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Cocoa plant productivity in West Africa under climate change: a modelling and experimental study

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Abstract

The potential effect of climate change on regional suitability for cocoa cultivation is a serious economic concern for West Africa—especially for Ghana and Côte d'Ivoire, whose cocoa cultivation accounts for respectively ∼19% and ∼45% of world production. Here, we present a modelling and observational study of cocoa net primary productivity (NPP) in present day and future West African climates. Our analysis uses a data assimilation technique to parameterise a process-based land-surface model. The parameterisation is based on laboratory observations of cocoa, grown under both ambient and elevated CO_2. Present day and end of 21st century cocoa cultivation scenarios are produced by driving the parameterised land-surface model with output from a high-resolution climate model. This represents a significant advance on previous work, because unlike the CMIP5 models, the high-resolution model used in this study accurately captures the observed precipitation seasonality in the cocoa-growing regions of West Africa—a key sensitivity for perennials like cocoa. We find that temperature is projected to increase significantly and precipitation is projected to increase slightly, although not in all parts of the region of interest. We find, furthermore, that the physiological effect of higher atmospheric CO_2 concentration ameliorates the impacts of high temperature and variation in precipitation thereby reducing some of the negative impacts of climate change and maintaining NPP in West Africa, for the whole 21st Century, even under a high emissions scenario. Although NPP is an indicator of general vegetation condition, it is not equivalent to yield or bean quality. The study presented here is, nevertheless, a strong basis for further field and modelling studies of cultivation under elevated CO_2 conditions.

1. Introduction

Cocoa is a major cash crop in West Africa. Changing suitability for its cultivation under climate change is thus a serious economic issue, especially for Ghana and Côte d'Ivoire, where cocoa accounts for respectively ∼3% and ∼7% of the GDP and ∼19% and ∼45% of world production (Bunn *et al* 2018). Recent studies have suggested that predicted changes to the climate would impact suitability for cocoa production in some regions of West Africa (Laderach *et al*, 2013, Schroth *et al* 2016). Here, we provide a more comprehensive assessment of this impact through a process-based exploration of the interaction between cocoa plant physiological processes, climate variability and atmospheric CO_2 levels.

In model projections, it is well known that changes in the mean climate are associated with changes in daily variability in temperature and precipitation (for example, Black 2009, Dunning *et al* 2018). Since daily variability in precipitation and temperature affect land-atmosphere interactions, changes in the weather are likely to affect future agriculture. For example, intensification of precipitation may reduce infiltration of water into the soil, because surface run-off is increased, and hence reduce root zone soil moisture during key parts of the growing season (for example, Eekhout *et al* 2018). Process-based land-surface and crop models that include parameterization of soil hydraulics provide a means of investigating the impact of changing precipitation variability on soil moisture, and hence crop productivity (for example, Seneviratne *et al* 2010, Osborne *et al* 2015, Asfaw *et al* 2018).

The effect of climate change on land-atmosphere interactions is modulated by the influence of elevated CO_2 levels on plant physiological processes. In C3 plants, such as cocoa, increased atmospheric concentrations of CO_2 lead to higher leaf internal concentrations of CO_2, and hence to increased rates of photosynthesis (the direct fertilization effect). Furthermore, higher internal CO_2 concentrations result in a decrease in stomatal conductance in many species, reducing transpiration (Lambers and Oliveira 2019). Reduced stomatal conductance will thus tend to reduce drought stress through maintenance of plant water status and increase plant productivity (Black *et al* 2012; Lemordant *et al* 2018). The effect of atmospheric CO_2 concentrations on productivity depends strongly on plant type (Ainsworth and Long 2005). It is critical therefore that land surface models are parameterized using experimental observations of cocoa photosynthesis under both ambient and elevated CO_2.

Unlike annual crops, which grow only during the rainy season, perennials such as cocoa are affected by the weather all year round (Wood and Lass 2008). Such crops are thus highly sensitive to changes in temperature and rainfall during both the wet and dry seasons, and hence to precipitation seasonality. Assessment of change in the seasonal cycle of precipitation requires a climate model that represents the present-day seasonal cycle accurately. In southwest Africa, although the low-resolution coupled models included in the multi-model ensemble that comprise CMIP5 (Coupled Model Intercomparison Project Phase 5—further described in section 3 of the supplementary material (available online at https://stacks.iop.org/ERL/16/014009/mmedia)) capture the mean climate fairly well (Roehrig *et al* 2013), they fail to simulate even the broad features of the rainfall seasonal cycle (Dunning *et al* 2017). The representation of the seasonal cycle is, however, much improved in a new suite of high-resolution global climate model simulations (see supplementary materials: section 1), offering an opportunity to investigate the impact of change in precipitation seasonality on perennial crops, such as cocoa.

Because of the complexities described above, assessments that infer climate change impacts on crop productivity solely from changes in climatological metrics cannot be considered robust. Our process-based approach thus advances on previous studies of future cocoa cultivation, in which the climatic conditions under which cocoa is currently cultivated are treated as an analogue for future cultivation suitability (Läderach *et al* 2013, Schroth *et al* 2016). To this end, we utilize a new suite of high-resolution climate model simulations, which accurately capture the observed seasonal cycle in precipitation. The climate model output is used to drive a process-based land-surface model, which includes a new photosynthesis and coupled stomatal conductance parameterization based on observations of cocoa cultivation in both present day and elevated CO_2 scenarios. These model simulations provide insights into how changes in the climate, together with changes in physiological processes affect photosynthesis, and hence cocoa productivity in the future.

2. Methodology

Our study takes a three-pronged approach. Firstly, we analyse changes in relevant metrics of temperature and precipitation, both in the CMIP5 models, and in an ensemble carried out using a single high-resolution climate model (section 2.1). Secondly, we carry out a series of controlled glass-house experiments of the response of cocoa plants to elevated CO_2 (section 2.2). Thirdly, we present a multi-factorial set of experiments, using the JULES land surface model (section 2.3) to explore the effect of changes in temperature, rainfall and CO_2 on net primary production of cocoa. Key to this is a new parameterisation for JULES, based on experimental observations of cocoa growth under present day and elevated CO_2 levels.

