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Research Article

Development and evaluation of introgression lines with yield enhancing genes of the Indian mega-variety of rice, MTU1010

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Abstract
MTU 1010 is an early maturing and high-yielding mega rice variety widely grown in an area of 3 Mha. It is characterised by limited grain number and panicle branching. To improve the grain number in MTU 1010, an IRRI breeding line, IR121055-2-10-5 was utilized as donor to transfer yield-enhancing genes *Gn1a* and *OsSPL14* (associated with increased grain number and better panicle branching, respectively) into MTU1010 by Marker-Assisted Backcross Breeding (MABB). At each backcross generation, foreground selection was carried out with *Gn1a* and *OsSPL14*-specific molecular markers, whilst background selection was done with a set of SSR markers polymorphic between the IR121055-2-10-5 and MTU1010. With the use of a gene-specific marker, homozygous BC_2F_2 plants carrying the yield-enhancing gene were identified and advanced through pedigree-method of selection till BC_2F_6 and best performing ten lines were selected and evaluated in replicated station trials for yield contributing traits, where grain number and brancing per panicle exhibited high significant and positive correlation with single plant yield. Three promising lines namely RP6353-5-8-13-24, RP6353-26-13-39-5 and RP6353-32-12-8-16 with higher grain number and yield than MTU1010 were identified and nominated for evaluation in Initial Varietal Trial-Aerobic (IVT-Aerobic) of All India Crop Improvement Programme on Rice (AICRP), of which RP6353-26-13-39-5 (IET28674), was promoted for further testing.

Keywords: Rice, Yield enhancing genes. *Gn1a*, *OsSPL14,* MABC

INTRODUCTION

Rice (*Oryza sativa* L.) is the most important cereal crop which feeds more than half of the world population. Rice has traditionally been a staple food in most Asian countries and its consumption is gradually increasing in African countries as well. The main risks to global rice production and food security are the continually growing world population, urbanization, changing climate and industrialization, which are reducing the amount of arable land accessible for rice farming. Rice production has seen a plateauing trend in countries like India and it is

expected that world yield increases of the major crops will be insufficient to meet the food requirement of estimated nine billion people by 2050 (Ray, 2013). Hence, one of the most important goals of rice breeding programmes around the world is to improve genetic yield potential per unit area. Rice grain productivity is a complex trait, which is determined by major yield contributing traits like number of productive tillers, number of grains per panicle and thousand grain weight.

Grain number per panicle is an important trait for higher yield in rice. A pioneering study by Ashikari *et al.* (2005) on the molecular analysis of indica rice variety Habataki resulted in identification of *Grain number 1a* (*Gn1a*) gene located on Chromosome 1, as a major QTL associated with high grain number. The *Gn1a* gene encodes cytokinin oxidase/and its accumulation in the inflorescence meristem increases the number of reproductive organs, resulting in enhanced grain number. The *OsSPL14*/ WFP/IPA1, a gene encoding squamosa promoter binding protein - like 14 in developing panicles and located on Chromosome 8 is associated with higher grain number per panicle and panicle architecture (Sakamoto and Matsuoka, 2008; Kovi *et al*., 2011a; Jiao *et al*., 2010; Miura *et al*., 2010).

MTU1010 (*Cottondora Sannalu*) is a high yielding rice variety grown in an area of ~ 3 million hectares, but possesses limited panicle branching and a lower number of grains per panicle. Keeping this in view, the current study aimed to improve MTU1010 for higher grain number and panicle branching using marker-assisted backcross breeding mediated transfer of the, *Gn1a* and *OsSPL14* genes, was done.

MATERIALS AND METHODS

A breeding line from IRRI, Philippines, IR121055-2-10-5, possessing the favourable alleles of the yield enhancing genes, *Gn1a* and *OsSPL14* was used as a donor parent for introgression into the variety MTU1010.

