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Effects of Drought Tolerant Quantitative Trait Loci on Flowering Traits, Panicle Exsertion Rate, Spikelet Sterility and Grain Yield of Rice under Rainfed Lowland Conditions

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ABSTRACT

Drought hinders rice production and yield stability in rainfed lowland ecosystems. Quantitative trait loci (QTL) for root traits on chromosomes 1, 2, 7 and 9 in backcross introgression lines (BIL) of elite rice variety IR64, derived from Azucena/IR64, were designated as Targets 1, 2, 7 and 9 in the present study. Severe stress developed during the period of optimum flowering as indicated by 98-100% yield reduction. Significant phenotypic variations in BIL were observed on days to flowering (DF), delay in flowering (DeF), panicle exsertion rate (PEX), percent spikelet sterility (PSS) and grain yield (GY). Variations among target QTL were also found in the traits studied, particularly under drought stress, indicating that BIL containing Targets 1 and 2 had early DF, higher PEX, lower PSS and higher GY under stress than those with Targets 7 and 9. Targets 7 and 9 lacked QTL for root thickness, indicating that it plays a role in drought tolerance under rainfed lowland conditions. Early flowering BIL had an advantage over later flowering ones because water can be extracted at the early drought stage, which can support the PEX and result in low PSS. In a very severe drought at the flowering stage, PSS directly affected GY. Further study of root morphology and early flowering under stress are necessary to improve rice yields under rainfed lowland conditions.

Keywords: drought tolerance, backcross introgression line, days to flowering, delay in flowering, panicle exsertion rate

INTRODUCTION

In Asia, around 45% of the total rice area is estimated to have no irrigation input (Crosson, 1995). These areas often experience severe water deficits due to low and uneven rainfall distribution patterns, and rice yields are greatly reduced by drought. Drought stress is a serious limiting factor

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to rice production and yield stability in rainfed areas and 18 million tonne of rice valued at USD 3,600 million is lost annually to drought (Ribaut and Poland, 2000). Drought can develop at any time during the growing season, due to unpredictable annual rainfall, and grain yield can be reduced substantially if drought occurs around flowering time (Hsiao, 1982; Boonjung and Fukai, 1996). Matsushima (1962) reported that rice is sensitive to water deficit from 20 d before heading (booting stage) up to 10 d after heading and O' Toole (1982) reported that the most sensitive stage is about 10 d before flowering until 7 d after flowering. During flowering time, drought-induced spikelet sterility can occur as well (O' Toole and Moya, 1981). Mild water stress in the vegetative stage might not have much effect on the heading time and yield. The most sensitive stage to water deficit is at flowering time as the deficit then may cause flowering delay, which has been suggested as an indicator of drought susceptibility (Pantuwan *et al.*, 2002b), with the effects being manifested in panicle exsertion, anther dehiscence and a reduced number of fertile spikelets per panicle, resulting in yield reduction (O'Toole and Namuco, 1983; Boonjung and Fukai, 1996). Recently, several studies have been undertaken to map quantitative trait loci (QTL) for root traits, which are associated with drought tolerance (DT) in rice (Champoux *et al.*, 1995; Redona and Mackill, 1996; Yadav *et al.*, 1997; Price and Coutois, 1999; Shen *et al.*, 1999; Shen *et al.*, 2001). QTL linked with root traits related to drought tolerance of the backcross introgression lines (BILs) of IR64 rice derived from Azucena/IR64 were developed. QTL for root traits and capacity for osmotic adjustment for drought tolerance have been identified previously on chromosomes 1, 2, 7 and 9 and designated as Targets 1, 2, 7 and 9 and were used as material in the present research to study: 1) the effects of root trait QTL on flowering and agronomic traits under water deficit; and 2) the relationships between flowering and agronomic traits and relate the results to root QTL that were introgressed to the BILs of IR64.

