been studied, partly because most studies (e.g. Balasimha, 2007; Govindaraj and Jancirani, 2017) are conducted at plot level. We expect that variation in tree size influences the direction and magnitude of pruning effects on yield. For instance, larger trees can exhibit higher levels of self-shading and may have larger carbohydrate reserves which together would contribute to a stronger compensatory response. On the other hand, respiration of non-photosynthetic tissue as a fraction of photosynthesis tends to increase with tree size (Collalti et al., 2020) which would imply a more negative effect of leaf loss for larger trees. We also expect that variation in competition will change the effects of pruning on yield. Intra-specific competition in cocoa stands has been suggested to be one of the causes of early decline in yield (Tahi et al., 2019), and thinning experiments showed that the removal of a portion of the trees results in a large increase in pod production in the remaining ones (Lachenaud and Oliver, 1998). Pruning may reduce competition between trees and is thus expected to be more beneficial for trees experiencing stronger competition.

In order to provide detailed scientific underpinning of the relation between pruning of cocoa trees, tree size and competition among trees, and to improve pruning recommendation in cocoa cultivation, we addressed the following the questions: (1) To what extent does pruning affect cocoa trees in term of light capture, growth and yield? (2) To what extent do these effects depend on tree size and the level of intraspecific competition? We performed a pruning experiment in a nine-year-old plantation in Côte d'Ivoire. We measured light interception, vegetative production and flower and pod production during one year after the pruning intervention. In order to facilitate future comparisons with other pruning studies we report our pruning protocol, the amount and fraction of biomass removed and we express pruning effects on annual dry bean yield per tree.

2. Materials and methods

2.1. Study site

The study was carried out in the research station of the *Centre National de Recherche Agronomique* (CNRA) located the municipality of Divo (5.769814 N, 5.236746 W), Côte d'Ivoire. The station has an average annual maximum and minimum temperature of 31.6 (±0.9) and 21.7 (±0.8)̊C and 1229 (±194) mm of precipitation yearly (average from 1972 to 2019, weather data from CNRA local weather station). Rainfall has a bimodal distribution with peaks in June and October, a dry spell in August, and a major dry season from December to the beginning of March.

2.2. Experiment design

The study took place between April 2018 and December 2019 in a nine-year-old full-sun field that was planted with a mix of Upper Amazonian cocoa hybrids, typically distributed to Ivorian farmers. The field was originally established as a fertilizer trial and all previous experimental and maintenance activity had ceased in 2015. We selected the eight plots that in the previous experiment had been assigned to two of the former fertilization treatments, i.e., plus 150 and 200 g of Triple Superphosphate. Soil analysis showed no significant residual differences in nutrient availability, pH, and cation exchange capacity between the two previous fertilizer treatments (results of T-tests in Table S 1). Additionally, we found no significant difference between former treatments in average tree size (Wilcox-test: $n = 48$, p-value=0.11) and amount of biomass removed with pruning (T-test: $n = 48$, p-value=0.70). All selected plots for our pruning experiment were re-fertilized to minimize possible nutrient limitation, with 193 kg ha^{-1} of Calcium Nitrate, 71 kg ha^{-1} Triple Superphosphate and 138 kg ha^{-1} of Potassium Sulphate per year (in line with Yara recommendation), applied in in March/April, June and September during both 2018 and 2019.

Each plot consisted of five rows of six trees planted at a distance of 2.5 × 3 m. Following the procedure described below, we pruned all trees (15 on average) in a randomly selected half of each plot. The other half of the plot was left unpruned. Among the pruned trees, only the three central trees were included in the measurements and analyses to minimize possible border effects (Fig. S 1). In total we thus included 24 pruned and 24 unpruned trees in the study.

2.3. Pruning treatments

No known pruning intervention had been carried out since the termination of the previous experiment in 2015. Therefore, to minimize the chance of an excessive reaction of the trees to pruning, we applied the pruning treatment at two moments in time: April 2018 and December 2018. Our pruning treatment followed a set of guidelines aimed at working towards an open cup shape of the tree crowns mimicking interventions carried out in overgrown farmer fields by private and public extension agencies. More specifically, after removal of dead, diseased and damaged branches, further removal of branches was aimed at (1) eliminating mispositioned and crossing branches; (2) reducing competition with neighboring trees by cutting back branches to the middle line between two consecutive trees; and (3) creating an open cup-shaped crown by removing vigorous branches in the center part of the crown to allow for a more homogeneous light distribution. Due to differences in size and architecture, the absolute amount of pruned material varied among trees. Fresh weight of removed leaf and wood material was determined in the field. Pruned materials were left in the plot to decompose and a sample of ten fully expanded leaves and five ~20 cm long branches per pruned tree was separately weighed and subsequently dried (at 70 ℃) to stable weight to calculate leaf and wood dry matter content (DMC). Average values of DMC were used to calculate dry weight of removed leaf and wood material.

In order to check how the amount of pruned biomass was related with tree size and to calculate the percentage of above ground biomass removed by our pruning treatment, we estimated tree aboveground biomass (AGB_{est}, kg) with a widely used allometric equation (Eq. (1)) for tropical trees (Chave et al., 2014):

$$AGB_{est} = 0.0673\ \left(\rho\ DBH^2\ H\right)^{0.976} \tag{1}$$

Where ρ is wood density (g cm^{-3}), DBH is diameter at breast height (cm), and H is tree height (m). ρ was set to 0.39 g cm^{-3} (Kotowska et al., 2015). Since we did not directly measure DBH on the focal trees, we transformed the measured diameter at 20 cm (D20, see Section 2.4.2) to DBH using a ratio DBH/D20 of 0.79 (SD: 0.14). This ratio was obtained from a separate dataset containing measurements of D20 and DBH of 101 trees in the same field. Tree height was measured using a graduated pole.

During the two pruning interventions we removed an average of 5.91 kg of dry biomass per tree (SD = 2.43, range 1.3 kg to 11 kg). This amount increased significantly with estimated aboveground biomass AGB_{est} (Fig. S 2a). On average our pruning treatment removed 26.4% of aboveground biomass (SD=8.73, range 14.8 to 46.3%). We did not find a significant relation between this percentage and AGB_{est} (Fig. S 2b).

