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Title: Breeding implications of drought stress under future climate for upland rice in Brazil

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Abbreviations: TPE, target population of environments; BC, bias correction; RCP, representative concentrations pathway; GCM, general circulation model; PCEW, actual to potential evapotranspiration ratio.

Abstract

Rice is the most important food crop in the developing world. For rice production systems to address the challenges of increasing demand and climate change, potential and on-farm yield increases must be increased. Breeding is one of the main strategies toward such aim. Here, we hypothesise that climatic and atmospheric changes for the upland rice growing period in central Brazil are likely to alter environment groupings and drought stress patterns by 2050, leading to changing breeding targets during the 21st century. As a result of changes in drought stress frequency and intensity, we found reductions in productivity in the range of 200-600 kg ha^{-1} (up to 20 %) and reductions in yield stability throughout virtually the entire upland rice growing area (except for the south-east). In the face of these changes, our crop simulation analysis suggests that the current strategy of the breeding program, which aims at achieving wide adaptation, should be adjusted. Based on results for current and future climates, a weighted selection strategy for the three environmental groups that characterise the region is suggested. For the highly favourable environment (HFE, 36–41 % growing area, depending on RCP), selection should be done under both stress-free and terminal stress conditions; for the favourable environment (FE, 27–40 %), selection should aim at testing under reproductive and terminal stress; and for the least favourable environment (LFE, 23–27 %), selection should be conducted for response to reproductive stress only and for the joint occurrence of reproductive and terminal stress. Even though there are differences in timing, it is noteworthy that stress levels are similar across environments, with 40–60 % of crop water demand unsatisfied. Efficient crop improvement targeted toward adaptive traits for drought tolerance will enhance upland rice crop system resilience under climate change.

Keywords: breeding, adaptation, simulation modelling, drought stress, environment groups

Introduction

Rice is the second most important staple crop globally, contributes to ca. 15 % of daily per capita calorie intake, and is the most important food crop across the developing world (Cassman, 1999; Khoury et al., 2014). In Latin America and the Caribbean (LAC), where dependence on rice as a staple food crop is substantial, annual rice consumption ranges between 6 and 57 kg $person^{-1}$ (Fitzgerald & Resurreccion, 2009; Kearney, 2010). Tropical LAC countries, in particular, have the largest rice consumption rates (Kearney, 2010). In addition to rice's current importance, global demand for rice is expected to increase as a result of population growth and economic development (FAO, 2010; Tilman & Clark, 2014). A recent global analysis showed that rice's dietary importance across the developing world has increased by 21 % in the last 30 years (Khoury et al., 2014).

Particularly for rainfed rice systems, which occupy large production areas in Asia and most of the production areas in Africa and Latin America (Hijmans & Serraj, 2008), concerns have been raised with regard to how rice production systems will be able to sustainably satisfy increasing demand in a context of stagnating potential and on-farm yield, increasing yield gaps and climate change-induced yield reductions (Challinor et al., 2014; Zhao et al., 2016). More specifically, the latest IPCC report showed that, in the absence of adaptation, tropical rice productivity is likely to decrease at a rate between 1.3 % and 3.5 % per degree of warming (Porter et al., 2014). Furthermore, increased temperatures can lead to heat stress-threshold exceedance and substantially lower yield (Li et al., 2015; Zhao et al., 2016). There is thus an increasing need for better adapted cultivars combining improved yield potential and lower drought sensitivity (Lafitte et al., 2006).

While there may be several potential avenues to increase rice yield, crop breeding is arguably one of the most promising strategies toward such aim (Dingkuhn et al., 2015; Ramirez-Villegas et al., 2015). Higher rice productivity has been attained in irrigated environments by improving yield potential while reducing crop duration, whereas less success has been achieved in drought-prone environments such as upland and rainfed cropping systems (Kamoshita et al., 2008; Serraj & Atlin, 2008). Under climate change, breeding targets may vary depending on how different abiotic stresses act during the growing season, as a result of increased temperature and geographically varying precipitation changes. For instance, a recent study for Australian wheat suggested shifted breeding focus under future climate due to increased prevalence of heat stress during flowering and a concomitant reduction in the importance of drought (Lobell et al., 2015). Similarly, Harrison et al., (2014) reported increased frequency of severe drought stress for maize in Europe. For upland rice in Brazil, where drought is a key limiting factor [30-40 % probability of occurrence, with up to 30 % yield reduction, Heinemann et al. (2008), Rabello et al. (2008)], a recent study by Heinemann et al., (2015) suggested that breeding should take account of drought stress patterns under current climate at early stages of breeding to improve yield under water-limiting conditions. Shifting stress patterns and their breeding implications for rice under future climate, however, are yet to be investigated.

Here, we assess changes in the prevalence and intensity of drought stress that result from climate change for upland rice in central Brazil (states of Goiás, Rondônia, Mato Grosso and Tocantins), the main upland rice growing area of Brazil and globally, and one of the largest rainfed rice growing area in Latin America. We hypothesise that the complex interplay between changing precipitation and increasing temperature during the rice growing period in central Brazil (November through to January) (Collins et al., 2013) and growth stimulation at elevated CO_2 concentrations (Krishnan et al., 2007; Kimball, 2016), is likely to alter the frequency of environment groupings and drought stress patterns by 2050. We discuss breeding implications of these changes and suggest potential future breeding directions for upland rice in Brazil.

Materials and methods

Overview

We used observed historical (1981-2005) weather from 51 weather stations in central Brazil (states of Goiás, Rondônia, Mato Grosso and Tocantins, Fig. 1) and bias-corrected projections (2041-2065) of an ensemble of 12 General Circulation Models (GCMs) with data for the four Representative Concentrations Pathways (RCPs, 2.6, 4.5, 6.0, 8.5) to simulate growth and development of upland rice. For all locations, we ran simulations with the ORYZA2000 crop model for a range of management scenarios and 7 soil types prevalent in the region. We employed clustering analysis on simulated yield to determine environment groups, and then for each group used the same classification method on the seasonal pattern of the actual-to-potential evapotranspiration ratio (PCEW) to determine the main drought stress patterns. Using the historical and future clustering results we finally assessed changes in the frequency of the environment groups and in the frequency and intensity of the drought stress patterns. We used these results to suggest potential avenues for future breeding.

Current and future weather data

Observed historical 1981-2005 weather data from 51 weather stations within the study region, hereafter referred to as the upland rice TPE (Target Population of Environments), were gathered from a previous study (Heinemann et al., 2015). Briefly, this dataset consists of daily observations of temperature, precipitation and solar radiation originally gathered from the Brazilian Meteorological Institute (INMET, http://www.inmet.gov.br), and thoroughly checked for gaps and errors. For all these weather stations, except the one corresponding to Santo Antônio de Goiás (49º 16’ 48” S, 16º 28’ 12” W, Fig. 1), daily solar radiation was estimated according to Richardson & Wright (1984).

For the three stations located in the state of Tocantins, which missed data from 1981-1989, were supplemented with other existing databases. More specifically, we gathered data from two databases: ANA (Agência Nacional de Águas, Brazil) and the CPC (Climate Prediction Center). We used ANA data to the maximum extent possible and used CPC data only for filling missing ANA entries. For minimum and maximum temperature and solar radiation we used the WATCH Forcing Dataset – ERA Interim (WFDEI) dataset (GPCC version) (Weedon et al., 2011). Following Hawkins et al. (2013) we `nudged` the means and variability of the WFDEI data for each variable for the period 1980-1989 (10 years), based on correction factors derived from the 10 years following 1989 (i.e. 1990-1999) before merging it with the observed time series 1990-2005. Visual checks of the final time series 1981-2005 helped ensuring there were no obvious errors or implausible changes in the behaviour of the time series.