Note that descriptions of the coupled model intercomparison (CMIP5) climate models and observed meteorological data used in this study are given in supplementary information.

2.1. Climate change analysis

Data were taken from the UK Met Office Unified Model (GA3) ensemble of 25 km resolution global atmosphere-only runs: The U.K. on Partnership for Advanced Computing in Europe (PRACE) Weather-Resolving Simulations of Climate for Global Environmental Risk (UPSCALE) project runs (herein these runs will be referred to as UPSCALE). The UPSCALE simulations use an atmosphere only AMIP (Atmospheric Model Intercomparison Project) type set up, in which an atmospheric model is driven with observed sea surface temperature (SST). Here, OSTIA SSTs represented present climate (Donlan *et al* 2012); and with OSTIA SSTs modified by HadGEM2 projected SST change (2090–2110 relative to 1990–2010; RCP8.5 scenario). CO_2 is set to constant values of 343 ppmv for the 1990–2012 runs and 935 ppmv for the future climate runs (Mizielinski *et al* 2014). The ensemble consists of five present day and three future integrations, generated through small perturbations to initial conditions.

The high-resolution model analysis is supplemented with analysis of model output from the 5th Coupled Model Intercomparison Project (CMIP5), which forms the basis of the IPCC 5th assessment. In this study, 29 models were used, comprising a range of modelling centres and including a range of resolutions and parameterisations. A full description of the CMIP5 dataset is given in Taylor *et al* (2012); and a table of the models used in this study, with information on horizontal resolution, is given in the supplementary material (table S3.1).

Lack of knowledge of future emissions is a key source of uncertainty in climate projections. The CMIP5 approach is to carry out climate model simulations for a range of greenhouse gas concentration trajectories, described by representative concentration pathways (RCPs) (Van Vuuren *et al* 2011). Although the RCPs are based on CO_2 concentrations, rather than emissions, the two are closely related. To explore the range of uncertainty related to future emissions, the following two RCPs were considered: RCP 4.5, a medium emissions scenario, with CO_2 emissions gradually increasing until ∼2040 and then declining; RCP 8.5, a high emissions scenario, with CO_2 emissions increasing at rates that are close to the present day throughout the 21st Century.

2.2. Observational chamber experiments

2.2.1. Plant growth conditions

Four-month-old seedlings of *Theobroma cacao* (var. Amelonado) were grown in 5L pots containing a mixture of sand, gravel and vermiculite (1:2:2 by vol) under controlled greenhouse conditions at the Controlled Environment Laboratories at the University of Reading. The seedlings were grown under two CO_2 concentrations for 154 days. Nine seedlings were placed in each of four greenhouses. Two compartments were maintained at a CO_2 concentration close to ambient (400 ppm) and two compartments were maintained at an elevated CO_2 concentration (700 ppm). Temperature conditions within each compartment were set to mimic typical conditions in Ghana in January. The target temperature cycled between a minimum of 19 °C at night and a maximum of 32 °C during the day. Average relative humidity in the compartments was 51%. All trees were irrigated to excess with a modified Long Ashton solutions six times daily.

2.2.2. Photosynthetic light response curves

Photosynthetic light response curves were measured on the youngest, fully expanded and hardened leaf which had developed under the experimental conditions using an LCpro + infrared gas analyser fitted with a light attachment and an internal CO_2 source (ADC BioScientific, Great Arwell, Herts., UK). All measurements were carried out between 08:00 h and 14:00 h. Photosynthesis was measured at irradiance levels of 696, 435, 261, 174, 7, 44, 26 and 0 μmol m^{-2} s^{-1}. CO_2 concentration within the IRGA chamber was set to the growth concentration. Average temperature within the IRGA chamber during measurements was maintained at 31 °C and average relative humidity was 47%.

2.3. Land surface modelling experiments

The Joint UK Land Environment Simulator (JULES) is the land surface component of the UK Met Office Hadley Centre climate model. JULES calculates the fluxes of energy and mass between the land surface and atmosphere. It explicitly models the temperature and water content of soil in an arbitrary number of layers, as well as the temporal evolution of leaf area index, when the TRIFFID vegetation model or phenology model is invoked.

In this study, rather than being coupled to a climate model, JULES is run offline — enabling us to explore sensitivities of the land-atmosphere system to individual elements of climate change. The choice of JULES, moreover, ensures consistency with the climate model study using UPSCALE, whose land-surface scheme is equivalent to JULES. In its offline mode, JULES is driven by observed or modelled meteorological variables. Information on soil and land surface properties is provided by ancillary files. The version used here is 5.1, which is described in full at http://jules-lsm.github.io/vn5.1/. A full description of JULES can be found in Clark *et al* (2011), and Best *et al* (2011).

Key to our study is model representation of photosynthesis, and the leaf-level exchange of water and carbon in C3 plants. In JULES, the leaf level stomatal conductance (g_s) is linked to the rate of photosynthesis (A) via the CO_2 diffusion equation:

$$A = g_s\left(C_c - C_i\right)/1.6 \tag{1}$$

where C_c and $\underline{C}_i$ are the leaf surface and internal concentrations of CO_2.

C_c and C_i are related by the Jacobs (1994) formulation:

$$\frac{C_i - C_*}{C_c - C_*} = f_0\left(1 - \frac{D}{D_*}\right) \tag{2}$$

where D is the leaf humidity deficit and C_* is the CO_2 compensation point (the point at which no further CO_2 is absorbed from the environment because the CO_2 required for photosynthesis is equal to the amount released by respiration). The variables f_0 and D^* are vegetation-specific calibration parameters (for full details see Cox *et al* 1998).

