Simulation of genotype performances across a larger number of environments for rice breeding using ORYZA2000

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ARTICLE INFO

ABSTRACT

Breeding line selection with conventional field methods is limited by time, cost, and appropriate environments. Crop models can be used as a tool to assist in breeding line selection by extrapolating the results of multiple-environment trials (MET) to large environments in a cost-effective and faster manner. This study is the first attempt to use ORYZA2000 for the selection of drought-resistant rice genotypes, and it provides a 'virtual' platform for a large number of environmental trials. In a case study, ORYZA2000 results from two field experiments in two environments were extrapolated to 669 environments in South Asia. For these two field experiments, the differences between simulated and field-measured grain yield and total above-ground biomass for all the 69 genotypes were within the standard deviations of the field measurements. This result confirmed that ORYZA2000 has the capability to correctly represent the growth and yield of rice genotypes under different environments. Using simulation outputs for 69 genotypes in 669 environments, the performance of these genotypes was evaluated for rainfed conditions with various drought stress. With the increase in the number of environments, the effect of the genotype on phenotypic performances across environments become much more significant than that of the effects of environment and genotype–environment interactions, and heritability was also increased. Desirable rice genotypes could then be selected by breeders based on the expected yield and adaptability to various environments generated by the model. The evaluation of rice genotypic performance by ORYZA2000, as 'virtual' multiple-environment trials, can improve the reliability of selected genotypes for a wide range of environments and enhance efficiency in terms of time consumption and cost effectiveness of the breeding process.

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1. Introduction

Rice genotypes react differently in different environments because of various climatic conditions, soil characteristics, and/or agronomic practices (Gravoic et al., 1991; Inthapanya et al., 2000; Mahajan and Prasad, 1986; Moeljopawiro, 1989; Olaleye et al., 2010; Ram et al., 1978; Sedghi-Azar et al., 2008). The interplay of genetic and non-genetic effects causing differential performance of different genotypes in different environments is the genotype by environment (G × E) interaction (Prabhakaran and Jain, 1992). Therefore, it is essential to quantify and interpret these interactions for the evaluation or prediction of the performance of rice breeding lines in a wide range of agro-climatic conditions. The G × E interaction introduces uncertainty in the superiority of rice genotypes across a target population of environments (TPE).

Stability and adaptability are paramount when assessing the relative performances of genotypes across a TPE. There are several versions of the definitions of the term stability (Becker and Leon, 1988; Lin et al., 1986; Westcott, 1987). Most breeders used the term stability to characterize a genotype with minimum variability in performance across environments. A stable genotype associated with a high mean yield has general adaptability. Breeders evaluate genotypes through multiple environment trials (METs) (Annicchiarico, 2002; Kang, 1998; Simmonds, 1991) in which the performance of a set of genotypes is assessed in a set of environments. The environments are chosen to form a sample of the TPE that shows the variations in environmental conditions. The methods that investigate genotypic stability accounting for G × E interaction patterns by approximating the G × E interaction term by one or few multiplicative terms. These include the Finlay–Wilkinson (1963) model, Eberhart–Russell model (1966) and AMMI models (Zobel et al., 1988; Gauch, 1992).

However, conventional MET studies have limitations on evaluations of breeding lines. First, the limited sample of MET

sites does not always fully represent the environmental diversity over large TPE regions. Second, the short time period of a MET study (normally 2–3 years) cannot fully capture the temporal variations of genotype performance caused by varying climate conditions. Finally, MET studies are conducted under currently available soil-climatic conditions, so they may provide reference information on the performance of breeding lines a few years later while a new variety is widely adapted on the basis of regression estimations, but the environmental uncertainties will continuously increase with the prolongation of variety adaptation because agro-climatic conditions always exceed the conditions in which a MET for the variety was implemented.

To overcome these difficulties and to undertake an extensive 'virtual' MET study, crop models, with their excellent potential for evaluating genetic improvement, for analyzing past genetic improvement from experimental data, and for proposing plant ideotypes for a target environment, have been used to evaluate the performance of breeding lines over wide ranges of environments. APSIM (Agricultural Production Systems IMulator), which involves a sorghum crop module, was used to identify genotype to phenotype relations of sorghum in Australia (Hammer et al., 2010). Casadebaig et al. (2011) demonstrated the capability of the SUNFLO model in identifying breeding traits for high yield of sunflower by extending the MET experiment results. Phakamas et al. (2010) evaluated the adaptability of 17 peanut genotypes over 112 locations using the simulation outputs of the CSM–CROPGRO–Peanut model. There is not yet a similar study for rice, the staple food of almost half the global population, although rice crop models are available for such studies.

ORYZA2000 is a rice simulation model developed for application in agricultural research (Bouman et al., 2001; Bouman and van Laar, 2006). This model has been widely used for various applications across a wide range of regions (Amiri and Rezaei, 2010, 2009; Belder et al., 2005; Boling et al., 2011, 2007, 2004; Bouman et al., 2007; Das et al., 2007; Feng et al., 2007; Jing et al., 2008, 2007; Kreye et al., 2009; Li and Wassmann, 2010; Li et al., 2005; Soundharajan and Sudheer, 2009; Tuong et al., 2003; Xue et al., 2008; Zhang et al., 2008). The ability of this model to predict growth and yield as influenced by local environmental conditions, agronomic practices, and cultivar traits offers an opportunity to evaluate the effects of a trait or a combination of traits on yield through model simulation without an actual incorporation of these traits of a genotype. Moreover, the strong capability of ORYZA2000 to quantify the influence of soil water on rice growth and yield (Bouman et al., 2007; Feng et al., 2007) extends its efficiency to evaluate the response of a rice cultivar under drought stress.

