PLANT SCIENCE TODAY
ISSN 2348-1900 (online)
Vol 12(2): 1-12
https://doi.org/10.14719/pst.6131

HORIZON
e-Publishing Group
HePG

RESEARCH ARTICLE

Evaluation of physio-morphological traits and yield performance of backcross inbred lines under drought stress across diverse environments

Arulmozhi R[1*], A John Joel[2], R Suresh[3], P Boominathan[4], K Sathya Bama[5], S M Indhu[6], R Pushpa[1], M Dhandapani[1], R Manimaran[1] & K Subrahmaniyan[1]

[1]Tamil Nadu Rice Research Institute, Aduthurai, Mahadanapuram 612 101, Tamil Nadu, India

[2]Centre for Plant Molecular Biology and Biotechnology Tamil Nadu Agricultural University Coimbatore 641 003, Tamil Nadu, India

[3]Department of Rice, Tamil Nadu Agricultural University Coimbatore 641 003, Tamil Nadu, India

[4]Department of Crop Physiology, Tamil Nadu Agricultural University Coimbatore 641 003, Tamil Nadu, India

[5]Department of Soil Science and Agricultural Chemistry, Tamil Nadu Agricultural University Coimbatore 641 003, Tamil Nadu, India

[6]Department of Genetics & Plant Breeding, Tamil Nadu Agricultural University Coimbatore 641 003, Tamil Nadu, India

OPEN ACCESS

ARTICLE HISTORY
Received: 08 November 2024
Accepted: 25 January 2025
Available online
Version 1.0 : 03 April 2025
Version 2.0 : 13 April 2025

Check for updates

Additional information

Peer review: Publisher thanks Sectional Editor and the other anonymous reviewers for their contribution to the peer review of this work.

Reprints & permissions information is available at https://horizonepublishing.com/journals/index.php/PST/open_access_policy

Publisher's Note: Horizon e-Publishing Group remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Indexing: Plant Science Today, published by Horizon e-Publishing Group, is covered by Scopus, Web of Science, BIOSIS Previews, Clarivate Analytics, NAAS, UGC Care, etc
See https://horizonepublishing.com/journals/index.php/PST/indexing_abstracting

CITE THIS ARTICLE
Arulmozhi R, Joel AJ, Suresh R, Boominathan P, Bama KS, Indhu SM, Pushpa R, Dhandapani M, Manimaran R, Subrahmaniyan K. Evaluation of physio-morphological traits and yield performance of backcross inbred lines under drought stress across diverse environments. Plant Science Today. 2025; 12(2): 1-12. https://doi.org/10.14719/pst.6131

Abstract

The present experiment was conducted using two sets of backcrossed inbred line (BILs) derived from two crosses *viz.,* ADT(R) 45 × Apo with Quantitative trait loci (QTLs) qDTY 1.1, 3.1 and 4.1 and ADT(R) 45 × Way Rarem with QTLs qDTY 12.1. The BILs and their parental lines were evaluated in an irrigated (EI) as well as two drought environments (EII and EIII) to understand the relationship and contribution of physio morphological traits responsible for developing potential genotype with high yield under drought environments by correlation and path coefficient analysis. Predominant association and high direct and indirect dependency were observed for the number of productive tillers per plant, panicle length, grains per panicle and spikelet fertility % with yield in stress and non-stress environments. The association of physiological traits, viz., leaf senescence, drying, rolling and drought recovery scores, showed a negative and significant relationship with grain yield in both moisture-stress environments. Despite the huge variations observed between the irrigated and drought environments, it was observed that 55 % of BILs carrying qDTY 1.1 and 71 % of BILs with qDTY3.1 showed 80 % drought recovery in the stress environment. Almost all the BILs harbouring qDTY 12.1 recorded 80 % drought recovery. This indicates that these QTLs allow the genotypes to tolerate water stress and recover from drought through the adaptive mechanism of secondary traits, *viz.,* leaf senescence, drying, rolling and drought recovery without yield loss under water stress conditions.

Keywords

BIL; drought; physiological traits; qDTY

Introduction

The sustainability of contemporary agriculture is seriously threatened by climate change. Farmers and scientists must work together to comprehend and develop solutions for and adjust to the changing environmental conditions to maintain sustainable crop production. The effect is especially noticeable for rice (*Oryza sativa* L.), a staple grain consumed by over half of the world's population. Millions of smallholder farmers in South and Southeast Asia depend on rice for their livelihoods, which is grown under various environmental circumstances (1). With a primary concentration on irrigated habitats, the Green Revolution increased rice output by 2.6 times since 1961 (2). Nonetheless, more than 40 million people in South and Southeast Asia rely on growing rice in marginal uplands that receive rainfall, substantially contributing to the world's rice production. Small and marginal farmers frequently grow rice in these regions with few infrastructure and inputs. About 30 % of the world's rice-growing land depends on rainfall and irregular rainfall patterns usually cause drought or floods, drastically lowering productivity (3).

An estimated 23 million ha of rice are affected by varied degrees of drought in Asia alone, making drought a significant abiotic stressor impacting rice productivity in rainfed countries. Climate change worsens these issues, increasing water shortages and making droughts more frequent and severe. Due to competition from urban and industrial needs, freshwater availability is decreasing even in areas with irrigation infrastructure (4). As a result, water stress is now a significant problem that restricts rice yield in irrigated and rainfed systems. Stabilizing rice production in rainfed areas is essential to addressing poverty and food insecurity, aligning with the United Nations' Millennium Development Goals (5). Direct seeding has replaced transplanting in rainfed rice agriculture areas due to frequent droughts and flash floods. Direct seeding has benefits, including a 90 % labour reduction compared to transplanting and a 14-day shorter crop growth period (6). Modern high-yielding rice cultivars cannot frequently endure early abiotic stresses, which results in poor seedling establishment despite these advantages (7). Farmers are forced to replant, which raises expenses and puts them at risk of terminal drought or leaving fields fallow. Creating cultivars resistant to several abiotic stresses is still challenging for plant breeders.

Development of drought-tolerant and high-yielding varieties requires a good knowledge of the physio-morphological mechanisms involved in yield under drought-related components. The genetic control of these secondary traits contributing to drought resistance will be key to improving stable rice production (8,9). Traditional rice varieties, drought resistant but non-responsive to improved management practices, are cultivated in marginal lands and receive comparatively lower inputs under subsistence agriculture. Hence, drought resistance and yield stability are the primary selection criteria in such ecosystems.

Considering the above situations, the present research focuses on the development of climate-resilient elite pre-breeding materials in rice by utilizing the backcrossed inbred lines (BILs) derived from the crosses ADT (R) 45*1/Apo and ADT (R) 45*1/ Way Rarem. ADT (R) 45 a high-yielding rice variety adapted to irrigated ecosystems, whereas Apo derived from an aus or tropical *japonica* germplasm group is reported to possess six drought QTLs,qDTY1.1, qDTY2.1, qDTY2.2, qDTY3.1,qDTY4.1 and QTY8.1 and Way Rarem which belongs to the *indica* group is reported to have a major QTL qDTY12.1showing high additive effects for grain yield under drought (10). The BIL population derived from the above crosses was analyzed for its genetic and phenotypic variability for yield and drought-related traits to identify elite genotypes for future abiotic stress breeding programs.

Hence, the present study has been formulated to address the facts mentioned above with the following objectives to assess the performance of QTLs governing yield under drought by employing a marker-assisted breeding approach in backcrossed inbred lines of ADT(R) 45*1/Apo and ADT(R) 45*1/Way Rarem and Phenotyping in Target Production Environment for better correlation of QTLs effects and secondary physiological traits for yield under stress.

