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Early flowering changes robusta coffee yield responses to climate stress and management

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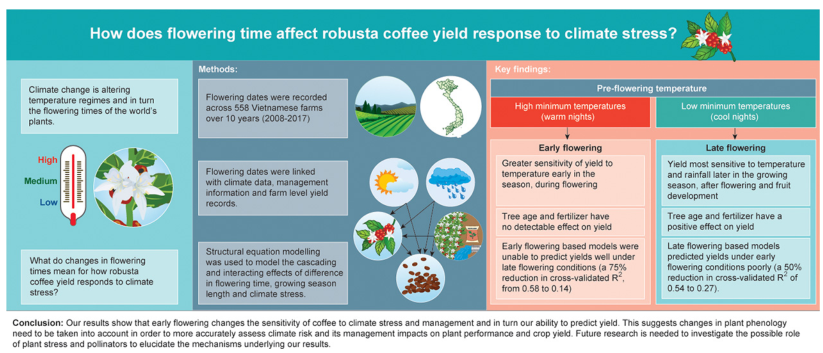
HIGHLIGHTS

- Climate change is changing plant flowering times with many unknown consequences.
- We combined climate, phenology and agronomy data with structural equation modelling.
- Early flowering increases coffee sensitivity to climate stress and management.
- Flowering time maximum temperatures more negatively affect early-flowering coffee.
- Early flowering reduces the positive effect of fertilizer use on coffee yield.

GRAPHICAL ABSTRACT



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ABSTRACT

A shift towards earlier flowering is a widely noted consequence of climate change for the world's plants. However, whether early flowering changes the way in which plants respond to climate stress, and in turn plant yield, remains largely unexplored. Using 10 years of flowering time and yield observations (Total $N = 5580$) from 558 robusta coffee (*Coffea canephora*) farms across Vietnam we used structural equation modelling (SEM) to examine the drivers of flowering day anomalies and the consequent effects of this on coffee climate stress sensitivity and management responses (i.e. irrigation and fertilization). SEM allowed us to model the cascading and interacting effects of differences in flowering time, growing season length and climate stress. Warm nights were the main driver of early flowering (i.e. flowering day anomalies <0), which in turn corresponded to longer growing seasons. Early flowering was linked to greater sensitivity of yield to temperature during flowering (i.e. early in the season). In contrast, when late flowering occurred yield was most sensitive to temperature and rainfall later in the growing season, after flowering and fruit development. The positive effects of tree age and fertilizer on yield, apparent under late flowering conditions, were absent when flowering occurred early. Late flowering models predicted yields under early flowering conditions poorly (a 50 % reduction in cross-validated R^2 of 0.54 to 0.27). Likewise, models based on early flowering were unable to predict yields well under late flowering conditions (a 75 % reduction in cross-validated R^2, from 0.58 to 0.14). Our results show that early flowering changes the sensitivity of coffee production to climate stress and management and in turn our ability to predict yield. Our results indicate that changes in plant phenology need to be taken into account in order to more accurately assess climate risk and management impacts on plant performance and crop yield.

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1. Introduction

Coffee is highly sensitive to climatic variability and, as such, is illustrative of the challenges that climate change poses to the world's plant species and to agricultural production more generally (Chemura et al., 2021; Kath et al., 2020; Moat et al., 2019; Moat et al., 2017). Sixty percent or more of wild coffee species are threatened with extinction – with climate a key contributing risk (Davis et al., 2019). Climate change is projected to cause large declines in the areas suitable for coffee production, resulting in up to 50 % declines in several key coffee producing countries (Bunn et al., 2015; Grüter et al., 2022; Moat et al., 2017). Even coffee species (e.g., robusta coffee, *Coffea canephora*) that are adapted to warmer conditions are exceptionally sensitive to climatic variation (Kath et al., 2020; Tournebize et al., 2022). While rising CO_2 levels may help offset some loses (Ainsworth and Long, 2021; Rodrigues et al., 2016) and new species of production coffee with increased ability to cope with hotter and drier conditions are being identified (Davis et al., 2021), understanding and managing climate impacts on coffee will be an ongoing challenge into the future as temperatures rise and rainfall patterns shift.

Less well documented than the direct impacts of climate variability and change on suitable coffee production areas are those associated with the more subtle disruptions to plant phenological cycles evident in changes in the timing of key biological processes or phenophases, such as flowering and fruiting (Wolkovich et al., 2012). Recent studies indicate that the timing of these critical plant phenophases are shifting considerably as the climate changes (Ge et al., 2015; Menzel et al., 2020; Stuble et al., 2021). Phenological studies across 1634 plant species suggest that, on average, for every degree Celsius of warming there is a 2.5 to 5-day advance in flowering time (Wolkovich et al., 2012). The relationship between warming and changes in flowering time for coffee remains unquantified.

The consequences of early flowering are potentially profound, but for coffee, as for many tropical plant species, these remain relatively unexplored (Stuble et al., 2021). There are potential physiological consequences; for example, early flowering may trigger stress responses making plants more vulnerable to stressors later in the season (Anwar et al., 2021; Takeno, 2016). Phenophase shifts may also result in a mismatch in the life cycles of co-dependent/mutualistic species, leading to population impacts and the loss of critical pollination related ecosystem functions (Boreux et al., 2013b; Imbach et al., 2017). The impact of early flowering, acting through ecological asynchronies and increased stress, could have significant consequences for how coffee responds to climate stress and by extension climate change.

Flowering initiation in coffee is a complex phenomenon that is poorly understood (Craparo et al., 2021). Even so, it is well accepted that coffee phenology is highly sensitive to climate. There is thought to be a strong relationship between temperature and coffee flowering, with warm temperatures particularly important for floral bud initiation (DaMatta and Ramalho, 2006). Rainfall, or more specifically rainfall at the end of the dry season, is also thought an important cue to trigger flowering (Haarer, 1962). While this relationship has been little tested or quantified, a number of studies (Boreux et al., 2013a; Masarirambi et al., 2009) show that, because of coffee's sensitivity to rainfall, irrigation can be used to synchronise coffee flowering.

While climate variability has been shown to be important for coffee phenology, the consequences of climate-induced phenological shifts (e.g., towards early flowering) remain relatively unexplored. Further, while recent studies on robusta coffee (e.g. Venancio et al., 2020) have highlighted the sensitivity of the flowering phase to temperature and rainfall, none have considered how this may change with a shift in flowering time. For example, does early flowering in coffee alter how it responds to climate stress? If so, what does this mean for our ability to predict and quantify the impacts of rising temperatures and shifting rainfall patterns on coffee production? This knowledge gap is especially pertinent for robusta coffee - the more heat-tolerant coffee production variety – which, despite accounting for 40 % of global coffee supply (ICO, 2022), has received relatively little detailed phenological research attention. Recent research has suggested important links between phenology and rust disease in robusta (Rosas et al., 2021) and points to important interactive effects between pollinators and management that influence robusta flowering, fruit set and ultimately production (Boreux et al., 2013b). However, on the whole, the complex interplay between flowering time and other factors (e.g., pollination, disease susceptibility and stress) that could greatly influence robusta coffee's vulnerability to climate remain largely unexplored. Understanding the consequences of early flowering, including altered exposure to climate stresses and how plants respond to these, will enhance our ability to predict the impacts of climate change and inform adaptive management strategies for maintaining productivity in key agricultural crops such as robusta coffee.