The rate of photosynthesis if there is no water stress (A_p) is represented as the minimum of three limiting regimes: (i) Rubisco-limited rate (W_C); (ii) light-limited rate (W_L); and (iii) rate of transport of photosynthetic products (W_E):

$$A_p = \min(W_C, W_L, W_E) \tag{3}$$

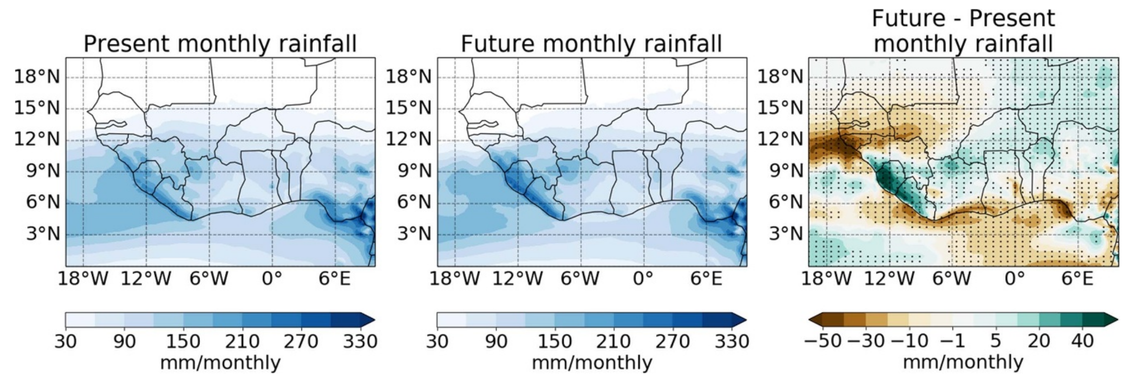

Figure 1. Present and future monthly rainfall from the UPSCALE simulations. The first column shows the mean rainfall across the five present climate UPSCALE simulations, the second column shows the mean rainfall across the three future climate UPSCALE simulations. The third column shows the future minus the present. Stippling indicates where the change is statistically significantly different at the 5% level (Mann Whitney U test).

Each of the limiting rates of photosynthesis is affected by environmental conditions (Collatz *et al* 1991). In C3 plants, all three limiting regimes are affected by temperature. Photosynthetically active radiation (PAR), however, only affects W_l. Both W_c and W_l are affected by the internal CO_2 concentration (C_i).

Leaf photosynthesis (A) is then derived by scaling A_p with a metric of root-zone soil moisture content (β):

$$A = A_P\beta \tag{4}$$

The means by which 'A' is scaled to canopy-level gross primary productivity (GPP) is described in Best *et al* (2011).

As was described above and in Clark *et al* (2011), the three limiting rates of photosynthesis and the CO_2 diffusion equation (equation (1)) include a number of plant-specific parameters. In order to account for these variations, JULES separates vegetation cover into plant functional types (PFTs). When developing a cocoa PFT, in this study, we begin by considering the response of the tropical broad-leaf PFT (Harper *et al* 2016) selected for being the closest morphologically to cocoa. To develop a PFT that resembles cocoa, we utilise a data assimilation (DA) method, ensuring that the rate of photosynthesis, and hence the canopy-scale GPP and NPP (Net Primary Productivity) is calculated using a cocoa specific parameterisation.

The method by which the observations described in section 2.2 are utilised to parameterise JULES for cocoa is summarized in the supplementary information section 2.

3. Results

3.1. Projected changes in the West African climate

Both rainfall and temperature are projected to change during the 21st Century in West Africa. Figure 1 shows that, in the high-resolution simulations, precipitation is projected to increase over much of West Africa, albeit with reduced precipitation projected in Western Guinea and in southern coastal regions of Ghana and Côte d'Ivoire. These findings are broadly consistent with the CMIP5 analysis presented in Roehrig *et al* (2013).

Cocoa is a perennial crop and is thus sensitive to the seasonal cycle in rainfall. A metric of rainfall seasonality (used in Laderach *et al* (2013) and Schroth *et al* (2016)) is the number of consecutive months of the climatological season cycle during which rainfall is less than 100 mm. It is suggested in these studies and in previously published work on cocoa (Wood and Lass 2008) that regions that climatologically experience more than three consecutive months of < 100 mm of rainfall are less suitable for cocoa cultivation, and that this determines the northern boundary of the cocoa belt in Ghana and Côte d'Ivoire. Figure 2 shows that the projected changes in rainfall do not result in large changes in this metric within the present-day cocoa growing regions delineated by Schroth *et al* (2016). There is some indication, however, that the projected increases in rainfall have a favorable effect on the cocoa growing capacity for some regions of Nigeria. These results are consistent with Schroth *et al* (2016), but may be considered more robust because of the improved representation of the seasonal cycle in the high-resolution climate simulations used in this study.

The projected changes in rainfall are small in comparison to variability between models (see supplementary information). This is not the case, however, for temperature. Figure 3 shows that minimum, maximum and mean daily temperature are all projected to increase in this region; by approximately 5 °C by the end of the 21st Century under an RCP8.5 scenario. Moreover, figure 4 indicates that the projected shifts in temperature are fairly uniform across the full range of values. In other words, a 30 °C event in the present occurs as often as a 35 °C event is projected to occur in the future; and the same is true for a 20 °C present/25 °C future event.

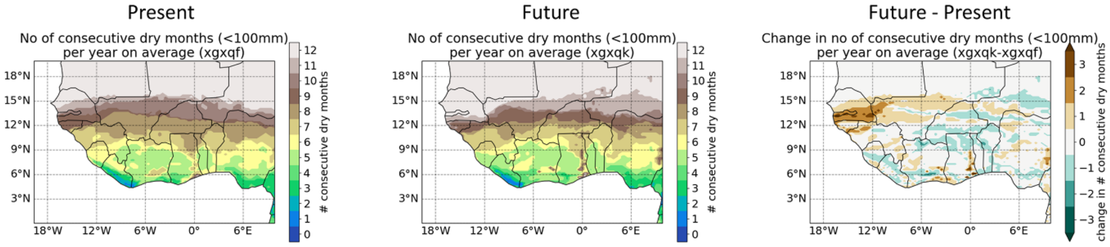

Figure 2. Average number of consecutive months with < 100 mm rainfall ('dry months') in a present climate UPSCALE simulation (left), a future climate UPSCALE simulation (middle) and the change (right).

