Experimental Agriculture (2025), vol. 61, e25, 1–12
doi:10.1017/S001447972510015X

CAMBRIDGE UNIVERSITY PRESS

RESEARCH ARTICLE

Effects of climate and within-tree competition on cocoa pod production in Ghana

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(Received 04 October 2024; revised 15 July 2025; accepted 01 August 2025)

Abstract

Cocoa production is highly variable and shows low yields globally, but the drivers of this variation are poorly understood. Climate has been proposed as one of the main drivers, but within-tree competition for resources and disease may also influence the number of cocoa pods produced. In addition, the relative importance of climate and within-tree competition for resources remains unknown. We evaluated the effects of climate, within-tree competition, and disease on cocoa pod dynamics in Ghana and assessed the relative importance of climate and within-tree competition. We monitored cocoa pod dynamics during three years for 1472 trees at 96 farms across Ghana. Counts of pods of different sizes were carried out every six weeks. Climate effects were evaluated based on monthly precipitation and temperature, including lag effects. Effects of within-tree resource competition on pod production were tested by assessing the effect of the number of larger-sized pods on a cocoa tree on the number of pods in smaller size classes using generalised linear mixed-effects models accounting for zero inflation. We consistently found that climate was a stronger driver of pod production than within-tree competition. Across size classes, the climatic conditions experienced at the time of fruit set had the strongest effect on the number of pods. For most pod size classes, both higher temperature and, unexpectedly, higher precipitation negatively influenced pod number. A larger number of large and mature pods negatively affected the number of cherelles (smallest pods), indicating within-tree competition among pods. This suggests that cocoa trees prioritise sustaining pods in larger sizes over producing new ones, for instance, through mechanisms like cherelle wilt. Our results suggest that higher precipitation increased the incidence of fungal diseases and indirectly reduced the number of pods produced. Thus, a combination of lagged climate effects and within-tree competition and disease drives the dynamics and development of pods on cocoa trees. Our results show that lagged climate effects should be considered for adaptation measures to climatic conditions (and climate change) and for determining the best timing for disease management interventions. These results help in understanding cocoa production dynamics and are important for yield and disease modelling.

Keywords: Cocoa production; climate; within-tree competition; disease

Introduction

Cocoa is one of the most important tropical commodities worldwide, but yields are typically low, and causes of this low yield remain poorly understood (Carr & Lockwood 2011; Asante *et al.* 2021). Causes of low cocoa production, for example, are limited management including aging cocoa trees, inadequate planting material, poor pruning practices, low economic returns from cocoa farming, aging farmers, high levels of pest and disease pressure (e.g. cocoa swollen shoot virus and black pod), and poor soil fertility (Groeneveld, 2010; Nalley *et al.*, 2014; Akrofi *et al.*, 2015; Artavia Oreamuno & Croppenstedt, 2023; Mensah *et al.*, 2023; Tosto *et al.*, 2022). Modelling and field studies suggest that climate change poses threats to cocoa production (Läderach *et al.*, 2013; Gateau-Rey *et al.*, 2018) and may cause loss of suitability in certain areas (Läderach et al., 2013; Schroth *et al.*, 2016; de Sousa *et al.*, 2019), due to drought stress (Santos *et al.*, 2018; da Silva *et al.*, 2017) and low pollinator abundance when cocoa is flowering (Toledo-Hernández *et al.* 2017; Arnold *et al.*, 2018). To assess the effects of climate change on cocoa production, an enhanced understanding of the drivers of cocoa pod production is needed.

Climate variables such as radiation, temperature, and precipitation largely drive cocoa vegetative growth and pod production (Alvim, 1977; Young, 1983, Zuidema *et al.*, 2005, de Almeida & Valle, 2007). Radiation, water availability, and temperature influence photosynthetic carbon assimilation, which directly determines pod growth and wilting of the small pods (cherelles) (Daymond & Hadley, 2008; Schwendenmann *et al.*, 2010; Lahive *et al.*, 2019). For instance, reduced water availability has been shown to decrease pod number by 10% and cocoa bean yield by up to 45% (Schwendenmann *et al.*, 2010). Pod production can also be severely reduced (up to 60%) by excessive rain (Bos *et al.*, 2007), through waterlogging or increased disease incidence, in Ghana, especially from black pod (*Phytophthora palmivora* and *Phytophthora megakarya)* (Akrofi *et al.*, 2015).

