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RESEARCH ARTICLE

Revealing the gene action of puffing-associated traits in rice (*Oryza sativa* L.) through generation mean analysis

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Abstract

Rice is the primary source of nutrition for billions of people and is one of the world's oldest and most significant staple foods. In addition to yield, it is equally essential to preserve quality. Puffed rice is a traditional, affordable and widely available prebiotic cuisine that stands out among the numerous rice-based products. A more profound comprehension of the genetic factors and physicochemical properties influencing puffing yield can significantly enhance production efficiency. The present study elucidates the genetics of 14 traits viz. days to initial flowering (DF), panicle length (PL), number of productive tillers per plant (NPT), number of filled grains per panicle (NFG), kernel length (KL), kernel breadth (KB), kernel L/B ratio (L/B ratio), plant height (PH), test weight (TW), single plant yield (SPY), puffing yield (PY), bulk density (BD), expansion volume (EV), expansion ratio (ER) by employing generation mean analysis in two crosses (Kuliyadichan × ASD 19 and ACK 15004 × Bhavani). The individual scaling and joint scaling tests were used to evaluate the adequacy of the additive dominance mode in addition to testing in the A, B, C and D scales. Epistatic interaction was observed for DF, PH, NPT, PL, NFG, puffing yield and KL of both crosses. Duplicate epistasis was predominant for the traits such as, PL, number of productive tillers, number of filled grains/ panicle, KL, L/B ratio, PH, TW, puffing yield and BD. Meanwhile, the traits such as KB and SPY showed complementary epistasis. Traits governed by epistatic gene action can be improved when the selection process is delayed until later generations are born. However, selection for traits governed by additive gene action can be effectively practised at the early breeding stages.

Keywords: additive; dominance; epistasis; gene action; puffing yield

Introduction

Rice, the heart of many meals around the globe, is more than just a food; it's a cultural icon that transcends borders and traditions, hence it is referred to as a global grain. It is a fundamental food source and a focal point of extensive research aimed at enhancing agricultural practices, improving food security and addressing nutritional needs. The world's top four rice producers are China (30 %), India (21 %), Indonesia (9 %) and Bangladesh (6 %) (1). In addition to production, quality research is also crucial, owing to its starch content, which is the most common dietary energy source and provides instant energy. Due to its high starch content, it is used to make various foods, including rice flour, rice flakes, canned rice, popped or puffed rice and fermented goods (2). One such product is puffed rice, a traditional, affordable, widely available prebiotic food (3). Puffed rice is an expanded breakfast cereal made from parboiled rice subjected to high temperatures for a short time. The physiochemical components include KL, BD, KB, starch polymorphism (SP), L/B ratio, amylose content, gelatinization temperature, gel consistency, EV and protein content. These components are either positively or negatively correlated with puffing yield (4). Hence, understanding the gene action of the puffing yield and the physiochemical components will help enhance the puffing yield (PY).

Materials and Methods

The experiment was conducted from late thaladi (October 2023) to the summer season (March 2024) at V.O.C. Agricultural College and Research Institute, Killikulam, Thoothukudi. The experimental materials were generated from the cross between the rice genotypes: Kuliyadichan x ASD 19 (cross I) and ACK 15004 x Bhavani (cross II). Among them, Kuliyadichan and ACK 15004 had low puffing yield, while ASD 19 and Bhavani exhibited high puffing yield (5). The puffing yield is the ratio of the weight of puffed rice obtained to the weight of the raw rice sample before puffing, which is expressed as a percentage (%). The parents and their F_1's were raised in the B block in October 2023. Each entry was transplanted in 2 rows of 3m length at 20 cm x 10 cm spacing in the main field, replicated four times in randomized block design (RBD).

True F_1's of these crosses were identified with the help of molecular markers such as RM225 and RM276 and advanced to F_2 by selfing. The backcross populations were developed by crossing the F_1s with the respective crosses' parents. A total of six generations for each two crosses were developed.

The phenotypic traits were assessed on the six generations for the fourteen traits namely, DF, PH, NPT, PL, NFG, TW, SPY, KL, KB, L/B ratio, BD, EV, ER and PY.

