

Heritability, Correlation and Path Analysis among Yield and Yield Attributing Traits for Drought Tolerance in an Interspecific Cross Derived from *Oryza sativa* x *O. glaberrima* Introgression Line under Contrasting Moisture Regimes

Surapaneni SAIKUMAR^{1,2,3,*}, Akula SAIHARINI¹, Dass AYYAPPA³,
Guntupalli PADMAVATHI³, V. Vinay SHENOY¹

¹Barwale Foundation, Barwale Chambers, #3-6-666, Street No.10, Himayathnagar, Hyderabad 500 029, India;

saikumar@barwalefoundation.org (*corresponding author)

²Department of Genetics, Osmania University, Hyderabad, India

³Directorate of Rice Research, Rajendra nagar, Hyderabad 500 030, India; ayyappadass81@gmail.com

Abstract

Drought is a major constraint for rainfed lowland and upland rice productivity throughout world. A backcross inbred population derived from ‘Swarna’ and ‘WAB450-I-B-P-157-2-1’ (*Oryza sativa* L. x *O. glaberrima*) was evaluated under both irrigated and lowland drought stresses for yield and yield related traits across three different seasons. Significant differences were found among all the analyzed traits. Coefficients of variation were recorded relatively high for filled grains per panicle, spikelet fertility, test weight, harvest index and grain yield and low for panicle length under both conditions during the study interval. Broad sense heritability varied from 0.28 (panicle number) to 0.83 (plant height) under stress and 0.31 (test weight) to 0.86 (plant height) under control. However, heritability estimates for grain yield and harvest index were found to be similar under both conditions. Traits such as filled grains per panicle, spikelet fertility, harvest index and grain yield recorded higher values of both heritability, as well as genetic advance under both conditions, indicating the suitability of these traits as selection criteria to derive high yielding genotypes for drought prone regions. Harvest index exhibited maximum positive direct effect on grain yield under both the conditions; in addition, filled grains per panicle, spikelet fertility and biomass had positive direct effect on grain yield under both irrigated and lowland drought stresses state. Hence, for improving the rice yield under lowland drought ecology, a genotype should possess a large number of panicles per plant, filled grains per panicle, high spikelet fertility and maintains higher biomass and harvest index.

Keywords: grain yield, genetic advance, heritability, path analysis, rice

Introduction

Rice is one of the most important food crops for Africa and Asia, as it plays an irreplaceable role in Indian national food security. It is cultivated in a wide range of ecosystems under varying temperature and water regimes. Majority of rice is contributed from irrigated ecosystem, where yield increase is now getting stagnated (Peng *et al.*, 1999). However, rainfed ecosystem contributes only with a quarter to the total rice production, even though it occupies 50% of the total rice area in the world (Macleán *et al.*, 2002). Drought is the major environmental constraints to rice productivity in rainfed areas (Farooq *et al.*, 2009; Serraj *et al.*, 2009). At all stages of rice growth and development,

drought is the major stress, but it has the greatest impact during flowering, when grain formation is suppressed. This results in considerable yield losses under rainfed and upland ecosystems (Serraj *et al.*, 2009). Sensitivity of rice to drought stress is more pronounced during the reproductive stage; even moderate stress can result in drastic reduction in grain yield (O’Toole *et al.*, 1982; Pantuwan *et al.*, 2002; Lanceras *et al.*, 2004; Venuprasad *et al.*, 2009).

Young seedlings can recover much better upon relief from drought, although reduction in yield may be better anticipated if leaf area damage and tiller numbers reduction are known (Cruz *et al.*, 1986). The severity of vegetative-stage drought stress will depend on the plant’s ability to avoid stress either through a deeper or more extensive root

system, or the ability to recover upon rewatering (Yoshida and Hasegawa, 1982) and increase the dry matter accumulation in sinks. The amount of accumulated dry matter in green leaves is different from one cultivar to another cultivar (Abarshahr *et al.*, 2011). Yambao and Ingram (1988) observed that withholding water for 15 days during the panicle initiation stage reduced yield by 70%, during flowering 88% and during grain filling 52%. Drought at anthesis can delay or prevent flowering, or result in pollen or spikelet sterility (Saini and Westgate, 2000). Drought significantly delays peduncle elongation, trapping a very large proportion of the panicle within the flag leaf sheath because the expression of cell-wall invertase genes is decreased (Ji *et al.*, 2005). Spikelet sterility is mainly due to the inhibition of starch accumulation in pollen grains or failure of anther dehiscence (Zhu *et al.*, 2004). Drought that occurs during these processes causes damage to reproductive organs. High yield under drought stress was associated with continued leaf area development, root growth, continued photosynthesis, maintenance of high biomass production, spikelet fertility and harvest index during reproductive phase (Bouman *et al.*, 2005; Atlin *et al.*, 2006).

To meet the ever-growing demand for rice by 2030, a significant increase, of at least 35% in yield is needed (Bouman *et al.*, 2007). Development of drought tolerant cultivars still remains a major objective for increasing productivity under rainfed ecosystem. Understanding the inheritance of the interest traits is the key for success in any breeding programme. However, progress in breeding for drought resistance has been slow (Fukai and Cooper, 1995). Breeding for drought tolerance in rice with high yield potential is quite challenging due to its complex genetic nature (polygenic nature), poor understanding of physiological as well as molecular mechanisms underlying the trait and intensity, timing and duration of drought stress in lowland and upland conditions across seasons

Another major concern in drought breeding programs is that by genetic variability, as manifested by various alleles that a breeder could choose from, inter-varietal breeding program is fast eroding. This has negatively impacted gain-per-cycle in crop improvement endeavor. It is imperative that the breeders seek new sources of genetic variability to keep up the pace of crop improvement lest the threat of yield plateau persists. Population with high variability serves as a prime source in developing high yielding genotypes coupled with drought tolerance for effective selection. Genetic improvement mainly depends on the amount of genetic variability present in the population which is a ubiquitous property of all species in nature. These genetic variations might be either heritable or non-heritable due to differences either in the genetic constitution of the individuals or influenced by the environment in which they are grown. The magnitude of variation due to heritable component is very important, because it would be a guide for selection of genitors for crop improvement. Importance of variability for drought tolerance, yield and yield related traits have been emphasized by many workers in past (Selvarani and Rangaswamy, 1997; Venkataramana and Hittalmani, 1999; Kumar *et al.*, 2007). Correlation analysis provides a good measure of the association between characters and helps to identify the most important character(s) to be considered for effective selection for

increasing yield. The extent of direct and indirect effects of component characters on yield, elucidated through path coefficient analysis using correlations, helps further to choose the right characters as selection criteria (Chakraborty *et al.*, 2010).