Drought is a major constraint to rice yield and its stability in rainfed and poorly irrigated environments, resulting in significant yield and economic loss (IRRI, 2009; Pandey and Bhandari, 2007, 2006). Breeding for drought tolerance is one of the major approaches to reduce yield loss and economic loss in drought-prone environments (Kumar et al., 2008). However, there is a wide range of drought-prone environments, differing in both the timing and severity of drought stress. It is therefore necessary to have a quick and cost-effective method for evaluating drought-tolerant breeding lines over a large number of environments.

This study aims to develop a method for evaluating the performance of breeding lines over a large number of environments across a spatial and temporal scale using the rice model, ORYZA2000, in order to generate essential information for rice breeders on the selection of breeding lines for different environments.
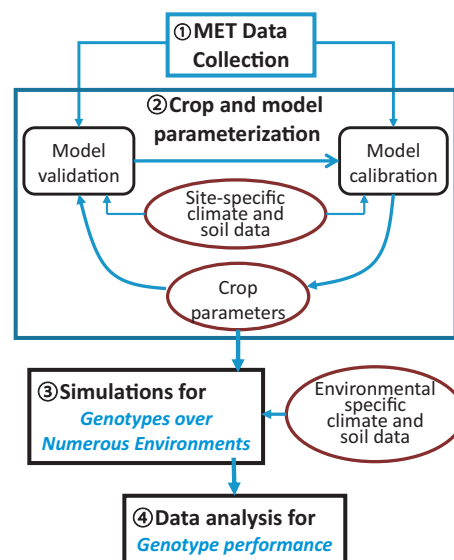

Fig. 1. The modeling approach framework for evaluating the adaptability and stability of rice genotypes across multiple environments.

2. Materials and methods

2.1. Framework of evaluation

A framework was developed to evaluate the adaptability and stability of rice genotypes across wide ranges of environments by using a modeling technique. It consists of four steps: data collection, crop parameterization, simulation, and simulation data analysis (Fig. 1).

2.2. Data collection

Data collection is the first and most important step in the modeling approach. Data quality and quantity are the key factors that determine the accuracy of genetic coefficients in the crop parameterization, model simulation outputs, and final evaluation on the adaptability and stability of genotypes. Table 1 lists three types of data requirements for crop parameterization and to address the study targets with different confidence levels for final results. Three types of data sets are: (1) a single location with multiple cropping seasons, (2) a single crop season in multiple locations, and, (3) ideally, multiple locations with multiple seasons. Three categories of data requirements are presented for different degrees of confidence of assessment. Detailed data significantly improve the confidence level of assessment. A decrease in the number of environments lowers the chance to fully capture the interactions of G × E in the parameterization, resulting in lower precision in crop parameterization and sequentially lowering confidence in the evaluation of genotypic performance across multiple environments.

In the case study, the source of data were the breeding line selection trials conducted by national collaborators of the drought breeding network of STRASA (Stress-Tolerant Rice for Africa and South Asia) in two sites in India: the Central Rainfed Upland Rice Research Station, Hazaribag, Jharkhand, in 2007, and the Central Rice Research Institute, Cuttack, Orissa, in 2008. Data were collected from advanced yield trials (AYT) for genotypes with 100–120 days' growth duration grown under water stress (rainfed in 2007) and non-water-stress (irrigated in 2008) conditions. Data quality and quantity met the criteria of 'fair data'. The data provided necessary information on 69 breeding lines (genotypes) for the simulation study.

Table 1
The quality and acceptability of data used for assessment of performance of breeding entries.

Item	Best data	Fair data	Usable data
Confidence level of results	*High*	*Acceptable*	*Uncertain*
Soil texture	√	√	
Soil organic carbon	√	√	
Soil organic N	√		
Daily radiation/sunshine	√ on-site	√	√
Maximum temperature	√ on-site	√ on-site	√
Minimum temperature	√ on-site	√ on-site	√
Rainfall	√ on-site	√ on-site	√
Wind speed	√ on-site	√	
Vapor pressure	√ on-site	√	
Nursery density	√	√	√
Field density	√	√	√
Sowing date	√	√	√
Planting date	√	√	√
Phenology	PI, FL, PM	FL, PM	PM
Biomass accumulation	>3 measurements, component	1 measurement, component	Final, total
N uptake	>3 measurements, component		
Final grain yield	√	√	√
Harvest index	√	√	√
Grain weight	√	√	
Transpiration	√		
Soil water	√	√	
Soil mineral N	√		
Irrigation	√	√	√
Fertilizer application	√	√	√
Pest & disease deduction	√	√	
Nutrient deficiency	√		

PI, *FL*, and *PM* are phenological stages of panicle initiation, flowering, and physiological maturity, respectively.
Component indicates the same type of measurement for different types of plant tissues. In this case, the components of measurements refer to biomass weight per unit land area or nitrogen weight per unit biomass weight separately for green leaf, dead leaf and stem in vegetative stage, or for green leaf, dead leaf, stem and panicle in reproductive stage.

