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Phenotypic stability and homeostasis in Assam rice landraces at varying nitrogen regimes

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Abstract

Aim : The present study was designed to identify stable rice (*Oryza sativa* L.) genotypes for nitrogen use efficiency (NUE), yield and its component traits and also to identify component traits associated with yield stability.

Methodology : Twenty-one landraces along with five high yielding varieties (HYVs) of rice were evaluated at three nitrogen levels (0, 40 and 60 kg N ha⁻¹) for two years (2014 and 2015). Eberhart and Russel's (1966) stability analysis were employed to assess the genotype × environment (GE) interaction and the stability of the genotypes across six environments. To study homeostasis, simple correlation analysis among ten different traits was done based on stability parameters.

Results : The present study revealed that environments created by graded nitrogen levels were fruitful for inducing environmental variations. The highly significant linear environmental variances were found for all ten traits. Linear GE interaction was significant for all the traits, except harvest index, grain nitrogen and nitrogen harvest index. The stability analysis identified four genotypes viz., Kolabor, Aki Bora, Rongdoi and Luha Sali with average stability whereas Betguti Sali was found to be stable below average. Correlation analysis based on stability parameters revealed the existence of homeostasis.

Interpretation: Present study revealed that genotypes namely Kolabor, Aki Bora, Rongdoi and Luha Sali are suitable to grow under both nitrogen limiting and nitrogen non-limiting environments whereas Betguti Sali was suitable for nitrogen non-limiting environments. Correlation analysis, based on stability parameters, revealed that yield stability was due to the plasticity of some other component traits under study.

Key words: GE interaction, Homeostasis, Landrace, Nitrogen use efficiency, *Oryza sativa*

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Introduction

Rice crop is grown in such an environment which is highly conducive to nitrogen loss. Among various biotic and abiotic factors, low NUE is a major constraint in agricultural systems, especially under lowland rice ecosystem. Nitrogen plays a key role in chlorophyll synthesis, formation of proteins and nucleic acids, and hence it is considered a major nutrient which is required more frequently and in large quantity than any other nutrient for rice production (Shadchina and Dmitrieva, 1995; Chen *et al.*, 2014). In order to get maximum productivity, nitrogen fertilizer is widely used by farmers, but applied nitrogen is not being used properly, thus expected yield can't be realized (Tian *et al.*, 2017). In most of the rice-producing regions of the world, nitrogen is one of the most yield limiting nutrients for rice production (Fageria and Baligar, 2001; Fageria and Barbosa Filho, 2001). It has, therefore, become urgent to breed rice varieties which can uptake nitrogen more efficiently even under nitrogen limiting environments. For abiotic stress improvement in crops, NUE has become second priority after drought, both in the private and public sector (Hirel *et al.*, 2011). Use of nitrogen efficient genotypes is an important complementary strategy in improving rice yield and reducing the cost of the production (Fageria and Barbosa Filho, 2001).

In Assam, most of the rice cultivated area is under lowland rice ecosystem, where winter/Kharif rice (June/July to November/December) is dominating crop of the state covering 17 lakh ha and contributing 73% of the total rice production (Ahmed *et al.*, 2010). Most cereal crops utilize only 30-40% of the applied nitrogen (Raun and Johnson, 1999) and the remaining portion is lost through a combination of leaching, surface run-off, denitrification, volatilization and microbial consumption (Fageria and Baligar, 2005), resulting in unexpected reduced yield per unit area. This low productivity discourage farmers to adopt input-intensive rice production technology during this season. It is estimated that 1% increase in NUE can save ~ \$1.1 billion annually (Kant *et al.*, 2012). Hence, attempts have to be made to develop rice varieties with higher NUE, which would be useful for low nitrogen input cultivation system (Glass, 2003; Kumagai *et al.*, 2009). NUE mainly depends on the nutrient status of soil, water availability, light intensity and disease infestation, and it fluctuates with changing the environmental conditions due to high GE interaction. Therefore, assessment of GE interaction for NUE, grain yield and its component traits is the need of the hour. Stability analysis facilitates in identifying suitable genotype(s) for the target environments.