Climatic conditions impact cocoa reproductive phenology (Young, 1983; Wuriandani *et al.*, 2018), including the number of flowers, pollination success, cherelle wilt, pod growth, and the number of beans per pod (Alvim, 1977; Marelli *et al.*, 2019; Toledo-Hernández et al., 2020). Due to the long time (5-6 months) required for pod ripening (Niemenak *et al.*, 2010; de Almeida & Valle, 2007), the effects of climatic conditions on cocoa yield can be delayed. For example, Wilson *et al.* (2019) used a delayed differential equation model to show lagged precipitation effects on cocoa yield. Temperature fluctuations may also affect cocoa yields. Glasshouse experiments showed a positive relationship between temperature and cherelle wilt and developmental rates of surviving pods, with the latter effect exhibiting strong genotypic variation (Daymond & Hadley, 2008).

Cocoa trees produce large amounts of flowers, but only few of those are successfully fertilised and develop into a pod (Adjaloo *et al.*, 2012; Groeneveld *et al.*, 2010; de Almeida & Valle, 2007). In addition, typically around 70% of the cherelles are lost by wilting (i.e. cherelle wilt), thus, critically reducing the number of pods that reach the mature stage and affecting final cocoa production (Young, 1983; Bos *et al.*, 2007). Data from Brazil suggest that pods are prone to wilting up to 70–90 days after pollination (Valle *et al.*, 1990). Cherelle wilt can be due to pollination-related deficits (Toledo-Hernández *et al.*, 2017) or due to within-tree competition for assimilates between pods or with other growing organs (de Almeida & Valle, 2007; Carr & Lockwood, 2011). This effect increases with pod load due to stronger within-tree competition among pods (Humphries, 1943). However, both mechanisms explaining cherelle wilt remain poorly understood.

Climate may also indirectly affect pod number through an effect on disease incidence (Groeneveld *et al.*, 2010), for example, the incidence of several diseases like black pod (*Phytophthora spp*) increases with rainfall and associated humidity (Ndoumbè-Nkeng *et al.,* 2009; Akrofi *et al.*, 2015; Marelli *et al.*, 2019). Infection of mature cocoa pods by diseases leads to an estimated yield loss of 30% worldwide (Ndoumbè-Nkeng *et al.,* 2009).

Previous studies focused mainly on the effects of either climatic variation or within-tree competition on cocoa pod dynamics. Yet, the interplay between climate and within-tree competition on pod production and disease occurrence remains poorly understood. To address this knowledge gap, we explore four research questions (RQ): (1) To what extent do temperature and precipitation influence pod number and with what time lag?; (2) To what extent is the number of small pods limited by within-tree competition with larger pods?; (3) What is the relative importance of climate and within-tree competition in determining the number of pods in different size classes?; and (4) Do precipitation and temperature influence the number of pods infected with black pod (*Phytophthora spp*)?.

We expect (i) the number of pods of all sizes to show lagged responses to climatic conditions with pod numbers increasing with increasing precipitation, because greater water availability could stimulate photosynthesis and growth, and decreasing with increasing temperature due to higher evapotranspiration or increased respiration; (ii) a negative effect of the number of larger pods on pod production caused by a higher rate of pod abortion due to within-tree assimilate competition; (iii) a stronger effect of climate than of within-tree competition on pod number, as climate mediates many physiological and reproductive mechanisms; and (iv) an increase in disease incidence with increasing precipitation, and a decrease with increasing temperature.

