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RESEARCH PAPER

Variation and impact of drought-stress patterns across upland rice target population of environments in Brazil

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Abstract

The upland rice (UR) cropped area in Brazil has decreased in the last decade. Importantly, a portion of this decrease can be attributed to the current UR breeding programme strategy, according to which direct grain yield selection is targeted primarily to the most favourable areas. New strategies for more-efficient crop breeding under non-optimal conditions are needed for Brazil's UR regions. Such strategies should include a classification of spatio-temporal yield variations in environmental groups, as well as a determination of prevalent drought types and their characteristics (duration, intensity, phenological timing, and physiological effects) within those environmental groups. This study used a process-based crop model to support the Brazilian UR breeding programme in their efforts to adopt a new strategy that accounts for the varying range of environments where UR is currently cultivated. Crop simulations based on a commonly grown cultivar (BRS Primavera) and statistical analyses of simulated yield suggested that the target population of environments can be divided into three groups of environments: a highly favorable environment (HFE, 19% of area), a favorable environment (FE, 44%), and least favourable environment (LFE, 37%). Stress-free conditions dominated the HFE group (69% likelihood) and reproductive stress dominated the LFE group (68% likelihood), whereas reproductive and terminal drought stress were found to be almost equally likely to occur in the FE group. For the best and worst environments, we propose specific adaptation focused on the representative stress, while for the FE, wide adaptation to drought is suggested. 'Weighted selection' is also a possible strategy for the FE and LFE environment groups.

Keywords: Breeding, environment classification, modelling, *Oryza sativa*, water deficit.

Introduction

Upland rice (*Oryza sativa* L.) (UR), also known as aerobic rice, plays an important social and economic role in the savannah region of central Brazil. In this region, corresponding to the target population of environments (TPE), UR constitutes a low-cost alternative to the irrigated intensive rice cropping systems of southern Brazil. In addition, Brazilian UR is a key part of the diets of central and northern Brazil, as well as an important source of income for smallholders across the Brazilian savannah.

In spite of the socio-economic and dietary importance of the UR system across many parts of Brazil, the cropped area has decreased by 57% in the last decade

Abbreviations: DAE, d after emergence; FE, favourable environment; HFE, highly favourable environment; LAI, leaf area index; LFE, least favourable environment; MAE, mean absolute error; MET, multi-environment trial; PCEW, weekly mean ratios of actual transpiration to potential transpiration; RMSE, root mean squared error; SD, standard deviation; TPE, target population of environments; UR, upland rice.

(IBGE: http://www.sidra.ibge.gov.br/bda/; Pinheiro *et al.*, 2006; Breseghello *et al.*, 2011). Decreases in the UR cropping area in Brazil have a variety of causes, including commercialization of UR grain type, strong competition from irrigated rice from southern Brazil in terms of both price and quality, substitution by less-risky and higher-revenue crops, and climatic variability (Ferreira, 2010). Importantly, however, a portion of this decrease can be attributed to the current UR breeding programme strategy (adopted since the 1980s), according to which direct grain yield selection is targeted primarily to the most favourable (i.e. stress-free) areas (Embrapa, 1981).

Direct grain yield selection in favourable areas is a cost-effective and efficient strategy, with mean yearly genetic gains in Brazil of 45.0 kg ha^{-1} (1.44%) from 2002 to 2009 (Breseghello *et al.*, 2011). However, such a selection strategy is often associated with a high risk of developing genotypes specialized for highly suitable areas, and hence can be inefficient when the climatic conditions differ significantly from optimal (Tardieu and Hammer, 2012). Several studies show that this is probably the rule rather than the exception (Chapman *et al.*, 2003; Chenu *et al.*, 2009). More specifically, in a TPE, genotype×environment interactions can hinder plant breeding progress for: (i) broad adaptation across the TPE; and (ii) adaptation to specific types of environments within the TPE (Löffler *et al.*, 2005; Dreccer *et al.*, 2007; Chenu *et al.*, 2011). In central Brazil, more specifically, newly developed UR cultivars often outyield traditional ones under optimal situations, but are outperformed under drought-stress situations (Heinemann *et al.*, 2011).

Developing new strategies for more-efficient crop breeding under non-optimal conditions is needed for Brazil's UR region, particularly due to the large drought-induced yield variations found within the region (Heinemann and Sentelhas, 2011). Such strategies should include a classification of spatio-temporal yield variations in environment groups, as well as a determination of prevalent drought types and their characteristics (duration, intensity, phenological timing, and physiological effects) within those environment groups (Heinemann *et al.*, 2008). Based on such information, a significant component of the genotype×environment interactions for grain yield may be explained and predicted, hence enabling the optimization of environmental screening and breeding itineraries (e.g. Chapman *et al.*, 2000*a*, *b*, *c*; Löffler *et al.*, 2005; Chenu, 2014). Due to the extent of the UR production region, however, the identification and characterization of environments is generally limited by the lack of multi-location agronomic experiments. To overcome this, crop model simulations have proved useful for many crops (Chapman *et al.*, 2000*c*; Heinemann *et al.*, 2008; Chenu *et al.*, 2011, 2013; Chauhan *et al.*, 2013). A characterization of environments that integrates weather, soil, crop, and management factors using crop simulation models to identify environments and characterize their stress patterns (in frequency and intensity) is useful in breeding strategies that target the development of stress-resilient, high-yielding germplasm (Löffler *et al.*, 2005; Chapman 2008; Chauhan *et al.*, 2013).

This study aimed to help support the Brazilian UR breeding programme to adopt a new breeding strategy that better fits the range of environments that exist in central Brazil. The specific objectives were to: (i) classify environment groups in the central Brazil UR production region based on achievable yields and their variability across years; and (ii) for each environment group, identify major drought-stress patterns, their frequency of occurrence, and the impact on crop yield.

Materials and methods

Observed data

Study region, weather, and soil data The study region, corresponding to the TPE, located in central Brazil between 7 and 20°S and 65 and 45°W (Fig. 1). The region is responsible for growing 90% of UR in Brazil (803 529 t in 2012; IBGE: http://www.sidra.ibge.gov.br/bda/). The climate is tropical, with a characteristic wet and dry period, and corresponds to the Köppen climate classification category 'Aw' (i.e. tropical wet and dry or savannah climate), with mean annual precipitation of 1000–1500 mm (mono-modal summer rains) and elevation ranging from 85 to 1190 m above sea level. Fifty-one sites with available daily weather data, where UR is currently grown and farmers have shown interest in growing this crop, were selected within the TPE for further analysis.

The historical daily weather data (i.e. precipitation and maximum and minimum temperatures) were downloaded from the INMET website (Brazilian Meteorological Institute: http://www.inmet.gov.br) and thoroughly checked for gaps and inconsistencies following D'Afonseca *et al.* (2012, 2013*a*, *b*) (Supplementary Table S1). Daily global solar radiation for all weather stations, except one station (ID=24, Supplementary Table S1) was estimated following the method of Richardson and Wright (1984). In order to develop spatially explicit crop simulations, the area of influence of each weather station within the TPE was first determined by Thiessen (or Dirichlet) polygons (Heinemann *et al.*, 2002). This method was chosen due to the limited range of altitudes across the TPE (see Supplementary Table S1 for altitude of weather stations). The seven most prevalent soil types in the production region, based on the American soil classification (texture) system, were then selected from a Brazilian soil database (Benedetti *et al.*, 2008; available at http://www.esalq.usp.br/gerd/BrazilSoilDB_08VI05.xls; see Fig. 1 for soil type distribution). Soil hydrological properties were calculated for use as crop model input for the seven soil types based on the equations listed in Supplementary Table S2 at *JXB* online (see values in Supplementary Table S3 at *JXB* online). Based on our field knowledge of UR systems, for each soil type we derived permanent wilting-point values by reducing the total soil water (difference between field capacity and residual soil water, each computed from equations in Supplementary Table S2) by an empirical factor. For clay soils, we used a factor of 0.56, whereas for the other soil types, we used a factor of 0.44 (J.C. Medeiros, personal communication) (Supplementary Table S3).

