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Identification and Genetic Characterization of a Novel Tillering Dwarf Semi-Sterile Mutant *tdr*1 in Rice

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Abstract

Tillering and plant height are important components of plant architecture and grain production in rice. We identified a novel high tillering, dwarf and semi-sterile mutant, as named *tdr*1 in a rice maintainer line E20 derived from the cross between between IR68888B and Luxiang 90. The investigation of tiller dynamic in the *tdr*1 line displayed 3 different phases: rapid increasing of tillers in the vegetative growth stage, producing no new tillers in the transition stage from the vegetative growth to reproductive growth, and regeneration of new tillers after heading. The assay of hormones showed the significant reduction of brassinolide level and no change of the levels of gibberellic acid, cytokinin and strigolactone in the *tdr*1 line. Genetic analysis indicated the phenotype of high tillering, dwarfism and semi-sterility is controlled by a recessive gene in several different segregation populations. The *TDR*1 gene was mapped in the 105 kb interval between RM3288 and RM6590 on chromosome 4. Cloning of *TDR*1 gene would provide a new opportunity to uncover the molecular mechanism of the development of plant height and tiller in rice.

Keywords

Rice, High Tillering, Dwarf, Semi-Sterile, Mapping

1. Introduction

Plant height and tillering are two important traits of plant architecture affecting grain yields in rice. Dwarfism improves plant lodging resistance to increase grain

*The co-first authors contributed equally to this work.

yield and harvest index [1]. Rice tillering determines the number of panicles per plant. Excessive tillering generally causes a high rate of unproductive tiller, small panicle size and poor setting rate [2]. It was proved that there was a negative correlation between tiller number and plant height [3].

Tillers originated from axillary buds in the axil of leaves and axillary buds are usually dormant after their formation. The outgrowth of axillary buds is regulated by the interaction of environmental and endogenous factors [4]. In rice, it is reported that the growth and development of tillers were associated with plant hormones such as auxin, cytokinin, gibberellins (GA), brassinosteroid and strigolactone [5]-[11]. A series of high-tillering dwarf mutants have been identified and characterized in rice in detail and some underlying genes have been cloned [12]-[17].

In this study, we identified a novel mutant plant *tdr*1 with high-tillering, dwarf and semi-sterile phenotypes from a rice maintainer line E20 derived from the cross between IR68888B and Luxiang 90. We investigated its phenotype and the response to plant hormones and performed mapping analysis.

2. Materials and Method

2.1. Plant Materials

In the spring of 2006, we found a mutant with multi-tillers, dwarfism and semi-sterility (named as *tdr*) in the F_4 progeny line E20 from the cross between IR68888B (female parent) and Luxiang 90 (male parent). We also created several F1populations derived from the crosses between the *tdr*1 line (female parent) and other *indica* lines E20, 931, IR68888B and Luxiang 90 (male parents).

2.2. Phenotypic Characterization and Assays of Phytohormone Level

In order to character the mutant phenotype, the mutant *tdr*, its wild type, and 9311 were grown in paddy field in Mianyang, Sichuan. A total of 30 plants from each of the above three lines were used to investigate several traits including tiller number, plant height, inter-node length, kilo-grain weight and pollen fertility.

Because the phenotypes of multi-tiller, dwarfism and semi-sterility were generally associated with plant hormones, exogenous gibberellins (1×10^{-4} mol/L GA3) and sterile water as control were sprayed for the *tdr* line, its wild type and 9311 at elongation stage in the greenhouse. The length of panicle, 1st, 2nd, 3rd, 4th and 5th upper internodes were measured for 10 plants each line at mature stage. Simultaneously, phytohormone levels were scored for young seedling using the ELISA kits (AndyGene) of four plant hormones including gibberellic acid (GA), cytokinin (CTK), brassinolide (BR) and strigolactone (SL) according to the corresponding protocols (http://www.andygene.com/index.php).