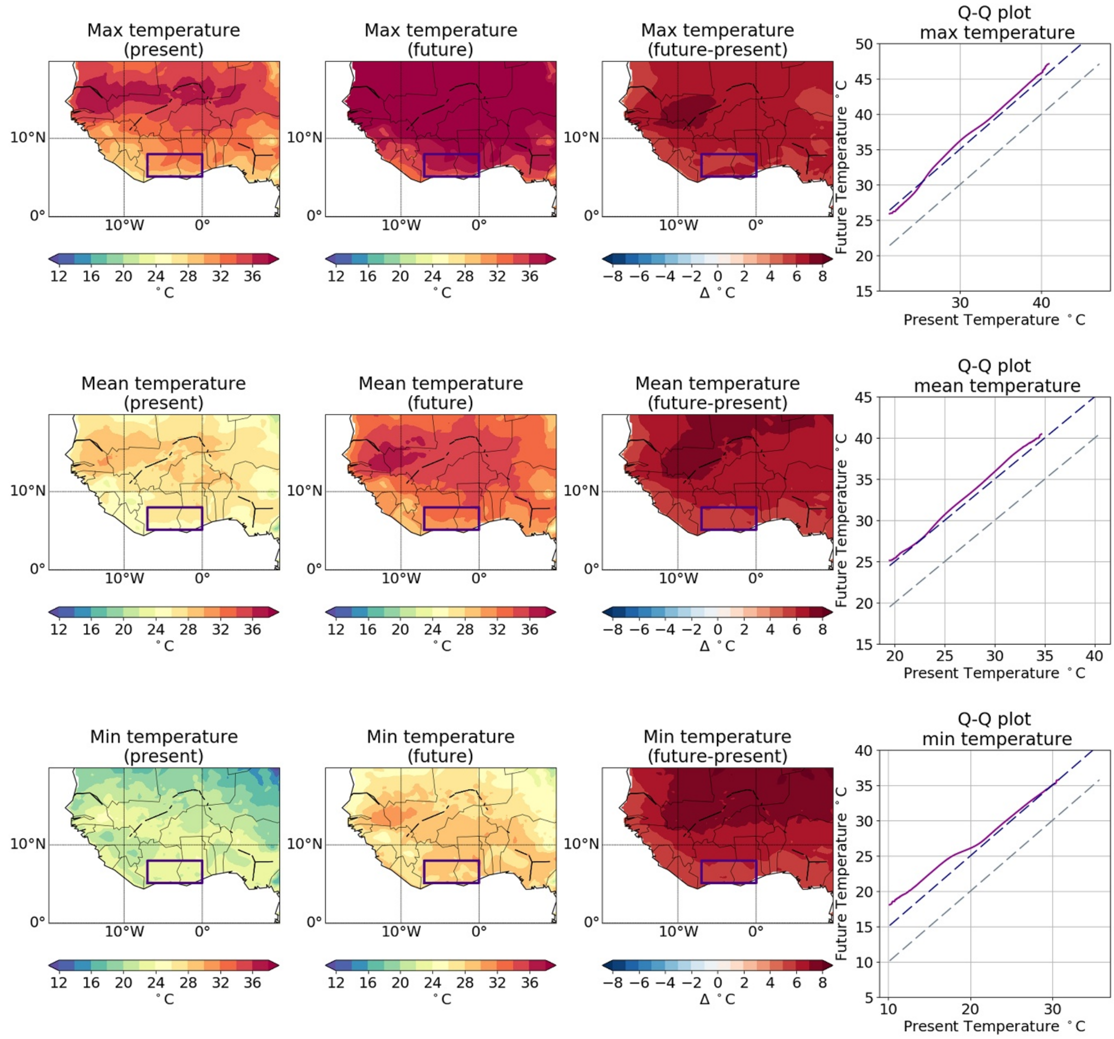

Figure 3. Comparison of temperatures from present climate and future climate UPSCALE simulations: daily maximum temperature (top row), daily mean temperature (middle row) and daily minimum temperature (bottom row). The first column shows temperature from the present climate UPSCALE simulation, the second column shows temperature from the future climate UPSCALE simulation, the third column shows the change. The furthest right column contains QQ plots comparing the temperature distribution under present climate and future climate UPSCALE simulations; the grey dotted line represents a 1:1 relation, the blue dashed line shows a 1:1 + 5 °C relation. The region used for the QQ plots (7°W–0°W, 5.1°N–8°N) is shown in the first 3 columns.

The high-resolution climate simulations provide detailed spatial information and a good representation of seasonality, but they are only available for the end of the 21st Century and for a high emissions scenario. Although there are deficiencies in the CMIP5 simulations, the multi-model mean broadly captures the spatial variability of present day mean annual rainfall amount and temperature (Roehrig *et al* 2013, Dunning *et al* 2017). There is value, therefore, in using the CMIP5 simulations to explore projected time series of regional annual temperature and rainfall, and to explore sensitivity to emissions scenarios.