Materials and Methods

This study focuses on genotyping backcross inbred lines (BILs) harbouring QTLs linked to drought tolerance in rice, which are genotyped and phenotyped drought. Backcross inbred lines (BILs) were developed using the elite recipient parent ADT (R) 45 (Table 1), incorporating QTLs such as *qDTY1.1, qDTY3.1, qDTY4.1* and *qDTY12.1* from donor varieties like Apo and Way Rarem during 2018-19 at the Plant Breeding Unit, Tamil Nadu Rice Research Institute, Aduthurai. The BIL populations were assessed under target production environments across three locations: Tamil Nadu Rice Research Institute, Aduthurai (Location I); Agriculture College and Research Institute, Eachangkottai (Location II) and Agricultural Research Station, Pattukottai (Location III) during 2019 and 2020 (Table 2). The collected data were analyzed statistically to draw meaningful conclusions.

Table 1. Details of parental genotypes used in this experiment

Sl.No.	Genotypes	Source	Designation	Description
1	ADT (R) 45	TRRI, Aduthurai, Tamil Nadu	Recipient parent	High yielding, fine grain quality, adapted to peninsular India, susceptible to drought stress
2	Apo	IRRI, Philippines aus/japonica	Donor parent	Upland Indica genotype with qDTY1.1, qDTY2.1, qDTY3.1 and qDTY4.1 governing grain yield under drought stress
3	Way Rarem	Indonesian Indica rice variety	Donor parent	Major QTL qDTY 12.1 for grain yield under drought and root traits

Table 2. Details of the experimental location

	TRRI, Aduthurai	AC & RI, Echangkottai	ARS, Pattukottai
Latitude	11°N	10° 40'N	10°25'E
Longitude	79°E	79° 09'E	79° 20' E
Average rainfall	1139.0 mm	930 mm	1106 mm
MSL	19.5m	58m	20.0 m
Soil type	Alluvial Clay soil	Sandy clay loam soil	Sandy soil

Materials

The study utilized two sets of backcross inbred lines (BILs) created using Apo and Way Rarem as donor parents to introduce QTLs for yield under drought stress into the ADT (R) 45 background. ADT (R) 45, a popular high-yielding short -duration variety, was initially crossed with Apo and Way Rarem. ADT (R) 45 was backcrossed once to the resulting progenies, ADT (R) 45/Apo and ADT (R) 45/Way Rarem. The BC_1F_2 population was developed using the seeds of the selfed BC_1F_1 plants from these crossings (ADT (R) 45/Apo/ ADT (R) 45 and ADT (R) 45/Way Rarem/ADT (R) 45). From this population, 160 plants from ADT (R) 45*1/Apo and 120 plants from ADT (R) 45*1/Way Rarem were selected and designated as BIL-A-1 to BIL-A-160 for ADT (R) 45/Apo and BIL-W-1 to BIL-W-120 for ADT (R) 45/Way Rarem. The single plant selection was used to advance the chosen plants to the BC_1F_3 generation.

The BC_1F_3 generation was grown under irrigated conditions at the Tamil Nadu Rice Research Institute (TRRI) Breeding Unit during Kuruvai, 2019. In each BIL, one agronomically superior plant was tagged for leaf sample collection for genotyping and further phenotyping at the BC_1F_4 stage. These tagged plants were selfed, harvested separately and raised in the Target Production Environment for phenotyping in the BC_1F_4 generation during 2020.

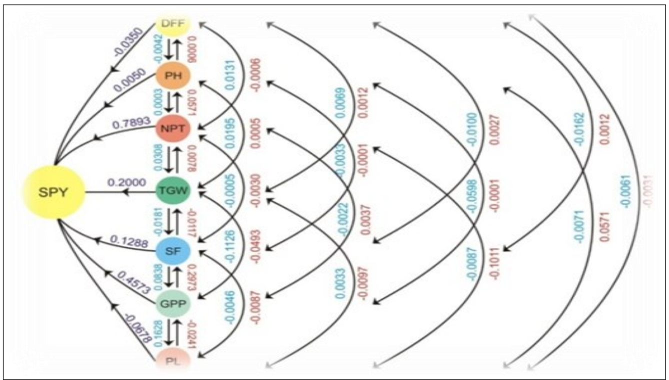
For genotyping, single plants from ADT (R) 45/Apo BILs were analyzed for QTLs *qDTY1.1, qDTY3.1* and *qDTY4.1,* while those from ADT (R) 45/Way Rarem BILs were genotyped for *qDTY12.1.*

Marker-assisted selection

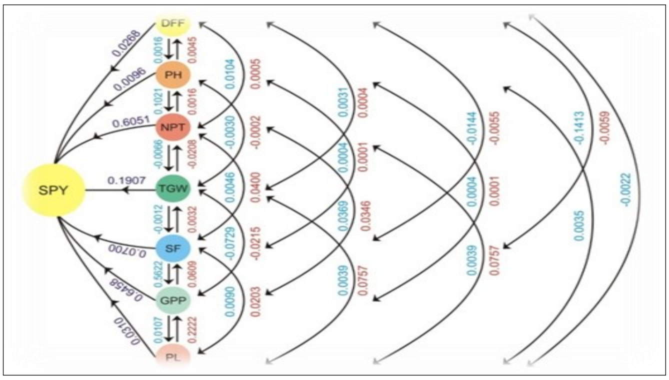
Genomic DNA isolation : A modified CTAB procedure was used to extract DNA from fresh leaf tissue (11). 0.8 % agarose gel electrophoresis was used to evaluate the isolated DNA's purity.

Foreground analysis of backcrossed progenies of ADT 45(BC_1F_3) : In this experiment, the drought-tolerant parents Apo and Way Rarem were used as male parents, while the high-yielding but drought-susceptible parent ADT (R) 45 served as the female parent in the hybridization program. To find drought QTLs - qDTY1.1, qDTY3.1 and qDTY4.1 in the backcross inbred lines generated from ADT (R) 45*1/Apo and QTL qDTY12.1 in the lines from ADT (R) 45*1/Way Rarem. Foreground selection was carried out in the BC_1F_3 generation. Foreground genotyping started with the selection process of monitoring qDTY loci with three peak markers, with one peak marker for each qDTY locus. In the foreground selection, the peak markers reported in an earlier study, namely RM11885, RM11928, RM261 RM520 (12) and RM511 (13), were used to confirm the presence of *qDTY1.1, qDTY3.1, qDTY4.1* and *qDTY12.1* respectively (Table 3 and Fig. 2).

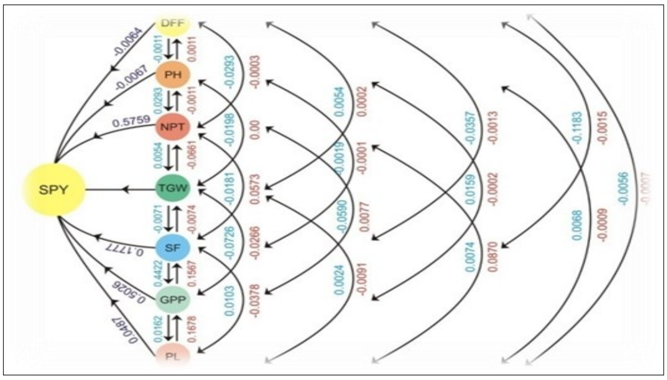
Field experiment for evaluation of backcross Inbred Lines (BILs) : The BC_1F_4 generation backcross inbred lines (BILs), both with and without drought QTLs, were evaluated in actual drought circumstances to assess the correlation between drought QTLs and the performance of the BILs under actual drought conditions. The experiment was conducted during the summer of 2020 across three locations: irrigated conditions at Tamil Nadu Rice Research Institute, Aduthurai; semi-dry conditions at Agricultural College and Research Institute, Echangkottai; and Agricultural Research Station, Pattukottai. Two Randomized Block Design (RBD) replications are used at each site to evaluate the genotypes.