Upland rice trial data Two sets of experiments were used. The first set was used for model calibration and consisted of six field trials, whereas the second set was used for model evaluation. Model calibration experiments were performed at the Embrapa Rice and Beans experimental station located at Santo Antônio de Goiás, GO, Brazil (latitude 16.47, longitude 49.28; ID=24 in Supplementary Table S1) during the wet season of 2008/2009 (planting dates 08/11 and 20/12), 2009/ 2010 (planting date 18/11), 2010/ 2011 (planting date 06/12), and 2012/ 2013 (planting dates 20/10 and 11/09). In these experiments, chemical fertilizers were applied in the soil at sowing, at intermediate to high rates compared with typical farmer management practices. Four out of the six sowing dates, hereafter referred to as PHE, were used for phenology calibration (these dates were the 08/11 and 20/12 planting dates in the 2008/ 2009 season, the 06/12 planting date in the 2010/ 2011 season, and the 20/10 planting date in the 2012/ 2013 season). For the PHE experiments, only the measurements of

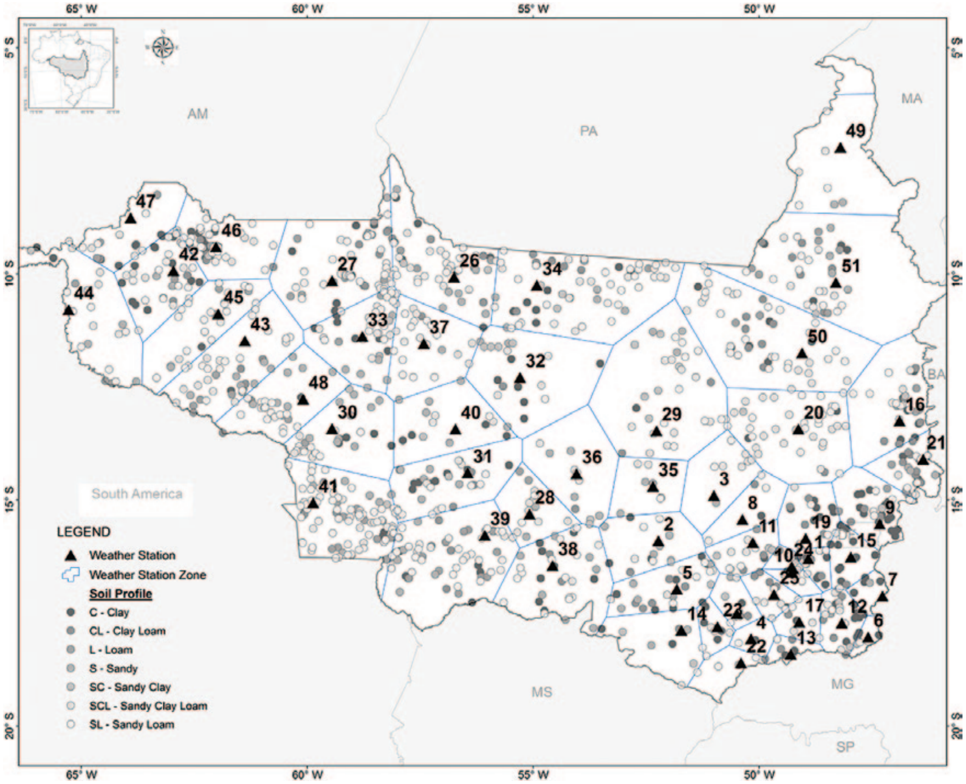

Fig. 1. UR TPE in central Brazil and the geographical distribution of weather station locations (triangles), weather stations coverage area (polygons), and soil type (dots). Numbers represent weather station identifiers described in Supplementary Table S1 at *JXB* online.

emergence dates, panicle initiation, flowering, and physiological maturity were used. For growth parameter calibration, all six experiments were used (hereafter indicated as GRO trials). GRO trials consisted of three rainfed experiments (planted on 08/11 and 20/12 in the 2008/ 2009 season and on 18/11 in the 2009/ 2010 season) and three irrigated experiments (planted on 06/12 in the 2010/ 2011 season and on 20/10 and 11/09 in the 2012/ 2013 season). In these experiments, measurements were taken of leaf area index (LAI), and leaf, stem, and panicle biomass. Using both well-watered and water-stressed experiments allowed calibration of the model under both potential and stressed conditions. High model skill in both conditions is critical for the reliability of the results presented here. In particular, we observed moderate water-stress levels in the rainfed experiment of 2009/ 2010, primarily during the reproductive stage.

The second set of experiments, referred to as EVAL, consisted of 11 rainfed experiments conducted during the period 2004–2011 by the UR breeding programme, with the aim of testing the value of candidate lines for potential varietal release. All trials were conducted at Santo Antônio de Goiás, GO, Brazil (location ID=24 in Supplementary Table S1 and Fig. 1). These trials reported only phenology and end-of-season yield, and were conducted in the rainy season without irrigation and with chemical fertilizers applied at planting with intermediate to high rates compared with typical farmer management. In the EVAL experiments, a range of environmental conditions were captured, including an intense drought in 2008. The physiological stress levels in both calibration and evaluation experiments are likely to be representative of a broad range of environments, although perhaps not completely representative of the lowest-yielding environments in the TPE. Table 1 presents a summary of the experiments, the variables reported, and their use within this study.

Model parameterization and evaluation

Crop model Oryza2000 is a process-based rice simulation model developed for application in agricultural research, and a general description of its structure can be found in Bouman *et al.* (2001). This model has been widely used for various applications across a wide range of regions (Li *et al*., 2009, 2013; Amiri and Rezaei, 2010; Li and Wassmann, 2010; Boling *et al.*, 2011; Heinemann *et al.*, 2012; Stone and Heinemann, 2012). Oryza2000 predicts growth and yield as influenced by local environmental conditions, agronomic practices, and cultivar traits. Its strong ability to quantify the influence of soil water on rice growth and yield (Bouman and Laar, 2006; Feng *et al.*, 2007) extends its efficiency to evaluate the response of a rice cultivar under drought stress (Li *et al.*, 2013).

The water dynamics were simulated in this study using the 'PADDY' soil water balance module. This is a one-dimensional multi-layer (up to 10) model that simulates soil water balance for a variety of growing conditions (e.g. puddled or non-puddled), with free or impeded drainage at some depth in the soil profile. The 'PADDY' module is well summarized by Boling *et al.* (2007). The same study demonstrated that the model is suitable for rainfed conditions.

Model calibration The Oryza2000 crop model was parameterized for a standard check variety, BRS Primavera. BRS Primavera is highly representative of varieties cultivated in central Brazil during the last 10 years, although it is currently being replaced by new varieties (BRS Esmeralda and BRS Sertaneja) due to its susceptibility to rice blast. As a check variety in breeding trials, BRS Primavera is also representative of materials that breeders are currently selecting. BRS Primavera is considered a short-cycle cultivar (~100 d from emergence to physiological maturity), with approximately 10 leaves on the main stem. It is planted in about 45% of the UR production region (Heinemann *et al.*, 2009).