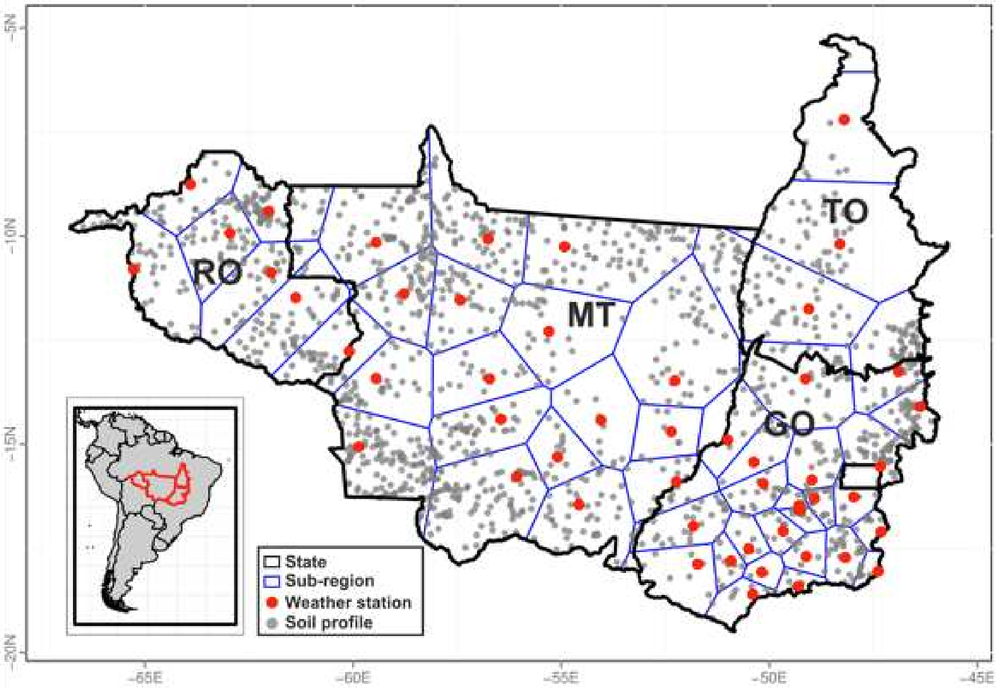

Figure 1 Upland rice study area in central Brazil. The area, also referred to as a Target Population of Environments (TPE), is formed by the states of Rondônia (RO), Mato Grosso (MT), Goiás (GO), and Tocantins (TO). The distribution of weather stations (red dots), their respective sub-regions (blue polygons), and the distribution of soil data used to construct the 7 soil types (light grey dots) are also shown.

Future climate data used here are from the CMIP5 ensemble (Taylor et al., 2012) for the all four RCPs and for the four variables needed for simulating rice growth, namely, daily precipitation, solar radiation, maximum and minimum temperatures. We restricted our analyses to the 12 GCMs that presented data for all variables and RCPs (Table S1). This was preferred to using different GCMs for each RCP, or to using fewer RCPs. Since GCM data at daily scale have inherent errors, bias correction (BC) was necessary before the future data was used into the crop model (Ramirez-Villegas et al., 2013). We bias-corrected the data using two different methods: (a) the delta method (DEL, hereafter), which applies a correction on the means, and (b) and the change factor method (CF, hereafter), which corrects both the means and the variability of the GCM output (Hawkins et al., 2013). The use of two bias correction methods allowed quantifying uncertainty from the choice of bias correction method, an often-neglected source of uncertainty in crop modelling studies [but see Koehler et al., (2013); Ramirez-Villegas and Challinor (2016)]. A combination of 12

[GCMs] x 4 [RCPs] x 2 [BC methods] for a total of 96 different climate scenarios for the period 2041-2065 were used.

Soil and management information

We used soil data from the study of Heinemann et al., (2015), who derived soil properties by applying pedotransfer functions to existing field measurements (Benedetti et al., 2008). A total of seven soil types of differing texture were finally selected for all simulations. Management information herein concerns the choice of cultivar, sowing dates, fertiliser use, and maximum rooting depth, all of which are necessary inputs to the crop model. We used a typical short-cycle cultivar named BRS Primavera (Primavera, hereafter), which is a common check cultivar in the upland rice breeding trials and thus representative of materials that breeders are currently selecting. Our choice of sowing dates is based on the Brazilian Government risk zoning for the upland rice TPE (Heinemann et al., 2015; http://www.agricultura.gov.br). We sampled the entire sowing calendar (from 1st November to 10th January) for upland rice at 10-day intervals (n=8), which allowed us to simulate typical farmer behaviour. Since the focus of this work is to quantify the seasonal behaviour of water stress and its impact, we assumed optimum nitrogen supply. Maximum rooting depth was set to 50 cm, based on field observations within the study region (Heinemann et al., 2015).

Crop model simulations

To perform spatially explicit crop simulations, we divided the study area into 51 sub-areas using the Thiessen polygons method (Heinemann et al., 2002), based on the weather stations locations (Fig. 1). For each sub-area, rice growth and development was simulated with the ORYZA2000 crop model (Bouman et al., 2001). ORYZA2000 is a process-based simulation model developed for field-scale simulation of rice productivity that simulates growth and development of rice under optimal, water-limited and nitrogen-limited situations. The model integrates modules for phenology, assimilation and biomass growth, leaf area dynamics, evapotranspiration, nitrogen dynamics, and soil water balance to produce crop simulations at a daily time step (Li et al., 2013). Here, we ran ORYZA2000 for rainfed conditions using the PADDY module, which is a one-dimensional water balance model developed to simulate a wide range of situations. For a more comprehensive description of ORYZA2000 the reader is referred to Bouman et al., (2001).

Simulation of CO_2 response was necessary under future climate. In ORYZA2000, CO_2 response acts to increase both initial and maximum assimilation rates following an exponential curve with CO_2 concentrations as the independent variable [Eq. 1-2].

$$CO2EFF = \frac{1-e^{-k1CO2*[CO_2]_f-k2CO2}}{1-e^{-k1CO2*[CO_2]_r-k2CO2}} \quad \text{[Eq. 1]}$$

$$AmaxCO2 = \frac{Amax1CO2}{Amax2CO2}\left[1-e^{\frac{-Amax3CO2*([CO_2]-Amax4CO2)}{Amax1CO2}}\right] \quad \text{[Eq. 2]}$$

where CO2EFF and AmaxCO2 are the initial and maximum rates of assimilation, respectively, $[CO_2]$ refers to the concentration of CO_2 in the atmosphere, with sub-indices indicating future (f, here defined by the mean concentration 2041-2065 for each RCP) and reference (r, the mean concentration during 1981-2005). The parameters k1CO2 (Eq. 1) and Amax3CO2 (Eq. 2) act as scaling factors to the response curve, whereas k2CO2=0.222 (Eq. 1), Amax1CO2=49.57 (Eq. 2), Amax2CO2=34.26 (Eq. 2), and Amax4CO2=60 (Eq. 2) are here assumed as prescribed constants. These response curves have been derived from observed Free-Air Carbon Enrichment (FACE) and Open Top Chamber (OTC) experiments with a limited number of rice cultivars by the ORYZA2000 development team, and have been built flexible to allow simulating other cultivars with stronger or weaker CO_2 fertilisation responses. ORYZA2000 thus simulates the expected response of assimilation, biomass and yield to increasing CO_2 concentrations (Kimball, 2016), although no reductions in stomatal conductance and transpiration are simulated.

Given that environment and drought stress pattern classifications and drought impact may vary depending on the extent of CO_2 response, we conducted simulations with two sets of parameters that represented the uncertainty envelope in simulated CO_2 response for rice. Specifically, we perturbed the scaling factors (k1CO2, Amax3CO2) in both response functions by increasing and decreasing their default values by 10 %. For k1CO2, the default value was 0.00305, whereas for Amax3CO2 the default value was 0.208. Thus, our `low stimulation` parameterisation used k1CO2=0.003355 (higher than default) and Amax3CO2=0.1872 (lower than default), whereas the `high stimulation` parameterisation used k1CO2=0.002745 (lower than default) and Amax3CO2=0.2288 (higher than default). We chose to perturb the parameters within ± 10 % since the resulting uncertainty in assimilation response to CO_2 was ≤ 20%, the typical range in observations of C3 crop response to carbon enrichment (Long et al., 2006). However, we note that this resulting uncertainty is lower than multi-model ensemble uncertainty estimates of CO_2 response (Li et al., 2015).

All simulations were conducted for cv. Primavera using parameter values from a previous study in which the model was thoroughly calibrated and evaluated for Brazilian conditions (Heinemann et al., 2015). In short, Heinemann et al., (2015) parameterised the ORYZA2000 model using data from 6 different field experiments (4 rainfed, 2 irrigated) conducted at Santo Antônio de Goiás (49º 16’ 48” S, 16º 28’ 12” W) and evaluated the model using data from 11 rainfed experiments conducted at the same location. ORYZA2000 simulated phenology in the evaluation data with less than 5 days of error, and yield with less than 350 kg ha^{-1} average error for a wide range of rainfed situations (see Heinemann et al., 2015), and is therefore deemed appropriate for this work. Here, for both historical and future climate conditions, we ran simulations for all soil (n=7) and sowing dates (n=8). Historical simulations used observed weather data from each of the 51 sub-regions (each containing one weather station), whereas future simulations were conducted for the 96 individual future climate projections (12 GCMs x 4 RCPs x 2 BC methods) and 2 CO_2 parameterisations for the period 2041-2065 at each sub-region. Thus, for each of the 51 sub-regions we conducted 7 (soils) x 8 (sowing dates) x 12 (GCMs) x 4 (RCPs) x 2 (BC methods) x 2 (CO_2 parameterisations), for a total of 10,752 future simulations per weather station region, each of 25 years. This totalled ca. 13.7 million model runs for the entire upland rice TPE.