A cross was made between IR121055-2-10-5 and MTU1010 during *Kharif* 2015. Hybridity of the F_1s were confirmed using PCR based functional markers for yield enhancing genes *Gn1a* and *OsSPL14* (**Table 1**). In *Rabi* 2015-16, the true heterozygous F_1s were then backcrossed with the recurrent parent, MTU1010, to generate BC_1F_1s progenies. Simultaneously, parental polymorphism analysis was carried out with 320 SSR markers and a set of 61 markers polymorphic between IR121055-2-10-5 and MTU1010 were identified. During *Kharif* 2016, the BC_1F_1 plants were screened for foreground selection with the gene-specific markers as mentioned above and two gene positive plants were subjected to background selection with parental polymorphic SSRs and backcrossing was continued till BC_2F_1s. A single heterozygous BC_2F_1 plant possessing target yield enhancing gene(s) with maximum recurrent parent genome recovery was selfed to develop BC_2F_2s in *Rabi* 2016-17 (**Fig. 1**). Homozygous positive BC_2F_2 plants possessing yield enhancing genes (i.e., homozygous for *Gn1a* and *OsSPL14*) were advanced further till BC_2F_6 generation.

During *Rabi* 2018-19, 10 promising two-gene pyramided lines at BC_2F_6 generation *viz.,* RP6353-1-5-11-35, RP6353-5-8-13-24, RP6353-9-18-20-8, RP6353-18-10-9-14, RP6353-22-18-5-12, RP6353-26-13-39-5, RP6353-27-15-18-4, RP6353-30-8-19-5, RP6353-32-12-8-16 and RP6353-35-15-21-12 were evaluated in Randomized Complete Block Design (RCBD) along with the parents namely IR121055-2-10-5 and MTU1010 under field condition at ICAR-IIRR, Hyderabad in 2 m^2 plots in three replications with a spacing of 15 x 20 cm. Data were recorded for eleven agro-morphological traits namely days to 50% flowering, plant height (cm), number of productive tillers per plant, panicle length (cm), grain number per panicle, flag leaf length (cm), flag leaf width (cm), primary branches per panicle, secondary branches per panicle, 1000 grain weight (g) and single plant yield (g). A two way ANOVA was used to determine the significant differences for different agro-morphological characters using SAS Version 9.2 (SAS Institute Inc., Cary, NC, USA) software program. PROC GLM procedure of SAS was used to conduct ANOVA to determine the significant variation between the lines. Critical Difference (CD), Coefficient of variance (CV), at $p = 0.05$ were calculated using standard errors of mean (S. E. M.±) using MS Excel package (Rekha *et al.,* 2018).

Table 1. Molecular markers used for foreground selection of two yield- enhancing genes

S.No.	Gene	Chromosome number	Marker's name	Forward primer Sequence (5'-3')	Reverse primer Sequence (5'-3')	Positive amplicon size (bp)	Negative amplicon size (bp)
1	*Gn1a*	1	*Gn1a*-INDEL 3F/R	GATCTAGATGCTCCAAAGTCC	CTGTACGTACGTGCACGTAG	275	205
2	*OsSPL14*	8	RMS-*OsSPL14*-INDEL-2F/R	ATCCCCAAATCCTCAAATCC	TCCCGGTTCAAAAGGTTAGA	400	440

