Original Research Article

Panicle Architecture in Enhancing Grain Yield in Rice (*Oryza sativa* L.)

ABSTRACT

The architecture of the rice panicle is a crucial focus in breeding for both high yield and quality. It stands as a significant agronomic trait that influences the number of grains per panicle, playing a direct role in contributing to the overall yield of rice grains. Unravelling the genetic basis of panicle architecture is crucial for improving the grain yield in rice. In this study, the panicle architecture traits were meticulously dissected into five distinct components viz., number of primary rachis, number of secondary rachis, grain number on primary rachis, grain number on secondary rachis and total grain number. These components were systematically phenotyped in F_2 and F_3 population derived from a cross between DRR Dhan 48 and Maudamani. 'DRR Dhan 48' is a biofortified elite fine grain medium slender grain type cultivar with high zinc (22 ppm in polished rice) and low glycemic index (51.1). It has resistance to bacterial blight with the incorporation of *xa5, xa13 and Xa21* in the background of Improved Samba Mahsuri. 'Maudamani' is a high yielding cultivar with high grain number and short bold grain type. Analysis of variance, histograms and boxplots revealed highly significant variation for the studied traits. Grain number in F_2 population ranged from 29 to 333 grain with a mean of 162.72 whereas in F_3, its varied from 49 to 368 with a mean of 184.17. Correlation analysis revealed significant correlation among the studied traits. The continuous variation observed in the population for panicle traits indicates that genetic control is governed by multiple minor loci. The presence of superior transgressive segregants highlights a complementary gene action influencing panicle architecture traits. The present investigation on panicle architecture offers scope for improving rice varieties and creating new germplasm resources and provides valuable information for further unravelling the genetic basis determining rice panicle architecture.

Key words: Panicle architecture, Primary rachis, Secondary rachis, Grain number, Correlations, Rice

1.INTRODUCTION

Rice (*Oryza sativa* L.) is one of the most important cereal crops, which provides food for more than half of the world's population. Given the rapid rise of the world population in this century, food shortage is becoming an even more serious global problem. There is an urgent need for increasing rice yield. Since it is a grain crop, rice panicle architecture, which refers to the number of both primary and secondary rachis branches on a panicle as well as the number of grains setting on these branches, is one of the most significant agronomical traits that contribute directly to grain productivity [1]. A mature rice panicle consists of one rachis (main axis), several primary rachis branches, tens of secondary rachis branches, and more than 100 spikelet's [2]. The rice inflorescence generates branches and spikelet meristems before producing floral meristems in a determinate pattern [3].

Grain yield is determined by plant architecture which includes plant height, tiller number and angle, and panicle architecture [4], which in turn comprises grain number, grain size and panicle size including branches [5]. The three major components directly influencing grain yield are number of panicles per plant, grain number per panicle and grain weight [6]. Of these, grain number per panicle is an important trait in determining grain yield and a major trait of concern for developing new plant types in rice [7,8,9]. Grain number per panicle is highly variable and depends on the structural features of the panicle including the number of primary and secondary branches, panicle length, and percentage of filled grains [10]. Grain number is controlled by multiple genes (QTLs) and therefore shows continuous variation in the segregating populations.

Increasing the grain number is the most direct route toward enhancing the grain yield in cereals. Grain number is mainly determined by the panicle architecture and branch differentiation, which are closely associated with the phytohormone pathways and vascular development [11,12,13]. Grain number per panicle is an important characteristic associated to ideal plant architecture which play a significant role in yield improvement in rice [8]. According to the ideal plant architecture model, low tillering and large panicle (200–250 grains per panicle) are the future targets for the breeding of rice [14]. The broad-sense heritability of grain number is relatively high, which ranged from about 70 to 90% in different studies [15,16], suggesting that genetic factors are the major determinant of grain number. Dissection of the genetic mechanism controlling grain number per panicle would thus be an effective way for breeders to improve rice yield.

Further, grain number is positively correlated with panicle length, number of primary and secondary branches [17,18]. Grain number is a typical quantitative trait affected by several genetic and environmental factors. The regulation of rice grain number is co-ordinately controlled by panicle architecture and branch differentiation, and many grain number associated genes exhibited pleiotropic effect in regulating tillering, grain size, flowering time, and other domestication related traits. It is also revealed that grain number determination is closely related to vascular development and the metabolism of some phytohormones. Therefore, it is essential to understand the molecular mechanism of grain number in rice.