Materials and methods

Study area

Cocoa reproductive phenology was monitored on 96 farms in the Ashanti, Western, Eastern, and Brong Ahafo regions in Ghana from August 2012 to August 2014 (Fig. 1a). Mean diurnal temperatures ranged from 25 to 30°C, and mean annual precipitation ranged from 1200 to 2000 mm (Fig. 2b). The farms were located in wet to mid-wet zones characterised by evergreen and deciduous climax vegetation (Abdulai *et al.,* 2020). All farms used shade trees in their cocoa stands, but shade tree density varied between farms, with an average of 15.9 trees per hectare (Asante *et al.*, 2021). Per farm, four plots were established and, within each plot, four cocoa trees were randomly selected to be monitored, resulting in a total of 16 trees per farm. In total, 1536 trees were monitored 17 times, at approximately 6-week intervals. The planting material was a combination of Amelonado and highly productive hybrids developed and distributed by the Cocoa Research Institute of Ghana (CRIG). All pods were counted and assigned to four size classes: cherelles (pods of 5–10 cm length), medium-sized pods (11–15 cm), large pods (>15 cm), and mature pods (>15 cm and with changing colour) (Fig. 1b). The number of pods infected with black pod (*Phytophthora spp*) per tree was also recorded. Pods were classified as infected when they exhibited black spots on the husks.

Farms and climatic clusters

Farms were clustered based on similar topographic characteristics to ensure that there was negligible climatic variation amongst the farms in the same cluster. We grouped farms if they were located (1) within 30 km distance from each other, and (2) within an altitude range of 100 m. We extracted the monthly average temperature and monthly sum of precipitation at the centroid of each cluster for the period of data collection (2012–2014) from the NASA Power database at a 0.5-degree resolution (~55 km) (Stackhouse *et al.* 2016) (Fig. 1b). We assume that the climate is homogeneous for farms within the same cluster.

Data analysis

To assess the effects of climate (at the level of farm clusters) and within-tree competition on cocoa pod number, we used generalised linear mixed-effects models (GLMMs) that account for the nested design of the study and for repeated observations per tree. Because of the large number of zero counts, we used zero-inflated GLMMs with a negative binomial distribution. To assess

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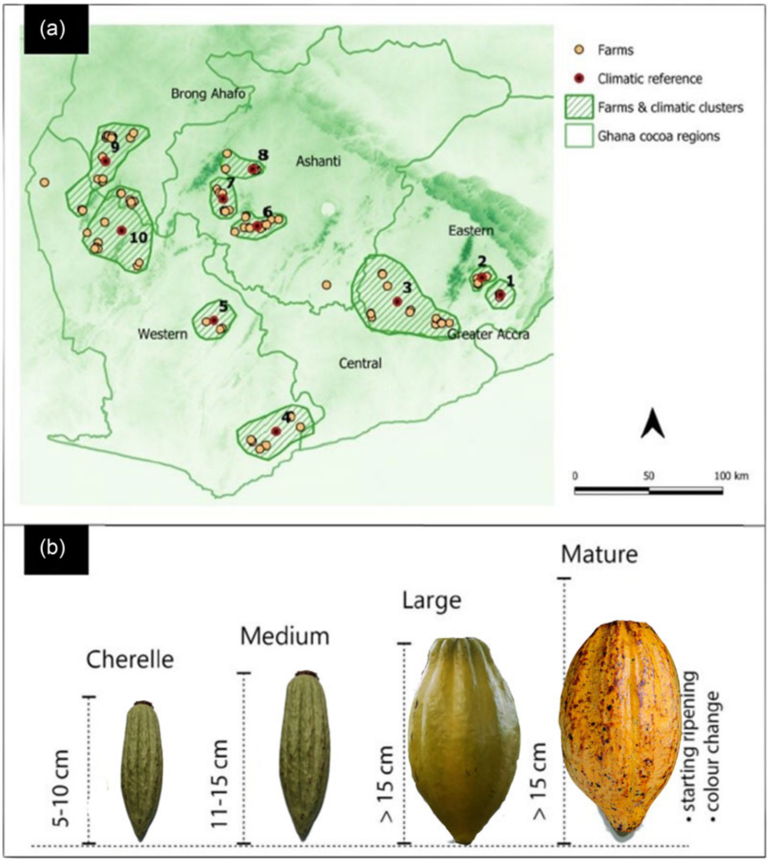