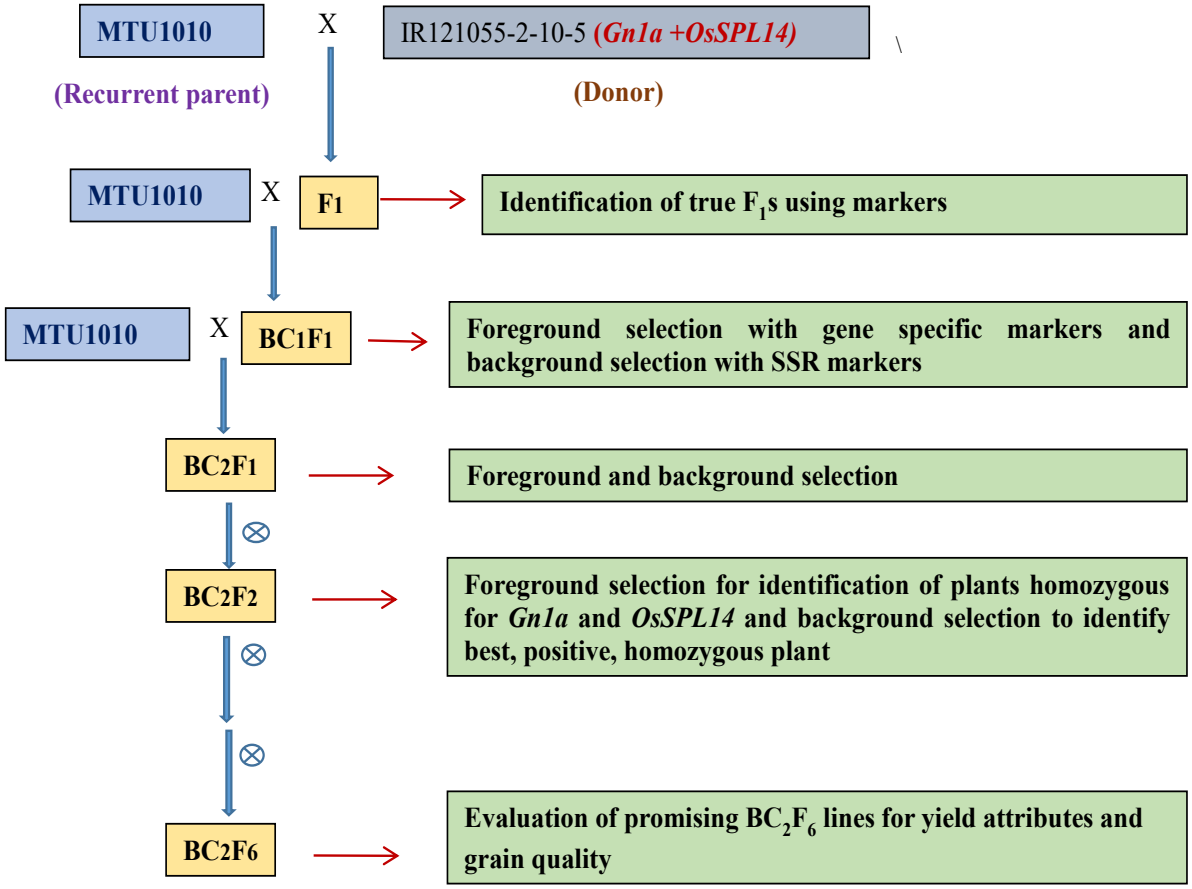


Fig. 1. Schematic representation of marker-assisted backcross breeding strategy to introgress yield enhancing genes into the genetic background of MTU1010

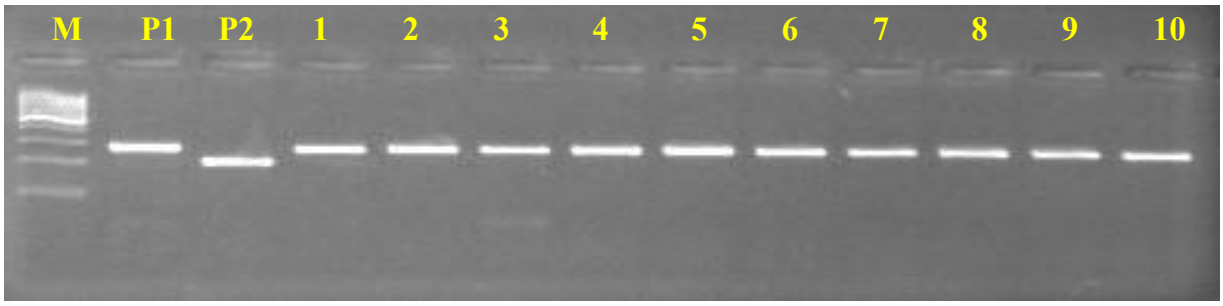
RESULTS AND DISCUSSION

MTU1010 (*Cottondora Sannalu*) is a short-duration, high-yielding, widely cultivated mega-variety of rice with long-slender grain type that was developed and released by ANGRAU (Acharya NG Ranga Agricultural University) in 2000 and is extremely popular among farmers for cultivation in both wet (i.e. *Kharif*) and dry (i.e. *Rabi*) seasons in India due to its wider adaptability. It is derived from the cross Krishnaveni / IR64 (Aruna kumari *et al*., 2016). Even though the variety is moderate to high-yielding, there is a significant scope to increase the grain number of the variety.