Numerous QTLs and genes have been identified for panicle traits due to their pivotal role in governing grain yield. Notable among these is *APO1* (Aberrant Panicle Organization1), identified in mutants, which affects panicle length [19]. *APO2* interacts with *APO1* to regulate panicle axis development [20]. *SP1* (Short Panicle 1) also influences panicle length [21]. *Ghd7, Ghd7.1*, and *Ghd8/DTH8* play roles in regulating panicle length, as well as the number of primary and secondary branches, in addition to influencing heading date [22,23]. *MOC1* (Monoculm 1) and *LAX1* (Lax Panicle) positively regulate panicle branching [24], while *FZP* (Frizzy Panicle) represses panicle branching [25]. *DEP1* (Dense and Erect Panicle1) regulates panicle grain density by affecting the number of primary and secondary branches [26]. *IPA1* (Ideal Plant Architecture 1)/*WFP* (Wealthy Farmer's Panicle) and*LP* (Larger Panicle) all contribute to regulating the number of primary and secondary branches [4,27,28]. Several genes also regulate the number of secondary and tertiary branches. Furthermore, various QTLs/genes such as *Gn1a* [29], *DEP* [26], *NOG1* [30], *qGN4.1* [10], *OsSPL14* [4], *GNP1* [31], and *qGN1c* [32] control the grain number trait and have been mapped, cloned, and functionally characterized in rice. *Gn1a* and *NOG1* specifically regulate grain number, while DEP1, IPA1/WFP, APO1, and GNP1 control panicle architecture and meristems. *NAL1* primarily governs panicle size and plant architecture [33,34]. *Ghd7* exhibits a substantial pleiotropic effect on the number of grains per panicle, heading date, and plant height [22,35]. The *R2R3 MYB* transcription factor, Regulator of Grain Number1 (*RGN1*), influences grain number and panicle architecture. Mutation of *RGN1* results in the absence of lateral grains on secondary branches, with RGN1 controlling lateral grain formation through the regulation of LONELY GUY (*LOG*) expression, thus influencing grain number and shaping panicle architecture. [36].

Although, many genes/QTLs are associated with panicle architecture and grain number have been characterized and their relevant genes have also been cloned, understanding of the molecular basis of rice panicle development is still a major concern. Moreover, to date, only a few genes like *Gn1a*, and *Dep1*mutants show favourable agronomic traits with high yield potential and can be used or have been used as germplasm resources for improving rice cultivars [29,26]. An in-depth analysis of panicle architecture would aid in designing an ideal panicle architecture for producing elite cultivars with high yield.

2. MATERIALS AND METHODS

In the present investigation, segregating population in F_2 and F_3 generations derived from the cross of two elite cultivars 'DRR Dhan 48' and 'Maudamani' was evaluated in wet season (WS) 2022 and dry season (DS) 2023 for panicle traits. 'DRR Dhan 48' is a biofortified elite fine grain medium slender grain type cultivar akin to popular cultivar Samba Mahsuri. It has high zinc (22 ppm in polished rice) and low glycemic index (GI) (51.1). It has resistance to bacterial blight with the incorporation of *xa5, xa13* and *Xa21* in the background of Improved Samba Mahsuri. It was released for cultivation in the Southern part of India in 2018. 'Maudamani' is a high yielding cultivar with compact panicle, high grain number and short bold grain type developed at ICAR-National Rice Research Institute.

Phenotyping

Observations were recorded on randomly selected three panicles in each plant in F_2 population for total number of grains in a panicle. A total of 612 F_2 plants were characterized for grain number. A sub set of 350 families in F_3 generation were evaluated for panicle traits. Observations were recorded on randomly selected three panicles in each line for total number of grains in a panicle, number of primary branches per panicle, number of secondary branches per panicle, grain number on primary branches and grain number on secondary branches. Data was subjected to various statistical analysis using R studio (version 4.3.1).

3.RESULTS AND DISCUSSION

The branching habit in a shoot and a panicle are most important in rice grain production as they are closely linked with yield potential in rice [37]. For developing superior varieties, it is quite essential to have large variation in the breeding material. In order to detect variability in the experimental material, the most commonly used statistical tool is ANOVA *i.e.,* Analysis of variance. In the present investigation, the data on panicle architecture traits viz., grain number (GN), number of primary rachis (PR), number of secondary rachis (SR), number of grains on primary rachis (PGN) and number of grains on secondary rachis (SGN) were subjected to ANOVA and the results revealed highly significant variance indicating presence of high variation among the studied traits (Table 1). Thus, there is ample scope for selection of panicle architecture traits for improvement of rice varieties for grain yield. Similar such inferences were drawn by Bai et al. (2016)[38].