Materials and methods

Location

The study was carried at experimental farm of the Barwale Foundation, Maharajpet, Hyderabad, India, located at latitude of 17° 24' N and longitude of 78° 12' E and an altitude of 536 m above mean sea level, during 2012 (dry season and wet season) and 2013 (dry season) under stress, as well as irrigated, ecosystems.

Plant material

Swarna, a semi-dwarf high yielding Indica line, occupies around 12% of the total rice production area in India. However, Swarna is highly susceptible to moisture stress (Venuprasad *et al.*, 2009). WAB450-I-B-P-157-2-1 is an upland ecotype derived from *O. glaberrima* and *O. sativa* by African rice center (WARDA), known for its drought tolerance, deep root, early vigor, weed competitiveness, pest or disease resistance, also known as a valuable genetic material for drought-prone environments (Saikumar *et al.*, 2014). Swarna (female) was crossed with WAB450-I-B-P-157-2-1 to produce a set of 202 BC₁F₆ back cross inbred lines (BILs) by single seed descent method. The obtained BILs along with their genitors and checks were evaluated for drought response at lowland reproductive stage stress for estimation of genetic variability parameters.

Field experiments

Six field experiments were conducted during 2012 and 2013 (dry season - DS and wet seasons - WS) with varied level of moisture stress. They comprised of three lowland irrigated trials (one each during DS 2012, DS 2013 and WS 2012), and three lowland stress trials (one each during DS 2012, WS 2012 and DS 2013). All the experiments were laid out as randomized complete block design with two replications. A plot size of 1.2 m² was used for lowland trials. 25-day old seedlings were transplanted into the main field. One seedling was transplanted per hill at a spacing of 20 cm between hills as well as rows. After transplanting, approximately 5 cm of standing water was maintained in the field until draining, before harvest for control trails. Inorganic NPK fertilizer was applied at the rate of 100-50-50 kg ha⁻¹. Weeds and insect pests were controlled chemically in order to ensure a healthy crop. Whereas for stress trials irrigation was withheld approximately 30 DAT until maturity for wet season trails. In dry season stress trials, DS 2012 and DS 2013, irrigation was withheld until the water level beneath the soil reaches to -100 cm with the help of piezo-meter or moisture tension reached -60 k Pa at 30 cm depth. Fields were then re-irrigated by flash flooding, and drained again after approximately 24 h to save the plants from being exposed to very severe stress that leads to a loss of all genetic variability for grain yield (GY) under reproductive stage stress (RS) in the mapping population (Kumar *et al.*, 2007). This cycle was repeated until harvest. Severe leaf rolling and leaf drying was observed during each

stress period. Crop received a rain fall of rainfall (335.0 mm (WS2012), 37.3 mm (DS 2012) and 0.0 mm (DS2013)) and evapo-transpiration (ET) was 842.0 mm (WS 2012), 957.2 mm (DS2012) and 987.5 mm (DS2013).

Data collection

In all the trials data was recorded on days to 50 percent flowering (DFF) as number of days from sowing to panicle emergence in 50 percent of the plants. At physiological maturity, plant height (PH), panicle number (PN), panicle length (PL), filled grains/panicle (FGP), spikelets number/panicle (SNP), spikelet fertility (SF), test weight (TW), grain yield (GY), biomass (BM) and harvest index (HI) were recorded. Physiological traits such as leaf chlorophyll content (SPAD) and canopy temperature (CT) were recorded at reproductive stage during dry season 2013 only. All the above mentioned traits were measured from three randomly selected plants per BIL per replication.

Mean data was generated for all the BILs under both control and stress conditions. For each genotype per replication analysis of variance and covariance were used as per methodology advocated by Panse and Sukhatme (1985). Correlation coefficients for all traits were estimated according to Johnson *et al.* (1955) for all three seasons. Broad-sense heritability was calculated for all traits in both stress and control conditions, for each season using

formula:

$$h^2_b = \sigma^2_g / \sigma^2_p \text{ or } \sigma^2_p = \sigma^2_g + (\sigma^2_e / r)$$

Where σ^2_p is the phenotypic variance, σ^2_g is the genotypic variance, σ^2_e is the error variance and r is the number of replications in the season.

Genotypic and phenotypic correlations were partitioned into direct and indirect effects through path analysis, using the technique outlined by Dewey and Lu (1959). All statistical analyses were carried out using the softwares GENERES and CROPSTAT version 7.2.3.

Results and discussion

Results from the analysis of variance revealed that significant genetic variation exists in BIL population for all traits studied, under both stress and control conditions during DS 2012, WS 2012 and DS 2013 ($p < 0.01$), which is mainly attributed to the large genetic variability present in the two parental lines used in breeding program. Such a wide variation indicated the scope for improving the population for these characters with respect to drought and other related quantitative traits. The BILs were compared with their parent's value distribution, considering the grain yield and other quantitative traits (Tab. 1).

Tab. 1. Range, mean and LSD 5% of the Swarna/WAB450-I-B-P-157-2-1 population and parents under reproductive stage stress (S) and control (C) conditions in DS 2013, WS 2012 and DS 2012