2.4. Data collection

2.4.1. Light measurements

To assess the impact of pruning on light penetration to soil level, light intensity below the canopy was measured right after the second pruning treatment (December 2018), after five months (May 2019) and after 11 months (November 2019). Four measurements per tree were conducted using an Onset HOBO MX2202 light sensor: one in each cardinal direction, half a meter from the stem. A second sensor was placed in unobstructed daylight in the proximity of the experimental field as a reference to calculate relative light intensity (I_{rel}).

To quantify the vertical profiles of light availability within the canopy, light measurements were taken along vertical transects in May and November 2019, on 14 pruned and 13 unpruned trees. All trees that were missing one or more direct neighbors or that were fully overgrown by their neighbors were excluded. To account for differences in light distribution due to the cupped shape of the crown we measured along two vertical transects, one in the center of the crown and the second one a meter south from the stem. Light intensity was measured every 50 cm from the top to the bottom of the crown using the light sensor mounted on an extensible pole. For these measurements we used the top measurement of each transect as the reference to calculate relative light intensity. All light measurements were taken between 11 am and 1 pm to ensure that all trees were measured under similar solar angle.

2.4.2. Vegetative and reproductive growth

Data on vegetative and reproductive response to pruning were collected from July 2018 to December 2019. Each week we recorded whether or not a tree was producing new leaves. Flushing activity was then calculated as the total number of weeks in which a tree was producing leaves. Counts of flowers, developing pods and wilted pods were conducted at a three-week interval and count was restricted to <2 m height on the stem. Flower counts included both open flowers and fully formed buds. Developing pods were divided in two classes: small pods, including younger pods from 0 to 7.5 cm, and large pods including more developed pod longer than 7.5 cm. This classification simplified the four-classes approached used by Daymond et al. (2015), by merging together their two smaller classes and the two larger classes. Wilted pods were removed after every count. Finally ripe pods were harvested and counted every three weeks from both stem and canopy.

To assess the impact of pruning on pod size we measured the fresh weight and the location in the tree (stem or crown) of each harvested pod at four harvests: two in the minor harvest season, April and May 2019, and two in the major season, October and November 2019. In November 2019 tree circumference at 20 cm from the ground was measured for all cocoa trees in the stand. In the case a tree was branching below 20 cm, the circumference of both stem and branch was used. We then calculated the basal area of central trees (BA_focal) as a proxy for tree size and the sum of the basal area of the direct neighbors (BA_neighbor) as a proxy for above- and belowground competition. Since some neighbor trees were missing, it is important to mention that 'BA_neighbor' consisted of the sum of the basal area of all existing neighbors, from a minimum of two to a maximum of four trees.

2.5. Statistical analysis

We restricted our statistical data analysis to measurements during the full year (2019) after the second pruning intervention which took place in December 2018. We applied generalized linear mixed effect modelling (GLMM) to explain variation in relative light intensity below the crown, flushing activity and annual total flower, pod production and pod weight by pruning treatment (pruned=1; unpruned=0), and BA_focal and BA_neighbor both as continuous variables. All continuous explanatory variables were scaled by subtracting the mean and diving by the standard deviation.

We also tested for interactive effects between pruning and BA_focal, and between pruning and BA_neighbor. This allowed us to test for possible modifying roles of cocoa tree size and neighbor tree size on the effect of pruning. A varying intercept for plots was included as random term to account for the non-independence of trees located in the same plot. For flower, pods and flushing we assumed data to follow a Poisson distribution, as these are count data. For pod size we added pod position (Stem = 0; Canopy = 1) and harvest season (Major seaso*n* = 0; Minor Seaso*n* = 1) as fixed factors, and checked for their interaction and the interactions with pruning. In this case we nested tree identity into plots as a random effect, to account for the non-independence of pods harvested from the same tree. Pod weight was assumed to follow a log-normal distribution. For the relative light intensity measured below the crown we also included the time of measurement as a fixed factor (December 2018 = 0; May 2019 = 1; November 2019 = 2) and checked for interaction with pruning. Since multiple measurements were taken per tree, tree identity was included as random term nested into plots and intercepts were allowed to vary. Relative light intensity below the crown was assumed to follow a log-gamma distribution.

To model I_{rel} along the vertical transect we used a non-linear mixed effect model approach (NLMM). For each measured light profile, I_{rel} data were fitted with a modified version of the Beer-Lambert equation (Eq. (2)), (Monsi and Saeki, 2005):

$$I_{rel} = e^{-k\ D} \tag{2}$$

where I_{rel} is the relative light intensity at point D, D is canopy depth (the distance from the top to the point of measurement) and k the light extinction coefficient. k was allowed to vary with all fixed and random terms mentioned in the analysis of I_{rel} below the canopy. Values above one were excluded from the analysis for a total of four data points for the center transect and eight data points for the South transects. In this case we assumed a normal distribution of the data.

To test the effect of pruning intensity on flushing, flower production and pod production we ran separate GLMMs on pruned trees only, with relative amount of AGB removed (Rel_P), BA_Focal, BA_neighbor and their interactions as explanatory variables. Similar to the analysis on the complete dataset, we standardized all explanatory variables, included varying intercepts for plots as random factor and assumed a Poisson distribution for all response variables.

In all analyses, collinearity was tested using Variance Inflation factors (VIF), that measures how much of the variance of an independent variable is explained by the other independent variables. All variables included in the final models had VIF <5 (max $= 3.5$). To determine the most parsimonious model for each response variable we performed a backward selection taking the model with the lowest AIC. In the case multiple models were within a ΔAIC<2, the most parsimonious model was selected. Confidence interval at 95% of each parameter was calculated as 1.96 times its standard error and parameters were considered significant if the CI did not overlap with zero. All analysis were performed using R 4.0.2 (R Core Team 2020). For GLMM we used the glmer function from the lme4 package and the glmmTMB function from the glmmTMB packages (in the case of light below the crown and pod weight, and supplementary analysis with Rel_P). NLMM were instead fitted using the nlme function from the nlme package. For the estimation of marginal and conditional pseudo-R^2 we used the r.squaredGLMM function in the MuMIn package.

2.6. Yield estimation

Our tree-level analysis of pruning effects, allowed to estimate the effect of pruning on annual dry bean yield for trees of different sizes and with different neighbors size. In line with the findings from statistical analyses of pod production, we estimated dry bean yield per tree (kg y^{-1}) for various combination of tree size and neighbors size (Table 4).