A total of 76 F_1 plants were analysed for their heterozygosity by using gene-specific markers of which 48 plants were observed to be true F_1's. Among these, a single positive plant (#RP6353-26) were backcrossed with MTU1010 to generate BC_1F_1s. Foreground selection was carried out in 154 BC_1F_1s, and among them, 23 plants were identified to be positive (i.e., plants possessing *Gn1a* and *OsSPL14,* respectively in heterozygous condition). Foreground selection of the targeted genes, *Gn1a* and *OsSPL14*, was carried out in the present work using gene-specific markers. Kim *et al*. (2016) designed a set of molecular markers for the selection of the gene which is specific for *Gn1a* i.e., *Gn1a-INDEL-3*. However, the markers did not show clear polymorphism and hence, an indel was identified within the candidate gene and designed a new marker, *OsSPL14*-Indel -2F/2R (specific for *OsSPL14*) and it showed a clear polymorphism between the donor parent IR121055-2-10-5 and MTU1010 and was used for foreground selection (**Fig. 2**).

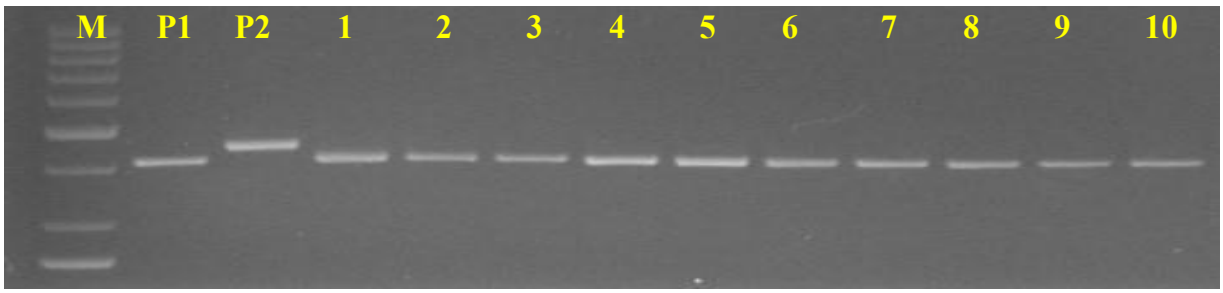
The positive BC_1F_1s were then screened for background selection with the parental polymorphic simple sequence repeat (SSR) markers, among which a single plant (RP6353-26-13) possessing maximum recovery of the recurrent parent genome (~ 75.3 %) was identified and backcrossed with the recurrent parent, i.e., MTU1010 to develop BC_2F_1s. A total of 61 parental polymorphic SSR markers with reasonable genome-wide coverage was used in the for background selection, featuring 14 polymorphic SSRs on Chromosome 1 (where *Gn1a* is located) and 17 markers on chromosome 8 (where *OsSPL14* is identified). This hastened the process of the recurrent parent genome (RPG) recovery

a. *Gn1a-INDEL-3F/3R*



M-50bp ladder, P1- IR121055-2-10-5, P2 - MTU 1010, Lanes 1-10 – Improved lines of MTU 1010.

b. **RMS-*OsSPL14-INDEL-2F/2R***



M-50bp ladder, P1- IR121055-2-10-5, P2 - MTU 1010, Lanes 1-10 – Improved lines of MTU 1010.