Statistical analysis

Generation mean analysis

For the two crosses, the mean values of P_1, P_2, F_1, F_2, BCP_1 and BCP_2 were computed for each of the six generations. The six generations' means are displayed in Fig. 1-4. The variance and the variance of the mean were also calculated for each of the six generations in the two crosses. The individual scaling tests (scale A, B, C and D) were used to evaluate the adequacy of the additive dominance model (6). The variances of the A, B, C and D were determined by calculating the corresponding variances of various generations. Data was also subjected to a joint scaling test in addition to testing on the A, B, C and D scales. The genetic effects were estimated by utilizing six-parameter models in the generation mean analysis if any scaling tests were significant (7). This approach was used to determine genetic parameters, including the mean (m), additive gene effects (d), dominance gene effects (h) and three types of non-allelic gene

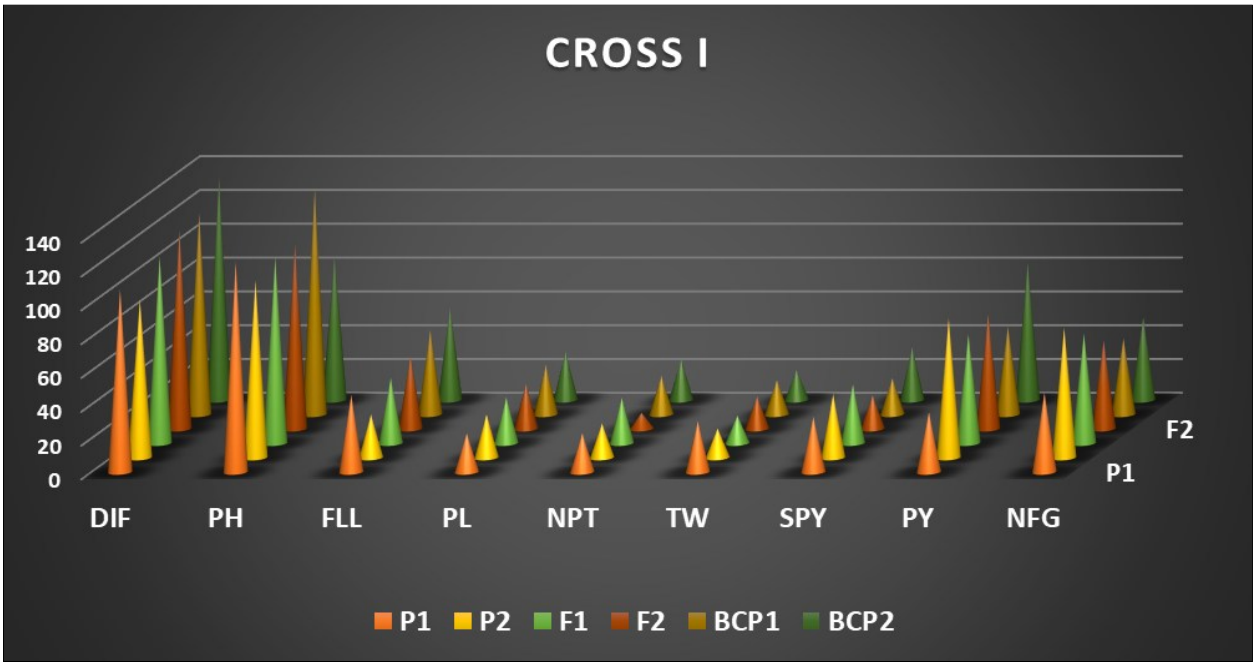

Fig. 1. Mean of six generations of cross I for traits viz. days to initial flowering, plant height, flag leaf length, panicle length, number of productive tillers per plant, test weight, single plant yield, puffing yield and number of filled grains per panicle.

