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Research Article

Association of flowering delay under stress and drought tolerance in upland rice (*Oryza sativa* L.)

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ABSTRACT : Days to flowering was negatively correlated with grain yield, panicle length, spikelet fertility and 1000 grain weight under moisture stress conditions. Delayed flowering under stress is a strong indication of susceptibility to drought because of retarded growth. Significant negative correlation of RWC with days to 50 per cent flowering (-0.37** and -0.41** in IB and TB NIILs, respectively) was noticed indicating RWC as an important indicator of plant water status which significantly influenced the plant phenology and productivity traits under drought stress.

KEY WORDS : Drought tolerance, Flowering delay, Physiological traits, Upland rice

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INTRODUCTION

Upland rice is grown in permanent fields in rotation with a range of winter crops like, wheat, vegetables, pulses, oilseeds or fallows, depending on the availability of residual soil moisture. These areas usually have a continuum from upland to lowland fields along the top sequence, with farmers often processing fields in all hydrological conditions. This system of rice cultivation is located mainly in South Asia and Bangladesh. The rainfed drill sown rice area in Karnataka is similar to this system, in which hydrological conditions like, upland, midland and lowlands are noticed all of which are drought prone (Hanamaratti *et al.*, 2005).

The rainfall pattern in rainfed drill sown rice area is generally mono-modal, with 800 to 1400 mm per annum with a peak in July-August. The terminal drought is most common situation which coincides with flowering/grain filling stage a most critical phase for moisture stress. However, the risk of intermittent vegetative stress is also not uncommon. The productivity in rainfed uplands is poor (0.8 to 1.2 t/ha) mainly because of erratic rainfall and moisture stress at flowering stage (Courtois and Lafitte, 1999; Singh, 2006). Therefore, association of flowering behaviour with productivity is more critical for selection and improvement of yield in upland rice.

A delay usually occurs in flowering date, when rice experiences a water deficit before flowering (Lafitte *et al*., 2003). The period of delay is partly related to extent of stress, the rice genotypes experienced and those with longer delay will tend to produce less grain (Ravindrakumar *et al*., 2003). The delay in heading under stress was negatively associated with plant water status indicators and stress yields (Blum *et al*., 1999 and Babu *et al*., 2003; Pantuwan *et al*., 2002). The delay in heading is an expression of growth retardation during the drying cycle as well as upon recovery and this delay is a strong indication of susceptibility to stress (Blum *et al*., 1999).

Absolute yield of the genotypes under stress represents their relative drought tolerance in terms of plant production,

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despite its association with potential yield and phenology. This may have occurred because phenology was changed drastically in response to stress (heading delay) and this itself represented a physiological response to stress. Therefore, this study was undertaken to understand the relationship of flowering behaviour with productivity and physiological traits under drought stress in upland rice.

EXPERIMENTAL METHODS

Two back-cross populations which were developed at IRRI using IR-64 (a high yielding widely adapted *indica* variety developed at IRRI) and Teqing (a high yielding upland adapted *indica* variety developed at China) as recurrent parents with Binam (a traditional *japonica* land race from Iran known to be drought tolerant) as donor. BC_2F_4 seeds of two introgressed populations along with genotypic data were provided by IRRI.

Fifty eight randomly selected near isogenic introgression lines (NIILs) from IR-64 x Binam (IB) and 55 NIILs from Teqing x Binam (TB) were evaluated preliminarily to know maturity duration. These NIILs were grouped based on maturity and evaluated along with popular upland land race, Dodiga and high yielding variety, MTU-1001 in three sets. The evaluation was done under Randomized Complete Block Design during summer 2005 under irrigation. The NIILs of each maturity group were planted in compact blocks separated by 2m in order to impose stress at particular stage by withholding irrigation. Each NIIL was planted in one row of 2m length with row spacing of 20 cm and 10 cm between plants. The recommended package was followed to raise the crop.