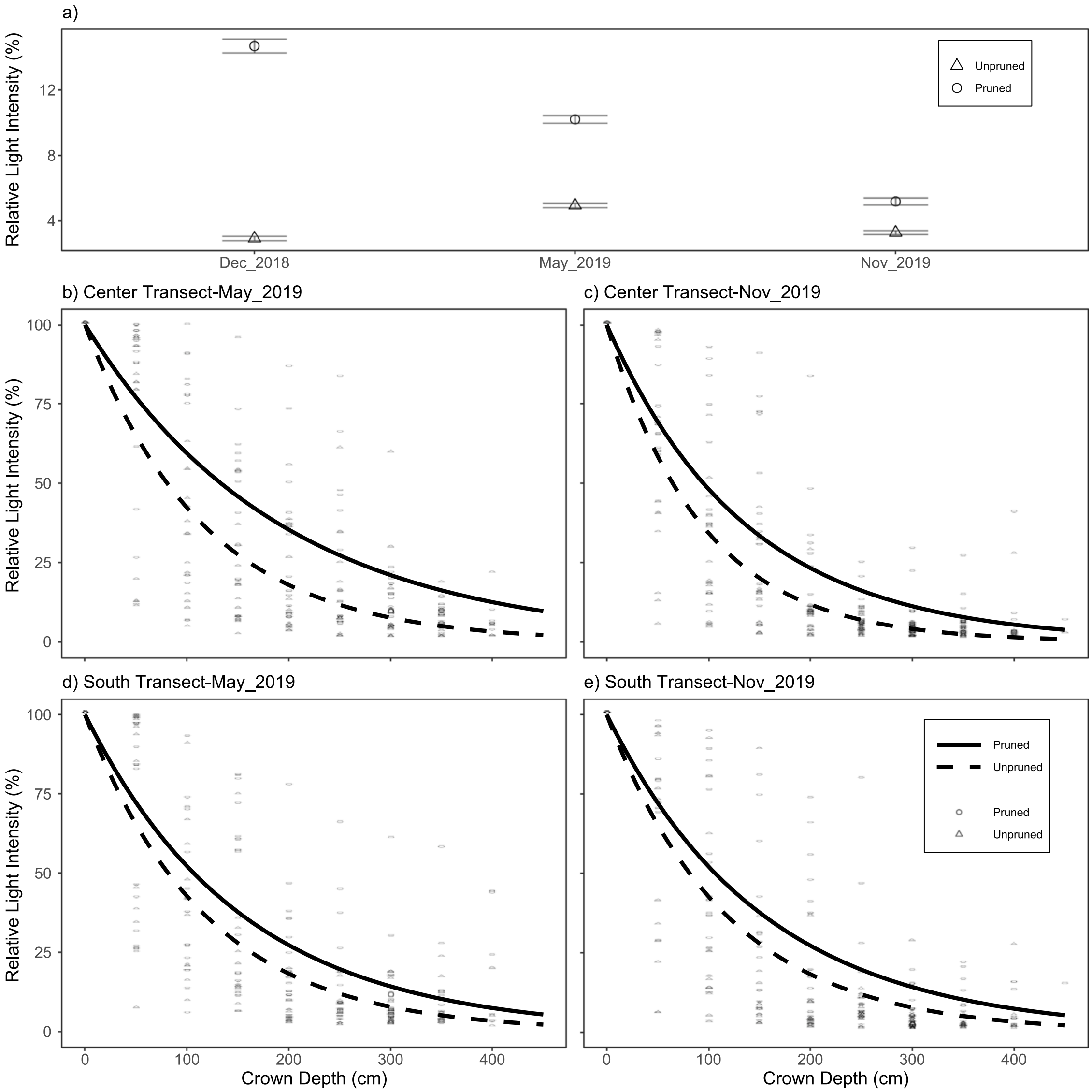

Fig. 1. Pruning effects on relative light intensity below and throw the crown. (a) Mean relative light intensity below the crown for pruned (circles) and unpruned (triangles) treatment at 0, 5 and 11 months after pruning, error bars indicate standard error. (b–e) Relative light intensity along the center and south vertical transect though the crown in May and November 2019 and predicted light extinction curve for pruned (circles, continuous lines) and unpruned (triangles, dashed lines) trees. Pruning took place in April and December 2018.

We estimated dry bean yield for each combination of tree size and neighbors size as follows. (1) Using a regression model for pod weight we estimated average fresh pod weight (kg) for stem and canopy pods in minor and major season and for pruned and unpruned trees. (2) Fresh pod weight was then converted into dry bean weight (kg) using the allometric equation estimated by Goudsmit et al. (2022) (Preprint) for trees in the same field (Eqs. ((S1), (S2)). (3) We separately predicted the number of pods produced on the stem and in the canopy in pruned and unpruned trees using the GLMMs for harvested stem and canopy pod number. (2) From the three-weekly data on pod count we calculated the proportion of pods produced during the major season (July-December) for stem (mean = 0.57) and canopy (mean = 0.51) pods. (3) We then converted pod counts to dry bean weight for each group, and (4) finally dry bean weight of the different groups was summed to calculated dry bean yield per trees (kg y^{-1}).

3. Results

3.1. Light measurements

Relative light intensity (I_{rel}) below the canopy varied between pruning treatments, month of measurement and their interaction (Fig. 1). The presence of an interaction showed that I_{rel} dynamics during the year differed between pruned and unpruned trees. As expected, directly after the pruning interventions (December 2018) I_{rel} was higher in the pruned trees. In May 2019, five months after pruning, I_{rel} was lower in pruned trees compared to December 2018 while for the unpruned trees there was no difference between these dates. Values for November 2019, 11 months after pruning, were lower than those for December 2018 in both pruned and unpruned trees, although the decrease was more pronounced for pruned trees (Table 1, Fig. 1 a).

The nonlinear mixed effect models fitted on I_{rel} measured along vertical transects through the crown (Eq. (2)) yielded different results for the center and the south transects. In the center transects, the light extinction coefficient (k) was lower in pruned trees compared to unpruned ones and was larger in November 2019 than in May 2019 (Table 2). This lower k reflected the relatively more uniform vertical light distribution in the pruned trees both in May and in November. Compared to May though, in November I_{rel} decreased faster with canopy depth, this being true also for unpruned trees (Fig. 1 b and c). In the south transect instead k was lower in pruned trees but we found no differences between May and November (Fig. 1 d and e).