Northeast India, particularly Assam is a biodiversity hotspot for rice and indigenous landraces of the region exhibit huge genetic diversity and valuable gene systems for future crop improvement to meet the ever-increasing demand for food production. Landraces of rice are in essence mixtures of pure lines and thus possess variability within them to resist unpredictable environmental changes more efficiently than the modern HYVs. (Joshi *et al.*, 2018). Further, landraces developed

a type of genetic homeostasis consequent upon considerable heterozygous balance maintained during the course of their long history of cultivation. Heterozygotes in these populations are the results of occasional cross-pollination between plants and subsequent segregation of heterozygous plants (Perez de la Vega and Garcia, 1997). Such genetically dynamic populations display equilibrium with the environment (Harlan, 1992). Many potential landraces of rice are increasingly replaced by HYVs to meet the growing food requirements. Despite being less productive they are known to have a high genetic variance for several biotic and abiotic stresses which make them valuable for rice breeding (Hanamaratti *et al.*, 2008; Huang *et al.*, 2010). Thus, rice landraces may serve as immediate potential genetic resources for low input or organic agriculture as it offers the most suitable solution for developing the agriculture sector and provides food security with the least negative impact on the environment.

Till date, not much effort has been made for evaluation of these potential rice germplasm of Assam for NUE and its stability. Thus, the opportunity ahead is to identify the outstanding nitrogen use efficient genotypes to sustain rice yields in low input or organic farming, and for further breeding high yielding nitrogen use efficient varieties suitable for rainfed lowland rice ecosystem. The present study was designed to evaluate a panel of twenty-six randomly selected rice genotypes adapted to lowland rice ecosystem of Assam under different nitrogen environment in order to assess NUE and other traits through stability analysis and to identify potential genotype (s) for evaluation under low input or organic farming and for recombination breeding.

Materials and Methods

Experimental materials and crop management: Field experiments were carried out during Kharif 2014 and 2015 at the Instructional-cum-Research Farm of Assam Agricultural University (AAU), Jorhat. Twenty-six winter rice genotypes consisting of Twenty-one landraces randomly sampled from different localities of Assam and five modern varieties developed by AAU, Jorhat were used in the present study. All the genotypes belong to late maturing group (140-170 days). The landraces were intermediate to tall (>110 cm) in stature while the modern varieties are semi-dwarf (<110 cm). The experiments were carried out in three different environments in the main field with variable nitrogen fertilization E1: 0 kg N ha⁻¹, E2: 40 kg N ha⁻¹ and E3: 60 kg N ha⁻¹ with fixed P and K @ 20 kg ha⁻¹. A randomized complete block design was followed in each environment with three replications.

The NPK doses were applied in the form of urea, single super phosphate [Ca(H₂PO₄)₂] and muriate of potash (KCl). One half of the total requirement of urea was applied at the time of final land preparation as a basal dose. The remaining urea was applied in two equal splits as top dressing at tillering and panicle initiation stage. Full doses of Ca(H₂PO₄)₂ and KCl along with vermicompost (contains 1% N, 0.25% P and 0.5% K) @ 10 t ha⁻¹

were applied as basal at the time of final land preparation. Thirty-five-day old seedlings were transplanted in the main field at a spacing of 20×20 cm in a plot of 6m×1m having five rows and standard management practices were followed.

Soil characteristics and meteorological observations: The soil of the experimental site belonged to the order Inceptisols with sandy loam texture and pH 4.8. Soil samples were randomly collected before land preparation from different spot of the experimental field for NPK estimation. The status of organic carbon (1.22%) and available potash (189.20 kg ha⁻¹) was medium and available nitrogen (211.35 kg ha⁻¹) and phosphate (14.08 kg ha⁻¹) was low. The minimum and maximum temperature ranged between 22°C to 31°C and 21°C to 30°C during *Kharif* 2014 and *Kharif* 2015, respectively. During the crop season, total rainfall was 43 mm in 2014 and 45 mm in 2015.