Irrigated environment (E- I), TRRI, Aduthurai



Drought environment (E– II), AC&RI, Echangottai

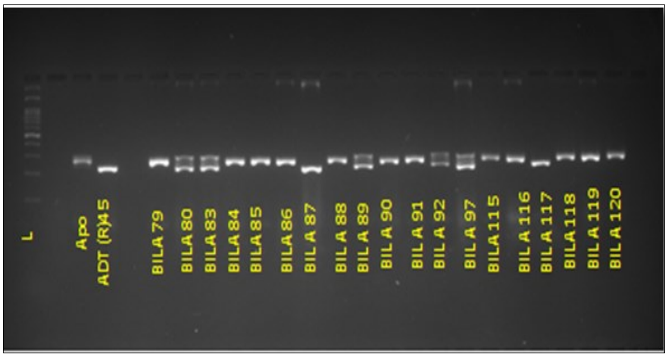


Drought environment (E– III), ARS, Pattukottai

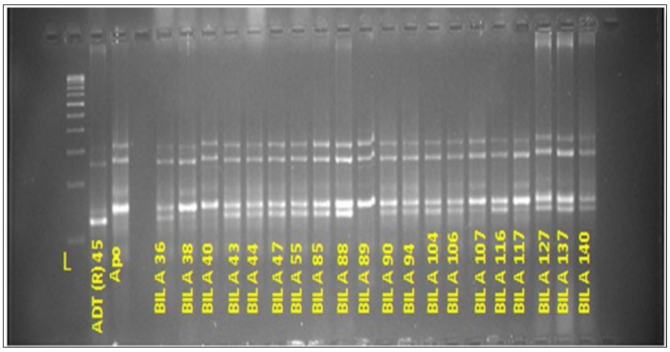
Fig. 1. Direct and indirect effects of yield and yield component trait in E-I, E-II and E-III.

Table 3. Details of primers used for foreground selection

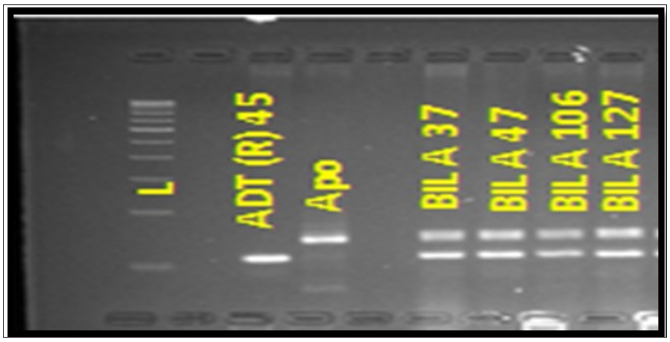
Sl. No.	QTL	Chromosome	Primer	Sequence
1	DTY 1.1	1	RM11885	'CTAGAGGCGAAAACGAGATG' 'GGGTGGGCGAGGTAATAATG'
2	DTY 1.1	1	RM11928	'CTAGAGGCGAAAACGAGATG' 'GGGTGGGCGAGGTAATAATG'
3	DTY 3.1	3	RM520	'AGGAGCAAGAAAAGTTCCCC' 'GCCAATGTGTGACGCAATAG'
4	DTY 4.1	4	RM261	'TCTTGCCCGTCACTGCAGATATCC' 'GCAGCCCTAATGCTACAATTCTTC'
5	DTY 12.1	12	RM511	'GACAGGGAGTGATTGAAGGC' 'GTTGATTTCGCCAAGGGC'



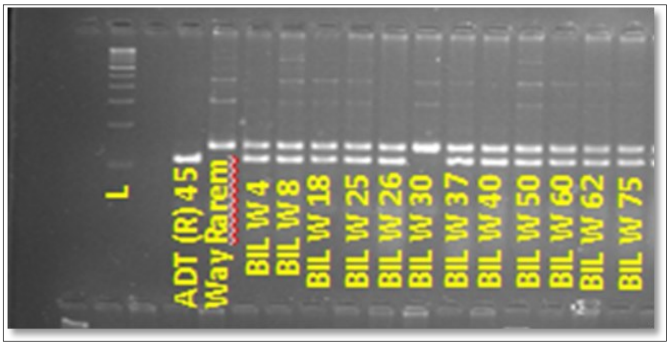
BILs qDTY1.1 amplified with SSR primer RM11928



BILs qDTY 3.1 amplified with SSR primer RM 520



BILs qDTY 4.1 amplified with SSR primer RM261



BILs qDTY12.1 amplified with SSR primer RM511

Fig. 2. Confirmation of drought QTLs in back cross population of ADT (R) 45*1 /Apo and ADT (R) 45*1 /Way Rarem.

Crop management in semidry condition : Under semi-dry conditions, BIL seeds from ADT (R) 45*1/Apo and ADT (R) 45*1/Way Rarem were directly sowed in dry, ground-up soil with a 20 cm gap between rows and a 15 cm gap between plants within each row in the Target Production Environment. On the 25th day after sowing, single seedlings per hill were maintained through thinning. The experimental plot measured 2 m in length, with two rows allocated per genotype and a 30 cm gap was maintained between genotypes. Recommended crop management and protection practices were implemented to ensure healthy crop growth. Regular irrigation was provided until the 60th day after sowing, after which irrigation was withheld to impose drought stress for 15 days, allowing soil cracks to develop due to moisture stress. Physiological parameters were recorded during the stress period and irrigation was resumed to enable crop recovery. Biometrical traits were measured and the BILs were harvested once the grains reached the physiological maturity stage.

Crop management in irrigated condition : As described above, the same experimental material was transplanted under irrigated conditions with the same spacing (20 × 15 cm), plot size (2 m with two rows per genotype) and crop management practices. Suggested crop production and protection methods were followed to ensure healthy crop growth. When the grains reached the physiological maturity stage, the crop was harvested and biometrical traits were recorded (14).

Recording quantitative traits : Biometrical observations were taken at appropriate stages of crop growth. The procedure for recording the various traits is outlined below:

Here are the procedures for recording various biometrical traits:

50 % flowering (days): For 50 % of the plants, the total number of days from seeding to the emergence of the first blooms was noted.

Plant height (cm): The height of the plants was measured in centimetres from the base to the tip of the boot leaf.

Number of productive tillers/plant : The number of producing tillers or panicles per plant was recorded during the maturity stage.

Panicle length (cm) : The primary panicle Length from the bottom of the panicle to the tip in each plant was measured in centimetres.

Grains per panicle (nos) : The number of filled grains in each primary panicle was counted and recorded.

Spikelet fertility : The number of viable spikelets (filled grains) in the chosen plants was counted and expressed as a percentage in Equation 1.

$$\text{Spikelet fertility (\%)} = \frac{\text{Number of filled grains}}{\text{Total number of grains (including filled and unfilled grains)}} \times 100 \quad \text{(Eqn. 1)}$$

1000 grain weight : One thousand well-filled grains selected randomly from each plant were weighed and expressed in gram.

Single plant yield (g) : The grain weight was measured and reported in grams after three plants from each Backcross Inbred Lines were harvested and dried individually.

Physiological observations (recorded in stress experiment) : The ability of a plant to grow satisfactorily when exposed to a period of moisture stress is called drought resistance. Drought resistance is a complex trait whose effect is a direct result of action involving several interacting physiological (reduced transpiration, high water-use efficiency, stomatal closure and osmotic adjustment), biochemical (accumulation of proline, polyamine, trehalose, etc., increased nitrate reductase activity and increased storage of carbohydrate) and morphological mechanisms (earliness, reduced leaf area, leaf rolling, wax content, efficient rooting system, awn, stability in yield and reduced tillering) for its adaption (15)

The plant uses different mechanisms to cope with drought stress. The four common crop adaptation mechanisms are drought escape, avoidance, tolerance and recovery. Each mechanism is associated with different traits and adapts based on their molecular responses and morpho-physiological changes (16). A thorough understanding of the various mechanisms that govern rice yield under water stress conditions is a prerequisite to facilitate the selection or development of drought-tolerant rice varieties.