Trait	Range	DS2013					WS2012					DS2012				
		Mean	LSD 5%	Swarna	WAB	Range	Mean	LSD 5%	Swarna	WAB	Range	Mean	LSD 5%	Swarna	WAB	
DFF	S	98.0-151.0	133.8	7.4	153.0	92.5	89.0-133.0	108.2	3.9	122.0	87.0	99.5-145.0	137.1	2.3	155.0	91.0
	C	90.0-126.0	113.2	3.1	125.0	84.0	87.5-120.0	105.1	7.5	117.0	83.0	89.0-120.0	109.5	3.4	115.8	87.5
PH	S	45.0-90.0	54.1	5.5	56.0	89.5	55.7-108.5	71.6	7.9	70.2	98.0	32.5-98.5	54.5	5.1	51.0	85.7
	C	63.3-106.1	78.3	4.0	82.7	115.3	78.3-123.0	94.1	9.2	90.3	125.7	72.5-119.0	92.7	7.5	89.5	116.0
PN	S	60-38.5	24.9	10.9	23.3	5.0	4.2-28.5	17.7	5.8	17.0	6.0	6.7-44.0	25.6	3.8	19.0	6.0
	C	6.8-43.4	20.1	4.5	25.0	7.0	3.9-23.3	15.2	0.2	17.0	7.0	4.0-24.8	16.5	5.8	21.0	8.0
PL	S	13.2-22.7	16.9	2.9	18.0	23.5	15.6-26.1	20.3	4.4	18.0	25.0	12.7-21.3	17.6	0.8	16.0	24.0
	C	16.5-26.7	20.8	0.7	20.3	28.0	19.0-28.8	22.7	0.1	22.0	29.0	19.8-27.3	23.0	2.2	18.7	28.1
FGP	S	0.0-161.0	45.2	67.1	0.0	76.5	26.0-176.0	145.7	90.8	33.0	108.5	22.0-131.7	59.8	8.5	0.0	66.0
	C	78.2-248.9	174.4	51.1	91.0	132.0	107.2-319.2	253.5	66.1	109.0	193.0	83.8-252.5	149.4	47.7	95.2	128.0
SF	S	0.0-78.0	26.5	17.4	0.0	70.0	23.7-87.0	62.4	29.4	34.2	80.6	15.1-82.5	52.3	6.6	0.0	69.1
	C	38.5-93.9	72.4	0.5	75.0	85.6	55.5-97.7	81.9	6.2	80.6	94.0	43.9-98.0	76.9	17.0	77.0	88.2
TW	S	0.0-18.6	7.2	2.8	0.0	24.2	6.0-31.5	14.5	6.0	8.0	27.0	5.5-26.0	12.1	0.7	0.0	25.0
	C	15.5-35.1	20.8	4.7	16.0	32.6	13.8-33.5	21.7	0.9	16.0	32.0	15.8-32.0	20.6	12.3	16.2	31.8
BM	S	4.8-13.7	7.8	3.5	9.8	7.7	4.6-15.3	8.5	3.3	10.8	6.8	4.6-15.6	8.7	0.4	7.4	6.1
	C	8.06-18.6	11.9	2.1	12.8	10.3	7.2-16.9	11.6	2.9	15.7	7.9	5.9-15.3	12.1	2.0	10.7	7.7
HI	S	0.0-0.3	0.06	0.04	0.0	0.16	0.0-0.5	0.2	0.1	0.05	0.23	0.0-0.3	0.1	0.0	0.0	0.2
	C	0.25-0.6	0.45	0.1	0.5	0.39	0.3-0.6	0.5	0.1	0.5	0.5	0.2-0.6	0.6	0.1	0.5	0.5
GY	S	0.0-2.1	0.43	0.2	0.0	1.2	0.0-4.0	2.2	1.0	0.5	1.5	0.0-2.6	0.7	0.5	0.0	1.5
	C	2.8-8.5	5.43	1.5	5.2	3.9	2.5-11.1	6.4	2.1	5.3	3.9	2.2-9.4	6.8	1.0	5.1	3.3
SPAD	S	38.5-45.2	42.8	2.1	45.7	44.0	-	-	-	-	-	-	-	-	-	-
	C	29.2-44.4	39.4	3.8	48.7	45.1	-	-	-	-	-	-	-	-	-	-
CT	S	35.2-42.2	37.3	3.8	39.5	36.2	-	-	-	-	-	-	-	-	-	-
	C	22.1-34.6	28.8	0.3	31.5	29.6	-	-	-	-	-	-	-	-	-	-

DFF: days to 50% flowering; PH: plant height (cm); PN: panicle number; PL: panicle length (cm); FGP: filled grains per panicle; SF: spikelet fertility; TW: test weight; BM: biomass (tha⁻¹); HI: harvest index; GY: grain yield (tha⁻¹); SPAD: chlorophyll content; CT: canopy temperature (°C); DS: dry season; WS: wet season; S: stress; C: control

Transgressive segregants with superior performance over the best yielding (under drought) of their genitors were observed during population screening under both the conditions. Such transgressive lines suggest either those favorable additive alleles are brought by both parents, and/or that complementary interactions occur between alleles of different origins. Range, mean, LSD5% of population in comparison with parents for all three seasons are presented in Tab. 1.

Variance and coefficient of variation

The magnitude of genetic variation and environmental effects involved in the expression of different characters were determined by phenotypic and genotypic coefficients of variation (Tab. 2). Magnitude of PCV was found to be higher than GCV for all the traits under both control and stress, and PCV was higher for stress experiments in comparison with control ones for all the traits across all seasons. Further traits such as GY, HI, FGP, SF and TW displayed very high coefficients of variation (GCV and PCV) among yield and yield attributing traits, high to moderate for DFF, PH, PN and BM and low for PL, SPAD (DS 2013) and CT (DS 2013) under both the conditions across all three seasons, indicating the influence of environment (water stress) in the expression of these traits,

with GY and HI being affected to a greater extent by stress environment. Further, there existed a large difference between the values recorded for GCV and PCV in the present study; such a large difference between GCV and PCV reflects a high environmental influence on the expression of traits. These findings for coefficient of variation (GCV and PCV) were similar to that of Akinwale et al. (2011) and Sadeghi et al. (2011). The GCV ranged from 9.8 (PL) to 136.1 (GY) in DS 2013, 7.1 (PL) to 52.7 (HI) in WS 2012 and 8.7 (PL) to 81.4 (HI) in DS 2012 under stress and 7.2 (PL) to 21.9 (FGP) in DS 2013, 7.3 (PL) to 23.8 (FGP) in WS 2012 and 5.5 (PL) to 16.5 (FGP) in DS 2012 under control conditions. Similarly, the values of PCV ranged from 13.1 (PL) to 195.6 (HI) in DS 2013, 11.7 (DFF) to 65.9 (GY) in WS 2012 and 12.2 (DFF) to 132.3 (HI) in DS 2012 under stress and 8.4 (PL) to 25.8 (FGP) in DS 2013, 8.2 (PL) to 27.3 (FGP) in WS 2012 and 7.3 (PL) to 23.2 (FGP) in DS 2012 under control environment. Further, physiological traits SPAD and CT during DS 2013 recorded lower values of both GCV and PCV (except in control), when compared to yield component traits. Transgressive segregation in both directions was observed for most traits under drought stress and control, indicating that both parents transmitted favourable alleles for each trait.