The three sets of NIILs were subjected to three different environments *viz.*, 1) Non-stress by maintaining wet throughout the cropping season (E_1); 2) Moisture stress at vegetative stage by withholding irrigation for 15 days at tillering stage (E_2) and 3) Moisture stress at reproductive stage by withholding irrigation for 15 days (E_3). The average soil moisture recorded in different environments was 22.49 per cent in (E_1), 11.74 per cent in E2 at peak stress and 7.50 per cent in E_3 at peak stress.

The observations on productivity and physiological traits were recorded on 10 randomly selected representative plants in all the genotypes in each replication during peak stress condition at both vegetative and reproductive stages. Photosynthetic rate and other gas exchange parameters were measured on the second fully expanded leaf of three representative plants per genotype with a portable photosynthesis system (LI-6400 LICOR, Nebraska, and Lincoln, USA). The measurements were made between 10.00 AM to 12.00 noon on all sampling dates on clear days. The measured parameters were as follows:

Parameters	Units
Photosynthetic rate (PH)	: μ mol of CO_2 m^{-2} s^{-1}
Transpiration rate (TR)	: m mol of H_2O m^{-2} s^{-1}
Stomatal conductance (SC)	: μ mol of CO_2 m^{-2} s^{-1}
Water use efficiency (WUE)	: μ mol CO_2/m mol H_2O
Radiation use efficiency (RUE)	: μ mol CO_2/ μ mol PAR
Leaf temperature (LT)	: ^0C

The analysis of variance, test of significance of variance components and broad sense heritability were carried out as suggested by Panse and Sukhatme (1967). To assess the association of morphological, physiological and yield components with grain yield and among them, simple correlation coefficients were computed from the mean of all traits over replications for all possible combinations of characters and tested for significance as per the procedure given by Panse and Sukatme (1967).

EXPERIMENTAL RESULTS AND ANALYSIS

The relative reduction in mean performance of most of the productivity traits was less in TB NIILs compared to IB NIILs except grains per panicle in E_3. Lower reduction of trait means between non-stress and stress condition was observed in TB NIILs than in IB NIILs for physiological traits except leaf area at vegetative stage. These findings suggested the importance of strong genetic back ground effect on expression of genes for drought tolerance as discussed by Xu *et al.* (2005). The per cent reduction was considerably low in TB NIILs than in IB NIILs for most of the productivity traits, which was supported by higher mean of TB NIILs in moisture stress conditions. More numbers of drought tolerant NIILs superior

Table 1 : Association days to flowering with productivity traits under non-stress (E1), moisture stress at vegetative stage (E2) and moisture stress at reproductive stage (E3) in two NILLs populations

Environments	NIILs #	Panicle length (cm)	Panicle weight (g)	Grain number/ panicle	Spikelet fertility per cent	1000 grain weight (g)	Grain yield / plant	Relative yield
E_1	IB	0.02	0.37**	0.44**	0.01	-0.30*	0.37**	-
	TB	0.16	0.10	0.14	-0.35*	-0.04	0.13	-
E_2	IB	-0.04	-0.12	-0.06	-	-0.15	-0.17	-0.20
	TB	-0.25	-0.09	-0.15	-	-0.08	-0.19	-0.13
E_3	IB	-0.29*	-0.05	-0.07	-0.09	-0.35*	-0.16	-0.26
	TB	-0.11	-0.12	-0.28	-0.33*	-0.14	-0.29*	-0.29*

* and ** indicate significance of values at P=0.05 and 0.01, respectively #: IB = IR-64 x Binam; TB= Teqing x Binam

to checks were observed in TB NIILs although transgressive segregants superior to recurrent parent were less compared to IB NIILs. This is because of superior performance of drought tolerant genotype Teqing (recurrent parent of TB NIILs) which as expected performed better in drought stress condition.

Similarly, Ali *et al.* (2006) reported differences in number of superior plants identified for different abiotic and biotic stress in different backcross populations. This may thus be attributed to the differences between the recurrent backgrounds at least partially with respect to differences in trait-enhancing alleles present in two recurrent parents.