Crop development rate was calculated using the observed crop phenology data from the PHE field experiments, i.e. emergence dates, panicle initiation, flowering, and physiological maturity (see Table 1). For deriving the crop growth cultivar-specific characteristics (i.e. maximum and minimum relative growth rate of leaf area, fraction of carbohydrates allocated to stems, fraction of nitrogen translocated from roots, maximum value of specific leaf area, and

Table 1. *Experimental data obtained at Santo Antônio de Goiás, GO (ID=24, Supplementary Table S1) used in this study based on the BRSPrimavera genotype*

Name	Description[a]	Measured variables used	Used for
PHE and GRO	(1) Wet season 2008/2009 planting 08/11 (RF)		Phenology calibration and growth parameter calibration
	(2) Wet season 2008/2009 planting 20/12 (RF)		
	(3) Wet season 2010/2011 planting 06/12 (RF)		
	(4) Wet season 2012/2013 planting 20/10 (IR)		
GRO only	(5) Wet season 2009/2010 planting 18/11 (RF)	Stem, leaf, and panicle biomass; leaf area index	Growth parameter calibration
	(6) Wet season 2012/2013 planting 11/09 (IR)		
EVAL	(1) Wet season 2004/2005 planting 23/11 (RF)	Flowering date; maturity date; yield	Model evaluation
	(2) Wet season 2004/2005 planting 18/11 (RF)		
	(3) Wet season 2005/2006 planting 20/12 (RF)		
	(4) Wet season 2005/2006 planting 15/12 (RF)		
	(5) Wet season 2006/2007 planting 03/11 (RF)		
	(6) Wet season 2008/2009 planting 07/12 (RF)		
	(7) Wet season 2008/2009 planting 06/12 (RF)		
	(8) Wet season 2008/2009 planting 09/12 (RF)		
	(9) Wet season 2010/2011 planting 22/12 (RF)		
	(10) Wet season 2011/2012 planting 05/12 (RF)		
	(11) Wet season 2011/2012 planting 07/12 (RF)		

[a] RF, rainfed; IR, irrigated (sprinkler irrigation).

upper limit leaf expansion), we applied the same method described by Li *et al.* (2013). To this aim, an iterative process based on the six experiments of the GRO dataset (Table 1) was applied until the differences between field measurements and simulated outputs were minimized in a given large number of iterations (10 000). The process was stopped when the differences between the measured (LAI, leaf, stem, panicle, and total biomass—considered as a target) and simulated values were within the range of measurement deviations. The iterative process is based on the minimization of absolute and normalized root mean square differences between simulated and measured values and takes into account the time series of target measurements. A more detailed explanation about the iterative process is available at https://sites.google.com/a/irri.org/theoryza2000/calibration-and-validation/model-evaluation. The crop growth cultivar-specific characteristics derived from the optimization process are shown in Supplementary Table S4 at *JXB* online.

Model evaluation Model evaluation efforts focused on assessing the differences between variables measured in the EVAL dataset (flowering and physiological maturity dates and end-of-season yield; Table 1) and their respective simulated pairs. The root mean squared error (RMSE) and mean absolute error (MAE) were used as measures of model skill.

Environmental characterization

Simulated scenarios Simulations were performed for a range of sowing dates (n=8), for each soil type (n=7), and weather station region (n=51) for the period 1980–2012, using recommended agronomic practices. Sowing dates were defined at 10 d intervals during the wet planting season, from 1 November to 10 January. This choice of potential crop calendars was based on the climatic-risk zoning for UR TPE developed by the Brazilian Government (http://www.agricultura.gov.br/). Model runs were initiated in February, regardless of sowing date, in order to allow the establishment of a realistic soil water profile on the basis of rainfall patterns occurring before the actual sowing date. All simulations were set for rainfed conditions, with no biotic constraints and no nitrogen limitations. In spite of the strong interactions between drought and nitrogen limitations, we focused here only on drought stress, as it is the main abiotic constraint on rice production in the UR region (Heinemann and Sentelhas, 2011). Potential transpiration and evaporation rates were calculated based on the Priestley–Taylor method. Maximum rooting depth was set at 50 cm based on soil samples in the calibration trials.

Determination of environment groups We used attainable (water and radiation-limited) yield to identify environment groups in the UR TPE. Towards this aim, we constructed a matrix consisting of simulated yields from 1980 to 2012 as a function of year, planting date, location, and soil type. An agglomerative hierarchical clustering method (Williams, 1976) was employed on simulated yield for classification with the squared Euclidean distance as the dissimilarity measure and incremental sum of squares (Ward, 1963) as the fusion criterion. The number of environment groups was defined based on the following criteria: (i) inertia gain, based on the Huygens' theorem, which allows decomposition of the total inertia (total variance) of between and within-group variance (Husson *et al.*, 2011); (ii) within-group sum of squares (Supplementary Fig. S3 at *JXB* online); and (iii) UR breeders' knowledge of the production area. The analysis was performed using the FactoMineR library in the R statistical package (R Core Team, 2014). In order to assess the differences among environment groups (clusters), a Kolmogorov–Smirnov non-parametric test was applied on the simulated yield (kg ha^{-1}), actual accumulated transpiration (mm per crop cycle) and total absorbed radiation (MJ m^{-2} per crop cycle).

Typology of stress patterns The Oryza2000 crop model assumes that there is a constant ratio of transpiration to gross photosynthesis under drought stress (Bouman *et al.*, 2001). This assumption might constitute a limitation in the simulation of assimilation under drought, but testing and/or improving it was beyond the focus of our study. Furthermore, extensive evaluation of the model suggests that this assumption is unlikely to affect crop simulations under current climates (Bouman *et al.*, 2001). Based on this, for each environmental group within the UR TPE, the main drought patterns were then determined using the temporal variation of weekly mean ratios of actual transpiration to potential transpiration (PCEW), which acts in the model as a daily photosynthesis reduction factor. To that aim, a matrix consisting of weekly PCEW values was created. The simulated drought-stress patterns were obtained by clustering the phenological sequence patterns of PCEW. The same classification method as for the determination of environment groups (above) was applied. In order to avoid bias in the stress pattern analysis resulting from the strong variation in PCEW during crop establishment, only the period from mid-vegetative stage [21 d after emergence (DAE)] to 2 weeks before physiological maturity (84 DAE) was considered. The strong variation in PCEW in the early vegetative stage is due to the initially shallow root system, but this has only small effects on subsequent growth. Similar drought classification procedures have been employed previously by Muchow *et al.* (1996), Chapman *et al.* (2000*b*), Heinemann *et al.* (2008), and Chenu *et al.* (2011). The agglomerative hierarchical clustering method was employed using R. The number of drought patterns for each environment was defined based on the same criteria applied by environmental groups: (i) inertia gain; and (ii) within-group sum of squares (see above).

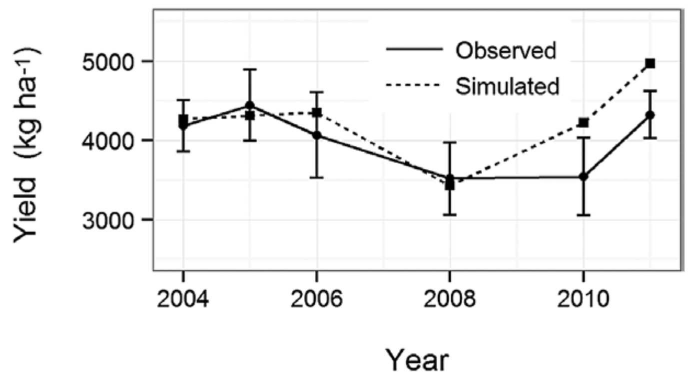

Fig. 2. Observed mean yield (continuous line) from UR multi-trial experiments at Santo Antônio de Goiás (EVAL dataset, see Table 1) and simulated yield (dashed line). Bars extend to 1 standard deviation (SD) of observed yield.

Results

Crop model skill

The Oryza2000 crop model showed a good performance for predicting UR phenology. The model showed a good performance for predicting panicle initiation, flowering, and physiological maturity dates of the PHE (phenology calibration) dataset (Supplementary Fig. S1A–C). All data points fell within the confidence intervals derived from the observed data (α=95%). The flowering date showed the largest RMSE (2.35 d, Supplementary Fig. S1B). For the EVAL dataset (Supplementary Fig. S1D, E), the RMSE and MAE values for flowering and physiological maturity date were 3.56 and 2.56, and 4.47 and 4.33, respectively. The crop model also captured well the seasonal variation in dry weight dynamics by organ for both rainfed (Supplementary Fig. S2A, B at *JXB* online) and irrigated (Supplementary Fig. S2C) conditions. LAI was also well simulated for rainfed (Supplementary Fig. S2D, E) and irrigated (Supplementary Fig. S2F) conditions. Yield evaluation based on the EVAL dataset showed low values of RMSE and MAE (349 and 249 kg ha^{-1}, respectively, Supplementary Fig. 2F). Oryza2000 also captured well the inter-annual variability of yield from 2004 to 2011 (Fig. 2). Yield overestimation was observed for the last two years, 2010 and 2011, due to blast disease incidence being stronger in 2010 than 2011.