Environment and drought stress pattern classification

We first determined environment groups within the upland rice TPE by clustering water- and radiation-limited (i.e. attainable) yield. Clustering was performed using the entire set of simulations (i.e. all planting dates, soils and sub-regions) but individually for each of the climate-by-CO_2 scenarios (i.e. 1 historical, and 96 x 2 = 192 future projections). We employed an agglomerative hierarchical clustering method with the Euclidean distance as the dissimilarity measure and the incremental sum of squares as the fusion criterion (Ward, 1963). For the historical period, the number of environmental groups (clusters) was defined by using the inertia gain [cf. Husson et al., (2011)], the within-group sum of squares and upland rice breeders knowledge of the production area. The latter was used mostly to verify that areas for each environmental group coincided with anecdotal knowledge of the region. For the future scenarios, the number of environmental groups determined in the historical period was kept. We then determined stress patterns for each environment group. To this aim, we first averaged weekly simulations of the actual-to-potential evapotranspiration ratio (PCEW), which acts in ORYZA2000 to reduce photosynthesis daily, and then clustered the phenological sequence patterns of PCEW using the same methods as for the environmental groups. Only simulated PCEW from 21-days after sowing (mid-vegetative stage) until 2 weeks before physiological maturity were used as this avoided the bias that would otherwise have been introduced by low PCEW values during crop establishment or during senescence (Heinemann et al., 2015). All clustering analyses were performed using the FactoMineR package in the R statistical framework (R Core Team, 2016).

Results

Shifted climate conditions under future climate

Projected changes in precipitation and temperature are shown in Fig. 2 for all RCPs for the period 2041-2065, relative to 1981-2005. Figures are specific to the rice growing period (November-March). Ensemble mean temperature increases are substantial, ranging from 1.5 ºC (minimum for RCP 2.6) to 3.1 (maximum for RCP 8.5). The largest temperature increases are projected to occur in the state of Mato Grosso (MT), the largest state within the TPE, whereas the least temperature increases are projected for the state of Tocantins (TO, northeast). Particularly for the northern areas of the TPE, future seasonal mean minimum and maximum temperatures for all RCPs are projected to be above 22 ºC and 33

°C (respectively), both of which are critical temperature limits for rice fertility (Peng et al., 2004; Jagadish et al., 2007).

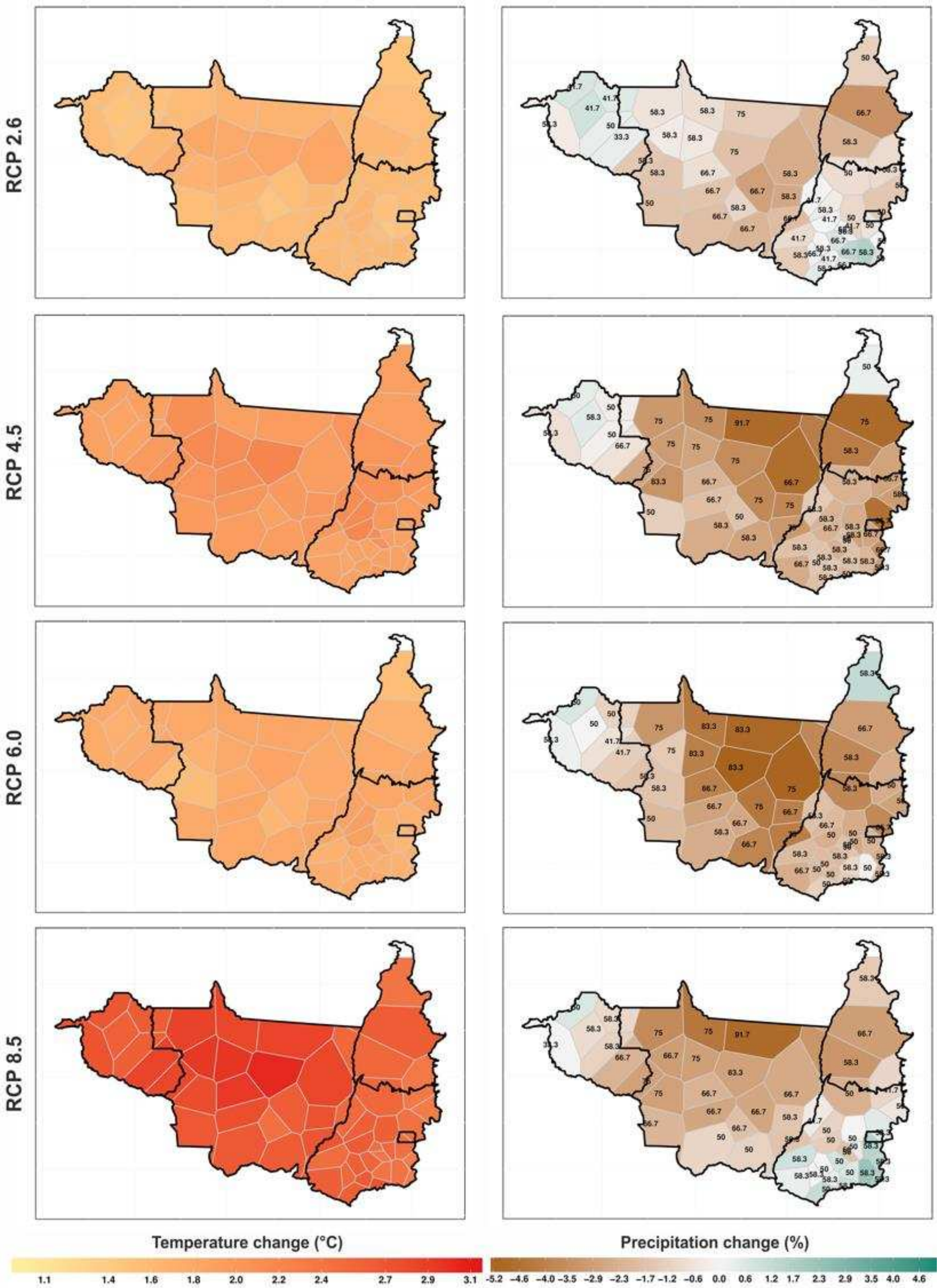

Figure 2 Projected changes in seasonal mean temperature (left) and seasonal total precipitation (right) across the upland rice growing region, for the period 2041-2065, relative to 1981-2005, for the rice

growing season (November to January). Bold numbers in the precipitation plots indicate the percentage of GCM projections that agree in the direction of change.

In contrast to temperature projections, expected precipitation changes were relatively small (mean regional changes between -2 and -5 %), geographically varied, and in some areas also highly uncertain (Fig. 2). Decreases in precipitation of up to 5 % are projected in the state of MT for all RCPs. Particularly in the northern part of MT, precipitation projections showed substantial (>70 %) agreement in the direction of the projected change. Elsewhere, however, uncertainty was large, with percentage agreement rarely reaching 60 %. For TO, climate change models indicated decreased precipitation. For Rondônia (RO), precipitation gains were projected mostly across the north-western areas. For Goiás (GO) projected precipitation changes differed across RCPs, with RCP 2.6 and RCP 8.5 showing precipitation gains in the south of the state, and RCP 4.5 and RCP 6.0 showing precipitation decreases across all the state. Goiás is also a state where GCM agreement is low (around 50 % in most weather station regions). Thus, future global emissions and climate sensitivity strongly condition future precipitation in the state.

Yield reduction and yield stability loss induced by climate change

Changes in seasonal mean temperature, total precipitation, solar radiation and CO_2 concentration interact to change historical mean yield and yield variability (Fig. 3). Current mean yield levels are in the range 500–4,500 kg ha^{-1}. The ensemble of simulations conducted here indicated that mean yield is projected to reduce across a most of the western part of the upland rice TPE, and increase across the east and south-east, with some differences between RCPs (Fig. 4A, B, Supplementary Fig. S1A, B). Mean yield changes ranged from –600 to 600 kg ha^{-1}, with the largest reductions (400 – 600 kg ha^{-1}) projected the central part of MT, followed by north-western and south-western MT (between 200 and 400 kg ha^{-1}). In these areas, model agreement, measured as the percentage of model simulations out of the 384 simulations per soil and weather station combination (i.e. 8 [sowing dates] x 12 [GCMs] x 2 [BC methods] x 2 [CO_2 parameterisations]) that were in the same direction of the median yield change, was generally above 60% (i.e. roughly two-thirds of the model simulations) for both RCPs, and, for RCP 8.5 specifically, also above 80 %. Yield gains were projected across the south-eastern part of GO, as well as across south-eastern and northern TO. Model agreement in these regions was, as in the areas of yield decline, above 60 % and sometimes above 80 % for both RCPs. Only in specific pockets within MT and RO (<10% of total area in the TPE) was model agreement close to 50% (no agreement, Fig. 4C, D, Supplementary Fig. S1C, D). In these areas, median projected yield changes were small, likely because of uncertainty in the direction of yield changes across model projections.