Figure 1. (a) Locations of the 96 included farms and of the clusters for climate data in Ghana. The polygons show the farm clusters with similar environmental conditions. Climate data were extracted at the centroid of each cluster. (b) Pod size classes used in the study.

possible lag effects of temperature and precipitation on pod number (RQ1), we built various models for each pod size class: for cherelle and medium pods, we tested models with monthly temperature and precipitation with a time lag of 1 to 3 months, while for large and mature pods, we tested time lags of 1 to 5 months (Table S1). For each model, we included precipitation and temperature with the same time lag. Simultaneously, in the models for each pod size class, the number of pods in larger pod size classes was included as fixed effect to assess the effect of within-tree competition for assimilates (RQ2). More specifically, the influence of pods in larger pod size classes on smaller pods was tested as follows: (1) for the number of cherelles, effects of the number of medium-sized, large, and mature pods were tested; (2) for the number of medium-sized pods, effects of the number of large and mature pods were tested; and (3) for the number of large pods, only the effect of the number of mature pods was tested. We only tested the effects of climate in the models for the number of mature pods, as this was the largest pod class.

To assess the relative importance of climatic variation and within-tree competition on pod number (RQ3), we compared the magnitude of the standardised coefficients of temperature, precipitation, and the number of larger-size pods for each pod size class. Finally, to evaluate the climate effect on black pod incidence (RQ4), we followed the same procedure as for RQ1, testing the effect of climate at different time lags on the number of diseased pods. In all the models, we also included all two-way interactions between pod size classes and temperature and precipitation.

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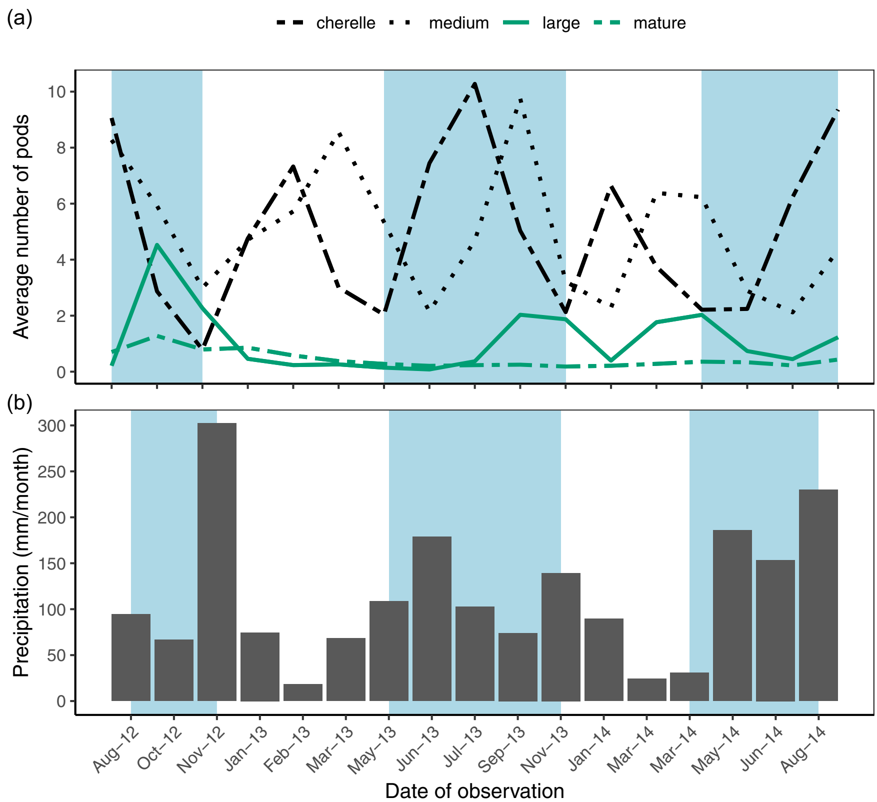

Figure 2. (a) Average number of cocoa pods per size class per observation date and seasonal patterns in precipitation for 96 cocoa farms in Ghana. The rainy seasons are indicated in light blue. (b) Monthly precipitation during the study period (mm/month).