Fig. 2. Foreground selection of selected backcross derived lines of MTU 1010 for targeted genes, Gn1a and OsSPL14 at BC_2F_6 generation

(Singh *et al.,* 2013). The number of backcross was limited to just two due to the use of marker based background selection and the fact that the donor genotype employed in this study, IR121050-1-8-5, is an elite breeding line developed by IRRI, Philippines with long slender grain type and semi-tall plant type similar to MTU1010.

A total of 210 BC_2F_1s were produced and 53 BC_2F_1 positive plants were confirmed through foreground selection. A single plant (RP6353-26-13-39) with 87.2 % recurrent parent genome recovery was identified through background selection and selfed to generate 345 BC_2F_2s. Among the BC_2F_2 plants, 38 were identified to possess *Gn1a* and *OsSPL14* in homozygous conditions. A single best plant *viz*., RP6353-26-13-39-5, possessing target yield enhancing genes with maximum 92.0 % recurrent parent genome recovery was identified through background selection and advanced through pedigree method of breeding (Sundaram *et al.,* 2008; Jena and Mackill 2008; Rekha *et al*., 2018; Anila *et al*., 2018; Vijay *et al.,* 2018) till BC_2F_6 generation (**Table 2**). Ten top performing breeding lines with targeted yield genes and phenotypic similarity with MTU 1010 were evaluated (**Fig. 2**), of which, three lines namely RP6353-5-8-13-24, RP6353-26-13-39-5 and RP6353-32-12-8-16, with yield superiority were nominated in AICRIP trials.

Phenotypic performance of improved lines of MTU1010 in presented in **Table 3; Fig. 3**. The ANOVA for eleven agronomic traits among the ten selected BC_2F_6 lines and the recurrent parent, MTU1010, revealed that the mean sum of squares due to treatments (<0.01) were highly significant for yield traits studied, indicating significant variability among the improved lines when compared to MTU1010 (**Table 3**). The yield contributing traits did not differ significantly among the selected BC_2F_6 lines, but differed with respect to MTU1010. The improved lines were 3-8 days earlier to complete 50% flowering, as compared to MTU1010. Also, plant height was observed to have significantly increased (2 – 4 cm) as compared to MTU1010. Significant increase in other major yield component traits such as grain number per panicle, primary and secondary branching per panicle, 1000 grain weight and single plant yield was also observed as compared to recurrent parent.

Table 2. Number of backcross plants screened in each generation

Cross combination	Particular of cross combination	Number of plants screened	Number of plants confirmed	Gene combination in the confirmed plants	Background genome recovery (%)
MTU 1010 x IR121055-2-10-5	F_1	76	48	*Gn1a* + *OsSPL14*	-
MTU 1010 x F_1	BC_1F_1	154	23	*Gn1a* + *OsSPL14*	75.3
MTU 1010 x BC_1F_1	BC_2F_1	210	53	*Gn1a* + *OsSPL14*	87.2
Selfed progeny of BC_2F_1	BC_2F_2	345	38	*Gn1a* + *OsSPL14*	92.0
Selfed upto	BC_2F_6		10	*Gn1a* + *OsSPL14*	-