Table 1. Analysis of variance for panicle architecture traits in the biparental population derived from cross of DRR Dhan 48 / Maudamani

Sources of variation	DF	SS	MSS	F-value	P value
Primary rachis	1	194927	194927	219.5	<2e-16***
Secondary rachis	1	228547	228547	288.6	<2e-16***
Grain number on primary rachis	1	356543	346543	836.6	<2e-16***
Grain number on secondary rachis	1	401431	401431	1347	<2e-16***

DF-Degrees of freedom, SS-sum of squares, MSS- mean sum of squares

In F_2 population, grain number ranged from 29 to 333 with a general mean of 163 while in F_3 population, it varied from 49 to 368 with a general mean of 184. The mean value of primary rachis ranged from 6 to 21 with a general mean of 11.56, secondary rachis from 4 to 49 with a mean of 21.11, grain number on primary rachis ranged from 16 to 192 with a general mean of 96.05 and grain number on secondary rachis ranged from 15 to 180 with a general mean of 88.11 (Table 2). Histogram for grain number in F_2 population was positively skewed and platykurtic with less kurtosis than normal distribution which indicated complementary gene action and relatively low probability of extreme events respectively (Figure 1A). While in F_3 generation, grain number followed a double exponential symmetric distribution, which when compared to the normal has a stronger peak, more rapid decay, and heavier tails with a skewness near zero and a higher kurtosis (Table 2 and Figure 1F). Similar double exponential symmetric distribution pattern was observed for number of grains on primary rachis (Table 2 and Figure 1C). For remaining panicle architecture traits (number of grains on secondary rachis, number of primary and secondary rachis), the phenotypic distribution was moderately skewed and leptokurtic with more kurtosis than normal distribution which indicated complementary epistasis gene action and a relatively high probability of extreme events respectively (Table 2 and Figure 1B, Figure 1D and Figure 1E). On a contrary, Deshmukh et al. (2010)[10] reported normal frequency distribution in the RILs without any significant skewness or kurtosis for grain number, primary branches and secondary branches.

Table 2. Descriptive statistics for panicle architecture traits in the biparental population derived from cross of DRR Dhan 48 / Maudamani

Traits	Mean	Min	Max	Range	SD	SE	Variance	Skewness	Kurtosis
Primary rachis	11.56	6.00	21.00	15	2.44	0.13	5.97	0.43	0.47
Secondary rachis	21.11	4.00	49.00	45	6.96	0.37	48.37	0.51	0.53
Grain number on primary rachis	96.05	16.00	192.00	176	19.92	1.06	396.89	0.76	4.71
Grain number on secondary rachis	88.11	15.00	180.00	165	23.83	1.27	567.75	0.37	2.37
Grain number	184.17	49.00	368.00	319	37.96	2.02	1440.76	0.64	4.26