Here we investigate the hypothesis that climate variability and management interventions have different impacts on robusta coffee yield that are dependent flowering time. We utilised a decade-long dataset with data on flowering time and yield from 558 farms across Vietnam, the world's most important robust coffee producing country. We calculated key phenological stages (flowering, fruiting and growing season) and linked this with daily climate data from ERA5: Fifth generation of ECMWF atmospheric reanalyses of the global climate (Hersbach et al., 2020) for each of the 5580 observations in our dataset. We used structural equation modelling to identify the key drivers of phenological (flowering time) shifts in robusta and test different model structures to identify whether early flowering changes response (yield) to climate and management factors (i.e., irrigation, fertilizer use and tree age).

2. Methods

2.1. Study area

The study area covers some of the world's most intensive robusta coffee (*Coffea canephora*) production provinces in the world - the Central Highlands region of Vietnam (Supplementary Material, Fig. S1), Southeast Asia. Vietnam is the world's most important producer of robusta coffee (40 % of total robusta supply) and accounts for 18 % of the world's total coffee production (ICO, 2022). The climate of Vietnam's coffee growing areas is characterised by a humid tropical climate with mean annual temperatures of around 24 °C and a total rainfall of c. 1833 mm per annum (Supplementary Material, Fig. S1). For further details on the climate and management of coffee farms in the study area please see Byrareddy et al. (2020), Byrareddy et al. (2019) and Kath et al. (2020).

The study dataset comprises yield and flowering time (day of year) for 558 farms (total $N = 5580$) collected over 10 years, from 2008 to 2017 (Supplementary Material, Fig. S2). We defined flowering time as the date of the first blossoming. We used the date of first flowering (instead of the range of dates over which full flowering occurs) because we are interested in how climatic variability influences the initiation of flowering, as opposed to the length or end of flowering. In robusta coffee farms the initiation of flowering is also immediately followed by irrigation, which is typically applied by farmers to synchronise flowering between trees (Byrareddy et al., 2020; Masarirambi et al., 2009).

Flowering is highly synchronous, and generally occurs for about 30–40 % of coffee plants on the same day, with all plants flowering within a day or two of each other. The same set of farms was assessed each year. Coffee farmers record the time of first flowering in their farm record books, along with harvesting time, which are maintained for coffee certification programs implemented by Sustainable Management Systems – ECOM Agroindustrial Corp. Ltd. (SMS-ECOM trading). The farmers in the SMS-ECOM supply chain are trained to collect the farm data by the agronomists. SMS-ECOM coffee agronomists also conduct farm surveys two to three times a year to collect and cross-check information and verify its accuracy. Farmers also record the date and amount of irrigation (litres $tree^{-1}$) and fertilizer (kg ha^{-1}) applied. Tree age is calculated based on planting year. For further details on the dataset and its collection please see Byrareddy et al. (2020), Byrareddy et al. (2019) and Kath et al. (2020).

2.2. Defining phenological stages

Using the flowering time data from each farm for each year we were able to approximate the key phenological stages of the coffee growth cycle. These were (1) pre-flowering, (2) flowering, (3) fruiting and (4) the growing season. Table 1 describes each of these phenological stages and the method used to delineate them. A graphical representation of the key phenological stages is in Supplementary Material, Fig. S3. Flowering day anomalies, relative to each site, were also calculated for each of the 5580 observations. The timing and duration of each phenological stage was then linked with daily climate data (ERA5) (Hersbach et al., 2020). For each phenological stage at each farm during each year, mean minimum temperature, mean maximum temperature and total rainfall were calculated (Fig. 1). See Kath et al. (2020) for further details on the climate data used in the study. The resulting dataset allowed us to precisely link climate conditions with the phenological stage of coffee at each farm, during each year.

2.3. Statistical analysis

To investigate the complex interlinked relationships between flowering time, climate stress and coffee yield we used structure equation models (SEM) (Lefcheck, 2016). SEM modelling has been well utilised in phenological studies (Esch et al., 2019; Li et al., 2021; Valdés and Ehrlén, 2021). There are two key features of SEM that differentiate this approach from traditional regression modelling and make it suitable for investigating how early flowering impacts coffee yield responses to climate. First, variables can appear as both predictors and responses (Lefcheck, 2016). This allowed us to construct models where the cascading and interacting effects of difference in flowering time, growing season length and climate stress could be captured holistically. Second, the links or paths between variables in an SEM represent hypothesized casual relationships (Lefcheck, 2016). SEMs were fit using the piecewiseSEM package (Lefcheck, 2016) in R (R Core Team, 2021) to construct structural equation models for both early- and late-flowering scenarios.

A simplified schematic showing the general SEM structure is shown in Supplementary Material, Fig. S4. Here climatic and management factors are predictors of flowering time, growing season length and yield (Supplementary Material, Fig. S4). Note here we show one box representing climatic factors, but in the full model these are separated into different phenological phases. In addition, the schematic shows that the links between flowering time, growing season length and yield are also evaluated in the model. The grey lines show the links between the different variables assessed, with beta (β) representing the parameter estimate of the relationship between the variables in the model. For further details on SEM please see Lefcheck (2016).

To evaluate the goodness-of-fit of the SEMs constructed we used Shipley's test of directed separation (Shipley, 2009), which tests whether variables are conditionally independent (i.e. there are no missing variables between unconnected variables) (Lefcheck, 2016). Tests of directed separation are done using Fisher's C (Lefcheck, 2016) and the hypothesized relationship is considered consistent with the data when there is weak support for conditional independence claims (i.e., P is greater than a given significance threshold, here we use $\alpha = 0.05$), after Lefcheck (2016). All models fit had a Fisher's C with $P > 0.05$ indicating adequate fit the data in each case.

As we used repeat observations from each farm over a 10 - year period we also fitted the SEMs using linear mixed models with a random effect for each site, nested within each province to account for any possible spatial autocorrelation. We also fitted each model within the SEM using an autoregressive process of order 1 to account for any potential temporal autocorrelation. We used flowering time anomalies (i.e. a measure of flowering time adjusted at the site level) as our response. As we used a site-level adjusted measure of flowering time we implicitly accounted for absolute differences in flowering day of year between sites that may have been caused, for example, by factors such as slope, aspect, soil and solar radiation, etc.

Correlated predictors were accounted for by adding error terms to remove the effect of correlated covariates on each other before computing their correlation with the response (Lefcheck, 2016). Correlations between all predictors are in Supplementary Material Fig. S5. As SEMs are sensitive to assumptions of normality, we normalised responses (i.e. flowering day of year, growing season length and yield) using Ordered Quantile (ORQ) normalization transformation in the bestNormalize package in R prior to model fitting (Peterson and Cavanaugh, 2019). SEMs were built for both flowering- and fruiting-period climate impacts, but, as results were similar for both these models (to be expected because one occurs directly after the other), we focus on the flowering-based results in the main text and provide results based on climate in the fruiting period in the Supplementary Material, Figs. S7–S10.

To test the effect that early flowering has on coffee responses to climate stress we compared the structure of three SEM models. The first of these used all available data. The second was restricted to all data showing early flowering (i.e., a flowering day anomaly <0). The third model was based on all late flowering (i.e., a flowering day anomaly >0). In all three models, coefficients were standardised [mean(x)/1.SD(x)] to allow the comparison of effect sizes among variables and between models (Gelman and Hill, 2006). To test the sensitivity of our results to the way we divided flowering day anomalies into early and late flowering. We also fit models based on very early flowering (i.e., a flowering day anomaly <5) and very late flowering (i.e., a flowering day anomaly >5) conditions.

Finally, for the yield subset of the SEM model, we tested how well a model built using only early flowering conditions predicted yields under late flowering (assessed using cross-validated R^2 values) and vice versa. We also carried out 1000 cross-validations (model built with a randomly selected 80 % of the data and tested on the remaining 20 %) for both an early and late flowering period to provide a baseline estimate of model performance. This test allowed us to assess the implications of predicting from models assuming either early or late flowering.