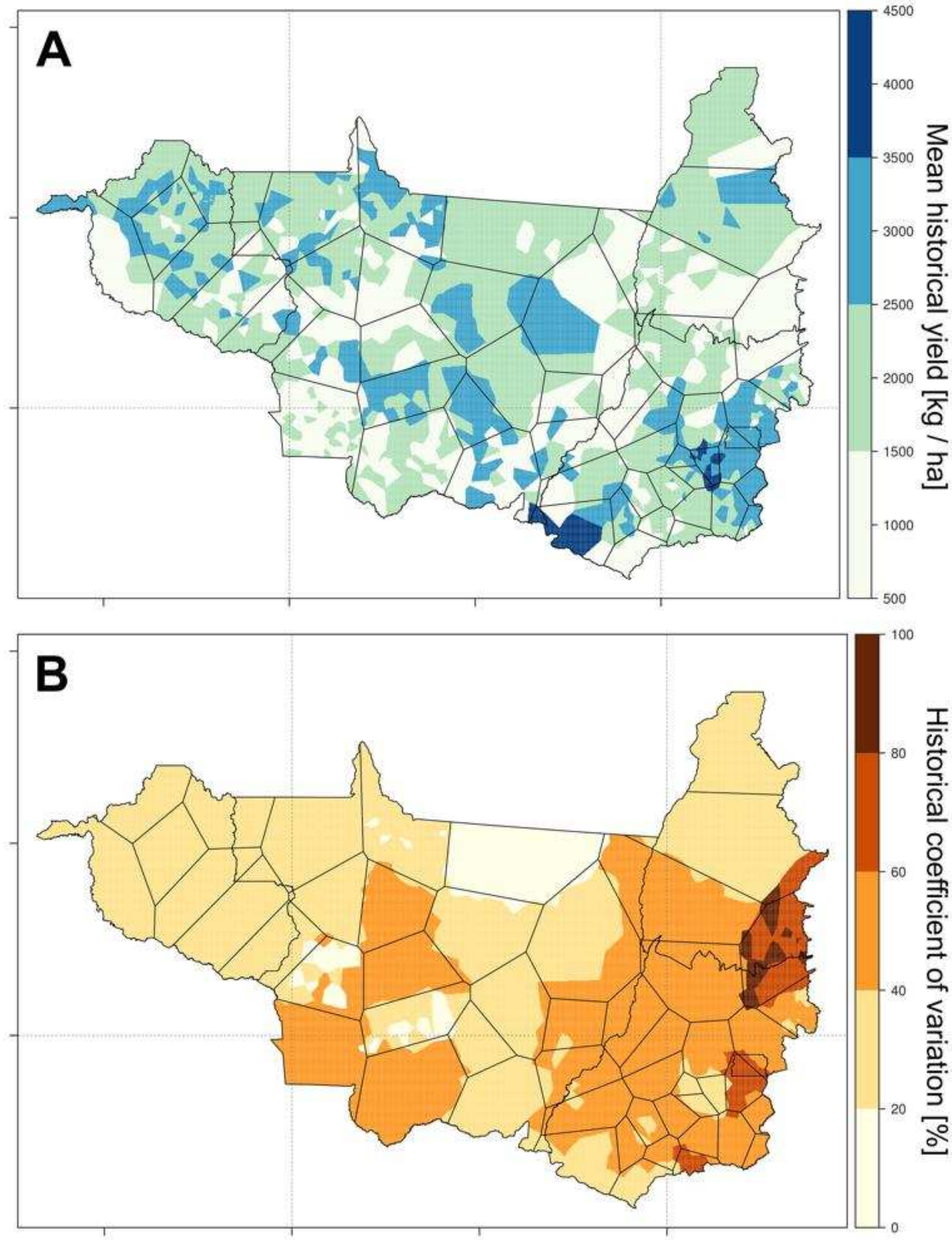

Figure 3 Historical mean yield (A) and coefficient of variation (B), as simulated with the ORYZA2000 model.

Importantly, yield stability is projected to decrease across virtually the entire TPE (Supplementary Fig. S2). Projections of yield coefficient of variation indicated increases in yield variability in all weather station and soil combinations within the TPE, except for south-eastern GO, where decreases in yield CV are projected. For central MT, eastern TO and northern RO, yield CV increases were above 10 percentage points and often above 20 percentage points, with high agreement (>80 %) in model projections.

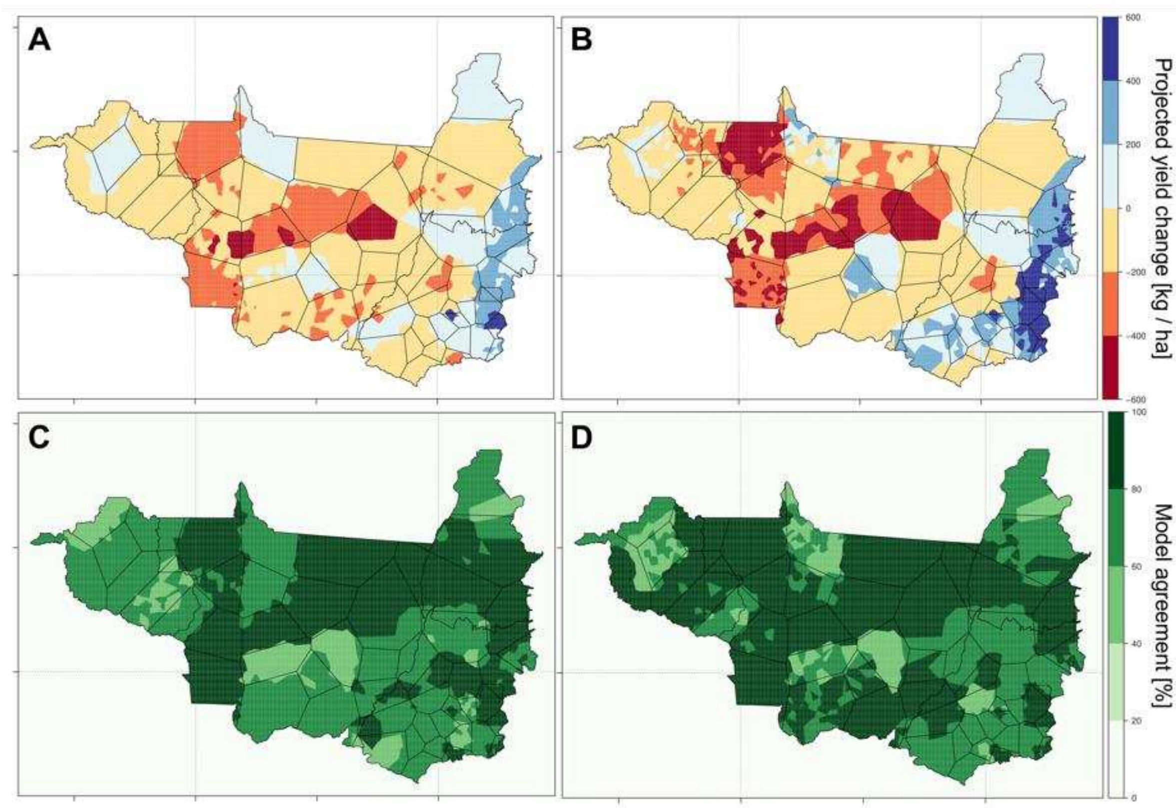

Figure 4 Median projected change in mean yield by 2050s (A, B) and model agreement (C, D) for RCP 2.6 (A, C) and RCP 8.5 (B, D) expressed as difference (in kg ha^{-1}) with respect to the historical mean yield. Model agreement (C, D) is calculated as the percentage of simulations out of the 384 future scenario simulations (8 sowing dates x 12 GCMs x 2 BC methods x 2 CO_2 parameterisations) that agree in the direction of the change with the median projected change that is shown in A and C. Results for RCP 4.5 and RCP 6.0 are in Supplementary Fig. S1.