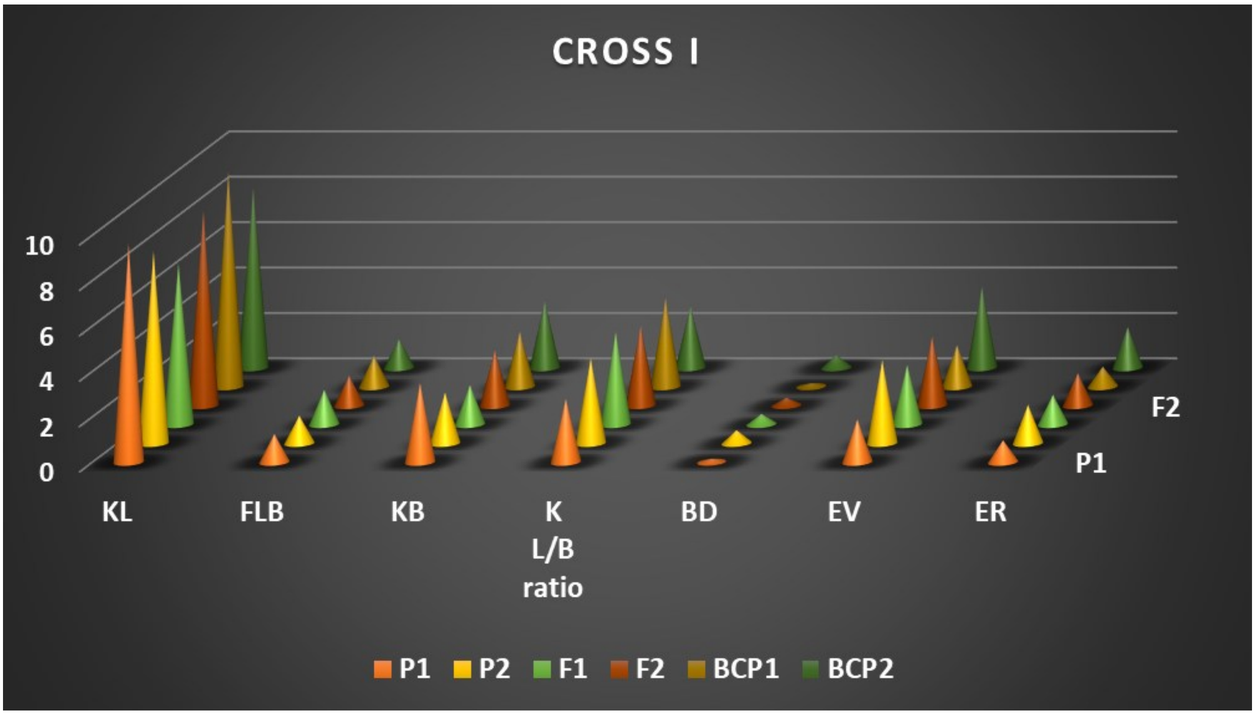

Fig. 2. Mean of six generations of cross I for traits viz. kernel length, flag leaf breadth, kernel breadth, kernel L/B ratio, bulk density, expansion volume and ratio.