MATERIALS AND METHODS

Plant materials

A total of 46 backcross-introgression lines (BILs) of elite rice variety, IR64, were used, which were developed to improve the root system via a molecular marker-aided backcross program at the International Rice Research Institute (IRRI) (Shen *et al.*, 1999). There were four QTL associated with root traits and their linkages to DNA markers were identified on rice chromosomes 1, 2, 7 and 9, designated as Targets 1, 2, 7 and 9, respectively. Different root characters were identified in the QTL targets such that Target 1 had total root weight, deep root weight, deep root per shoot ratio, deep root per tiller, maximum root length and root thickness. On the other hand, Target 2 had deep root per shoot ratio, deep root per tiller, maximum root length and root thickness. With the exception of root thickness, Targets 7 and 9 had similar root QTL as in Target 1 (Shen *et al.*, 2001).

Field experiments

A total of 46 BILs and recurrent parent IR64 were germinated at Kasetsart University, Kamphangsaen, on December 4, 2006 and transplanted on January 11, 2007 in two replications using a randomized complete block design. The field experiments were conducted under two sets of conditions, that is under irrigation and secondly under stress. Seedlings were affected by low temperature and transplanting was delayed until 39 d after seeding (DAS). The seedlings were transplanted into plot sizes of 1.25 × 0.5 m at 25 × 25 cm spacing (6 × 3 hills). For the stress field conditions, the water was drained out on February 20, 2007 (79 DAS) at the appropriate time for drought stress around panicle initiation stage (PI).

Soil samples were collected every week to monitor the change in soil moisture after draining the water and for the duration of the experiment. Rainfall records were obtained from the Nakhon Pathom Meteorological Station.

Data collection

The days to 100% flowering (DF) of each plot were recorded. The delay in flowering (DeF) was determined as the difference between flowering dates under stress and those under irrigated conditions. In each plot, three panicles were randomly tagged and the panicle exsertion rate (PEX) was measured when a small portion of the panicle was exserted until full length was obtained, which took approximately 3-4 d under irrigation and 4-5 days under stress conditions. At maturity, the three panicles were harvested and the grains from each panicle were counted to determine the percentage of seed sterility (PSS). The yield (GY) from each plot was converted into standard units of tonnes (t ha^{-1}).

Statistical analysis

Analysis of phenotypic variances was carried out using the multifactor ANOVA procedure of the statistical analysis software program CropStat for Windows (version 7.2. 2007.2) to check the genetic variation based on the randomized complete block design. A least significant difference (LSD) level of $P \leq 0.05$ was used to determine phenotypic variations among BILs and variations among targets and in BILs within a target by comparing with the recurrent parent of IR64.

RESULTS AND DISCUSSION

Pattern of drought stress development in field experiment

Water was drained from the field at 79 d after sowing (DAS) and the soil moisture content decreased continuously to 19, 14, 12, 11 and 12% at 85, 91, 97, 103 and 109 DAS, respectively. There were rainfall interruptions of 0.03, 2.41, 10 and 4 mm at 97, 109, 121 and 127 DAS, respectively (Figure 1). In this experiment, continuous drying was experienced particularly at the flowering period (91-120 DAS) resulting in successful stress at the reproductive stage. The rainfall interruption