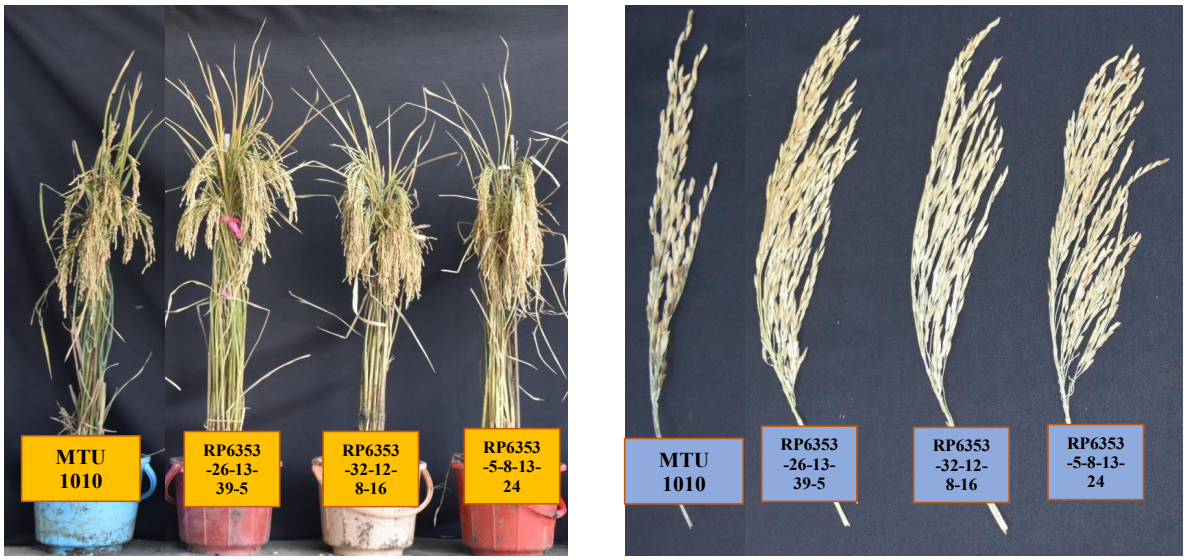


Fig. 3. a) Improved backcross derived plants b) panicle features of the selected improved lines of MTU1010 having the gene combination, *Gn1a* + *OsSPL14* along with recurrent parent, MTU1010

To compare the variation among traits, phenotypic, genotypic coefficients of variation, heritability, genetic advance and genetic advance in per cent mean and correlation coefficient are calculated and the results are furnished in **Table 3 and 4**, respectively. The phenotypic Coefficient of Vriation (PCV) values were higher than Genotypic Coefficient of Variation (GCV) for all the traits studied, indicating role of environment in expression of the traits. The highest PCV (%) was observed for primary branching per panicle (18.07) and the lowest was for recorded for days to 50% flowering (2.63). The GCV (%) was highest for grain number per panicle (16.96) and the lowest was for days to 50% flowering (0.89). Heritability in broad sense estimate varied from 11.38 per cent for days to 50 % flowering and 96.51 per cent for grain number per panicle. Genetic advance (GA) was highest for grain number per panicle (74.62) and lowest for days to 50 % flowering (0.61), while for genetic advance in per cent of mean (GAM %) the highest was for Grain number per panicle (34.32) and the lowest for flag leaf width (0.08). Similar results were observed for the analysis of genetic parameters for yield contributing characters in rice by Kumar *et al.,* 2018 and Allam *et al*. 2015.

Correlation studies revealed that single plant yield exhibited highly significant positive correlation with plant height (0.67), 1000 grain weight (0.559), grain number per panicle (0.56) and secondary branches per panicle (0.513) and positive and significant association with flag leaf length (0.413). However, it recorded non-significant and positive correlation with number of productive tillers (0.324), flag leaf width (0.275) and primary branching per panicle (0.183) and negatively non- significant association with days to 50% flowering (-0.206). Earlier studies by Singh *et al*., 2022, indicated that number of productive tillers, panicle length, flag leaf length and width and 1000 grain weight had positive relationship with yield in rice.

To meet the expanding food demands for the rapidly growing world population, increase in rice yield and production is of utmost importance. This could be achieved by developing genetically superior genotypes

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Table 3. Evaluation of agronomic characters of the improved lines of MTU1010 under field conditions during *Rabi* 2018-19