Environmental characterization

Based on the results obtained by cluster analysis of simulated yields, three environment groups were identified in the UR TPE: a highly favorable environment (HFE), a favourable environment (FE), and a least favorable environment (LFE) (Fig. 3A). HFE was characterized by having one category of soil type and two predominant categories of sowing date, whereas LFE was characterized by two predominant categories of soil type and sowing date. Within FE, conversely, there was no predominant sowing date. Not surprisingly, HFE showed the highest probability of reaching high simulated yields, followed by FE and LFE (Fig. 4A). Based on the Kolmogorov–Smirnov test, simulated yield, actual accumulated transpiration, and absorbed radiation showed significant differences among the environmental groups (Table 2).

HFE

This environment showed yields higher than overall means (i.e. all environments in the entire analysis region) for all years (1980–2012, Fig. 4B). The average simulated yield, actual transpiration, and absorbed radiation in this environment were 3168 kg ha^{-1}, 213 mm, and 372 MJ m^{-2} per crop cycle, respectively (Table 2). For this environment, the average flowering date and standard deviation (SD) were 71 DAE and 3 d, respectively. The annual precipitation was higher than overall means (1581 vs 1505 mm), while annual global radiation, annual temperature amplitude, annual temperature, and annual minimum temperature were lower than overall means (6894 MJ m^{-2}, 0.98 °C, 23.78 °C, and 18.06 °C vs 6944 MJ m^{-2}, 0.99 °C, 24.23 °C, and 18.23 °C). The main characteristic of this environment was the predominance of clay soil, with sowing dates concentrated towards the beginning of the sowing window (01/11 and 10/11) (Fig. 5), indicating that management practices had a significant impact on the frequency of occurrence of this environment across time and space. The frequency of occurrence for this environment represented only 19% of the UR TPE.

FE

This environment showed higher yields than overall means (all environment groups) for all years (1980–2012), but lower than those in the HFE (Fig. 4B). The mean yield, actual transpiration, and absorbed radiation in this environment were 2,610 kg ha^{-1}, 178 mm, and 326 MJ m^{-2} per crop cycle, respectively (Table 2). For this environment, the average flowering date and SD were 70 DAE and 2 d, respectively. The predominant soils of this environment group were sandy clay loam (28% occurrence) and clay loam (24%) (Fig. 5). The frequency of occurrence for this environment was 44% across the UR TPE.

LFE

This environment showed yields lower than overall means (all environments) for all years (1980–2012) (Fig. 4B). The mean

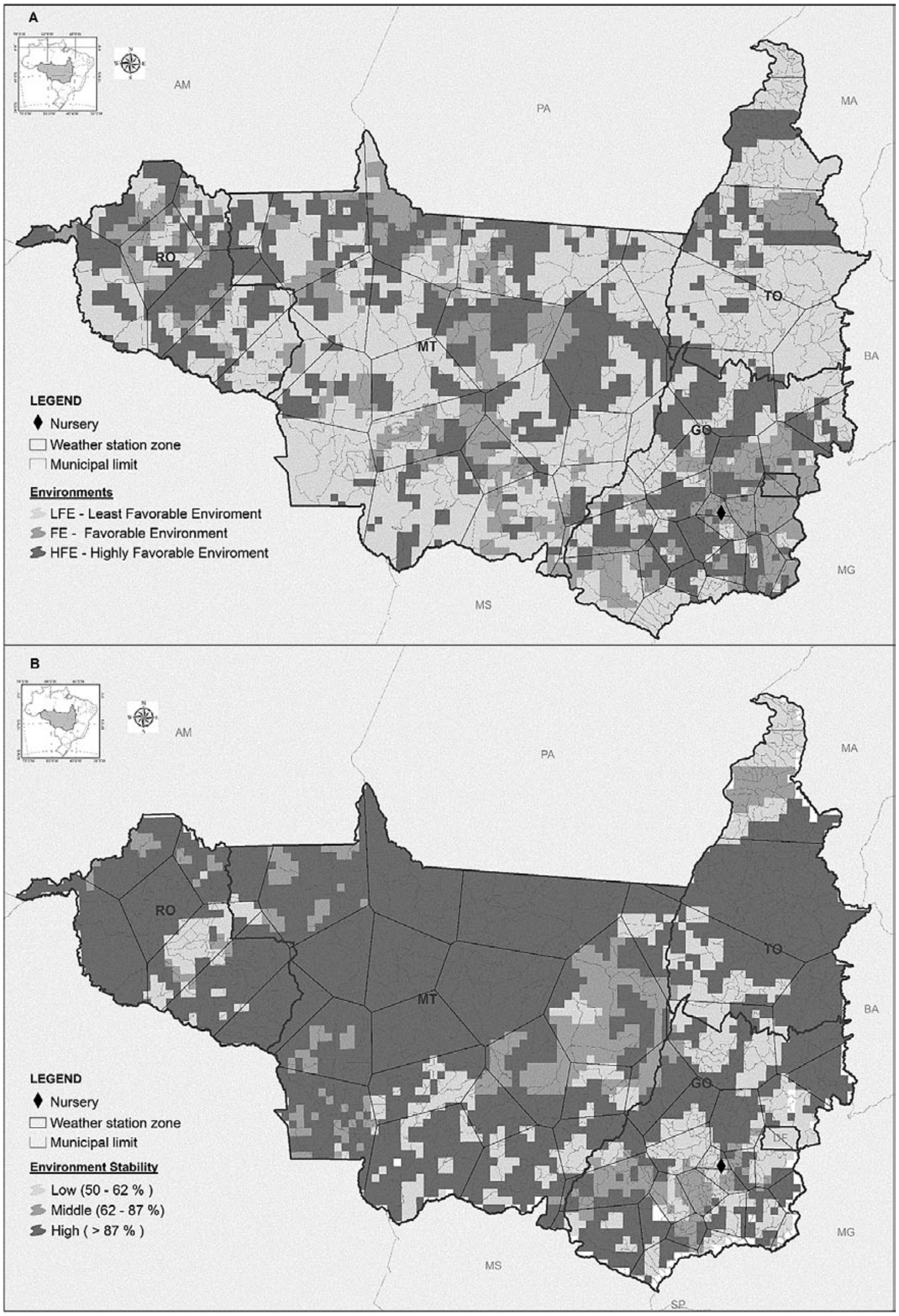

Fig. 3. Maps of environments distribution (HFE, FE, and LFE), nursery location, and weather station coverage area (A) and environment stability, nursery location, and weather station coverage area (B) on the UR TPE. Stability refers to how frequently the environment occurred in the simulated period (1980–2012).

yield, actual transpiration, and radiation absorbed in this environment were 1661 kg ha^{-1}, 132 mm, and 293 MJ m^{-2} per crop cycle, respectively (Table 2). The average flowering date and SD were the same as for FE (70 DAE and 2 d, respectively). In this environment, the total annual precipitation was lower than overall means (1465 vs 1505 mm), while annual global radiation, annual temperature amplitude, annual temperature, and annual maximum and minimum temperature were higher than overall means. The main characteristic of this environment was the predominance of sand and sandy loam soils (33 and 41%, respectively), with sowing dates concentrated towards the end of the sowing window (30/12 and 10/01) (Fig. 5). The frequency of occurrence of this environment was 37% across the UR TPE.