2.3. Model calibration and validation for crop parameterization

The modeling approach for genotype evaluation assumes that the performance of a given genotype in a given set of environmental conditions is the result of the superimposition of environmental effects on genetic characteristics, and genetic characteristics would not change with environments. The genetic characteristics are represented by crop parameters in a crop model. Most crop parameters, for instance, maximum assimilation rate, maximum light use efficiency, radiation interception, the relationship between leaf nitrogen content and assimilation rate, optimal assimilate allocation among crop organs, maximum remobilization rate of non-structural carbon and nitrogen from stem to grain, and maximum rates of water and nitrogen uptake, are measurable directly from field experiments while the crop is grown under optimal conditions. Unfortunately, both optimal and non-optimal growth conditions are very difficult to achieve because the optimal conditions are hardly identified for almost all crop genotypes. The measurements are therefore phenotypic expressing parameters of genetic parameters rather than real genetic parameters, but could be their approximated values. The measurable and immeasurable genetic parameters can be derived by the crop model through iterating the calibration and validation processes (the step 2 in Fig. 1) using site-specific climate and soil information and crop measurements in multiple environments if the crop model has physiologically sound mechanisms, and can quantify and integrate crop responses to genetic, environmental, and management factors.

The process of deriving crop genetic characteristics is crop parameterization (Fig. 1), which includes calibration and validation of the crop model with two independent datasets. The crop parameters needed by the model are adjusted from initial values in the calibration process using available field measurements (Li et al., 2009; Yadav et al., 2011), particularly biomass accumulation and grain yield. These parameters were used to generate simulation outputs for another independent dataset in the validation process. The calibration and validation processes were iterated until the differences between field measurements and simulation outputs were minimized for calibration and validation datasets in a given large number of iterations (it was 10,000 in this case), and the values of crop parameters are close to the genetic parameters for a given genotype. The iteration was stopped when the differences between the measured and simulated values were already within the range of measurement deviations. Using these genetic parameters, the crop model can estimate crop growth and yield in a wide range of different environments.

To achieve the objectives of this study, ORYZA2000 was used as a tool to evaluate the performance of genotypes over large number of environments where rice may suffer various drought stresses. ORYZA2000 is an ecophysiological rice model (Bouman et al., 2001) with adequate features to represent genetic and environmental interactions. It has the ability to evaluate the effects of drought stress on rice growth and yield with its series of equations to quantify the reductions of transpiration, assimilation, leaf growth, root growth and spikelet fertility, the changes of assimilate allocation to the root, stem, leaf and panicle, and the delay of phenology under drought stress (Boling et al., 2011, 2007; Belder et al., 2005; Bouman et al., 2001; Li et al., 2009).

In the case study, ORYZA2000 was used to derive the genetic parameters of 69 genotypes through iterating calibration and validation processes with initial values of crop parameters from a widely cultivated variety, IR72. The calibrated and validated parameters were specific leaf area; light extinction coefficient; allocation of assimilates between root and shoot as well as among leaf, stem, and panicle; senescence coefficient of leaf; remobilization rates of carbohydrates to storage from reserve pools of stem, root, and leaf; drought sensitivity; and maximum rooting depth.

Calibration used the measured data from field experiment in 2008 under irrigated conditions (no drought stress) while validation used the measured data from field experiment in 2007
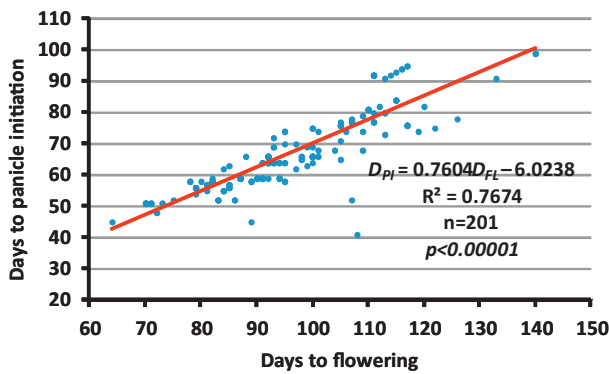
Fig. 2. The relationship between days to flowering and days to panicle initiation derived from field observations for various rice genotypes, environments, and agronomic practices across Asia.

Fig. 3. Histogram illustrating the distribution of drought stress of the 669 environments under rainfed condition. The drought stress is represented by the ratio of actual to potential evapotranspiration (ETa/ETp) during growth season under rainfed condition. Rainfed rice was safe in 37% of the 669 environments because of none to minor drought stress (ETa/ETp $\geq$ 0.9), suffered severe drought stress (ETa/ETp $\leq$ 0.60) in 28% of these environments, and experienced moderate drought stress (0.6 < ETa/ETp < 0.9).

under rainfed with drought stress conditions (see Section 2.2). The rice development rates in juvenile, photoperiod-sensitive, panicle development, and reproductive phases, which are the parameters controlling plant development, were calculated from observed phenological dates of sowing, transplanting, panicle initiation, flowering, and physiological maturity based on accumulative thermal time in each phase. However, the date for panicle initiation was not available in the case study. It was estimated by an empirical equation (Eq. (1)) derived from the detailed phenological data in field experiments conducted for various rice genotypes, environments, and agronomic practices across Asia (Fig. 2).

$$D_{PI} = 0.76 D_{FL} - 6.02 \tag{1}$$

where D_{FL} and D_{PI} are the days from sowing to flowering and to panicle initiation for a given genotype.

After calculation of the development rate for all 69 genotypes, for each genotype, its measured rice grain yield (GY) and total above-ground biomass (TB) were used as criteria in the calibration and validation to derive its crop parameters where the same set of parameters of development rates were used in both processes. The cropping and land management practices in the simulations of calibration and validation were set as what happened in field experiments, and field measured daily climate information and site-specific soil information was used in these processes.

2.4. Simulations across multiple environments

The objective of the case study was to evaluate the performance of drought-tolerant rice breeding lines in drought-prone environments; the drought stress was therefore the additional limiting factor to rice growth and yield in all simulations. To examine drought stresses of different severity that may exist naturally in environments, rice growth conditions in simulations were set as rainfed. Using calibrated and validated crop genetic parameters, simulations for 69 genotypes and 669 locations (environments) and a 10-year period were conducted to generate the data for evaluating the adaptability and stability of genotypes across multiple environments using ORYZA2000.