Climate change increases the contrast between high and low yielding environments

Yield variability projections already provide some insight on the changes within growing environments in the TPE, by suggesting that climate change could enhance the contrast between the high and low yielding environments found in the historical period. In the historical period, the upland rice TPE can be divided in three environments (Fig. 5A): a highly favourable environment (HFE), a favourable environment (FE), and a least favourable environment (LFE) [also see Heinemann et al. (2015)]. These environments showed different probabilities of occurrence spatio-temporally and different median yield in the historical period: HFE is associated with a probability of 19.4 % (median yield 3,023 kg ha^{-1}), FE with 44.6 % (2,184 kg ha^{-1}) and LFE with 36.0 % (1,297 kg ha^{-1}).

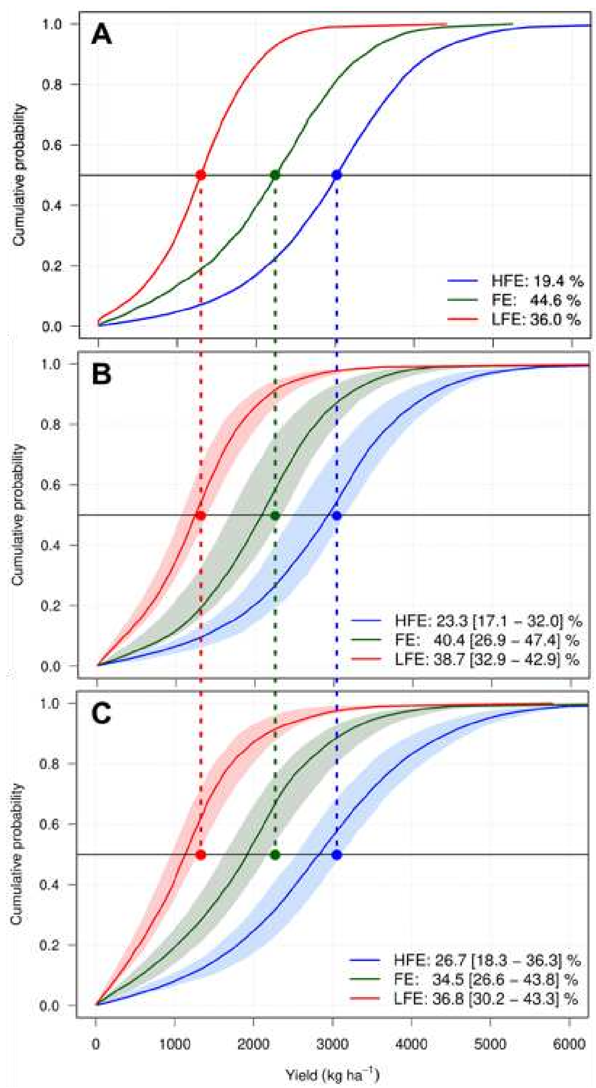

Figure 5 Current and future upland rice environment groups and their associated cumulative probability density function (CDF) and frequencies of occurrence in the historical period (A) and in 2050 for RCP 2.6 (B) and RCP 8.5 (C). Shading indicates the interquartile range of the future scenario simulations. Vertical dashed lines indicate the position of the historical median relative to the future climate CDFs for each environment group. The horizontal black line indicates the median (50^{th} percentile). Numbers on the bottom-right of panel (A) indicate the probability of occurrence of each environment group, and for panels (B, C) they indicate the median for the RCP, with the interquartile range shown in brackets. CDF plots for RCP 4.5 and RCP 6.0 are shown in Supplementary Fig. S3.

A more detailed analysis of environment group probabilities of occurrence and yield under climate change showed reduction in the median yield for the three environments, particularly under RCP 8.5 (Fig. 5B, C, Supplementary Fig. S3). However, perhaps most importantly, we found a change in the probabilities of occurrence of the three environment groups, with significant dependence on the RCP trajectory chosen. Results indicate that, under RCP 2.6, the most likely environment remained to be FE, although with a reduction in its probability of occurrence (40.4 %). For the rest of the RCPs, however, the most likely environment became LFE: 36.6 % probability for RCP 4.5, 41.2 % for RCP 6.0 and 36.8 for RCP 8.5. At the same time, HFE also became more likely for all RCPs. In all cases, these changes occurred at the expense of reducing the probability of having FE-type environments, implying increased contrast between high and low yielding upland rice environment groups.

Homogenisation of drought stress within environments

In setting up breeding priorities under climate change for upland rice, it is important to determine not only the TPE-level environment group composition, but also the within-environment-group composition of drought stress patterns. Under historical conditions, three drought stress profiles were found for LFE and FE, and two for HFE. These profiles are typified depending on the intensity of the drought experienced by the crop, as measured by the PCEW (ratio of actual to potential evapotranspiration). Figure 6 and Supplementary Fig. S4 show the yield probability distribution, whereas Figure 7 and Supplementary Fig. S5 show the seasonal variation in PCEW (top rows correspond to the historical period). For

LFE, three stress profiles exist, namely, reproductive stress (68 % probability of occurrence, SP1), reproductive-to-grain filling stress (17 %, SP2), and terminal stress (15 %, SP3). For FE, three stress profiles exist: reproductive stress (41 %, SP1), terminal stress (40 %, SP2), and severe reproductive stress (19 %, SP3); and for HFE two stress profiles were found: stress-free (69 %, SP1) and terminal stress (31 %, SP2). In general, despite differences in the timing of the stress, the intensity of drought is similar across environment groups. Stress levels, measured as percentage of unsatisfied water demand (i.e. the PCEW), were typically in the range of 40–60 %.

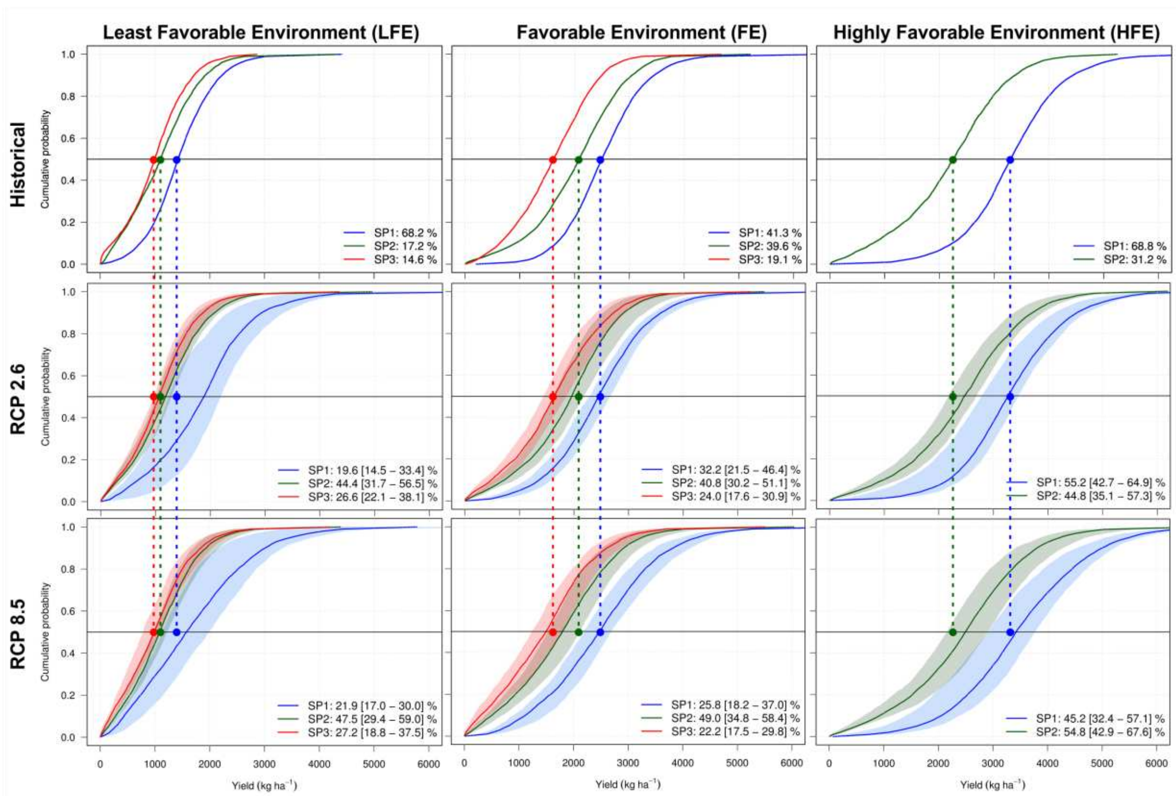

Figure 6 Cumulative probability density function (CDF) and frequencies of occurrence for upland rice stress profiles (SP) in the historical period (top row) and in 2050 for RCP 2.6 (middle row) and RCP 8.5 (bottom row) for all three environment groups: least favourable environment (LFE, left column), favourable environment (FE, middle column) and highly favourable environment (HFE, right column). Shading indicates the interquartile range of the future scenario simulations. Vertical dashed lines indicate the position of the historical median relative to the future climate CDFs for each environment group. Numbers on the bottom-right of the top row panels indicate the probability of occurrence of each profile in the environment group, and for the middle and bottom row panels they

indicate the median for the RCP, with the interquartile range shown in brackets. CDF plots for RCP 4.5 and RCP 6.0 are shown in Supplementary Fig. S4.