Major water-stress patterns

HFE

Two predominant stress patterns were identified for HFE (Fig. 6A), denominated drought-stress free [1] and terminal

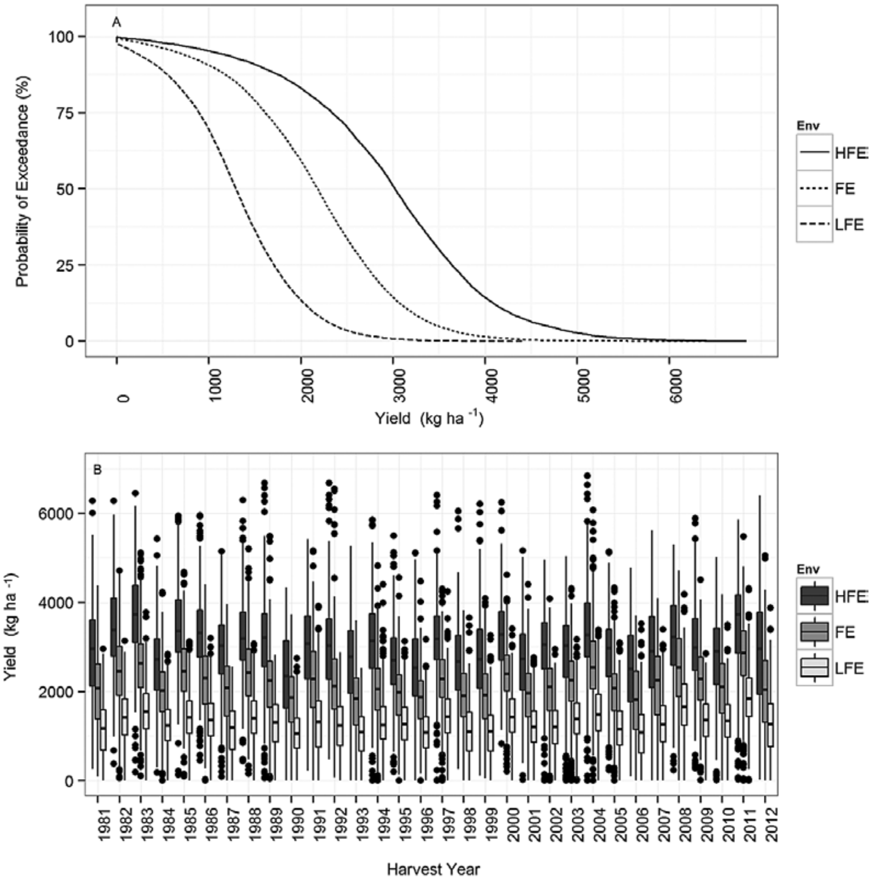

Fig. 4. Simulated rice yields across environments: yield exceedance probability for the UR environment groups (A) and simulated yield across the years (B). For the boxplot (B), boxes extend to the 25th and 75th sample percentiles of yield, the thick horizontal line is drawn at the median, and whiskers extend to 1.5 times the interquartile range.

Table 2. *Summary of simulated yield, actual transpiration, and radiation absorbed for each environment and the P value of the Kolmogorov–Smirnov (K-S) test between environments*

	LFE	**HFE**	**FE**	**LFE**	**HFE**	**FE**	**LFE**	**HFE**	**FE**
	Simulated yield (kg ha^{-1})			**Actual transpiration accumulated (mm)**			**Radiation absorbed (MJ m^{-2} per crop cycle)**		
Min	0	0	0	2	19	19	0	47	45
1st quartile	893.3	2339	1614	89	199	150	216	345	293
Median	1297	3023	2184	110	229	1783	254	378	329
Mean	1661	3168	2610	132	213	178	293	372	326
3rd quartile.	1709	3640	2700	136	260	203	294	412	363
Max.	4407	6839	6552	323	356	338	699	680	602
K-S test (*P* value)	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01

drought stress [2]. The most frequent stress pattern (69% frequency of occurrence) was stress-free [1] (Fig. 6A). This stress pattern was responsible for the highest simulated yields (Fig. 6D) with a mean of 3324 (±893) kg ha^{-1}. The most severe but least frequent stress (31%) was terminal drought stress [2], for which onset occurred at the beginning of the reproductive phase (49 DAE) with intensity increasing until the end of grain filling. This stress caused a yield reduction of 34% with respect to stress-free conditions [1]. The average and SD flowering date for both stress patterns, drought-stress-free [1] and terminal drought stress [2], were 71 DAE and 3 d, and 72 DAE and 3 d, respectively.

The seasonal variations in meteorology, i.e. mean weekly rainfall, mean daily maximum and minimum temperature, mean daily solar radiation, and total accumulated rainfall by crop cycle for both stress pattern are presented in Fig. 7A–D. For stress-free conditions [1], weekly rainfall increased from the vegetative to the end of the reproductive phase, followed by a decrease at the beginning of the grain-filling phase. For conditions of terminal drought stress, there was decreased

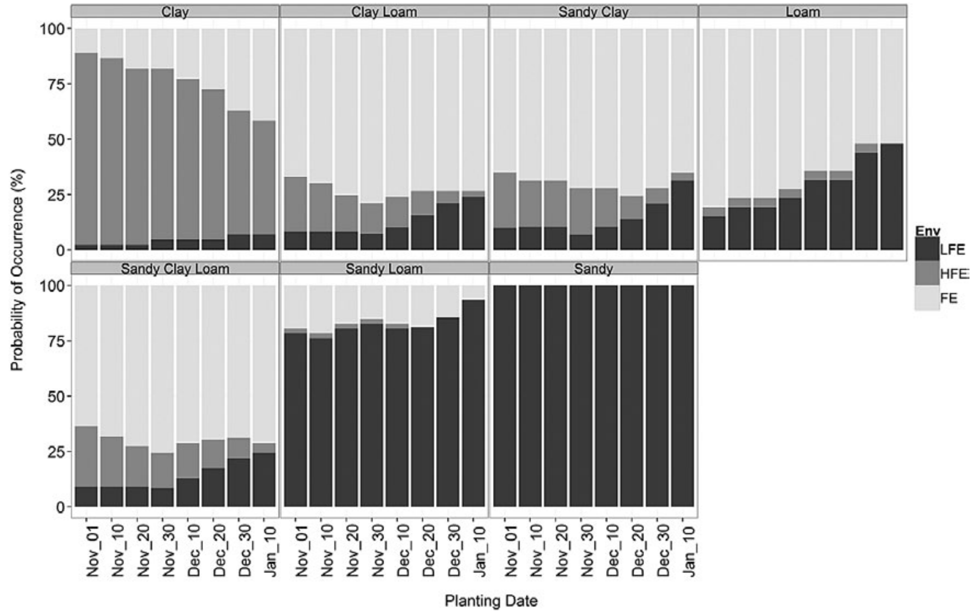

Fig. 5. Frequency of occurrence of the three environments across planting dates (top row) and soils types (bottom row).