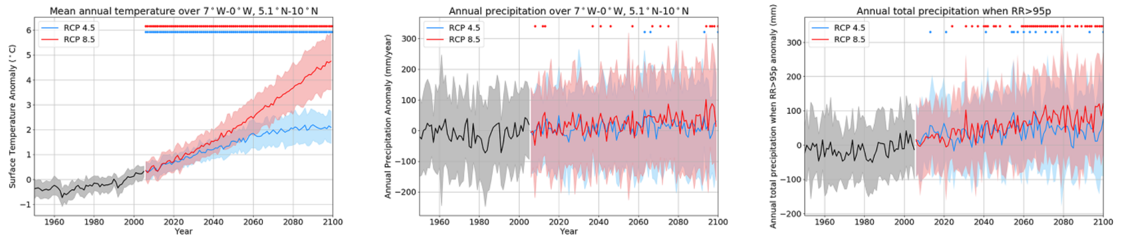

Figure 4. Change in temperature and precipitation through time: Timeseries of mean annual temperature (left) and mean annual precipitation (middle) and annual total precipitation when the rainfall rate is over the 95th percentile (right) from 29 CMIP5 models over 1950–2100 over 7°W–0°W,5.1°N–10°N. The black line/grey shading shows the mean and standard deviation for each year across the 29 models for the historical simulation; the blue and red lines/shading are for RCP4.5 and RCP 8.5 respectively. The anomalies are calculated relative to 1986–2005. The dots indicate when the range of values from 29 models for that year is significantly different from the range for 1986–2005 at the 5% level, using a Mann–Whitney U test.

Figure 4 shows time series of anomalies in temperature, total rainfall, and amount of rain during intense events for 7^0 W–0, 5^0N –10^0 N—comparing RCP4.5 and RCP8.5 emissions scenarios for 29 CMIP5 models. The dots show where the multi-model anomaly distribution for a given year is significantly different to the multi-model anomaly distribution for the climatological period (1986–2005)—in other words, when the signal of climate change emerges from the noise of internal model variability. The anomalies are calculated relative to each model's own climatology. As would be expected, there is a large warming trend. Scenario differences become apparent in the 2030s, but significant warming relative to 1986–2005 is evident for both scenarios throughout the future model integration.

In contrast to temperature, when averaged over a large region, a signal of increase or decrease in annual precipitation barely emerges from the noise, even by the end of the 21st Century. Comparing RCP4.5 and RCP8.5, there is some indication that differences between models are slightly greater at the end of the 21st Century for the RCP8.5 scenario, but beyond that, there is little sensitivity to scenario. Previous studies have shown, however, that even when the projected change in mean precipitation is small, there may be significant projected changes in the daily extremes (Field *et al* 2012). The bottom panel of figure 4 shows that the amount of seasonal precipitation during high rainfall days is projected to increase by the end of the 21st Century in RCP8.5.

3.2. Parameterisation of JULES for cocoa

As was described in section 2, the first step of the modelling is using a DA technique to parameterize the land-surface model for cocoa (Pinnington *et al* 2020). The results of the DA are shown in figure 5. Figure 5 (top left panel) shows the observations and the prior JULES prediction before DA. The observed photosynthesis initially increases with irradiance and then saturates at around 250 μmol m^{-2} s^{-1} (consistent with cocoa being a shade-adapted plant). In comparison, the photosynthetic rate for JULES has only just begun to saturate at 450 μmol m^{-2} s^{-1}, as is typical for standard C3 vegetation. For both model and observations, the level of photosynthesis for the plant is always higher under increased CO_2 levels. Figure 5 (top right panel) is the same as the top left panel but now using the new parameterisation after applying the DA technique to the JULES model and observational data. It is clear that after DA, the JULES model predictions fit the cocoa observations well and are always within the standard deviation of the observations. This is further illustrated by the scatter plots in two bottom panels of figure 5, where, after DA, the value of r^2 increases whereas root-mean squared error (RMSE) decreases considerably, for the JULES predictions compared to the observations. These findings provide evidence that we now have a version of the JULES model capable of representing key aspects of photosynthetic response of cocoa to changes in CO_2 and other key atmospheric variables.

3.3. Process-based investigation of changes in cocoa productivity

In order to explore the effect of climate change on cocoa productivity, net primary productivity was simulated using JULES driven with the present and future CO_2 levels and climates. NPP is the accumulation of biomass by plants before any litter or mortality. Although it is not a direct indicator of yield it does represent the resource available to the plant for growth, including allocation into fruiting bodies. In this study, we focus on NPP rather than GPP because NPP is more closely related to crop yield. The driving data were derived from the same high-resolution climate simulations described in section 2.1, and all results are presented for the JULES cocoa PFT (see section 2.3).

Over much of West Africa, NPP is projected to increase (figure 6), suggesting that cocoa trees will become more productive. Over the key cocoa growing regions, highlighted in the box plots, the changes are significant at the 95% level. Small decreases (<10%) are seen in the coastal and northwest regions, in which precipitation is projected to decline. In the light of previous studies (Laderach *et al* 2013, Schroth *et al*

