GENETICS OF SHATTERING RESISTANCE IN RICE (*Oryza sativa* L.)

By

AKHIL K. P.

(2018-11-032)

Department of Plant Breeding and Genetics

COLLEGE OF HORTICULTURE

VELLANIKKARA, THRISSUR – 680656

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DECLARATION

I hereby declare that this thesis entitled **"Genetics of shattering resistance in rice (*Oryza sativa* L.)"** is a bonafide record of research work done by me during the course of research and that the thesis has not previously formed the basis for the award of any degree, diploma, fellowship or other similar title, of any other University or Society.

Vellanikkara

Date : 16-12-2020

AKHIL K. P.
(2018-11-032)

CERTIFICATE

Certified that this thesis entitled **"Genetics of shattering resistance in rice (*Oryza sativa* L.)"** is a bonafide record of research work done independently by **Mr. AKHIL K. P. (2018-11-032)** under my guidance and supervision and that it has not previously formed the basis for the award of any degree, diploma, fellowship or associateship to him.

Vellanikkara

Date : 16-12-2020

Dr. S. Biju
Assistant Professor
Department of Plant Breeding and Genetics
College of Horticulture, Vellanikkara.

CERTIFICATE

We, the undersigned members of the advisory committee of **Mr. AKHIL K. P. (2018-11-032)**, a candidate for the degree of **Master of Science in Agriculture** with major field in Plant Breeding and Genetics, agree that this thesis entitled **"Genetics of shattering resistance in rice (*Oryza sativa* L.)"** may be submitted by **Mr. AKHIL K.P.** in partial fulfillment of the requirement for the degree.

Dr. S. Biju
Assistant Professor
Department of Plant Breeding and Genetics
College of Horticulture, Vellanikkara

Dr. Jiji Joseph
Professor and Head
Department of Plant Breeding and Genetics
College of Horticulture, Vellanikkara

Dr. T. Girija
Professor and Head
Department of Plant Physiology
College of Horticulture, Vellanikkara

Dr. Dijee Bastian
Professor
Department of Seed Science and Technology
College of Horticulture, Vellanikkara

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Introduction

1. INTRODUCTION

Rice the most important food crop of the world feeds more than half the population. It is the staple food across Asia where the world's poor people live and it is becoming increasingly important in Africa and Latin America. It is spectacularly diverse, both in the way it is grown and how it is used by humans. Rice is unique because it can grow in wet environment that other crop cannot survive. Cultivated rice originated from *Oryza rufipogan* (Fuller, 2007). Domestication of rice is considered as one of the most important developments in history and now thousands of rice varieties are cultivated on every continent except Antarctica. *Oryza sativa* and *Oryza glaberrima* are two important popular rice species cultivated in different parts of the world. Among these, *O. glaberrima* is cultivated only in parts of West Africa while *Oryza sativa* is grown in all other regions.

Rice feeds more than 60 per cent of the Indian population. The area under rice in India increased from 30.81 mha in 1950-51 to 44 mha in 2017-18 .Yield per hectare increased from 668 kg/ha in 1950-51 to 2665 kg/ha in 2019. A record total production of 117.47 million was reported during the year 2019-20 which was 9.67 million tons higher than the five years' average production of 107.80 million tonnes. In India, major share of rice production is from kharif season. In Kerala rice occupies 7.46 per cent of the total cropped area. Productivity of the crop in the state is very low (2790 kg/ha). The state is currently a major importer of rice as it is the staple food of the region hence there is an urgent need to enhance the production potential of the crop.

Elimination of seed shattering was a critical evolutionary step during rice domestication, as easy shattering will cause major loss in productivity. Varieties that shatter easily are not ideal for use by farmers as shattering reduces yield under all type of harvesting practices (Li and Gill, 2006). In rice breeding seed shattering remains an important target trait, particularly in *Indica* type. It is an important trait that distinguishes plants from their wild and weedy counter parts. This trait is essential for seed harvesting in the production of cereal crops, and therefore has attracted great attention of scientists to study the underlying genetic mechanism of seed persistence/shattering during crop domestication (Yao *et al.*, 2015).