3.2. Among-individual variation and seasonal patterns

Among-individual variation in tree size and neighborhood was large (Table 3). Basal area (BA_focal) varied nearly six-fold between the smallest and largest tree, while the sum of neighbor's basal area (BA_neighbor) varied nearly five-folds, the latter being caused both by the size and number of neighboring trees. Importantly, we found no initial difference in BA_focal (*T*-test, *p*-value=0.40) or BA_neighbor (*T*-test, *p*-value=0.66), between pruned and unpruned trees.

Table 1
Results of mixed effect models for light interception. Shown are mean and standard error (SE) of intercepts and coefficients of explanatory variables for relative light below the crown (Light% below; GLMM). Significant levels indicate whether effect of explanatory variable was significantly different than zero. Marginal and conditional R^2 are reported.

	Light % below	
	Mean	**SE**
Intercept (Unpruned Dec_2018)	-2.88**	0.15
Pruned	1.22**	0.08
May_2019	0.14	0.06
Nov_2019	-0.46**	0.06
Pruned X May_2019	-0.68**	0.08
Pruned X Nov_2019	-0.87**	0.08
	n = 48	
	R^2 0.48/0.80	

*P < 0.05; **P < 0.01

Table 2
Results of mixed effect models for light extinction. Shown are mean and standard error (SE) of intercepts and coefficients of each level of explanatory variables for light extinction coefficient (k; NLMM) for center and south vertical transects. Significant levels indicate whether effect of explanatory variable was significantly different than zero.

	k center transect		k south transect	
	Mean	**SE**	**Mean**	**SE**
Intercept (Unpruned May_2019)	0.0086**	0.0010	0.0085**	0.0008
Pruned	-0.0034*	0.0011	-0.0020*	0.0009
Nov_2019	0.0021**	0.0004		
	n = 427		n = 402	

*P < 0.05; **P < 0.01

The trees also varied greatly in their vegetative and reproductive performances (Table 3). Both flushing activity and the number of harvested pods varied by an order of magnitude between trees. For all other pod counts as well as flower count, minimum and maximum values differed by two orders of magnitude between trees. The range of variation was similar though in pruned and unpruned trees for total harvested pods (Fig. 2 a). The large variation in explanatory and response variables supports our choice to conduct statistical analysis of pruning effects at individual tree level, and not at plot level.

The temporal dynamics of the harvested pods from stem and canopy showed a bimodal pattern, which is typical of Upper Amazonian cocoa hybrids (Fig. 2 b). These dynamics seemed to vary between pruned and unpruned trees, but those temporal differences were not further analysed.

3.3. Vegetative and reproductive responses to pruning

The flushing activity strongly increased after pruning and was negatively affected by summed neighbor basal area (BA_neighbor, Fig. 3 a). By contrast, flower production on the stem increased with BA_neighbor and, to a lesser extent, by focal tree basal area (BA_focal). The presence of a positive interaction between BA_focal and pruning and between BA_neighbor and pruning indicated that those increases were stronger in pruned than in unpruned trees (Fig. 3 b). Similar to flower count, the annual production of small developing pods on the stem showed a positive relation with BA_focal and a positive interaction between both BA_focal and BA_neighbor and pruning. Unlike for flower count, we did not find an overall effect of BA_neighbor, indicating that only in pruned trees, the production of small pods on the stem increased with neighbors size (Fig. 3 c). Yet, the annual amount of large developing pods on the stem was not significantly different between treatments, but increased with BA_focal and decreased with BA_neighbor (Fig. 3 d).

The number of wilted pods on the stem decreased with BA_focal. We also found a positive interaction of pruning and BA_neighbor on the number of wilted pods, indicating that wilting increased with neighbors size in pruned trees only (Fig. 3 e). The number of harvested pods on the stem was not impacted by pruning, and was only positively affected by BA_focal (Fig. 3 f).

The variation explained by the models for pod- and flower number on the stem was relatively low, with marginal R^2 ranging from 0.04 for harvested pods to 0.24 for large pods. By contrast, the model for annual number of pods harvested in the canopy explained a large part of observed variation (marginal R^2 of 0.62). Number of pods harvested in the canopy increased strongly with BA_focal while BA_neighbor had an opposite effect of comparable magnitude. We also found positive interactions of pruning with both focal and neighbor basal areas (Fig. 3 g).

Table 3.
Summary statistics of explanatory and response variables. P= pruned, U= unpruned.

		Mean		Sd		Min		Max	
	unit	U	P	U	P	U	P	U	P
Explanatory variables									
BA_focal	*cm2*	211.16	235.64	104.95	93.87	81.5	92.00	471.80	389.90
BA_neighbor	*cm2*	856.87	886.77	248.49	224.39	288.00	482.00	1373.10	1349.40
Response variables									
Harvest Pods- All	*n*	60.46	54.58	54.10	30.13	2	3	202	130
Harvested Pods-Stem	*n*	19.38	18.04	12.43	11.27	1	2	42	47
Harvested Pods-Canopy	*n*	41.63	36.25	47.43	26.11	1	1	160	96
Flowers	*n*	177.63	181.00	158.36	119.66	0	6	639	452
Small Pods	*n*	77.42	83.50	52.34	61.68	5	2	214	225
Large Pods	*n*	83.42	86.04	54.28	54.50	2	11	181	214
Wilted Pods	*n*	20.96	23.96	30.43	25.28	0	1	151	110
Flushing	*weeks y-1*	13.33	21.54	10.25	12.03	2	6	37	46