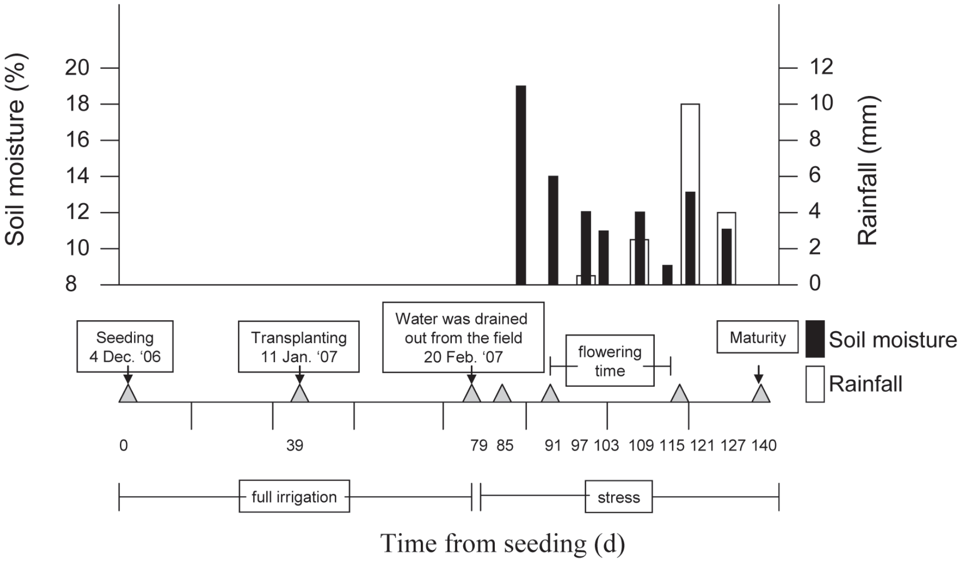

Figure 1 Pattern of rainfall (☐) and soil moisture content (■) in screening field at Kasetsart University, Kamphaeng Saen (KPS) in dry season 2007.

did not affect plant recovery, although there was 10 mm rainfall at 121 DAS, which was the maximum flowering time recorded under stress. The yield reduction in the stressed field revealed that there was 98-100% reduction in all lines, including IR64, indicating drought stress was highly severe and that the small amount of rainfall had not reduced the stressing of the rice plants.

Genotypic variations among BILs, and targets and trait correlations

Highly significant variations for DF under irrigated and stress conditions were observed (Table 1), indicating that the IR64 introgression lines were genetically different in terms of flowering time even under normal conditions. Under irrigated conditions, BILs with Target 2 had the earliest DF (94 d), whereas Target 7 had the longest DF (99 d). On the other hand, BIL with Targets 1 and 9 had DF values that were not significantly different from that of IR64 (97 d). Under stress conditions, BIL possessing Target 2 had early DF (94 d) too, while BIL with Targets 7 and 9 had DF values that were not different from IR64 (102 d), but were longer than BIL with Target 1 (98 d) (Table 2). Under water deficit conditions, stress occurred more or less 10 d before flowering until 7 d after flowering which is the most sensitive stage of rice to water deficit (O'Toole, 1982). DF under stress was correlated positively with DeF (0.82**) (Table 3). This signified that a delay in flowering may not be due to stress but rather to the inherent variation in flowering time. It was determined that lines with longer DF had also higher PSS, and hence the positive correlation between these two factors (0.39**) (Table 3). On the other hand, DF was negatively correlated with PEX and GY, although significant correlation was observed only between DF and PEX (-0.50**) (Table 3). Severe drought was encountered in this experiment, thus the longer the DF, the higher the likelihood that plants would be exposed to stress. The lack of available water prevented the extension of the peduncle from the leaf sheath, as the leaf water potential could not be maintained under very severe conditions (Jongdee *et al.*, 1997; Jearakongman, 2005). It has been observed in drought tolerant *indica* landraces that thicker roots had wider xylem vessels (Umayal *et al.*, 2001) and that the xylem diameter contributes to maintenance of xylem water conductivity (Sibounheuang *et al.*, 2006). Since the introgression lines contained QTL for root traits, it may help in maintaining the higher water potential of lines, which would support longer PEX and therefore shorter DF. Earlier flowering genotypes showed an advantage over late flowering ones in terms of higher spikelet fertility, higher harvest index and higher grain yield (Lafitte and Courtois, 2002).

DeF ranged from -5 d (no delay) to 16 d

Table 1 Phenotypic variations among BILs and IR64 for days for flowering, delay in flowering, panicle exertion rate, percent seed sterility and grain yield under irrigated and stress conditions in dry season of 2007.