Panicle exertion : Panicle exertion of the single plant was scored according to the Standard Evaluation System (14) (Table 4).

Leaf rolling : The levels of leaf rolling were assessed during midday for each plant after panicle exertion, using the Standard Evaluation System scoring system (14) (Table 5).

Leaf drying : The occurrence of leaf drying due to severe water loss and inadequate transpirational cooling was evaluated in each plant after panicle exertion. The extent of leaf tissue drying was scored using the standard evaluation system (14) (Table 6).

Leaf senescence : Leaf senescence was assessed in each plant after panicle exertion based on the scoring system from the Standard Evaluation System (14) (Table 7).

Drought recovery score : The drought recovery score was determined three days (72 hours) after rewatering plants under stress. The score ranged from 1 to 9 according to the Standard Evaluation System for rice (14) (Table 8).

Statistical analysis

Analysis of variance (ANOVA) was carried out for each character and subsequently, ANOVA was used to determine whether there were any differences in the traits studied among BILs. Differences were called statistically significant at $p<0.05$. Correlation and path analysis were performed using the GENRES 1994 Pascal Intl software version 3.01.

Table 4. Panicle exertion scoring

Score	Panicle exertion
1	Well exerted
3	Moderately well exerted
5	Just exerted
7	Partly exerted
9	Enclosed

Table 5. Leaf rolling scoring

Score	Leaf rolling
0	Leaves healthy
1	Leaves start to fold (Shallow V shape)
3	Leaves folding (deep V shape)
5	Leaves fully cupped (U-shape)
7	Leaf margins touching (O-shape)
9	Leaf tightly rolled

Table 6. Leaf drying scoring

Score	Leaf drying
0	No symptoms
1	Slight tip drying
3	Tip drying extended up to 1/4th length in most leaves
5	1/4th to1/2 of all leaves fully dried
7	More than 2/3rd of all leaves fully dried
9	All plants apparently dead

Table 7. Leaf senescence scoring

Score	Leaf senescence
1	Late and slow (Leaves have natural green colour)
5	Intermediate (Upper leaves yellowing)
9	Early and fast (all the leaves yellow or dead)

Table 8. Drought recovery scoring

Score	Drought recovery score
1	90 -100 % of plants recovered
3	70-80 % of plants recovered
5	40-69 % of plants recovered
7	20-39 % of plants recovered
9	0-19 % of plants recovered

Analysis of variance

The data for different characters were statistically analyzed using the randomized block design methodology (17) (Table 9). The "F" table values were used for the significance test (18).

Table 9. Analysis of variance (ANOVA)

Source of variation	d.f.	SS	MSS	F ratio
Replications	r-1	RSS	RMSS	RMSS/EMSS
Treatments	t-1	TrSS	TrMSS	TrMSS/EMSS
Error	(r-1)(t-1)	ESS	EMSS	
Total	(rt-1)	TSS		

r = Number of replications, t = Number of genotypes or treatments, df=Degrees of freedom, SS= Sum of squares, MSS = Mean sum of squares, RSS = Replication sum of squares, ESS = Error sum of squares, TSS = Total sum of squares, RMSS = Mean sum of squares due to replications, TrMSS = Mean sum of squares due to treatments, EMSS = Mean sum of squares due to error.

Path coefficient analysis

Path coefficient analysis was used to split the genotypic correlation coefficients into measures of direct and indirect effects (19) (Table 10).

Table 10. Path coefficient analysis -direct and indirect effects

Value of Direct or Indirect effects		Rate or scale
More than 1.00	:	Very high
0.30 to 0.99	:	High
0.20 to 0.29	:	Moderate
0.10 to 0.19	:	Low
0.00 to 0.09	:	Negligible

Results

Significant differences were found for every character among genotypes examined in every habitat, according to the analysis of variance (Table 11-13).

Path coefficient analysis

Path coefficient analysis helps to identify the causes and assess the relative contribution of each factor to yield (20). Understanding the key yield attributes and their interrelationships is crucial for developing effective breeding strategies to create high-yielding varieties. The present study, which examines location-specific associations, provides insights into stable trait relationships and their dependencies, aiding the selection of the best genotypes with key yield-contributing traits.

By dividing the trait correlation into direct and indirect effects, this technique enables a thorough investigation of how yield components affect yield at three distinct sites and in a pooled study across all locations. Such location-based and combined analyses reveal stable trait associations, offering valuable information for plant breeders (Table 14-16 and Fig. 1).

50 per cent Flowering (DFF)

At E1, DFF showed a slight negative direct effect, but at E2 and E3, it showed weak positive direct effects. The height of the plant and productive tillers per plant at E1 and E3, respectively, demonstrated indirect beneficial effects on yield. DFF also had indirect detrimental effects on single plant yield through characteristics including panicle length, grains per panicle and spikelet fertility % at E1, E2 and E3.

Plant height

Height of the plant showed positive effect on single plant yield at E1 and E3, but negatively at E2. Plant height exhibited favourable indirect impacts on yield through the number of productive tillers in all environments (E1, E2 and E3). With the exception of 1000 grain weight, plant height in the irrigated environment (E1) had a slight negative indirect influence through 50 % flowering, length of the panicle, grains per panicle and spikelet fertility percentage. 50 % flowering, productive tillers, panicle length and grains per panicle all showed favourable indirect effects on yield in E2 and E3 respectively.

Number of productive tillers per plant

In all conditions, the number of productive tillers had a significant and beneficial direct effect on grain yield (E1, E2 and E3). This indicates that productive tillers play a substantial role in enhancing productivity. The indirect effects of this trait, through other components such as plant height, 50 % flowering and 1000 grain weight, were minimal across all environments. Positive indirect effects

Table 11. Analysis of variance - Environment-I

Source	Df	DFF	PH	NPT	PL	GPP	SF	GW	SPY
Total	523	16.455	82.220	19.710	13.671	510.589	125.954	5.456654	102.022
Replication	1	0.017	2.583	4.641	0.022	241.022	90.360	0.117301	0.883
Genotypes	261	32.524*	161.830*	38.867*	25.944*	1000.150*	243.469*	10.735278*	201.940*
Error	261	0.450	2.915	0.609	1.450	22.060	8.577	0.198488	2.493

Table 12. Analysis of variance - Environment-II

Source	Df	DFF	PH	NPT	PL	GPP	SF	GW	SPY
Total	523	16.107	42.421	9.553	9.885	536.202	289.617	5.0133	31.971
Replication	1	0.154	5.371	0.302	0.641	34.300	1.651	0.7878	116.650
Genotypes	261	31.723*	83.290*	19.004*	19.525*	1064.574*	573.947*	9.8878*	62.1619*
Error	261	0.553	1.693	0.137	0.280	9.753	6.391	0.1550	1.457

Table 13. Analysis of variance - Environment-III

Source	Df	DFF	PH	NPT	PL	GPP	SF	GW	SPY
Total	523	15.188	57.923	12.481	10.874	537.981	283.020	4.8745	43.9148
Replication	1	0.374	2.151	0.725	0.960	129.242	142.617	0.5376	0.615
Genotypes	261	30.178*	87.490*	24.758*	21.290*	1063.244*	555.856*	9.6287*	86.946*
Error	261	0.255	1.984	0.250	0.497	14.284	10.723	0.1369	1.0496

DFF- Days to 50 % Flowering, PH-Plant height, NPT-Number of productive tillers, PL-Panicle length, GPP- Number of grains per panicle, SF- Spikelet fertility, GW-1000 Grain weight and SPY-single plant yield