3. Results

3.1. Early flowering exposes coffee to different climatic conditions

When flowering occurred early, coffee plants were exposed to significant differences in temperature and rainfall across the flowering and

Table 1
Phenological phases and their calculation methods. The below is adapted from Dinh et al. (2022).

Phase	Start	End	Duration
Pre-flowering. This stage captures the end of the ~6 week dormancy period when the plant is preparing for flowering.	30 days prior to the commencement of flowering	At the commencement of flowering	30 days
Flowering. Here we focus on the start of the ~8 week flowering period as we want to focus on the flowering initiation period (~30 days).	When first flowering is evident (see methods for details)	30 days after commencement of flowering	30 days
Fruiting. This stage captures the pinhead stage, when the fruit is first forming, and the start of expansion towards bean formation. Again we focus on the start of the fruit development period, which we approximate as running for 30 days.	From the end of flowering	30 days from the commencment of fruiting	30 days
Growing. This is the period after the fruit has developed – the period of cherry growth (i.e. the development of the coffee bean) - until harvesting occurs. This includes the maturation phase.	From the end of the fruiting phase	Ends at harvest	From fruiting to harvest

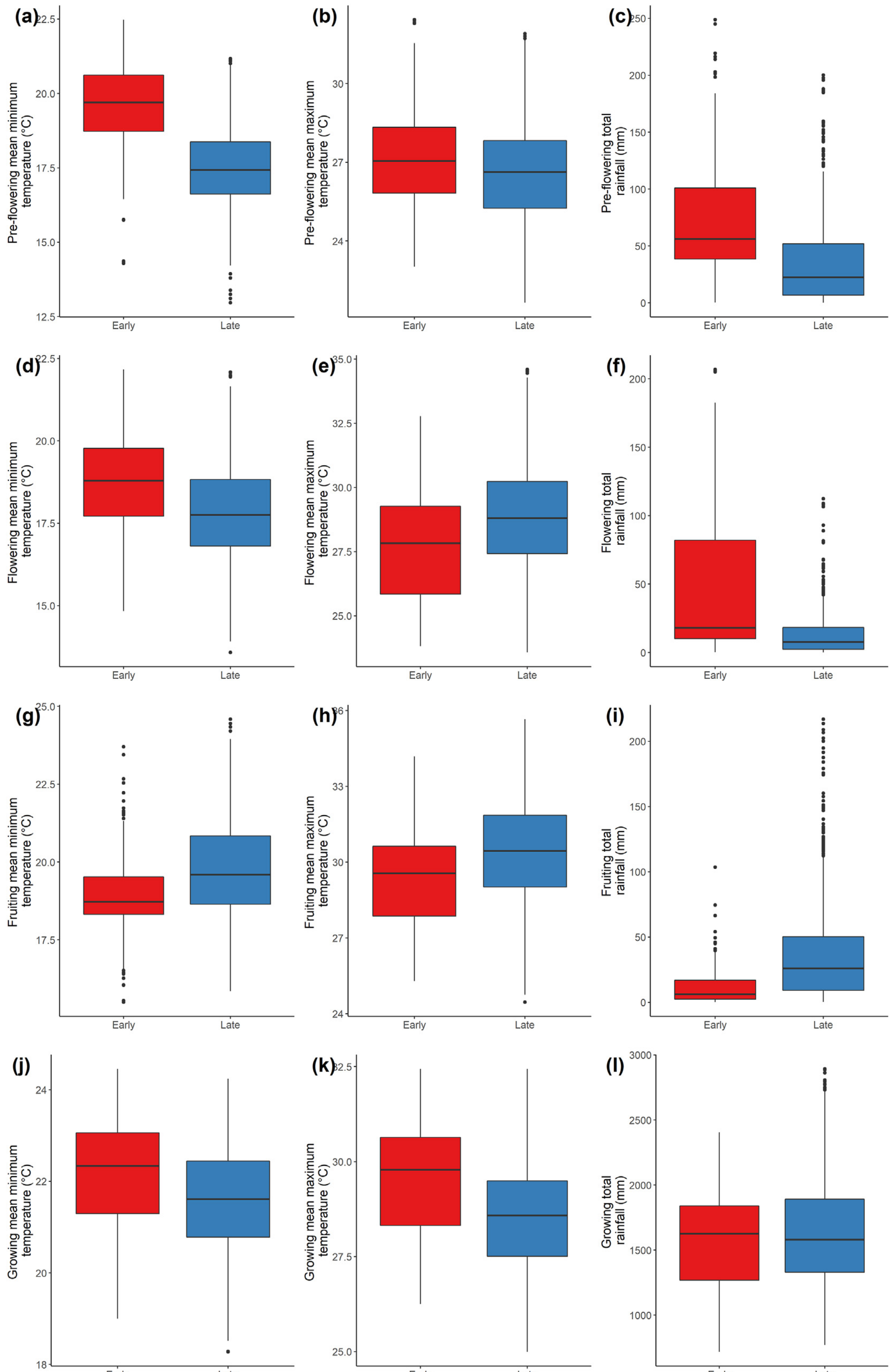

Fig. 1. Red (early flowering) and blue (late flowering) boxplots showing the distribution (center horizontal line is the median, lower and upper sections are 25th and 75th percentiles, respectively, whiskers show the full range of the data, except for outliers which are shown as points) of climate predictors (a–c) prior to flowering, (d–f) during flowering, (g–i) during fruiting and (j–l) during the growing season.

fruiting seasons but not the growing season (see Table 1 for details of phenophases), compared to late-flowering plants (Fig. 1; Table S1). Prior to flowering (i.e., pre-flowering), coffee that underwent earlier flowering was subject to warmer and wetter conditions (Fig. 1a–c), warmer minimum temperatures and higher rainfall (Fig. 1d, f), and lower maximum temperatures (Fig. 1e) (Table S1). Climatic conditions also differed during fruiting, with earlier flowering corresponding to cooler temperatures and lower rainfall in this period (Fig. 1g–i). Finally, while growing season climatic conditions were warmer for earlier-flowering coffee (Fig. 1j, k), there was no difference evident in rainfall conditions in this period (Fig. 1l) (Table S1). Coffee yield responses to irrigation and tree age also varied between early and late flowering, while fertilizer use did not (Supplementary material, Fig. S6) (Table S1).

3.2. Early flowering strongly correlates with growing season length

Earlier flowering in the study area occurred across most years, with the exception of 2009, 2013 and 2014 (Fig. 2a), and was most apparent in the later years of our dataset (2015–2017). The earlier that flowering occurred, the longer the total growing season (Fig. 2b, c); for each day earlier that flowering occurred there was on average a 1.025 day increase in the length of the growing season (Fig. 2c). The length of the dormancy period (i.e., the period from harvest to flowering the next season) was also reduced when earlier flowering occurred (Supplementary Material Fig. S3). Note that harvest time is less flexible (harvest day anomalies are only ±6 days) than flowering time and that growing season length is influenced by socio-economic conditions (i.e., the need to meet supply contracts, transport requirements, labor availability etc.) that constrain when harvest can occur.

3.3. Minimum temperature drives early flowering

Higher minimum temperatures in the month before flowering were the strongest driver (standardised $\beta = -0.73$) of early flowering (Fig. 3). In contrast, higher maximum temperatures were associated (standardised $\beta = 0.27$) with later flowering (Fig. 3). The mean effect of pre-flowering minimum temperature was 2.38 times stronger than that of maximum temperatures. Older trees were also more likely (standardised $\beta = -0.17$) to flower earlier, while increased irrigation was associated (standardised $\beta = 0.11$) with later flowering. The relative impact (i.e., the standardised β) of tree age and irrigation was much lower than the effect of temperature variables (Fig. 3).

