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Exploring assumptions in crop breeding for climate resilience: opportunities and principles for integrating climate model projections

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Abstract

Crop breeding for resilience to changing climates is a key area of investment in African agricultural development, but proactively breeding for uncertain future climates is challenging. In this paper, we characterise efforts to breed new varieties of crops for climate resilience in southern Africa and evaluate the extent to which climate model projections currently inform crop breeding activity. Based on a survey of seed system actors, we find that the prioritisation of crops and traits is only informed to a limited extent by modelled projections. We use an ensemble of CORDEX models for mid and end of century for southern Africa to test some of the assumptions that underpin current breeding activity, particularly associated with breeding for reduced durations and drought tolerance in maize, and demonstrate some of the ways in which such projections can help to inform breeding priorities and agenda setting (e.g. through the case of assessing cassava toxicity risk). Based on these examples, we propose five potential applications of climate models in informing breeding priorities. Furthermore, after unpacking the sources of uncertainty within the presented model projections, we discuss general principles for the appropriate use of climate model information in crop breeding.

Keywords Climate change · Resilience · Crop breeding · Projections · Agriculture · Africa

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1 Introduction

Crop breeding is a key area of investment in African agricultural development, as supported by the Comprehensive Africa Agricultural Development Platform and large donor-funded programmes. As climate risks and incidences of acute stress (both climatic and non-climatic) intensify across southern Africa, impacting on agricultural production and food security, the development and adoption of improved seeds are looked to as a way of building climate resilience (Cairns et al. 2013; Thornton et al. 2018; Rosenstock et al. 2019). Analysis by Cacho et al. (2020) suggests that climate-resilient seeds offer significant economic benefit to national agricultural economies in Africa. International programmes such as the CGIAR's Drought Tolerant Maize for Africa (DTMA) (Cairns and Prasanna 2018) and Next Generation Cassava (Maxmen 2019), and national agricultural research and development initiatives, are stimulating a rapid expansion in the release of certified climate-resilient varieties across sub-Saharan Africa (Cairns and Prasanna 2018).

Climate-resilient varieties in SSA are largely selected and bred to confer traits that indicate expanded viability at the extreme ranges of current climate, for instance by testing under controlled irrigation to simulate mid-season dry spells (Whitfield 2015). Programmes targeting the development, release and commercialisation of new varieties require significant investment of resource and time. Across southern Africa, such initiatives often involve a partnership between National Agricultural Research Systems (NARS), international centres under the CGIAR system such as the International Maize and Wheat Improvement Centre (CIMMYT), the International Institute for Tropical Agriculture (IITA) and the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) and the private sector (Langyintuo et al. 2010). At a regional level, the Southern African Development Community (SADC), via its Seed Security Network, has supported the harmonisation of seed regulation across the region and the cross-regional dissemination of seed information, giving breeding initiatives the scope to cover a range of contemporary growing conditions and become more efficient and flexible in the sharing and transfer of material across these diverse conditions (Kuhlmann 2015). However, this harmonisation has also been associated with concerns about effects on genetic diversity and food sovereignty (Lewis and Masinjila 2018).

Analysis by Challinor et al. (2016), which compares typical cycles of crop development and release with the rate of change of climate conditions, suggests that by the time new varieties are released, prevailing conditions may be significantly different from those under which they were initially selected and bred. This timeline can be reduced to some extent by the application of modern breeding tools such as marker-assisted selection and genomic-assisted breeding (Kole et al. 2015). Others have drawn on future climate projections to question whether crop breeding research and investment is being directed towards the right crops, based on their future viability (Manners and Van Etten 2018). In light of such evidence, there is growing recognition of the value of climate information within crop breeding programmes, to support pro-active germplasm selection, diversification and breeding for projected future climates. Atlin et al. (2017) highlight the importance of evaluating new crops under the range of climate conditions that they are likely to be grown in during their commercialisation window, and Thiele et al. (2017) highlight the downscaling of climate crop information as a first step in their climate smart breeding framework. The underutilised potential for collaboration between climate impacts modelling and crop breeding has also been highlighted in the CCAFS (CCAFS 2019) Breeding Foresight workshop report.

At a more systemic level, McGuire and Sperling (2013) recognise that climate-resilient seed systems should have ‘temporal breadth’ such that seed is available in a timely manner in response to short-term needs, but that systems are also planned with long-term foresight and sustainability. While the former may require a shortening of the breeding, delivery and adoption times for new varieties, that has been calculated as ranging between 10 and 30 years, and a higher uptake and turnover of improved varieties (Cairns and Prasanna 2018; Langyintuo et al. 2010; Challinor et al. 2016; Setimela and B Mwangi 2009), the latter points to the need for forecast information, not only of climates but also of markets, diets and more.

Climate change is not the only, or even necessarily the most important, motivation within crop breeding programmes in Africa. Market demand for foods with a variety of consumer defined traits—about quality, nutrition, perishability and more—is a key driver of breeding activity. Even for those programmes with a climate resilience focus, concerns about productivity; nutrition; tolerance to pests and disease; and distribution, access and affordability of seeds make up a multifaceted agenda (Defries 2018). Optimising for all of these priorities is unrealistic and, as such, setting priorities and targets for breeding programmes is by no means straightforward. Decisions about which crops and which traits to target inevitably involve assumptions about potential marginal gains, analyses of market demand and the allocation of limited resources. These questions sit within a context of historical institutional legacies and built expertise that may favour a continued focus on particular crops or traits. Indeed, McGuire and Sperling (2013) further highlight that resilient seed system interventions are directed by a careful weighing up of trade-offs and risks. We should not assume that climate information, in itself, can determine the trade-offs and risks of particular crop breeding strategies, let alone be sufficient to dictate breeding priorities and resource investment.

