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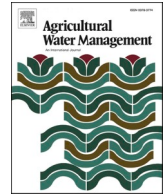
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Negative effects of water deficit on cocoa tree yield are partially mitigated by irrigation and potassium application

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ABSTRACT

Yields of most tropical crops are strongly reduced by drought, but this may be partially mitigated by irrigation and potassium application. Understanding the mechanisms regulating these relationships is essential to select crop varieties reaching high yield under environmental stress. We conducted a 2-year field experiment (2020–2022) to investigate the effects of seasonal irrigation, potassium application and their interaction on cocoa reproduction and yield, using six genotypes in Côte d'Ivoire. Potassium application increased pod number and size, contributing significantly to annual yield, but this effect was conditional to soil water availability. Similarly, irrigation when combined with potassium application almost doubled yield from 1.5 to 3.0 kg/tree (2000 kg ha⁻¹ yr⁻¹ to 4000 kg ha⁻¹ yr⁻¹, respectively). This yield effect was mostly the result of positive effects of irrigation on pod number per tree and, to a lesser extent, due to its positive effects on bean number per pod and bean mass. Irrigation effects on pod number were associated with an increased number of cherelles whereas the larger pod number during the major harvest compared to the minor harvest was associated with lower cherelle wilt. We also found a more than two-fold genotypic difference in yield, with the genotypes CI02 and CI03 and to a lesser extent hybrid M having lower yields than the genotype CI01. These genotypic yield differences were associated with differences in both cherelle wilt and initial cherelle production rates. The effects of withholding irrigation on yield were significantly dependent on the genotype, reflecting a potential genotypic difference in drought tolerance. The development of climate adaptive strategies for cocoa production requires integrating effects of irrigation, potassium application and cocoa genotype on yields. Future research should focus on unraveling the underlying genotypic and ecophysiological mechanisms of the results presented here, and identifying other potential approaches to enhance the resilience of cocoa to increasing water deficit under climate change.

1. Introduction

More than 70% of world cocoa is produced in West Africa. Nearly two million small-scale farmers cultivate this crop across an estimated six million hectares of forested lands, with Côte d'Ivoire being the largest producer with 800,000 smallholder farmers and about 2 million hectares of land (Wessel and Quist-wessel, 2015; Schulte et al., 2020; ICCO, 2021; CIFOR-ICRAF, 2021). Cocoa yield is susceptible to variable and reduced rainfall (Balasimha et al., 1988; de Almeida and Valle,

2007; Schroth et al., 2016). For instance, model simulations identified that dry-season rainfall and temperature accounted for 70% of the variation in simulated cocoa yields (Zuidema et al., 2005). Hence, concerns were raised about possible yield declines in many cocoa growing regions under climate change (ICCO, 2012), which is projected to result in more erratic rainfall, especially at the drier end of the cocoa belt (Asante, 2023). In addition to its direct effects, drought can induce a higher susceptibility to pests and pathogens (CacaoNet, 2012). The aforementioned adverse effects of climate change pose significant

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challenges to future cocoa production (Schroth et al., 2016) worldwide. Therefore, it is crucial to develop strategies that enable cocoa farmers to cope with water deficits and ensure the sustainability of their livelihoods.

Cocoa yield is defined as being very sensitive to drought conditions as a result of rainfall reduction (Gateau-Rey et al., 2018; Bae et al., 2008). Optimal growth is achieved at annual average rainfall between 1400 and 2000 mm yr⁻¹. Growth and yield decline when annual rainfall drops below 1200 mm (Alvim, 1977) and also when dry seasons are prolonged (Zuidema et al., 2003; Dohmen et al., 2018). Drought stress occurs when potential water loss through transpiration exceeds the ability of the tree to absorb water, thus reducing various physiological processes and tissue growth. The most obvious agronomic measure to deal with water shortages is to apply irrigation when shortages occur (e. g. during the dry season). An old study on mature cocoa (Hutcheon, 1973) showed that irrigation during the dry season reduced cherville wilt and increased pod setting and yield by over 40%. Similar effects were found in rain exclusion studies, resulting in a 10% decline in cocoa yield (Moser et al., 2010). So far, most studies on drought effects in cocoa have focused on seedlings and – as far as we know – few published studies have analyzed dry-season irrigation effects on yield in adult field-grown cocoa trees. Therefore, there is relatively little knowledge on the effects of dry-season irrigation on cocoa production and how these effects are modified by genotype.

An important agronomic practice in cocoa is ensuring adequate potassium availability. Cocoa requires large amounts of potassium to produce high yield (Thong and Ng, 1980). Potassium accounts for about 70% of the nutrient load in the xylem sap of cocoa trees (Martins, 1976) and it is the most exported mineral in cocoa pod husks during harvest (Almeida and Valle, 2007; Hougni et al., 2021). In cocoa seedlings, potassium application (3–4 g plant⁻¹) increased biomass during water deficit and promoted drought recovery survival (Kaba et al., 2022) and enhanced cocoa resilience to drought (Djan et al., 2018). These findings suggest that potassium application can help to mitigate negative effects of water deficit on cocoa seedling growth (de Almeida and Valle, 2007; Djan et al., 2018; Kaba et al., 2022) which has been documented in other crops such as cassava (Chua et al., 2020) and banana (Taulya, 2013). Yet, studies on cocoa, have been mostly limited to seedlings to greenhouse conditions. In a previous study (Adet et al., 2024), K fertilizer application and irrigation did not have any significant interactive effects on physiological characteristics such as stomatal conductance, leaf water potential or specific leaf area. Nonetheless, the role of potassium application on pod formation and yield of mature cocoa trees has not been studied. Therefore, it is important to understand the extent to which potassium availability and irrigation have interactive effects on yield and the extent to which possible effects of potassium are driven by effects on pod dynamics.

The environmental and management effects on cocoa may differ between different cocoa genotypes (Medina et al., 2017; Kaba et al., 2022). For instance, studies on drought tolerance have found that negative effects of water deficit on yield varied among cocoa genotypes (End et al., 1988; de Almeida and Valle, 2007; Daymond and Hadley, 2008; Gateau-Rey et al., 2018). This genotypic variation represents a resource for developing climate-resilient genotypes that better tolerate the impacts of water deficit and maintain high productivity (Lahive et al., 2019; Raza et al., 2019; Nasser et al., 2020). So far, few published studies have analyzed genotypic difference in cocoa yield in responses to variation in dry-season irrigation and potassium application in adult trees under field conditions. Therefore, we study various components of cocoa yield under water stress for a number of genotypes.

This study aimed to investigate the effects of irrigation, potassium application and their interactions on yield, yield components and reproductive components of adult trees of six cocoa genotypes under field conditions. We hypothesize that: (1) water deficit decreases annual yield, pod number and mass and bean size; (2) water deficit decreases cherville number and increases the fraction of chervilles that wilt, as well

as pest and pathogen occurrence on pods; (3) potassium application increases annual yield, yield components and reproductive components in water deficit conditions, thus mitigating effects of drought stress, and (4) the before mentioned responses are modified by genotype effects.