3.4. Early flowering has minimal direct effect on yield

Flowering day anomaly had only a minimal direct effect (standardised $\beta = -0.06$) on coffee yield. Early flowering strongly affected (standardised $\beta = -0.81$) the length of the growing season (Fig. 2a), but there was no detectable effect of growing season length on yield in the overall SEM (Fig. 3). The effect of climate and management predictors on yield was generally much stronger than the effect of flowering time and growing season length (Fig. 3).

3.5. Higher growing season maximum temperatures limit yield

Maximum temperature during the growing season was the most important predictor of coffee yield, with high maximum temperatures corresponding (standardised $\beta = -0.82$) to lower yields (Fig. 3). High rainfall during flowering also had a negative effect (standardised $\beta = -0.14$) on yield (Fig. 3). In contrast, higher minimum temperatures (standardised $\beta = 0.18$) during the growing season, tree age (standardised $\beta = 0.83$), irrigation (standardised $\beta = 0.38$) and fertilizer use (standardised $\beta = 0.44$) were all associated with higher yields. It should be noted that the relative impact of management predictors, apart from tree age, was far lower than the effect of growing season maximum temperature (Fig. 3).

3.6. Earlier flowering alters coffee yield responses to climate and management

The sign and magnitude of the effect of flowering and growing season temperature and rainfall predictors varied between the early and late flowering SEMs (Figs. 4, 5 & 6). When early flowering was considered, climatic conditions during flowering were most strongly associated (e.g. flowering maximum temperatures had a standardised $\beta = -0.99$) with yields (Fig. 4), while growing season climatic conditions seemingly had a relatively minimal effect (e.g. growing season minimum temperatures had a standardised $\beta = -0.39$) on coffee yield (Fig. 6). In contrast, under late flowering conditions climatic conditions during the growing season were the most important (Fig. 5). As in the overall SEM, growing

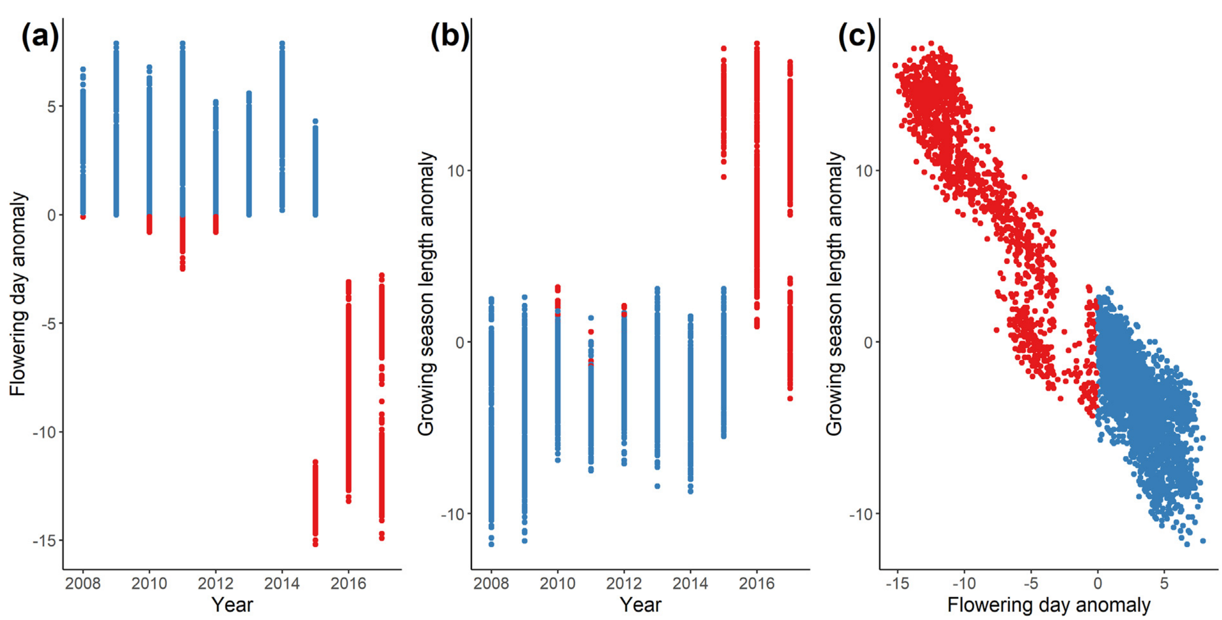

Fig. 2. (a) Flowering day anomaly and (b) growing season length anomaly over the duration of the study (2008–2017) across the 5580 observations and (c) the relationship between flowering day anomaly and growing season length anomaly (Pearson $r = -0.94$). Red dots are early flowering observations (Flowering day anomaly <0) and blue dots are late flowering (Flowering day anomaly <0).

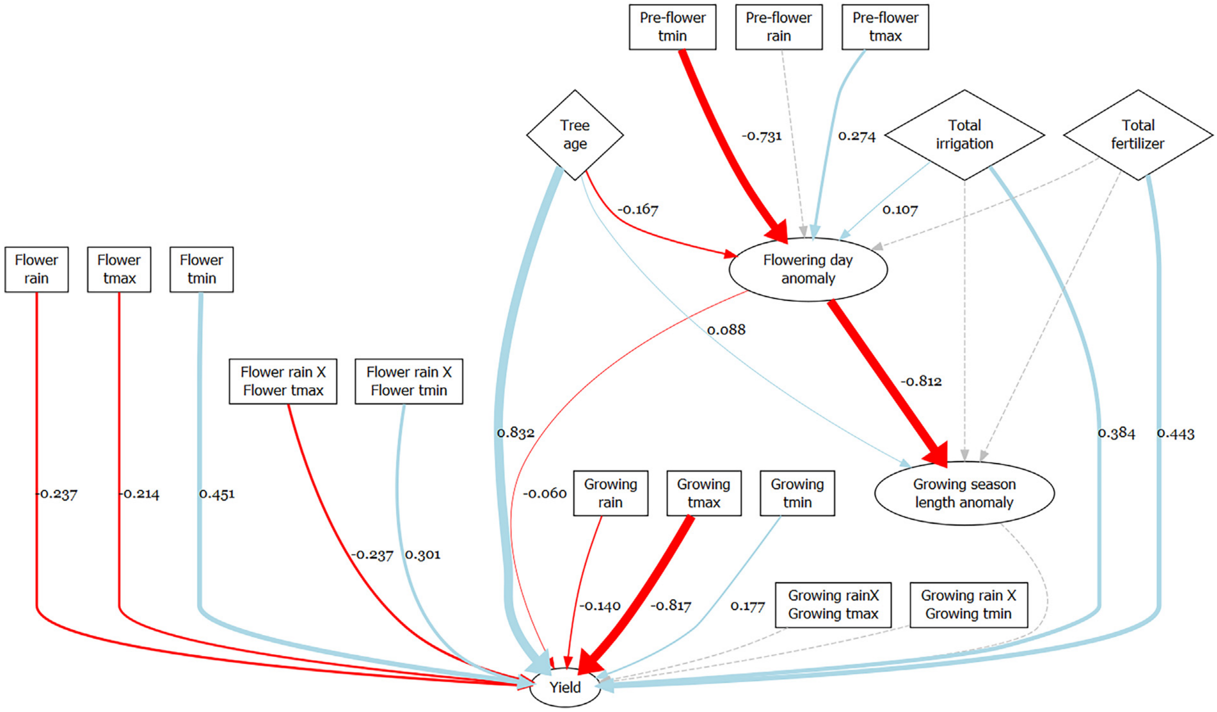

Fig. 3. Structural equation model (SEM) incorporating all data (N = 5580) exploring the relationship between flowering time, growing season length, climate and management. Blue arrows denote positive relationships, and red arrows negatives ones. Arrows for non-significant paths ($P \geq 0.05$) are shown by grey dashed lines. The thickness of the significant paths has been scaled based on the magnitude of the standardised regression coefficient, given in the associated box. R^2s for component models for each of the response variables are the conditional R^2c based on the variance of both the fixed and random effects (Flowering day anomaly $R_c^2 = 0.61$; Growing season length anomaly $R_c^2 = 0.71$ and Yield $R_c^2 = 0.81$).

season maximum temperatures (standardised β = −1.02) were the chief constraint on yield under late flowering conditions (Figs. 5 & 6).