In this study, though, we begin from the premise that there is significant potential for climate projections and derived analyses of future crop impacts to contribute to crop breeding. This includes contributing to discussions of the risks and benefits of crop and trait targeting, informing germplasm sourcing and sharing, and even playing a role in the ongoing debate in many African countries over GM technology. With the exception of some of the studies highlighted above, there have been few attempts to apply climate projections and climate impacts analysis to answering crop breeding–specific questions. Of these attempts, fewer still (with the notable exception of Manners and van Etten (2018)) take as a starting point an understanding of existing crop breeding priorities and activity. However, knowing that climate impacts do not act in isolation to shape breeding, and in light of the influence of complex multifaceted priorities and institutional legacies, in directing breeding activity and investment, there is particular value in framing climate analysis within a concurrent analysis of contemporary breeding activity.

In this paper, we present and use the findings of a mixed methods analysis of seed systems in southern Africa to highlight some of the dominant strategies employed in breeding for climate resilience. We then interrogate these strategies on the basis of climate model projections (to the middle and end of the century) to analyse the strength of long-term climate evidence base for such strategies. We conclude with a discussion and recommendations for crop breeding programmes for integrating climate and climate impacts analysis in the pursuit of more climate-resilient seed systems.

2 Materials and methods

We ran an online survey disseminated to broadly defined seed systems stakeholders across Africa. This included those involved in crop breeding, testing, regulation, marketing and sales. The survey asked about priority crops and crop traits that they develop or work with, their use of climate information (at different temporal scales) in informing seed system activity and bottlenecks in building seed system resilience. The survey received 238 responses; this was comprised of 12% of respondents working in seed bank management, 31% in crop breeding trials, 15% in crop testing, regulation and certification, 30% in seed multiplication and marketing and the remainder in other aspects of the seed system. In this paper, we present an analysis of a subset of this data, focusing on those respondents based in southern Africa[1] ($n = 145$). This was supplemented by a review of grey and academic literature documenting case studies of crop breeding projects in the region, and data from the CGIAR's Diffusion and Impact of Improved Varieties in Africa (DIIVA) project, held within the ASTI database. This includes data on varietal releases (between 1960 and 2011) and an estimation of employment and investment in different agricultural research fields (including crop breeding), all disaggregated by crop, for ten southern African countries.[2]

From this combination of survey and literature review, we extracted information about the frequency of crops and traits identified as targets or priorities in breeding programmes, and analysed the extent to which climate information at different time horizons[3] is used to inform breeding strategies. Based on the survey findings, our climate analysis focused on interrogating the evidence base for the following strategies: (1) breeding for early maturity in maize, (2) breeding for drought tolerance in maize and (3) breeding alternative cereal and starch crops to maize, in order to provide and assess illustrative examples of climate model applications within crop breeding. We used regional climate model projections to evaluate whether efforts to breed for early maturity are compatible with the changing duration of the growing season for maize, and to evaluate how investment in drought tolerance compares to anticipated trends in dry spell occurrence, based on an assessment of consecutive dry days and mid growing season dry days. Finally, we take the example of cassava, and consider the viability and suitability of this as an alternative to maize, by analysing the effect of future climates on thresholds in cassava quality, specifically related to toxicity.

The models and methods used in this analysis are described below.

2.1 Models

We used the regional climate models available from CORDEX-Africa. These models are available at a 0.44° × 0.44° resolution. The multi-model ensemble for RCP8.5 includes 6 RCMs (regional climate models) with 11 different GCMs (global climate models) providing initial and boundary driving conditions, and for RCP4.5 7 RCMs and 9 different GCMS. The matrix of GCM/RCM combinations is presented in Supplementary Material Table 1. We used 1971–2000 as the historical period, 2031–2050 as the mid-century period and 2071–2100 as the end of century period, except for the HadGEM models which end in 2099.

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[1] For the purpose of this analysis, we define southern Africa as being comprised of the following countries: Angola, Botswana, Democratic Republic of Congo, Kenya, Lesotho, Madagascar, Malawi, Mozambique, Namibia, Rwanda, Swaziland, Tanzania, Uganda, South Africa, Zambia and Zimbabwe

[2] https://www.asti.cgiar.org/diiva

[3] 1–5 days, seasonal, 1–5 years, 5–20 years, and 20+ years

2.2 Rainy season onset

The rainy season onset, cessation and duration were estimated following the method of Dunning et al. (2016). First, grid cells are classified as having a bimodal or unimodal rainfall regime using harmonic analysis. The onset and cessation of the rainy season for each year are then found using the cumulative daily precipitation anomaly.

2.3 Growing degree days

The time taken for maize to reach maturity was calculated using growing degree days (GDDs). Growing degrees are a measure of heat accumulation. GDDs were calculated as the accumulation of daily mean temperature between the base and maximum temperature thresholds ($GDD = Tavg{-}Tbase$), as per the degree day calculation of Mathieu and Aires (2018). We used 10 °C as the base temperature, which is commonly used for maize (Skaggs and Irmak 2012), and 35 °C as the maximum temperature. Outside of these thresholds, GDDs were zero. GDDs were accumulated daily, starting from the first day of the rainy season.

A maximum, or upper, temperature threshold is not always used in the calculation of GDDs; however, we have chosen to use one as maize is sensitive to high temperatures (Lobell et al. 2011). Various temperature thresholds are reported in the literature for maize, varying from 30 °C for optimal temperatures to 45.3 °C for maximum temperature (Dieng et al. 2018; Food and Agriculture Organization of the United Nations 2007; Lobell et al. 2011). We chose 35 °C as the maximum temperature threshold, following Dieng et al. (2018), as a balance between the reported thresholds.