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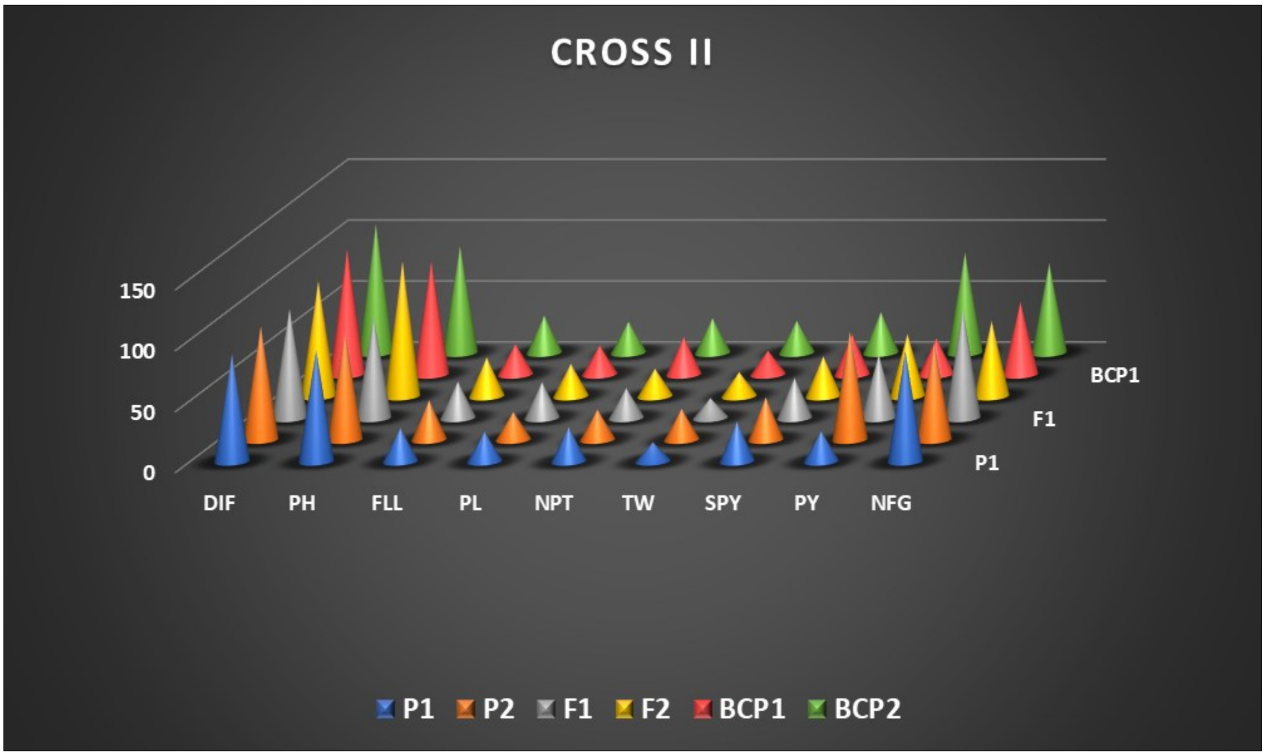

Fig. 3. Mean of six generations of cross II for traits viz. days to initial flowering, plant height, flag leaf length, panicle length, number of productive tillers per plant, test weight, single plant yield, puffing yield and number of filled grains per panicle.