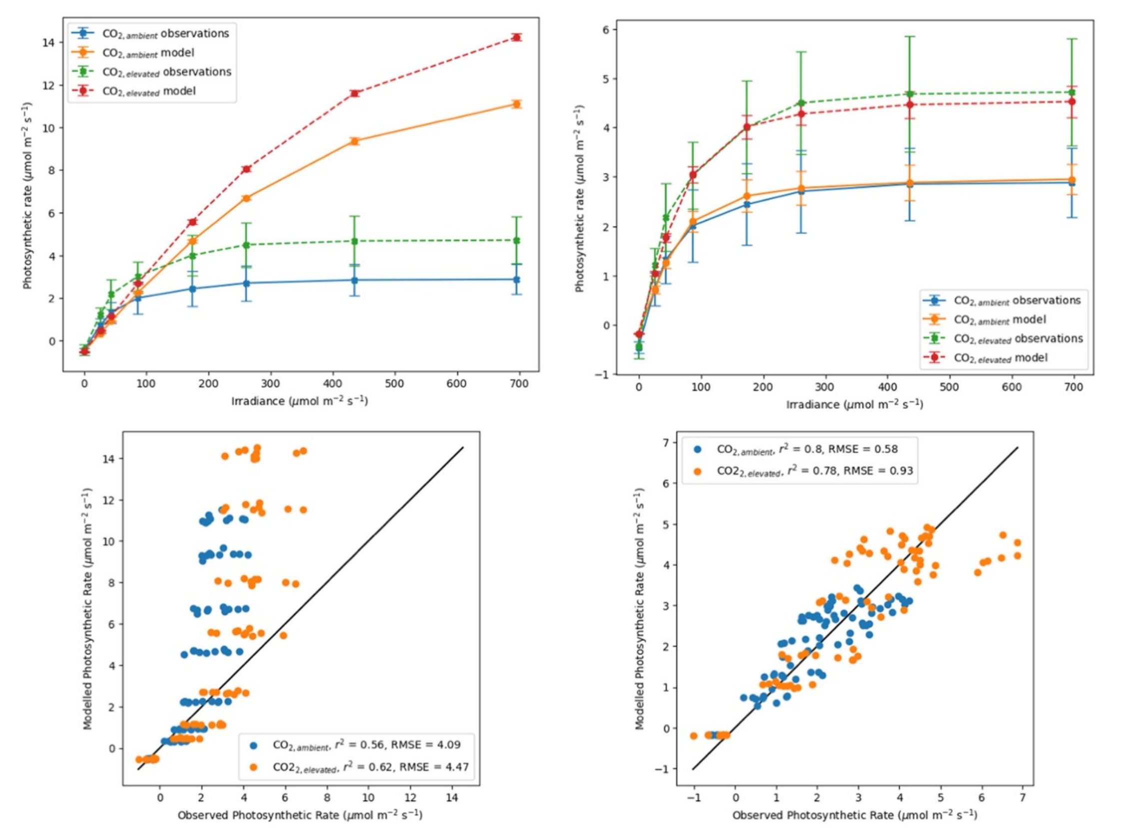

Figure 5. The effect of assimilating observations on the representation of photosynthesis: Observed and modelled photosynthesis light response curves for cocoa under 2 different CO_2 regimes, vertical lines represent $\pm$ 1 standard deviation from the modelled and observed mean, before DA using default JULES parameters (top left), after assimilating observations from a leaf chamber attached to an infrared gas analyser and optimising 8 leaf level photosynthesis parameters in JULES (top right). Observed photosynthetic rate versus JULES modelled photosynthetic rate before DA using default JULES parameters (bottom left), and after DA (bottom right).

2016), the increases in NPP might seem unexpected, given that temperatures are higher and the projected precipitation changes are small.

To investigate further, a series of idealised experiments was conducted, in which temperature, precipitation and specific humidity were altered in turn for both present day and elevated CO_2 (figures 7 and S2.1). In these experiments, temperature was increased by a uniform value, and precipitation and humidity were altered by a uniform proportion. Two sets of scenarios were considered, representing CMIP5 RCP8.5 average temperature, precipitation and humidity changes for the middle and end of the 21st Century, under an RCP8.5 scenario. Additional sets of simulations, in which the vegetation suffers no water stress at all—i.e. β is kept at 1 throughout the simulation period (equation (4)), were carried out for both scenarios. Areal mean NPP for all the experiments for the region highlighted in figure 6 is shown in figure 7. Comparison between the idealized runs suggests that the projected increase in NPP is driven primarily by elevated CO_2, with the effect modulated by change in temperature, precipitation and humidity. As would be expected, NPP increases with higher precipitation and atmospheric humidity—both of which act to reduce water stress (which affects photosynthesis, see equation (4)). The sensitivity to water stress is confirmed by the high NPP in the simulations in which water stress is set to zero, i.e. $\beta = 1$. These effects are highlighted in figures S2.1(b) and S2.1(c). Here, the projected increase in specific humidity has a greater effect on NPP than the projected increase in precipitation, especially for the end of century scenarios. It should be noted that because of the large warming, in the full future climate scenarios, the projected increase in specific humidity is still generally associated with a reduction in relative humidity, and hence an increase in vapour pressure deficit (D). In the model, the effect of increased D is to reduce the internal concentration of CO_2 and hence to reduce the rate of photosynthesis (equation (2)).

The response to regional temperature change is more difficult to anticipate. GPP and hence NPP will be reduced if the temperature is either well below or well above the optimum for photosynthesis. As temperature increases towards the optimum, the rate of photosynthesis increases and then decreases sharply once the optimal temperature is exceeded (Lambers and Oliveira 2019). In West Africa, field studies have shown a weak positive correlation between

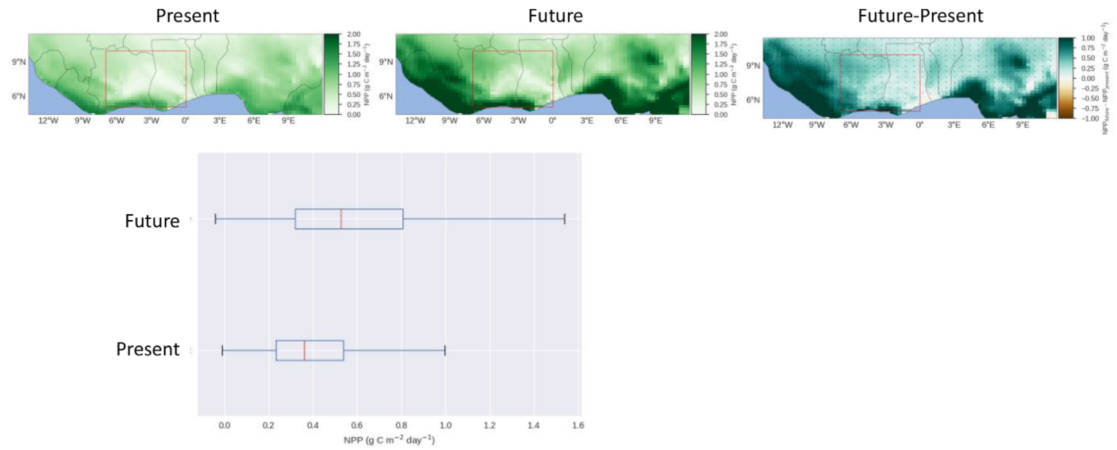

Figure 6. Comparison between present and future NPP: Maps of NPP for the JULES cocoa PFT when run using UPSCALE present climate (top left) and future climate (top middle) and difference between projected future and present NPP (top right). Box plots of Net Primary Productivity (NPP) for the JULES cocoa PFT when run using UPSCALE present climate and UPSCALE future climate for the rectangle box included on the maps (bottom).