We considered short-, medium- and long-duration maize crops, requiring 500, 1000 and 1500 GDDs, respectively, to reach maturity. These thresholds span the wide variety of GDD requirements reported in the literature for maize, from 100 to 1500 (Dieng et al. 2018; Moeletsi and Walker 2013; Moeletsi and Walker 2012; Tsimba et al. 2013).

2.4 Consecutive dry days and number of dry days in the rainy season

We calculated the mean yearly maximum length of dry spells using the consecutive dry days (daily rainfall < 1 mm) equation from the Expert Team on Climate Change Detection and Indices (Zhang et al. 2011). These indices were developed to be a set of standard indices, allowing comparisons between different studies (Tank et al. 2009; Zhang et al. 2011). We also calculated the number of dry days in the rainy season (daily rainfall < 1 mm) as a percentage of the total duration of the rainy season for each model and each year.

2.5 Cassava toxicity

We counted the number of months in the historical and future time periods where the conditions for increased cassava toxicity were met. A month was considered toxic for cassava if the average minimum and maximum temperatures were equal to or above 25 °C and 38 °C, respectively, and if the month was a drought month, defined as having a Standardized Precipitation and Evapotranspiration Index (SPEI) < -1.

The minimum and maximum thresholds for cassava were based off Brown et al. (2016), who found in field experiments that in conditions of high temperatures ($TMIN \geq 25$ °C and $TMAX \geq 38$ °C) and drought conditions applied for 1 month, cyanogenic compounds in the cassava root increased by a factor of 6–7.

We defined droughts using the SPEI as defined by Vicente-Serrano et al. (2010), which is a commonly used drought index that performs well compared to alternatives (Labudová et al. 2017), and has been used in Africa (e.g. Abiodun et al. 2019; Adejuwon and Olaniyan 2019; Ghebrezgabher et al. 2016; Oguntunde et al. 2017; Polong et al. 2019; Ujeneza and Abiodun 2015). We used 1955–1970 as the reference period, and looked at droughts over 1 month and used the log-logistic distribution. We performed the calculation using the 'SPEI' package for the R statistical software (Begueria and Serrano 2017; R Core Team 2013).

3 Results

3.1 Characterising crop breeding activities and priorities

Survey findings indicate that the majority of effort and investment in crop breeding in southern Africa is in maize. A total of 74% of survey participants identified maize as a key crop in their work, and within the DIIVA database maize ranks as the highest crop, by a significant margin, in regard to the rate of varietal release and the number of crop breeders employed (Table 1).

Although maize breeding initiatives are helping to expand the productive range of this main staple crop (Cairns and Prasanna 2018), keeping pace with the rate of change in maize-relevant climate conditions is a significant challenge (Challinor et al. 2016). Indeed, in some areas of southern Africa, conditions are moving outside of existing, and projected, suitability ranges, pointing to a need for transformational adaptation, i.e. a shift in which crops are produced where (Rippke et al. 2016). Grain crops such as sorghum (which ranked as the 6th most common focal crop within our survey), and tuber or root crops such as cassava (which ranked 4th), are important

Table 1 The seven crops most commonly worked on by survey respondents, with an indication of the proportion of respondents identifying each. Data from the DIIVA database (https://www.asti.cgiar.org/about) is presented alongside this to indicate number of identified varieties for each crop and total number of full-time equivalent crop breeders employed in government, non-profit organisations and education agencies, across the countries documented in the database.

Crop	Survey	DIIVA database		
	Focal crops (% of respondents (and rank))	Number of varieties released (to 2011)	Crop breeders employed at government, nonprofit and higher education agencies (FTE equivalent)	Countries included in the database
Beans	51 (2)	183 (2)	20.8 (2)	CD, MW, MZ, RW, TZ, UG, ZM
Cassava	42 (4)	158 (3)	15.9 (3)	AO, CD, KE, MW, MZ, TZ, UG, ZM, ZW
Groundnuts	46 (3)	44 (6)	5.02 (6)	KE, MW, TZ, UG, ZM
Maize	74 (1)	724 (1)	83.5 (1)	AO, KE, MW, MZ, TZ, UG, ZM, ZW
Sorghum	40 (6)	21 (7)	1.5 (7)	KE, TZ
Soybeans	39 (7)	111 (4)	6.1 (5)	CD, KE, MW, TZ, UG, ZM, ZW
Sweet potatoes	41 (5)	86 (5)	7.6 (4)	MZ, RW, TZ, UG

AO, Angola; *CD*, Democratic Republic of Congo; *KE*, Kenya; *MW*, Malawi; *MZ*, Mozambique; *RW*, Rwanda; *TZ*, Tanzania; *UG*, Uganda; *ZM*, Zambia; *ZW*, Zimbabwe staple crops across the region (FAO 2019) and represent an alternative sources of starch carbohydrates from plants with greater resilience to heat and drought stress than maize (Schittenhelm and Schroetter 2014; Hadebe et al. 2017; Okogbenin et al. 2013; El-Sharkawy 2003). Jarvis et al. (2012) show that climate suitability for cassava is expected to increase in large areas of southern Africa to mid-century, although recent research using convection permitting regional climate models also suggests that there will be a decline in suitability for cassava over significant areas of the region (Chapman et al. 2020). In accordance with the findings of Manners and van Etten (2018), our data suggests that there is a particular bias, within crop breeding, towards maize over many other crops with significant climate resilience characteristics.

Three target traits that specifically relate to climate resilience were highlighted as priorities within crop breeding by survey respondents, two relate to tolerance to stresses: dry spells within the growing season, and extreme heat. These align closely with a justification for maize alternatives that naturally confer such traits. The third climate resilience trait relates to variability and changing durations of rains, which is particularly addressed by the targeting of short duration/early maturity varietal traits (Table 2).

