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RESEARCH ARTICLE

Association studies in rice introgression lines contributing to high yielding ability

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Abstract

Introgression lines (IL) from crosses between elite cultivars and wild species are important resources for mapping quantitative trait loci (QTLs) for yield. In order to evaluate the relationship between morphological characters and yields in rice, 25 ILs (KMR3 × *Oryza rufipogon*) at BC_4F_6 generation were grown during *Rabi* 2014. Transgressive segregations were observed for most traits. The results suggested that genetic variation for these traits were largely controlled by additive genes. Statistical analysis on important agronomic traits showed that maximum standard deviation belonged to the total grain number per plant followed by number of grains per panicle and grain yield per plant. Grain yield per plant was positively correlated and was significant to tiller number, number of panicle per plant, number of grains per panicle and grain weight per panicle. This study revealed that selection based on total number of grains per panicle, grain weight per panicle and panicle per plant will be highly effective for yield improvement in rice breeding programs. Overall, there was high genetic variation which promised high rate of arising elite transgressive individuals and moderate heritability for most traits in the populations tested. It is feasible and efficient to use wild rice abundant genetic diversity to develop rice cultivars for high yield.

Keywords: Wild species, introgression lines, yield, yield components

Introduction

Rice (*Oryza sativa* L.) is one of the most important cereals and provides the staple food for more than 50% of the world's population. The first green revolution brought rice grain yield to a new level by utilizing the *semi-dwarf* 1 gene (sd1) in the 1960s. However, the contradiction between world food supply and consumer demand has become increasingly sharp due to the continuously increasing population. To meet the food demands of 9 billion people by 2050, genetic improvement that increases rice production will be important. Grain yield is one of the most important index in rice breeding, which is governed by quantitative trait loci (QTLs). Different mapping populations have been used to explore the QTLs controlling yield related traits. Primary populations such as F_2 and recombinant inbred line populations have been widely used to discover QTLs in rice genome-wide, with hundreds of yield-related QTLs detected. To date, 20 QTLs directly affecting rice grain and its components have been cloned with NIL-F_2 populations and 14 new grain QTLs have been validated in the NILs. Wild relatives of rice are a rich source of desirable genes not only for yield but also for disease resistance and stress tolerance. Currently, the narrow genetic data base of breeding programs has resulted in a bottleneck effect in rice cultivar development (Tanksley and McCouch 1997). Unlocking the tremendous genetic potential from wild rice will bring and enormous improvement in the modern cultivar with the aid of molecular selection (Zamir, 2001). Noticeably, several yield-enhancing QTLs have been identified from common wild rice (*Oryza rufipogon*), as the progenitor of Asian cultivated rice (*O. sativa* L.) (Xiao *et al.,* 1996, 1998; Moncada *et al.,* 2001; Brondani *et al.,* 2002; Li *et al.,* 2002; Septiningsih *et al.,* 2003; Thomson *et al.,* 2003; He et al., 2006; Tian *et al.,* 2006a). In order to identify and use the desired genes from wild rice, it is still very important to develop *Oryza rufipogon* x *O. sativa* introgression lines.