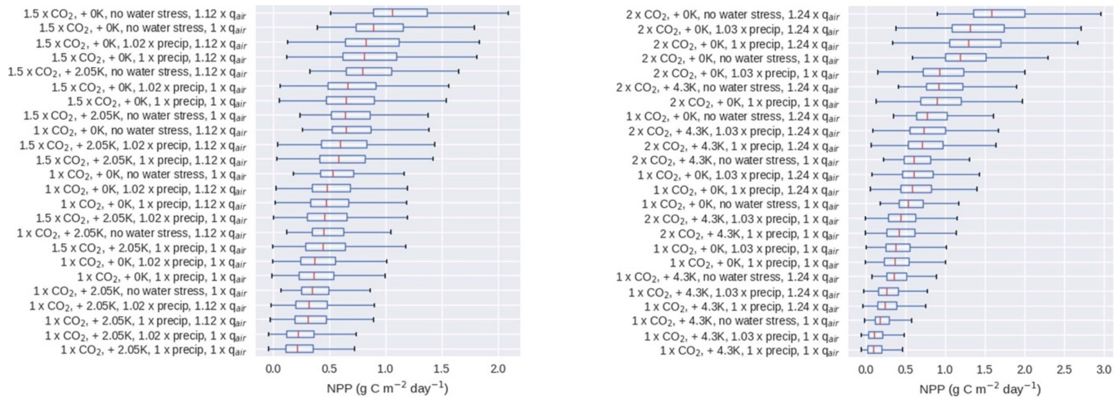

Figure 7. Box plots of Net Primary Productivity (NPP) for factorial experiments using UPSCALE present climate and varying CO_2 concentration, temperature, precipitation and specific humidity: using CMIP RCP8.5 mid-century values (left), using CMIP RCP8.5 end of century values (right). The region over which the averaging is carried out is shown as a rectangle on figure 6.

temperature and cocoa production (Ojo and Sadiq 2010, Lawal and Emaku 2007), suggesting that in the present day, the optimum temperature for cocoa is not frequently exceeded in hot years, and also that the temperature is not so far below the optimum that it becomes the primary limitation on yield. This is consistent with the relationship between temperature and GPP in the model experiments (figure 8), which shows that for the West African climate, GPP is not heavily dependent on daily temperature. Note that we compare GPP, rather than NPP against temperature in order to make inferences about changes in the optimal temperature for photosynthesis. At the highest temperatures, however, there is a sharp drop off in GPP, suggesting that the optimal temperature for photosynthesis is exceeded on the hottest days in both the present and future climate.

Based on these results, we would expect that if temperature were to increase by the amount projected in RCP8.5 simulations by the end of the century, GPP would be low because temperatures are frequently well above the optimum. And indeed, this behaviour is evident in the factorial experiments (figure 7). However, the factorial experiments also show that when CO_2 is elevated, GPP at high temperatures is similar to that simulated for present day conditions. The reason for this can be inferred from figure 8, which plots GPP against temperature for present day and future conditions (with no water stress). This comparison suggests that the optimal temperature increases as CO_2 increases and that the temperatures found in the future are not as far beyond the optimum as would be expected if the optimal temperature was the same as for the present day. This shift in optimal temperature under elevated CO_2 is an emergent property of the land surface model, related to changes to the limiting conditions on photosynthesis (Sage and Kubien 2007).

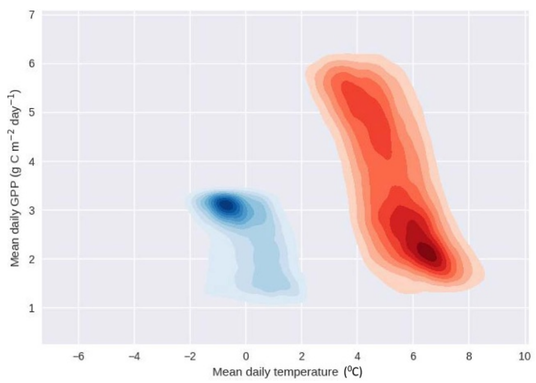

Figure 8. Plot of mean daily GPP versus daily temperature anomaly for all points in red box in figure 6. The blue and red shading indicates where the majority of points are for different combinations of mean daily GPP and mean daily temperature. Temperatures are anomalies calculated relative to the UPSCALE present day aerial mean climatology. The blue shading is for present day CO_2 and the red shading is for elevated CO_2.

4. Discussion

Previous studies of the effect of climate change on cocoa cultivation in West Africa have either been based on observational and experimental results (Lahive *et al* 2019, Ojo and Sadiq 2010, Lawal and Emaku 2007) or on climate 'envelopes', which assess the prevalence of favourable climatic conditions in the future (Läderach *et al* 2013, Schroth *et al* 2016). Here we combine these approaches, by parameterising a land-surface model using DA techniques combined with observations of cocoa productivity under elevated CO_2, and then applying the model to simulations of present and future climate.

Our study finds that in the regions where cocoa is currently grown in Ghana, Côte d'Ivoire and Togo (delineated in Schroth *et al* 2016), NPP is projected either to stay the same or to increase slightly. The small decreases in NPP in the southernmost parts of these countries predominantly concern regions where cocoa is less widely cultivated, although it should be noted that some cocoa is cultivated in south-west Ghana. Further east, in Nigeria, and further west in Liberia, modest increases in vegetation productivity are projected. There is some suggestion that projected increases in rainfall during the dry season may extend the regions suitable for cocoa cultivation slightly further north in Ghana, Togo and Côte d'Ivoire, but the abrupt drop in NPP north of $\sim$ 11.5 N persists in the future simulations. Changes in the timings of the wet and dry seasons during the year will impact on cropping patterns and establishment success of seedlings.