Climatic stresses are often not the main focus of breeding initiatives. Survey results identify a variety of target crop traits in breeding, including nutritional quality, yield and pest and disease resistance, all of which have a similar level of prioritisation to the more explicitly climate-focused trait priorities (Table 2), and many crop breeding research programmes focus on the combining, or stacking, of desirable climatic and non-climatic traits (Whitfield 2015).

Table 2 The 8 most commonly identified priority traits with the number of respondents identifying those traits as a priority (column A); including their priority ranking by crop (based on filtering responses to those respondents working on each crop) 1 = highest priority, 8 = lowest priority (column B); and the proportion of those identifying a particular trait as a priority that use (beyond 5 years) future climate projections to inform crop breeding activity (column C)

Crop Trait	A. No (and %) of respondents identifying as priority	B. Priority ranking (1-8) of crop traits by crop							C. No (and %) of A. using 5+ year climate information
		Beans	Cassava	Groundnuts	Maize	Sorghum	Soybean	Sweet potato	
Enhanced nutritional content (iron, vitamin A, protein etc.)	90 (63)	6	4	6	6	5	6	3.5	18 (20)
High yield/biomass	107 (74)	3	6	4.5	1.5	4	2	5.5	23 (21)
Resistance to pests/insects	104 (72)	2	3	1.5	3	2.5	1	3.5	20 (19)
Resistance to viruses/fungi/bacteria	95 (66)	4.5	5	3	4	6	3	5.5	22 (23)
Short duration/early maturity	98 (68)	4.5	2	4.5	5	2.5	5	2	20 (20)
Tolerance to dry spells within the growing season	105 (72)	1	1	1.5	1.5	1	4	1	22 (21)
Tolerance to heat stress	62 (43)	8	8	7.5	8	7	8	7	17 (27)
Tolerance of soil nutrient deficiencies	68 (47)	7	7	7.5	7	8	7	8	17 (25)

Indeed, caution should be taken in translating metrics of yield under stress conditions as a complete indicator of the superior climate resilience of crops/varieties. There are complex interactions between climatic conditions and the quality and nutritional properties (which Manners and van Etten (2018) emphasise as important basis on which to prioritise crop breeding investment), exposure to and sensitivity to biotic stresses (accounted for to some extent in the Jarvis et al. (2012) projections) and long-term soil dynamics that are associated with different crops.

Table 2 also presents data that gives an indication of the extent to which future climate information is helping to inform breeding strategies and activities. Across all of these target traits, only 19–27% of respondents suggested that they make use of climate projections with a time horizon of more than 5 years (i.e. information about anticipated climates associated with the timescales of breeding and delivery of new varieties). In the following section, we demonstrate how such information (with time horizons of the middle and end of the century) might be used to test some of the assumptions and objectives of crop breeding in southern Africa. This is an illustrative set of examples rather than a comprehensive climatic assessment of all breeding activities. We focus here on the priorities of short duration/early maturity varieties and drought-tolerant varieties of maize, and consider climate-crop quality interactions in relation to cassava, a crop widely considered as being a climate-resilient alternative to maize.

3.2 Testing assumptions about breeding for climate resilience

Under optimal circumstances, the maturity period of a maize variety would be equal in length to the growing degree days within the rainy season in which it is grown, such that the crop can fully mature within the rainfall window of the growing season, while converting the full extent of energy potential to biomass. This can represent an important trade-off. Even under circumstances of a shortening of the rainy season, targeting crops with a shorter duration may not be the most appropriate strategy if this is counterbalanced by an increase in average temperatures (and therefore in the number of growing degree days) within that season.

Across the region, CORDEX models project a shortening of the rainy season to the end of the century, under both RCP 4.5 and RCP 8.5. However, it should be noted that these projections are associated with significant inter-model variability (Fig. 1a). However, this does not translate into a reduction in the number of growing degree days within the season (Fig. 1b).

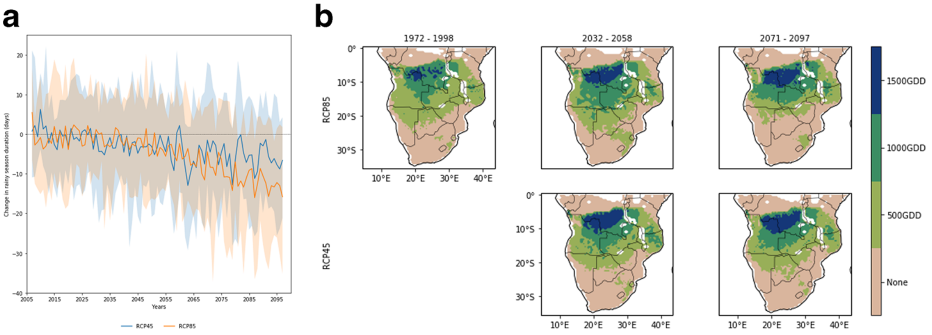

Fig. 1 **a** Projected average change in rainy season duration (days) to the end of the century based on RCP 4.5 (blue) and RCP 8.5 (orange) for southern Africa. Shaded area represents intermodal range. **b** Areas where the number of growing degree days (1500, 1000, 500) are met within the rainy season in 95% of CORDEX models (21 RCP8.5, 20 RCP4.5), and 95% of years (25 years). Areas with a bimodal rainy season excluded

Our results indicate that in the present day, 500 GDDs are acquired in the rainy season for most maize-growing areas, particularly across a central belt of the region that runs through Angola, Zambia, Malawi, Tanzania, Zimbabwe and Mozambique. There are some more equatorial regions in Tanzania and the Democratic Republic of Congo in particular where 1000 GDDs are met, and a smaller subset of this area that reaches 1500 GDDs.