We included a random intercept, per tree, plot and farm, in a nested random effects structure. For each pod size class, we compared all models based on the Akaike Information Criterion (AIC) and selected the best model for each pod class based on the lowest AIC. All predictors were standardised by subtracting the mean and dividing by the standard deviation to be able to compare effect sizes (Gelman & Hill, 2006). All statistical analyses were performed in R 4.0 (R Core Team, 2021). Zero-inflated GLMMs were fitted using the glmmTMB package (Brooks *et al.*, 2017).

Results

First, we assessed how climate influenced pod number, and at what time lag (RQ1). We found that the best model explaining the number of pods in each of the size classes included average monthly temperature (T) and monthly sum precipitation (P) at the moment of fruit set (Fig. 3). For cherelles, the best model included the climate one month ago; for medium-sized pods, the climate of two months ago; and for large and mature pods, the climate of four and five months ago, respectively. Thus, in all classes, the weather at pod-set was the most important climatic predictor of pod number. In all pod size classes, the number of pods decreased with increasing temperature and precipitation. For cherelles, large and mature pods, temperature had a stronger effect compared to the other predictors, while for medium-sized pods, precipitation had the strongest effect (Fig. 3).

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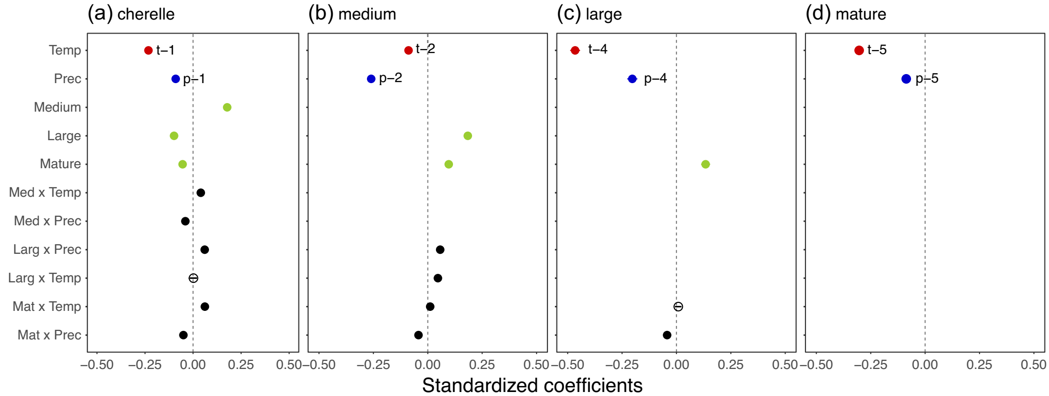

Figure 3. Effects of lagged temperature and precipitation and the number of larger pods on cocoa pod numbers in four size classes: (a) cherelles, (b) medium-sized pods, (c) large pods, and (d) mature pods. Standardised coefficients from the best generalised linear mixed-effects model per pod size class are shown. Interactions are indicated for the two factors interacting in the model (Med=the number of medium-sized pods; Larg=large pods; Mat=mature pods; Temp=temperature; Prec=precipitation). The labels within the plots indicate the time lags of temperature (t) and precipitation (p), for example, p-1 means precipitation one month prior to pod count. Closed circles indicate significant effects, while open circles indicate non-significant effects.

Second, we assessed whether the number of small pods is influenced by the number of large pods (within-tree competition; RQ2). The number of cherelles was negatively influenced by the number of large and mature pods, but was positively influenced by the number of medium-sized pods. Instead, the number of medium-sized pods increased with an increasing number of large and mature-sized pods, and the number of large-sized pods increased with an increasing number of mature pods (Fig. 3).

Third, we determined the relative importance of climate and within-tree competition in determining the number of pods in different size classes (RQ3). The number of cherelles was strongly affected by the number of large and mature pods, but temperature had a stronger effect than the number of pods in larger-size classes. In contrast, for medium-sized pods, precipitation had the strongest effect. Additionally, the positive effect of medium-sized pods on the number of cherelles was stronger than the negative effects of the number of large and mature pods. Furthermore, the number of large pods had a stronger effect than the number of mature pods on the number of cherelles. For medium-sized pods, the positive effect of the number of large pods was stronger than the effect of temperature but weaker than the effect of precipitation. For large pods, both temperature and precipitation had stronger effects than the number of mature pods, with temperature having the strongest effect (Fig. 3).