2. Material and methods

2.1. Plant material and study area

The experiment was performed in Côte d'Ivoire at the Nestlé R&D research centre in Zambakro 6°49'13.98"N, 5°16'36.26"W located at 20 km from Yamoussoukro that has an equatorial climate comprising four seasons. The long dry season from mid-November to mid-March is characterized by the presence, in December and January, of the 'harmattan', a dry wind from the Sahara, which considerably lowers air humidity. The long rainy season is from mid-March to mid-July, while the short dry and short wet seasons run from mid-July to mid-September and from mid-September to mid-October, respectively. Average rainfall amounts vary from 900 to 1100 mm with a highly variable temporal distribution from year to year. It ranges from 15 mm in the driest month (January) to 165 mm in the wettest one (June). Diurnal temperatures average 26 °C, with a relative humidity ranging from 75% to 85%, dropping to 40% during the 'harmattan' (Nov-Jan) and rising to 80–90% in the rainy period.

Planting material for six genotypes produced through somatic embryogenesis was used for the experiment, including five clones (CI01, CI02, CI03, CI07, and CI14) and one hybrid (Mercedes, M) the most currently distributed material to cocoa farmers. The same trees, and the same genotypes, were used over the two years of the experiment. The stand, established in 2015, consisted of 240 trees (2.5 × 3 m intervals, 1320 plants ha⁻¹) cultivated in full sun. The study was conducted over two years (2020–2022), with N and P fertilizers applied with or without K fertilizer. All trees received N in the form of Nitrobor (487 kg ha⁻¹) and P in the form of Di-Ammonium Phosphate (DAP, 156 kg ha⁻¹). The K-fertilized trees received KCl (207 kg ha⁻¹) with three applications in March, July, and September 2020–2021 at 0.125 kg N, 0.04 kg P, and 0.053 kg K per tree.

2.2. Irrigation treatments

The experiment was set up as a split-plot randomized block design with irrigation and potassium application as treatments. The cocoa stand was divided into irrigated and non-irrigated blocks, further subdivided into sub-plots being either fertilized with potassium or not. Irrigation was initiated in January 2020 and involved drip irrigation with a flow rate of 1 L h⁻¹. Trees were located between two emitters, spaced 80 cm apart, and received irrigation four times weekly, providing 9.3 mm day⁻¹ (~ 967 mm yr⁻¹ during dry periods).

2.3. Yield

Yield per tree was measured by multiplying individual bean dry mass (BeanMass) by the number of beans per pod (PodBeanN) and the number of pods produced per tree (PodCount) throughout different seasons over two years of production.

$$\text{Yield} = \text{BeanMass} \times \text{PodBeanN} \times \text{PodCount} \quad (\text{A.1})$$

The yield figures represent either main and small season yields or annual yields (the sum of the main and minor harvests) in kg per tree averaged over the two years of production. We present yield per tree rather than values converted to field-level values per hectare because plots were relatively small so the assumptions of a continuous field may not fully hold.

2.4. Cherelle dynamics and yield components

Healthy cherelles (length < 5 cm) were counted monthly and the fraction of wilted cherelles was calculated as wilted cherelles / (wilted + healthy cherelles). Two harvest seasons were defined: the main harvest in November where pods developed mainly during the major wet season, and the small harvest in April with pods having mainly developed during the major dry season. The total ripe pods per tree (PodCount) was counted and removed during both harvests. A random subsample of 16 pods from a group of 8 trees (2 pods tree⁻¹) for each genotype was collected, measured, weighted for fresh weight (PodMass), with fresh beans (PodBeanN) counted and weighed.

Then, a random sample of 50 dry beans were individually weighed to determine the average bean mass (BeanMass). Pathogen damage (e.g., black-pod disease, *Phytophthora palmivora* & *megakarya*) that appeared during the development of the experiment and on harvested pods was registered as the percentage of pods that was attacked when still on the tree:

$$\% \text{ of Attack} = \frac{N^{\circ} \text{ of pods affected}}{N^{\circ} \text{ of pods harvested}} * 100 \quad (\text{A.2})$$

2.5. Data analysis

Linear mixed-effects models (LMMs) were used to evaluate the effects of irrigation, potassium application and their interaction, and of genotype on yield and yield components. The analysis was performed in two steps. First, we tested whether there was an effect of the harvest season (small vs main), irrigation and their interaction on yield and yield components. The period in which pods developed during dry months, and then irrigation was turned on, was considered as the small harvest. The main harvest was the period in which pods were developed during wet months, and irrigation was turned off. We included the harvest season (small vs main), irrigation and the two-way interaction between irrigation and harvest season as fixed effects, with a random intercept per tree. In the second step, we tested the effects of irrigation, potassium application and genotype on cocoa annual yield and yield components using annual means or totals. We included irrigation, potassium application, genotype and the interaction between irrigation and potassium as fixed effects and a random intercept per tree. Models were compared based on Akaike's information criterion (AIC), selecting the most parsimonious models with the lowest AIC values indicating the best fit (Burnham and Anderson, 2002). We also assessed whether yield, and effects of irrigation and potassium application on yield, varied among years. To do so, we added year, and interactions between year and irrigation and year and potassium application as fixed effects to the best model, but adding these effects did not significantly improve model fit. Effects were considered significant, if bootstrapped 95% confidence intervals of the model coefficients did not overlap with zero. Marginal R-squared (R²_m) and conditional R-squared (R²_c) values were calculated; R²_m indicates the variation explained by the fixed effects only, R²_c indicates variation explained by both the fixed and random effects (Nakagawa and Schielzeth, 2013).

Statistical analyses were performed using R3.1.0 software (R Core Team). LMMs were performed using the "glmmTMB" R package (Brooks et al., 2017).

3. Results

3.1. Effects of season and irrigation on annual cocoa yield and yield components

Results showed that irrigation and potassium treatments influenced both soil and plant water status, consequently affecting yield components (Fig. A3). The details regarding the variation in microclimate and soil moisture (Fig. A3) were as described in Adet et al., (2024).