By mid-century, 1000 GDDs are acquired within the rainy season for a significantly greater proportion of maize-growing areas in RCP8.5 and RCP4.5, with this area expanding down into Angola, Zambia and Mozambique. This is primarily due to increases in temperature despite a shortening of the growing season (as indicated in Fig. 2). These observed duration effects remain relatively consistent from mid-century to end of century, and particularly under RCP 8.5 we observe a contraction of the total maize-growing area that reaches this minimum 500 GDD threshold within the growing season. As indicated in Fig. 2, and supported by the findings of Chapman et al. (2020), under RCP 8.5 by the end of century we anticipate an increase in the length of the dry season, and associated shortening of the rainy season, across the region.

The largest increases in consecutive dry days are in areas that are already dry and these correlate to some of the areas in which we see the GDD accumulation fall below 500 for the growing season. The contraction of area meeting the 500 GDD by the end of century in northern parts of Namibia and Botswana, and in parts of Zimbabwe, Zambia, Malawi and Mozambique are consistent with Rippke et al.'s (2016) findings about the timescales of transformation away from maize to alternative crops. There are some small areas near the

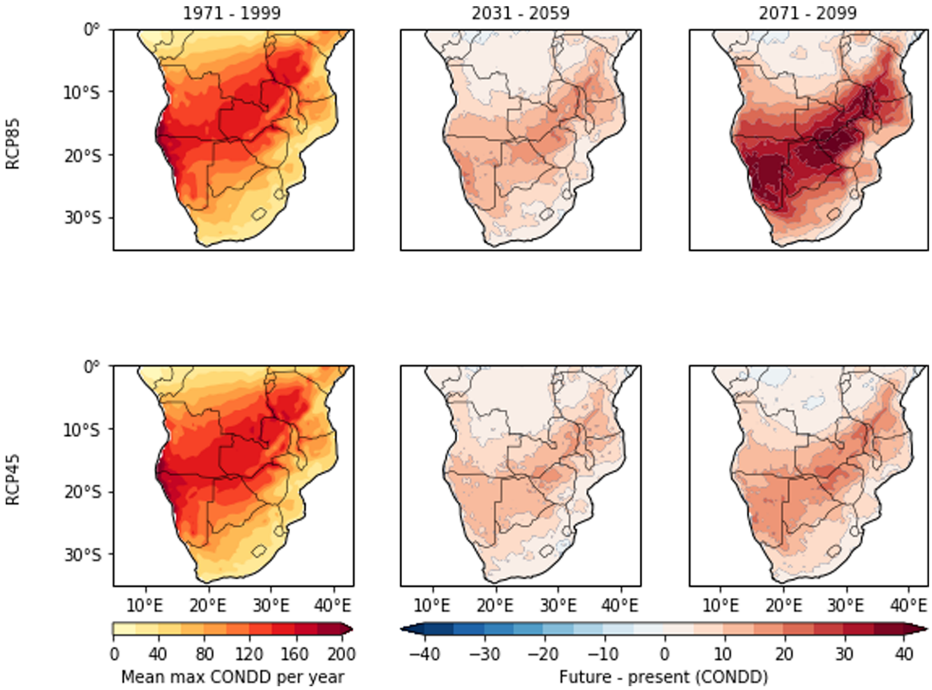

Fig. 2 Ensemble mean maximum number of consecutive dry days (CONDD) per year in the historical period (1971–1999), and the difference between the future and historical periods for mid (2031–2059) and end of century (2071–2099) for RCP8.5 and RCP4.5

equator in the Democratic Republic of Congo which may have small decreases in the number of consecutive dry days. This may reflect that in that region, there may be increases in the amount of precipitation and a possible lengthening of the rainy season (Chapman et al. 2020). However, it should be noted that across the region there is model disagreement over projected changes in the timing and length of the rainy season (Chapman et al. 2020).

These results broadly challenge some of the logic of investment in early maturity varieties, as they suggest a trend towards increasing duration for large parts of the maize-growing area of the region over the timescales of the current breeding programmes. However, there is spatial variability in this, and such analysis can also help to identify transitions of areas into longer or shorter duration conditions and point to regions of comparable contemporary conditions, from which breeding material might be sourced and adapted for addressing these transitional needs.

While the mean maximum consecutive dry day increases in most areas, the rainy season also becomes drier in the northern SADC region by mid-century under both RCP4.5 and RCP8.5. This may mean that rainfall may become more intermittent during the rainy season in these areas, even if the duration or overall amount of rainfall does not change. This is not the case everywhere however, and parts of Tanzania and South Africa may have fewer dry days, as a percentage of the overall length of the rainy season, in the future (Fig. 3).

These findings suggest that dry spells within the growing season will continue to be a feature of the climatic variability that crop production must adapt to in the region, and such climate model evidence can help to support and strengthen the case for the continued investment in breeding for drought tolerance across the region, as well as identifying geographic areas for which such effort may be particularly important.