2.3. Extraction of DNA and Mapping of *TDR* Gene

DNA was prepared using the modified hexadecyltrimethylammonium (CTAB)

method. Ten normal plants and 10 dwarf plants from the F2 population derived from *tdr* and 9311 were used to create the dominant and recessive bulks, respectively. Fine mapping of *TDR* gene was conducted with SSR and InDel markers. InDel markers were designed according to the genomic sequences of *indica* line 9311 and *japonica* line Nipponbare.

3. Results

3.1. Phenotypic Characterization of *tdr*1 Line

The mutant *tdr* showed dwarfism, high tillering ability, small grain and low setting rate (Figure 1). Ten plants from each lines *tdr*, its wild type and 9311 were characterized. Compared with the wild type, the maximum number of tillers in *tdr*1 line is up to 81.4 and its plant height is not enough half (45.5 cm) of the plant height of its wild type (109.86 cm). Its kilo-grain weight is 15.36 gram, the setting rate is only 32.47% and lots of unstained pollens were observed.

To fully understand tillering dynamics of *tdr*1 line, we continuously investigated the number of tillers of 10 plants for *tdr*1 line, its wild type and 9311 every 5 days after transplantation. We found that the *tdr*1 line has rapidly increased the tiller number since June 13th (Figure 2) and the number of tillers reached a plateau for the *tdr*1 line on July 8rd. For the wild type and 9311, the number of tillers have become immobile since June 28th, but new tillers occurred again on about August 7th (the heading day of *tdr*1 line) for the *tdr*1 line, which indicates that the transition from vegetative to reproductive stages could inhibit the growth of axillary buds and the end of the transition phase could relieve the dormancy of axillary buds in the *tdr*1 line again.

3.2. Effect Evaluation of Exogenous Gibberellin and Phytohormones Determination

In previous reports, GA plays an important role for plant height and tillering. In order to understand the effect of GA for the *tdr*1 line, we treated the *tdr*1 line, its wild type and 9311 with exogenous GA3 (1×10^{-4} mol/L). We found that exogenous GA can increase the plant height for the above three lines, but showed different effect for the three lines (Figure 3). For the *tdr*1 line, the 2nd and 3rd upper internodes were significantly elongated, but its plant height was not fully recovered. For its wild type, the length of the 1st, 2nd and 3rd upper internodes were remarkably increased. For 9311, the panicle, 1st, 2nd, 3rd and 4th internodes were significantly elongated. These above results indicate that the phenotype of the *tdr*1 line is not caused by the signal transduction pathway of GA.

To fully understand the change of phytohormones in the *tdr*1 line, we measured the content of phytohormones such as gibberellins (GA), cytokinin (CTK), brassinolide (BR) and strigolactone (SL) in the *tdr* line and its wild type. Compared with in the wild type (GA 113.02 pmol/L, CTK 41.99 pmol/L, SL 37.08 pmol/L), the levels of GA (109.34 pmol/L), CTK (43.05 pmol/L) and SL (35.18 pmol/L) did not significantly change in the *tdr*1 line, but the level of BR (165.22