The delay in flowering was more in stress at vegetative stage (E_2), while it was not so much in stress at reproductive stage (E_3). The flowering was delayed more in drought susceptible genotypes like, IR-64. Flowering delay because of stress was lower in TB NIILs compared to IB NIILs in E_2 indicating the TB NIILs are less suffered due to drought stress. This was also supported by realization of high frequency of drought tolerant genotypes in TB NIILs.

Delay in flowering under drought is associated with an apparent delay in floral development. With the onset of stress occurring from 5-10 days before heading, flowering is slowed mainly due to slower elongation of the panicle and supporting tissues. Genetic variation in respect of delayed flowering under drought has been reported and only part of this variation depended on measured plant water status (Pantuwan *et al*., 2002). A delay in flowering date was also reported in rice, when it experiences water deficit before flowering (Lafitte *et al*., 2003). The length of delay is partly related to severity of stress the rice genotype experiences and those with longer delay will tend to produce less grain yield under drought (Ravindrakumar *et al*., 2003).

Drought also affects the process of starch deposition in pollen grains before heading, resulting in unviable pollen and poor anther dehiscence. Genetic variation in respect of pollen formation has been observed independent of plant water status (Liu *et al*., 2005). Panicle desiccation can occur when drought coincides with flowering. Variety specific mechanisms that can refill cavities in xylem elements of shoots may be important to limit panicle failure under stress (Stiller *et al*., 2003) under stress conditions. Accordingly, the variation in spikelet fertility had positive association with grain yield in drought stress in the present investigation.

Relationship between grain yield under stress and non-stress:

There was highly significant positive correlation between grain yields under non-stress (E_1) and moisture stress at vegetative stage (E_2) (r =0.43**) in IB NIILs. Similarly, significant positive correlation (r = 0.31*) was observed between grain yield in non-stress and that under moisture stress at reproductive stage (E_3) in TB NIILs. Similar relation between potential yield under non-stress and yield under water stress

Table 2 : Association days to flowering with physiological traits under non-stress at vegetative stage (E1), moisture stress at vegetative stage (E2), non-stress at reproductive stage (E1R) and moisture stress at reproductive stage (E3) in two NILLs populations

Environments	NIILs#	Leaf area at maturity (LA)	Boot leaf area (BLA)	Photosynthetic rate (PH)	Stomatal conductance (SC)	Transpiration rate (TR)	Relative transpiration rate (RTR)	Leaf temperature (LT)	Water use efficiency (WUE)	Radiation use efficiency (RUE)	Relative water content (RWC)	SPAD meter reading	Leaf drying score (DS)
E_1	IB	0.26	0.13	-0.18	0.01	-0.04	-	-0.15	-0.02	-0.18	0.08	-0.16	-
	TB	0.32*	0.29*	-0.15	-0.04	-0.11	-	-0.17	0.02	-0.15	0.04	-0.27	-
E_2	IB	0.30*	0.34*	-0.16	0.04	-0.18	-0.20	0.34*	0.11	-0.16	-0.37**	-0.35*	0.07
	TB	0.13	0.17	-0.18	-0.02	-0.28	-0.35*	0.19	0.29*	-0.18	-0.41**	-0.29*	0.12
E_1R	IB	-	-	0.13	0.18	0.03	-	-0.03	-0.06	0.13	0.02	0.30*	-
	TB	-	-	0.02	0.1	0.13	-	0.17	-0.14	0.02	0.15	-0.08	-
E_3	IB	0.37**	0.29*	0.13	0.0002	0.03	-0.02	0.29*	0.07	0.13	0.14	0.12	-
	TB	0.50**	0.38**	0.14	0.06	0.0001	-0.09	-0.03	-0.04	0.14	0.28	0.1	-