Introgression lines population were effectively used in mapping quantitative trait loci (QTLs), identifying favorable genes, discovering hidden genetic variation, evaluating the action or interaction of QTLs in multiple conditions and providing the favorable experimental materials for plant breeding and genetic researches. Due to its simple genetic background, introgression lines (ILs) become a useful experimental material for genetic analysis and molecular breeding and could be used to evaluate the action and interaction of genes over multiple years and in multiple site experiments (Grandillo *et al.,* 1996; Eshed and Zamir 1995, 1996; Yamamoto *et al.,* 1998, 2002; Monforte and Tanksley 2000b). In this study, 25 introgression lines were used which were developed from a cross between common wild rice (*Oryza rufipogon*), as the donor and an elite cultivar KMR3 as the recipient, was selected its high grain yield in field trials and characterized in detail for yield and its related traits from seed to seed in BC_4F_6 and BC_4F_7 generations. Introgression lines are homozygous lines with small chromosomal segments from the donor into the recurring parent by consecutive backcrossing and selfing (Tian *et al.,* 2006). Two yield QTLs, yield 1.1 and yield 2.1 which helped in increasing the yield by 18%, were identified in a Malaysian accession of *O. rufipogon* (Xiao *et al.,* 1996, 1998). This accession was used as a donor in many studies and using different recipients resulting in identification of many QTLs for yield and its related traits Xiong *et al.,* 1999; Moncada *et al.,* 2001; Septiningsih *et al.,*2003; Thomson *et al.,*2003; McCouch *et al.,*2007). Using introgression lines several authors have demonstrated that ILs are useful genetic material for improving various agronomic traits in popular varieties, identification of new genes and for map-based cloning of QTLs in rice (Xie *et al.,*2008; Rahman *et al.,* 2007; Yoon *et al.,* 2006). Ideotype breeding has been advocated specially to obtain high yield from indica x japonica crosses (Peng *et al.,*2008). It is important to know which yield related trait or yield components can help to enhance yield and up to what extent but this has not been analyzed in introgression lines. It would be useful if guidelines for selecting key traits of importance can be developed for backcross derivatives of elite x wild crosses. This paper reports on characterization and analysis of yield and related traits associated from seed to seed in a set of 25 high yielding KMR3x *Oryza rufipogon* ILs. Hence, the objectives of this study were to evaluate the phenotypic diversity of rice based on morphological traits and identification of the morphological traits responsible for the yield difference among the rice genotype.

Materials and methods

Plant materials used in the present study was originated from the mapping population KMR3 × *rufipogon.* In order to evaluate the relationship between morphological characters and yield in rice, 25 ILs at BC_4F_6 generation were grown with a plant to plant distance of 15 and 20 cm between rows during *Rabi* 2014. The observations were recorded on five selected plants for thirteen traits including yield and its component trait. 25 ILs were selected based on morphological performance and important agronomic traits like, seed germination %, coleoptiles growth rate %, plant growth rate %, plant height (cm), tiller numbers, number of panicle per plant, panicle length (cm), panicle weight (cm), grain numbers per panicle, grain numbers per plant, grain weight per panicle (g), thousand grain weight (g), grain length (mm), grain width (mm), grain yield/plant (g) and grain yield per plot (g) were recorded on those genotypes based on the standard evaluation system (SES) of rice (IRRI, 2002). The statistical analysis, including estimation of descriptive statistics, coefficient of correlation and mean percentage phenotypic variation was conducted by using SAS (Statistical Analysis System) version 9.2 (SAS Institute 2008).

Results and discussion

Transgressive segregation and field performance

Phenotypic transgressive segregation was observed for all the traits with all ILs in BC_4F_6 families. The values of thirteen yield related traits in BC_4F_6 and KMR3 showed largest variation (Table 1). The coefficient of variation for yield per plant was highest i.e., 29.57, while lowest was observed for GW i.e., 4.19. Yield per plant and plot yield for 25 IL was recorded in the field (Fig. 1). Yield per plant was highest in IL SS7 (85.9 g) where as lowest yield per plant was recorded in IL SS 14 (25.2 g). Plot yield did not consistently reflect the yield per plant. Plot yield was highest in IL SS 7 (3622.1 g). However, IL SS 14 had lowest (1015.5 g) plot yield compare to KMR3.

Seed germination

Rate of seed germination was analyzed in 25 high yielding ILs till 7 days after sowing (Fig. 2). The control line KMR3 showed a late straight line pattern of germination and 100% seeds germinated even after 7 days. The highest yielding ILs such as SS 5 and SS 15 also showed same pattern of germination as compare to KMR3 (100% and 95% after 7 days respectively). However, IL SS 25 which was among the high yielding lines of the 25 lines, showed a step slow (late germination i.e., only 80% of the seeds germinated after 7 days).