Observations on plant traits: A random sample of ten hills per plot was observed for ten different traits viz., panicle length (PL), spikelet fertility (SF), 1000-grain weights (TGW), biological yield (BY), grain yield (GY), harvest index (HI), grain nitrogen (Ng), physiological nitrogen use efficiency (PNUE), nitrogen utilization efficiency (NUE) and nitrogen harvest index (NHI). The plant nitrogen content was determined by Micro-Kjeldahl's method (Jackson, 1974). In the present investigation, PNUE was determined as the ratio of biomass production to total plant nitrogen at maturity (Matsunami *et al.*, 2013), and NUE and NHI were estimated following the method of Moll *et al.* (1982) and Singh *et al.* (1998), respectively.

Statistical analyses: Six environments were characterized based on weather data and simple regression analysis was performed in MS Excel 2007. The mean data for six environments were subjected to pooled analysis of variance over environments to study GE interaction and phenotypic stability as per model suggested by Eberhart and Russel (1966). Stability analysis was performed in Windostat v. 9.2. Simple correlation coefficients were calculated among ten different traits based on stability parameters and their significance (at 1% and 5%) were tested using t-test with (n-2) degrees of freedom (d.f.) (Gomez and Gomez, 1968).

Results and Discussion

In order to predict the environmental difference under study, regression lines were fitted taking nitrogen levels at Y-axis and NUE related traits and GY at X-axis which revealed linear relationship of these traits with nitrogen levels. There was a positive linear relationship of nitrogen level with Ng (Fig. 1A) and GY (Fig. 1E) corroborates previous studies of Kang *et al.* (2013) for Ng and Zhang *et al.* (2009) for GY. Though graded nitrogen levels were different, but similar trend was observed. However, the slope of regression was negative in PNUE (Fig. 1B), NUE (Fig. 1C) and NHI (Fig. 1D) implying that the average increase in nitrogen levels corresponds to decrease of these traits (Zhang *et al.*, 2009; Artacho *et al.*, 2009). These findings revealed

differential responses of each trait with varying nitrogen levels. Thus, these environments created by graded nitrogen levels were effective in inducing environmental variations to assess GE interaction with respect to nitrogen levels.

The analyses of variance for stability of traits revealed significant differences among the genotypes for all traits over the environments (Table 1). The highly significant linear environmental variance for all traits suggested considerable difference among the environments and their predominant effect on the traits. The linear GE interaction was significant for all the traits, except HI, Ng and NHI, indicating predictable phenotypic performance in varying test environments. The pooled deviations were significant for all the traits, except HI and NUE. Further, both linear GE interaction and pooled deviation mean squares were found to be significant for the traits namely PL, SF, TGW, BY, GY and PNUE, suggesting that GE interaction was due to both linear and non-linear components for these traits. For the trait NUE, linearity was most evident from the significant linear GE interaction alone. These results indicated that variation among the genotypes could be largely explained by differences in regression slopes for most of the traits. Thus, the response of genotypes to the changing environments could be portrayed as orderly and predictable with respect to these traits. The phenotypic performance of genotypes could not be accurately predicted for Ng and NHI showing significant non-linear component of GE interaction. The significant linear and non-linear GE interaction for various traits in rice has been reported by Singh *et al.* (2016) and Ajmera *et al.* (2017) which confirm the findings of the present investigation.