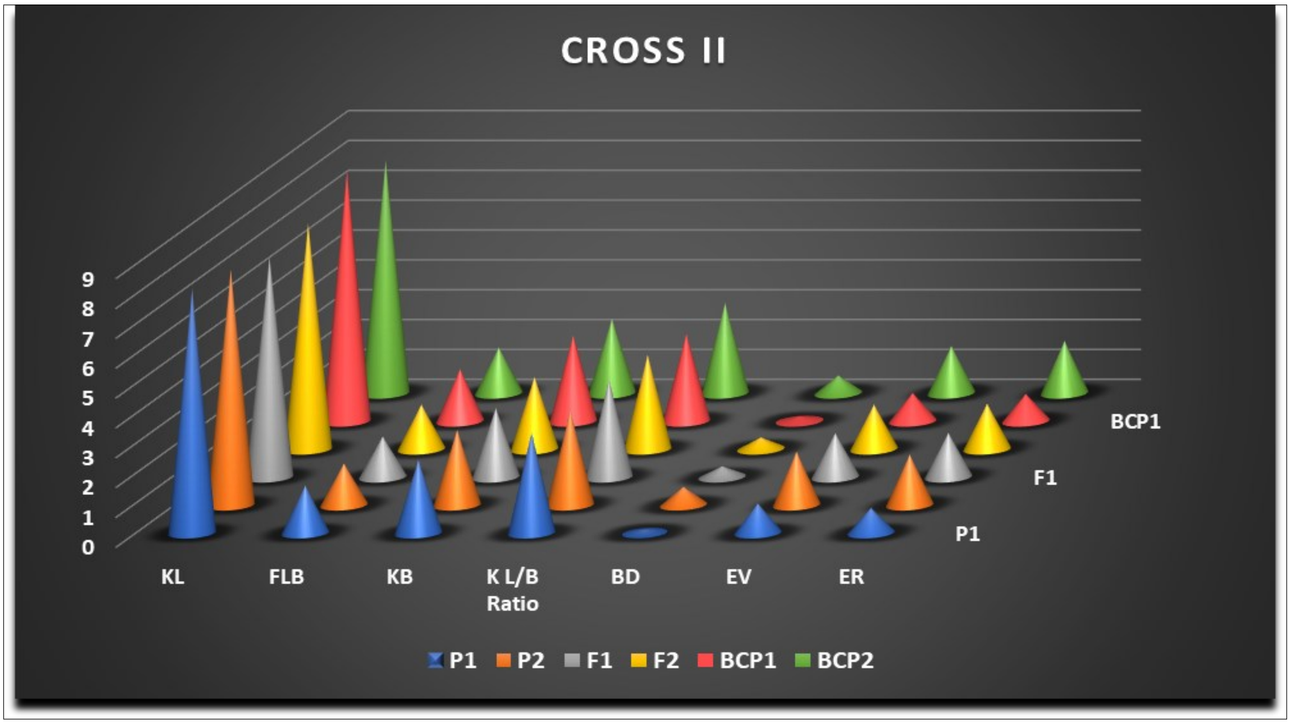

Fig. 4. Mean of six generations of cross II for traits viz. kernel length, flag leaf breadth, kernel breadth, kernel L/B ratio, bulk density, expansion volume and ratio.

interactions: additive x additive (i), additive x dominance (j) and dominance × dominance (l).

Results and Discussion

The presence of epistasis was investigated using the simple and joint scaling tests for the inheritance of the 14 traits subjected to the experiment. Both scaling tests had been used to determine whether epistasis is present in the inheritance of various traits in paddy (8, 9). The presence of epistasis was observed for all the traits except TW of cross I, SPY, KB, L/B ratio and BD of cross II and the EV and ER of both crosses (Table 1 & 2).

A six-parameter model was employed to identify further the kind of non-allelic gene interaction controlling the inheritance of the traits. Days to initial flowering were significantly positive for additive (d) gene action, followed by the negative significance of additive × dominant (j) gene action in cross I. Hence, this negative interaction (j) may hinder the selection process in cross I. A previous study also observed similar results of additive gene action for this trait (10). In cross II, the additive (d) gene action was negatively significant and the dominant (h) gene action was positively significant, followed by the negative significance of dominant × dominant gene action and

Table 1. Genetic parameters for puffing-associated traits in cross I (Kuliyadichan x ASD 19)

Traits	m	(d)	(h)	(i)	(j)	(l)	Scaling test			
							A	B	C	D
DF	68.351± 6.09	7.250* ± 0.37	151.964 ± 11.96	32.899 ± 6.40	-39.167* ± 1.46	-109.565± 6.03	*	*	-	-
PL	14.358 ± 1.49	-1.375 ± 0.29	36.146 ± 3.02	10.017 ± 1.57	4.083 ± 0.93	-23.340 ± 1.59	*	-	-	-
NPT	-34.669 ± 2.22	1.375 ± 0.33	114.713* ± 4.53	56.294*±2.33	-4.750 ± 1.50	-53.044*± 2.43	-	-	*	*
NFG	98.400 ± 8.87	-15.000*± 0.41	-135.800 ±17.38	-36.400±9.32	22.000* ± 1.63	102.400 ± 8.74	*	*	-	-
KL	13.346* ± 0.34	0.588 ± 0.11	-12.022 ± 0.68	-4.284 ± 0.36	1.558 ± 0.21	6.475 ± 0.37	-	*	-	-
KB	3.094* ± 0.13	0.625 ± 0.10	-0.831 ± 0.28	-0.219 ± 0.13	-1.583* ± 0.18	-0.429 ± 0.16	-	*	-	-
L/B ratio	4.170* ± 0.20	-0.480 ± 0.09	-2.480 ± 0.43	-0.880 ± 0.21	3.400* ± 0.22	2.400 ± 0.25	-	*	-	-
PH	111.680 ± 6.29	9.778* ± 0.46	-10.338 ± 12.32	3.097 ± 6.62	78.445* ± 1.03	8.858 ± 6.18	*	*	-	-
TW	24.080 ± 1.39	6.400* ± 0.24	-11.660 ± 2.82	-	-	-	-	-	-	-
SPY	9.627 ± 7.33	-2.364*± 0.23	15.836 ± 14.38	25.644 ± 7.71	-14.606* ± 1.35	9.510 ± 7.22	*	*	-	-
PY	64.703* ± 0.93	-23.509*± 0.42	13.366 ± 2.74	-5.587 ± 0.97	-11.249 ± 2.35	-13.424 ± 1.87	-	*	*	-
BD	0.344 ± 0.24	-0.211*± 0.01	-0.112 ± 0.48	0.030 ± 0.26	-0.404* ± 0.04	0.234 ± 0.24	*	-	-	-
EV	-2.330 ± 0.48	-0.888*± 0.11	10.107 ± 0.97	-	-	-	-	-	-	-
ER	8.156 ± 3.35	-0.365*± 0.02	-13.584 ± 6.55	-	-	-	-	-	-	-