Seed germination from a total of 20 seeds was counted after 3 days and recorded after every 24 h till 7 days. Data represented here is mean of 5 individual experiments. On the other hand, IL SS20 and SS 18 which were among the lowest yielding lines of the 25 lines, late germination i.e., 80% and 85% germination after 7 days). It was significant that the highest yielding line IL SS 7 showed a straight-line slope for rate of germination and reached 100% after 7 days. The high yielding line IL SS 15 also followed similar pattern of germination like KMR3 although with higher rate. The IL SS 19 and SS 18 having lowest rate of germination could also show considerable increase in yield over KMR3. It appears that late and steady germination as in ILs SS 7 and SS 15 may be an adaptation to ensure highest survival and growth in unpredictable environmental conditions. Overall, there was high genetic variation which promised high rate of arising elite transgressive individuals and moderate heritability for most ILs tested. The highest yield of IL SS 7 was associated with its slow but steady rate of germination, highest number of grains per panicle followed by more number of grains per plant. The panicle weight, grain weight per panicle, number of secondary branches per panicle and number of panicles per plant was positive and significant. The traits negatively associated with high yield IL SS 7 was plant height, tiller number, panicle length, panicle weight and number panicles per plant compared to KMR3. The slow rate of germination indicated a communicative behavior of the sibling roots and could be an advantageous feature for seedling establishment in case of an unpredictable or unfavorable environmental delay in germination as reported in Arabidopsis (Biedrzycki *et al.,*2010).The next highest yielding IL SS 15 had also lower rate of seed germination, longer shoot length in seedling stage, higher growth rate, highest increase in number of panicles and moderate increase in seed weight per panicle compared to KMR3.

Correlations between traits tested

On the basis of these traits the genotypes, which perform better with respect yield and yield contributing traits were selected for the further genetic analysis for the improvement of the rice crop. The quantitative traits, that is, number of spikelets per panicle, number of seeds per panicle, seed weight per panicle and thousand grain weight that directly contributed to the yield of the rice genotypes. Other traits i.e. plant height, number of tillers per plant, plant growth rate, panicle length, flag leaf area, primary branches per panicle, secondary branches per panicle and maturity days were also important with respect to the yield of the plants. Phenotypic correlations among twelve morphological traits are shown in the (Table 2). In this study, plant yield (YP) was positively and significantly correlated with tiller number (0.34) (TN), number of panicles per plant (0.33) (NP), grain number per panicle (0.70) (GN) , grain number per plant (0.887) (GNP), grain weight per panicle (0.73) (GW) and thousand grain weigh (0.34) (TGW). Panicle length was positively and significantly associated with panicle weight (0.682), grain weight per panicle was positively and significantly associated with grain number per panicle (0.94) and grain number per plant (0.54). Thousand grain weight was positive and significant with grain weight per panicle (0.51). Grain number per plant was also positively and significantly associated with tiller number (0.47), number of panicles per plant (0.46) and grain number per panicle (0.60). Thousand grain weight (-0.34) and grain weight per panicle (-0.40) was negatively associated with plant height (PH). However, high yield in the present KMR3 ILs was associated with dwarfness, panicle weight, grain weight per panicle, grain number per plant height 1000-seed weight and early flowering. The strategies of the KMR3 ILs to increase yield do not strictly support the earlier reports. In the present study, it is shown that each IL follows different paths to increasing yield. Recently, it was also shown that yield based selection is as effective as phenotypic trait based selection in the late generations of breeding (Yuan *et al.,* 2011) supporting the results of this study. The associated factors for high yield are different in different ILs and were considered as follows.

Analysis of mean percentage phenotypic variation of top six high-yielding ILs and assessment of yield and it related traits

Greater number of evidence suggest that introgression lines are useful genetic materials for the identification of new genes (Eshed and Zamir 1994, 1995, 1996; Chetelat *et al.*,2000; Kubo *et al.*,2002) for distinguishing pleiotropy versus linkage as well as pseudo-over dominance versus true-dominance (Yamamoto *et al.,*1998; Monforte *et al.,*2000) and for the map-based cloning of QTLs (Alpert and Tanksley 1996; Grandillo *et al.,* 1996; Yamamoto *et al.,*2000; Yano *et al.,*2000). However, two key factors, the range of phenotypic variation in the ILs population and the coverage ratio of the donor genome, should be considered during the course of developing introgression lines. The top 6 ILs having higher grain yield per plant were selected for the analysis of mean percentage phenotypic variation of some seedling and phenotypic traits (Fig. 3).