Min-minimum, Max-Maximum, SD-standard deviation, SE-standard error

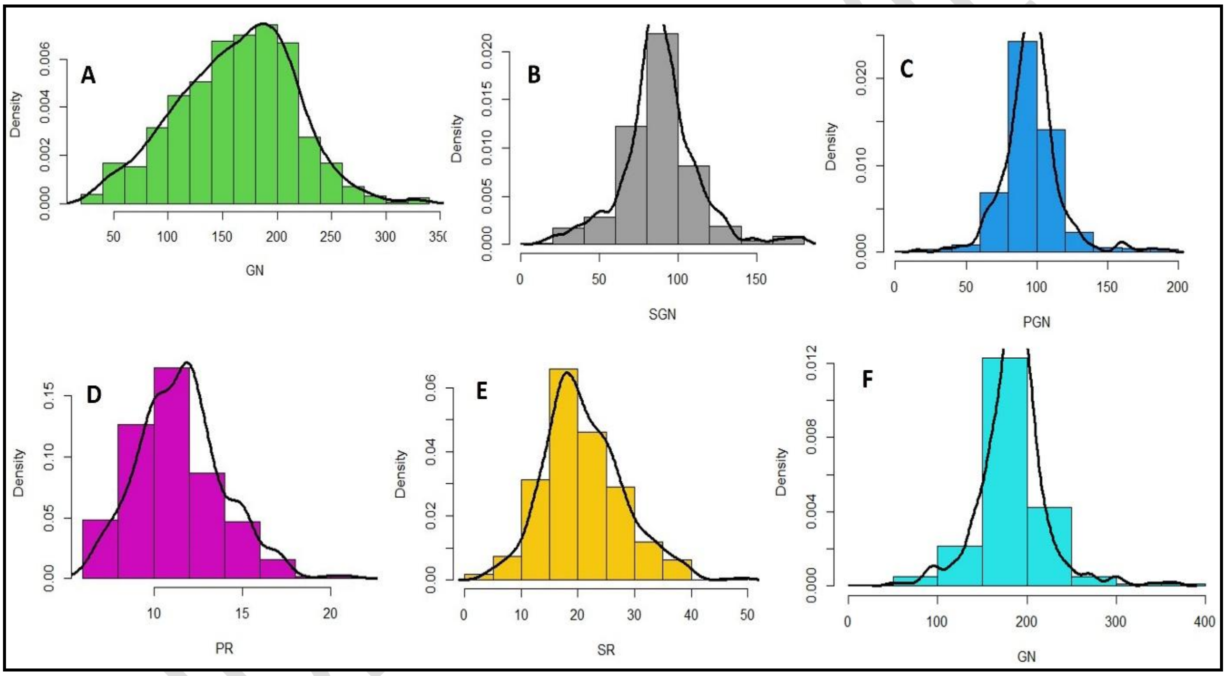

Figure. 1. Histogram for panicle traits in segregating populations from the cross of DRR Dhan 48/Maudamani. X-axis represents the trait and Y-axis represents the density of the population. (a) Normal distribution pattern for grain number in F_2 generation with positive skewness, (b) Number of grains on secondary branches per panicle in F_3 population, (c) Number of grains on primary branches per panicle in F_3 population, (d) Number of primary branches per panicle in F_3 population, (e) Number of secondary branches per panicle in F_3 population, (f) Total grain number per panicle in F_3 population.

Similarly, box plots revealed the extent of variability and distribution pattern for the studied panicle traits in F_2 and F_3 segregating generations (Figure 2). Median value for grain number concentrated at 170 to 180 with uniform distribution of the population in all the quartiles which indicated even distribution of events in the population (Figure 2A and Figure 2F). For primary rachis, medium value concentrated at 12 with restricted 3rd quartile (Figure 2B) and for secondary rachis at 20 with restricted 2nd quartile (Figure 2C). Again, in case of number of grains on primary and secondary rachis, population was uniformly distributed in all the quartiles with median value concentrated at 100 and 80 respectively (Figure 2D and Figure 2E).