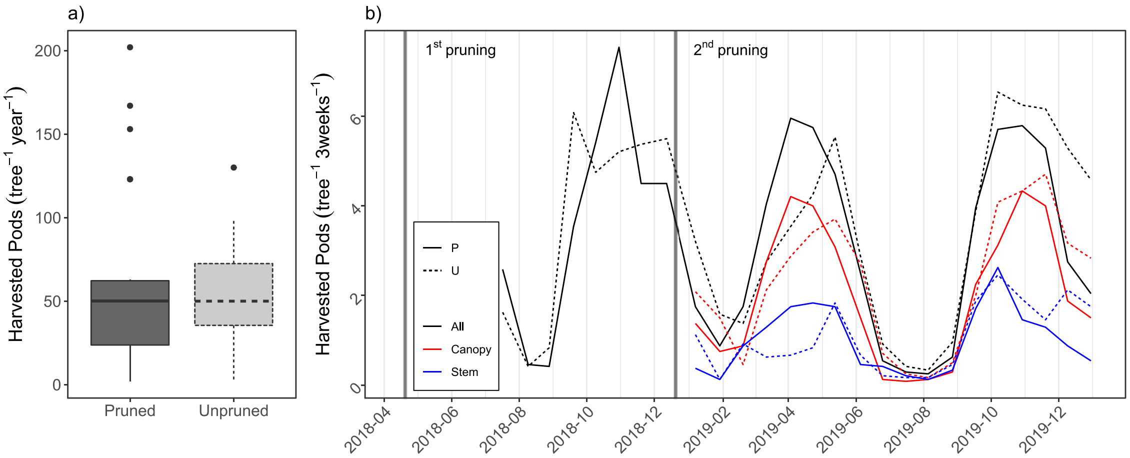

Fig. 2. Descriptive results of cocoa yield during the pruning experiment. (a) Distribution of Annual pod yield (number of pods) of pruned and unpruned trees in 2019. (b) Temporal dynamics of total pod yield (black lines) of pruned (continuous) and unpruned (dashed) trees during the experiment. From January 2019 onwards, stem (blue) and canopy (canopy) pods were recorded separately. The 2019 data were used in statistical analyses.

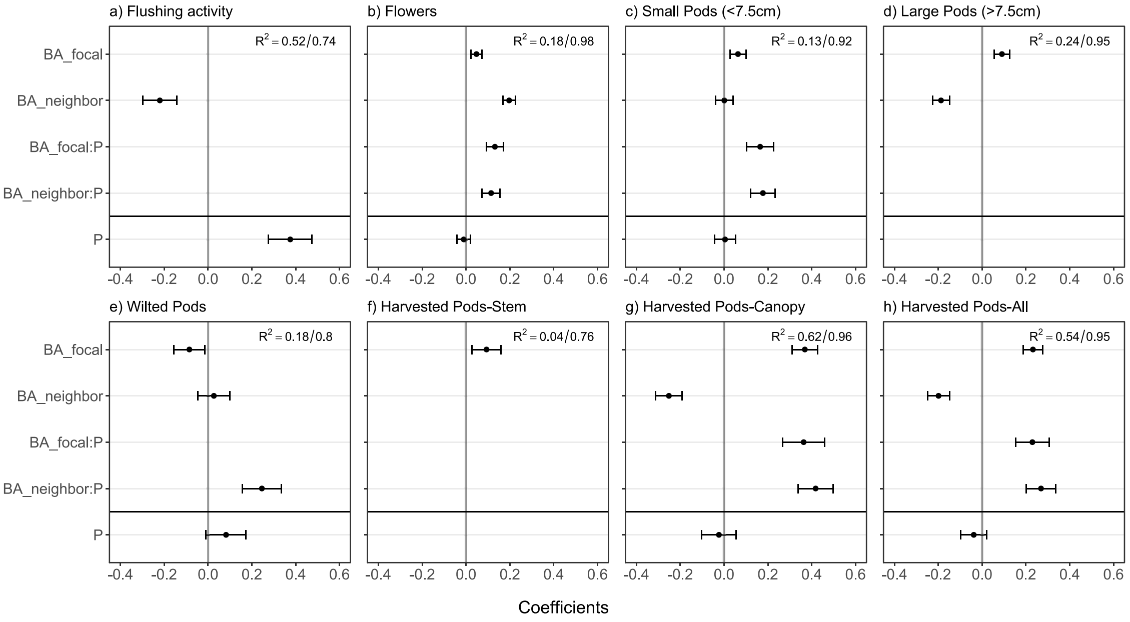

Fig. 3. Effects of pruning, tree size and neighbor size on vegetative growth, reproduction and yield, as derived from generalized linear mix effect models. Shown are means and 95% confidence interval of the coefficients for pruning (P), tree basal area (BA_focal) and summed neighbor basal area (BA_neighbor) and their interactions. Tested variables are flushing activity (a), annual flower production (b), annual number of small (c) and large (d) developing pods and annual number of wilted pods (e), annual number of harvested pods on the stem (f) and in the canopy (g) and total annual number of pods harvested (h). Panel b to f refer to counts on the stem only (up to 2 m in height). All coefficients apart from pruning (P) are standardized. Marginal and conditional R^2 are reported for each model.

Since canopy pods made up approx. 60% of total harvested pods, we found similar results for total pod production (i.e., the sum of canopy and stem pods). In this case though, effects sizes and the marginal R^2 were slightly lower (Fig. 3 h).

When neighbors size was kept constant at mean value, our model predicted that tree size will have a stronger positive effect on pod production in pruned trees than in unpruned trees (Fig. 4 a). By contrast, assuming an average tree size, the strongly negative effect of neighbor size on pod production, is largely mitigated by pruning (Fig. 4 b). Thus, pruning effects on pod production mostly manifest themselves as interactions with tree size and neighbor size rather than as main effects. The predicted net effect of pruning intervention, expressed in percentages, on annual number of pods per tree of all possible hypothetical combinations of BA_focal and BA_neighbor within the range measured in this study (Fig. 5) ranged from -58% for small trees under with small neighbors, to +150% for large tree with large neighbors.

Results of the analysis on pruned trees only were largely consistent with the analysis on the full dataset, both in term of direction of effects and of variation explained by models (Fig. S 3). Yet, for flushing, flowers and small and large developing pods we found a negative interaction between Rel_P and BA_neighbor, indicating that a heavier pruning intervention in combination with the presence of larger neighbors reduced the value of those response variables when compared with a lighter pruning and smaller neighbors (Fig. S 3 a–d). For canopy pods and total number of pod we found only main positive effect of Rel_P, BA_focal and BA_neighbor (Fig. S 3 g, h).

In contrast to results for pod number, the weight of individual pods was not associated with size of focal and neighboring trees. We did find that pods produced in the canopy were lighter than those on the stem and pods harvested in the minor season were lighter than those in the major season. We also found a positive interaction between season and pruning, indicating that in the minor season pods were heavier in pruned trees compared to unpruned trees (Table S 2).