** Significant at 0.01 level of probability, * Significant at 0.05 level of probability

Table 14 . Direct and Indirect effects of yield and its component traits in environment I

Characters	DFF	PH	NPT	PL	GP	SF	GW
DFF	**-0.0350**	0.0006	0.0131	-0.0061	-0.0162	-0.0100	-0.0069
PH	-0.0042	**0.0050**	0.0571	-0.0071	-0.0598	-0.0033	0.0195
NPT	-0.0006	0.0003	**0.7893**	-0.0087	0.0022	-0.0005	0.0078
PL	-0.0031	0.0005	0.1011	**-0.0678**	0.1626	0.0087	-0.0097
GP	0.0012	-0.0007	0.0037	-0.0241	**0.4573**	0.0838	-0.0493
SF	0.0027	-0.0001	-0.0030	-0.0046	0.2973	**0.1288**	-0.0181
GW	0.0012	0.0005	0.0308	0.0033	-0.1126	-0.0117	**0.2000**

Diagonal values represent direct effects Residual Effect= 0.3120239

Table 15 . Direct and Indirect effects of yield and its component traits in environment II

Characters	DFF	PH	NPT	PL	GP	SF	GW
DFF	**0.0064**	-0.0011	-0.0293	-0.0056	-0.1183	-0.0357	0.0054
PH	0.0011	**-0.0067**	0.0945	0.0068	0.0159	-0.0019	-0.0198
NPT	-0.0003	-0.0011	**0.5759**	0.0074	0.0590	0.0181	-0.0212
PL	-0.0007	-0.0009	0.0870	**0.0487**	0.1678	0.0378	0.0091
GP	-0.0015	-0.0002	0.0677	0.0162	**0.5026**	0.1567	-0.0266
SF	-0.0013	0.0001	0.0573	0.0103	0.4422	**0.1777**	-0.0074
GW	0.0002	0.0007	-0.0661	0.0024	-0.0726	-0.0071	**0.1847**

Diagonal values represent direct effects Residual Effect= 0.3591801

Table 16. Direct and Indirect effects of yield and its component traits in environment III

Characters	DF	PH	NPT	PL	GP	SF	GW
DF	**0.0268**	0.0016	0.0104	-0.0022	-0.1413	-0.0144	0.0031
PH	0.0045	**0.0096**	0.1021	0.0035	0.0085	0.0004	-0.0030
NPT	0.0005	0.0016	**0.6051**	0.0039	0.0369	0.0046	-0.0066
PL	-0.0019	0.0011	0.0757	**0.0310**	0.2222	0.0203	0.0241
GP	-0.0059	0.0001	0.0346	0.0107	**0.6458**	0.0609	-0.0215
SF	-0.0055	0.0001	0.0400	0.0090	0.5622	**0.0700**	0.0032
GW	0.0004	-0.0002	-0.0208	0.0039	-0.0729	0.0012	**0.1907**

Diagonal values represent direct effects Residual Effect= 0.2539698

on yield were observed through panicle length, grains per panicle and spikelet fertility percentage in stress environments E2 and E3, respectively.

Panicle length

The trait had low positive indirect effects on yield through the number of productive tillers, grains per panicle and spikelet fertility percentage in all environments (E1, E2 and E3). Additionally, a small unfavourable indirect effect was recorded through 50 % flowering across all environments. In the irrigated environment (E1), panicle length negatively impacted single plant yield. In contrast, it positively affected yield in stress environments (E2 and E3).

Number of grains per panicle

Across all environments, this biometrical trait demonstrated a strong positive direct effect on single plant yield. The number of productive tillers, spikelet fertility percentage and days to 50 % blooming were identified as the traits that had favourable indirect effects on yield. Nonetheless, in E1, E2 and E3, the number of grains per panicle had a detrimental indirect impact on yield through 1000 grain weight. Furthermore, it demonstrated favourable indirect effects on yield in E2 and E3 through panicle length.

Spikelet fertility percentage

In all three environments, grain yield was positively impacted by spikelet fertility %. It also exhibited indirect positive effects on yield through the number of grains per panicle in all environments. The irrigated environment (E1) had a negative indirect influence through traits such as plant height, number of productive tillers, panicle length and 1000-grain weight. In the stress environments E2 and E3, spikelet fertility had a positive indirect effect through plant height, number of productive tillers and panicle length.

1000 grain weight

In all the environmental conditions, the weight of 1000 grains had a moderately favourable direct impact on single plant yield. It also expressed indirect positive influences through days to 50 % flowering and panicle length. However, it had a detrimental indirect influence on grain yield through the number of grains per panicle in E1, E2 and E3.

Association of physiological traits with yield

The interconnections of various physiological traits influencing grain yield were examined in a study on the photosynthetic parameters of Backcross Inbred Lines (BILs) and parental lines under moisture-stress conditions. Among the five physiological traits, Panicle exertion, leaf rolling, leaf drying, leaf senescence and drought recovery score, only leaf rolling showed a positive direct and indirect effect on single plant yield in both stress environments (E2 and E3). All other traits exhibited low adverse direct and indirect impact on yield in these stress environments (E2 and E3) (see Tables 17-18).

Table 17. Direct and Indirect effects of yield and physiological traits in environment II

Characters	PE	LR	LD	LS	DRS
PE	**-0.0257**	0.0227	-0.1072	-0.0562	-0.1517
LR	-0.0081	**0.0725**	-0.1581	-0.1159	-0.1877
LD	-0.0089	0.0373	**-0.3075**	-0.1903	-0.2669
LS	-0.0049	0.0288	-0.2009	**-0.2913**	-0.2855
DRS	-0.0085	0.0297	-0.1794	-0.1818	**-0.4573**

Diagonal values represent direct effects Residual effect = 0. 4582244

PE- Panicle exertion, LR- Leaf rolling, LD- Leaf Drying, LS- Leaf senescence, DRS- Drought recovery score and SPY- Single plant yield

Table 18 . Direct and Indirect effects of yield and physiological traits in environment III

Characters	PE	LR	LD	LS	DRS
PE	**-0.0162**	0.0124	-0.1021	-0.0898	-0.1517
LR	-0.0039	**0.0515**	-0.1381	-0.1557	-0.1904
LD	-0.0057	0.024	**-0.2893**	-0.2334	-0.2426
LS	-0.0040	0.0222	-0.1873	**-0.3606**	-0.2480
DRS	-0.0061	0.0244	-0.1746	-0.2225	**-0.4019**

Diagonal values represent direct effects Residual effect =0.4545771

Discussion

50 percent flowering

In the irrigated condition, the number of days until 50 % blooming had a minimally detrimental direct impact on yield (E-I). In contrast, a low positive direct effect was observed in the drought environment (E-II). Previous studies have emphasized how the floral pathway affects drought tolerance (21). Flowering marks the transition from the vegetative to the reproductive stage, which is governed by various genetic pathways, including responses to vernalization, photoperiod and gibberellic acid biosynthesis, all of which are impacted by environmental elements (22). Flowering initiation timing is a crucial period for crop production, as it triggers the activation of specific genes that are upregulated during drought stress, accelerating the floral transition and shortening the vegetative phase (23-24). This process is part of the plant's drought-escape strategy, allowing it to complete its life cycle under water scarcity conditions quickly. The current study's findings on the negative relationship between accelerated flowering during drought stress and grain yield suggest that this adaptation benefits yield under moisture stress conditions.