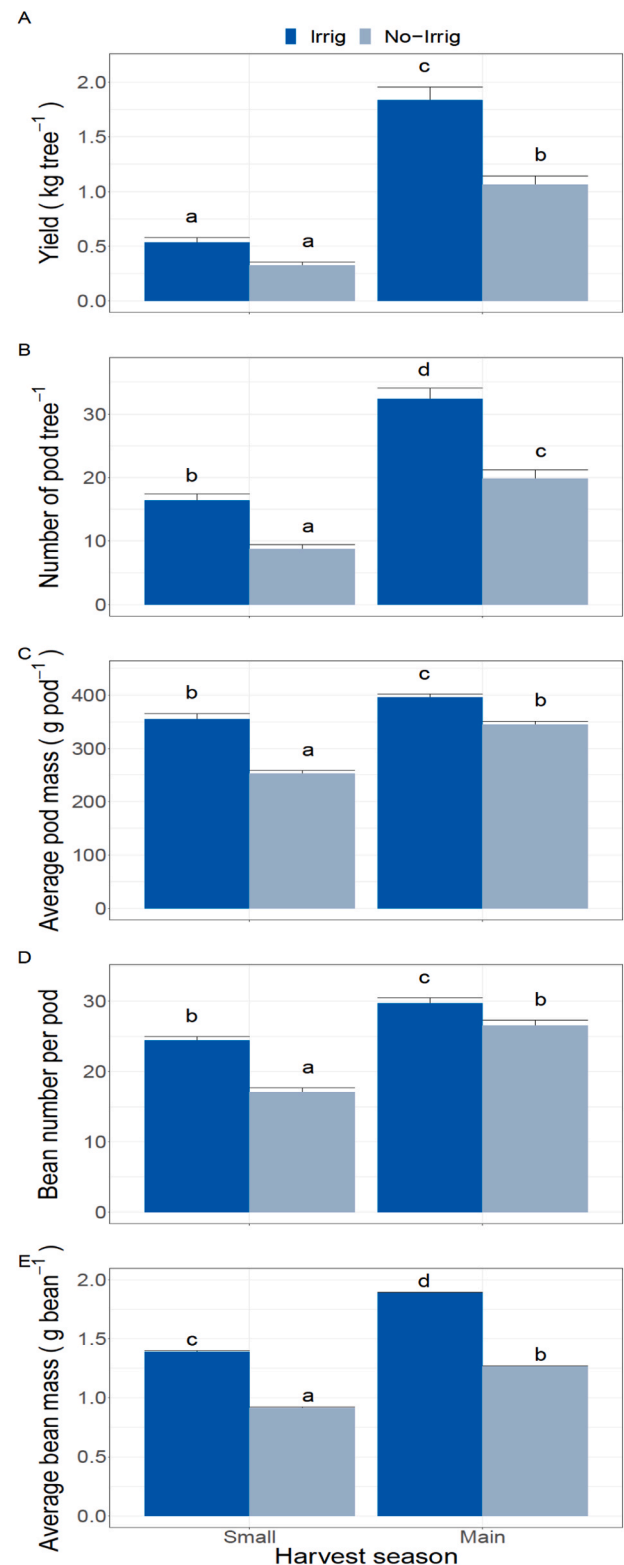


Fig. 1. Effects of irrigation (Irrig = irrigated vs No-Irrig=non-irrigated) and harvest season (Small vs Main) on annual cocoa yield and yield components. The mean and standard errors (whiskers) are shown for (A) annual yield per tree (B) number of pods per tree, (C) pod mass, (D) number of beans per pod and (E) individual bean mass. Pods harvested during the main harvest have developed during the wet season; those from the small harvest have developed during the dry period. Treatment and season effects are shown in Table 1. Different letters above the bars indicate a significant difference.

Table 1

Results of linear mixed-effects models to explain variation in four yield variables and three reproductive variables of experimental cocoa trees. Explanatory variables are season (small vs main season, Seas), irrigation (Irrig) treatment and their interaction (:), and are marked, with “sig” when significant. Variable names: cocoa annual yield, number of pods per trees (PodCount), average pod mass (PodMass), number of beans per pod (PodBeanN), and mass of an individual bean (BeanMass), average number of cherelles (Cher), fraction of wilted cherelles (Wilt), percentage of attacked and diseased pod (Attack). Marginal R^2 (R_m^2): variation explained by fixed effects only. Conditional R^2 (R_c^2): variation explained by both fixed and random effects.

Variables Response	Unit	Predictors in best model			R_m^2	R_c^2	
Yield Components	Yield	kg tree ⁻¹	Seasons ^{Sig}	Irrig ^{Sig}	Seasons:Irrig ^{Sig}	0.06	0.17
	PodCount	-	Seasons ^{Sig}	Irrig ^{Sig}	Seasons:Irrig ^{Sig}	0.19	0.29
	PodMass	g pod ⁻¹	Seasons ^{Sig}	Irrig ^{Sig}	Seasons:Irrig ^{Sig}	0.13	0.16
	PodBeanN	-	Seasons ^{Sig}	Irrig ^{Sig}	Seasons:Irrig ^{Sig}	0.14	0.31
	BeanMass	g bean ⁻¹	Seasons ^{Sig}	Irrig ^{Sig}	Seasons:Irrig ^{Sig}	0.14	0.15
Reproductive components	Cher	-	Seasons ^{Sig}	Irrig ^{Sig}	Seasons:Irrig ^{Sig}	0.04	0.05
	Wilt	-	Seasons ^{Sig}	Irrig ^{Sig}	Seasons:Irrig ^{Sig}	0.03	0.06
	Attack	%	Seasons ^{Sig}	Irrig ^{Sig}	Seasons:Irrig ^{Sig}	0.07	0.08

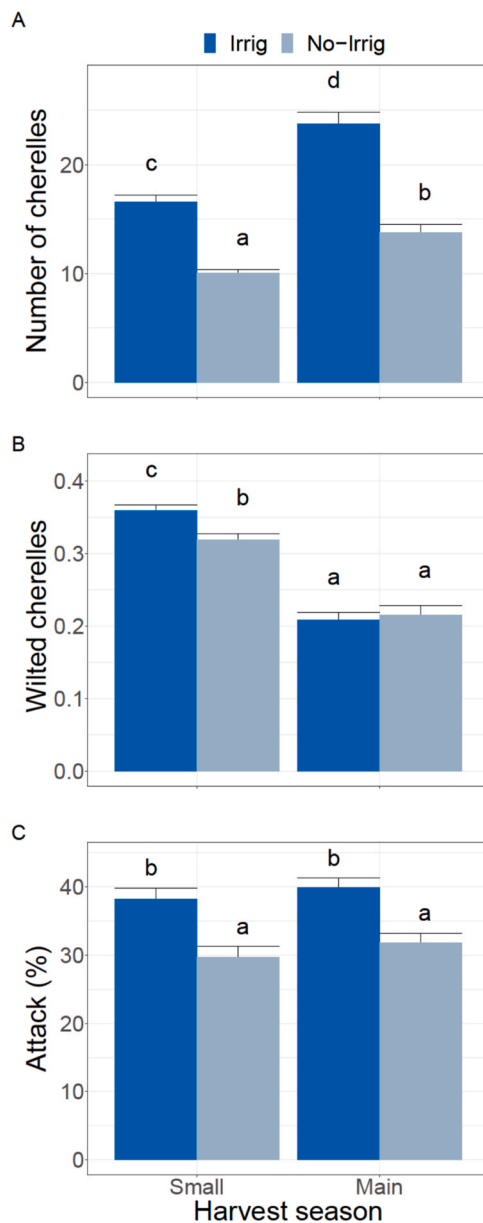


Fig. 2. Effects of irrigation (Irrig=irrigated; No-Irrig=non-irrigated) and harvest season (Small vs Main) on cocoa reproductive components. Means and standard errors (whiskers) are shown for (A) Average number of cherelles (B) Fraction of wilted cherelles, (C) Percentage of attacked and diseased pods (Attack). Treatment and season effects are shown in Table 1. Letters are shown as in Fig. 1.

Irrigation significantly increased yield in the main harvest (~77% increase), but not in the small harvest season (Fig. 1, Table 1). This positive effect extended to all yield components, particularly the number of pods per tree (PodCount) and to a somewhat lesser extent on the average dry bean mass. Differences between main and small harvests were consistent across all components, with during the main harvest a stronger positive responses to irrigation than during the small harvest (Fig. 1).

Irrigation increased cherelle numbers in both seasons, especially in the main season (Fig. 2. A). However, irrigation increased the fraction of wilted cherelles only in the small harvest (Fig. 2. B), while it increased the loss of pods due to greater percentage of attacked pods in both seasons (Fig. 2. C). This implies that the positive effect of irrigation on pod number resulted from increased cherelle production rather than reduced cherelle loss. On the other hand, the difference in pod number between the main and small harvest season was associated with both more cherelles being produced and relatively lower rates of cherelle wilt during the main season (Fig. 1. B, C; Fig. 2. B, C).