For the combination of tree size and neighbors size that we simulated, yield estimation ranged widely from a maximum of 2.84 kg y^{-1} of dry beans for a hypothetical unpruned large tree (75th percentile) with small neighbors (25th percentile), to a minimum of 1.42 kg y^{-1} of dry beans for a pruned small tree (25th percentile) with small neighbors (25th percentile). The net effect of pruning, expressed in percentage, ranged from -40.7% percent for small trees with small neighbors to +32% for large trees (75th percentile) with large neighbors (75th percentile, Table 4). The simulated net pruning effect on dry bean yield is not directly comparable with the simulated annual number of pod produced per trees because the effect on stem and canopy pods were estimated separately for dry bean yield estimation and because canopy

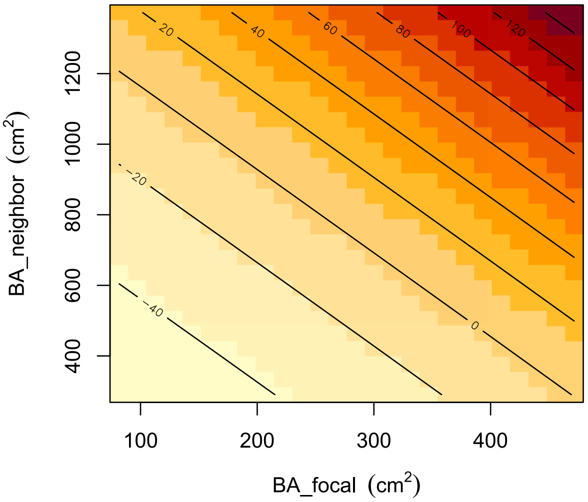

Fig. 5. Net effect of pruning for all possible combinations of basal area of the focal tree (BA_focal) and summed basal area of neighbors (BA_neighbor) on pod production (stem + canopy), as predicted by the generalized mixed effect model. Net pruning effects is expressed as a percentage of change in pod production: [pruned-unpruned]/unpruned * 100%. Lighter and yellow colors indicated a negative net effect and darker and red colors indicate a positive net effect. Contour lines of 20% increment are shown.

Table 4
Yield estimates per tree in kg y^{-1} of dry beans for pruned and unpruned fields of various combination of tree size (BA_focal) and neighbors size (BA_neighbor) expressed in percentile of the measured range. Net pruning effects is expressed as a percentage of change.

BA_focal percentile	BA_neighbor percentile	Unpruned Kg y^{-1} tree^{-1}	Pruned Kg y^{-1} tree^{-1}	% of change
0.25	0.25	2.40	1.42	-40.7
0.25	0.50	2.01	1.44	-28.5
0.25	0.75	1.70	1.46	-14.4
0.50	0.25	2.60	1.84	-29.3
0.50	0.50	2.18	1.86	-14.4
0.50	0.75	1.84	1.89	+2.9
0.75	0.25	2.84	2.56	-9.9
0.75	0.50	2.38	2.60	+9.6
0.75	0.75	2.00	2.65	+32.3

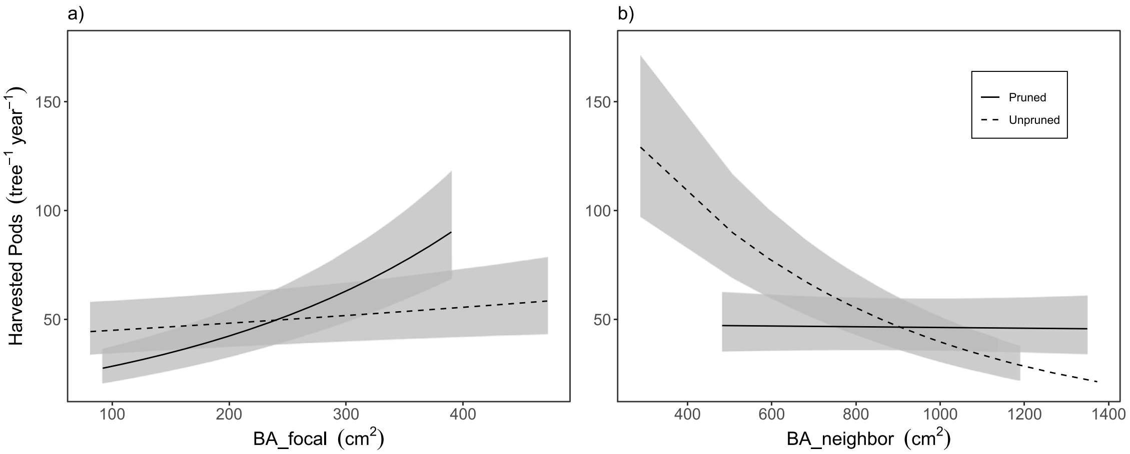

Fig. 4. Predicted interactive effects of pruning on the annual number of pods produced per tree, based on generalized mixed effect models. (a) Interactive effect of pruning and tree basal area (BA_focal). Summed neighbor basal area (BA_neighbor) was kept at the mean value. (b) Interactive effect of pruning and summed neighbor basal area (BA_neighbor). Basal area of focal tree (BA_focal) was kept at mean value. Grey shading represents the 95% confidence interval.

pods, being smaller than stem pods, contributed relatively less than stem pods to final yield.

4. Discussion

In this study we investigated how pruning affects cocoa tree light interception, growth and pod production and whether this effect depends on tree size and neighbor size. Pruning induced a compensatory response, enhancing flushing activity in pruned trees compared to unpruned ones. When only pruned trees were considered, we found this response to be mediated by pruning intensity and neighbor size. Additionally, as expected, tree size and neighbors size influenced the direction and magnitude of pruning effect on yield. Larger pruned trees performed better than smaller pruned trees and pruning strongly mitigated the negative effect of larger neighbors on pod production.

4.1. Pruning effect on light interception efficiency and induced compensatory growth

After one growing season pruned trees recovered their light interception while maintaining a more homogeneous vertical light distribution than unpruned trees. Light interception efficiency of pruned trees was enhanced, meaning that the average light interception per unit leaf area increased, with leaves deeper in the crown receiving more light in pruned trees than in unpruned ones. Hence the pruning intervention successfully changed the architecture of the trees toward a more open cup shape structure, with a better light penetration in the crown and a lower level of self-shading. Higher light interception efficiency has been reported in apple trees with an open center structure compared to a close center one (Willaume et al., 2004) and similar conclusion were drawn for simulated open center peach trees using a 3D modelling approach (Tang et al., 2015).