Tab. 2. GV, PV, GCV, PCV, broad-sense heritability (h^2_b), genetic advance (GA) yield and yield components of the Swarna/WAB450-I-B-P-157-2-I population under reproductive stage stress (S) and control (C) conditions in DS 2013, WS 2012 and DS 2012

Trait		DS2013						WS2012						DS2012					
		GV	PV	GCV	PCV	H	GA	GV	PV	GCV	PCV	H	GA	GV	PV	GCV	PCV	H	GA
DFF	S	4640	5864	161	200	0.79	32.6	895	123.1	8.7	11.7	0.73	17.7	171.7	220.1	95	122	0.78	196
	C	1083	131.8	9.1	109	0.82	18.7	680	82.4	7.8	8.6	0.82	14.7	55.9	66.5	7.4	8.3	0.84	147
PH	S	380	45.7	11.4	135	0.83	21.4	35.3	51.4	8.2	15.0	0.69	14.1	42.6	53.8	11.9	14.0	0.79	22.9
	C	37.9	43.9	7.8	8.6	0.86	15.3	27.4	33.8	8.1	9.6	0.81	8.5	31.5	37.5	5.9	8.4	0.84	10.3
PN	S	122	43.0	14.0	26.3	0.28	15.3	4.2	12.9	11.5	20.2	0.32	13.6	49.9	91.2	27.6	48.6	0.55	54.8
	C	9.1	14.4	15.0	18.8	0.63	24.6	6.8	8.8	17.1	22.3	0.77	35.2	3.5	6.1	11.2	10.5	0.57	12.3
PL	S	2.8	4.9	9.8	13.1	0.56	15.1	2.1	7.1	7.1	13.1	0.30	8.0	2.4	4.5	8.7	13.8	0.52	17.3
	C	2.3	2.8	7.2	8.4	0.83	14.5	2.8	3.1	7.3	8.2	0.89	15.1	1.6	2.8	5.5	7.3	0.57	8.6
FGP	S	2311.0	3471.1	106.2	130.2	0.67	78.5	1392.5	2712.9	25.9	41.2	0.51	33.6	452.8	904.2	35.6	89.9	0.50	71.8
	C	1372.1	1652.2	21.9	25.8	0.83	44.1	3662.4	4786.8	23.8	27.3	0.76	43.0	604.1	1191.6	16.5	23.2	0.51	24.3
SF	S	686.2	957.1	98.8	130.5	0.71	92.8	59.6	101.2	12.3	26.9	0.59	21.7	327.2	689.6	34.5	69.5	0.47	70.0
	C	129.1	149.7	15.6	18.1	0.86	32.3	74.8	84.8	10.5	11.2	0.88	20.4	75.2	149.6	11.2	15.9	0.50	16.4
TW	S	46.1	156.6	93.4	310.0	0.29	87.8	11.2	30.6	22.9	31.1	0.37	34.9	11.4	32.5	27.9	79.1	0.35	57.3
	C	2.7	8.5	7.8	13.9	0.31	1.9	22.5	46.5	21.8	25.8	0.48	44.8	3.0	7.5	8.4	5.6	0.40	4.6
BM	S	1396383.9	4503702.0	13.3	27.3	0.31	17.4	917674.8	2612189.2	11.3	15.7	0.35	24.1	3384689.3	6483516.8	21.1	37.6	0.52	40.4
	C	1976698.6	2380141.0	21.7	23.8	0.83	20.9	2805522.0	4097718.0	14.8	17.8	0.68	25.2	2045458.3	3819606.0	11.8	16.2	0.53	17.8
HI	S	0.003	0.005	131.1	195.6	0.63	114.9	0.013	0.018	52.7	63.4	0.71	91.2	0.004	0.009	81.4	132.3	0.45	113.6
	C	0.006	0.008	16.3	21.0	0.76	29.5	0.006	0.011	13.9	19.2	0.57	21.8	0.002	0.003	11.5	9.8	0.60	18.4
GY	S	158336.1	259562.3	136.1	179.7	0.61	125.9	686123.9	1205315.8	49.8	65.9	0.57	77.3	326017.6	775389.3	81.3	125.5	0.42	108.6
	C	893608.3	1332621.0	17.4	20.4	0.67	28.2	1504676.8	2728539.0	20.1	27.1	0.55	30.7	1059208.6	2101772.5	15.1	21.3	0.50	22.1
SPAD	S	0.3	6.4	1.1	12.5	0.05	0.2	-	-	-	-	-	-	-	-	-	-	-	-
	C	4.6	8.4	5.4	7.3	0.55	8.3	-	-	-	-	-	-	-	-	-	-	-	-
CT	S	0.7	3.1	2.2	4.8	0.21	2.1	-	-	-	-	-	-	-	-	-	-	-	-
	C	3.9	12.9	6.8	32.3	0.30	14.0	-	-	-	-	-	-	-	-	-	-	-	-

DFF: days to 50% flowering; PH: plant height (cm); PN: panicle number; PL: panicle length (cm); FGP: filled grains per panicle; SF: spikelet fertility; TW: test weight; BM: biomass (tha-1); HI: harvest index; GY: grain yield (tha-1); SPAD: chlorophyll content; CT: canopy temperature (0c); DS: dry season; WS: Wet season; S: stress; C: control

Heritability and genetic advance

Heritability estimates were observed to be high for DFF (0.82 to 0.86), PH (0.81 to 0.84), high to moderate for PN (0.57 to 0.77), PL (0.57 to 0.89), FGP (0.51 to 0.83), SF (0.50 to 0.88), BM (0.53 to 0.83), HI (0.57 to 0.76) and GY (0.50 to 0.67), moderate for SPAD (0.55) and low for TW (0.31 to 0.48) and CT (0.30) under control conditions across all seasons. Under stress environment, heritability is high for DFF (0.73 to 0.79) and PH (0.69 to 0.83), high to moderate for PL (0.30 to 0.57), FGP (0.50 to 0.67), SF (0.47 to 0.71), HI (0.45 to 0.71) and GY (0.42 to 0.61), moderate to low for PN (0.28 to 0.55), TW (0.29 to 0.35), BM (0.31 to 0.52) and CT (0.21) (DS 2013) and very low for SPAD (0.05) (DS 2013) for all three seasons (Tab. 2). High to moderate heritability was reported for different quantitative traits studied in rice (Berneir *et al.*, 2007; Abarshahr *et al.*, 2011; Akinwale *et al.*, 2011; Sadeghi *et al.*, 2011; Vikram *et al.*, 2011; Saikumar *et al.*, 2014). Similarly DTF and PH were also highly heritable across other studies (Berneir *et al.*, 2007; Vikram *et al.*, 2011; Saikumar *et al.*, 2014).