Tree age and fertilization had strong positive effects (standardised β ranging between 0.31 and 0.83) on yield in the overall SEM (Fig. 3) and under late flowering conditions (Fig. 5). In contrast, tree age and fertilization had no effect under early flowering conditions (Figs. 4 & 6). That is, the older the tree the higher the yield, but only under late flowering conditions (Fig. 6). Similarly, as fertilizer application increased so did yields, but again only under late flowering conditions (Fig. 6). Irrigation had a similar positive effect (standardised β = 0.29 and 0.24 respectively) (95 % confidence intervals overlap) under both early and late flowering conditions (Fig. 6).

The relationships we found between climate and management with robusta yield were similar under the different divisions of our data (i.e. also based on flowering anomaly of ±5 days, instead of with 0 as above) (Supplementary Material, Fig. S11). Flowering climatic conditions still diverged under this ±5-day division, with parameter estimates overlapping (Supplementary Material, Fig. S11). Growing season climate parameters also had a largely similar effect regardless of whether a 0- or 5-day division was used, although maximum temperature effects were more positive under very late flowering (i.e. when the data were restricted to a positive 5-day anomaly), and more negative under very early flowering (i.e. a negative 5-day anomaly) (Supplementary Material, Fig. S11). Irrigation affects were again similar between a 0- and 5-day anomaly division, but not so for tree age and fertilizer (Supplementary Material, Fig. S11). Tree age and fertilization had similar parameter estimates when comparing early (<0 days) and very early divisions (<−5 days), but not when comparing late (>0) and very late (>+5 days) (Supplementary Material, Fig. S11).

3.7. Early and late flowering models poorly predict yields under different flowering times

The late flowering model predicted yields under late flowering well (cross-validated R2 = 0.54) (Fig. 7). Similarly, the early flowering model predicted yields in early flowering conditions well (cross-validated R^2 = 0.54). These results were also consistent across repeated cross-validations (×1000 times) within both late flowering (minimum cross-validated R^2 = 0.43, maximum cross-validated R^2 = 0.57) and early flowering (minimum cross-validated R^2 = 0.42, maximum cross-validated R^2 = 0.70) models (Supplementary Material, Fig. S12). In contrast, models based on late flowering predicted yields under early flowering conditions poorly (a c. 50 % reduction in cross-validated R^2 of 0.54 to 0.27). Likewise, models based on early flowering were unable to predict yields well under late flowering conditions (a c. 75 % reduction in cross-validated R^2, from 0.58 to 0.14).

4. Discussion

Warmer temperatures and changing rainfall patterns are causing many plants to flower earlier globally (Wolkovich et al., 2012). However, while the broad ecological consequences of early flowering have been well researched (Cleland et al., 2007; Piao et al., 2019; Rafferty and Ives, 2011), how shifting flowering times influence the sensitivity of agricultural productivity to climate and management has not been much explored, but see Fraga et al. (2016). We used an observational industry-based farm-level flowering time and yield dataset collected under real-world production conditions. Using this extensive long-term dataset (N = 5580) of robusta coffee flowering times we showed that early flowering changes how climate affects coffee yield. Early flowering also affected the influence of management interventions, such as fertilization, on coffee yield. Importantly, we also showed that models based on late flowering conditions poorly predicted yields under early flowering conditions and vice versa.

Early flowering increased the sensitivity of coffee yield to higher temperatures earlier in the season, during flowering itself. In contrast, when late flowering occurred, yield was most sensitive to temperature and rainfall later in the growing season, after flowering and fruit development had occurred. Tree age and fertilizer had no effect on yield when flowering

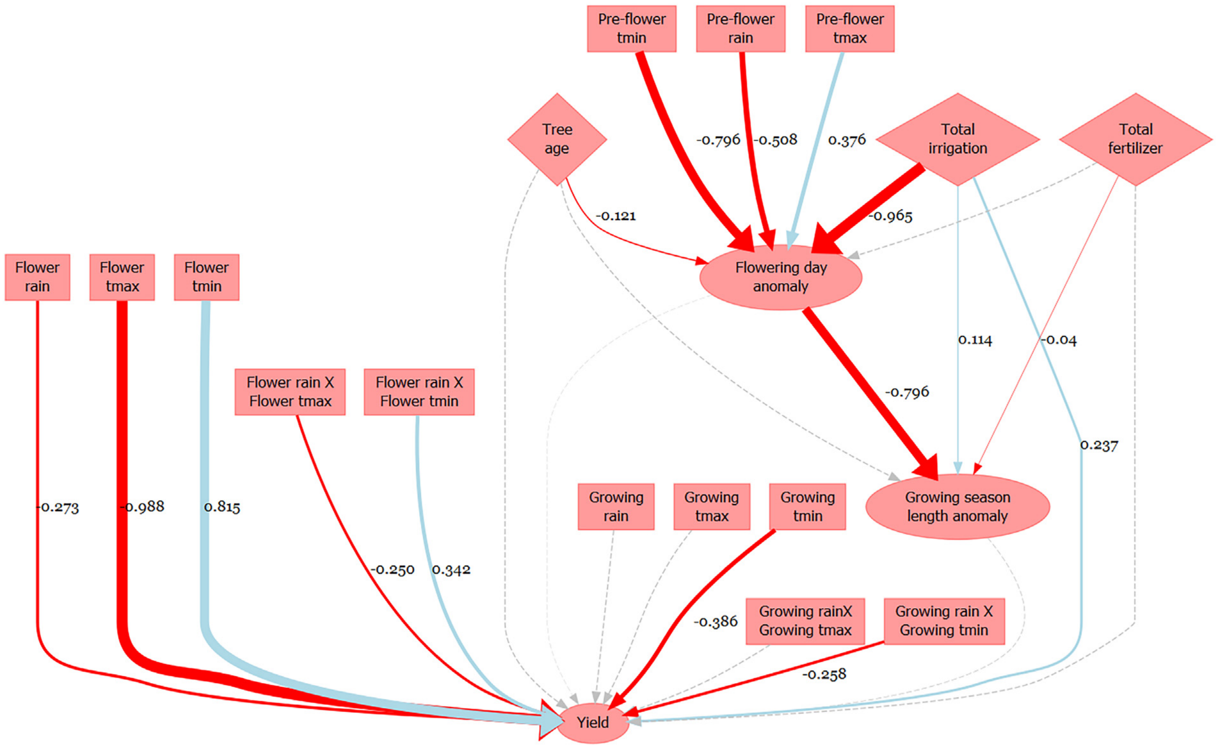

Fig. 4. Structural equation model (SEM) built when flowering occurs early (i.e. flowering day anomaly <0) (N = 1382) exploring the relationship between flowering time, growing season length, climate and management. Blue arrows denote positive relationships, and red arrows negatives ones. Arrows for non-significant paths ($P \geq 0.05$) are shown by grey dashed lines. The thickness of the significant paths has been scaled based on the magnitude of the standardised regression coefficient, given in the associated box. R^2s for component models for each of the response variables are the conditional R^2c based on the variance of both the fixed and random effects (Flowering day anomaly $R_c^2 = 0.80$; Growing season length anomaly $R_c^2 = 0.69$ and Yield $R_c^2 = 0.84$).

occurred early, but increased yield under late flowering conditions. In effect, early flowering altered the factors (i.e., seasonal climatic conditions and management) most limiting coffee yield. We postulate two mechanisms, possibly interacting, which could explain these findings.