	Days to flowering (d)		Delay flowering (d)	Panicle exertion rate (cm day^{-1})		Percent seed sterility (%)		Grain yield (t ha^{-1})	
	Irrigated	Stress		Irrigated	Stress	Irrigated	Stress	Irrigated	Stress
IR64	97	102	5	7.1	5.5	13.2	96.6	5.71	0.01
Mean	96	98	2	7.6	5.7	12.8	95.4	4.95	0.02
Minimum	92	91	-5	4.9	2.2	6.1	78.2	2.95	0.00
Maximum	108	121	16	11.1	8.0	27.9	100.0	6.95	0.11
Level of significance	**	**	**	ns	**	**	**	**	**
LSD	2	4	3	2.4	2.2	6.5	5.3	1.09	0.01
CV (%)	1	2	32	15	18	25	2	11	3

LSD-Least Significant Difference

CV-Coefficient of Variation

** indicates level of significance (significant at 99%); ns = not significant in the BIL, while IR64 showed a five-day delay in flowering (Table 1). The current study proved that BIL with Targets 7 and 9 showed longer DeFs (3 and 5d, respectively) whereas those with Targets 1 and 2 exhibited short DeF (Table 2). As mentioned above, the delay in flowering may have been due to the long flowering time of lines, rather than the result of drought stress, since those with Targets 7 and 9 with long flowering time also showed delays in flowering. In general, DeF due to stress was not observed, but there were some lines within the same frame of flowering time under the irrigated conditions that showed different responses in delayed flowering. DeF was found to be correlated positively (0.82**, 0.39**) with DF and PSS, respectively, and correlated negatively (-0.50**) with PEX (Table 3). The positive correlation between DF and DeF is again

Table 2 Phenotypic variations in targets compared with IR64 for days for flowering, delay in flowering, panicle exertion rate, percent seed sterility and grain yield under irrigated and stress conditions in dry season of 2007.

Trait	IR64	Target 1	Target 2	Target 7	Target 9
Days to flowering (d)					
Irrigated	97c	96bc	94a	99d	97c
Stress	102c	98b	95a	102c	103c
Delay flowering (d)	5c	2a	1a	3b	5c
Panicle exertion rate (cm day^{-1})					
Irrigated	7.1a	7.7a	7.8a	7.7a	7.2a
Stress	5.5a	6.9a	6.1a	5.1a	5.2a
Percent seed sterility (%)					
Irrigated	13.2a	12.2a	13.2a	12.1a	13.9a
Stress	96.6b	93.1a	92.8a	96.6b	95.5b
Grain yield (t ha^{-1})					
Irrigated	6.01c	5.10b	4.82a	4.91a	5.04b
Stress	0.10a	0.44a	0.24a	0.14a	0.13a

Letters a,b,c,d, in a row indicate significant difference of the trait mean values among targets and IR64

Table 3 Correlation coefficients among days for flowering (DF), delay in flowering (DeF), panicle exertion rate (PEX), percent seed sterility (PSS) and grain yield (GY) under stress conditions in dry season of 2007.

Trait	DF	DeF	PEX	PSS	GY
DF	1				
DeF	0.82**	1			
PEX	-0.50**	-0.48**	1		
PSS	0.39**	0.28ns	-0.40**	1	
GY	-0.21ns	-0.21ns	0.24ns	-0.33*	1

** indicates level of significance (significant at 99%); ns = not significant an indication that DeF did not result from drought stress. The study conducted by Pantuwan *et al.* (2002b), exemplified the real effect of drought stress to DeF, wherein no relationship (r=0.03; not significant) between DF and DeF was found. The inability to exsert the panicle from the leaf sheath resulted in an increase in spikelet sterility, which was observed in the present experiment and that of Pantuwan *et al.* (2002b). Pantuwan *et al.* (2002c) suggested that rice that was able to maintain relatively high panicle water potential had less DeF.

Variation in PEX under stress was observed among BIL, but not under irrigated conditions (Table 1). Under stress, PEX was found in the range 2.2-8.0 cm. When PEX was compared among targets, no difference was identified, although Targets 7 and 9 had shorter PEX (5.14 and 5.12 cm, respectively) compared with Targets 1 and 2 (Table 2). Rice is sensitive to water stress during reproductive development from panicle exsertion to emergence (Selote and Chopra, 2004). The effect of water stress during the elongation of internodes resulted in a decreased panicle exsertion and may be a consequence of a failure in the maintenance of internal plant water potential (Zou *et al.*, 2007). In stressed plants, peduncle elongation is hindered. The interruption in peduncle elongation affected PEX, which consequently caused a delay in the heading. Peduncle elongation can only resume after re-watering the plants (Liu *et al.*, 2006). As expected, PEX was found to be correlated negatively (-0.40**) with PSS (Table 3). In the present experiment, the potential spikelet number per panicle may not have been affected, but spikelet sterility may have increased due to less PEX which was also observed by Selote and Chopra (2004).