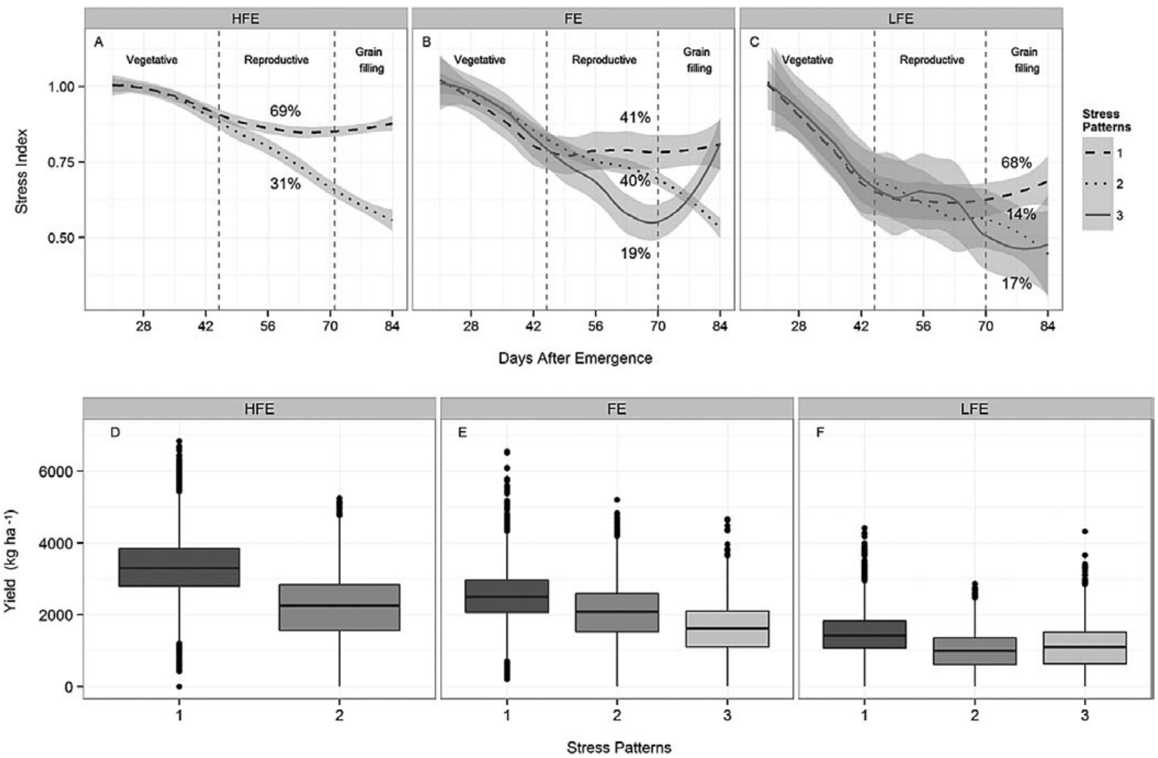

Fig. 6. Drought-stress patterns (A–C) and simulated yields per drought-stress pattern (D–F) for HFE, FE, and LFE for UR target population environment groups. (A–C) Stress types for each environment with numbers representing the frequency of occurrence of stress patterns in environmental groups. The first and second vertical dashed lines show the average panicle initiation and flowering dates for each environment group, respectively. Reproductive phase is defined as the period from panicle initiation to (50%) flowering. Grey shaded bands represents the 95% confidence interval around the average stress patterns. (D–F) In the box plot, boxes extend to the 25th and 75th sample percentiles of yield, the thick horizontal line is drawn at the median, and whiskers extend to 1.5 times the interquartile range.

rainfall during the reproductive phase (Fig. 7A). For stress-free conditions [1], daily solar radiation decreased from 21 to 19 MJ m^{-2} d^{-1} during the crop cycle and was lower than that of terminal drought stress [2] (Fig. 7C). The stress-free pattern [1] had a rainfall accumulation per crop cycle of 750 mm, 150 mm higher than that of terminal stress [2] (Fig. 7D). The drought-stress impact on LAI, actual transpiration, and dry matter is presented in Fig. 8. For stress-free [1] conditions, the maximum LAI expected was 2.9 and for terminal stress [2] it was 2.2 (Fig. 8A). The stress-free pattern [1] had higher maximum actual transpiration (4.2 mm) than terminal drought stress [2] (3 mm). The total accumulated dry matter simulated

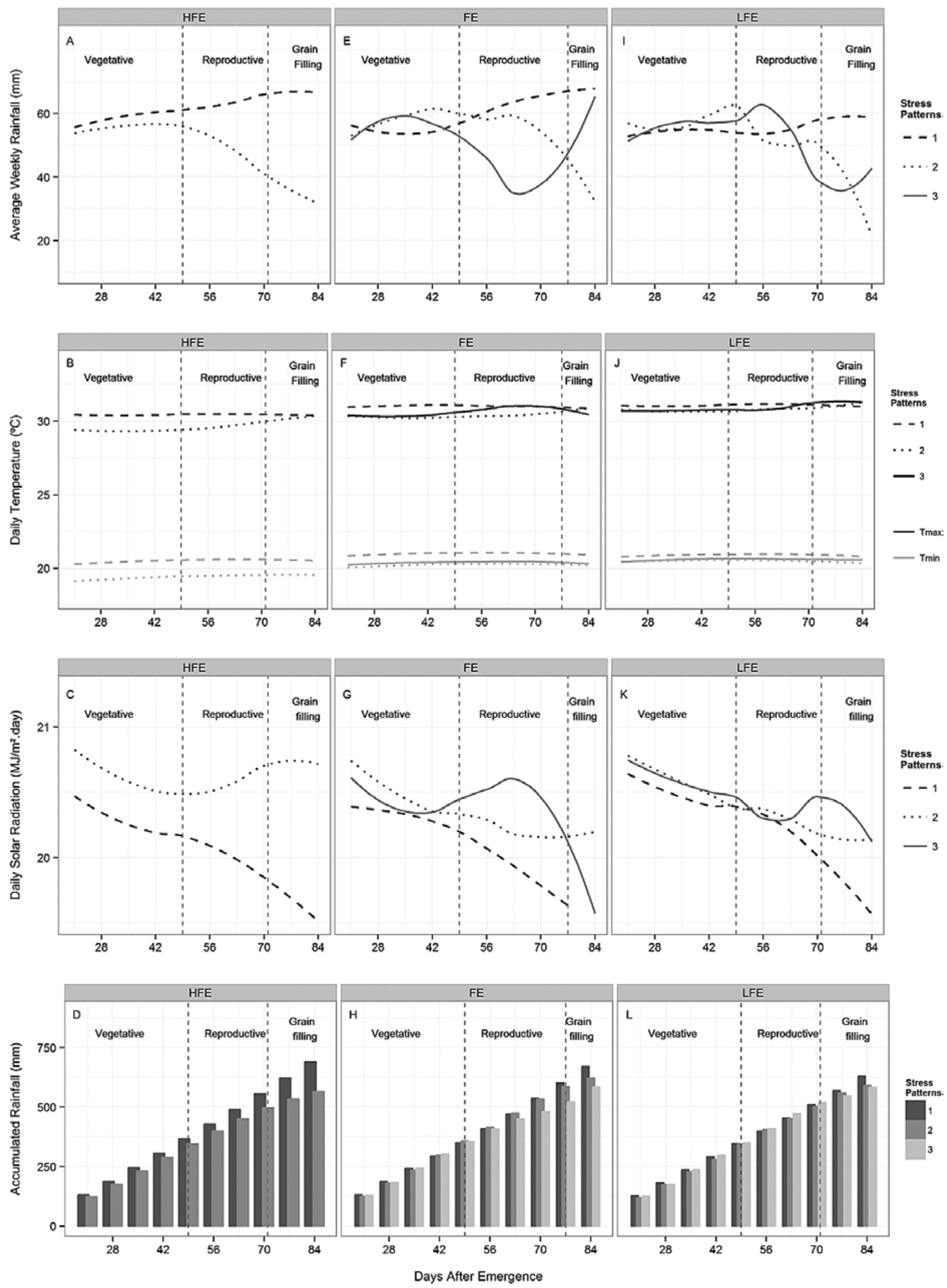

Fig. 7. Variation in climate, i.e. mean weekly rainfall, mean daily maximum and minimum temperature, mean daily solar radiation, and mean total accumulated rainfall, for each drought-stress pattern in the three environments groups (HFE, FE, and LFE).

for stress-free conditions [1] was 8067 kg ha^{-1}, 29% higher than with terminal drought stress [2] (Fig. 8B).