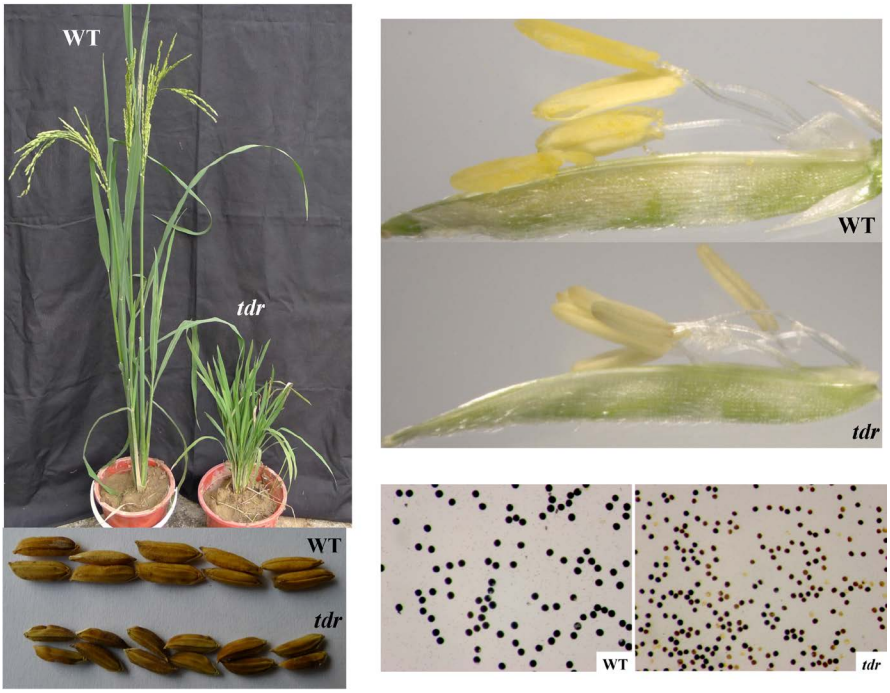

Figure 1. The variant phenotype of the *tdr1* line including plant height, the size of anthers and seeds and the fertility of pollen.

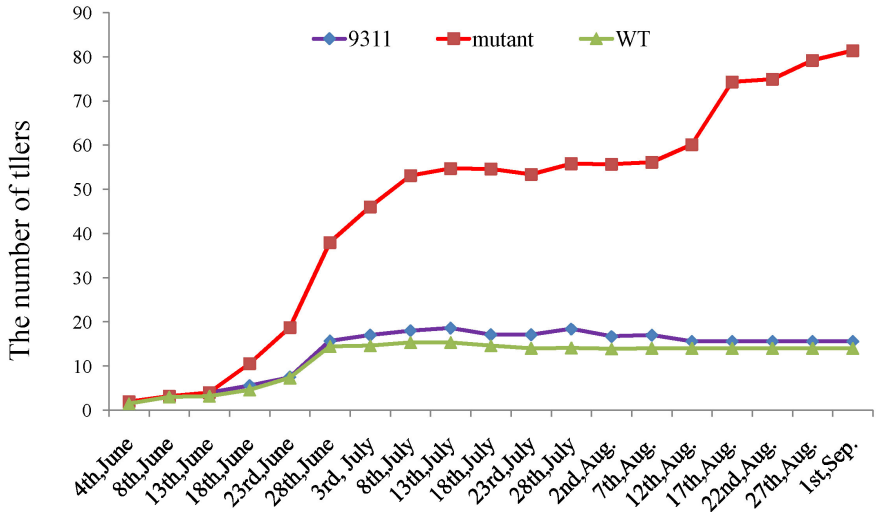

Figure 2. The dynamics of tiller number of the *tdr1* line, its wild type and 9311.

pmol/L) remarkably decreased in the *tdr*1 line (**Figure 4**), implying the biosynthesis of brassinolide might play roles for the phenotype of *tdr*1 line.

3.3. Genetic Segregation of *tdr* Phenotype

To determine the inheritance pattern of the phenotype of high-tillering, dwarfism and semi-sterility in the mutant *tdr*1 line, we used the *tdr*1 line and four normal semi-dwarf lines with different genetic background such as its wild type E20, 9311, IR68888B and Luxiang 90 to construct several F_2 populations and 1