Under climate change, we found changes in the composition of each environment group as well as in the similarity between stress patterns across environment groups. For LFE, two key differences were observed in the future scenarios with respect to the historical period. First, there was a three- and two-fold increase in the probabilities of occurrence of SP2 (reproductive-to-grain filling stress) and SP3 (terminal stress), respectively, and a halving in the probability of SP1 (reproductive stress), indicating a shift in the timing of drought (Fig. 6, first column). Secondly, SP2 and SP3 became increasingly similar between them, but more distant to SP1 both regarding yield impact and in the seasonal pattern of PCEW (Fig. 6-7, first column).

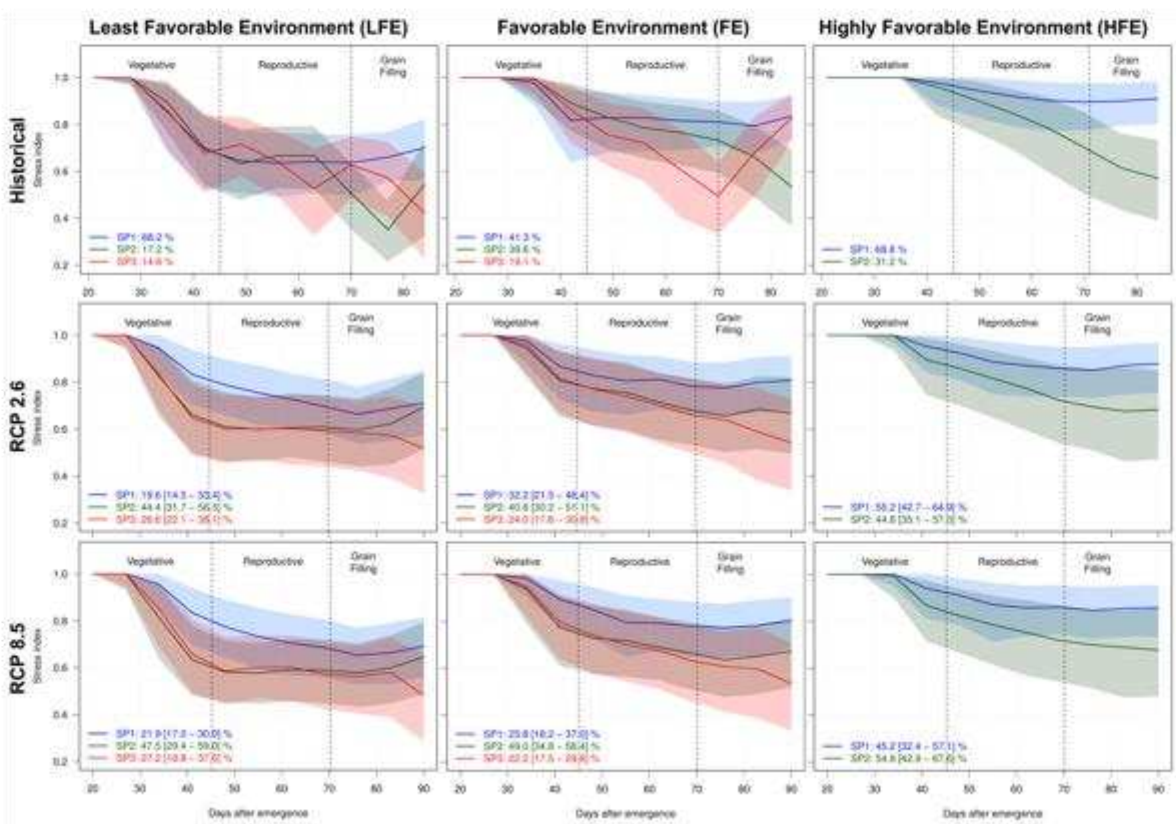

Figure 7 Current and future upland rice stress patterns and frequencies of occurrence in the historical period (top row) and in 2050 for RCP 2.6 (middle row) and RCP 8.5 (bottom row) for all three environment groups: least favourable environment (LFE, left column), favourable environment (FE, middle column) and highly favourable environment (HFE, right column). Shading reflects the

interquartile range of the spatio-temporal variation of each stress profile. Numbers on the bottom-right of the top row panels indicate the probability of occurrence of each profile in the environment group, and for the middle and bottom row panels they indicate the median for the RCP, with the interquartile range shown in brackets. Profile plots for RCP 4.5 and RCP 6.0 are shown in Supplementary Fig. S5.

For FE, a similar behaviour was observed, whereby SP2 (terminal stress) and SP3 (severe reproductive stress) both became more likely and similar. In this case, the probability of occurrence of SP2 increased by roughly 20 %, whereas that of SP3 increased by roughly 15 % (median across the crop-climate ensemble of simulations). In both LFE and FE, SP1 (reproductive stress) either increases or maintains its yield levels under future climate scenarios, as a result of reduced stress levels at the beginning of the reproductive period; however, it becomes much less frequent than under historical conditions (ca. 70 % reduction for LFE and 40 % reduction for FE for all RCPs). For HFE, we found a systematic reduction in the probability of occurrence of stress-free conditions (SP1, Fig. 6-7, right column) to the extent that it becomes almost as likely as the terminal stress profile (SP2). At the same time, SP2 becomes less severe. The latter resulted in increased yield for this stress profile.

At the environment group-level for LFE and FE, therefore, while in the historical period there are three distinct drought stress profiles, results suggest that seasonal drought conditions are likely to become more uniform within these environments under climate change.

Shifted growing conditions and breeding priorities for upland rice

At the TPE level, the above results imply a substantial shift in growing conditions for upland rice, and thus of breeding priorities. In the historical period, there was a general trend for reproductive (52 % overall probability of occurrence) and terminal (29 %) stress to occur separately across the entire upland rice TPE, with only 13 % of probability of occurrence of stress-free conditions and 6 % probability for the crop to jointly experiencing reproductive and grain-filling stress during the season. Under future climate, the probability of occurrence of the joint reproductive and grain-filling stress (i.e. reproductive-to-grain-filling stress) ranged between 25–28 % (depending on the RCP chosen), thus becoming the most important stress after terminal stress (29–40 % overall probability). The probability of reproductive stress reduced to less than half (to 17–21 %, depending on the RCP), whereas the probability of stress-free conditions remained the lowest (12-13 %).

Discussion

Implications of projected changes in mean yield and yield stability

For upland rice across the savannah region in Brazil, reductions in productivity are expected across most of the TPE, except for the easternmost area (see Fig. 4 and Supplementary Fig. S1). Expected reductions in rice crop yield in these areas have been reported by global studies. A previous global study where gridded simulations of multiple crop models were used reported rice yield declines between 5–10 % by 2100 (Rosenzweig et al., 2014). Another study based on statistical models also reported expected yield losses in the range 3–7 % by 2030 (Lobell et al., 2008). On the contrary, Muller et al. (2015), project little yield impact in Central Brazil. None of these studies, however, reported upland and irrigated rice production systems separately for Brazil, or for other countries or regions, none include or use the ORYZA2000 crop model, and the Lobell et al. (2008) study did not include CO_2 response. Moreover, it is noteworthy that the study of Rosenzweig et al. (2014) reports large uncertainty as a result of the crop model used, with models that consider nitrogen stress showing large yield decreases [also see Webber et al. (2015)]. An earlier global study where the Decision Support System for Agrotechnology Transfer (DSSAT) model was used (Nelson et al., 2010) to perform gridded simulations at a relatively high resolution reported yield decreases between 5–25 % by 2050 in the Brazilian savannah region, though that study assumed cropping systems in the savannah are irrigated. Despite methodological differences, there is some agreement between existing and our estimates of climate change impacts on rice crop yield for the Brazilian savannah region. In addition, the substantial agreement across individual model projections in our analysis suggests our results are robust.

Increase in yield variability was also projected to occur from climate change (Supplementary Fig. S2). Reduction in yield stability has been reported elsewhere as a major limitation for cropping systems under climate change (Challinor et al., 2014; Porter et al., 2014). To the knowledge of the authors, however, studies specifically addressing climate change impacts on yield variability in rice for Latin America or Brazil, or even globally are scarce or do not exist.