For each genotype in each environment, rainfed rice yield was computed by ORYZA2000 for 24 sowing dates in a year (starting on 1 January with 15 days interval) and a period of 10 years (i.e. 240 simulations). The settings for agronomic practices were the same in all simulations: 10 cm rice field bund height, transplanted 21-day-old seedlings, plant density of 1000 seedlings m^{-2} in the seedbed, 25 hills m^{-2} with 2 plants per hill in the main field, no nitrogen stress, no impact of pests and diseases, full water and nutrient supply in the seedbed, full nutrient supply in main field, and water management under rainfed conditions that was effective
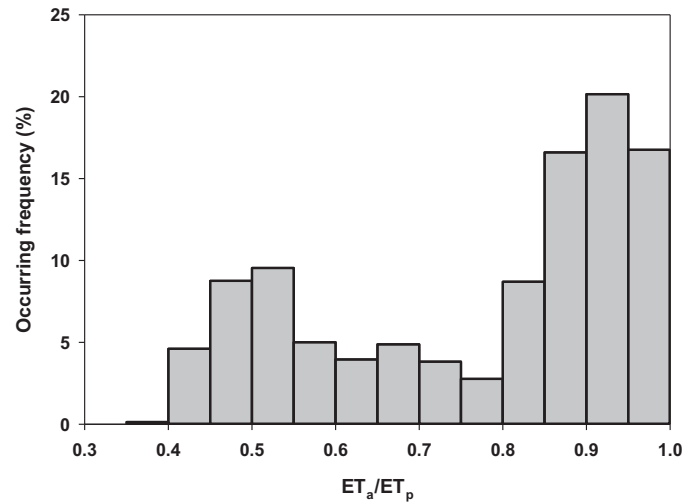
immediately after transplanting. With these simulation settings, possible water deficiency (drought stress) is only an additional factor limiting yield except for the local temperature and radiation conditions of the given environment. The simulated rainfed rice yield was defined as the simulated grain biomass plus 14% moisture content.

For a genotype, above simulations were repeated for all 669 environments. These simulations were further repeated for all 69 genotypes. The total number of simulations in the case study with 69 genotypes in 669 environments was 11,078,640.

The 669 environments in this study presented partial combinations of soil and weather types in the current rice production area of South Asia, and had none to severe drought stress to rainfed rice (Fig. 3). The available soil and weather information were in 5 arc-minutes and 2.18 arc-degrees of geographic resolutions, respectively. Referencing to the geo-coordinate of the 669 environment in South Asia, the soil information was extracted from World Inventory of Soil Emission Potential (WISE) (Batjes, 2006), while daily climate information for a period from 2009 to 2019 (weather information of 11 years were needed for simulation period of 10 years) was download from the CGCM projection results (http://www.cccma.ec.gc.ca/data/cgcm3/cgcm3.shtml).

2.5. Data analysis

2.5.1. Data reorganization

For each genotype in each environment, data matrix P is composed by the simulated rainfed rice yield (Eq. (2)), where the subscript k is the number of simulation years and s indicates the number of sowing dates in a simulation.

$$P = \begin{vmatrix} p_{11} & \cdots & p_{s1} & \cdots & p_{r1} \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ p_{1k} & \cdots & p_{sk} & \cdots & p_{rk} \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ p_{1l} & \cdots & p_{sl} & \cdots & p_{rl} \end{vmatrix} = p_{ks} \quad (k = 1, 2, 3, \cdots, r; \ s = 1, 2, 3, \cdots, l) \tag{2}$$

A best p_s can be selected from all p_{ks}, for which the average grain yield of a sowing date across all tested years is the highest

compared with that of all other sowing dates. The best p_s, which is a one-dimensional matrix p_k for a best rainfed sowing date, is the representative of maximum rainfed yield for a genotype in an environment.

All p_k for all genotypes and environments constitute a three-dimensional matrix A (Eq. (3)), where subscripts i, j and k are the numbers of genotypes, environments and years, respectively:

$$A = a_{ijk} \quad (i = 1, 2, 3, \cdots, n; j = 1, 2, 3, \cdots, m; k = 1, 2, 3, \cdots, r) \quad (3)$$

2.5.2. Data analysis for evaluation of genotype performance across environments

Conventional two-factor ANOVA with replication was first carried out with genotype and environment considered as two factors and the year treated as replication. Referencing Delacy et al. (1996), Atlin (2003), Verulkar et al. (2010), and Anputhas et al. (2011), from data matrix A in Eq. (3), the performance of genotype i in environment j and year k was modeled as y_{ijk} (Eq. (4)),

$$y_{ijk} = \mu + g_i + e_j + (ge)_{ij} + \varepsilon_{ijk} \quad (4)$$

where i, j, and k have the same means as in Eq. (3), μ is overall mean, g_i is the effect of the genotype i, e_j is the effect of the environment j, $(ge)_{ij}$ is the interaction effect associated with the genotype i and h environment j, and ε_{ijk} is the error component associated with each estimated yield.

From data matrix A and Eq. (4), variance components were also calculated. With the variance, the broad-sense heritability or repeatability (H) of performance over all genotypes and environments was calculated as Eq. (5) (Verulkar et al., 2010; Cooper et al., 1996):

$$H = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\sigma_{ge}^2}{m} + \frac{\sigma_e^2}{rm}} \quad (5)$$

where r represents the replications in an environment (years in the case study), m is the total number of environments, σ_g^2 is the genotypic variance, σ_{ge}^2 is the G × E interaction variance, and σ_e^2 is the error variance.