When compared with KMR3, these high yielding ILs showed an apparent increase in Y/P by 2% in IL SS 4 to 49% in IL SS 7. However, all the 6 ILs showed increase in plot yield compared to KMR3 which ranged from 0.2% in IL 4 to 48.9% in IL SS 7. All the 6 ILs outperformed the recurrent parent KMR3 by 3-57%, 5-38%, 1-73% and 3-46% for grain number per panicle, grain number per plant, grain weight per panicle and number of secondary branches per panicle respectively. The highest yielding IL SS 7 showed an increase in yield per plant, yield per plot, 1000 grain weight, grain weight per panicle, number of secondary branches per panicle and grain number per panicle up to 49%, 48.9%, 10%, 73%, 46% and 57% respectively. The flag leaf area was 18% more in IL SS 7 compared to KMR3, but it was less by -8-41% among all the 5 ILs. Almost all the high yielding ILs showed early flowering as compared to KMR3. Seedling germination %, coleoptiles growth, seedling root length, number of primary branches per panicle were less compared with KMR3 in almost all the ILs indicating that these traits are negative indicators of higher yield. Hence it can be concluded that the grain number per panicle, grain number per plant and number of secondary branches per panicle are the major positive traits influencing the yield of the ILs. The 25 ILs showed a wide range of variance in morphological and yield-related traits. Several investigations have been made earlier to define a robust method of selection for yield which can withstand dynamic and unfavorable environment.

All the genotypes showed highly significant variations for all the traits studied. Furthermore there was a significant effect of genotypic into environmental interaction on all the traits. The extent of variability for any character is very important for the improvement of crop through breeding. Significant variation in all the traits studied indicated the presence of high genetic diversity among all the genotypes of rice. Nearly 88%, and 32% of the ILs were showed, higher plant height and higher number of tiller per plant than KMR3. Number of panicles per plant and panicle length was more than KMR3 in 20% of the ILs. However, the highest yielding line IL SS 7 showed 22% increase in number of panicles per plant (Fig. 4). Germination percent was higher than KMR3 in 16% ILs and less in 84% of ILs. 92% ILs showed increase in number of secondary branches per panicle. 52% and 32% of the plants also showed increase in grain number per panicle and grain yield per plant than KMR3. All the ILs outperformed KMR3 for yield per plant with a range of increase from 2% to 49%. The line IL SS7 showed the highest increase in yield. Days to 50% flowering was less in all the high yielding ILs compared to KMR3. These results indicate that for increasing yield in case of introgressions from *Oryza rufipogon* following traits need improvement. Early flowering is a positive trait. Obviously, number of panicles, grain number per panicle and grain weight per panicle has to be higher than the restorer line KMR3. Vegetative traits like leaf length and weight only indicate higher initial vigor of the plant but not necessarily higher yield. Long shoot and root in seedling stage is a positive trait and may confer vigor in the adult plant.

These results confirm that genes introgressed from *Oryza rufipogon* into an elite background can improve key agronomic traits, even though *Oryza rufipogon* is phenotypically inferior to the cultivated variety. To this end, ideotype approach (Peng *et al.*, 2008), pedigree selection (Ali, 2011) and many other (Sofi *et al.*, 2006) have been shown to be beneficial in various studies. Various selection strategies and genes have been shown to increase productivity by delaying heading date, increasing plant height and panicle size (Ali 2011; Xue *et al.*, 2008). The plant height, tiller number, panicle weight, grain number per panicle, grain number per plant grain weight per panicle and thousand grain weight was positive and significant. The negatively parameters associated with IL SS15 were coleoptiles growth, seedling root growth, low flag leaf area and less number of primary branches per plant. The ILs SS 10, SS 25, SS 19 and SS 4 showed nearly similar pattern of increase and decrease in traits with. Overall, there was high genetic variation which promised high rate of arising elite transgressive individuals and moderate heritability for most traits in the populations tested. Jennings (1964) proposed that selection for the stay-green trait combined with large, erect flag leaves is a valuable breeding objective for increased yield potential. Donald (1968) proposed the ideotype approach for plant breeding. He defined crop ideotype as an idealized plant type with a specific combination of characteristics favorable for photosynthesis, growth and grain production. Later Peng *et al.,* (1994) proposed New Plant Type (NPT) and then a revised ideotype was proposed later (Peng *et al.,* 2008) to define a plant type that was theoretically efficient. However, the results obtained in this study of the ILs do not support their ideotype concept. Yuan *et al.,* (2011) suggested that yield-based selection was as effective in increasing rice grain yield as trait-based selection in the late generations of the breeding cycle supporting our results in the present study. These results from KMR3*x Oryza rufipogon* introgression lines are also supported by observations on Swarna x *O. nivara* introgression lines. It is feasible and efficient to use wild rice abundant genetic diversity to develop rice cultivars for high yield.