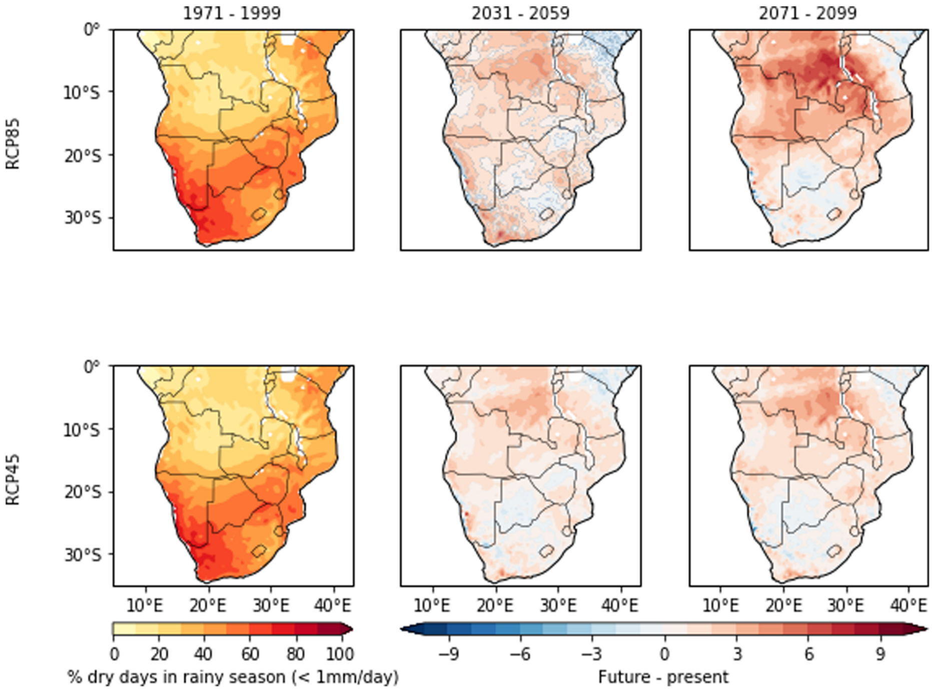

Fig. 3 Ensemble mean of percentage of rainy season which is a dry day (< 1 mm rainfall) in the historical period (1971–1999), and the difference between the future and historical periods for mid (2031–2059) and end of century (2071–2099) for RCP8.5 and RCP4.5

Focusing breeding effort on alternatives to maize may be particularly important in areas that are projected to fall below the 500 GDD threshold, but beyond impacts on biomass accumulation, there are a variety of climate-related impacts on crop quality for which modelled information may usefully help to highlight breeding challenges and priorities. Here, we take cassava, a root crop with a typical duration of 9 to 18 months, as a case in point. Under the changing consecutive dry days projected in Fig. 2, there will be a mixed picture in terms of suitability across the southern African region by the end of the century, with some benefit from increased temperatures in some areas, and the exceedance of critical heat and drought thresholds in others (Chapman et al. 2020). However, the protracted consecutive dry days is a challenge not only for cassava productivity but also for quality. Under conditions of high temperature and reduced water availability, there has been an observed increase in cyanogenic compounds in the cassava root. In order to be safely consumed, cassava has to be processed to remove its toxicity, but improperly processed cassava has been associated with cyanide-related health disorders (Kashala-Abotnes et al. 2019) (Fig. 4).

In the present day, conditions for large increases in cassava toxicity (6–7x) are rare, primarily as while droughts may be common, the temperature thresholds are not met, although it should be noted here that CORDEX models tend to be cooler than observations, and so these projections may include a systematic under-estimate (see Chapman et al. 2020). These conditions remain rare in the mid-century, but by the end of the century start to occur more regularly, particularly in RCP8.5. In RCP8.5, toxic months occur in parts of Zambia, the Congo, Mozambique and Tanzania on a yearly basis. The main limiting factor is the temperature thresholds, as droughts become more frequent in both RCP4.5 and RCP8.5 by

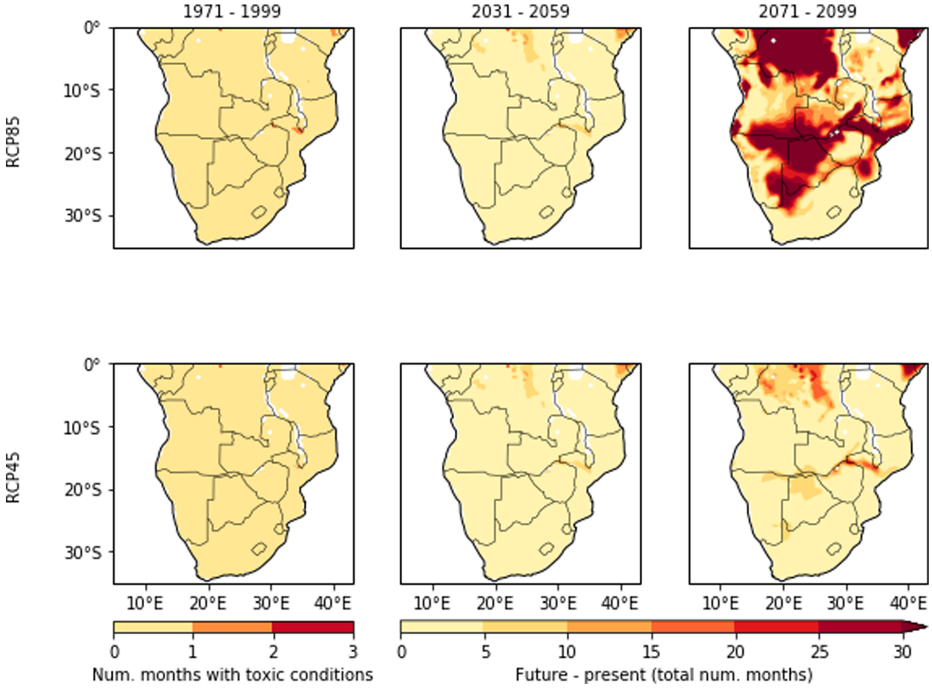

Fig. 4 Change in total number of months (future – present) that meet the criteria for cassava toxicity (SPEI < − 1 and TMIN ≥ 25 °C and TMAX ≥ 38 °C). Column 1 shows total number of months in historical period for models included in RCP4.5 and RCP8.5 ensemble

mid-century. Droughts themselves also increase cassava toxicity by 4× (Vandegeer et al. 2013) (see supplementary material Figure 2 for details of SPEI and temperature thresholds).