Using the heritability, the expected performance yield for a genotype was calculated as Eq. (6):

$$y_i = H\overline{a_{i..}} \quad (6)$$

where $\overline{a_{i..}}$ is the average yield of a genotype over all environments and all years.

Using data matrix A, the stabilities of a genotype on a spatial (multiple locations) (SS) and temporal (multiple years) (ST) scales were calculated as the inverse of variation coefficients:

$$SS_i = \frac{\overline{a_{i..}}}{sd_{\overline{a_{ij.}}}} \quad (7)$$

$$ST_i = \frac{\overline{a_{i..}}}{sd_{\overline{a_{i.k}}}} \quad (8)$$

where $sd_{\overline{a_{ji.}}}$ is the standard deviation for genotype i across multiple environments in which $\overline{a_{ij}}$ is the average yield of genotype i in multiple years for environment j. The $sd_{\overline{a_{i.k}}}$ is the standard deviation for genotype i across multiple years where $\overline{a_{i.k}}$ is the average yield of genotype i in multiple environments for year k.

Across all genotypes, the relative stability index for spatial (r_{ss}) and temporal stabilities (r_{st}) was the normalized results for the minimum and maximum values of all SS_i or ST_i, respectively, thus facilitating the identification of the top stable genotypes on a spatial and temporal scale.

3. Results and discussion

3.1. Calibration and validation of ORYZA2000

In the case study, the recorded crop phenology (dates of sowing and transplanting, and days to 50% flowering and harvest), measured crop GY and TB data in 2008 were used to calibrate crop parameters. Fig. 4a and b and Table 2 present the calibration results for 69 genotypes. During the calibration, the crop parameters were adjusted to achieve minimum difference between measured and simulated GY and TB. The simulated and measured GY and TB were highly correlated ($r^2 > 0.95$), with no significant difference and very low root mean square error ($RMSE_n < 4.2\%$). The model efficiency was close to 1.0 for both GY and TB, which implied that the measurements were nearly 100% captured by the model.

Using these calibrated crop parameters, a validation was conducted for all 69 genotypes under the environmental conditions of 2007 (severe drought stress, $ET_a/ET_p = 0.59$), in which management and weather conditions were different from those of 2008. Comparing validation with calibration results, the simulated TB and GY agreed with measurements to a lower degree (Fig. 4c and d), the $RMSE_n$ was 2–7 times higher, and model efficiency was also lower (Table 2). However, the simulated TB and GY were not significantly different from the measurements, and the $RMSE_n$ between simulated and measured values (<16%) was lower than the variation coefficient derived from replications of field measurements (24%). GY, which was the key output used in assessing the performance of breeding genotypes, was accurately estimated

Table 2
The statistical analysis results of model calibration using the data from an irrigated condition experiment at the Central Rice Research Institute, Cuttack, Orissa, India in 2008, and of model validation using data from a rainfed condition experiment at the Central Rainfed Upland Rice Research Station, Hazaribag, Jharkhand, India in 2007where the actual evapotranspiration was 65% of potential one during the growth season.

Item	Mean		Mean		Regression parameters			$p(t)$	RMSE	$RMSE_n$	M_e
	Mean	sd	Mean	sd	a	b	r^2				
Calibration											
TB	9.61	3.566	9.589	3.553	0.034	0.994	0.996	0.486	0.233	0.024	0.996
GY	2.65	0.630	2.618	0.613	0.078	0.959	0.971	0.386	0.110	0.042	0.969
Validation											
TB	5.437	0.805	4.904	0.787	0.000	1.259	0.670	0.471	0.822	0.151	0.055
GY	1.576	0.362	1.612	0.333	0.270	0.256	0.860	0.874	0.133	0.084	0.864

sd is the standard deviation of measured and modeled values.
a, b, and r^2 are the interception, slope, and correlation of regression analysis using measurements as X and modeled values as Y.
$p(t)$ is the probability of Student t test to refute the hypothesis of non-equal means.
RMSE is the root mean square error while $RMSE_n$ is the normalized RMSE by mean of measurements.
M_e is model efficiency with a value of 1.0 indicating that the model can represent the measurements by 100%.

by the model. In addition, the similar accuracy of this study to many prior modeling studies of ORYZA2000 with different rice varieties, locations (environments) and agronomic practices (Amiri and Rezaei, 2010, 2009; Belder et al., 2005; Boling et al., 2011, 2007, 2004; Bouman et al., 2007; Das et al., 2007; Feng et al., 2007; Jing et al., 2008, 2007; Kreye et al., 2009; Li et al., 2005, 2009; Soundharajan and Sudheer, 2009; Tuong et al., 2003; Xue et al., 2008; Yadav et al., 2011, 2012) also confirmed the capability of this model to estimate rice yield of multiple genotypes in environments. In summary, the model can estimate GY in very different environments (no drought stress in 2008 vs. severe drought stress in 2007) with acceptable accuracy. Using simulated GY, the performance of genotypes was evaluated by conventional G × E analysis methods introduced by Delacy et al. (1996), but it was examined for many more environmental conditions than those of a field MET.

3.2. Analysis of variance and estimates of variance component

Through the simulations for rainfed conditions, genotypes experienced various drought stresses across spatial and temporal scales due to various weather and soil conditions. For a given environment, different genotypes experienced different severities of drought stress because of the variations in genotypic drought tolerance and interactions between genotype and environment. The simulated maximum rainfed rice yield (MRY) was significantly influenced by genotypes, environments, and interactions of genotype and environment (Table 3). For the MRY, the magnitude of genotypic variance was found to be substantially greater than that of the magnitude of environmental variance. The means of G × E interaction and error variance were very minor in comparison with the means of other two types of variance. This finding was contrary to the results of Verulkar et al. (2010) for rice genotypes with a small number of environments, in which the G × E interaction and error variance were about 20% of genotypic variance (Table 3). With the increase in the number of environments, the influence of genotype on grain yield was isolated from the influences of environment and interaction of G × E. This isolated genotypic influence was helpful for the effective selection of breeding lines.