Eberhart and Russell (1966) proposed regression coefficient (b_i) as a parameter of response or sensitivity to environmental changes while deviation from regression (S^2_{di}) measures the stability of the genotypes. According to Eberhart and Russell (1966), a stable genotype is one which shows high trait mean, unit regression ($b_i = 1$) and least deviation from regression ($S^2_{di} = 0$). Genotype is considered to be 'below average stable' if regression coefficient is significantly greater than unity ($b_i > 1$) and 'above average stable' if regression is significantly less than unity ($b_i < 1$). In the present study, the result of the stability analysis (Table 2) revealed that four genotypes namely Kolabor, Aki Bora, Rongdoi and Luha Sali exhibited average stability for GY while Betguti Sali was found to be below average stable. The genotypes Kolabor, Betguti Sali, Mashuri and Ranjit were registered as average stable and Luha Sali exhibited below average stability for NHI. Similarly, for NUE, Lothabor, Luha Sali, Kolabor, Aki Bora and Gitesh exhibited average stability and Betguti Sali was found to be below average stable. The genotypes Luha Sali, Betguti Sali, Aki Bora and Manohar Sali were found to be average stable for PNUE. For HI, Luha Sali, Kolabor, Aghoni Bora and Gitesh had average stable. Similarly, Lothabor, Aki Bora, Mal Bhog, Kon Joha and Manohar Sali registered as average stable for BY. Average stability for TGW has been found in Kolabor, Betguti Sali, Moina Bora and Aki Bora. Kabori and Jahinga had average stability for SF. Similarly, for PL, Kolabor and Aki Bora were recognized as average stable.

Fig. 1: Relationship of N levels with (A) Ng, (B) PNUE, (C) NUtE, (D) NHI and (E) GY. The line represents fitted function.

The grain yield of rice fluctuates considerably with the change in environmental conditions (Al-Salim *et al.*, 2016). Hence, a variety possessing stability for yield is desirable for minimizing the risk of yield loss in harsh environments of unpredictable rainfed lowland ecosystem. The high yielding genotypes with average stability for GY were Kolabor, Aki Bora, Rongdoi and Luha Sali which also exhibited average stability for other traits. Kolabor registered as average stable for the majority of the traits including Ng, NHI, NUtE, PNUE, BY, HI, PL and TGW, and the latter six traits also being average stable for Aki Bora.

Likewise, both Rongdoi and Luha Sali were also found to be average stable for NUtE, PNUE and HI. Rongdoi had average stability for NHI and BY as well. Thus, these landraces were most desirable for stable yield performance with greater adaptation in the test environments. However, the genotype Betguti Sali having below average stability for GY and NUtE would be suitable for nitrogen non-limiting environments.

Pearson correlation coefficients among the traits based on mean values revealed strong positive correlations of PL

Table 1: Pooled analysis of variance for stability of 26 winter rice genotypes over 6 environments for NUE, yield and related traits

Source of variation	d.f.	PL (cm)	SF (%)	TGW (g)	BY (g)	HI
Varieties	25	25.395**	139.972**	76.262**	133.516**	0.008**
Env. + (Variety × Env.)	130	2.136**	35.326*	1.066**	29.218**	0.001
Environments (Linear)	1	112.810**	639.109**	34.449**	2552.531 **	0.027 **
Variety × Env. (Linear)	25	2.001*	50.821**	2.139**	15.528*	0.001
Pooled Deviation	104	1.104**	25.796**	0.487**	8.247**	0.001
Pooled Error	300	0.170	2.785	0.201	4.952	0.001
Total	155	5.887	52.205	13.194	46.040	0.002
Source of variation	d.f.	Ng (%)	PNUE (kg kg ⁻¹)	NUtE(kg kg ⁻¹)	NHI (%)	GY (g)
Varieties	25	0.091**	27.201**	6.423**	46.214**	34.753**
Env. + (Variety × Env.)	130	0.067**	14.796**	1.881**	25.271**	7.370**
Environments (Linear)	1	6.649 **	1445.281 **	172.745 **	2572.393 **	691.190 **
Variety × Env. (Linear)	25	0.021	7.203**	1.185**	6.920	3.173*
Pooled Deviation	104	0.015**	2.866**	0.405	5.190**	1.804*
Pooled Error	300	0.004	1.806	0.493	2.235	1.289
Total	155	0.071	16.797	2.613	28.648	11.787