A higher efficiency in light capture does not necessarily ensure a better performance due to possible differences in total leaf area between pruned and unpruned trees. However Yapp and Hadley (1994) reported that light penetration through the canopy had a greater influence than light interception on yield in a mature cocoa plantation with a closed canopy. Cocoa is in fact a shade-tolerant species (Almeida and Valle, 2008) and a reduction in the amount of leaf area fully exposed to the sun together with an increase in the photosynthetic rate of shade leaves can have a positive impact on carbon assimilation. As cocoa has relatively low light-saturated rates of photosynthesis and associated light-saturation points (Da Matta et al., 2001), sun leaves do not make full use of the intercepted radiation, while shading the leaves deeper in the crown. The excessive radiation can result in photoinhibition and photodamage (Lahive et al., 2019), thus potentially reducing the contribution of those leaves to tree carbon assimilation.

When compared with unpruned trees, pruned trees exhibited a fast compensation of light interception that was clearly associated with an increase in leaf flushing activity. The latter is commonly reported in tree crops subjected to pruning, including cocoa (Leiva-Rojas et al., 2019), mango (Persello et al. 2019) and apple (Fumey et al., 2011). More generally, several compensatory mechanisms may contribute to the rapid vegetative production in response to pruning. These include: remobilization of stored carbohydrates, changes in biomass allocation towards the tissue types that were lost (in this case leaves and branches) and enhanced photosynthetic activity of the remaining leaves (Anten et al., 2003; Trumble et al., 1993). The relative importance of those factors varies with phenological phases (Davie et al., 2000), intensity (Fumey et al., 2011) and type of pruning (Sharma and Singh, 2006). In order to decompose the contribution of the different factors that contributed to the observed compensatory growth, measurements on photosynthesis, starch concentration and sap flow are needed.

Flushing activity was reduced by the presence of large neighbor cocoa trees. This result is in line with the observation by Mayer (1972), who found that cocoa trees in the middle of a stand had shorter flushing periods than isolated trees. When only pruned trees were considered, the negative effect of the presence of large neighbors was even stronger in trees that were more heavily pruned compared to tree that received a lighter pruning. A heavier pruning had most probably removed more photosynthetic biomass and the presence of larger neighbor trees might have resulted in lower amounts of stored reserves (Anten et al., 2003), thus limiting the potential for compensatory growth. As production of new leaves in cocoa is known to rely heavily on stored carbohydrates (Machado and Hardwick, 1988; Taylor, 1988), detailed studies on flushing in relation to non-structural carbohydrate concentrations, that take into account flushing intensity (i.e. percentage of flushing branches, number of leaves per flush) in addition to flushing activity, could shed more light on these compensatory responses. Repeated pruning interventions may lead to full depletion of reserves making trees less resilient to adverse climatic conditions or pest damage (Kobe, 1997). Understanding the dynamic of non-structural carbohydrate dynamics in response to pruning in multiyear experiments is therefore of much importance. Finally, since soil fertility in small holder cocoa fields are low (Ali et al., 2018), and nutrient limitation can alter plant compensatory responses (Hawkes and Sullivan, 2001) and competition (Coates et al., 2013), further research on pruning-fertilizer interactions are needed to provide specific pruning advice for unfertilized fields.

4.2. The indirect effect of pruning on pod production

In our one-year experiment, pruning acted as a modifier of other effects: it enhanced the positive effect of tree size and mitigated the negative effect of neighbor tree size on pod production. If only pruned trees were considered, pod production was positively affected by both tree and neighbor tree size, as well as by pruning intensity.

In general, larger trees produced more pods, as was recently reported for cocoa trees of similar hybrid mix (Trebissou et al., 2021). Larger trees in fact are expected to have larger root systems, as this scales nearly isometrically with above ground biomass (Niklas, 2005) and larger leaf areas and thus a greater capacity for resource acquisition and photosynthesis.

The positive relationship between tree size and canopy photosynthesis is curvilinear, largely because larger trees have deeper crowns and thus more self-shading (Ferree and Schupp, 2003). Therefore the positive impact of pruning through reduction of self-shading on canopy photosynthesis was probably stronger in larger than in smaller trees and it probably increased with pruning intensity. Additionally the positive impact of pruning on pod production in large trees may be explained by their larger carbohydrate reserves. In contrast, in small trees, the smaller leaf area, the possible initial lower level of self-shading and the expected lower reserve stock may have limited any positive effects of pruning on pod production.

The observed negative effect of neighbor trees size on pod production is in line with the findings of Trebissou et al. (2021). Interestingly, that study reported a comparable degree of variation in pod production among trees as we found here, possibly also influenced by the genetic diversity among trees (Tahi et al., 2019). Our findings are also consistent with the observed positive effects of pruning on fruit production in very dense avocado stands (Stassen et al., 1999), although in that study the effect of neighbor size was not explicitly quantified. Attribution of the mitigating effect of pruning on neighbor trees size to a release in either light or water limitation is hard and not possible without additional measurements. On the one hand, one can argue that the positive pruning effect in trees surrounded by larger trees is consistent with a release of light competition since we cut back all branches that were overshadowing or intruding neighboring crowns. On the other hand, it can also be argued that trees suffering more from water stress due to stronger competition for this resource with larger neighbors could have benefited more from the likely increase in soil moisture availability due to pruning than those trees that had fewer or smaller competing neighbors. This below-ground pruning effect may have played a role because our second pruning intervention (December 2018) took place right before the dry season. Pruning-induced reductions in transpiration were indeed found in studies measuring sap flow and tree water status in tree crops such as apple (Li et al., 2003), nectarine (Conesa et al., 2019) and wild cherry (Molina et al., 2019), while Martínez-Ramos et al. (2009) reported reduced drought induced mortality in defoliated palms. The increase in average weight of pods on pruned trees during the minor harvest further supports the hypothesis that pruning could have reduced water stress. In general, pods produced during the minor harvest were lighter than those from the major harvest as they developed during the dry season, when carbohydrate acquisition can be limited by water shortage and drought induced decrease in leaf area index (LAI) (Zuidema et al., 2005). Studies on timing of pruning intervention and sap flow measurements are required to further understand the impact on pruning on reduction of water stress.