Such projections add further nuance to the interpretation of crop suitability assessments as a means to targeting priority crops, and may also help to identify priority traits (such as reduced toxicity) for building varietal resilience to climate within suitable crops. In the following discussion, we reflect on some of the ways in which multi-layered climate model projections, such as those presented above, can help to inform crop breeding activities and highlight some conditions and caveats for the use and integration of such information within crop breeding.

3.3 Sources of uncertainty

Across the analyses of future climate impacts presented above, there are multiple sources of uncertainty. This uncertainty comes not only from broad-scale emission trajectories and the internal variability of the climate system but also from the challenges of simulating these processes at regional scales (Chapman et al. 2020) and translating them, within climate impacts models, into representations of crop responses (Challinor et al. 2018). These challenges arise from the interactions between uncertainties in crop science, genotypic variation in key traits, gaps in information and structural uncertainty in climate impacts models. Below, we highlight some examples of limitations and uncertainty within our analysis.

In our analysis, we have conducted runs across an ensemble of RCMs, driven by different combinations of GCMs and representative concentration pathways (RCP 4.5 and RCP 8.5), as exists within the CORDEX dataset. We present projections of growing degree days, consecutive dry days, rainy season dry days and high cassava toxicity months for both of these RCP. In the case of the rainy season duration analysis, we also present inter-model variability. In doing so, we illustrate the ranges that result from these two sources of uncertainty.

In this paper, we took a simplified approach to modelling crop phenology. We acknowledge that there is some evidence to suggest that cardinal temperatures for maize may vary during different parts of the growing season (Sánchez et al. 2014); however, it is far from settled that this is the case (Parent et al. 2019) nor is there consensus on cardinal temperature thresholds at different growth stages. Since in this analysis we cannot know exactly when the crop transitions from one growth phase to another, we employ the simplification that cardinal temperatures remain constant throughout the growing season. As a sensitivity test, we also ran the growing degree days analysis using a maximum temperature of 35 °C and 45.3 °C. Figure 5 shows changes in GDD classifications—i.e. where < 500, 500, 1000, and 1500 GDD are met within the rainy season—between runs with the lower and higher temperature threshold.

Although this threshold is considered to be one of the most significant uncertainties in modelling climate impacts on maize (Lobell et al. 2011), our analysis showed little sensitivity to maximum temperature threshold in our results on changes to growing degree day categorisations in either mid or end of century runs for either RCP 4.5 or RCP 8.5. In this case, the lack of sensitivity is largely due to the fact that the 35 °C is rarely exceeded within the model projections for the region. The only exception to this is that under the end of century RCP 8.5 runs there are a small number of grid cells that experience a reduction in the GDD accumulated during the rainy season.

We also acknowledge that crop development can be driven by day length as well as temperature, and that there is evidence of photoperiod sensitivity in tropical maize cultivars (Coles et al. 2010). Since maps showing which cultivars are grown where are not available in

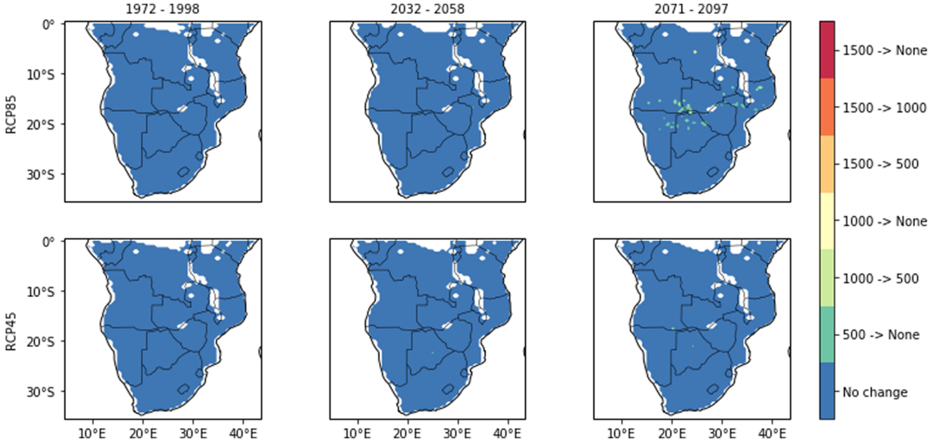

Fig. 5 Changes in areas where the number of growing degree days (1500, 1000, 500) is met within the rainy season when applying a 45.3 °C cardinal temperature threshold for the GDD calculation compared to a 35 °C cardinal temperature threshold

our study region, and the biggest genotypic differences in photoperiod sensitivity are between tropical and temperate cultivars (Bonhomme et al. 1994), we make the simplifying assumption that cultivars are fully adapted to the prevailing day lengths in which they are grown.

In the case of cassava toxicity, we must also acknowledge the uncertainty in the assumptions that we adopt about threshold responses to drought. This is a phenomenon that has only been observed and tested under a limited range of cultivars and conditions. The impact of reduced water availability on plants varies in different types of soil (Fernandez-Illescas et al. 2001), for example, and differences in soil properties have been shown to be an important component of the overall uncertainty in climate impacts (Folberth et al. 2016). We have further simplified the cassava response to drought that was observed by Brown et al. (2016) for the purpose of modelling affects by categorising drought conditions on a monthly timescale.

As a result, our projections of changes in growing degree days and cassava toxicity risk should be considered as indicative of challenges and conditions, for which a resilient crop breeding strategy may accommodate rather than a clear signal of the specific conditions that should be bred for. In the discussion below, we outline applications of climate modelling with crop breeding initiatives context. However, we also emphasise the importance of acknowledging and communicating uncertainty in climate model projections, so that they can be appropriately inform crop breeding.