Table 2. Genetic parameters for puffing-associated traits in cross II (ACK 15004 X Bhavani)

Traits	m	(d)	(h)	(i)	(j)	(l)	Scaling test			
							A	B	C	D
DF	52.467* ± 4.02	-2.500* ± 0.33	131.400* ± 7.56	38.700 ± 4.64	-0.500 ± 0.80	-93.867* ±4.12	*	*	-	-
PL	31.530* ± 2.73	0.750 ± 0.23	-17.100 ± 5.21	-7.780 ± 3.15	-4.800 ± 0.83	15.160 ± 2.71	*	-	-	-
NPT	-1.133 ± 4.09	1.667* ± 0.24	69.850 ± 7.75	27.800 ± 4.72	1.667 ± 1.07	-43.967* ±4.01	*	*	-	-
NFG	66.100* ± 4.32	6.000* ± 0.58	-40.700 ± 8.79	18.900 ± 4.98	-39.500* ± 2.39	64.600* ± 4.92	*	*	*	-
KL	5.946* ± 0.30	0.150 ± 0.06	5.093 ± 0.61	2.104 ± 0.35	0.900 ± 0.16	-3.674 ± 0.36	*	-	-	-
KB	1.302 ± 0.26	-0.035 ± 0.11	3.480 ± 0.52	-	-	-	-	-	-	-
L/B ratio	4.013* ± 0.36	0.093 ± 0.13	-2.634 ± 0.70	-	-	-	-	-	-	-
PH	173.100* ± 14.43	2.000 ± 0.58	-157.050 ±26.82	-83.100 ± 16.66	6.500 ± 1.57	66.300 ± 13.50	*	-	-	-
TW	8.650 ± 2.46	-4.783 ± 1.03	37.683 ± 4.98	12.167 ± 2.97	-3.633 ± 1.68	-29.833* ± 2.97	-	*	-	-
SPY	32.172* ± 3.12	-1.088 ± 0.42	2.133 ± 6.80	-	-	-	-	-	-	-
PY	37.587 ± 5.43	-31.995* ±0.92	39.957 ± 10.35	19.408 ± 6.72	-41.285* ± 2.12	-25.193 ± 5.63	*	*	-	-
BD	0.420 ± 0.08	-0.252* ± 0.02	-0.038 ± 0.17	-	-	-	-	-	-	-
EV	2.312* ± 0.13	-0.403* ± 0.03	-2.428 ± 0.33	-	-	-	-	-	-	-
ER	2.023* ± 0.18	-0.427* ± 0.04	-1.453 ± 0.41	-	-	-	-	-	-	-

these results were in accordance with the outcome of another study (11). Hence, the reciprocal recurrent selection would be employed to improve this trait.

The PH of cross I showed that the scales A and B were positively significant for additive (d) gene action, followed by the positive significance of additive × dominant (j) gene action in cross I. The magnitude of (j) was greater than the additive effect; hence, reciprocal recurrent selection will be employed for this trait. The results of another experiment also explained that the gene action of PH is governed by additive and dominance effects (12). This was reported earlier by several other studies (10, 11, 13-15).

The combined effect of (h) and (l) was higher than the fixable interaction (i) for the number of productive tillers per plant. The additive, dominance and epistatic gene effects are harnessed by reciprocal recurrent selection, which helps the improvement of this trait in cross I. It had been previously reported in other studies (11, 16). In cross II, the additive (d) gene action and the negative significance of dominance x dominance (l) gene action may hinder selection. This result of the cross II was in accordance with the findings of other experiments (14, 17-20).

