Exploring cacao genetic diversity for resilience to climate change – validating or contradicting current predictive models of production suitability

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Abstract

A number of modelling studies predict that climatic change will negatively affect cacao productivity. The anticipated increased evaporative and water demands cannot realistically be compensated with increased irrigation in many cocoa producing regions, and moving to new production areas will imply a stimulus for deforestation. Thus, maximizing current production areas by integrating climate-ready management practices and stress-tolerant planting materials is an important part of the solution. But even though modelling studies paint a bleak future for cacao production, many of the tolerance mechanisms and adaptation responses in the genetic diversity of cacao are still little understood and greater efficiency and inclusiveness is warranted in such analysis. Before these modelling results can be translated into action, we must work towards better modelling approaches. This paper suggests important avenues to enhance the applicability and use of cacao climate modelling exercises. These gaps could be filled with future collaborative investigations, new areas of modelling and research to be further explored to identify novel and tolerant genetic material, using big data analysis and crowdsourcing.

To contribute to a more careful assessment of the available options, this paper also presents a summary of the current status of physiological research on cacao and abiotic stresses, focusing on increased drought, temperature and CO_2 levels, and the role of genetic diversity for greater resilience. It then examines climate impact studies relevant to cacao production. While it finds that these studies represent cacao physiological responses to climate-induced stresses in a narrow way and generally are short on validation or sensitivity analysis, the bulk of the data suggests that the extent of how drought or heat affects cacao is determined by the individual genotype's inherent traits that allow avoidance, tolerance or escape. Thus, if the genetic diversity is fully exploited, for development of improved planting materials, both by research institutes and farmers, there is great potential for increased cacao resilience through selective breeding, and identification of tolerant genotypes. The key lies in tapping the genetic potential of cacao as a way to fully understand production limits and constraints.

Introduction:

Unpredictable weather patterns are affecting countless cacao producing regions. A broad literature review on climate change and variability found that areas in Sub-Saharan Africa are already experiencing significant variations (1) and numerous data sets from the global climate centres provide evidence of a drying trend, particularly in parts of West Africa (2). Climatic data of a 40-year period (1951-2000) from the Ghana Meteorological Agency supports the notion of decreased annual precipitation, with southwestern Ghana most affected. Records show that precipitation has decreased by up to 20% in the forest regions, and by 10% in the Savannah areas (3). Similarly, an assessment of Nigerian climatic data for a fifty-year period (1961-2010) recognized rainfall had a significant negative coefficient at < 5%, and temperature a significantly positive coefficient, revealing that coupled with rising temperature, overall rainfall has been continually decreasing (4). These findings are concerning given originally an understory tree in the tropical Amazon, cacao has intrinsic characteristics that can make it susceptible to extreme weather patterns (5,6).

Farmers are already witnessing these climatic changes and their impacts to current production. Nigerian farmers indicate changing climates have delayed flowering, delayed or reduced pod development, and diminished seedling

establishment (7). Similarly, Ghanaian farmers unanimously confirmed that weather conditions have been changing over the last 20 years (8). Although there are cacao-growing regions in Malaysia and West Africa where temperatures can exceed 40 °C without significant negative effects, early studies such as Wood and Lass 1985 cite the maximum daily temperatures at which cacao can be grown without reducing yield to be between 30 °C and 32 °C (9), with growth and development, flowering, and fruit development are all highly dependent on temperature (10–12). Yet the extent of how these changes, increasing temperatures and reductions in precipitation, will continue to progress and affect cacao production are unknown.

The role of climate models towards achieving greater resilience in these evolving weather patterns is indisputable, they are useful tools that help decision-making, and the understanding of interactions between complex traits or scenarios that may occur. Thus, with some concerning conclusions generated thus far, models have been used to evaluate the impact of expected climatic variations in several cacao producing regions. Although there is knowledge on the genetic, morphological, and physiological differences across the diverse range of cacao genotypes, models and climate predictions have not taken this information into consideration for their analysis or conclusions. The literature highlights numerous physiological responses cacao holds for protection against severe climate patterns, each with differing levels on the conclusiveness on their effectiveness. Additionally, while there is much yet that needs to be explored, the research carried out thus far suggests that increased CO_2 concentrations will help to ameliorate the impacts from water deficits (13–16), yet more evidence is needed. This potential amelioration of some of the impacts from drought and increased weather patterns are also excluded from modelling exercises and conclusions.