Plant height

In the 1960s, Peta's tall variety was crossed with the sd-1 gene, which was first discovered in the Dee-geo-woo-gen variety, to produce the semidwarf cultivar IR8. The development of dwarf, high-yielding, lodging-resistant and fertilizer-responsive rice cultivars was transformed by introducing the sd-1 gene, leading to notable yield improvements and improved food security. This was a significant achievement in agricultural research. The Green Revolution (GR) varieties, which were bred for irrigated ecosystems, significantly boosted global food security. However, low productivity and yield losses persist in rainfed rice-growing regions subjected to abiotic stresses. The drought sensitivity of GR varieties is partially to blame for this. Its repulsion with the sd-1 allele was connected to the qDTY1.1 allele's loss during the GR (25). The present study found a low correlation between plant height and yield, suggesting that plant height alone cannot indicate high yield because modern rice varieties and cultures have been incorporated with the *sd1* gene (26-27). While the sd-1 gene helps improve lodging resistance in drought-prone environments, overly short plants may suffer from poor growth, reducing biomass and yield potential. Therefore, breeding semidwarf rice varieties with drought tolerance, more tillers and higher panicle and grain weight will help create climate-resilient rice cultivars suitable for abiotic stress.

Number of productive tillers per plant

Tillering is crucial for crop recovery, as water deficit stress affects photosynthesis membrane stability and increases reactive oxygen species. Osmotic adjustment, accumulating soluble sugars and proline, helps plants recover after rewatering. Tolerant cultivars recover better than susceptible ones (28). The study showed that an increase in productive tillers strongly correlates with higher grain yield across all three environments, highlighting the importance of productive tillers in improving yield.

Panicle length

Length of the panicle was positively associated with grain yield and number of grains per panicle across all environments, with a direct positive effect observed even under drought stress. This suggests that longer panicles contribute to higher biological yield, even under moisture stress. The genotype BIL W60, with a 6 % reduction in panicle length, demonstrated a strong link between panicle length, grain yield, number of filled grains per panicle and fertility percentage of spikelet, indicating that these plant traits are interdependent across different environments.

Spikelet fertility percentage

Grain filling, which affects grain number, is sensitive to environmental factors. The study showed that grains per panicle were positively correlated with spikelet fertility in all environments. Genotypes such as BIL A127, BIL A129, BIL W37 and BIL W40, which maintained stable yield across environments, exhibited minimal reductions in grains per panicle compared to irrigated conditions. The mobilization of organic solutes for sink development was enhanced by ideal panicle architecture and early flowering (29, 30). A positive relationship between grains per panicle, spikelet fertility and yield indicates that more grains increase the likelihood of fertile seeds, thereby boosting grain yield.

1000 grain weight

Water deficit stress during the reproductive phase disrupts several mechanisms, including starch accumulation in pollen grains, panicle exertion, anther dehiscence, spikelet fertility, pollen fertility and other yield components, ultimately reducing grain yield (31-34). Moisture stress also reduces peduncle elongation, which affects panicle exertion, leading to partial panicle emergence (35). Spikelets confined inside the flag leaf usually become sterile due to impaired fertilization. Among the seven yield components studied, spikelet fertility percentage showed the strongest positive association with yield under drought and irrigated situations. The indirect influence of spikelet fertility on grains per panicle was also positive in both environments, highlighting its significant role in improving grain yield through increased grains per panicle. BILs such as BIL A 20, BIL A 21, BIL A 30, BIL A 36, BIL A 67, BIL A 129, BIL A 159, BIL W 10, BIL W 37, BIL W 40 and Apo, which exhibited stable yields across environments, maintained over 60 % spikelet fertility under drought stress, emphasizing the importance of this trait in enhancing grain yield under stress.

The relationship between 1000 grain weight and single plant yield was positively correlated but not statistically significant in irrigated and drought conditions. Most traits exhibited a negative correlation with 1000-grain weight across environments. However, a positive association was recorded between 1000 grain weight, days to 50 % flowering and spikelet fertility under moisture stress, suggesting that early flowering could facilitate grain filling before the onset of terminal stress. Despite this, the indirect effects of 1000 grain weight through other traits were minimal, indicating that environmental factors may have masked its overall impact (36, 37).

Evaluation under moisture stress for yield and physiological parameters

In addition to yield, secondary traits play a significant role in drought resistance, indirectly contributing to yield improvement under moisture stress. Physiological parameters such as panicle exertion, senescence, leaf rolling, leaf drying and drought recovery score are crucial for drought tolerance. These traits were evaluated through visual observation under drought conditions, with significant differences noted for all characteristics, reflecting the impact of water stress on various physiological aspects (Fig. 3).

Panicle exertion

Panicle exertion is a key trait linked to yield, with poor panicle exertion being a significant cause of spikelet sterility, which ultimately reduces yield (33). In this study, the parent genotype Apo exhibited well-exerted panicles, scoring a 1 and 59 BILs with drought QTLs (*qDTY 1.1, 3.1, 4.1 and 12.1*) also showed well-exerted panicles and higher yield under drought conditions (38). These results emphasize the importance of panicle exertion in improving grain yield under drought-prone environments. However, 116 BILs without drought QTLs showed moderate panicle exertion but suffered yield reduction due to decreased fertility. The genotypes Way Rarem and ADT (R) 45 displayed partial panicle exertion, reducing yield through shorter panicle length and fewer fertile grains. The critical drought period overlaps with the panicle development and anthesis stages and the study showed significant variation in panicle exertion across BILs, which corresponded with increases or decreases in grain yield. According to related research, moisture stress between the flowering and booting phases disrupts panicle initiation, resulting in fewer panicles, decreased grain filling, spikelet fertility and 1000-grain weight, eventually leading to low grain yield (39-41).

Leaf senescence

Senescence is an important trait influencing productivity under drought, as the carbohydrate remobilization associated with senescence is vital for grain filling. This study found variable expression of leaf senescence across the population. BILs with drought QTLs (qDTY 1.1,qDTY 3.1,qDTY 4.1 and 12.1) and the drought-tolerant parent Apo had low leaf senescence scores (below 3) in both stress environments, indicating their ability to delay senescence. Conversely, the susceptible parent ADT (R) 45 exhibited higher leaf senescence scores (above 5), suggesting it maintains higher photosynthesis rates under stress. Stable genotypes such as BIL A 20, BIL A 67, BIL A 129, BIL W 8, BIL W 37, BIL A 47, BIL A 68, BIL W 106, BIL W 50 and Apo exhibited low senescence. They maintained a natural green colour, demonstrating late senescence, a favourable trait under drought stress.

Leaf rolling

Leaf rolling is a key mechanism for drought avoidance, enabling plants to reduce the exposed leaf area under water stress, which helps minimize transpiration and gas exchange through the stomata (42). Additionally, leaf-rolling changes support photosynthesis's continued function during drought (43). The crucial function leaf rolling plays in drought stress resistance is highlighted by choosing cultivars that can modify their leaf water potential in drought circumstances (44). Morphological traits such as leaf blade width and length are essential in expressing the physiological adaptation of leaf rolling to drought and reducing leaf water status (45). In this study, the donor parent Apo and 24 BILs with drought QTLs exhibited shallow V-shaped leaf rolling, which supported optimal photosynthesis and the translocation of assimilates, a crucial component of drought adaptation.

In contrast, the recipient parent ADT (R) 45 and 147 BILs without drought QTLs showed higher degrees of leaf rolling, indicating its involvement in moisture stress tolerance. Genotypes such as BIL A 67, BIL A 114, BIL A 129 and BIL W 60, which displayed shallow leaf rolling, maintained stable grain yields under moisture stress. Therefore, minimal leaf rolling in drought-tolerant genotypes is linked to better osmotic adjustment, maintenance of leaf water potential and efficient photosynthesis, all contributing to improved assimilate translocation during stress.

Leaf drying

Leaf drying in response to stress was minimal in the donor parent Apo and BILs with drought QTLs, which exhibited low scores, indicating a slight drying at the leaf tips. In contrast, the recipient parent ADT (R) 45 and 132 BILs without drought QTLs showed higher scores, indicating significant leaf drying, a sign of sensitivity to severe stress. The results confirm that parental lines without drought QTLs performed poorly, resulting in reduced yields under stress.