FE

In this environment, the most frequent stress patterns were reproductive stress [1] and terminal drought stress [2], with a frequency of occurrence of 41 and 40% (respectively) (Fig. 6B). Reproductive stress [1] began around 34 DAE and reached its highest intensity during the reproductive phase. This stress pattern showed the highest simulated yields in this environment with a mean of 2498 (±722) kg ha^{-1}. Terminal drought stress [2] had its highest intensity during the grain-filling stage, with yields 18% lower in relation to the reproductive stress pattern [1] (Fig. 6E). The most severe stress, but least frequent (19% of frequency of occurrence), was severe reproductive stress [3]. This stress pattern had its highest intensity during the reproductive stage and caused a yield reduction of 36% with respect to the more moderate reproductive stress [1] pattern (Fig. 6E). The average and SD flowering date for reproductive stress [1], terminal drought stress [2], and severe reproductive stress [3] were 70 DAE and 2 d, 71 DAE and 3 d, and 70 DAE and 2 d, respectively. The

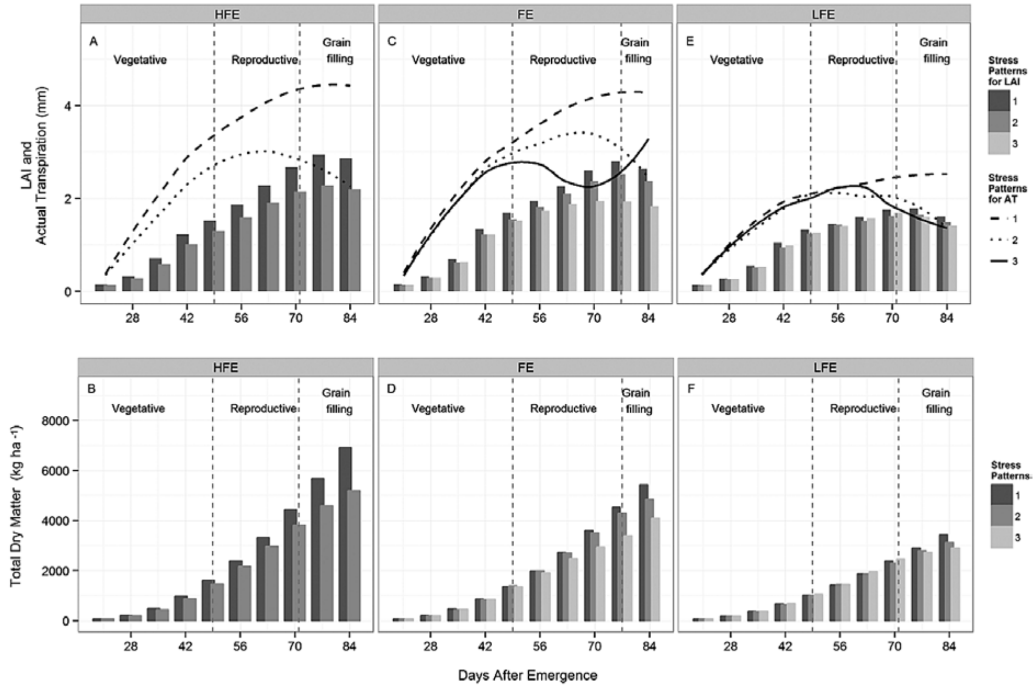

Fig. 8. Effect of each drought-stress pattern on crop traits of LAI and actual transpiration (AT) (A, C, E) and total dry matter (B, D, F) for HFE, FE, and LFE.

main difference between reproductive stress [1] and the other two stress patterns was that, for reproductive stress, rainfall increased after the reproductive phase, whereas for the others there was a decrease after the reproductive phase. Mean daily solar radiation for reproductive stress [1] and terminal drought stress [2] had almost the same seasonal pattern (Fig. 7G). The mean maximum LAI value simulated (average value across sowing×year combinations of the maximum LAI simulated within the crop cycle) for reproductive stress [1], terminal drought stress [2], and severe reproductive stress [3] was 2.4, 2.1, and 1.6, respectively. Total accumulated dry matter observed for reproductive stress was 6314 kg ha^{-1}, 16 and 23% higher than under terminal drought stress [2] and severe reproductive stress [3], respectively (Fig. 8D).

LFE

Three predominant stress patterns were also identified for LFE (Fig. 6C), denominated reproductive [1], terminal [2], and reproductive-to-grain-filling [3] stresses. In this environment group, the most frequent stress pattern was reproductive stress [1] with a frequency of occurrence of 68%. This stress pattern began at 28 DAE, had its highest intensity during the reproductive stage, and showed the highest simulated yields (Fig. 6F) with a mean of 1461 (±589) kg ha^{-1} (Fig. 6F). The reproductive-to-grain-filling stress [3] had its highest intensity at the beginning of grain filling. This stress pattern caused a yield reduction of 24% in relation to the reproductive stress [1] pattern. The most severe but least frequent (14% of frequency of occurrence) stress pattern for this environment was terminal stress [2]. This stress pattern had its highest intensity during the grain-filling stage and led to a yield reduction of 32% with respect to the reproductive stress [1] pattern. The average and SD flowering date for reproductive [1], terminal [2], and reproductive-to-grain-filling [3] stress were the same: 70 DAE and 2 d.

For reproductive stress [1], weekly rainfall was almost constant during the crop cycle. For the other stresses, terminal [2] and reproductive-to-grain-filling [3], rainfall decreased during the reproductive phase (Fig. 7I). The total accumulated dry matter was 3934 kg ha^{-1} for reproductive stress [1], whereas terminal drought stress [2] and reproductive grain-filling stress [3] showed a total dry matter of 3391 (16% lower) and 3362 kg ha^{-1} (17% lower), respectively (Fig. 8F).

Discussion

Breeding activities for UR in Brazil since the 1980s have focused on direct selection for grain yield and for wide adaptation to the undivided target region. In this strategy, the screening of the early generation yield test (nursery) was done in a single site, Santo Antônio de Goiás, GO, Brazil, under stress-free conditions. In such a scheme, new crop varieties are exposed to abiotic stresses only at later breeding stages, when genotypes are fewer and genetic variation lower. Testing sites, or 'multi-environment trials' (METs), are not selected on the basis of environmental characterization, and when drought is prevalent in trials, these are generally discarded. These selection criteria may increase the risk of developing genotypes specialized for highly favourable areas that do not have enough plasticity and hence do not respond well under stressed conditions. Below, we discuss potential ways to address this issue for UR in Brazil.

Distribution and usefulness of the environmental classification

Based on the yield simulations using historical weather data, three major environments types, HFE, FE, and LFE, were identified to characterize the UR TPE (Fig. 4). While statistical methods were useful in determining likely groupings (Supplementary Fig. S3), expert knowledge was also incorporated into the framework, thus resulting in a classification that is arguably more useful to breeders. Meetings with breeders were held during the course of this research to gain a better knowledge of UR TPE and a better understand the criteria for selecting MET locations. This allows empirical observations from breeders and experimentalists (mostly based on field trials) to feed back into their expectations from the classification (Setimela *et al.*, 2005; Hernandez-Segundo *et al.*, 2009). This also allowed the incorporation of both empirical and anecdotal knowledge that would otherwise be difficult to incorporate into a model-based framework. For instance, according to UR breeders, MET locations are chosen mainly according to partner availability, with environmental representativeness playing a minor role. The nature of the present work provides an objective measure of environmental representativeness with which current MET locations can be re-assessed. The classification presented here is thus robust and reflects both breeder knowledge and the main sources of yield variability in the region. The classification also agrees well with previous work. Specifically, Heinemann and Sentelhas (2011) based on UR survey yield data from 1976 to 2006 also identified three environments in the same TPE. With respect to Heinemann and Sentelhas (2011), average simulation yields in HFE and FE were higher since the crop simulations of the present study did not account for biotic and nitrogen stress (a potential issue for future work). However, we demonstrated that crop simulations captured well the spatial and temporal variability for these two environments (Supplementary Figs S1 and S2 and Fig. 2). For LFE, the average simulated yield was lower than that of Heinemann and Sentelhas (2011), perhaps because the crop model overestimated the drought effect on yield in some cases (an issue to be addressed in the 'PADDY' submodel) (Bouman *et al.*, 2001; Boling *et al.*, 2007).