With a large number of environments, genotypes experienced different severities of drought stress varying from no stress to very severe stress (Fig. 3). The heritability with a large number of environments was calculated to be 0.9993 (≈1.0) (Eq. (4)). This heritability was much higher than what Venuprasad et al. (2007), Kumar et al. (2008), and Verulkar et al. (2010) reported. High heritability values for grain yield indicated that selection for
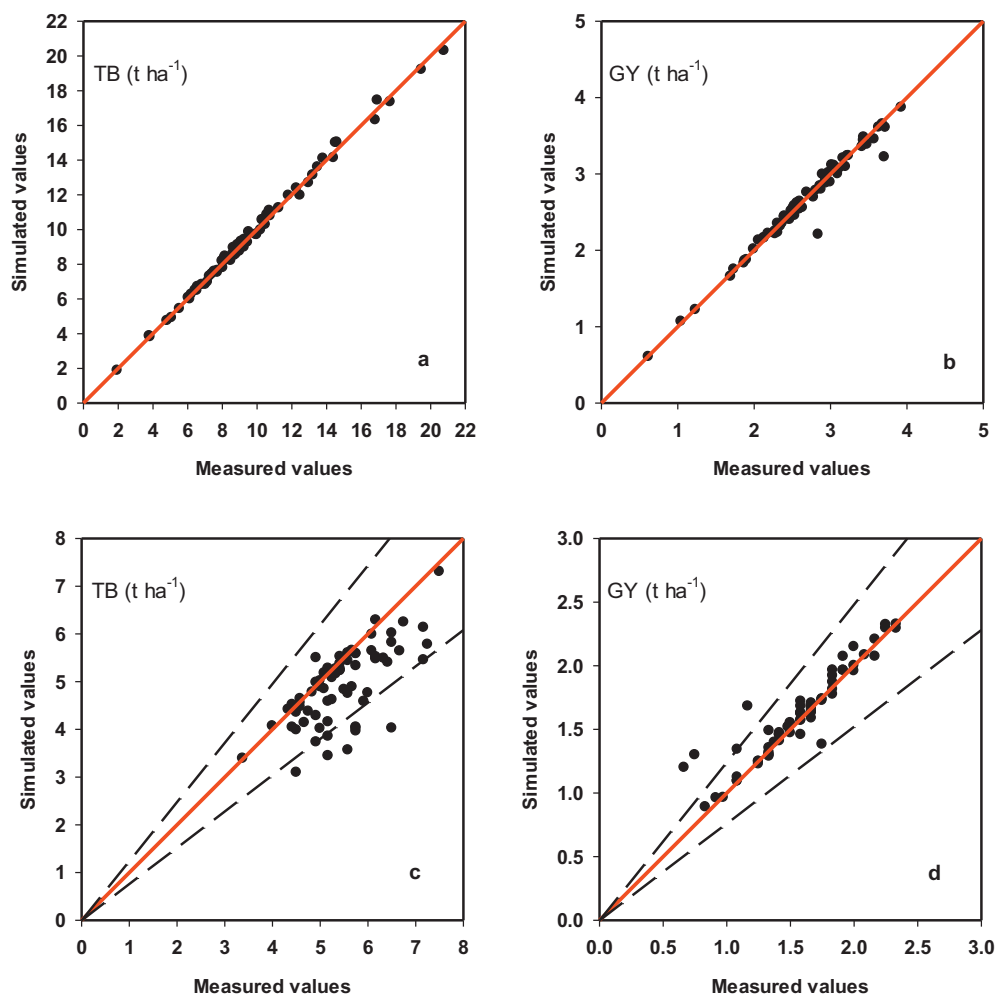

Fig. 4. The measurements and simulated total above-ground biomass (TB) and grain yield (GB) for calibration (a and b) and validation (c and d) datasets. The calibration dataset is the field measurements of advanced yield trials (AYT) with 100–120 days growth duration at the Central Rice Research Institute, Cuttack, Orissa, India, in 2008 under full irrigation, and the validation dataset is the field measurements of an AYT at the Central Rainfed Upland Rice Research Station, Hazaribag, Jharkhand, India, in 2007 under severe drought stress (ETa/ETp = 0.59).

Table 3
The results of ANOVA using simulated maximum rainfed grain yield for 69 breeding entries (genotypes) and 669 environments across South Asia. A 10-year period was treated as a replication in each environment, and the reference results of ANOVA re-estimated from Table 3 of Verulkar et al. (2010), which was derived from field experimental data with 36 genotypes and 4–7 environments in 3 years in South Asia, the study area. Some genotypes were used in both studies.

Source of variation	SS	df	MS	F	P-value	F crit
The results from this study using simulation data						
Environment (E)	1,090,615.31**	668	1632.66	617.68	0.00	1.09
Genotype (G)	988,885.36**	68	14,542.43	5501.81	0.00	1.30
G × E	352,465.90**	45,424	7.76	2.94	0.00	1.01
Residual (error)	1,098,118.68	415,449	2.64			
Total	3,530,085.25	461,609				
Reference results re-estimated from Table 3 of Verulkar et al. (2010)						
Environment (E)	292,001.00	(14)	(20,857.21)	(62.42)		
Genotype (G)	98,113.00*	35	(2803.23)	(8.39)		
G × E	251,454.33*	(490)	(513.17)	(1.54)		
Residual (error)	327,466.67*	(980)	(334.15)			
Total	969,035.00	(1619)				

SS is square summary of difference, *df* is degrees of freedom, *MS* is mean of *SS*, and numbers in brackets were derived from text information, but not direct data in tables in the paper of Verulkar et al. (2010).