3.2. Effects of irrigation and potassium on annual yield and yield components

Annual bean yields varied between 0.5 and 3 kg tree⁻¹ across treatments and seasons. Given the density of 1320 trees ha⁻¹, this converts to about 650 – 4000 kg ha⁻¹ though this extrapolation needs to be taken with caution as plot sizes were relatively small. For this reason, we have chosen to report values per tree. Irrigation approximately doubled yield from ~1.5 to ~3 kg tree⁻¹, but only when K fertilizer was applied (Fig. 3), as indicated by the significant irrigation x K interaction (Table 2). This pattern was fairly consistent across the six genotypes (Fig. 4).

Positive irrigation and K effects on yield were observed in all yield components, especially in the number of pods per tree, which doubled from ~30 to ~60 pods when both irrigation and potassium were applied (Fig. 3 A, B-D, E). K application alone did not increase yield under non-irrigated conditions, but only increased pod mass, with small effects on bean number and bean mass (Fig. 3 C, D, E).

Considering the reproductive dynamics, irrigation had a large positive effect on the number of cherelles (Table 2; Fig. 5. A) and potassium application significantly increased the number of cherelles under irrigation. However, irrigation slightly increased the fraction of wilted cherelles and attacked pods (Table 2; Fig. 5. B, C). There was a significant K by irrigation interactive effect on the fraction of wilted cherelles (Table 2), wilting tending to slightly decline with K application in the irrigated plots but the opposite seemed to occur in the non-irrigated plots though neither trend was significant in the post-hoc analysis (Fig. 5. B). To summarize, water deficit led to fewer pods per tree, reduced cherelle wilt and resulted in smaller pods and beans. K application only stimulated pod production and yield when combined with irrigation.

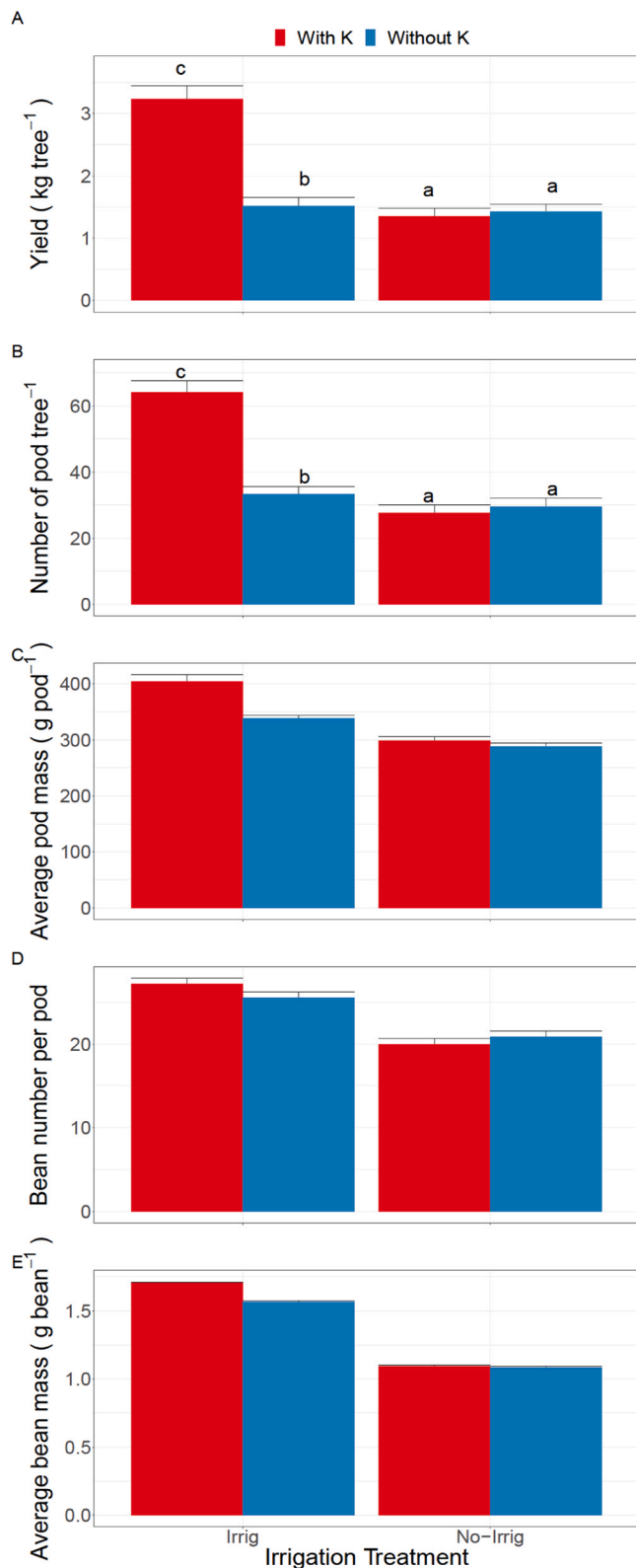


Fig. 3. Effects of irrigation (irrigated vs non-irrigated) and potassium application (with K vs without K) on cocoa annual yield and yield components. Mean and standard errors (whiskers) are shown for (A) annual yield per tree (B) number of pods per tree, (C) pod mass, (D) number of beans per pod and (E) individual bean mass. Letters are shown as in Fig. 1.

3.3. Genotypic effects and their interaction with irrigation and potassium application

Overall, yield differed between genotypes (Table 2) with CI02 and to a lesser extent CI03 exhibiting lower yield ($0.3 - 1 \text{ kg tree}^{-1}$, depending on K and irrigation levels) compared to especially CI01 and CI14 ($0.6 - 3 \text{ kg tree}^{-1}$). There was a significant genotype by irrigation effect on yield (Table 2) indicating that the effect of irrigation differed between genotypes. While yields were consistently reduced by withholding irrigation for all genotypes, this effect was significant only in CI01 when considering genotypes separately (Fig. 4).

There was also a genotype by K interactive effect on yield. The effects of K on yield under irrigation were positive across all genotypes but only significantly in CI01. Genotypic variation in yield was mostly associated with variation in the number of pods per tree (Fig. 3, Fig. A1). Genotype effects on pod mass were relatively small and inconsistent. However, there were very weak genotypic differences in the response of pod mass to K as indicated by the significant K by genotype interaction (Table 2).

Genotype effects were observed for all reproductive components (Table 2). The low-yielding genotype CI03 tended to produce more cherelles compared to other genotypes whereas the other low yielder CI02 tended to produce fewer cherelles than the other genotypes. Other genotypic differences in reproductive traits were relatively inconsistent (Fig. 5, Fig. A2)

4. Discussion

This study explored the effects of irrigation, potassium (K) application and their interaction on yield and yield components, as well as genotypic differences in these traits. Results showed significant yield responses to seasons, irrigation, K, and their interactions. Annual yield approximately doubled from $\sim 1.5 - 3 \text{ kg tree}^{-1}$ (roughly $\sim 2000 - 4000 \text{ kg ha}^{-1}$) with application of $\sim 960 \text{ mm}$ dry season irrigation amounting to about 87% of the total annual rainfall (1100 mm). Irrigation mainly increased the number of mature pods and young cherelles that were produced, but also led to higher cherelle wilt incidence. K positively affected yield only under irrigation, and hence did not mitigate the negative effects of withholding irrigation on yield.

In the most favorable treatment (K fertilizer and irrigation), we observed a three-fold difference in yield across genotypes indicating the large genotypic variation in yield that exists in cocoa. There was also evidence for genotypic differences in drought tolerance, the response only being significant and also largest in CI01. These results provide significant knowledge to develop climate adaptive cocoa planting material and agronomic practices.