Conclusion

The study while confirming the view that the progenitor species consisted of the largest source of unfolded variability for traits of complex inheritance like yield and it components have helped identifying additional novel variability for yield improvement. High genet variation was observed in the offsprings derived from the cross between KMR3 and *Oryza rufipogon* and great genetic variation promises high rate of arising transgressive segregation. The current study indicated that while introgressing from *Oryza rufipogon* the following traits need to be improved for increasing yield: (1) tiller number and number of panicles per plant should be higher; (2) early flowering (3) steady rate of germination and (4) high seed weight per panicle. Seedling phenotypes did not show strong correlation with increasing yield in this study. Yield/plant does not always reflect the plot yield. The novel association of seed germination rate of these high yielding ILs need further study to dissect its link with high yield. Late and steady germination may be an adaptation to ensure highest survival and growth in unpredictable environmental condition as shown by highest yielding ILs in this study. Thus, it is clear that it is possible to have diametrically opposite strategies in each yield component to increase yield and restricting to a specific ideotype in selection approaches may be counterproductive in rice breeding. In high yield breeding of *Oryza rufipogon* utilization, grain number per panicle, grain weight per panicle, and grain yield per plant should be the most important traits to be considered. It is efficient and feasible to utilize *Oryza rufipogon* abundant genetic diversity to develop rice cultivars for high yield. More research are required to unearth novel yield related gene blocks hidden in closely related wild/weedy species and primitive cultivars, if the rice dependent world want to assure food security. This study indicated that each ILs has a different strategy or a combination of different yield traits to attain high yield. High yield in these ILs was associated with early flowering, high number of tillers, panicles weight and grain weight per panicle.

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Table 1. Descriptive Statistics of KMR3 and 25 ILs for some agronomic traits

Variable	KMR3	Range	Mean	Standard Deviation	Coefficient of Variation (%)
Plant Height at Maturity(cm)	107.67	79.67-133	117.11	10.72	9.15
Number of Tiller/Plant	20.67	15.00-31.33	20.39	4.42	21.71
Number of Panicles/Plant	21.00	14-30	19.73	4.26	21.59
Panicle Length (cm)	24.67	19.33-28	22.88	2.39	10.45
Panicle Weight (g)	2.57	1.30-3.67	2.61	0.61	23.34
Grain Number/ Panicle	138	87.67-217.33	142.97	32.25	22.56
Grain Number/ Plant	2730	1050-3780	2393.56	629.12	26.28
Grain Weight/Panicle (g)	2.76	0.72-4.78	2.75	0.72	26.18
Grain Length (mm)	5.54	5.16-6.12	5.44	0.23	4.23
Grain Width (mm)	2.40	2.04-2.55	2.31	0.10	4.19
Thousand Grain Weight (g)	20.00	17-22	19.14	1.49	7.80
Yield / Plant	57.68	25.19-85.9	51.74	15.30	29.57
Yield / Plot	2432.73	1015.46-3622.14	2162.65	622.37	30.63

Where, PH=Plant Height at Maturit (cm), NT=Number of Tiller/Plant, NP=Number of Panicles/Plant, PL=Panicle Length (cm), PW=Panicle Weight (g), PG=Grain Number/ Panicle, GNP=Grain Number/ Plant, GWP=Grain Weight/Panicle (g), GL= Grain Length (mm), GW=Grain Width (mm), TWG=Thousand Grain Weight (g), YP=Yield / Plant, YPP=Yield / Plot

Table 2 Simple correlations among different morphological traits of rice under field condition