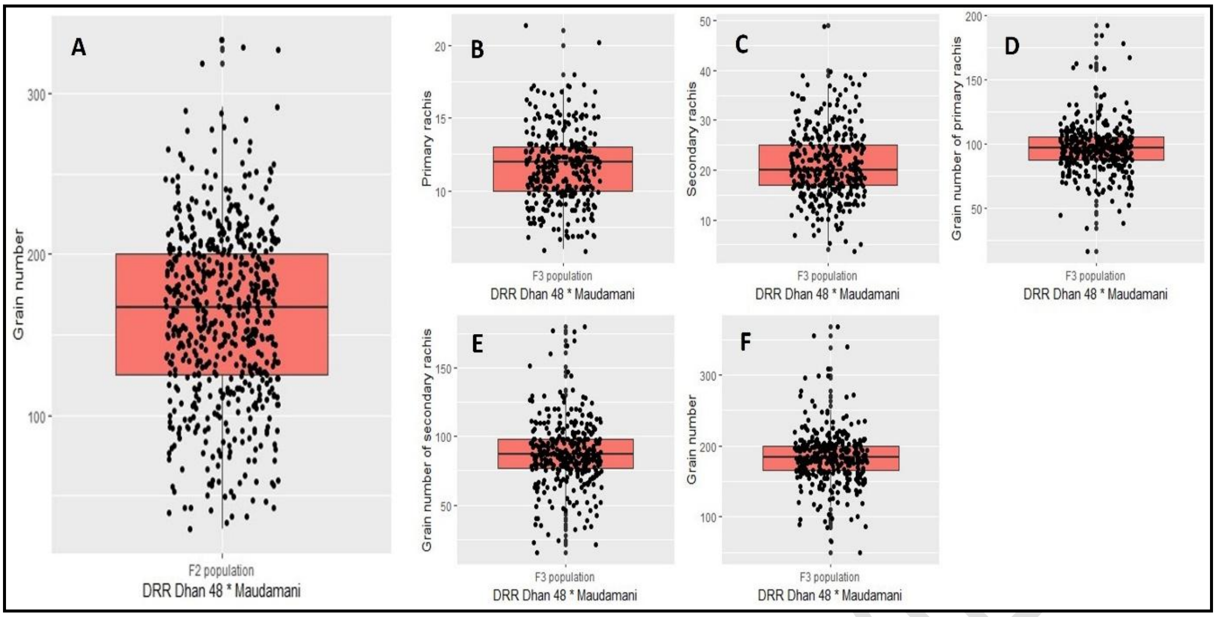

Figure. 2. Box plots showing variation for panicle architecture traits in in segregating populations from the cross of DRR Dhan 48/Moudamani. Box plot showing graphical representation of frequency distribution for each trait. The box indicating the existence of the 50% of the data within the box, the lower end of the box is 1st quartile (Q1), the upper end of the box is 3rd quartile (Q3) which shows the existence of the 25% of data above the Q3 and below the Q1, remaining 25% of the data is distributed, with solid line indicating the median value of the data distribution, the points above the outlier are the maximum value for the traits. The upper, median and lower quartiles represent the 75th, 50th and 25th percentiles of the genotypes, respectively. The vertical lines represent the variation in the population. Dots represent the outliers.

Corrplot depicted highly significant positive correlation among the panicle architecture traits (Figure 3). Among them, highest was observed between secondary rachis and grains on secondary rachis. While grain number has significant positive correlation with all the studies panicle architecture traits, it was highest with number of grains on primary rachis followed by number of grains on secondary rachis, secondary rachis and primary rachis. Grain number showed extremely significant positive correlations with primary branches (PB) and secondary branches (SB) representing that an increase in the number of PB and SB will increase the number of grains per panicle Deshmukh et al. (2010) [10]. Similarly, Rebolledo et al. (2016)[17] reported absolute positive correlation of grain number with number of primary and secondary branches in rice. However, the length of branches (PBL and SBL) was not significantly correlated with variables related to number of branches (PBN and SBN), suggesting independent genetic control.

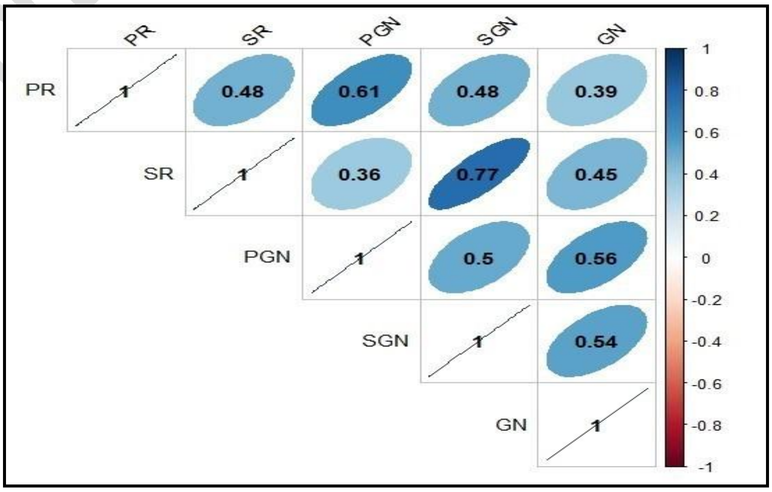

Figure. 3. Graphical representation of correlation coefficients among panicle architecture traits. Intensity of colour in each box represents the significance of correlation.

Presence of phenotypic extremes beyond the parental values revealed transgressive segregation for all the panicle traits studied. There were five superior transgressive segregants with higher value than parent ‘Maudamani’ for all studied panicle architecture traits. The percentage of transgressive segregation ranged from 0.42 to 56.6%. For grain number, there were 20 superior transgressive segregants over the better parent Maudamani. Presence of transgressive segregation indicated complementary effects of minor alleles from both parents for the panicle architecture traits in the present investigation. Similarly, Gunashekaran et al (2023) [39]reported newer stable genetic sources for high grain number with high additive gene effects for important panicle traits to exploit transgressive segregants. The present study demonstrates the ideal choice of the parents in the development of mapping population for panicle architecture traits as important loci from both the parents can be identified. The population is further advanced and genotyping combining advanced molecular tools like QTL seq and 1K RiCA platform and phenotyping is underway.

4.CONCLUSION

Rice panicle architecture is a key target of selection when breeding for yield and grain quality and it is one of the most important agronomical traits that directly contribute to grain yield in rice. High correlation exists between panicle traits and also there is highly significant variation between traits. More grain number on secondary rachis in a panicle leads to high grain number per panicle. Presence of superior transgressive segregants with complementary gene action for the panicle architecture traits validated the choice of parents DRR Dhan 48 and Maudamani for improvement of grain number in rice. This provides valuable information and resources for further unravelling the genetic basis determining rice panicle architecture.

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