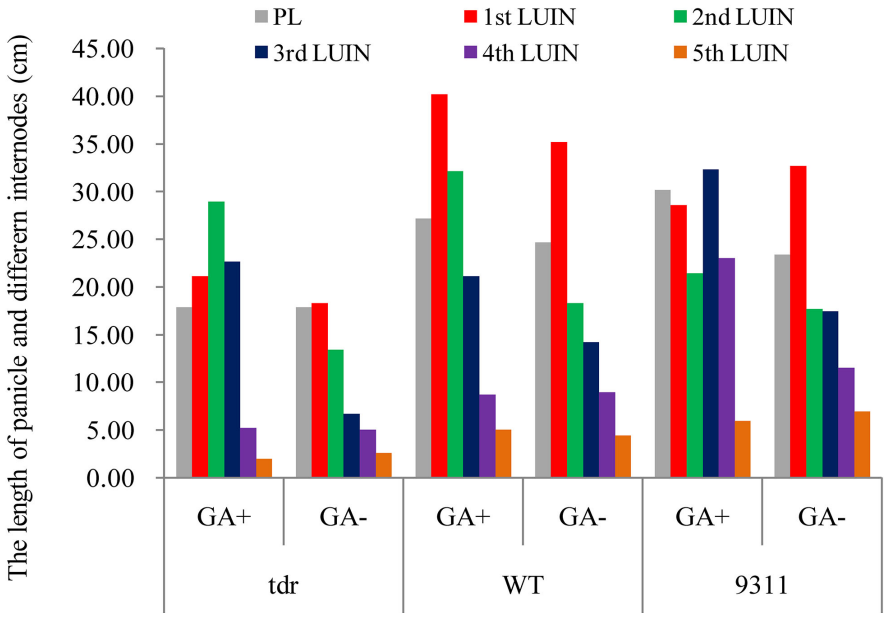

Figure 3. Effects of exogenous GA on the length of different internodes and panicles in *tdr*1 line, its wild type and 9311.

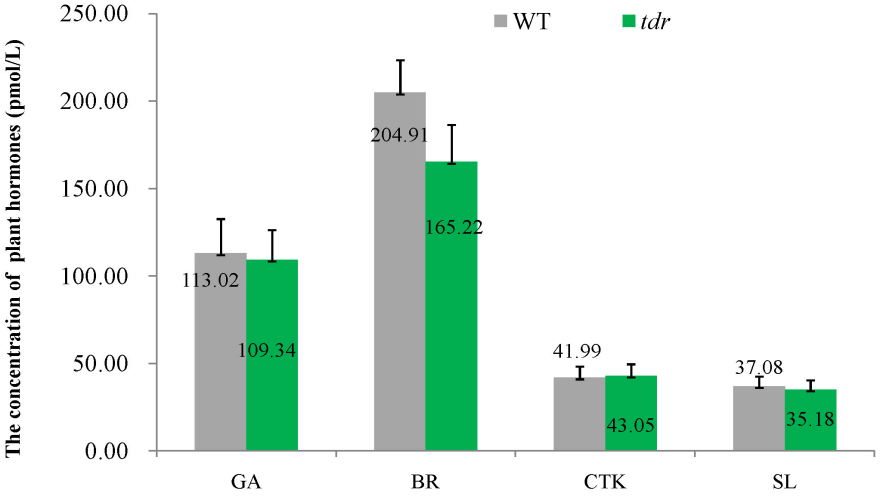

Figure 4. The assays of four phytohormones including GAs, CTKs, BRs and SLs in the leaves of the *tdr1* line and its wild type.

backcross population (BC_1F_1). We scored plant height of the parent lines, their F_1, F_2 and BC_1F_1 progenies and investigated the segregation ratios of plant height in F_2 and BC_1F_1 populations (Table 1). All the F_1 plants from the four crosses showed the wild-type phenotype, and all of these F_2 progenies have a segregation ratio of 3:1 between wild-type and mutant plants ($\chi^2 < 3.84$), indicating this phenotype is controlled by a recessive gene.

3.4. The Mapping of *TDR*1 Gene

Genetic analysis showed that the phenotype of high-tillering, dwarfism and semi-sterility was controlled by a recessive gene. We selected the F_2 population

Table 1. The phenotype of plant height in the different lines and progenies.