4.1. Irrigation effects on yield

Dry bean yield almost doubled from an estimated ~ 2000 to $\sim 4000 \text{ kg ha}^{-1}$ by applying 960 mm as irrigation water during the dry season albeit only when trees were also fertilized with K. This clearly indicates the importance of dry season irrigation for cocoa in relatively dry areas, like the northern part of the cocoa belt in Côte d'Ivoire, as supported by crop models emphasizing the sensitivity of cocoa yield to dry season water availability (Zuidema et al., 2005; Asante, 2023). Daymond et al. (2020) found greater seasonal variation in yields in areas with more pronounced dry seasons. This suggests that the dry season, with its associated water stress and other environmental factors, likely contributes to the increased variability in cocoa yield. Also, an experiment in Malawi revealed that more frequent irrigation treatments (1600 mm yr^{-1}) during the dry season led to a 15% yield increase compared to less frequent irrigation (920 mm yr^{-1}) (Lee, 1975). This result aligns with our finding that dry season irrigation (960 mm yr⁻¹) led to a two-fold increase of yield in combination with potassium application. Huan et al. (1986) reported a $\sim 40\%$ increase in pod number and annual dry bean yield (60%) due to irrigation. Our results are also

Table 2

Results of linear-mixed effects models to explain variation in four yield variables and three reproductive variables of experimental cocoa trees, as a function of genotype (Gen, CI07, CI14, CI01, CI03, CI02, M), irrigation (Irrig), potassium application (Pot) treatment and their interaction. Significant predictors in the best model are marked with “sig”. Variables names: cocoa annual yield, number of pods per tree (PodCount), average pod mass (PodMass), number of beans per pod (PodBeanN), and mass of an individual bean (BeanMass), average number of cherelles (Cher), fraction of wilted cherelles (Wilt), percentage of attacked and diseased pods (Attack). Marginal R² (R_m²): model variation explained by fixed effects only. Conditional R² (R_c²): model variation explained by both fixed and random effects.

Variables Responses	Annual Yield	Unit	Significant Predictors in best model							R _m ²	R _c ²
			Gen ^{sig}	Pot ^{sig}	Irrig ^{sig}	Gen:Irrig ^{sig}	Gen:Pot ^{sig}	Irrig:Pot ^{sig}	Gen:Irrig:Pot ^{sig}		
Yield Components	PodCount	-	Gen ^{sig}	Pot ^{sig}	Irrig ^{sig}	Gen:Irrig ^{sig}	Gen:Pot ^{sig}	Irrig:Pot ^{sig}	Gen:Irrig:Pot ^{sig}	0.16	0.22
	PodMass	g pod ⁻¹	Gen ^{sig}	Pot ^{sig}	Irrig ^{sig}	Gen:Irrig ^{sig}	Gen:Pot ^{sig}			0.06	0.07
	PodBeanN	-	Gen ^{sig}		Irrig ^{sig}	Gen:Irrig ^{sig}				0.16	0.22
	BeanMass	g bean ⁻¹	Gen ^{sig}	Pot ^{sig}	Irrig ^{sig}	Gen:Irrig ^{sig}	Gen:Pot ^{sig}		Gen:Irrig:Pot ^{sig}	0.10	0.11
Reproductive Components	Cher	-	Gen ^{sig}	Pot ^{sig}		Gen:Irrig ^{sig}	Gen:Pot ^{sig}	Irrig:Pot ^{sig}	Gen:Irrig:Pot ^{sig}	0.12	0.15
	Wilt	-	Gen ^{sig}	Pot ^{sig}	Irrig ^{sig}	Gen:Irrig ^{sig}	Gen:Pot ^{sig}	Irrig:Pot ^{sig}	Gen:Irrig:Pot ^{sig}	0.15	0.19
	Attack	%	Gen ^{sig}	Pot ^{sig}	Irrig ^{sig}	Gen:Irrig ^{sig}	Gen:Pot ^{sig}			0.03	0.03

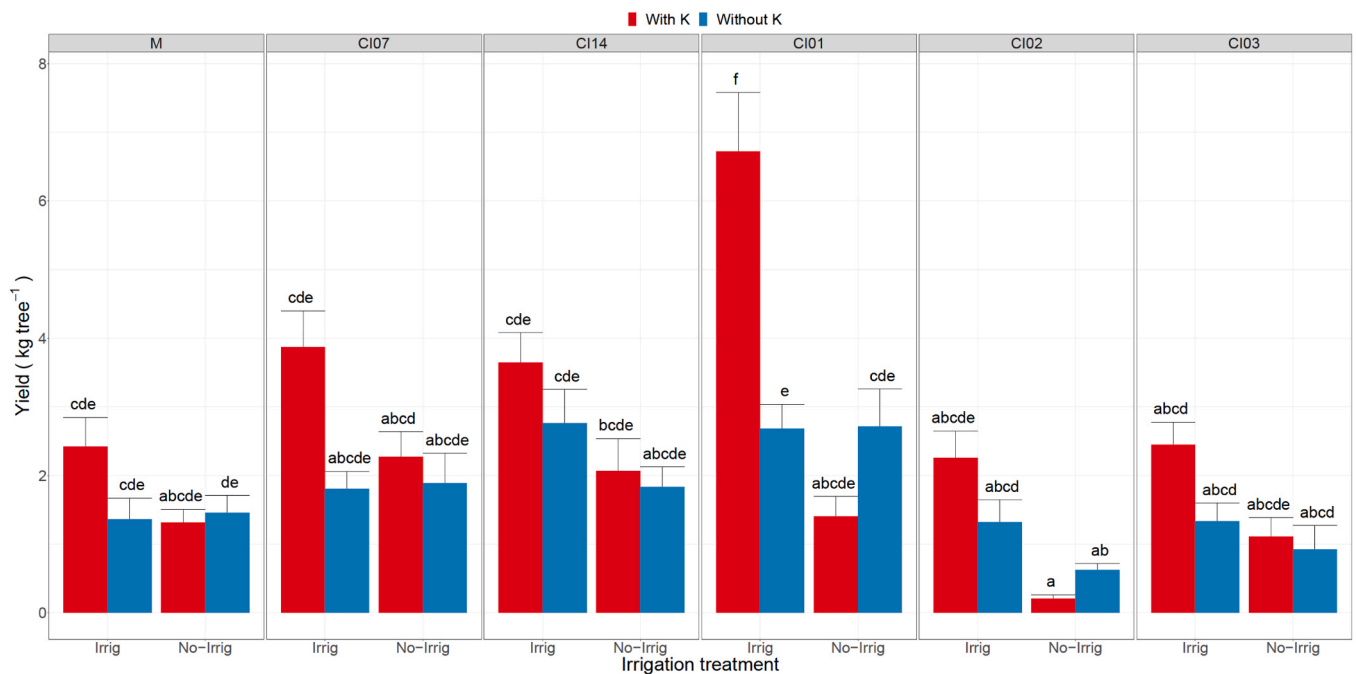


Fig. 4. Effects of irrigation (irrigated vs non-irrigated), potassium application (with K vs without K) on yield of six cocoa genotypes (M, CI07, CI14, CI01, CI02, CI03). Mean and standard errors (whiskers) are shown for the annual yield per tree. Letters are shown as in Fig. 1.

consistent with the substantial yield increases documented by Diczbalis et al. (2010) under specific irrigation conditions, likely associated with differences in climate, local evapotranspiration and soil characteristics between sites. These studies show that irrigation practices can have profound positive effects on cocoa yield, emphasizing the role of water management in maximizing productivity. Cocoa yield and effects of irrigation (along with potassium application) did not vary among years, thus the yield response was present in the first year of the experiment already, indicating that there was no indication of a delayed response in yield after changes in ecophysiological traits and/or in vegetative growth. Further research on irrigation effects on cocoa yield is needed to determine optimal irrigation regimes for different climatic conditions considering the often existing limited availability of water resources for irrigation and the existence of competing claims on water from other uses such as the production of food crops.