The implications of high upland rice yield variability and lower mean yield are substantial for both farmers, the national economy, as well as for the global food system (GFS UK, 2015). High yield variability and lower mean yield can cause income instability and food insecurity in a region where farmers have limited access to resources and low technology adoption levels (Strauss, 1991; Marcolan et al., 2008). High yield variability under climate change, in particular, will also increase the already high risk of cultivating upland rice, which will likely accelerate the current trend towards reducing upland rice cropped areas (Pinheiro et al., 2006; Marcolan et al., 2008; Ferreira, 2010). Urban centres in Central Brazil can also be impacted due to instability in the flow of produce to the markets and in market prices (Nelson et al., 2010; Chen et al., 2012). Deeper investigation of these impacts is warranted in future studies.

The area cultivated with upland rice in Central Brazil has been in continuous decline since the early 2000s (Marcolan et al., 2008; Ferreira, 2010). Farmers normally prefer soybean and maize, which are less sensitive to drought stress than rice and count with well-established value chains in the region. The perspective of a less favourable climate only makes it more difficult for upland rice to reverse the trend of declining areas. On the other hand, upland rice is a good option of agronomic rotation with soybean and, in the absence of drought stress, allows similar profitability. Therefore, improving the drought tolerance of upland rice may be the only possibility of maintaining upland rice as a significant component of agricultural systems in Central Brazil. The biological limit of adaptation of this species to drought stress is still unknown.

Projected changes in crop yield and loss in yield stability will thus bring numerous challenges for upland rice cropping in Brazil, highlighting the need for adaptation. Adaptation strategies for cropping systems are numerous, and range from short-term coping strategies through to longer-term transformations (Rippke et al., 2016). Kim et al. (2013), for temperate rice, found that cultivar and planting date adaptation can counteract negative climate change impacts. For Central Brazil, Heinemann et al. (2015) suggest early planting dates can increase yield. Moreover, efficient breeding and delivery systems are needed under future climate so as to deliver novel varieties that are adapted to and respond well under the specific drought conditions found here (Silva et al., 2009; Breseghello et al., 2011; Challinor et al., 2016).

Breeding implications of changes in environment groups and stress profiles

The current upland rice breeding strategy in Embrapa is composed of two separate breeding programs: (i) the conventional breeding program, focusing on increasing grain yield, stability and adaptability to the undivided TPE; and (ii) a drought tolerance breeding program created in 2004. The conventional breeding program uses two main breeding methods: modified pedigree and recurrent selection. In both methods, the first three generations are conducted in a single location under good environmental conditions (Santo Antonio de Goiás, GO). The fourth generation genotypes ($F_{2:4}$ or $S_{0:2}$) are tested in multi-location trials of at least 5 sites. This implies in exposing the progenies to different local weather conditions, including drought stress. The best progenies, based on the results of these trials' joint statistical analysis, are selected for single plant selection (modified pedigree) or recombination (recurrent selection). With time, the upland rice breeding program is improving its genetic stability while exploiting the GxE interactions through seeking wide adaptability. The same philosophy is applied from generation F_6 to F_{10} of the pedigree method, as the homozygosity gets higher, the number of lines declines, tested in a growing number of sites. The network must represent the TPE, including the stresses that occur routinely (Heinemann et al., 2015). With the modified pedigree methodology and a very broad network represented by the multi-location trials (around 40 trials with F_{10} elite lines in the upland rice production area in Brazil), it is possible to evaluate and select lines with high stability in a wide range of environments. This strategy aims to select high yielding elite lines with the capacity to respond favourably to changes in the environment (i.e. with wide adaptation) and at the same time to have a highly predictable performance in different environmental conditions (Colombari Filho et al., 2013). Currently, the modified pedigree method achieves a yield gain of 2.66 % per cycle (Martinez et al., 2014), but it has a tendency to reduce drought tolerance (Pinheiro et al., 2006; Silveira et al., 2015).

A drought tolerance breeding program was created in 2004. In such program, the strategy is to select genotypes with high yield potential under optimal conditions that are able to maintain good productivity under drought. This program is conducted in the drought phenotyping site of Porangatu, state of Goiás, Brazil (Martinez et al., 2014). The program started in 2004 with the identification of drought tolerant donors and the cross of those with lines or varieties with a minimum level of drought tolerance. Nowadays, the progenies are in $F_{2:4}$ generations, and the first releases are expected to occur within the next 10 years. All generations are subjected to SP1 and SP2 drought stress patterns.

Under current climate, we found that unstressed conditions occur roughly 13 % of the time, whereas under future climate we find that this probability of occurrence either remains unchanged or reduces for all RCPs (12 % in RCP 8.5 to 13 % in RCP 2.6). The existing breeding strategy results in high-yielding cultivars with a medium tolerance under stressful conditions, and therefore still leave risks to farmers that adopt such varieties. It enhances wide adaptation and has led to improved genotypic stability, but selection weights equally all stresses, and there is no consideration of environmental co-variables (e.g. weather, soil water contents) in the statistical analysis. Due to the diversity of stresses found, a revised breeding strategy is suggested for upland rice in Brazil both under current and future climate.

The results shown in this work will improve the breeding program to deal with climate changes aiming to deliver cultivars adapted to the new TPE. Foremost, the early evaluation should be done in sites of the multi-location network chosen based on our clustering analysis of historical and future yield (also see Heinemann et al. 2015), in which the upland area is classified in HFE, FE and LFE. Combining that with the weather data evaluation from each site, will make a detailed weighted selection possible. A better process of selection will help breeders to select the desired progenies, lines, cultivars adapted to the future. Another improvement in the breeding program could be the modification in the drought stress protocol normally used in drought phenotyping site of Porangatu to apply the same type of stress predicted for 2050.

Under current climate, a differentiated strategy that isolates drought stress profiles is recommended, since this would allow to control for GxE interactions (Heinemann et al., 2015, 2016). The best strategy under current conditions would be: for HFE, specific adaptation to stress-free conditions (i.e. selection for yield potential); for FE, wide adaptation to drought, or selection for yield under drought, weighted by the probability of different drought profile conditions; and for LFE, specific adaptation to reproductive drought stress, or a weighted selection strategy as in FE.

Results presented here indicated that the selection strategy can be adjusted. For HFE, a weighted selection strategy whereby genotypes are tested both under stress-free and terminal stress conditions may be needed, since these two stress profiles each have ~50 % probability of occurrence. For FE, selection should aim at testing under reproductive (probability of occurrence 62–70 %) and terminal stress (ca. 30–38 %) and then weighting genotype performance according to these probabilities. For LFE, breeders could also adopt a weighted selection strategy, but trials should be conducted for response to reproductive stress (20–25 % probability) and for the joint occurrence of reproductive and terminal stress (75–80 %). As demonstrated by previous studies (though on a different cereal crop), weighted selection can help isolating the environmental components of observed drought impacts from the genotypic component, thus allowing for quicker breeding gains under stressful environments (Chenu et al., 2011). Stress levels were similar across environments, with the percentage of unsatisfied water demand being typically in the range of 40–60 %.

It is noteworthy that we have focused only on one genotype (Primavera), whereas environment groups and stress patterns may depend on the type of cultivars grown by the farmers (i.e. GxE interaction). While Primavera is currently used as a check cultivar in the conventional breeding program and is hence representative of genotypes released to the public, clearly, as a result of the breeding process at Embrapa, changes have occurred and will continue to occur in the characteristics of the germplasm released and grown by farmers in the last 30-40 years, leading to changes in the environments and stress patterns. In particular, during 1980s and 1990s a major shift from releasing landraces (e.g. cv. Douradão) to releasing modern cultivars (e.g. cv. Primavera) occurred in the breeding program, whereas in late 1990s wide hybridizations were carried out, introducing indica genes into a predominant japonica background with significant increase of yield potential especially under highly favorable conditions (Martinez et al., 2014). These activities have resulted in cultivars with longer growing cycle, and lower root length density, but generally less drought tolerance (Pinheiro et al., 2006; Breseghello et al., 2011). In fact, cv. Primavera has been reported to be more drought sensitive than its predecessors (Pinheiro et al., 2006; Heinemann et al., 2011; Silveira et al., 2015). Further changes will likely continue to occur as upland rice breeding continues in Brazil, especially as genotypes developed by the drought-tolerant breeding program created in 2004 are released and adopted. Therefore, while we argue that the current production situation in central Brazil is well represented by cv. Primavera, continuous updating of environmental groups and stress patterns will be required in the next decades. Future studies that include a wider variety of varieties, with different levels of drought tolerance and different growing cycles can help in analysing the genotypic dependencies of the environmental and stress types identified here. These will further help the breeding program in designing selection trials and defining the selection strategy.