The practically absent overlap among environmental groups (HFE, FE, and LFE) observed in Figs 3 and 4 indicates that subdivision of areas into environmental groups and selection for specific adaptation in these environments is a potential strategy to increase selection response. Based on our results, we hypothesize that improved selection procedures should target efforts to specific zones and planting dates, rather than searching for wide adaptation within the undivided TPE. Several results support this hypothesis. For instance, Colombari Filho *et al*. (2013), based on a study of stability and adaptability of Brazilian UR elite lines from 27 years of METs), showed that crossover interaction among sites was higher than among years, which makes the selection of cultivars with wide adaptation in an undivided TPE difficult. In addition, Breseghello *et al.* (2011) argued that one of the factors limiting the genetic gain for grain yield is the vast geographical region represented by the UR TPE, which encompasses a large range of soil, climate, and crop-management variation. They suggested that subprogrammes focused on more-specific environments could result in faster genetic gains for grain yield.

Some limitations may, however, arise when attempting to put into practice an environment-specific germplasm selection strategy. Most importantly, UR is not a for-profit crop such as soybean and maize, and consequently there are only a few seed companies interested in replicating seeds that privilege cultivars of broad adaptation with more marketing options as opposed to cultivars adapted to specific environments (Breseghello *et al.*, 2011). In addition, there is a practical limit on the number of environments that can be covered in a breeding programme, especially when these efforts are conducted by public institutions, such as for the UR breeding programme, since the resources required for separate efforts to develop new varieties need to be appropriately justified (Fischer *et al.*, 2012). While only *ex-ante* and *ex-post* impact assessments would be able to confirm if costs are justified by the impact of a more environmentally disaggregated UR breeding strategy, the classification reported here would significantly facilitate germplasm selection. This is because such a strategy would isolate genotype×environment interactions to the maximum extent possible while also covering the entire geographical space. The fact that optimal conditions occur only approximately 19% of the time (Fig. 3) across the UR TPE analysed here, and that UR is commonly cultivated in the production region mainly by smallholders with limited or no use of fertilizers, suggests that the socio-economic impact of the breeding programme would be larger if direct selection was done in non-optimal conditions, even if genetic gains are generally lower under such conditions.

Environment-specific breeding strategies

HFE was characterized by the highest yields (Table 2) and the lowest frequency of occurrence in the UR TPE (19%), and with mostly stress-free conditions [1] (69% occurrence, Fig. 6A). In this environment, our simulation results support the UR breeding strategy to base rice selection mainly on yield potential. The best sites for METs in this environment are located in the centre north of the UR TPE, which showed high environmental stability (Fig. 3). In the early generation yield test (nursery), located at Santo Antônio de Goiás, GO, Brazil, HFE had a 62.5% probability of occurrence (Fig. 3A), and is suitable for selection of cultivars for potential yield, if sowing is done at the beginning of November, in clay soil. However, this area is classified as middle environmental stability (Fig. 3B). Therefore, irrigation would be necessary to avoid drought stress whenever terminal drought stress occurs.

FE was characterized by average yields lower than HFE but higher than LFE, and had the highest frequency of occurrence in the UR TPE (44%). FE had two predominant stress patterns: reproductive stress and terminal stress (Fig. 6B), with 41 and 40% frequency of occurrence. Specific adaptation to a single stress pattern type in such an environment could be a risky strategy, unless rainfall could be forecasted before the sowing date with accurate predictions of the seasonal environment stress pattern. In FE, farmers should target cultivars that provide a good income (high yields) in the best years, and adequate income to cover more than production costs in poor years. An appropriate breeding strategy for this environment could be wide adaptation to drought. A similar strategy for wheat TPE in Australia, in which none of the stress types clearly dominated within any of the regions, was suggested by Chenu *et al.* (2011). Another possible option for this environment is the application of weights to genotype performance from the METs to match the representativeness of their growing environment-type expectations in the TPE, referred to as 'weighted selection'. This strategy has been shown to increase the response to selection (Podlich *et al.*, 1999), mainly when genotype×environment interactions are large (Chenu *et al.*, 2011), as is the case when drought is prevalent and varies substantially in its timing. The potential sites for METs where there is a high probability of occurrence of this environment can be seen in Fig. 3A. Sowing should be done preferentially in sandy clay loam and clay loam soil types to increase the probability of occurrence of FE (Fig. 5A).

LFE is characterized by the lowest yields, with a frequency of occurrence in the UR TPE of 37%, and reproductive stress [1] (69% occurrence, Fig. 6C) as the dominant stress pattern. For this environment, a specific adaptation to this stress pattern would be the most effective and reasonable breeding strategy. A weighted selection strategy, described above, is also feasible in this environment. The best locations for METs in this environment are presented in Fig. 3A. Trials should be sown towards the end of the sowing period (end of December) in sand and LS soils.

It is worth noting that only one cultivar, i.e. the check cultivar BRS Primavera, was used for the characterization presented in this study. However, other genetic materials with different cycles could be parameterized to evaluate their performance across the UR TPE even before being tested in the fields. Such assessments could help to determine more robustly the stability of the different environments found here. In addition to this, further analyses might be needed to determine how stable these environments are, how drought stress might change under future projected climate, and whether or not other stresses may become important in the future (IPCC, 2013). Such analyses could provide useful information to adjust the UR breeding strategy in the coming decades.

Conclusion

The detailed characterization of UR TPE undertaken in this study suggested that the UR TPE could be divided into three environment groups: HFE, FE, and LFE. For the best (HFE) and worst (LFE) environments, where there is a predominant stress pattern (stress-free and reproductive stress, respectively), we suggest that a specific adaptation should be applied focusing on such stresses, whereas for FE, with no predominant stress pattern, wide adaptation to drought is suggested. Weighted selection is also a possible strategy for the FE and LFE environmental groups. Nevertheless, it is important to note that the feasibility of adjusting the UR breeding strategy will depend on both the biophysical impact of the improved varieties and the non-biophysical constraints such as seed systems and farmers' socio-economic conditions. Biophysically, we found that the frequency of occurrence of the three environment groups in the study area was as follows: FE (44%)>LFE (37%)>HFE (19%). Because the current breeding strategy focuses primarily on the highly suitable areas for stress-free conditions, this results in only approximately 14% coverage (from all possible growing conditions in the TPE). However, an additional 42% of coverage (again, from total) would be possible if breeders were to focus on reproductive stress (which corresponds to 41 and 68% within LFE and FE, respectively), as well as on optimal conditions. The extent to which this potential can, nevertheless, be realized will depend on whether seed systems are in place and whether farmers are likely to adopt the new germplasm—clearly an area meriting future analyses.

Supplementary data

Supplementary data are available at *JXB* online.

Supplementary Table S1. Weather station identification, latitude, longitude, altitude (m), number of years with daily weather data available and soil type distribution among weather stations.

Supplementary Table S2. Equations applied to calculate soil hydrological properties.

Supplementary Table S3. Physical and hydrological soil attributes used as soil input for the crop model simulations.

Supplementary Table S4. Crop growth values derived from iterative calibrated process.

Supplementary Fig. S1. Simulated vs measured panicle initiation, flowering and physiological matur for parameterization process and flowering, and physiological matur and yield for evaluation process based on the upland rice rainfed trial experiments at Santo Antônio de Goiás, GO.

Supplementary Fig. S2. Simulated and measured total dry matter, leaves, stems, and panicles, and leaf area index for the rainfed wet season 2009/2010, wet season 2008/2009, and irrigated wet season 2010/2011.

Supplementary Fig. S3. Numbers of clusters for the simulated yield data within-cluster sum of squares and inertia gain method (Husson *et al.*, 2011) for different numbers of clusters.

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