Lines or population	Progeny	Plant height (cm)	The number of plants		The ratio of segragation	The value of χ^2
			Normal	Dwarf		
tdr	-	59.04 ± 3.24	-	10	-	-
E20	-	103.41 ± 1.16	10	-	-	-
9311	-	105.28 ± 3.47	10	-	-	-
IR68888B	-	102.24 ± 2.15	10	-	-	-
Luxiang 90	-	98.47 ± 2.36	10	-	-	-
tdr/E20	F_1	100.22 ± 2.38	10	-	-	-
tdr/9311	F_1	104.13 ± 2.30	10	-	-	-
9311/*tdr*	F_1	103.58 ± 2.34	10	-	-	-
tdr/ IR68888B	F_1	99.62 ± 3.17	10	-	-	-
tdr/Luxiang 90	F_1	97.17 ± 3.02	10	-	-	-
tdr//*tdr*/9311	BC_1F_1	-	68	71	0.96	0.065
tdr/E20	F_2	-	248	82	3.02	0.001
tdr/9311	F_2	-	279	108	2.58	1.312
tdr/IR68888B	F_2	-	83	25	3.32	0.197
tdr/Luxiang 90	F_2	-	68	19	3.58	0.464

from the cross between 9311 and the *tdr*1 line to map the *TDR* gene. Thirty nine SSR markers showed the polymorphism between 9311 and *tdr*1 line in about 600 used SSR markers evenly distributed on 12 chromosomes in rice. We used these polymorphic SSR markers to perform the linkage analysis for 392 F_2 recessive plants and finally the underlying gene *TDR*1 was located in the 2.1 cM interval between RM252 and RM303 on Chr.4 (**Figure 5**, **Table 2**).

For fine mapping of the *TDR*1 gene, we further screened the polymorphic markers between RM252 and RM303 based on the Nipponbare reference genome and obtained 7 polymorphic markers in this interval. The 1620 recessive plants in the F_2 population were used to fine map the *TDR*1 gene. Finally, the *TDR*1 gene was mapped in the 105.4 kb interval between RM3288 and RM6590. Based on the Nipponbare reference genome (https://rapdb.dna.affrc.go.jp/), there are 20 annotated genes including D17/HTD1 (Os04g0550600) and OsSPL7 (Os04g0551500) (**Table 3**).

4. Discussion

Recently lots of high-tillering dwarf rice mutants were reported and some underlying genes were mapped and cloned. Phytohormones play important roles for plant growth and development. In this study, the *tdr*1 mutant displayed the capability of high tillering, dwarfism, small seeds and the reduction of fertility. The *tdr*1 line was treated with exogenous GA3 and its height was not fully recovered, which indicates the *tdr*1 mutant is independent of the GA pathway. The

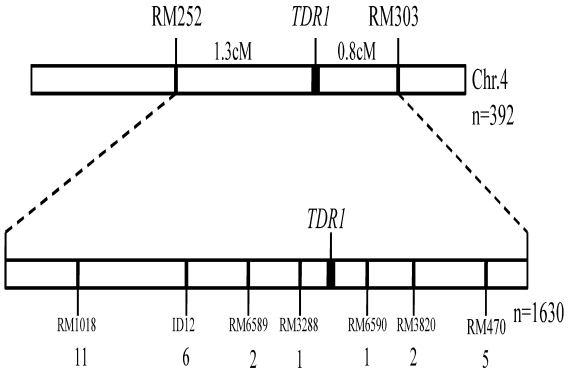

Figure 5. The linkage map of *TDR1* gene.

Table 2. Lists of the primers used for mapping the underlying gene *TDR*1.

Markers	Forward primer (5'-3')	Reverse primer (5'-3')
RM252	TTCGCTGACGTGATAGGTTG	ATGACTTGATCCCGAGAACG
RM303	GCATGGCCAAATATTAAAGG	GGTTGGAAATAGAAGTTCGGT
RM1018	ATCTTGTCCCACTGCACCAC	TGTGACTGCTTTTCTGTCGC
ID12	TCGCCAAATAAGATCGCTGA	ACCAAGCAGCAGATTTAGTG
RM6589	AAGTTCACAACACGTCGTCG	CGACGCTGTTGATCAGCC
RM3288	CTCGTACCGTCAAAAGACC	AATCTGGAGGCACTGTCAC
RM6590	TTGCGTCGGTGTAGAGGC	CACATGTCATCCTCACACCC
RM3820	CTCTGCTAGCCTGCACACAG	GTGGCTTTCAATGGTTGGAG
RM470	TCCTCATCGGCTTCTTCTTC	AGAACCCGTTCTACGTCACG