We found significant interactions between climate and the number of pods in larger-size classes, indicating that the effects of within-tree competition depended on temperature and precipitation, but overall, the interaction effects were weak (Fig. 4).

Last, we evaluated the effect of precipitation and temperature on the number of pods infected with black pod (RQ4). The best model testing the effects of climate conditions on the number of damaged pods by black pod included a four-month time lag for precipitation and temperature. The number of infected pods increased with increasing precipitation and decreased with increasing temperature (Fig. 5).

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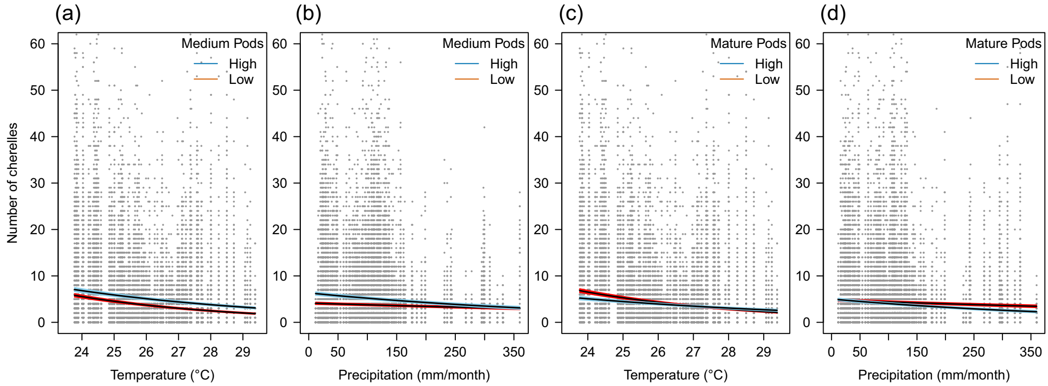

Figure 4. Effects of climate and the number of pods in larger-size classes on the number of cherelles. Medium-sized pods (a & b) and mature pods (c & d). The number of pods was kept constant at either a high (90th percentile, blue line) or a low (10th percentile, red line) value. Confidence intervals are indicated in blue and red.