	PH	TN	NP	PL	PW	GP	GNP	GW	TWG	YP	DM
PH	**1**										
TN	0.033	**1**									
NP	0.058	0.983*	**1**								
PL	0.154	0.053	-0.004	**1**							
PW	0.131	0.018	-0.018	0.682*	**1**						
GP	-0.299	-0.283	0.316	0.236	0.258	**1**					
GNP	-0.184	0.472*	0.461*	0.221	0.294	0.603*	**1**				
GW	-0.408^8	-0.320	-0.334*	0.128	0.171	0.948*	0.549*	**1**			
TGW	-0.342*	0.268	0.215	-0.235	-0.096	0.221	0.030	0.511*	**1**		
YP	-0.297	0.340*	0.335*	0.184	0.240	0.702*	0.887*	0.734*	0.345*	**1**	
DM	-0.121	0.032	0.026	0.271	0.225	0.207	0.071	0.108	-0.246	0.043*	**1**

Level of significance $p<0.05$= * ; Where, Plant Height (PH), Tiller Number (TN), Number of Panicles (NP), Panicle Length (PL), Panicle weight (PW), Grain/Panicle (GP), Grain Number per Panicle (GNP),Grain Weight (GW), Thousand Grain Weight (TGW), yield per Plant (YP), Maturity Days (DM)

Fig. 1: **Yield of 25 introgression lines in the field study compared to KMR3. Yield per plant-average weight of filled grains (g) from 5 plants and plot yield-average weight of filled grains from 42 plants (21 plants in 2 rows)**