4.1. Ecological asynchrony as a possible driver of shifting climate sensitivity

First, early flowering may cause ecological asynchronies that trigger a switch in the limiting effect of climate on yield from the growing season to the flowering season. Coffee, like numerous other plant species, is highly dependent on pollinators to ensure fruit set (Classen et al., 2014; Hipólito et al., 2018; Imbach et al., 2017). However, the type and abundance of pollinators present in an area may differ over time. Early flowering in the tropical tree fruit, longan (*Dimocarpus longan* Lour.), reportedly attracts a greater frequency of mainly dipterans, rather than mainly wild bees that are found in later flowering trees; as dipterans are less-effective pollinators than wild bees, the result is lower fruit set under early flowering (Sritongchuay et al., 2021). Climate change acting through the coupled effects of early flowering and changes in habitat and climatic suitability for pollinators could therefore cause significant spatial and temporal mismatches in pollinator availability (Hegland et al., 2009; Imbach et al., 2017).

This mismatch in the availability and type of pollinators could be further exacerbated if the pollinators available during early flowering are more sensitive to temperature conditions than those present during late flowering. Floral temperature regulates plant-pollinator interactions, both by promoting or modifying pollinator behaviour and by altering the floral reward signals that attract pollinators (Creux et al., 2021; Harrap et al., 2017; Heinrich and Raven, 1972). Further, pollinators can change their preferences depending on flower temperatures, possibly selecting plants in cooler areas when it is hot, or plants in warmer areas when it is cold (Norgate et al., 2010).

The strong negative maximum temperature effect we find during flowering could therefore be a consequence of pollinator sensitivity to temperature. In other words, the suite of pollinators available when early coffee flowering occurs may be sensitive to high day time temperatures and thus pollinate less coffee, in turn resulting in lower fruit set and yield. Alternatively, the suite of pollinators available when flowering occurs later in the season may be less sensitive to temperature and thus pollination is not limited by temperatures during flowering. However, we found no evidence for this in this study; when earlier flowering occurred, maximum temperatures were not warmer compared to later flowering. This result is more consistent with the idea that it is not a shift in climate per se causing the increased sensitivity to maximum temperatures, but instead some other biological mechanism (e.g., a change in the sensitivity of available pollinators, as hypothesized above).

4.2. Earlier flowering stress and vulnerability as a possible driver of shifting climate sensitivity

A second possible mechanism, possibly acting alongside the effects of ecological asynchronies, is based on the potential impact of sequential physiological stresses on plants. Early flowering is a stress inducing event (Takeno, 2016) and thus any follow up stresses occurring in close succession, say during flowering, may be particularly damaging to the plant and difficult for it to tolerate compared to when the plant is exposed to stresses spread over a longer period of time (Anwar et al., 2021) or under conditions when a stressful earlier flowering event has not occurred. In our study the possible stresses caused by early flowering may increase coffee's sensitivity to follow up stresses – in this case high maximum temperatures during flowering. In general, high temperatures negatively affect coffee productivity, through for example increasing atmospheric evaporative demand in the air, which triggers stomatal closure and in turn decreases photosynthesis (DaMatta and Ramalho, 2006). Whether this is the same pathway through

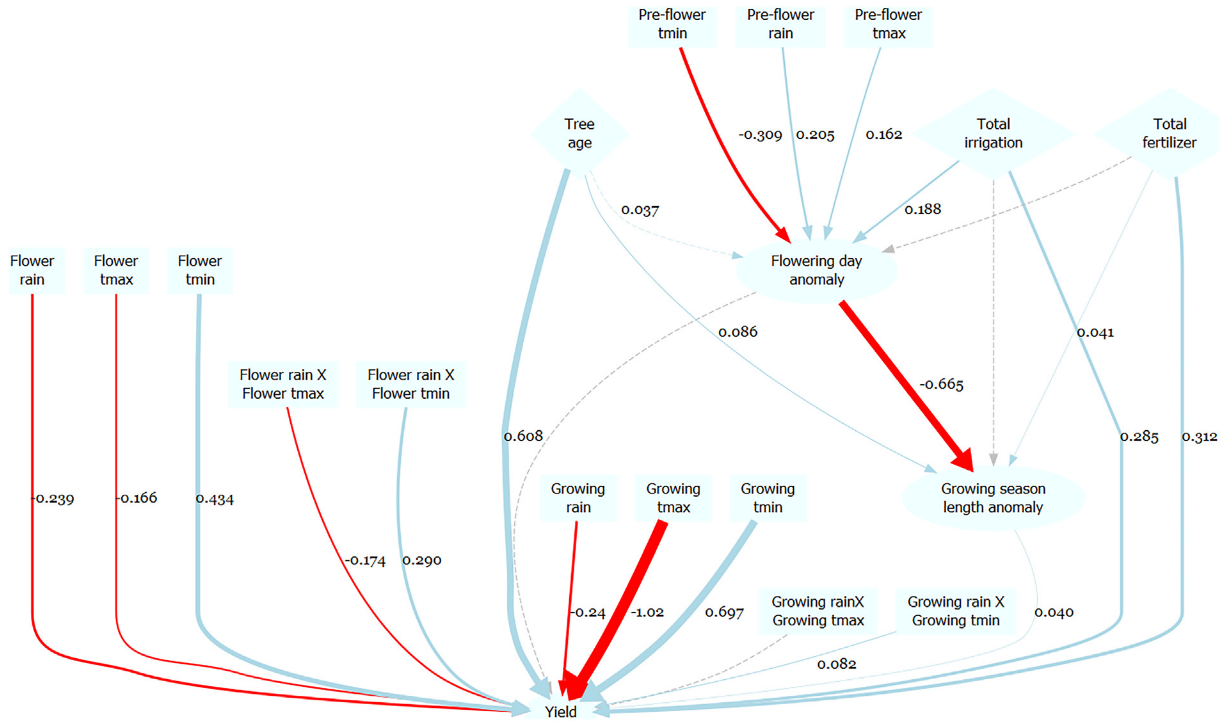

Fig. 5. Structural equation model (SEM) built when flowering occurs late (i.e. flowering day anomaly > 0) ($N = 4181$) exploring the relationship between flowering time, growing season length, climate and management. Blue arrows denote positive relationships, and red arrows negatives ones. Arrows for non-significant paths ($P \geq 0.05$) are shown by grey dashed lines. The thickness of the significant paths has been scaled based on the magnitude of the standardised regression coefficient, given in the associated box. R^2s for component models for each of the response variables are the conditional R^2c based on the variance of both the fixed and random effects (Flowering day anomaly $R_c^2 = 0.43$; Growing season length anomaly $R_c^2 = 0.45$ and Yield $R_c^2 = 0.78$).

which high temperature stresses coffee under early flowering needs to be tested through further experimental physiological studies.