Further, all traits were influenced by stress environment (drought stress), which is evident from the lower values of heritability estimates in stress with respect to control condition, except for HI and GY in WS 2012. Traits such as PN and BM were affected to maximum extent by the environment, in comparison with the rest of the traits. However, TW showed lower values of heritability in both the conditions. Further, the heritability for GY under stress was found similar to that under control in all three years, indicating that selection for GY under reproductive stage stress has practical applicability in improving the GY for drought prone environments. Similar results in the case of heritability for GY under reproductive stage stress were reported in previous studies also (Kumar *et al.*, 2007; Berneir *et al.*, 2007; Abarshahr *et al.*, 2011; Vikram *et al.*, 2011; Saikumar *et al.*, 2014). Selection for GY under RS is now a well-recommended selection criterion for breeding drought-tolerant rice varieties (Kumar *et al.*, 2008). Low heritability indicates a greater role of the environment on the expression of traits (Seyoum *et al.*, 2012).

Similar to the coefficient of variation the value of genetic advance expressed in percent of mean was also high for GY (77.3 to 125.9 (S) and 22.1 to 30.7 (C)), HI (91.2 to 114.9 (S) and 18.4 to 29.5 (C)), FGP (33.6 to 78.5 (S) and 24.3 to 44.1(C)), SF (31.7 to 92.8 (S) and 20.4 to 32.3 (C)) and TW (34.9 to 87.8 (S) and 21.9 to 44.8) and low for PH (14.1 to 22.9 (S) and 8.5 to 15.3 (C)), PL (8 to 15.1 (S) and 8.6 to 15.1 (C)), SPAD (0.2 (S) and 8.0 (C)) and CT (2.1 (S) and 14.0 (C)) under both the conditions, where as moderate estimates of genetic advance were noticed in case of DFF (17.7 to 32.6 (S) and 14.7 to 18.7 (C)), PN (24.6 to 54.6 and 12.3 to 15.1 (C)) and BM (17.4 to 40.4 (S) and 17.8 to 25.2 (C)). High values of genetic advance were recorded for all the studied traits for stress trails rather than control, and dry season trails over wet season, except for PN, PL and BM.

Further traits such as FGP, GY and HI recorded high heritability as well as GA under both control and stress conditions, consistently across the seasons. Similar results were reported previously (Manickavelu *et al.*, 2006; Yadav *et al.*, 2011). Although other traits showed high heritability

values, expected GA was low or moderate to inconsistent.

However, a suitable selection procedure could be followed only when the high broad-sense heritability estimate was coupled with high genetic advance. Since high heritability does not always indicate high genetic gain, heritability with genetic advance should be used in predicting selection of superior genotypes (Ali *et al.*, 2002). The three traits above mentioned, having high values of heritability and genetic advance in percent of mean have emerged as ideal traits for improvement through selection. Further these traits showed high GCV and PCV values, suggesting that they may provide a high response to selection, owing to their high transmissibility and variability.

Correlation

Magnitude of correlation coefficient at phenotypic level was higher than inherent associations at genotypic level, between different traits in the population. GY was significantly and positively correlated at both phenotypic (p) and genotypic (g) level with FGP (0.35 to 0.71 (p) 0.67 to 0.85 (g)), SF (0.30 to 0.75 (p) 0.67 to 0.83 (g)), TW (0.30 to 0.64 (p) 0.59 to 0.75 (g)) and HI (0.94 to 0.97 (p) 0.98 to 0.99 (g)), negatively and significantly correlated with DFF (-0.33 to -0.56 (p) and -0.34 to -0.77 (g)) under stress conditions consistently. Whereas under control, traits such as FGP (0.17 to 0.24 (p) 0.29 to 0.39 (g)), SF (0.18 to 0.29 (p) 0.40 to 0.41 (g)), BM (0.54 to 0.76 (p) and 0.39 to 0.73 (g)) and HI (0.64 to 0.77 (p) and 0.70 to 0.78 (g)) were positively and significantly correlated with GY, and DFF (-0.18 to -0.21 (p) and -0.26 to -0.28 (g)) was negatively correlated with GY consistently across all three seasons (at $p < 0.05$ and $p < 0.01$) (Tab. 3). PH and PN found to positively correlated with GY under stress condition only. BM showed a weak negative correlation with HI under stress during dry season experiments, and was positively correlated with HI under WS 2012 stress and all control conditions. In addition, DFF was also negatively correlated with HI under both conditions. The positive correlation between GY and PH, FGP, SF, TW, BM and HI has been also emphasized previously by many researchers (Lanceras *et al.*, 2004; Berneir *et al.*, 2007; Vikram *et al.*, 2011). Similarly, the negative correlation between GY and DTF has also been reported (Garrity and O'Toole, 1994; Lanceras *et al.*, 2004; Abarshahr *et al.*, 2011; Varma *et al.*, 2012). In contrast, the negative correlation between PH and GY was revealed by Laffite *et al.* (2006).

However, under both conditions HI, FGP and SF were found to be highly correlated with GY consistently, when compared to other quantitative traits, under both the conditions at $p < 0.01$. Whereas, for FGP, SF and HI values of correlation coefficients were found to be high with GY under stress, rather than under control conditions, at both levels. Further, DFF was found to be highly negatively correlated with GY under both the conditions among all the studied traits. As the level of stress increased, correlation between GY and HI increased significantly. Similarly, the negative correlation between GY and DTF emphasized with the increase in stress level. Canopy temperature (DS 2013) was negatively and significantly correlated with GY and other yield related traits. Such a negative correlation between GY and CT is reported in earlier studies also (Hongyan *et al.*, 2005).

HI, BM, PH were the determining factors for GY under both the conditions, with HI being the major determinant, indicating that genetic improvement in GY can be accompanied by an improvement in HI (Fukai *et al.*, 1999; Babu *et al.*, 2003)

Path analysis

Path coefficient analysis permits the separation of the correlation coefficient into components of direct and indirect effect on GY. Path analysis carried out with the help of genotypic correlation coefficients under stress revealed HI had high positive direct effect on GY ranging from 0.90 to 1.40 (HI) and followed by BM (0.12 to 0.30),

SF (0.21 to 0.29) and FGP (0.16 to 0.23) (Tab. 4). On the other hand, PN (-0.02 to -0.12) was found to have direct negative effect on GY under stress conditions, during all three seasons. The direct effects of five other traits and two physiological traits were too low or inconsistent to be considered for any consequence. However, most of the traits exhibited indirect influence on grain yield under stress through HI, traits such as PH (0.12 to 0.51), PN (0.11 to 0.46), FGP (0.41 to 0.64), SF (0.52 to 0.71) and TW (0.52 to 0.86) had an indirect positive effect and DFF (-0.32 to -0.97) and BM (-0.07 to -0.37) had an indirect negative effect on GY under stress.