** Significant level of 0.01 in the ANOVA analysis.
* Significant level of 0.05 in the ANOVA analysis.

yield under drought stress was highly repeatable. Indeed, crop modeling techniques can improve breeding by expanding MET results from a small number of environments to numerous environments.

3.3. Performance of genotypes across environments

Table 4 presents the MRY and stability across spatial and temporal scales for all genotypes in the case study. Among 69 examined genotypes, the expected MRY varied from less than $0.4 \, t \, ha^{-1}$ to up to $8.3 \, t \, ha^{-1}$. Fig. 5 illustrates the range of simulated MRY of 69 genotypes over environments. The measurements from an irrigated environment at the Central Rice Research Institute, Cuttack, Orissa, India, in 2008 were in the range except for 5 out of 69 genotypes. This result confirmed that the

simulation outputs for multiple environments were highly reliable.

The purpose of breeding line selection is to choose for genotypes with both higher yield and good stability across various environments. If both spatial and temporal stability indices were higher than 0.75 (i.e. stability in the top 25% of all 69 genotypes), genotypes ARB5 and IR78908-142-B-3-B had yield higher than $2 \, t \, ha^{-1}$, and only ARB5 had yield above $3 \, t \, ha^{-1}$ (Table 4). Similarly, if both spatial and temporal stability indices were higher than 0.5, 9 genotypes (ARB3, IR78875-23-B-2-B, IR78908-105-B-2-B, IR79959-B-217-1-2, RF5329, IR77778-B-8-1-2-1, IR78875-123-B-4-B, IR79899-B-179-2-3, and IR79906-B-192-2-3) were expected to have MRY higher than $4 \, t \, ha^{-1}$, and the last 4 genotypes yielded higher than $5 \, t \, ha^{-1}$ while the MRY for IR79906-B-192-2-3 even surpassed $6 \, t \, ha^{-1}$.
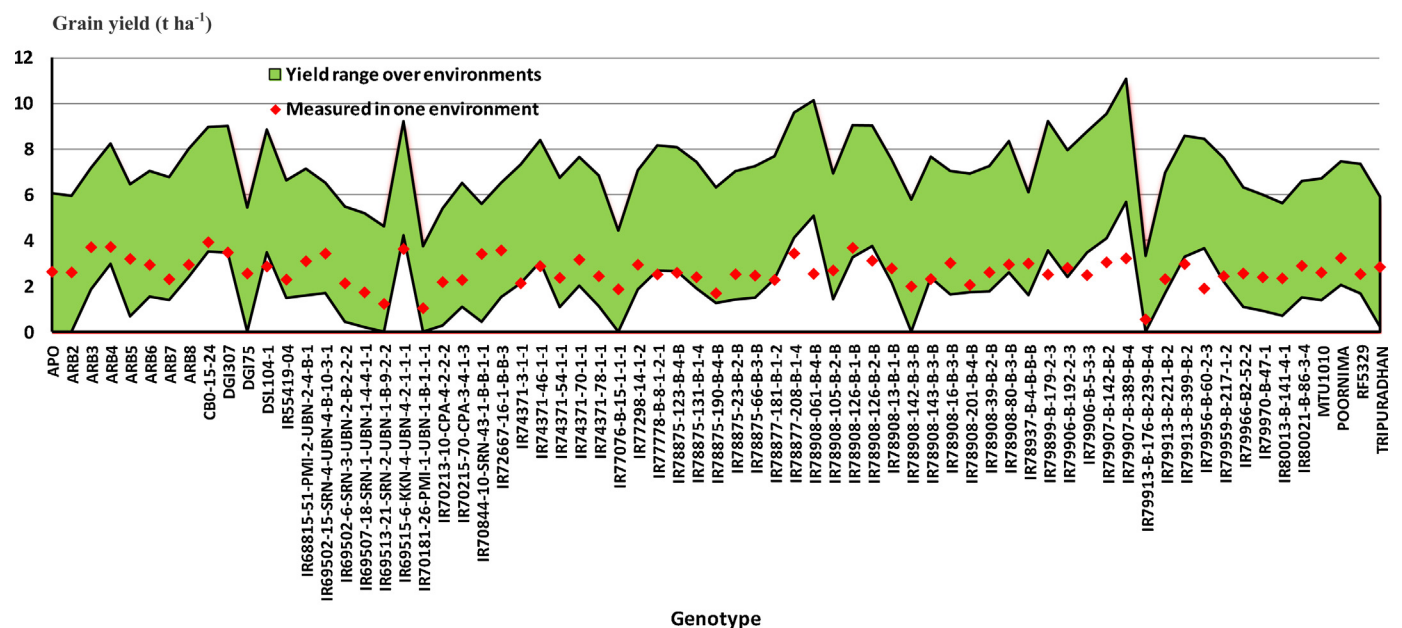

Fig. 5. The varying ranges of simulated maximum rainfed grain yield over all environments (shaded area) and measured yield (dots) and measured deviation in irrigated conditions for all 69 genotypes.

Table 4

Expected maximum rainfed yield for genotypes pooled across environments (location × year × various drought stress), relative stability index of yield across spatial (r_{ss}) and temporal (r_{st}) scales, and combined identification of genotypes.