S.No.	Plant identity	DFF	PH	NPT	PL	TGW	GNPP	FLL	FLW	PBP	SBP	SPY
1	MTU1010	94 ± 1.5	104.7 ± 1.5	12 ± 1.5	21.0 ± 1.2	20 ± 0.9	124.0 ± 3.5	28.3 ± 1.5	1.6 ± 0.1	10.0 ± 1.2	23.0 ± 1.0	17.9 ± 1.3
2	IR121055-2-10-5	90 ± 1.5	123.0 ± 1.7	16 ± 1.5	25.7 ± 1.5	23.3 ± 0.6	276.6 ± 5.5	40.9 ± 1.6	2.1 ± 0.1	16.0 ± 1.5	39.0 ± 1.2	25.7 ± 1.5
3	RP6353-1-5-11-35	90 ± 1.2	108.7 ± 1.8	13 ± 1.2	21.7 ± 1.5	19.6 ± 0.4	238.3 ± 4.9	35.0 ± 1.7	1.6 ± 0.1	12.0 ± 1.0	31.0 ± 1.0	20.0 ± 1.2
4	RP6353-5-8-13-24	91 ± 1.2	109.3 ± 1.5	13 ± 1.5	22.2 ± 1.3	20.2 ± 0.8	241.0 ± 6.1	35.0 ± 1.2	1.8 ± 0.1	12.3 ± 0.9	34.3 ± 1.5	21.0 ± 1.2
5	RP6353-9-18-20-8	86 ± 1.2	107.0 ± 1.7	11 ± 1.5	19.4 ± 1.4	20.3 ± 0.4	198.0 ± 4.4	32.3 ± 1.5	1.8 ± 0.1	10.7 ± 1.3	31.0 ± 1.5	19.0 ± 1.2
6	RP6353-18-10-9-14	88.3 ± 1.5	106.3 ± 1.8	12 ± 1.5	19.3 ± 1.3	19.1 ± 0.5	197.3 ± 4.6	32.8 ± 1.6	1.7 ± 0.1	12.0 ± 1.2	32.0 ± 1.5	18.7 ± 1.2
7	RP6353-22-18-5-12	93 ± 1.2	107.0 ± 1.7	12 ± 1.5	18.7 ± 1.5	19.7 ± 0.7	207.3 ± 4.1	33.0 ± 1.7	1.7 ± 0.1	13.0 ± 1.5	34.3 ± 0.9	18.7 ± 1.2
8	RP6353-26-13-39-5	90 ± 1.5	110.0 ± 1.7	14 ± 1.5	23.3 ± 1.5	21.2 ± 0.5	246.3 ± 5.2	35.3 ± 1.5	2.0 ± 0.1	14.0 ± 1.0	38.0 ± 1.0	22.3 ± 1.5
9	RP6353-27-15-18-4	90 ± 0.9	107.3 ± 1.5	12 ± 1.2	20.7 ± 1.5	19.6 ± 0.8	214.3 ± 3.5	33.0 ± 1.2	1.9 ± 0.1	11.3 ± 0.9	30.3 ± 0.9	20.0 ± 1.2
10	RP6353-30-8-19-5	89 ± 1.5	108.0 ± 1.7	12 ± 0.9	21.7 ± 1.5	18.5 ± 0.8	218.3 ± 4.6	33.0 ± 1.2	1.8 ± 0.1	11.7 ± 0.9	31.0 ± 1.0	20.7 ± 1.8
11	RP6353-32-12-8-16	89 ± 0.9	106.7 ± 1.5	13 ± 1.2	22.0 ± 1.2	20.8 ± 0.5	230.7 ± 4.1	35.7 ± 1.5	1.8 ± 0.0	13.0 ± 1.2	34.7 ± 1.3	21.0 ± 1.2
12	RP6353-35-15-21-12	90 ± 1.5	107.7 ± 1.8	12 ± 1.2	21.0 ± 1.2	19.0 ± 0.5	216.3 ± 4.6	33.7 ± 1.5	1.7 ± 0.1	11.7 ± 0.9	31.7 ± 0.9	18.3 ± 1.2
	Mean ± SE	90.4± 1.2	108.6 ± 1.5	13 ± 0.8	21.3 ± 1.3	20.1 ± 0.6	217.3 ± 4.0	33.9 ± 1.3	1.7 ± 0.1	12.3 ± 1.1	32.5 ± 1.2	20.4 ± 1.2
	MSS	0.2473	<0.0001	0.0676	0.0654	0.0022	<0.0001	0.0013	0.1428	0.0754	<0.0001	0.0176
	CV%	2.48	2.52	11.34	10.6	5.37	3.22	6.98	10.72	15.58	6.43	10.76
	CD	3.8	4.65	2.51	3.83	1.82	11.86	4.02	0.32	3.24	3.54	3.73
	F value	1.34	7.71	1.89	2.07	3.58	71.84	4.23	1.51	1.98	9.84	2.62
	P value	0.2646	<.0001	0.0904	0.0638	0.0042	<.0001	0.0015	0.189	0.0763	<.0001	0.0224
	GCV (%)	0.89	4.05	6.84	6.45	5.5	16.96	7.53	5.13	9.14	12.1	8.44
	PCV (%)	2.63	4.77	13.25	12.41	7.69	17.26	10.27	11.89	18.07	13.7	13.68
	H2 (%)	11.38	72.06	26.7	27.03	51.26	96.51	53.79	18.62	25.62	77.94	38.12
	GA	0.55	7.71	0.95	1.47	1.63	74.62	3.87	0.08	1.17	7.15	2.20
	GAM	0.61	7.08	7.29	6.91	8.12	34.32	11.38	4.56	9.54	22.01	10.74