Similarly, under control conditions in addition to HI

Tab. 3a. Phenotypic and genotypic correlation coefficients between yield and yield components traits of the Swarna/WAB450-I-B-P-157-2-1 population under reproductive stage stress (S) (above the diagonal) and control (C) (below the diagonal) conditions in DS 2013

		DS 2013 S											
		DFF	PH	PN	PL	FGP	SF	TW	BM	HI	CC	CT	GY
Phenotypic correlation	DFF	1.00	-0.07	0.07	-0.11	-0.36**	-0.40**	-0.37**	0.01	-0.35**	0.08	0.15	-0.33**
	PH	0.04	1.00	-0.10	0.68**	0.40**	0.32**	0.34**	0.04	0.30**	0.15*	-0.15	0.31**
	PN	0.32**	-0.16	1.00	0.01	-0.29*	-0.26*	-0.28*	0.24*	-0.23*	0.08	0.04	0.16*
	PL	0.09	0.53**	0.02	1.00	0.30**	0.22*	0.24*	0.05	0.14	0.16*	-0.13	0.11
	FGP	-0.36**	0.12	-0.15	0.11	1.00	0.85**	0.71**	-0.13	0.71**	-0.13	-0.40**	0.71**
	SF	-0.34**	0.03	-0.18	-0.09	0.58**	1.00	0.85**	-0.15	0.74**	-0.08	-0.09	0.75**
	TW	-0.32*	0.27**	-0.16	0.22*	0.13	0.08	1.00	-0.18	0.66**	-0.08	-0.10	0.64**
	BM	0.06	0.11	0.29*	0.06	0.13	0.10	0.02	1.00	-0.25*	-0.02	-0.09	-0.10
	HI	-0.48**	-0.14	-0.21*	-0.10	0.20*	0.28*	0.16*	-0.14	1.00	-0.09	-0.12	0.96**
	CC	-0.21*	-0.12	-0.15	-0.10	-0.16	-0.13	0.07	-0.04	-0.02	1.00	-0.07	-0.07
	CT	0.11	0.18*	0.05	0.07	-0.17	-0.08	0.01	0.05	-0.16	-0.04	1.00	-0.12
	GY	-0.21*	-0.03	0.02	-0.04	0.24*	0.29*	0.14	0.54**	0.75**	-0.04	-0.10	1.00
	Genotypic correlation	DFF	1.00	-0.07	0.15	-0.15	-0.44**	-0.44**	-0.39**	0.03	-0.37**	0.15	0.38**
PH		0.05	1.00	-0.21*	0.92**	0.47**	0.35**	0.37**	0.04	0.37**	0.31**	-0.33*	0.36**
PN		0.41**	-0.17	1.00	-0.25*	-0.67**	-0.56**	-0.50**	0.49**	-0.48**	0.27*	-0.43**	0.19*
PL		0.10	0.58**	0.05	1.00	0.36**	0.30**	0.32**	0.05	0.22*	0.35**	-0.34**	0.14
FGP		-0.37**	0.13	-0.19	0.12	1.00	0.95**	0.89**	-0.32*	0.89**	-0.14	-0.33*	0.83**
SF		-0.35**	0.02	-0.22*	-0.10	0.58**	1.00	0.92**	-0.33*	0.81**	-0.16	-0.29*	0.83**
TW		-0.53**	0.52**	-0.30*	0.37**	0.22*	0.14	1.00	-0.37**	0.74**	-0.18	0.24*	0.75**
BM		0.09	0.14	0.41**	0.10	0.16	0.13	0.09	1.00	-0.29*	-0.05	0.30**	-0.22*
HI		-0.54**	-0.14	-0.31*	-0.13	0.23*	0.31**	0.34**	-0.28*	1.00	-0.14	-0.23*	0.98**
CC		-0.21*	-0.13	-0.18	-0.10	-0.16	-0.13	0.13	-0.05	-0.03	1.00	0.09	-0.06
CT		0.14	0.28*	0.10	0.09	-0.23*	-0.10	0.22*	0.12	-0.24*	-0.06	1.00	-0.29*
GY		-0.28*	-0.03	-0.03	-0.05	0.36**	0.41**	0.39**	0.39**	0.78**	-0.04	-0.11	1.00

(0.72 to 0.96), BM (0.66 to 0.68) was also found to have high positive direct effect on GY, followed by SF (0.11 to 0.17) and FGP (0.09 to 0.12). Similar to stress, even under control, the indirect effect exerted by most of the traits is mainly via HI, where FGP (0.29 to 0.39), SF (0.40 to 0.41) and BM (0.39 to 0.73) had the positive indirect effect, and DFF (-0.26 to -0.28) had the negative indirect effect on GY through HI. Yadav *et al.* (2008), Pandey *et al.* (2012) found high direct contribution of HI on GY in rice. Indirect

influence of various yield related traits via HI on GY has been proposed by Singh and Chaudary, (2006), Kotal *et al.* (2010) and Pandey *et al.* (2012).

In past, many researchers have emphasized the importance of several quantitative yield component traits as selection criteria for deriving high yielding genotypes in different ecosystems in rice: for example, biomass and harvest index (Lanceras *et al.*, 2004), days to 50% flowering, flag leaf width and harvest index (Abarshahr *et al.*, 2011),

harvest index (Kumar *et al.*, 2009) under lowland stress, harvest index, plant height and panicle length (Mehetre *et al.*, 1994), filled grains per panicle, spikelet fertility (Seyoum *et al.*, 2012) in upland condition. Spikelet fertility, biomass and harvest index (Pandey *et al.*, 2012), number of spikelets per panicle (Zheng *et al.*, 2003), harvest index, test weight (Kishor *et al.*, 2008), harvest index (Ganesen *et al.*, 1998), number of spikelets per panicle, flag leaf length, plant height (Abarshahr *et al.*, 2011) under irrigated condition. Thus, practical applicability of yield and yield attributing traits,

such as days to 50% flowering, plant height, panicle number, harvest index, spikelet fertility, test weight, biomass and harvest index in rice breeding programme either individually or in combination, as selection criterion represent an effective and feasible approach for pursuing higher yield in the case of rice, which may be due their high direct or indirect effect on GY.