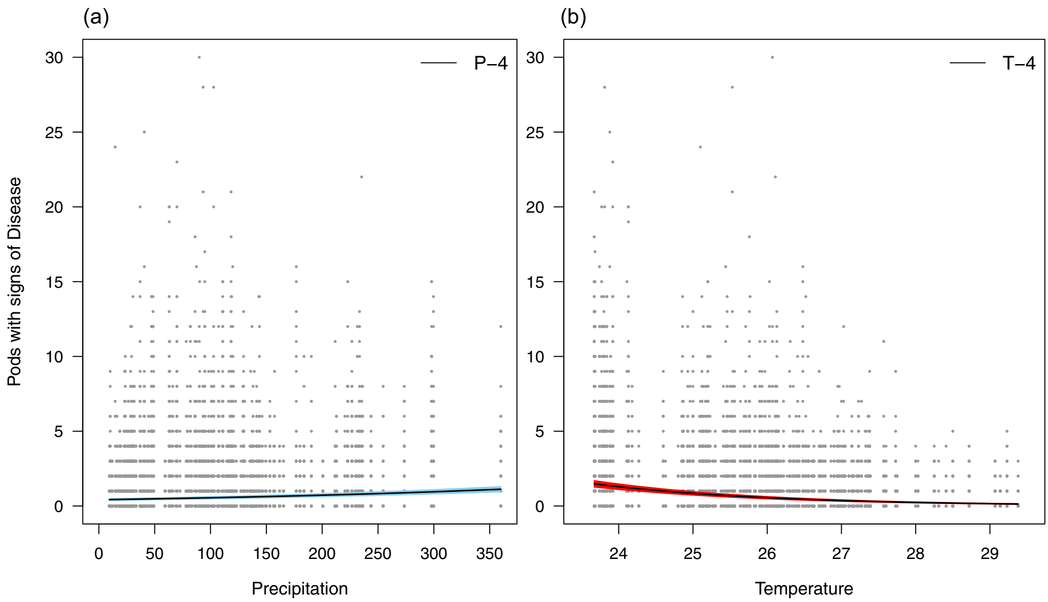

Figure 5. Relation between precipitation (a) and temperature (b) and the number of large and mature diseased pods. Precipitation and temperature include a 4-month time lag, thus measured four months before the count of diseased pods. Confidence intervals are indicated in blue and red.

Discussion

Lagged climate effects on pod production

Our results show that the number of cocoa pods in all size classes was best predicted by the climatic conditions in the period of fruit set, with negative effects of both increasing temperature and increasing precipitation (RQ1). Our findings agree with those of other studies that showed that the period of fruit set has a major impact on yields of several crops (Holzschuh *et al.*, 2012;

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Garibaldi *et al.*, 2013; Forbes & Northfield, 2017). Cocoa has shown delayed effects to water limitation. For example, cocoa dry bean weight decreased more than 50% after recovery to water deficit months before (Moser *et al.*, 2010). Similarly, after the strong 2015-16 El Niño event in Brazil, cocoa tree mortality was high and yield was reduced by more than 80% up to 9 months after the drought event (Gateau-Rey *et al.*, 2018).

The negative effects of temperature during the period of fruit set on the number of pods confirmed our hypothesis that high temperatures limit cocoa pod production. Higher temperatures can lead to lower nutrient transport within the plant, higher evapotranspiration, and potentially reduced pollination success, ultimately negatively affecting pod production (Young, 1994; de Almeida *et al.*, 2016; Asante *et al.*, 2021). In addition, higher temperatures increased cherelle wilt in greenhouse experiments, possibly due to stronger competition for assimilates within cocoa trees (Daymond & Hadley, 2008), reducing the number of pods produced.

Contrary to our hypothesis, we found negative effects of precipitation on the number of pods produced. This could be the result of high humidity associated with intensive or long periods of rain, leading to waterlogging and/or an increase in the incidence of diseases (Ndoumbè-Nkeng *et al.*, 2009). We found that the occurrence of pods with signs of disease significantly increased with increasing precipitation, indicating that excessive rainfall, and potentially high humidity, reduces pod production (see section *Climate effects on disease incidence*). These findings show the importance of lagged climate effects on cocoa production, which is of high relevance in the current and future climate change conditions to improve predictability and timely management. A recent study on the future effects of climate change on cocoa production in West and Central Africa showed that, in Ghana, a combination of higher temperatures but wetter dry seasons and elevated CO_2 could maintain and even increase cocoa yields with moderate projected climate scenarios in 2060, if management practices like nutrient inputs, adequate pruning, and disease management are promoted (Asante *et al.*, 2025). Including lagged climate effects in such studies can have the potential to help more accurately predict future yields (for both short-term yield forecasting, as well as long-term yield projections under climate change), as it will allow greater accuracy in determining the timing of climate effects.

Effects of within-tree competition on pod number

We found that an increasing number of large and mature pods had a negative effect on the number of cherelles (RQ2). This suggests the occurrence of a within-tree competition effect, in agreement with our hypothesis that within-tree competition among pods will increase with an increasing number of larger pods. Nevertheless, the positive effect of medium-sized pods on the number of cherelles was unexpected, and also, the number of pods in medium, large, and mature-size classes was positively associated with the presence of larger pods. The fact that only the number of cherelles decreased with an increasing number of large and mature pods suggests that cherelle wilt is the main mechanism that regulates within-tree competition for assimilates. This effect was documented already in Humphries (1943): *"the young fruits tend to wilt at progressively earlier stages as the growing season advances"*. The allocation of assimilates and nutrients towards larger pods has indeed been found to generate higher rates of cherelle wilt (Stephenson, 1981; Bridgemohan & Mohammed, 2019). Larger pods are not affected by wilting because they have passed the wilting phase (up to 70–90 days from fruit set) (Valle *et al.*, 1990), and may, therefore, be experiencing less within-tree competition for assimilates (Daymond & Hadley, 2008). However, the effects of within-tree competition on other aspects, such as final pod weight and bean size and bean quality, require additional research.