Genotype	Yield (t ha⁻¹)	Relative stability index		Stability in top 25% (r_{ss} and $r_{st} \geq 0.75$) and yield level		Stability in top 50% (r_{ss} and $r_{st} \geq 0.5$) and yield level		
		r_{ss}	r_{st}	≥2.0	≥3.0	≥3.0	≥4.0	≥5.0
APO	3.03	1.00	0.32					
ARB2	2.93	0.98	0.54					
ARB3	4.52	0.52	0.61			✓	✓	
ARB4	5.61	0.48	0.21					
ARB5	3.57	0.81	0.95	✓	✓	✓	✓	
ARB6	4.29	0.63	0.24					
ARB7	4.08	0.56	0.19					
ARB8	5.21	0.69	0.06					
CB0-15-24	6.24	0.60	0.26					
DGI307	6.25	0.66	0.23					
DGI75	2.71	0.61	0.64					
DSL104-1	6.17	0.55	0.00					
IR55419-04	4.06	0.41	0.87					
IR68815-51-PMI-2-UBN-2-4-B-1	4.37	0.66	0.30					
IR69502-15-SRN-4-UBN-4-B-10-3-1	4.11	0.21	0.40					
IR69502-6-SRN-3-UBN-2-B-2-2-2	2.96	0.35	0.29					
IR69507-18-SRN-1-UBN-1-4-4-1-1	2.70	0.31	0.89					
IR69513-21-SRN-2-UBN-1-B-9-2-2	2.15	0.28	0.44					
IR69515-6-KKN-4-UBN-4-2-1-1-1	6.73	0.31	0.21					
IR70181-26-PMI-1-UBN-1-B-1-1-1	0.80	0.87	0.64					
IR70213-10-CPA-4-2-2-2	2.84	0.40	0.44					
IR70215-70-CPA-3-4-1-3	3.80	0.58	0.53			✓		
IR70844-10-SRN-43-1-B-B-1-1	3.02	0.42	0.21					
IR72667-16-1-B-B-3	4.02	0.32	0.23					
IR74371-3-1-1	4.73	0.44	0.82					
IR74371-46-1-1	5.73	0.52	0.33					
IR74371-54-1-1	3.92	0.73	1.00			✓		
IR74371-70-1-1	4.84	0.71	0.30					
IR74371-78-1-1	3.98	0.77	0.35					
IR77076-B-15-1-1-1	1.95	0.29	0.31					
IR77298-14-1-2	4.47	0.45	0.93					
IR77778-B-8-1-2-1	5.43	0.61	0.59			✓	✓	✓
IR78875-123-B-4-B	5.37	0.59	0.52			✓	✓	✓
IR78875-131-B-1-4	4.67	0.65	0.40					
IR78875-190-B-4-B	3.79	0.35	0.16					
IR78875-23-B-2-B	4.23	0.71	0.83			✓	✓	
IR78875-66-B-3-B	4.37	0.80	0.15					
IR78877-181-B-1-2	5.01	0.55	0.44					
IR78877-208-B-1-4	6.87	0.61	0.42					
IR78908-061-B-4-B	7.61	0.34	0.26					
IR78908-105-B-2-B	4.18	0.64	0.65			✓	✓	
IR78908-126-B-1-B	6.16	0.80	0.27					
IR78908-126-B-2-B	6.40	0.49	0.21					
IR78908-13-B-1-B	4.84	0.55	0.37					
IR78908-142-B-3-B	2.90	0.81	0.91	✓				
IR78908-143-B-3-B	5.02	0.50	0.82					
IR78908-16-B-3-B	4.34	0.57	0.21					
IR78908-201-B-4-B	4.33	0.44	0.38					
IR78908-39-B-2-B	4.52	0.62	0.47					
IR78908-80-B-3-B	5.48	0.78	0.38					
IR78937-B-4-B-B-B	3.86	0.00	0.32					
IR79899-B-179-2-3	6.39	0.73	0.76			✓	✓	✓
IR79906-B-192-2-3	5.18	0.66	0.74			✓	✓	✓
IR79906-B-5-3-3	6.13	0.50	0.40					
IR79907-B-142-B-2	6.83	0.60	0.42					
IR79907-B-389-B-4	8.39	0.55	0.12					
IR79913-B-176-B-239-B-4	0.37	0.88	0.09					
IR79913-B-221-B-2	4.33	0.49	0.89					
IR79913-B-399-B-2	5.94	0.50	0.51					
IR79956-B-60-2-3	6.06	0.18	0.64					
IR79959-B-217-1-2	4.90	0.58	0.58			✓	✓	
IR79966-B2-52-2	3.71	0.46	0.89					
IR79970-B-47-1	3.46	0.37	0.13					
IR80013-B-141-4-1	3.17	0.27	0.27					
IR80021-B-86-3-4	4.05	0.38	0.25					
MTU1010	4.05	0.52	0.07					
Poornima	4.76	0.57	0.29					
RF5329	4.52	0.74	0.70			✓	✓	
Tripuradhan	3.07	0.76	0.58			✓		

4. Conclusions

Field selection of drought-tolerant varieties through the drought breeding network, which included multiple experimental locations and field experiments with different degrees of drought stress has proved to be a successful approach. Using data from field selection, the modeling approach exposes genotypes to a larger number of environments and various degrees of drought stress than multiple environment trials. By increasing the variation in environment, the influence of genotype on grain yield can be isolated from that of environment and interaction of genotype and environment. Thus, selection by crop modeling techniques for grain yield, as a 'virtual' selecting platform, is effective and highly repeatable, which can accelerate the selection process and reduce selection costs.

Acknowledgment

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fcr.2013.05.006.

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