assay of phytohormone level also showed that this mutant phenotype was not related with GA, CTK and SL and could be caused by the reduction of BR. It is proved that BR plays crucial roles in the development of lateral organs including lateral organogenesis, plant height, seed size and fertility [18] [19] [20]. On the aspect of tiller dynamics, the *tdr*1 line rapidly increases of tillers in the vegetative growth phase, stops producing new tillers in the transition phase from the vegetative growth to reproductive growth, and regenerated new tillers after heading. The *htd*1 mutant has been reported to still keep the high tillering capacity [21].

In our paper, the underlying gene *TDR*1 was located in the about 105 kb region of chromosome 4. In this candidate region, 20 genes are annotated and includes *D*17/*HTD*1 and *OsSPL7* causing the phenotype of high tillering and dwarfism. *D*17/*HTD*1 was proved to be associated with strigolactone biosynthesis [22] [23]. However, our hormone assays also indicates that there is no significant change for strigolactone in the *tdr*1 line and its wild type. *OsSPL7* was reported as a target of miR156f and binds directly the *OsGH*3.8 promoter to regulate tiller and plant height, and the miR156f/*OsSPL7* pathway was involved in the regulation of plant architecture mediated by auxin [24]. Currently, it is

Table 3. The candidate genes in the mapping interval of *TDR*1 gene.

Gene ID	Position	Annatation information
Os04g0550200	chr04:27539878..27540865	Pathogenesis-related transcriptional factor and ERF domain containing protein. OsERF34
Os04g0550300	chr04:27544416..27545300	Hypothetical protein
Os04g0550400	chr04:27551423..27560074	E3 ligases of H2Bub1, Transcriptional regulation of anther development. OsHUB1
Os04g0550500	chr04:27563230..27566440	Similar to N-acetyl glutamate kinase 2
Os04g0550600	chr04:27567824..27570449	Negative regulation of the outgrowth of axillary buds, Strigolactones biosynthesis. D17/HTD1
Os04g0550700	chr04:27570555..27572699	Uncharacterised conserved protein UCP012943 domain containing protein
Os04g0550800	chr04:27575661..27576994	Major intrinsic protein family protein
Os04g0550833	chr04:27576034..27576647	Hypothetical protein
Os04g0550866	chr04:27595181..27595879	Hypothetical protein
Os04g0550900	chr04:27595492..27596105	Aquaporin TIP2-3
Os04g0551200	chr04:27605166..27608318	Similar to Cytoplasmic malate dehydrogenase
Os04g0551300	chr04:27608423..27612487	Similar to Growth regulator like protein
Os04g0551400	chr04:27609034..27611514	Non-protein coding transcript
Os04g0551500	chr04:27614776..27618001	Squamosa promoter-binding-like protein 7. OsSPL7
Os04g0551550	chr04:27614946..27617739	Hypothetical protein
Os04g0551600	chr04:27627478..27628262	Zinc finger, FYVE/PHD-type domain containing protein
Os04g0551700	chr04:27633216..27637876	PAP fibrillin family protein
Os04g0551800	chr04:27638063..27643857	Similar to T-complex protein 1, alpha subunit (TCP-1-alpha) (CCT-alpha)
Os04g0552000	chr04:27645701..27647185	Barwin-related endoglucanase domain containing protein
Os04g0552066	chr04:27646851..27647183	Hypothetical protein

found that there is the interaction between auxin and brassinosteroid regulating plant growth and development. Auxin could promote the expression of *DWARF*4, a crucial hydroxylase for BR biosynthesis to control endogenous BR level and also inhibit the binding of BZR1 to the promoter of *DWARF*4 [25] [26]. In our study, the level of BRs is significantly reduced in the *tdr*1 line, compared with its wild type. Because the level of auxin was not tested, we can not know whether the auxin-BR interaction was destroyed to cause the phenotype of high tillering, dwarfism and semi-sterility in the *tdr*1 line.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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