The impact of pruning on neighbor competition can be placed in the wider context of the so-called Tragedy of the Commons, according to which an individual overinvestment in resource acquisition organs leads to a general decrease of stand performance (Anten and Vermeulen, 2016). As a result, LAI of vegetation stands may be larger than the optimal value for maximum photosynthesis (Anten, 2002). Thus, removal of leaves and branches through pruning could increase performance as it decreases leaf area and thus brings LAI closer to that of an optimal stand. Empirical tests of such stand-level effect of pruning on LAI are hard to implement in practice. An alternative for such empirical assessments is the development of 3D plant models that allow experimental manipulation and estimation of LAI implications (Louarn and Song, 2020). Such models exist for apple (da Silva et al. 2014), peach (Tang et al., 2015) and mango (Boudon et al., 2020), and are currently developed for cocoa. Such a modelling approach would facilitate the understanding of how size and competition mediated impact of pruning can shift with pruning intensity and for example, shade levels, as many cocoa fields are agroforestry systems. This approach would also aid the design of pruning intervention that are more context specific, therefore contributing closing the cocoa yield gap.

Our predictive models of the interactive effects of tree size, neighbor trees size and pruning on pod production at tree level (Fig. 5 and Table 4) reveal large variation in pruning effects. Within the range of tested conditions, the extreme scenario for small trees surrounded by small neighbors shows that these are strongly negatively impacted by pruning. In practice, this would correspond to expected pruning effects on less vigorous or younger trees. At the other extreme strong positive effects of pruning were found for large trees with large neighbors. This would correspond to more vigorous or older cocoa trees. Clearly, in most cases the net pruning effect will be somewhere between those two extremes, also because focal tree size and neighbor size are negatively correlated (data not shown; Trebissou et al., 2021). The variable pruning effects found here are consistent with – and may help explaining –the wide variation in published pruning responses. Given the large size heterogeneity in cocoa farms, our findings of size-mediated pruning effects suggests that the effectiveness of pruning interventions is a function of the size and competition distribution in cocoa fields.

4.3. What limits pod production in pruned cocoa trees?

Pruning influenced the number of small developing pods present on the stem but did not change the number of harvested pods on the stem. The increase in fruit abortion in pruned trees under strong competition probably caused the pruning effect to shift from a stimulation of small pod production to no (main or interactive) effect for harvested pods on the stem. Those trees may have had less resource available to sustain a high number of developing pods. Fruit abortion (cherelle wilt) is indeed a well-known mechanism of cocoa trees to adjust the number of developing pods to the amount of resource available (Valle et al., 1990).

Due to size and architectural complexity of the tree crowns we could not directly count flowers, developing and wilting pods in the canopy, thus we can only formulate likely hypotheses on the causes of the increase in number of pods that was observed in the crown. First, pruning may have stimulated flower production in the canopy, possibly in response to the improved light condition (Ferree and Schupp, 2003). Second, pruning may have reduced fruit wilting in the canopy because of the higher light availability (Byers et al., 1991) due to deeper light penetration into the crown and thus created a higher local availability of resources, allowing more pods to develop and ripen. Some support for this second hypothesis is provided by the lack of effects of pruning on stem pod production: if higher availability of carbohydrates in the canopy are used locally to support the development of a higher number of canopy pods, the amount of assimilates reaching the stem could have remained unchanged after pruning. As highlighted in a recent review on cocoa physiology, however, mechanisms of environmental control on cocoa flowering and carbohydrate partitioning among different organs in relation to the cauliflorous nature of the crop remain largely unknown (Lahive et al., 2019), and direct measurements of flowering and wilting dynamics in a representative part of the crown could shed some light on those mechanisms.

4.4. Implication for cocoa pruning management

Our study has implications for the measurement and analyses of results in pruning studies and demonstration plots. The strong interactions of pruning effects with tree size and neighbor trees size highlights the importance of a tree-based assessment of pruning treatments, instead of the conventional plot-based assessments that dominates pruning literature. The field measurements and statistical methods used here are an example of such tree-level analysis. The development, documentation and free availability of statistical packages and analyses tools for mixed-effect models allow wide application of tree-level analyses. We also stress that caution is recommended when reporting and interpreting yield values that are derived from pruning effect estimates at plot level, especially if plot size is small and/or tree size distribution is not taken into account.

Based on our results, we formulate three suggestions for pruning practices for adult cocoa trees. First, we recommend pruning treatments to aim at reducing competition between cocoa trees and size differences within the stands. By focusing on large trees and trees experiencing more competition, the effects of pruning can be maximized. Second, our results suggest that pruning can help avoiding overcrowding and optimizing LAI and thus prevent yield reduction that is commonly observed in cocoa field from a certain age onwards (Lachenaud and Oliver, 1998; Tahi et al., 2019). Third, the variation in net effect of pruning on pod production suggests that, in practice, pruning interventions need to be tree specific, and more attention should be given to tree-level pruning assessment and treatment in manuals and trainings.

Finally, one of the most important strategies to increase yields of most crops in the past has been increasing plant density and creating less competitive plant types that have traits that give high yield per unit area at such densities (Duvick and Cassman, 1999). While selection for less competitive types is difficult in cocoa because of the long breeding cycle, our results show that competition among individuals could be effectively reduced by pruning suggesting that pruning can play a critical role in cocoa systems intensification. Further density-pruning experiments are however needed to support this development.

Data availability

The data used in this study are available on the DANS-EASY database, doi: 10.17026/dans-xt7-mbgq.

CRediT authorship contribution statement

Ambra Tosto: Conceptualization, Methodology, Investigation, Formal analysis, Visualization, Writing – original draft. **Pieter A.**

Zuidema: Conceptualization, Methodology, Writing – review & editing, Supervision. **Eva Goudsmit:** Methodology, Investigation, Writing – review & editing. **Jochem B. Evers:** Conceptualization, Methodology, Writing – review & editing, Supervision. **Niels P.R. Anten:** Conceptualization, Methodology, Writing – review & editing, Supervision, Funding acquisition.

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.

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