Wide variation in PSS was observed among BIL under irrigation (6.1-27.9%) and stress (78.2-100%) conditions (Table 1). Under fully irrigated conditions, even though PSS across BIL was significant, differences between targets and IR64 showed no significant variation. Significant differences were observed under stress conditions. The results showed that BIL with Targets 1 (93.1%) and 2 (92.8%) had PSS, which was lower than BIL with Targets 7 (96.7%) and 9 (95.5%). The PSS of BIL in Targets 7 and 9 was not statistically different from IR64 (96.6%) (Table 3). High PSS was due to stress mainly, which inhibited the elongation of the peduncle and while some may have continued growing, they did not achieve the lengths attained under irrigated conditions. Liu *et al.* (2006) observed that florets that were kept under the leaf sheath or emerged too late for anthesis were all sterile and this was observed to be the same in the present experiment. Spikelet fertility is most sensitive to drought stress at flowering (Boonjung and Fukai, 1996) and the increase in sterility may be attributed to severe stress experienced during the peak flowering time (91-120 d). Garrity and O'Toole (1994) reported that seed sterility contributed the most to grain yield reduction. The reduction in GY may have been due to the reduction in filled spikelets per panicle, spikelet fertility, filled grain weight per panicle and 20 grain weight (Praba *et al.*, 2009). In the present experiment, only the PSS was found to be correlated significantly with GY (-0.33*) (Table 3), and therefore contributed directly to the decrease in GY.

IR64 yielded 5.71 t ha^{-1} and the range of GY in the BIL was 2.95-6.95 t ha^{-1} signifying highly significant genotypic variations in GY under irrigated conditions (Table 1). Under irrigated conditions, the GY values of BIL with Targets 1 and 9 were not statistically different, but were higher than those possessing Targets 2 and 7 (Table 2). IR64 yielded higher GY values than all targets. On the other hand, under stress conditions, very low GY was observed in BIL ranging from 0 to 0.11 t ha^{-1} and was 0.01 t ha^{-1} in IR64 (Table 1). Due to severe drought stress, all targets had GY values that were not different statistically from IR64 (Table 2), although those possessing Targets

1 and 2 showed higher GY values than IR64 and Targets 7 and 9. In an experiment conducted by O'Toole *et al*. (1984), it was observed that rice panicles lack a mechanism to impede water loss, particularly when drought stress occurs during flowering, and this finding supports the present results, where prolonged stress lessened the PEX, which may have been due to the low panicle water potential and its consequent effect on the elongation of the peduncle. Poor PEX resulted in increased PSS and, therefore, decreased GY. The present results agreed with those of Liu *et al*. (2007) who suggested that the water status in grains and panicles probably has more direct effect in spikelet fertility, grain filling and final yield.

CONCLUSION

The results showed that QTL for root traits were associated with drought tolerance in rice, particularly in BIL of IR64. The introgressed QTL segments linked to root traits were linked to chromosomes 1, 2, 7 and 9 and those with Targets 1 and 2 had root thickness QTL which were not found in Targets 7 and 9. The results indicated that root thickness is a necessary trait for rice to perform well under rainfed lowland conditions. Moreover, under very severe drought stress, early maturing genotypes had an advantage by supporting panicle exsertion that resulted in less spikelet sterility, although the flowering time affected indirectly the grain yield, while the percentage of spikelet sterility contributed directly to yield loss. Therefore, it is suggested that combating drought stress under rainfed lowland conditions requires: thick root morphology to support panicle exsertion; high filled-grain percentage; and grain yield coupled with early maturity.

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