Early flowering also coincides with a shorter dormancy period in our coffee study. Dormancy is critical for many plants, helping plants buffer themselves against unfavourable conditions and playing an important role in bud break, flowering and fruiting (Beauvieux et al., 2018; Shefferson et al., 2005). As the timing of harvest is set each year, based on socio-economic and logistic constraints (e.g., availability of labour) the period of dormancy is reduced in direct proportion to flowering time (Supplementary Material Fig. S1). Despite the potential importance of dormancy, research on the impact of dormancy length on coffee is absent from the literature. Disentangling the possibly compounding stresses of a shorter dormancy and early flowering could be an important avenue for future research and help elucidate why coffees climate sensitivity may shift as a result of early flowering.

4.3. Earlier flowering and reduction in the benefit of fertilization and tree age

A mismatch in pollinator availability, or a stress response that limits effective flowering and subsequent fruit set, could also explain why management factors, such as fertilizer application and tree age have a strong positive effect on coffee yield under late flowering, but not when early flowering occurs. The benefits of tree age and fertilization are only likely to be realised if there is effective conversion of flowers to fruit. If stress or a lack of pollinators prevents this, then management interventions that occur after flowering and fruiting would have little effect on yield. As such, the application of fertilizer, which occurs later in the growing season well after flowering (Byrareddy et al., 2020), becomes less important. The positive benefits of fertilizer application are thus only able to be realised if there is sufficient pollination and fruit set. Likewise, the benefits of having older and larger trees also become negligible, as again the main limiting factor becomes pollination effectiveness in flowering. In contrast, the similar positive impact of irrigation observed under both early and late flowering may be because irrigation occurs during the flowering period to help ensure synchronisation of coffee flowering (Byrareddy et al., 2020; Masarirambi et al., 2009). Future research invesigating the role of irrigation (and water stress) on flowering time would help clarify this.

Interestingly, the positive effect of tree age and fertilization on robusta yield was absent when we restricted our data to only very late flowering (here defined as +5-day flowering day anomaly). This again may be because of a mismatch between pollinator availability and flowering times, but also potentially results from a mismatch between the robusta coffee cherry's growth stage and its subsequent nutrient demand. For example, in canola, the timing of nitrogen application has a significant impact on yield (Ma and Herath, 2016). Equivalent research on fertilizer timing on robusta coffee yield under different phenological stages appears lacking in the literature. Our results suggests that experimental research testing the relationship between fertilizer application, tree age and yield is an important next step for disentangling these effects and for identifying a mechanism that might explain our results.

4.4. Temperature as a driver of earlier flowering in coffee

Our results align with other research suggesting that warm nights, prior to flowering, are a key driver of early flowering (Perrella et al., 2020; Thines et al., 2014). The strong relationship between temperature and coffee flowering is also well documented in the literature, with warm temperatures believed to be important for floral bud initiation (DaMatta and Ramalho, 2006). Rainfall, especially at the end of the dry season, is also believed to be an important cue to trigger flowering (Haarer, 1962). However, more recent research testing and quantifying this phenomenon is lacking in the literature. Our findings indicate that the effect of rainfall at the end of the dry season (i.e. the pre-flowering phase in our model) may be relatively less important for robusta coffee phenology than temperature in this managed and irrigated system.

Our results suggest a relationship between water availability (rainfall or irrigation) and flowering time, but that this seems to change depending on

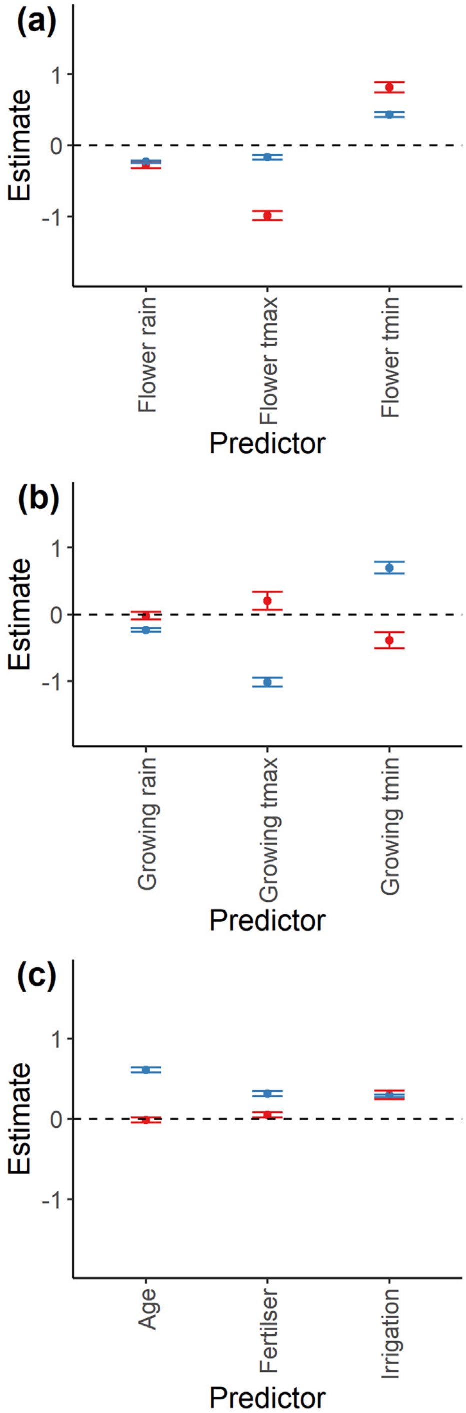

Fig. 6. Comparison of flowering and growing season climate stressors and management predictors estimated standardised effect size on coffee yield under early (red) and late (blue) flowering times. Points are the mean estimates and error bars are 95 % confidence intervals.

whether flowering occurs early or late. We suggest that it is possible that the cooler conditions pre-flowering associated with later flowering trigger physiological changes in coffee that alter how it responds to rainfall. Regardless of the mechanism, our results underscore that flowering initiation in coffee is a complex phenomenon and not yet adequately understood (Craparo et al., 2021) and that further experimental research is needed to disentangle the interacting climatic and management factors that trigger flowering.

One factor that we did not assess, but which is important for flowering time, is photoperiod and solar radiation (Renner, 2007; Wang et al., 2020; Yeang, 2007). In woody plants a longer photoperiod can advance flowering by 1–5.6 days (Wang et al., 2020). Around the equator the annual cycle of solar radiation intensity is likely an important trigger of flowering for tropical plants (Yeang, 2007). In the rubber tree (*Hevea brasiliensis*), which flowers at the same time every year, solar radiation is thought to be the chief determinant of flowering, as opposed to rainfall and temperature, which vary year to year (Renner, 2007; Yeang, 2007). In contrast, our study, with sites between a latitude of 10–15 degrees north, showed that robusta coffee flowering time varied substantially from year to year (up to −15 to +8 days at a farm). For this reason, we focused on seasonal dynamic climatic parameters (e.g. temperature and rainfall) that drive flowering time anomalies in the field, whereas photoperiod and solar radiation are largely, although not completely we acknowledge, a function of landscape position, so generally relatively stable from year to year.

4.5. Implications of early flowering changing coffee responses to climate stress and management

Our results have two important implications for understanding and managing the impacts of climate change on coffee and the world's plant species more generally. First, failure to take into account shifts in flowering time could result in the misalignment and misidentification of the climate stressors of most importance for this and other significant socio-economic crops. For instance, studies assessing the seasonal impacts of climate that don't specifically consider conditions at flowering time may mean that the period over which climate statistics are considered may be misaligned by several weeks or more, making it difficult to accurately quantify the seasonal impacts of climatic change on plant species, including major cropping species. More importantly, as shifts in flowering time appear to alter the effect of climate stressors, models for predicting the impacts of climate change may be either over- or underestimating the effect of particular climate variables at different times of the year. In this study, early flowering switched the period of highest vulnerability from the growing season to the flowering phase, consistent with Kath et al. (2020).