The positive irrigation effect on yield was largely associated with a positive effect on the number of healthy and mature pods produced per tree and to a lesser extent with more beans per pod, and higher bean mass. However, pod mass was not affected by irrigation. These factors, identified in various studies as key yield determinants (Lachenaud, 1995; Doaré et al., 2020) show the complexity of cocoa yield responses

to environmental changes. Apart from irrigation, the number of pods produced often depends on environmental factors other than water availability, and is also heritable (Cilas, 1991; Cilas et al., 1999). The pod number in turn is mediated by the reproductive dynamics discussed in the next section.

4.2. Irrigation effects on reproductive components

Pod production is determined by the number of young pods (cherelles) produced, the fraction of cherelles that wilt (cherelle wilt) and the pods damaged by pests and diseases, particularly pod fungal disease (*Phytophthora palmivora* and *P. megakarya*). Dry season irrigation resulted in more cherelles being produced which could have been associated with a greater assimilate availability (i.e., through a greater stomatal conductance and leaf area) (Balasimha et al., 1991; Adet et al., 2024). Previous studies reported that water deficit led to greater cherelle wilt and reduced pod load in cocoa (Hadley et al., 1994; Daymond et al., 2002). The proposed explanation is that cherelle wilt is linked to a reduced assimilate supply, although the exact mechanism remains poorly understood (Valle et al., 1990; Bos et al., 2007; Melnick, 2016; Goudsmit et al., 2023). The argument is that drought conditions,

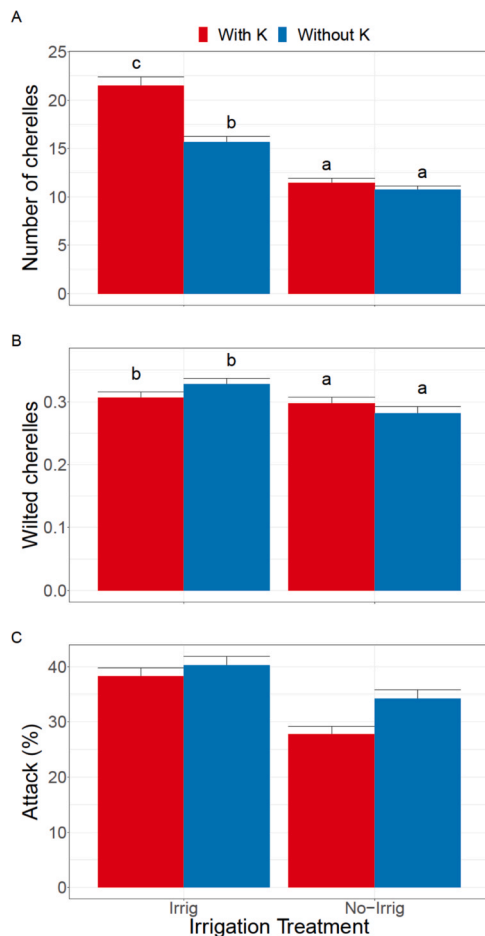


Fig. 5. Effects of irrigation (irrigated vs non-irrigated) and potassium application (with K vs without K) on cocoa reproductive components. Mean and standard errors (whiskers) for (A) Average number of cherelles (B) Fraction of wilted cherelles, (C) Percentage of attacked and diseased pods (Attack). Letters are shown as in Fig. 1.

through low assimilate reserves, would trigger cherelle wilt as trees have fewer resources to grow pods up to maturity. However, seemingly in contradiction with this, in our study, irrigated trees had a higher fraction of cherelle wilt. It is possible that the greater number of cherelles in the irrigated trees caused more competition for resources, e.g. between larger and smaller cherelles, in turn causing more of the smaller ones to wilt. Clearly, the mechanisms of assimilate allocation in cocoa trees and their impact on pod growth and cherelle wilt require more in-depth research. Particularly the question whether irrigation affects synchronicity of pod growth and its impact on cherelle wilt need more investigation, which our data resolution did not allow us to answer.

4.3. Effects of potassium application on cocoa yield

K strongly increased yield, but only for irrigated trees, in line with the idea that a limiting production factor has a stronger effect when other factors are not limiting (Harmsen, 2000). However, this contradicts our hypothesis that K application would mitigate the negative impact of water deficit. The positive effect of K on yield can be attributed to its role in maintaining osmotic potential in the phloem, facilitating assimilate transport, enhancing stomatal functioning and photosynthesis (Cakmak, 2005; Gattward et al., 2012; Djan et al., 2018; Xu et al., 2020; Anokye et al., 2021). Our results demonstrate that applying $\sim 200 \text{ kg ha}^{-1}$ of K doubled annual yield and improved pod number in irrigated conditions (Fig. 2), which is consistent with previous studies showing the positive effect of K application on pod number (Lachenaud,

1991; Verlière, 1981; Uribe et al., 2001). Combined with nitrogen and phosphorus fertilization, the effect of K application on pod number is even more pronounced (Snoeck et al., 2016) and hence consistent with our findings as we applied N and P fertilizers to all treatments. Results highlight that fertilizer application is more effective when other yield limiting factors – in this case water availability – are controlled for. They also emphasize that climate adaptation strategies, such as irrigation, are most effective when integrated with proper agronomic practices (Asante et al., 2021).

4.4. Genotypic response to irrigation and potassium application

The yield varied almost three-fold across genotypes, ranging from $\sim 0.8 \text{ kg tree}^{-1}$ in CI03 to 3.4 kg tree^{-1} in CI01 under irrigated and K-fertilized conditions. This confirms other work (e.g., Daymond et al., 2002) of there being strong genetic variation in yield potential in cocoa and thus potential for breeding. The relationship between yield and yield components also differed between genotypes. For instance, CI02 produced fewer pods than most other genotypes due to lower cherelle production, while CI03 had lower pod numbers due to a higher rate of cherelle wilt. Yield responses are likely influenced by distinct physiological mechanisms regulating cherelle production and wilt as reported by Bekele et al., (2022). Furthermore, some of the clones (notably CI01) had higher yields than the currently widely used hybrid Mercedes, indicating that there is potential for yield increases through use of different genotypes than the ones currently disseminated to farmers.

There was a genotype by irrigation effect on yield indicating there was at least some degree of genotypic variation in drought tolerance in our selection. This variation may help provide a basis for breeding more climate-resilient cocoa. Yet, breeding in cocoa has focused on yield and disease resistance and relatively little work has been done to breed for climate resilience (Lahive et al., 2019). Post-hoc analysis of our analysis revealed that while all genotypes exhibited yield reductions due to withholding irrigation, the effect was only significant in CI01 and this genotype also exhibited the largest absolute reduction in mean yield ($> 1 \text{ kg tree}^{-1}$). Interestingly, in our previous study (Adet et al., 2024), CI02 and CI03 exhibited the reductions in LAI and light capture when irrigation was withheld, but this pattern was not reflected in our yield data. Overall, probably due to our limited number of replicates at genotype level, our data are insufficiently accurate to determine which genotypes are most drought tolerant. Further research, including more genotypes and environmental conditions, is necessary to develop cocoa genotypes with combined high yield and drought tolerance.