* indicate significance of values at P=0.05 and 0.01, respectively

#: IB = IR-64 x Binam; TB= Teqing x Binam

Table 3 : Association of productivity traits with photosynthetic rate and related traits under non-stress at vegetative stage (E1), moisture stress at vegetative stage (E2), non-stress at reproductive stage (E1R) and moisture stress at reproductive stage (E3) in two NILLs populations

Traits	Environments	NIILs#	Panicle length (cm)	Panicle weight (g)	Grain number/ panicle	Spikelet fertility per cent	1000 grain weight (g)	Grain yield/ plant	Relative yield	Drought susceptibility index
Photosynthetic rate	E_1	IB	0.08	-0.08	-0.19	0.04	0.32*	0.25	-	-
(m mol M^{-2} S^{-1})		TB	0.11	0.18	0.14	0.13	0.07	0.22	-	-
(PH)	E_2	IB	0.02	0.05	0.09	-	0.08	0.17	0.12	-0.12
		TB	0.01	0.26	-0.05	-	0.03	0.30*	0.32*	-0.32*
	E1R	IB	0.12	0.09	0.04	-0.02	0.09	0.31*	-	-
		TB	-0.03	-0.02	-0.02	0.15	0.06	0.10	-	-
	E_3	IB	-0.04	0.19	0.34*	0.23	-0.09	0.24	0.15	-0.15
		TB	-0.23	-0.10	-0.04	0.10	0.09	0.16	0.12	-0.12
Transpiration rate	E_1	IB	0.10	-0.03	-0.02	-0.01	-0.01	-0.18	-	-
(μ mol M^{-2} S^{-1})		TB	-0.12	-0.54**	-0.56**	-0.31*	0.17	-0.30*	-	-
(TR)	E_2	IB	0.12	0.05	0.15	-	-0.14	0.01	0.13	-0.13
		TB	0.05	0.12	0.15	-	-0.04	0.24	0.24	-0.24
	E1R	IB	0.07	0.08	0.05	-0.14	0.06	0.07	-	-
		TB	0.09	-0.37*	-0.34*	-0.36*	0.03	-0.23	-	-
	E_3	IB	0.19	0.28*	0.24	0.11	0.08	0.04	0.01	-0.01
		TB	-0.06	0.11	-0.05	-0.03	0.07	0.17	0.04	-0.04
Relative water content	E_1	IB	0.04	-0.01	-0.06	-0.05	0.17	0.23	-	-
(%)		TB	-0.10	0.34*	0.21	0.17	0.17	0.39**	-	-
(RWC)	E_2	IB	0.15	0.24	0.10	-	0.14	0.42**	0.34*	-0.34*
		TB	0.04	0.30*	0.09	-	0.19	0.40**	0.21	-0.21
	E1R	IB	-0.10	-0.10	-0.13	-0.11	0.12	0.15	-	-
		TB	-0.15	0.24	0.15	-0.10	0.09	0.12	-	-
	E_3	IB	-0.05	0.16	0.15	0.24	0.12	0.27*	0.20	-0.20
		TB	-0.05	0.27	0.28	0.19	0.13	0.10	0.08	-0.08

* and ** indicate significance of values at P=0.05 and 0.01, respectively #: IB = IR-64 x Binam; TB= Teqing x Bina

was reported in rice (Babu *et al.*, 2003; Lafitte *et al.*, 2004). The correlation of grain yield under non-stress with that in drought stress indicated that, there is high probability that genotypes performing well under non-stress conditions will also perform well under drought, even if the relative yield reduction of these genotypes is large. This is because of spillover effects of yield potential (Blum, 1988). In the present investigation, most of the NIILs yielded better under stress than would have been expected on the basis of their non-stress yields, This was evidenced by weaker associations between yield under non-stress and stress in respect of IB NIILs in E_2 (0.24) and TB NIILs in E_3(0.12). Such NIILs could be the candidates for further study to identify drought adaptive traits.