Leaf rolling under drought stress | Spikelet sterility under drought stress | Leaf senescence under drought stress | Leaf drying under drought stress

Fig. 3. Recording observation for physiological stress following SES, IRRI (1996).

Drought recovery

The ability of a plant to recover after drought stress is considered even more critical than its ability to tolerate drought (46, 47). This study found that 55 % of the BILs carrying qDTY 1.1 and 71 % of those with qDTY 3.1 demonstrated drought recovery rates of 80 % or higher. Furthermore, all BILs, except for BIL W 25 with qDTY 12.1, showed 80 % or better drought recovery, highlighting the significant contribution of qDTY 12.1 to drought tolerance. This underscores the need for further research to quantify the contribution of qDTY 12.1 among rice's drought QTLs.

Genotypic correlation between yield and physiological traits under drought conditions revealed a significant negative correlation with grain yield, viz., panicle exertion, leaf senescence, leaf rolling, leaf drying and drought recovery score. Panicle exertion, leaf senescence, drying and rolling had significant mutual positive intercorrelations. Traits like leaf rolling, leaf drying, leaf senescence and panicle exertion can reflect the internal water status under water deficit conditions. These traits can be considered integrative traits to identify drought-resistant genotypes.

Therefore, genotypes such as BIL A 20, BIL A 37, BIL A 47, BIL A 62, BIL A 67, BIL A 68, BIL A 127, BIL A 129, BIL W 4, BIL W 8, BIL A 37, BIL A 40, BIL A 50, BIL W 60 and Apo, which showed low scores for physiological traits like panicle exertion, leaf rolling, leaf drying, leaf senescence and rapid drought recovery upon rewatering, present excellent candidates for selection. These genotypes could further enhance drought tolerance by adapting secondary traits.

Conclusion

The findings from this study suggest that, for selection in both irrigated and moisture-stress environments, emphasis should be placed on all traits except plant height. However, when breeding for drought tolerance, special attention should be focused on identifying genotypes with early flowering, an increased productive tiller, longer panicle and more grains per panicle. It is also crucial for the plant to overcome spikelet sterility, even under drought stress, during flowering initiation. Among the physio-morphological traits studied, panicle exertion, leaf rolling, drying, senescence and drought recovery scores showed extremely strong negative associations with grain yield. Conclusively, the outcome of this research indicated that qDTY QTLs *viz.,*qDTY 1.1, qDTY 3.1, qDTY 4.1 and qDTY 12.1 played a major role in physio-morphological traits which facilitated for the stable performance of the BILs across environments under moisture stress condition. Out of which the alleles studied, the QTL qDTY 12.1 contributed maximum for drought tolerance without loss of yield trait. Further advancement of these two BILs carrying qDTY QTLs may be rewarding to isolate several adaptive drought tolerance mechanism with substantial yield under drought. Therefore, breaking the linkage between these traits through various breeding strategies could lead to more successful outcomes.

Acknowledgements

The authors acknowledge Tamil Nadu Rice Research Institute for providing financial support. Financial support from the Department of Science and Technology (Science and Engineering Research Board) through a grant - EMR/2016/003147 for this research is gratefully acknowledged.

Authors' contributions

RA carried out all the field and laboratory work, performed statistical analysis and drafted the manuscript. AJ coordinated the research work and provided critical comments, a time-to-time review and a streamlining of the research work and draft corrections. KSB and PB helped conduct the experiments and record the observations. SMI contributed to the analysis of statistical data and interpretation of results. Author RS generated essential financial assistance for field and laboratory works and supported the planning and execution of research work.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

References

1. Mahajan G, Kumar V, Chauhan BS. Rice production in India. In: Chauhan BS, Khawar J, Mahajan G, editors. Rice production worldwide. Newyork: Springer; 2017. p. 53–91. https://doi.org/10.1007/978–3–319–47516–5
2. Khush GS. Green revolution: preparing for the 21st century. Genome. 1999;42(4):646–55. https://doi.org/10.1139/g99–044
3. Fahad S, Adnan M, Noor M, Arif M, Alam M, Khan IA, et al. Major constraints for global rice production. In: Mirza H, Masayuki F, Jiban KB, editors. Advances in rice research for abiotic stress tolerance; 2019. p.1–22. https://doi.org/10.1016/B978–0–12–814332–2.00001–0
4. Molden D, Oweis TY, Pasquale S, Kijne JW, Hanjra MA, Bindraban PS, Bouman BAM, et al. Pathways for increasing agricultural water productivity. In Molden D, editor. Water for food, water for life: a comprehensive assessment of water management in agriculture. London, UK: Earthscan; Colombo, Sri Lanka: International Water Management Institute; 2007.p.279–310
5. Cairns JE, Audebert A, Mullins CE, Price AH. Mapping quantitative trait loci associated with root growth in upland rice (*Oryza sativa* L.) exposed to soil water–deficit in fields with contrasting soil properties. Field Crops Res. 2009;114(1):108–18. https://doi.org/10.1016/j.fcr.2009.07.009
6. Pandey S, Velasco L. Economics of direct seeding in Asia: patterns of adoption and research priorities. In Pandey S et al., editors. Direct seeding: research strategies and opportunities. Manila: IRRI; 2002. p. 3–14
7. Dar MH, Bano DA, Waza SA, Zaidi NW, Majid A, Shikari AB, et al. Abiotic stress tolerance–progress and pathways of sustainable rice production. Sustain. 2021;13(4):2078. https://doi.org/10.3390/su13042078
8. Zaharieva M, Gaulin E, Havaux M, Acevedo E, Monneveux P. Drought and heat responses in the wild wheat relative *Aegilops geniculata* Roth: potential interest for wheat improvement. Crop Sci. 2001;41(4):1321–29.

https://doi.org/10.2135/cropsci2001.4141321x

9. Passioura JB. Phenotyping for drought tolerance in grain crops: when is it useful to breeders?. Func Pl Biol. 2012;39(11):851–59. https://doi.org/10.1071/FP12079

10. Dixit S, Singh A, Kumar A. Rice breeding for high grain yield under drought: a strategic solution to a complex problem. Int J Agron. 2014;2014(1):863683. https://doi.org/10.1155/2014/863683

11. Hoisington D. Laboratory protocols: CIMMYT applied molecular genetics laboratory. Mexico: CIMMYT; 1992. https://onlinelibrary.wiley.com/doi/10.1155/2014/863683

12. Venuprasad R, Dalid CO, Valle DM, Zhao D, Espiritu M, Cruz SMT, et al. Identification and characterization of large-effect quantitative trait loci for grain yield under lowland drought stress in rice using bulk–segregant analysis. Theor Appl Gene. 2009;120:177–90. https://doi.org/10.1007/s00122–009–1168–1

13. Bernier J, Kumar A, Ramaiah V, Spaner D, Atlin G. A large effect QTL for grain yield under reproductive stage drought stress in upland rice. Crop Sci. 2007;47(2):507–16. https://doi.org/10.2135/cropsci2006.07.0495

14. International network for genetic evaluation of rice. Standard evaluation system for rice. Baños, Laguna: IRRI; 1996

15. Fleury D, Jefferies S, Kuchel H, Langridge P. Genetic and genomic tools to improve drought tolerance in wheat. J Exp Bot. 2010;61 (12):3211–22. https://doi.org/10.1093/jxb/erq152

16. Fukai S, Cooper M. Development of drought–resistant cultivars using physiomorphological traits in rice. Field Crops Res. 1995;40 (2):67–86. https://doi.org/10.1016/0378–4290(94)00096–U

17. Cochran WG, Cox GM. Experimental designs. New York: John Wiley and Sons; 1950 .https://doi.org/10.1097/00010694–195008000–00014

18. Wishart J. Statistical tables for biological agricultural and medical research. Nature. 1939;144:533. https://doi.org/10.1038/144533a0