Lower attacked pod percentages in CI02 and CI03 suggest promising tolerance to biotic stress, potentially related to hormonal signals and immune responses (Ku et al., 2018; Iqbal et al., 2022). Genotypes could possess specific receptors that recognize pathogen and/or environmental changes. These receptors may induce the closure of stomata on the pods' exocarp (Flores et al., 1994; Iwaro et al., 1997) and leaf epidermis, preventing pathogens from entering the organs (Schulze-Lefert and Robatzek, 2006; Ku et al., 2018).

5. Conclusion

This study found that dry-season irrigation had strong positive effects on cocoa yield, but only when K was added. Thus, K application in combination with irrigation positively influences cocoa yield, potentially due to improved nutrient uptake and use. Contrary to our expectation, K did not mitigate the side effects of water deficit on yield. In water-limited conditions, even if sufficient K is present in the soil, the trees may struggle to take it up, limiting their potential to enhance yield. Finally, we observed a very large genotypic difference in yield as well as a genotype effect on yield responses to irrigation. These findings clearly show that managing drought conditions and maximizing yield in cocoa require a comprehensive approach that includes water management, fertilizer application and genotype selection, and overall crop

management practices.

CRedit authorship contribution statement

Danaë Rozendaal: Formal analysis, Methodology, Supervision, Validation, Writing – review & editing. **Arthur Tapi:** Resources. **Lucette Adet:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Visualization, Writing – original draft, Writing – review & editing. **Niels Anten:** Funding acquisition, Supervision, Writing – review & editing. **Pieter Zuidema:** Supervision, Writing – review & editing. **Philippe Vaast:** Supervision, Writing – review & editing.

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. : Effect of irrigation and potassium on each genotype

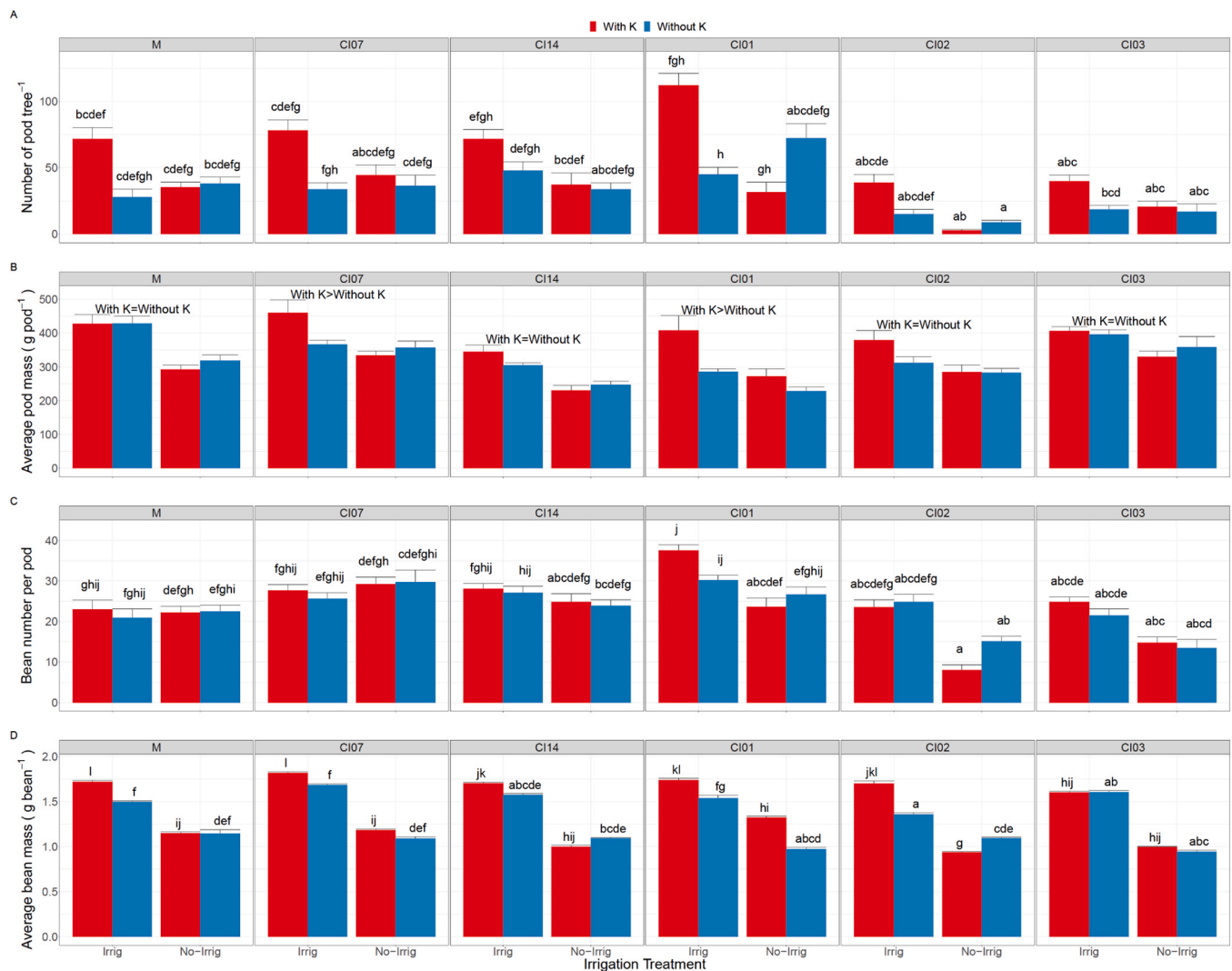


Fig. A1. Effects of irrigation (irrigated vs non-irrigated) and potassium application (with K vs without K) on cocoa yield components for six genotypes. Mean and standard errors (whiskers) are shown for (A) number of pods per tree, (B) pod mass, (C) number of beans per pod and (D) individual bean mass. Different letters above the bars indicate a significant difference.