With the goal of evaluating what is known about cacao climatic resilience, and in order to generate a comprehensive perspective and understanding of what questions remain, this report highlights significant advances of published research in cacao drought and temperature tolerance, summarize climate modelling predictions and presents possible innovative alternatives for seeking more robust, and real-time knowledge on cacao climate resilience. From the extensive review of research on the effects of drought and temperature stress and increased CO_2 on cacao and the role of genetic diversity to address climate change (17) it appears that while future climatic predictions are worrisome, the genetic materials held within national and international collections offer much potential in the development of improved planting material.

Cacao physiological responses to drought

Cacao productivity, development and quality are strongly affected by the amount, distribution and duration of rainfall (10,18,19). Though we need to enhance our understanding of cacao physiological responses to stress, several studies have been carried out on cacao physiology and its reaction to environmental stress. Four main types of responses are briefly presented here: osmotic adjustment, stomatal conductance, water potential and root responses.

i. Osmotic adjustment

Osmotic adjustment is defined as the active accumulation of solutes or osmolytes. It has been recognized as an important drought tolerance response in many crops. Osmotic adjustment has also been seen as a positive mechanism for water deficit response in cacao.

Table 1: Summery table on cacao osmotic adjustment literature.

Authors	Trial Location	Trial Type	Main Conclusions
De Almeida (2002)	Brazil	Greenhouse	Three clones were identified as being drought tolerant based on the degree of osmotic adjustment recorded (SPA5, SIAL70, TSH516)(20).
Rada et al. (2005)	Venezuela	Field	Osmotic adjustment and sustained leaf turgor was observed in the initial 12, yet not sustained over a period of 25 days (21).

Moser (2010); Köhler (2010); Schwendenmann (2010);	Indonesia	Field	Localized osmotic adjustment response in the root tissue is hypothesized to have aided in the stabilization of plant water status, as well as sustained leaf, stem and root growth.(19,22,23).
Araque et al. (2012)	Venezuela	Field	Observed variation in osmotic adjustment between the genotypes was enough to categorize some as more tolerant than others, but not enough to rescue the plants from significant decrease in stomatal conductance and photosynthetic activity (24).

The ability of osmotic adjustment to confer drought tolerance to cacao, might still be limited. More research is needed to better understand the potential of osmotic adjustments as a method to enhance cacao water-deficit tolerance.

ii. *Stomatal conductance*

Stomatal conductance measurements estimate the rate of gas exchange and transpiration through leaf stomata (25). When plants are exposed to increased evaporative demand, turgor and stable water potential values can be attained through stomatal control among other responses (26–29). Stomatal opening in cacao has been observed to be very sensitive to water deficit and relative humidity, with proven genetic variation in the level of sensitivity (30–32):

Table 2: Summery table on cacao stomatal conductance literature.

Authors	Trial Location	Trial Type	Main Conclusions
Nunes (1967)	Sao Thomé	Greenhouse	Variations in stress levels were attributed to differences in stomatal response, cultivars with greater stomatal sensitivity were able to better regulate water loss (33).
Balasimha et al. (1988)	Nigeria	India	Effective stomatal regulation is a key drought tolerance response that can result in decreased transpirational water loss (34).
Apshara (2013)	India	Field	Three accessions presented greater resilience to water deficit by reducing transpirational water loss through greater stomatal sensitivity and induced stomatal closure (35).
Ofori et al. (2014)	Ghana	Field	Considerable genetic variation for traits related to drought resistance were observed. While many responses, including stomatal conductance, were induced by environmental factors, inherent genetic induction was responsible for the differential responses (36).
Almeida, Tezara and Herrera (2016)	Venezuela	Field and Greenhouse	In the greenhouse, stomatal closure was an effective mechanism to preserve leaf-water status, indicated by maintenance of relative water content. Lower stomatal conductance was observed in the field, yet water potentials of all the clones substantially decreased as the dry period progressed (37).

| Ayegboyin (2016) | Nigeria | Greenhouse | Leaf area, stomatal conductance and photosynthetic rates had linear and positive relationships with water status. Data showed frequency of irrigation rather than amount is most important for seedling establishment (38). |

With priven genetic diversity for sensitivity, cacao's ability to regulate stomatal closure toward sustained relative water content, despite drought, suggests that stomatal sensitivity is an interesting target for future tolerance breeding efforts.

iii. Water potential (Ψ)

Like in many crops, cacao stem and leaf water potentials are used as indicators of plant water status, and tolerance to water deficit. Below a summery on what has been found.