4 Discussion

Building climate resilience within seeds is increasingly being prioritised with African crop breeding programmes. McGuire and Sperling (2013) argue that in order to build resilience in seed systems, interventions (such as crop breeding initiatives) should be directed by a careful weighing up of benefits and risks, i.e. weighing up the relative benefits of pursuing one breeding strategy over another. Some of these risks arise because of uncertainty over future climatic conditions. Climate model projections can play a valuable role in helping to parameterise and inform such decisions.

Even if the choice of which crops to invest in and which traits to target was purely motivated by a climate agenda, resilience is not something that can be objectively optimised for. As climates transition in and out of the suitability ranges of different crops, there are value judgements to be made about whether to maintain or even increase investment in the adaptive breeding of status quo staple crops, or redirect investment and effort towards improving crops, for which the conditions are becoming more favourable. Similarly, value judgements are embedded in the metrics through which resilience is conceived: whether this is reflected in crop productivity or quality under projected climate changes; whether such performance should be considered under projected averages, across variability ranges or at extremes; which agro-climatic variables should be the focus of such projections?

Climate model projections can play a valuable role in helping to parameterise and inform such choices, but cannot directly answer them, no more than they can provide an adequate basis for setting breeding priorities. Here, we outline five potential applications of climate models in helping to weigh up breeding priorities:

1. Understanding changing durations: by identifying at what point in time the prevailing conditions will more frequently favour a long duration variety/crop over a short one for a given location
2. Understanding critical constraints on productivity and quality: by identifying what climate thresholds might have the most significant effect on the viability and quality of particular crops (e.g. toxicity in cassava) over medium to long timescales
3. Understanding breeding and testing conditions: by identifying significant differences in the agro-climatic conditions over the timescales of the breeding, delivery and adoption cycle of new seeds to indicate where artificial or analogue environments for breeding might have some value for trait evaluation
4. Understanding crop selection (and crop breeding investment) options: by identifying transitions into and out of the suitability window, for different crops based on these critical constraints
5. Understanding variability: by identifying, for all of the above, the range of conditions experienced into the future and the frequency with which critical thresholds or extremes are expected to be experienced (e.g. the season frequency with which a long duration variety may not reach maturity), including critical thresholds in variability itself

Our survey result suggests that such applications of climate model projections are underutilised within crop breeding activity in southern Africa, and this can result in decision making about breeding for climate resilience that is not as fully informed about future conditions as it could be, and potential for misplaced assumptions about such conditions.

There is an inevitable degree of uncertainty in breeding for future conditions. The use of climate projections can help to highlight key trends and narrow down the parameters of these future conditions. However, in utilising climate and climate impacts projections in these ways, it is important to acknowledge the embedded assumptions and limitations that also exist within model projections (Challinor et al. 2018; Whitfield 2013). If uncertainty is not sufficiently characterised, modelling assumptions can quickly become masked in simple representations of future crop suitability and response, and the translation of model projections into adaptation and crop breeding recommendations (Challinor et al. 2018, Whitfield 2013). As such, it is important that model projections are communicated with a clear explanation of sources of uncertainty and underlying model assumptions.

To be particularly useful in informing crop breeding priorities, climate model analysis is conducted across space and time dimensions in order to understand the sensitives, dynamics and timescales across which agro-climatic thresholds change (particularly for comparison with the timescales of breeding). The GDD analysis presented in the paper highlights that a trend towards increasing growing degree days to the middle of the century is not necessarily expected to continue to the end of the century (as the rainy season shortening becomes a more dominant factor), and this points to some of the trade-offs between breeding for short- and long-term dynamics (relative to the timescales of breeding) that should be weighed up in crop breeding investments. At the same time, spatial analysis at appropriate resolutions can help to provide a geographic picture that might indicate variation in these trade-offs across regions and countries and potentially point to analogous environments or opportunities for sourcing of useful genetic material.

It is similarly important that such modelling should not focus too narrowly on individual indicators, where we expect that there might be multiple interactions between climate and crop responses, in productivity, quality and varied biotic and abiotic impacts. This is particularly important because of the potential for indirect climate impacts on crop pests and diseases, soils and other factors. In the paper, we use cassava toxicity as one example of an often-overlooked crop quality consideration that is linked to future climates, and highlights an additional consideration when thinking about future crop suitability. Many of the conditions and priorities for crops to be adapted for are not climatic in nature. They relate, for example, to the imperatives for foods to have nutritional value; for seeds to be accessible, affordable and trusted; for plants to be resilient to abiotic and biotic stresses and have multifunctional characteristics. Combining multiple simulations, and using crop models for example, in an integrated way (including by integrating other knowledge and perspectives) can help to ensure that climate models do not point to maladaptive strategies or traits with significant trade-offs.

There is a danger that modelled projections become misused as an objective source of information that legitimises certain priorities and preferences over others (Whitfield 2015; Challinor et al. 2018; Stirling 2010). It is important to highlight gaps in information and assumptions where these are present. This should involve the use of ensemble models and sensitivity analyses to generate output ranges and an exposing of the influencing of different assumptions within them. Rather than undermining the value of model evidence for informing breeding priorities and activity, a clear elicitation of uncertainty can strengthen the case for targeting diversity in crop breeding (e.g. not being too narrowly focused on early maturity), while also informing some of the trade-off calculations described above.

There will be much to learn from efforts to integrate climate modelling with crop breeding programmes in southern Africa, and inevitably assumptions to be exposed in the knowledge that underpin both of these, conventionally distinct, areas of research. However, bringing this knowledge together has the potential to support pro-active efforts to build resilience to climates that are changing significantly, even within the timescales of breeding programmes. Designing modelling approaches to address specific questions (e.g. about changing duration) can help to both challenge the assumptions that underpin this breeding activity and strengthen evidence bases for investment in climate-resilient seeds.

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