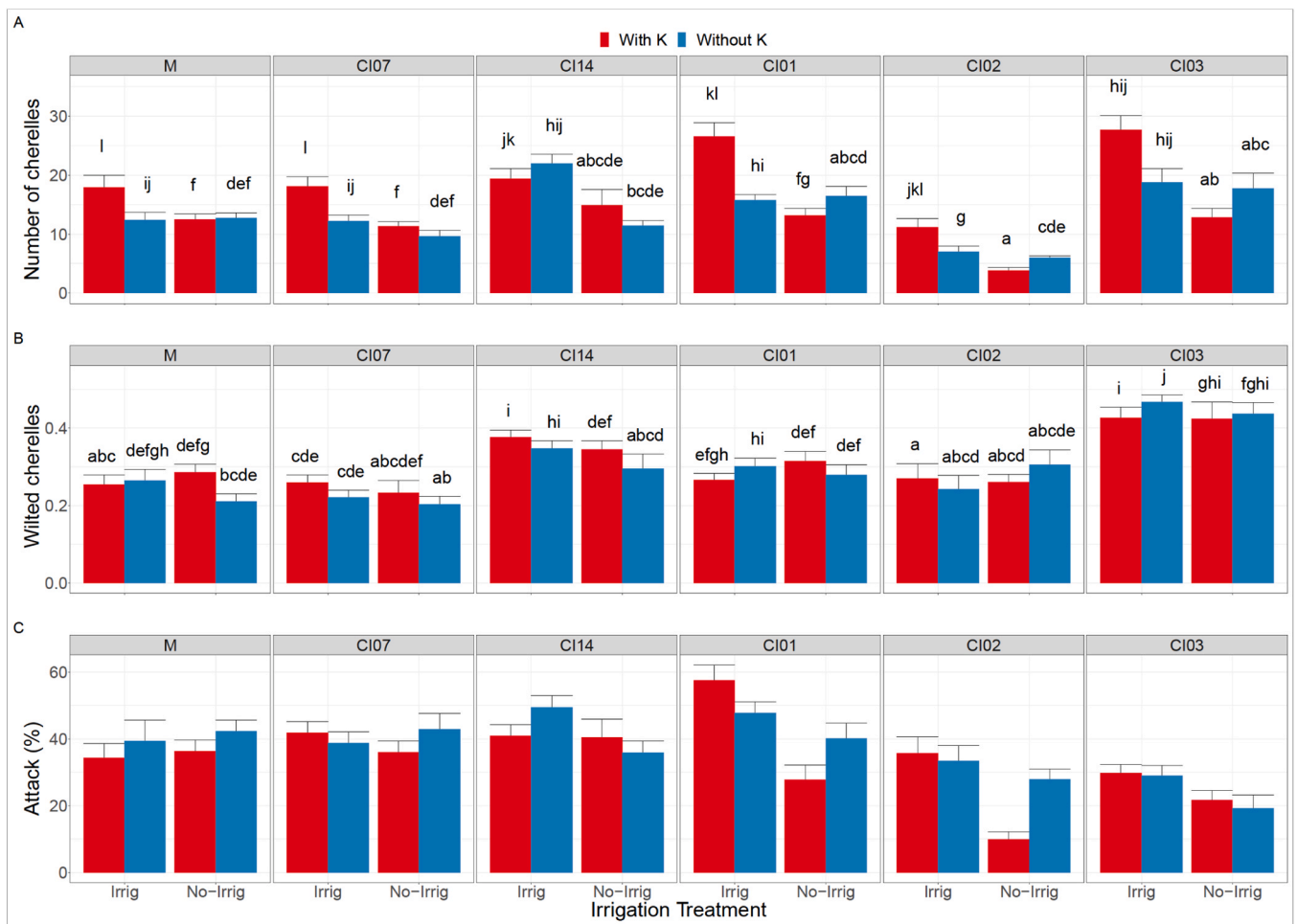


Fig. A2. Effects of irrigation (irrigated vs non-irrigated) and potassium application (with K vs without K) on reproductive components of six cocoa genotypes (M, CI07, CI14, CI01, CI02, CI03). Mean and standard errors (whiskers) are shown for (A) Average number of cherelles (B) Fraction of wilted cherelles, (C) Percentage of attacked and diseased pods (Attack). Different letters above the bars indicate a significant difference.

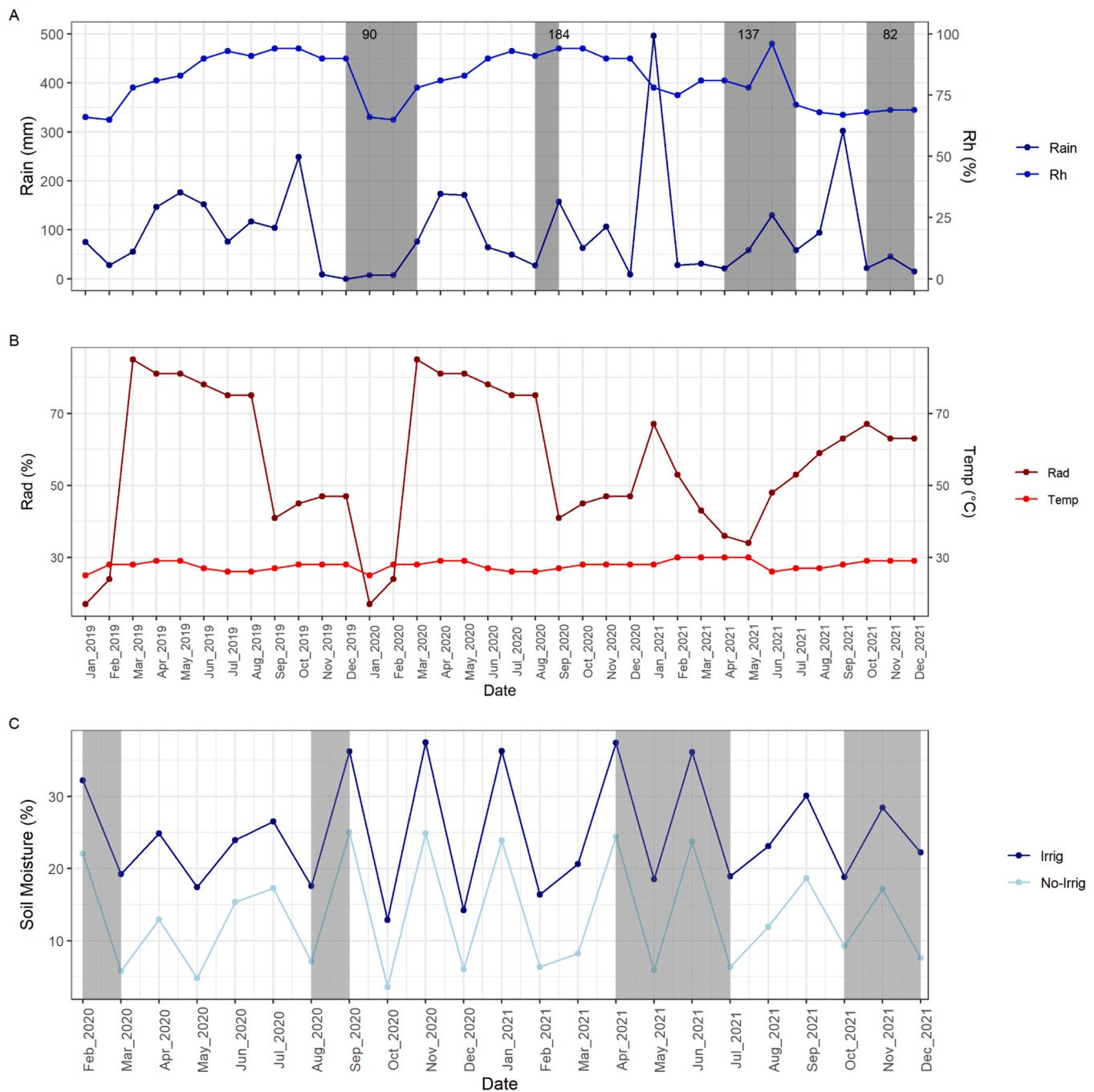


Fig. A3. Monthly averages of microclimate variables throughout the experiment. (A) Rainfall (Rain; mm) on the left y-axis and relative humidity (Rh; %) on the right, (B) Solar radiation (the percentage of time with sunshine Rad; %) on the left y axis and air temperature (Temp; °C) on the right axis, (C) Soil volumetric water content (%) for irrigated (Irrig) and non-irrigated (No-Irrig) plots. The grey areas indicate the dry months in which the irrigation treatment was applied; the numbers in the grey area indicate the total rainfall received in that period. Copied with permission from Adet et al., (2024).

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