19. Dewey DR, Lu K. A correlation and path-coefficient analysis of components of crested wheatgrass seed production. Agron J. 1959;51 (9):515–18. https://doi.org/10.2134/agronj1959.00021962005100090002x

20. Lenka D, Misra B. Path coefficient analysis of yield in rice varieties. Ind J Agric Sci.1973;43:376–79.

21. Wagner D. Key developmental transitions during flower morphogenesis and their regulation. Curr Opinion Gene Develop. 2017;45:44–50. https://doi.org/10.1016/j.gde.2017.01.018

22. Zhang T, Wang J, Zhou C. The role of miR156 in developmental transitions in *Nicotiana tabacum*. Sci China Life Sci. 2015;58:253–60. https://doi.org/10.1007/s11427–015–4808–5

23. Riboni M, Galbiati M, Tonelli C, Conti L. Gigantea enables drought escape response via abscisic acid–dependent activation of the florigens and suppressor of overexpression of Constans1. Pl Physiol. 2013;162(3):1706–19. https://doi.org/10.1104/pp.113.217729

24. Wei H, Chen C, Ma X, Zhang Y, Han J, Mei H, Yu S. Comparative analysis of expression profiles of panicle development among tolerant and sensitive rice in response to drought stress. Front Pl Sci. 2017;8:437. https://doi.org/10.3389/fpls.2017.00437

25. Vikram P, Swamy BM, Dixit S, Singh R, Singh BP, Miro B, et al. Drought susceptibility of modern rice varieties: an effect of linkage of drought tolerance with undesirable traits. Sci Rep. 2015;5(1):14799. https://doi.org/10.1038/srep14799

26. Spielmeyer W, Ellis MH, Chandler PM. Semidwarf (sd–1),"green revolution" rice, contains a defective gibberellin 20-oxidase gene. Proceed Nat Acad Sci. 2002;99(13):9043–48. https://doi.org/10.1073/pnas.132266399

27. Kovi MR, Zhang Y, Yu S, Yang G, Yan W, Xing Y. Candidacy of a chitin-inducible gibberellin-responsive gene for a major locus affecting plant height in rice that is closely linked to Green Revolution gene sd1. Theoret App Genet. 2011;123:705–14. https://doi.org/10.1007/s00122–011–1620–x

28. Abid M, Ali S, Qi LK, Zahoor R, Tian Z, Jiang D, et al. Physiological and biochemical changes during drought and recovery periods at tillering and jointing stages in wheat (*Triticum aestivum* L.). Sci Rep. 2018;8(1):4615. https://doi.org/10.1038/s41598–018–21441–7

29. Sakamoto T, Matsuoka M. Identifying and exploiting grain yield genes in rice. Curr Opinion Pl Bio. 2008;11(2):209–14. https://doi.org/10.1016/j.pbi.2008.01.009

30. Xu JL, Lafitte HR, Gao YM, Fu BY, Torres R, Li ZK. QTLs for drought escape and tolerance identified in a set of random introgression lines of rice. Theoret App Genet. 2005;111:1642–50. https://doi.org/10.1007/s00122–005–0099–8

31. Liu JX, Liao DQ, Oane R, Estenor L, Yang XE, Li ZC, Bennett J. Genetic variation in the sensitivity of anther dehiscence to drought stress in rice. Field Crops Res. 2006;97(1):87–100. https://doi.org/10.1016/j.fcr.2005.08.019

32. Mishra KK, Vikram P, Yadaw RB, Swamy BM, Dixit S, Cruz MT, et al. qDTY 12. 1: a locus with a consistent effect on grain yield under drought in rice. BMC Gen. 2013;14:1–0. https://doi.org/10.1186/1471–2156–14–12

33. Boonjung H, Fukai S. Effects of soil water deficit at different growth stages on rice growth and yield under upland conditions. 2. Phenology, biomass production and yield. Field Crops Res. 1996;48(1):47–55. https://doi.org/10.1016/0378–4290(96)00039–1

34. Saini HS, Westgate ME. Reproductive development in grain crops during drought. Adv Agron. 1999;68:59–96. https://doi.org/10.1016/S0065–2113(08)60843–3

35. He H, Serraj R. Involvement of peduncle elongation, anther dehiscence and spikelet sterility in upland rice response to reproductive-stage drought stress. Environ Exp Bot. 2012;75:120–27. https://doi.org/10.1016/j.envexpbot.2011.09.004

36. Pham HT, Do KT, Truong MN, Tran XD, Nguyen LT, Bui BC. Path analysis for yield traits in F2 generation and molecular approaches for breeding rice tolerant to drought and submergence. Afr J Agric Res. 2016;11(26):2329–36. https://doi.org/10.5897/AJAR2016.11153

37. Hossain S, Salim M, Azam MG, Noman S. Variability, correlation and path analysis in drought tolerant rice (*Oryza sativa* L.). J Biosci Agric Res. 2018;18(02):1521–30. https://doi.org/10.18801/jbar.180218.187

38. Subashri M, Robin S, Vinod KK, Rajeswari S, Mohanasundaram K, Raveendran TS. Trait identification and QTL validation for reproductive stage drought resistance in rice using selective genotyping of near flowering RILs. Euphytica. 2009;166:291–305. https://doi.org/10.1007/s10681–008–9847–6

39. Pantuwan G, Fukai S, Cooper M, Rajatasereekul S, O'Toole JC. Yield response of rice (*Oryza sativa* L.) genotypes to different types of drought under rainfed lowlands-Part 3. Plant factors contributing to drought resistance. Field Crops Res. 2002;73(2–3):181–200. https://doi.org/10.1016/S0378–4290(01)00194–0

40. Fabre D, Siband P, Dingkuhn M. Characterizing stress effects on rice grain development and filling using grain weight and size distribution. Field Crops Res. 2005;92(1):11–16. https://doi.org/10.1016/j.fcr.2004.07.024

41. Acuna TB, Lafitte HR, Wade LJ. Genotype × environment interactions for grain yield of upland rice backcross lines in diverse hydrological environments. Field Crops Res. 2008 ;108 (2):117–25. https://doi.org/10.1016/j.fcr.2008.04.003

42. Richards RA. Increasing the yield potential of wheat: manipulating sources and sinks. Increasing yield potential in wheat: breaking the barriers. Mexico, D.E: Cimmyt; 1996

43. Price AH, Cairns JE, Horton P, Jones HG, Griffiths H. Linking drought-resistance mechanisms to drought avoidance in upland rice using a QTL approach: progress and new opportunities to integrate stomatal and mesophyll responses. J Exp Bot. 2002;53 (371):989–1004. https://doi.org/10.1093/jexbot/53.371.989

44. Dingkuhn M, Farquhar GD, De Datta SK, O'toole JC, Datta S. Discrimination of 13C among upland rices having different water use efficiencies. Aus J Agric Res. 1991;42(7):1123–31. https://doi.org/10.1071/AR9911123

45. Cal AJ, Sanciangco M, Rebolledo MC, Luquet D, Torres RO, McNally KL, Henry A. Leaf morphology, rather than plant water status, underlies genetic variation of rice leaf rolling under drought. Pl Cell Environ. 2019;42(5):1532–44. https://doi.org/10.1111/pce.13514

46. Fang Y, Xiong L. General mechanisms of drought response and their application in drought resistance improvement in plants. Cell Mole Life Sci. 2015;72:673–89. https://doi.org/10.1007/s00018-014-1767-0

47. Chen D, Wang S, Cao B, Cao D, Leng G, Li H, et al. Genotypic variation in growth and physiological response to drought stress and rewatering reveals the critical role of recovery in drought adaptation in maize seedlings. Front Pl Sci. 2016;6:1241. https://doi.org/10.3389/fpls.2015.01241