Some of these findings contrast with previous work (Läderach *et al* 2013, Schroth *et al* 2016). In particular, it was suggested in that although drought stress would not worsen, even by the 2050s, increases in maximum temperature would reduce the suitability for cocoa production in all countries apart from Cameroon (Schroth *et al* 2016). Underlying this result is the assumption that the present-day optimum temperature for cocoa will stay the same in the future. Our modelling, however, suggests that the temperature range tolerated by cocoa is raised by rising CO_2 concentrations—a finding consistent with previous observational and modelling studies (Long 1991, Sage and Kubien 2007, Bagley *et al* 2015, Dusenge *et al* 2019). In coffee, for example, photosynthesis under supra-optimal temperatures declined less under elevated CO_2 compared to that under ambient CO_2 (Rodrigues *et al* 2016). Survey of the CMIP5 ensemble indicates, furthermore, that an upward shift in optimum temperature in high CO_2 scenarios is an emergent property of most CMIP5 models (figure S3.9). The published literature suggests that this is caused by a shift in the transition from carbon limited to export limited photosynthesis (Long 1991, Sage and Kubien 2007). It is, nevertheless, clear from figures 7 and 8 that the highest daily temperatures in West Africa are detrimental to NPP in both present and future climate scenarios. Moreover, it should be noted that the optimal temperature for photosynthesis is variety dependent, and that there is thus a clear need for further experimental observations on cocoa to corroborate these model findings.

An additional factor, not accounted for in previous statistical studies of future cocoa production, is the direct fertilization effect. Experimental observations indicate that the rate of photosynthesis increases as a result of elevation in CO_2 (figure 5). Comparison between model output and observations (see figure 5) suggests that, if anything, the new cocoa parameterization slightly underestimates the direct fertilization effect. Our study, however, assumes that the instantaneous effect of increased CO_2 concentration on the rate of photosynthesis persists indefinitely. In practice, the response of vegetation to increased CO_2 concentration may be affected by acclimation—a phenomenon in which the initially positive response of photosynthesis rate to elevated CO_2 declines after weeks/months of exposure (Sage *et al* 1989). Acclimation is related to inhibition of photosynthesis (down-regulation), through various processes caused by accumulation of photosynthetic products in plant leaves, and increased stomatal resistance (Xu *et al* 2015 and references therein). Genetic experiments confirm that the severity of down-regulation is linked to the availability of 'sinks' for additional photosynthetic products (Ainsworth *et al* 2004). The magnitude of the acclimation effect is thus expected to vary between plant species. Extended large scale Free-Air CO_2 Enrichment (FACE) experiments, in which plants are grown under elevated CO_2 in natural environments, provide insights into the long-term plant response to elevated CO_2. Such experiments indicate, for example, that coffee does not acclimate significantly to elevated CO_2 (Ghini *et al* 2015, Rakocevic *et al* 2018). These findings are consistent with leaf-level observations, which demonstrate that photosynthesis in coffee plants is not down-regulated in high CO_2 environments (Ramalho *et al* 2013). In general, woody perennials, which have relatively large available sinks for photosynthetic products, tend to acclimate less to elevated CO_2 than plants with smaller sinks (Ainsworth and Long 2005, Ainsworth and Rogers 2007). It should also be noted that the responses modelled here are based upon measurements made on juvenile cocoa growing under ideal greenhouse conditions (see section 2.2). Enhancement of growth and photosynthesis in response to elevated CO_2 may be constrained by limitations in other key resources such as nutrient supply and may differ in mature trees.

There are no long-term observations of cocoa grown under high CO_2 conditions. In this context, however, coffee is a good analogue. Coffee and cocoa are both woody perennials, and thus both have relatively large sinks for photosynthates. Furthermore, unusually for C3 plants, neither has a strong stomatal response to high concentrations of CO_2 (Ghini *et al* 2015, Lahive *et al* 2018) Batista *et al* 2012. As an understory tropical species which evolved in an environment where water limitations are likely to have been infrequent there was probably not a strong selection pressure for stomatal sensitivity in cocoa. A recent study has highlighted that a lack of sensitivity in stomatal response to elevated CO_2 is not unusual and tends to be most prevalent amongst woody species from warm, dry environments (Purcell *et al* 2018).

A potentially detrimental effect of increased stomatal resistance is reduced plant transpiration, which in turn reduces atmospheric humidity and hence precipitation—changes that might partly offset the expected improved drought tolerance (Peters *et al* 2018). In practice, however, cocoa's weak stomatal response to CO_2 means that these processes are likely to be of secondary importance, compared to the impact of larger scale climate change. The response of shade trees and natural forest fragments present in the cocoa landscape will also have a potential impact here.

In our study, we only consider total biomass (as represented by NPP). We do not consider how changing environmental conditions may affect the allocation of biomass to cocoa pods and final yield. Plant reproductive development is generally considered to be more sensitive to rising temperatures than vegetative development. However, there are limited data on this subject in cocoa (e.g. Daymond and Hadley 2008). We also do not have sufficient observational data to explore how projected environmental changes may affect the cocoa bean quality; bean size and fat content being key traits of importance to the industry. Nevertheless, assessment of general climatic suitability, defined here as modelled changes in NPP, is the first step towards making decisions on future cultivation of cocoa.

In conclusion, a process-based modelling study, supported by experimental observations, indicates that even under a high emissions scenario, NPP will be maintained in the regions of West Africa where cocoa is currently grown throughout the 21st Century.

Data availability statement

The data that support the findings of this study are available upon reasonable request from the authors.

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