GY under well-watered condition was important in determining GY under water-limiting conditions. Better performance of cultivars with high potential yield under rainfed lowland regions was proposed (Fukai *et al.*, 1999).

Tab. 3b. Phenotypic and genotypic correlation coefficients between yield and yield components traits of the Swarna/WAB450-I-B-P-157-2-1 population under reproductive stage stress (S) (above the diagonal) and control (C) (below the diagonal) conditions in WS 2012

		WS 2012 S										
		DFF	PH	PN	PL	FGP	SF	TW	BM	HI	GY	
WS 2012 C	Phenotypic correlation	DFF	1.00	0.15	-0.09	-0.34**	-0.41**	-0.26*	-0.45**	0.23*	-0.65**	-0.56**
		PH	-0.21*	1.00	-0.29*	0.12	0.04	0.02	-0.03	0.12	-0.16	0.15*
		PN	-0.01	-0.13	1.00	0.10	0.02	0.05	0.09	0.27**	-0.01	0.15*
		PL	-0.22*	0.41**	-0.14	1.00	0.17*	0.09	0.32**	-0.02	0.24*	0.24*
		FGP	-0.23*	0.23*	-0.08	0.17*	1.00	0.63**	0.16*	-0.03	0.36**	0.35**
		SF	-0.43**	0.18*	0.40**	0.10	0.56**	1.00	0.15	-0.01	0.31**	0.30**
		TW	-0.01	0.14	-0.13	0.13	0.19*	0.01	1.00	-0.03	0.31**	0.30**
		BM	0.16**	0.08	0.11	-0.03	0.10	0.00	0.12	1.00	-0.12	0.16*
		HI	-0.57	0.03	-0.04	0.04	0.17*	0.34**	-0.04	0.19*	1.00	0.94**
	GY	-0.21*	0.07	0.05	0.01	0.18*	0.22*	0.11	0.76**	0.77**	1.00	
	Genotypic correlation	DFF	1.00	0.20*	-0.13	-0.62**	-0.64	-0.59**	-0.61**	0.76**	-0.80**	-0.77**
		PH	-0.24*	1.00	-0.66**	0.17*	-0.06	-0.15	-0.04	0.45**	-0.13	0.18*
		PN	-0.01	-0.17	1.00	-0.17	-0.33	-0.25*	0.16*	0.19*	0.10	0.16*
		PL	-0.24*	0.55**	-0.14	1.00	0.36	0.17*	0.72*	-0.48**	0.63**	0.70**
		FGP	-0.25*	0.33**	-0.09	0.19*	1.00	0.86**	0.24*	-0.27*	0.80**	0.67**
		SF	-0.49**	0.26*	0.05	0.11	0.62**	1.00	0.11	0.21*	0.97**	0.82**
		TW	-0.01	0.20*	-0.14	0.13	0.21*	0.01	1.00	-0.09	0.54**	0.59**
		BM	0.24*	0.15	0.14	-0.03	0.11	0.01	0.15	1.00	-0.67**	-0.27*
HI		-0.74**	0.10	-0.05	0.05	0.17*	0.47**	-0.04	0.04	1.00	0.99**	
GY	-0.26*	0.16*	0.07	0.02	0.29*	0.40**	0.16*	0.73**	0.70**	1.00		

Although yield potential has no direct genetic relationship to drought tolerance, under drought stress it contributed to higher grain yield. On the other hand, GY under very severe stress was mainly related to BY and HI. In a study conducted on pearl millet under drought stress condition (Yadav *et al.*, 2002) HI and the GY would likely be accompanied by an improvement of BM. The indirect effect of FGP and SF under stress through HI indicated that direct selection using FGP and SF along with HI to select high yielding genotypes will be effective under stress condition, whereas under control condition selection based on traits such as FGP, SF, BM and HI will be quite useful in breeding programs. The strong genetic correlation between GY and HI resulted in a high direct effect on grain yield.

The value of residual effect ranged from 0.17 to 0.21 under stress and 0.21 to 0.25 under control, indicating that the effect of component traits leading to genetic variability

on GY is ranged from 83% to 79% in stress and 79% to 75% under control conditions by the ten common traits across all three seasons and two physiological traits (DS 2013) that were studied under both the conditions (Tab. 4).

Conclusion

Results from the above study suggest that there is an adequate genetic variability present in the material studied under stress and irrigated condition. Further characters viz. harvest index, filled grains per panicle, spikelet fertility, panicles per plant, plant height, biomass and days to 50% flowering influenced the yield either directly or indirectly. Genotypes that are capable of maintaining high harvest index, biomass, spikelet fertility, more filled grains per panicle, panicles per plant and reduced plant height and

Tab. 3c. Phenotypic and genotypic correlation coefficients between yield and yield components traits of the Swarna/WAB450-I-B-P-157-2-1 population under reproductive stage stress (S) (above the diagonal) and control (C) (below the diagonal) conditions in DS 2012