**Significant at 1% level of probability; *Significant at 5% level of probability

Table 2: Stability status of rice genotypes under study on the basis of stability parameters

	GY (g)	NHI (%)	NUtE (kg kg ⁻¹)	PNUE (kg kg ⁻¹)	Ng (%)	HI	BY (g)	TGW (g)	SF (%)	PL (cm)
Genotypes with AS	Kolabor Aki Bora Rongdoi Luha Sali	Kolabor Betguti Sali Mashuri Ranjit Gitesh	Lothabor Luha Sali Kolabor Aki Bora	Luha Sali Betguti Sali Aki Bora Manohar Sali		Luha Sali Kolabor Aghoni Bora Gitesh Manohar Sali	Lothabor Aki Bora Mal Bhog Kon Joha	Kolabor Betguti Sali Moina Bora Aki Bora	Kabori Jahinga	Kolabor Aki Bora
Genotypes with BAS	Betguti Sali	Luha Sali	Betguti Sali							
Genotypes with AAS					Mashuri Ranjit			Manohar Sali Khaui	Moina Bora Aghoni Bora	

AS: Average stability; BAS: Bellow average stability; AAS: Above average stability

(0.6938), SF (0.4979), TGW (0.5126), BY (0.6770), HI (0.6136), PNUE (0.6867), NHI (0.4998) and GY (0.9372) with NUtE. A strong positive correlation with NUtE was exhibited by Ng and PNUE with respect to 'bi' values and GY for 'S²di' values. Therefore, any generalization regarding the stability of a genotype for all the traits is too difficult as the genotypes did not exhibit uniform responses and stability patterns. These two attributes namely, responsiveness and stability appeared to be specific for individual traits of a given genotype and were not similar for all the traits of that genotype. It is well known that yielding ability and response to environmental changes are two independent attributes of a genotype and are governed by separate gene systems (Singh and Gupta, 1984). Thus, bringing together of diverse gene constellations for the stability of several

attributes into a single genotype would provide stable genotype for most of the traits.

The desirable genotypes may show low GE interaction for agriculturally important traits but, at the same time, be more flexible for the other traits; such genotypes are said to be 'well buffered', as they can adjust their genotypic states in response to environmental changes and this phenomenon is called genetic homeostasis (Lerner, 1954). The plasticity of certain yield components and stability in some other yield component compensates in such a way as to result in stability in yielding ability (Grafius, 1956). Grafius (1956) emphasized that the studies of individual GY components could lead to a simplification of genetic explanation of yield stability. If traits associated with high yield stability could be found, the plant breeder might

Table 3 : Pearson correlation coefficients among the traits for mean values

Traits	PL	SF	TGW	BY	HI	Ng	PNUE	NUtE	NHI
PL									
SF	0.3659								
TGW	0.6768**	0.6556**							
BY	0.6411**	0.3113	0.4716*						
HI	0.1788	0.3673	0.2084	-0.0383					
Ng	0.1282	0.0558	0.1092	0.4184*	0.4069*				
PNUE	0.7037**	0.3381	0.5094**	0.8948**	-0.1385	0.0033			
NUtE	0.6938**	0.4979**	0.5126**	0.6770**	0.6136**	0.3017	0.6867**		
NHI	0.3288	0.1396	0.2205	0.5304**	0.4212*	0.9060**	0.2171	0.4998**	
GY	0.6069**	0.4450*	0.4531*	0.7256**	0.6531**	0.5924**	0.5789**	0.9372**	0.6908**