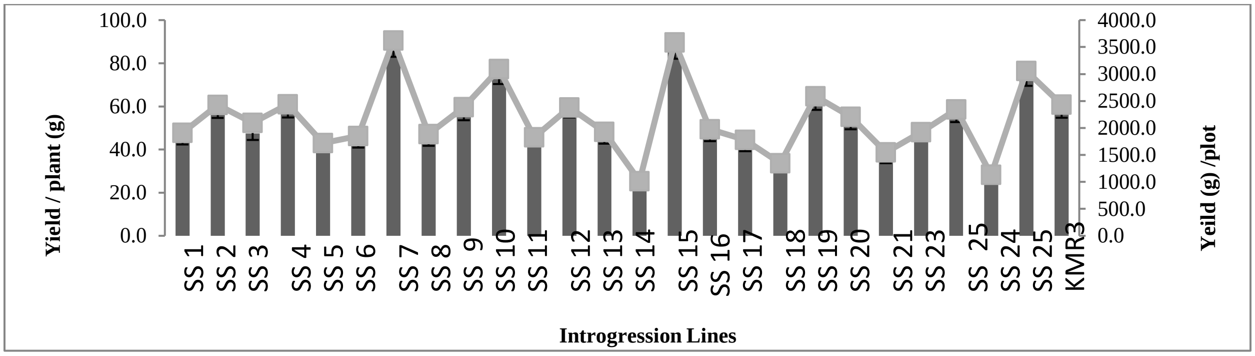


Fig. 2: Germination time course of 25 high yielding introgression lines of KMR3

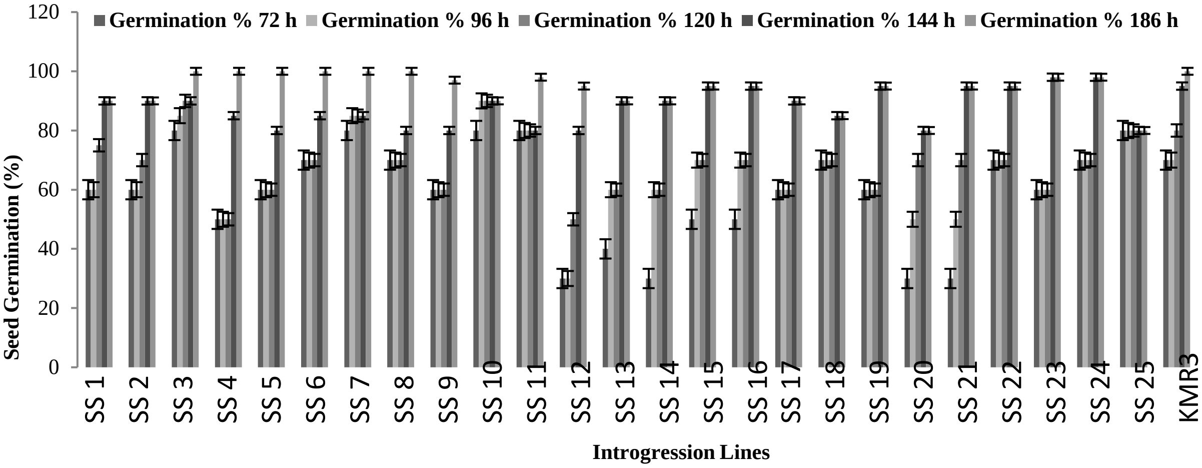
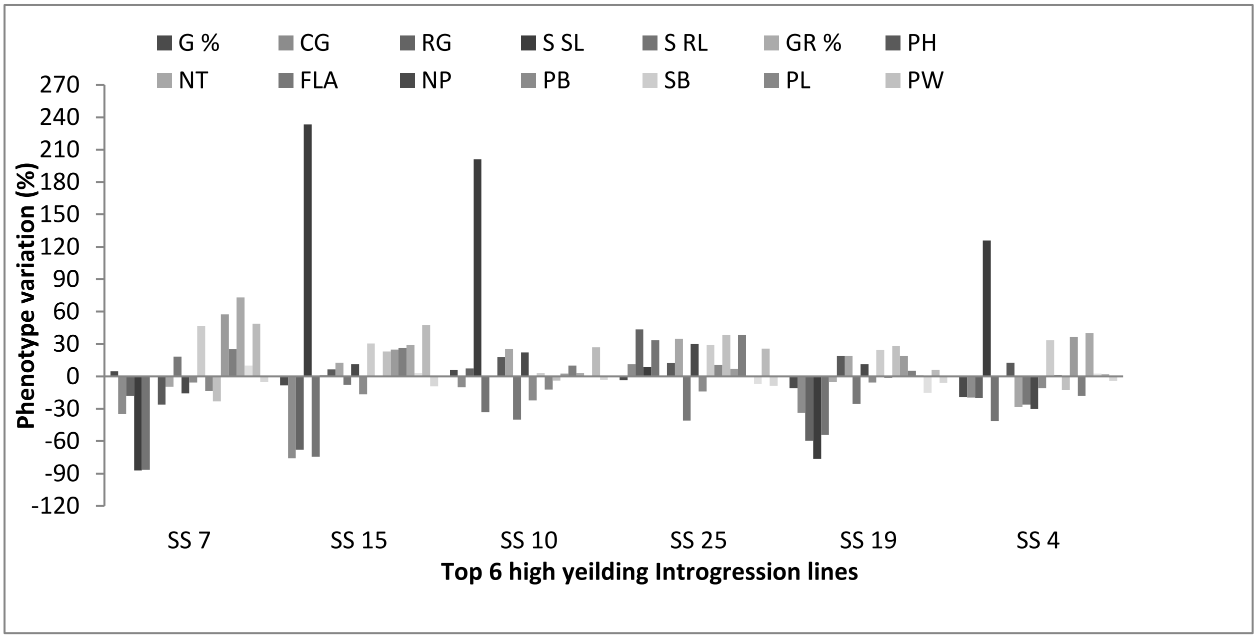


Fig. 3 Analysis of top 6 high-yielding ILs



Where, mean percentage phenotypic variation (Δ%) over the recurrent parent KMR3 for Germination % (G%), Coleoptile Growth (CG), Root Growth (RG), Seedling Shoot Length (SSL), Seedling Root Length (SRL), Growth Rate (GR%), Plant Height (PH), Number of Tiller (NT), Flag Leaf Area (FLA), Number of Panicles (NP), Primary Branches (PB), Secondary Branches (SB), Panicle Length (PL), Panicle Weight (PW), Grain/Panicle (GP), Grain Number/Plant (GNP), Grain Weight/Panicle (GWP), Thousand Grain Weight (TGW), Yield/Plant (YP) and Yield/Plot (YPP). The Δ% was calculated as 100(IL-mean of KMR3)/Mean of KMR3. Horizontal line at ordinate zero represents KMR3 value