The costs of conducting breeding and selection trials for a wide range of drought conditions to be able to weight genotype selection across the entire TPE could, however, constrain its applicability. This is particularly true for publicly funded breeding programs. In such situations, a viable option for each environment type or even for the undivided TPE would be to develop genotypes with wide adaptation to drought. Drought tolerance in upland rice can be achieved by selecting for high grain yield in stress environments, or by using marker-assisted selection on less complex traits (Bernier et al., 2008). An example of this strategy comes from the upland rice in Brazil. The last variety released, BRS Esmeralda, is the first variety from Embrapa's breeding program with drought tolerance. BRS Esmeralda was directly selected under a variety of weather conditions, including drought stress. Its high stability is shown by Colombari (Colombari Filho et al., 2013). Additionally, success in other publicly-funded breeding programs such as those of maize in Africa and common beans in Central America and Africa provides evidence of the potential for breeding drought-tolerant materials for adaptation to climate variability and change (Beebe et al., 2011; Cairns et al., 2013).

Identifying the key physio-morphological traits that confer drought tolerance is also critical for the efficient selection of genetic material in breeding trials. Although more research will be required for a complete understanding of which traits are desirable for a specific environment and drought pattern, existing research suggests that improved root characteristics, shorter cycles (i.e. drought escape), osmotic adjustment, as well as quicker and larger assimilate translocation from stems to panicles would likely be desirable traits to improve drought responses (Fukai & Cooper, 1995; Dingkuhn et al., 2015).

Uncertainty and decision making in breeding programs

Model projections of climate change impacts can help guide decisions on adaptation (Ranger & Garbett-Shiels, 2011), and, in this case, help establishing clear targets for the upland rice breeding program in Brazil. Large uncertainty in model projections, however, can preclude these decisions (Vermeulen et al., 2013). Hence, further to what has been discussed above on the representativeness of cv. Primavera, limitations arise in our analysis, most notably, because future climate projections are inherently uncertain, and because, as in any model-based analysis, the crop model used does not capture crop response perfectly (e.g. limitations in simulating CO_2 response, heat stress, or site-specific farmer management). Here, we accounted for a range of uncertainty sources, namely, emissions pathways (RCPs), simulated climate sensitivity (using multiple GCMs), bias correction methods, and rice crop response to enhanced CO_2 concentrations. Importantly, our study is one of the first crop simulation studies that explicitly quantifies the response of the crop CO_2 concentrations and of different bias correction methods [also see Ramirez-Villegas and Challinor (2016)]. Agreement across model projections of yield and yield stability was found throughout most of the upland rice TPE (see Fig. 4C, D). Also, despite variability across crop-climate model projections for environment-specific yield distributions and drought profiles, differences between the medians were substantial, and overlaps between uncertainty bounds were small, indicating our results are robust towards modelling uncertainties (Fig. 5-6). Recent studies have also shown that predictability can be achieved for certain crop processes (Challinor et al., 2016), at long timescales (Rippke et al., 2016), or for certain model outcomes [e.g. adaptation vs. no adaptation, Ramirez-Villegas and Challinor (2016); Porter et al. (2014)]. The latter studies are particularly relevant to our analysis, since they specifically emphasise that while uncertainty is prevalent in model projections of crop yield, there is robustness as to the direction and impact of adaptation strategies. Nevertheless, we argue that, despite the uncertainties and limitations, the benefits of breeding drought-tolerant upland rice will be substantial during the 21st century. If the current level of drought tolerance is not improved, upland rice may be replaced by other, more drought tolerant, cash crops.

Conclusions

In this study, we assessed changes in the prevalence and intensity of drought stress due to climate change for upland rice in central Brazil, with a view on the implications that these changes have on the current breeding strategy for upland rice in Brazil. In the face of climate change-induced decreases in mean yield and losses in yield stability, our results suggest that the current strategy of the breeding program can be improved to minimize the impact of drought stress on new cultivars.

Under climate change scenarios, based on our results and on those of a previous study that focused on historical climates (Heinemann et al., 2015), we recommend a weighted selection strategy for all the environment groups in the TPE. Although only economic ex-ante and/or ex-post technology impact assessments will allow determining whether it is economically feasible to change the current breeding strategy to be modified, it is necessary to consider future projected climatic conditions in the breeding pipeline. Improving the adaptive traits of germplasm to respond better under drought stress will ultimately facilitate upland rice systems adaptation to climate change, improving food security and farmer livelihoods.

There are a variety of future research avenues that could be pursued based on the results presented here. Although the ORYZA2000 model already simulates heat stress, future studies could use available and/or new experimental data to evaluate heat stress response in the model, and then use it to quantify the occurrence of heat-stressed environments. Heat has been reported as being of major importance for rice globally (Teixeira et al., 2013; van Oort et al., 2015), and specifically also for the southern part of the upland rice TPE studied here (Teixeira et al., 2013). Future work could also involve the validation of the growing environments reported here with field trials, and the determination of potential parents and physio-morphological traits that are key for drought tolerance. Finally, clearly, the drought stress profiles and yield environments that we find can change as new cultivars become available and adopted, and future analyses will be required to determine if the breeding strategy is indeed on track, and yield progress is being made under the different drought types that exist in the target region.

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Figure captions

Figure 1 Upland rice study area in central Brazil. The area, also referred to as a Target Population of Environments (TPE), is formed by the states of Rondônia (RO), Mato Grosso (MT), Goiás (GO), and Tocantins (TO). The distribution of weather stations (red dots), their respective sub-regions (blue polygons), and the distribution of soil data used to construct the soil scenarios (light grey dots) are also shown.

Figure 2 Projected changes in seasonal mean temperature (left) and seasonal total precipitation (right) across the upland rice growing region, for the period 2041-2065, relative to 1981-2005, for the rice growing season (November to January). Bold numbers in the precipitation plots indicate the percentage of GCM projections that agree in the direction of change.

Figure 3 Historical mean yield (A) and coefficient of variation (B), as simulated with the ORYZA2000 model.

Figure 4 Median projected change in mean yield by 2050s (A, B) and model agreement (C, D) for RCP 2.6 (A, C) and RCP 8.5 (B, D) expressed as difference (in kg ha^{-1}) with respect to the historical mean yield. Model agreement (C, D) is calculated as the percentage of simulations out of the 384 future scenario simulations (8 sowing dates x 12 GCMs x 2 BC methods x 2 CO_2 parameterisations) that agree in the direction of the change with the median projected change that is shown in A and C. Results for RCP 4.5 and RCP 6.0 are in Supplementary Fig. S1.

Figure 5 Current and future upland rice environment groups and their associated cumulative probability density function (CDF) and frequencies of occurrence in the historical period (A) and in 2050 for RCP 2.6 (B) and RCP 8.5 (C). Shading indicates the interquartile range of the future scenario simulations. Vertical dashed lines indicate the position of the historical median relative to the future climate CDFs for each environment group. The horizontal black line indicates the median (50^{th} percentile). Numbers on the bottom-right of panel (A) indicate the probability of occurrence of each environment group, and for panels (B, C) they indicate the median for the RCP, with the interquartile range shown in brackets. CDF plots for RCP 4.5 and RCP 6.0 are shown in Supplementary Fig. S3.

Figure 6 Cumulative probability density function (CDF) and frequencies of occurrence for upland rice stress profiles (SP) in the historical period (top row) and in 2050 for RCP 2.6 (middle row) and RCP 8.5 (bottom row) for all three environment groups: least favourable environment (LFE, left column), favourable environment (FE, middle column) and highly favourable environment (HFE, right column). Shading indicates the interquartile range of the future scenario simulations. Vertical dashed lines indicate the position of the historical median relative to the future climate CDFs for each environment group. Numbers on the bottom-right of the top row panels indicate the probability of occurrence of each profile in the environment group, and for the middle and bottom row panels they indicate the median for the RCP, with the interquartile range shown in brackets. CDF plots for RCP 4.5 and RCP 6.0 are shown in Supplementary Fig. S4.

Figure 7 Current and future upland rice stress patterns and frequencies of occurrence in the historical period (top row) and in 2050 for RCP 2.6 (middle row) and RCP 8.5 (bottom row) for all three environment groups: least favourable environment (LFE, left column), favourable environment (FE, middle column) and highly favourable environment (HFE, right column). Shading reflects the interquartile range of the spatio-temporal variation of each stress profile. Numbers on the bottom-right of the top row panels indicate the probability of occurrence of each profile in the environment group, and for the middle and bottom row panels they indicate the median for the RCP, with the interquartile range shown in brackets. Profile plots for RCP 4.5 and RCP 6.0 are shown in Supplementary Fig. S5.