Table 3: Summery table on cacao water potential literature.

Authors	Trial Location	Trial Type	Main Conclusions
Joly and Hahn. (1989)	USA	Greenhouse	Net photosynthesis started to decline in response to water deficit once Ψ fell below about -0.8 to -1.0 MPa(39).
Deng et al. (1990)	USA	Greenhouse	The distribution of ^{14}C-labelled assimilates showed that moderate stress occurs when values Ψ reaches -0.8 to -1.2 MPa, and severe stress below -1.76 MPa (40).
Balasimha et al. (1991)	India	Field	Genotypes able to maintain higher Ψ values during midday hours, even under drought, were considered the most tolerant (18).
Balasimha (2013)	India	Field	Ψ levels are stable indicators of resilience/tolerance, especially when a particular genotype is able to maintain high levels of Ψ despite severe water limitations (41).
Kacou et al. (2016)	CPCRI	Greenhouse	Important to breed for maintenance of water status, gas exchange and photochemical activities as genotypic for these is present in cacao (42).

Leaf water potential is a dependable indicator of tolerance, genotypes able to sustain high relative water content, despite the drought are more resilient.

iv. Root responses

The root system is one of the most sensitive and responsive tissues of a plant, and allocation of carbohydrates to increase root proliferation typically allows for access to deeper water reservoirs during periods of water deficit. Several studies mention increased root mass as being a possible trait for increased drought tolerance.

Table 4: Summery table on cacao root responses literature.

Authors	Trial Location	Trial Type	Main Conclusions
Deng, Joly and Hahn (1990)	USA	Greenhouse	A reduction in ^{14}C-labelled assimilates exported to sink leaves and to expanding flush leaves, but an increase of those allocated to roots was recognized as a positive

			response allowing roots to access deeper water reservoirs (40).
Schwenden mann (2010);	Indonesia	Field	*Gliricidia* appeared to be a good companion tree even in prolonged periods of water stress, with complementary ecophysiological responses as the cacao trees withdrew water mainly from the top portions of the soil profile, with more than 80% of cacao's fine root biomass located in the top 40 cm's (23).

Although cacao has relatively deep taproots, the depth from where water can be taken up depends on the length of the taproot's lateral roots responsible for water absorption (43). While shallow-rooted cacao may not have great potential for deeper water extraction, such characteristics serve for the design and planning of agroforestry systems that mitigate water deficit via other microclimatic services.

Increased CO_2 and environmental interactions

Initial work to understand how rising concentrations of CO_2 could impact cacao physiology was conducted by researchers at USDA. The UoR in the UK has played a leading role in continuing to investigate how environmental changes can impact cacao yield and the physiological determinants of yield.

Table 5: Summery table on literature of cacao's response to increased CO_2 concentrations.

Authors	Trial Location	Trial Type	Main Conclusions
Baligar et al. (2005)	USA	Greenhouse	Plants growing in higher CO_2 concentration increased uptake of all mineral nutrients and tended to increase the shoot and root growth parameters measured (14).
Baligar et al. (2008)	USA	Greenhouse	Increasing CO_2 significantly enhanced photosynthesis when raised from 85 to 680 cm^3 m^{-3}, minimally when increased from 680 to 850 cm^3 m^{-3}. Increasing CO_2 decreased stomatal conductance by about 65%. The increasing ambient CO_2 concentrations potentially improves cacao water-use efficiency (13).
Lahive (2015)	UK	Greenhouse	Elevated CO_2 offset some negative effects of water deficit. Vegetative growth, maximum photosynthesis and water-use efficiency were significantly enhanced under elevated CO_2. Increased CO_2 could potentially mitigate some drought impacts (15).