The PL of both crosses exhibited the significance of scale A, indicating epistatic interaction for this trait, but no significant epistatic effect was observed. Another study also observed that the gene effects, viz. additive (d), dominance (h) and additive x additive (i) genetic effects did not contribute to the expression of PL (21).

In both crosses, the magnitude of (l) was higher than the additive effect, stating that reciprocal recurrent selection or random mating would be favorable for improving the NFG. These results closely resemble the outcome of previously conducted experiments (11, 12, 15, 17, 22, 23).

Additive (d) gene action was observed for TW. Hence, it is considered a fixable trait and a simple selection techniques or hybridisation followed by pedigree breeding is suggested to improve this trait. Other studies also reported similar results of TW being governed by additive gene action (10, 11, 13, 22, 24). Moreover, it was also noted that the inheritance of TW was governed by epistatic gene action (25).

The additive (d) gene action and the additive x dominant (j) gene action were negatively predominant for SPY in the study, as reported earlier by other investigators (10, 13, 14, 17, 26-28). Hence, the negative interaction of (j) over the adverse additive effect may hinder the selection process. In case of cross II, all the scales were non-significant, denoting the absence of epistasis for this trait.

The scales B of cross I and A of cross II were significant for indicating epistatic interaction. Non-allelic interaction for KL has also been observed (29) and it has been noted that most grain quality traits are governed by additive, dominance and epistatic interaction (30). For KB, significance was found with scale B of cross I and the additive × dominance (j) type of gene action; a similar observation was reported in an earlier study (31). Both the additive and dominant gene action were non-significant for KB in cross II, which was in accordance with the findings of another study (15). The genetic parameter additive x dominance (j) type of gene action alone was positively significant for the L/B ratio. This implied that this trait would be improved by postponing the selection for later generations to get the desired type of segregants.

In both crosses, the negative fixable gene action (d) and the negative influence of (j) were observed, indicating that selection has to be postponed for later generations to improve BD. In both crosses, all the scales were non-significant, evidencing the absence of epistatic effect over the trait EV, which was concurrent with the findings of a previously conducted study (16). Only the additive (d) gene action in both crosses was negatively significant for the ER. Hence, selection has to be delayed for the subsequent generations. The additive (d) gene action was negatively significant for the puffing yield in cross I, but in cross II, the negative significance of additive gene action and the negative additive x dominance gene action indicated the negative interaction of (j) over the additive effect and it hindered the selection process. To exploit these types of gene action in both crosses, selection in later generations would be beneficial to improve this trait.

The estimates of components of genetic variance indicated that duplicate epistatic (15:1) interaction (h and l having opposite sign) was predominant for the traits such as DF, PL, number of productive tillers, number of filled grains/ panicle, KL, L/B ratio, PH, TW, PY and BD. These results were similar to those of other studies (11, 26, 32, 33). It was also reported that the PL was governed by duplicate epistasis (34). Meanwhile, the traits such as KB and SPY showed complementary epistasis (9:7) (h and l having the same sign). These findings corresponded with one study (15) while contradicting the other (35).

Conclusion

Most of the traits included in this study are controlled by epistasis. Hence, some traits, such as DF of cross II, PH and NPT of cross I, NFG of both crosses, can be improved by reciprocal recurrent selection based on their gene action, but some traits, such as DF of cross I, L/B ratio, BD, ER and EV, are improved by postponing the selection to later generations. The genetic analysis indicates that additive gene action negatively impacts puffing yield in both crosses, making the early-generation selection less effective. Understanding gene action will help breeders improve the trait effectively. The features that demonstrated complementing epistasis can be utilized as a metric to evaluate the selected plant's genetic value for future development. However, selection procedures will be ineffective in improving a trait that exhibits duplicate epistasis or a high number of epistasis for that characteristic.

Authors' contributions

SJH and MAP conceived this review. SB, SJH, AKP and RV wrote the manuscript and SA and JRJ reviewed it. MT edited the manuscript. All authors have read and approved the final version.

Compliance with ethical standards

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

Ethical issues: None

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