In our study, models based on late flowering conditions poorly predicted robusta coffee yields under early flowering conditions, and vice versa. This result indicates that coffee models that do not account for whether flowering has occurred late or early may be at risk of incorrectly extrapolating the consequence of future climatic conditions on coffee growing productivity and suitability. As such, any projections of the impact of climate change on coffee yield based on annual averages (e.g. Bunn et al., 2015; Chemura et al., 2021; Grüter et al., 2022), phenologically adjusted conditions (Fraga et al., 2016; Guo et al., 2021; Kath et al., 2020; Venancio et al., 2020) and potentially even genomic variability (Tournebize et al., 2022) that do not account for potential changes in the effects of climate with early flowering may misidentify the climate stressors/season of most importance and in turn the consequences of climate change. Our results therefore highlight an important avenue for future experimental and field level-based work, which appears lacking in literature for many agro-ecosystems at the moment, but see (Fang et al., 2020; Koebsch et al., 2020), on integrating the consequences of phenological shifts with predictions of climate change impacts (Richardson et al., 2012).

Further, even though climate change is causing a trend towards early flowering, year to year climatic variability means that there is still likely to be high inter-annual variation in flowering times. Inter-annual variability in flowering times means that managing the consequences of early flowering (e.g. increased vulnerability to temperature during flowering) may need to occur dynamically year to year depending on pre-flowering climatic conditions. In practice this could mean management interventions, such as fertilizer application may need to be dynamically altered depending on whether early flowering has occurred or not. Indeed, our results suggest that if early flowering occurs then the application of fertilizer may be less beneficial to yield. The economic and environmental implications of this

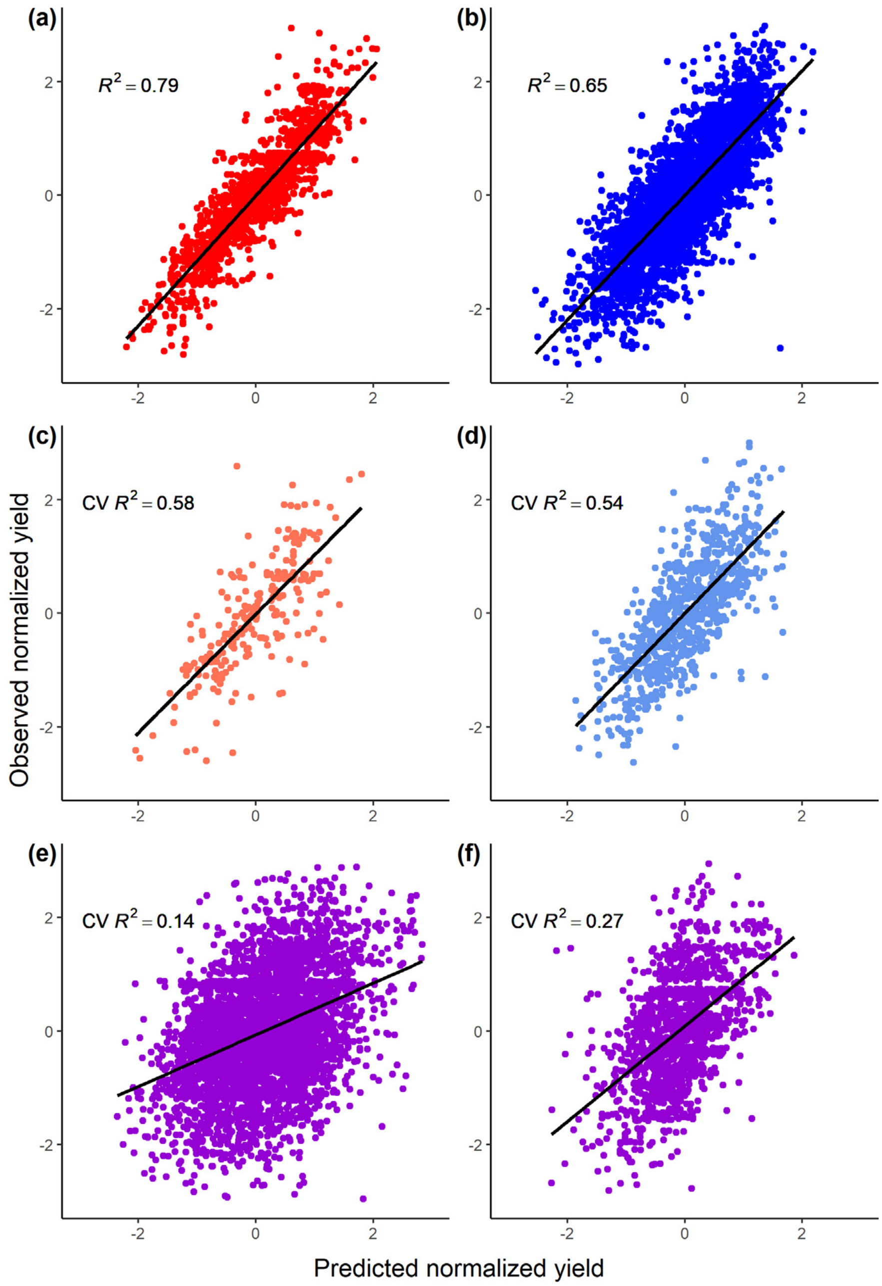

Fig. 7. Yield model component of the SEM showing the ability to predict yields when predicting from models based early flowering (a, c, e) or late flowering (b, d, f). (a) Early flowering model predicting to all data (red points) used to build the model, (b) Late flowering model predicting to all data (blue points) used to build the model, (c) cross-validation of the early flowering model testing how well it predicts yield observations (light red points) for early flowering coffee held-out of the model, (d) cross-validation of the late flowering model testing how well it predicts yields for late flowering coffee yield observations (light blue points) held-out of the model, (e) cross-validation of the early flowering model testing how well it predicts yields for late flowering coffee yield observations (purple points) held-out of the model and (f) cross-validation of the late flowering model testing how well it predicts yields for early flowering coffee yield observations (purple points) held-out of the model. Cross-validations were based on 80/20 split of the data (see methods for details). See Supplementary Material. Fig. S8 for summarised results of repeated (randomised 1000 times) cross-validations.

for coffee production are potentially far-reaching. Fertilizer is an important input cost for coffee farmers, while runoff from excess fertilizer is an important environmental concern in the high rainfall tropical areas coffee is grown (Byrareddy et al., 2019; Tully et al., 2012). Understanding the implications of early flowering in determining the effectiveness of management interventions, and related environmental consequences, is therefore an important line of future enquiry. Given the important environmental and economic consequences of fertilization, field experiments quantifying the costs and benefits of adjusting nutrient management practices based on flowering time are needed. Further research is also needed to identify the degree of early flowering difference that would justify management changes as presumably small anomalies (e.g. 1 to 2 day differences in flowering time) would have minimal impact.

CRediT authorship contribution statement

Jarrod Kath: Conceptualization, Analyses, Writing- Original draft preparation, review and editing. **Vivekananda Mittahalli Byrareddy:** Data collection, Conceptualization, Writing- Original draft preparation, review and editing. **Kathryn Reardon-Smith:** Conceptualization, Writing- Original draft preparation, review and editing. **Shahbaz Mushtaq:** Writing, review and editing.

J.K conceived the study and performed the analysis and led the write-up. KRS and VMB contributed to conceptual development of the study and the writing of the manuscript. V.M.B collected the data. All authors critically reviewed the paper and assisted with the interpretation of results and writing of the paper.

Data availability

Data and code underlying the study is stored at HARVARD Dataverse https://doi.org/10.7910/DVN/VVIQGI

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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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.158836.

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