Climate Models

While there is no general agreement on how climate change has or will affect cacao production, there is a wide-ranging consensus that climate instability is impacting production (1,8,44–49). A number of studies have looked at past production data as a key to future effects of climate change (for example, Oyekale 2008). These studies show that weather variables, and especially rainfall, have an impact on variability in cacao production between years, with generally a larger role for rainfall than for temperature.

Extrapolation from these studies towards the future, however, is problematic because season-to-season variation does not match the decadal time-scale on which climate change operates. If long-term trends shift climate averages, not only the response of cacao trees to climate will change, but farmers may also shift management practices.

To address long-term trends, Species Distribution Models (SDMs) have been used to understand how climate will affect the suitability of cacao producing regions. SDMs use current geographic data on the presence of cacao, create a predictive model that uses climatic and other environmental variables to predict current cacao presence. Current data are then replaced with future climate projections in these models, which result in future predictions of land suitability for cacao. A first study was done by Laderach et al. (2011) who predicted a drastic contraction of areas suitable for cacao production in West Africa (Cote d'Ivoire and Ghana) (50). Applying the same model (Maxent), Laderach et al. (2013) predicted much less drastic changes (51). In the publication, the authors do not explain the reason behind these stark differences in results. Schroth et al. (2016) further updated this study, focusing on a larger area in West Africa, finding similar results (52). An interesting hypothesis generated by this study is that the maximum temperature during the dry season may be driving suitability changes more than drought stress.

It is difficult to judge the degree of uncertainty of these studies, as the model evaluation measure they reported (area under the curve, AUC) is not accepted as an uncertainty measure in the modelling literature (53). Also, these studies do not show awareness of the need to control for "spatial sorting bias", a technical point invalidates a large number of studies (54). Thus, caution is warranted in interpreting these studies for decision-making purposes. Future studies need to be based on a much stronger grasp of the physiology of cacao and need to be much more geared to the full range of possible options available to address the climate adaptation in cacao.

Recommendations

Based on our study, we made a number of (intentionally provocative) recommendations to improve science and decision-making to address climate adaptation in cacao.

1. *Focus on variation and diversity in responses rather than trends and averages*. Much variation remains hidden in the modelling exercises. For example, training a cacao geographic distribution model with data from one part of a cacao growing region and projecting (extrapolating) the results onto another part (and the other way around) would provide a highly transparent way to evaluate the models visually that any decision-maker can understand. Also, this could reveal areas where cacao would not be expected, based on the climate-crop relations in the other part of the region, or where cacao systems in which climate adaptation is possibly already more advanced than elsewhere. Future modelling and empirical studies could focus specifically on finding so-called "positive deviants" and describing their management practices (55) to inform decision-making. At the same time, the physiological studies summarized above already show that much genetic diversity is available, a crucial resource for climate adaptation. Exploitation of cacao genetic diversity will rely more on the identification of exceptions, variation and responses to extreme conditions, than on deeper understanding of long-term trends or averages.

2. *Drastically increase the use of existing and new data to understand climate responses*. Traceability programmes are creating large amounts of data. Companies could pool these data with third parties through carefully designed data sharing agreements and do "pre-competitive" research to do climate research in real-time and with high spatial resolution. On the other hand, citizen science approaches can add specific farmer-generated data, based on observations or simple, but massively executed, experiments, leading to physiological insights that are directly relevant to field conditions ((56)).

3. *Include knowledge on physiological trends and responses into conclusion generating exercises.* There is knowledge on cacao physiological responses, yet none has been included in modelling exercises or the conclusions made from such exercises. We encourage future discussions to include this important information, along with the data generated in response to cacao's interaction with increased ambient CO_2 (15,16).

4. *Generate insights for robust decision-making rather than only try to improve uncertain predictions.* Climate change is not the only stressor in agricultural systems or the only factor that affects the bottom line or social impact of companies. Taking a broader decision science approach will make it possible to put climate adaptation in   a broader context and focus on those aspects that are most critical for decision-making and invest efforts in those types of information that will affect decision-making most (cf. (57)). In some cases, the possibility of robust decisions that work well across a number of future scenarios reduces the need for improved predictions. In other cases, the reduction of uncertainty involves long-term investments in data generation and data-driven decision-making as part of the business model and will lead to better informed decision-making over a longer period of time.

Acknowledgements

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