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Relative importance of climate and within-tree competition for pod production

For pods of all sizes, we found that climatic conditions had a stronger effect on the number of pods produced than within-tree competition, confirming our hypothesis for RQ3. At the same time, the effects of the number of large and mature pods on the number of cherelles were weaker than the positive effect from the number of medium-sized pods. This could indicate that favourable weather conditions at the time of fruit set would translate into a bigger number of both cherelles and medium-sized pods, regardless of the presence of larger pods. Nevertheless, other studies indicate that under stress conditions, cocoa plants prioritise vegetative over reproductive development (Moser *et al.*, 2010; Schwendenmann *et al.*, 2010; Lahive *et al.*, 2019), meaning that a stronger negative effect of climate can increase within-tree competition, thus increasing cherelle wilt and reducing bean size. We also found significant interactions between climate (precipitation and temperature) and the number of pods in larger-size classes, but the interaction effects were weak.

Climate effects on disease incidence

We found that the number of pods with visible damage from black pod disease significantly increased with increasing precipitation, indicating that excessive rainfall indirectly reduces pod production (RQ4). Our results are in line with those of Bridgland (1953), who found negative precipitation effects on cocoa pod numbers with a time lag of 4–5 months. Similarly, Ali (1969) reported a negative effect of precipitation on cocoa during the rainy season, while the effects of precipitation were positive during the dry season. The increased incidence of infected cocoa pods with increasing precipitation was consistent with results from Anim-Kwapong and Frimpong (2004), who found that black pod incidence (*Phytophthora spp)* increased under humid and shaded conditions in Ghana. This effect can be explained by more effective spore propagation in fungal diseases at high humidity levels (Marelli *et al.*, 2019). Lower disease incidence at higher temperatures was likely due to higher radiation and drier conditions, which inhibit the release of spores (Marelli et al, 2019). However, finding effects of climate on disease at a four-month time lag was unexpected given that infection by black pod, especially from *Phytophthora megakarya,* occurs within a few days to weeks (Akrofi *et al.*, 2015; Marelli *et al.*, 2019).

Conclusions

Our results suggest that cocoa pod production is driven by the combined effects of climate and within-tree resource competition, but the effects of climatic conditions were the strongest. Increasing temperature, and unexpectedly also precipitation, at the time of fruit set had a negative effect on the number of pods produced. The number of pods in larger-size classes had a negative effect on the number of cherelles, indicating within-tree competition for assimilates. The number of diseased pods increased with precipitation and decreased with temperature at a time lag of four months. Higher disease levels under humid conditions may explain the negative effect of precipitation on pod production. Our results are also useful for determining the best timing for disease management interventions, such as reducing shade cover to minimise excessive humidity and fungicide application. These results help in understanding cocoa production dynamics and are important for yield and disease modelling, for example, for the projection of climate change effects on cocoa production.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S001447972510015X

Author contributions. EMS, AT, NA, and PZ formulated the research questions. All authors designed the study. EMS, DR, AT, and PZ carried out the study and analysed the data. All authors contributed to the interpretation of the results and to writing the manuscript.

Funding statement. This work was supported by the Costarican Ministry of Science and Technology for funding the studies of first author's master program (MICITT; grant P300P2_174477 to EMS); the Netherlands Foundation for the Advancement of Tropical Research (NWO-WOTRO; grant W08.250.305 to AT); and Mondelez International for providing access to the data. Funders had no role in the design, analysis, or writing of this article.

Competing interests. The authors have no competing interests.

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Cite this article: Montero-Sánchez EA, Rozendaal DMA, Tosto A, Anten NPR, and Zuidema PA. Effects of climate and within-tree competition on cocoa pod production in Ghana. *Experimental Agriculture*. https://doi.org/10.1017/S001447972510015X