Note: $p \leq .001^{***}$, $p \leq .01^{**}$, $p \leq .05^{*}$, $p \geq 0.1^{+}$

DFF - Days to 50% flowering, PH - Plant height (cm), NPT- Number. of productive tillers, PL - Panicle length (cm), TGW - Thousand grain weight (g), GNPP - Grain number per panicle, FLL - Flag leaf length (cm), FLW - Flag leaf width (cm), PBP - Primary branches per panicle, SBP - Secondary branches per panicle, SPY - Single plant yield(g), Mean- Standard error mean; CV - Coefficient of variation, CD - Critical difference; PCV - Phenotypic Coefficient of Variation, GCV - Genotypic Coefficient of variation, H2-Broad sense of heritability, GA-Genetic advance and GAM – Genetic advance in % of the mean.

Table 4. Correlation coefficient analysis for different yield and its related characters of selected improved lines of MTU 1010

	DFF	PH	NPT	PL	TGW	GNPP	FLL	FLW	PBP	SBP	SPY
DFF	1	-0.095	-0.019	-0.187	0.052	-0.324	-0.199	-0.202	-0.07	-0.274	-0.206
PH		1	0.591**	0.463**	0.683**	0.623**	0.698**	0.37*	0.545**	0.565**	0.67**
NPT			1	0.354*	0.493**	0.57**	0.547**	0.388*	0.526**	0.49**	0.324
PL				1	0.304	0.475**	0.494**	0.413*	0.43**	0.44**	0.344*
TGW					1	0.371*	0.447**	0.3	0.505**	0.442**	0.559**
GNPP						1	0.781**	0.406*	0.566**	0.8**	0.56**
FLL							1	0.269	0.479**	0.665**	0.413*
FLW								1	0.574**	0.457**	0.275
PBP									1	0.593**	0.183
SBP										1	0.513**
SPY											1

** Significant at 1% level of significance, *significant at 5% level of significance
DFF - Days to 50% flowering, PH - Plant height, NPT - Number of productive tillers, PL - Panicle length, TGW - Thousand grain weight, GNPP - Grain number per panicle, FLL - Flag leaf length, FLW - Flag leaf width, PBP - Primary branches per panicle, SBP - Secondary branches per panicle, SPY - Single plant yield.

with high yield potential. From this study, the promoted entry RP6353-26-13-39-5 (IET28674) could help farmers for increasing higher yield to fulfil the food demand and offer the best genetic resources for crop breeding programme.

Authors' contribution Conceptualization of research (SRM); Designing of the experiments (SRM, BSM and PE); Contribution of experimental materials (JKK); Execution of field/lab experiments and data collection (PE, KMBVN, CK, HG, DT, AD, RG, MSK, KRR, AM, HSK, AD, SRK, LPB, SP, VG); Analysis of data and interpretation (FRA, SP); Preparation of the manuscript (PE, KMBVN, SRM, FRA, SP).

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