Relation between flowering delay and productivity traits:

Days to 50 per cent flowering was positively correlated with grain yield and important productivity traits (panicle weight and grains per panicle) in both IB and TB NIILs under non-stress (E_1) situation. However, this association was negative under moisture stress conditions (Table 2). Days to 50 per cent flowering, was also negatively associated with panicle length, spikelet fertility percentage and 1000 grain weight under stress. Pantuwan *et al.* (2002) also reported negative association of delayed flowering with grain yield, fertile panicle percentage and filled grains percentage, when drought stress developed before flowering. However, Yue *et al.* (2005) reported positive correlation of delay in flowering with relative spikelet fertility in black soil, but the correlation was negative in upland sandy field. This suggested that, the effect of delayed flowering time by drought stress on yield stability depends on soil type and condition of screening as well. Productivity under moisture stress was negatively associated with days to flowering (Garrity and O'Toole, 1994; Lanceras *et al.*, 2004) and delay in flowering under stress (Babu *et al.*, 2003). This suggested that, delayed flowering is a strong indication of susceptibility to drought because of retarded growth during the drying cycle and upon recovery (Blum *et al.*, 1999). Lafitte *et al.* (2004) reported no association between yield and flowering date when stress level was mild.

Relation between flowering delay and physiological traits

Days to flowering under moisture stress at vegetative stage was negative with photosynthetic rate and its related traits like stomatal conductance, transpiration rate, relative transpiration and chlorophyll meter (SPAD) reading in both IB and TB NIILs. This indicated that the genotypes showing delay in flowering under drought suffered more stress (Blum *et al.*, 1999; Babu *et al.*, 2003) by reduced assimilation processes under stress resulting in reduced productivity. This was also depicted by negative correlation of the yield and yield traits with days to flowering (Table 1) and positive correlation with photosynthetic rate, transpiration rate and RWC especially in moisture stress at vegetative stage (Table 3) in this study.

Relative transpiration was negatively correlated with days to 50 per cent flowering indicating that relatively less drought affected genotypes maintain higher transpiration rate under stress. The association between leaf temperature and days to 50 per cent flowering was significantly positive in E2 and E3 in case of IB NIILs. This correlation was also positive in TB NIILs in E_2. This indicated that genotypes, where flowering is delayed to a greater extent under moisture stress condition experience more stress as well as heat stress and reduce transpiration rate drastically.

There was positive correlation between WUE and days to 50 per cent flowering under E_2 indicating that, genotypes flowering late were better for WUE but such WUE genotypes would be poor in productivity. Significant positive correlation of WUE was observed with yield and yield related traits in E_1 in case of TB NIILs. This positive association can be explained on the basis that, the condition of screening in this study was almost aerobic even under non-stress conditions with some limitation of water. Hence, judicious moisture utilization of a genotype would have been an important factor for better productivity under non-stress aerobic condition.

Phenotypic correlations of RWC, a moisture stress indicator were significant with plant phenology and production traits in moisture stress at vegetative stage. Leaf RWC was negatively correlated with days to 50 per cent flowering (-0.37** and -0.41** in IB and TB NIILs, respectively) under vegetative stage stress similar to earlier findings (Babu *et al.*, 2003). Likewise, RWC was also negatively associated with physiological traits like leaf temperature and WUE in E_2 and E_3 in case of both IB and TB NIILs. SPAD reading was negatively correlated with days to 50 per cent flowering under E_2 indicating that presence of sufficient chlorophyll under stress which in turn may help in avoiding delay in flowering and affecting assimilation rate and productivity under stress.

Flowering delay has negative impact on grain yield and productivity traits like panicle length, spikelet fertility and 1000 grain weight under moisture stress conditions. This is a strong indicator of susceptibility to drought because of retarded growth. Leaf RWC is an important indicator of plant water status which significantly influenced the plant phenology and productivity traits and has strong association with delayed flowering under drought stress. Hence flowering delay under stress is the strong indicator of drought susceptibility.

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