		DS 2012S										
		DFF	PH	PN	PL	FGP	SF	TW	BM	HI	GY	
DS 2012S	Phenotypic correlation	DFF	1.00	-0.32*	-0.15	0.01	-0.47**	-0.53**	-0.42**	0.01	-0.62**	-0.45**
		PH	-0.03	1.00	0.04	0.40**	0.39**	0.40**	0.51**	0.28*	0.22*	0.26*
		PN	0.06	-0.09	1.00	-0.12	0.15	0.10	-0.31*	0.28*	0.20*	0.23*
		PL	0.25*	0.26*	0.00	1.00	0.37**	0.27*	0.32**	0.27*	-0.02	0.03
		FGP	-0.04	0.18*	-0.18	0.05	1.00	0.86**	0.53**	0.21*	0.48**	0.51**
		SF	-0.32*	0.14	-0.07	-0.21*	0.53**	1.00	0.62**	0.15	0.47**	0.46**
		TW	-0.04	0.09	-0.10	0.11	-0.03	-0.07	1.00	0.18*	0.42**	0.43**
		BM	0.21*	0.23*	0.32**	0.24*	0.03	0.05	-0.06	1.00	0.17*	0.32**
		HI	-0.53**	-0.08	-0.21*	-0.07	-0.14	0.13	0.04	-0.06	1.00	0.97**
	GY	-0.18	0.12	0.10	0.12	0.17*	0.18*	-0.02	0.72**	0.64**	1.00	
	Genotypic correlation	DFF	1.00	-0.35**	-0.15	0.12	-0.48**	-0.54**	-0.43**	0.01	-0.91**	-0.60**
		PH	-0.03	1.00	0.04	0.45**	0.43**	0.44**	0.55**	0.31**	0.37**	0.44**
		PN	0.10	-0.49**	1.00	-0.13	0.16*	0.11	-0.04	0.32**	0.33**	0.39**
		PL	0.36**	0.36**	-0.21*	1.00	0.39**	0.29*	0.33**	0.31**	0.02	0.09
		FGP	-0.04	0.32**	-0.70**	0.03	1.00	0.86**	0.55**	0.21*	0.68**	0.74**
		SF	-0.44**	0.34**	-0.25*	-0.35**	0.17*	1.00	0.63**	0.14	0.65**	0.67**
		TW	-0.16	0.55**	-0.11	0.42**	0.11	0.03	1.00	0.19*	0.62**	0.67**
		BM	0.34**	0.15	0.38**	0.48**	-0.10	0.05	-0.24*	1.00	-0.09	0.17*
HI		-0.71**	-0.01	0.15	-0.05	-0.14	0.24*	-0.09	-0.01	1.00	0.98**	
GY	-0.27*	0.09	0.20*	0.14	0.39**	0.41**	0.18*	0.57**	0.74**	1.00		

Tab. 4a. Direct (diagonal values) and indirect effects of different characters on grain yield at genotypic level under stress DS 2013, WS 2012 and DS 2012

		DFF	PH	PN	FGP	SF	TW	BM	HI	Genotypic correlation with GY
DS 2013 S	DFF	0.02	0.00	0.00	-0.01	-0.06	0.00	0.00	-0.32	-0.34**
	PH	0.00	0.12	0.01	0.01	0.05	0.00	0.00	0.31	0.36**
	PN	0.00	-0.02	-0.03	-0.01	-0.07	0.00	0.09	0.18	0.19*
	FGP	-0.01	0.05	0.02	0.23	0.12	-0.01	-0.05	0.58	0.83**
	SF	-0.01	0.04	0.02	0.03	0.29	-0.01	-0.02	0.58	0.83**
	TW	-0.01	0.04	0.02	0.03	0.12	-0.01	-0.03	0.68	0.75**
	BM	0.00	0.00	-0.02	-0.01	-0.05	0.00	0.12	-0.37	-0.22*
	HI	0.00	0.04	0.02	0.03	0.11	-0.01	-0.05	0.90	0.98**
R=0.17										
WS 2012 S	DFF	-0.02	0.00	0.00	-0.01	-0.02	-0.01	0.11	-0.77	-0.77**
	PH	0.00	-0.02	0.02	0.00	-0.01	0.00	0.06	0.12	0.18*
	PN	0.00	0.02	-0.02	0.00	-0.01	0.00	0.05	0.11	0.16*
	FGP	0.01	0.00	0.01	0.21	0.03	0.00	-0.04	0.41	0.67**
	SF	0.01	0.00	0.01	0.01	0.23	0.00	0.03	0.51	0.82**
	TW	0.01	0.00	0.00	0.00	0.00	0.01	-0.01	0.52	0.59**
	BM	-0.02	-0.01	0.00	0.00	0.01	0.00	0.14	-0.34	-0.27*
HI	0.02	0.00	0.00	0.01	0.03	0.01	-0.09	0.96	0.99**	
R=0.21										
DS 2012 S	DFF	0.10	-0.01	0.02	0.03	0.01	0.05	0.00	-0.80	-0.60**
	PH	-0.09	0.03	0.00	-0.02	0.00	-0.07	0.09	0.51	0.44**
	PN	-0.04	0.01	-0.12	-0.01	0.00	0.00	0.09	0.46	0.39**
	FGP	-0.13	0.01	-0.02	0.16	0.08	-0.07	0.06	0.64	0.74**
	SF	-0.15	0.01	-0.13	0.05	0.21	-0.08	0.04	0.71	0.67**
	TW	-0.12	0.01	0.00	-0.03	-0.01	-0.12	0.06	0.86	0.67**
	BM	0.00	0.01	-0.04	-0.01	0.00	-0.02	0.30	-0.07	0.17*
HI	-0.25	0.01	-0.04	-0.01	-0.07	-0.03	1.40	0.98**	0.98**	
R=0.18										

Tab. 4b. Direct (diagonal values) and indirect effects of different characters on grain yield at genotypic level under control DS 2013, WS 2012 and DS 2012

		DFF	FGP	SF	TW	BM	HI	Genotypic correlation with GY
DS 2013 C	DFF	-0.05	0.01	0.06	0.02	0.06	-0.38	-0.28*
	FGP	0.02	0.09	-0.01	-0.01	0.10	0.17	0.36**
	SF	0.02	0.00	0.11	0.00	0.08	0.20	0.41**
	TW	0.03	0.00	0.00	-0.04	0.06	0.32	0.39**
	BM	0.00	0.00	0.00	0.00	0.66	-0.27	0.39**
	HI	0.03	0.00	0.00	-0.01	-0.19	0.96	0.78**
	R=0.24							
WS 2012 C	DFF	0.06	-0.01	0.00	0.00	0.17	-0.47	-0.26*
	FGP	-0.02	0.12	0.00	0.00	0.06	0.10	0.29**
	SF	-0.03	0.01	0.17	0.00	0.01	0.24	0.40**
	TW	0.00	0.01	0.00	0.02	0.10	0.04	0.16*
	BM	0.02	0.00	0.00	0.00	0.68	0.03	0.73**
	HI	-0.05	0.00	0.00	0.00	0.03	0.72	0.70**
	R=0.25							
DS 2012 C	DFF	-0.02	0.00	0.02	0.00	0.23	-0.49	-0.27*
	FGP	0.00	0.10	0.09	0.00	0.06	0.15	0.39**
	SF	0.01	0.02	0.15	0.00	0.03	0.19	0.41**
	TW	0.00	0.01	0.02	0.02	0.05	0.08	0.18*
	BM	-0.01	0.00	0.00	0.00	0.69	-0.10	0.57**
	HI	0.01	0.00	-0.01	0.00	-0.01	0.74	0.74**
	R=0.21							

days to 50% flowering can be considered as suitable for improving the grain yield in rice breeding programs targeting lowland drought.

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