**Significant at 1 % level of probability; *Significant at 5 % level of probability

Table 4 : Pearson correlation coefficients among the traits for bi values

Traits	PL	SF	TGW	BY	HI	Ng	PNUE	NUtE	NHI
PL									
SF	0.0555								
TGW	-0.1664	-0.1278							
BY	0.1081	0.0396	-0.1109						
HI	0.3479	0.1246	0.1357	-0.4068*					
Ng	0.2453	0.1020	0.0426	0.4895*	0.1774				
PNUE	-0.0051	0.1849	0.0878	-0.0129	0.2611	0.5474**			
NUtE	-0.1181	0.1036	0.2317	0.2623	-0.1565	0.4481*	0.6051**		
NHI	0.0018	0.0978	-0.1862	-0.3742	0.1101	-0.4875*	0.0103	-0.0633	
GY	0.4789*	0.0782	0.0580	0.5391**	0.4903*	0.6964**	0.2489	0.1990	-0.2383

**Significant at 1 % level of probability; *Significant at 5 % level of probability

Table 5 : Pearson correlation coefficients among the traits for S²di values

Traits	PL	SF	TGW	BY	HI	Ng	PNUE	NUtE	NHI
PL									
SF	0.2266								
TGW	0.0024	0.1207							
BY	-0.1266	0.0897	-0.1427						
HI	-0.3168	0.0207	0.1490	-0.2569					
Ng	0.0598	-0.0698	-0.1390	0.2123	0.1393				
PNUE	-0.0784	-0.0600	0.0326	0.0141	0.3378	0.5758**			
NUtE	-0.1319	-0.0169	0.0210	0.2309	0.1495	0.2602	0.4449*		
NHI	-0.2216	0.0038	-0.0317	0.1151	0.3282	0.2318	0.3397	0.3179	
GY	-0.3387	-0.2251	0.0695	0.3771	0.3236	0.3661	0.2635	0.6188**	0.3525

**Significant at 1 % level of probability; *Significant at 5 % level of probability

effectively select for GY stability by selecting for these correlated traits. Thus, to know the genetic association of GY with its component traits and among them, correlation analysis based on stability parameters was done. Correlation studies based on mean values (Table 3) revealed that all the traits had a significant

positive correlation with GY. This result was in agreement with the findings of Fageria and Barbosa Filho (2001). Further, most of these traits were interrelated among themselves. The 'bi' values for GY were significantly and positively associated with those for Ng, PL, BY and HI (Table 4), indicating that the genotypes had

similar responses to the change in environment with respect to these traits. However, correlations of 'S²d' values of these traits with that of GY were non-significant (Table 5). Correlations based on non-linear component revealed that 'S²d' value of NUTe exhibited significant positive correlation with value of GY; suggesting that stability for GY and NUTe could be simultaneously improved. These findings suggested that a genetic homeostatic device operating in a rice landrace in response to environmental fluctuations might play an important role in the expression and compensation of the component traits finally conferring yield stability of the genotype.

The landraces provide traits for more efficient nutrient uptake and utilization and are sources of useful genes for adaptation to stress environments (Dwivedi *et al.*, 2016) and thus can cope with climate changes. The genetic diversity of traditional landraces is the most immediately useful and economically valuable component of rice biodiversity (Wood and Lenne, 1997). In the present study, we identified four promising stable landraces viz., Kolabor, Aki Bora, Rongdoi and Luha Sali across the varying nitrogen regimes. These landraces could serve as immediate breeding material for evaluation under low input or organic farming situation. The other potential use of traditional varieties could be breeding for both nitrogen limiting and nitrogen non-limiting environments.

A highly nitrogen-responsive landrace Betguti Sali could be used for developing nitrogen-responsive HYVs. The landraces have a long history of cultivation in the farmers' field and these could be grown in other areas of small farmers and marginal environment with minimal testing. A systematic evaluation of landraces will unveil the pattern of diversity and facilitate identifying the alleles for yield enhancement and abiotic stress adaptation, thus raising the productivity and stability of crops in vulnerable environments. Therefore, a further study with these diverse genotypes was suggested to understand the genetics of NUE and linking the traits of interest to appropriate molecular markers for precision breeding.

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