Apart from the steady reduction in the land area under rice cultivation, losses of grains in the field as well as during post-harvest transport are considered as major reasons for reduced production. The degree of shattering can be categorized into several types like easy-shattering, moderate shattering, and hard or non-shattering. It is an important parameter when selecting mechanical harvesting methods to prevent loss of yield during harvest. For the past few years in Kerala, most of the cultivation practices have been mechanized. Due to scarcity of farm labour as well as high efficiency of machines, in near future the entire rice cultivation and harvesting operations will be done by farm machines. In such a situation plants with moderate or medium shattering habit will be more preferable than shattering habit for combine harvester.

In early shattering varieties, harvest loss occurs in the process of reaping and conveying the plant to the threshing section of the machine apart from field loss. On the other hand, in hardy shattering varieties grains may not be removed completely from the panicle. Though there are a number of high yielding rice varieties in Kerala, the post-harvest loss is still a major factor in reducing yield. One of the major disadvantages of Jyothi, the most popular high yielding rice variety of the state is the increased shattering of grains at maturity.

Rice genotypes shows wide variability in response to seed shattering hence; transferring shattering resistance to high yielding varieties and studying the inheritance of seed shattering trait may contribute to planning and executing breeding strategy there by leading to their genetic improvement. Reducing seed shattering in rice can save valuable resources and improve the productivity of rice in Kerala.

With this background the present work is taken up with the following objectives

1. To transfer shattering resistance to popular rice varieties

2. To understand the genetics of shattering resistance

Review of Literature

2. REVIEW OF LITERATURE

The available literature on origin, dispersal, cultivation and variation of rice, character association, mode of inheritance and methods to evaluate shattering are presented in this chapter.

2.1 Origin, dispersal and domestication of rice germplasm in relation to grain shattering

2.2 Genetic parameters

2.3 Gene associated to grain shattering and character association

2.4 Mode of character inheritance

2.5 Methods to evaluate shattering

2.1 Origin, dispersal and domestication of rice germplasm in relation to grain shattering

There are two cultivated and twenty-one wild species of genus Oryza. *O. sativa*, the Asian cultivated rice is grown all over the world while the African cultivated rice, *O. glaberrima* is grown on a small scale in West Africa. The genus *Oryza* probably originated about 130 million years ago in Gondwanaland and different species got distributed into different continents with the breakup of Gondwanaland. The cultivated species originated from a common ancestor with AA genome. Perennial and annual ancestors of *O. sativa* are *O. rufipogon* and *O. nivara* and those of *O. glaberrima* are *O. longistaminata*, *O. breviligulata* and *O. glaberrima* probably domesticated in Niger river delta. Varieties of *O. sativa* are classified into six groups on the basis of genetic affinity. Widely known *indica* rice correspond to group I and *japonica* rice to group VI. The so called *javanica rices* also belong to group VI and are designated as tropical japonicas in contrast to temperate *japonicas* grown in temperate climate. *Indica* and *japonica* rice had a polyphyletic origin. *Indicas* were probably domesticated in the foothills of Himalayas in Eastern India and *japonicas* somewhere in South China. *Indica* rice is dispersed throughout the tropical and subtropical regions of India. It is estimated that about 120000 varieties of rice exist in the world (Khush, 1997).

Plants during development shed leaves, flowers, fruits, or seeds resulting from cell expansion and separation in the abscission zones. These are considered as the general adaptation in plants (Roberts *et al*., 2002)

A study by Thomson *et al*. (2003) in advanced backcross population between an accession of *Oryza rufipogan* (IRGC 105491) and the US cultivar Jefferson (*O. sativa* SSP Japonica) were developed by revealed That QTLs for plant height, shattering, tillering type and awns were found clustered on chromosome 1 and 4 and these morphological traits were related to the domestication process.

2.2 Genetic parameters

Padmaja *et al*. (2008) studied the genetic variability, heritability and genetic advance of 150 rice genotypes for eleven characters. Significant variance was observed for all characters except leaf width and 100 seed weight. Almost all characters recorded high GCV and PCV. They also reported high heritability coupled with high genetic advance for all characters except days to 50% flowering and panicle length. Leading to the conclusion that these characters are controlled by additive gene action.

Bisne *et al*. (2009) conducted an experiment with eight testers, four CMS lines and thirty two hybrids and estimated genetic parameters for yield and its corresponding characters for thirteen characters related to yield in rice. High heritability and high genetic advance was observed in characters like harvest index, total numbers of filled spikelet per panicle, 100 grains weight and spikelet fertility percentage. Direct selection may be effective for these characters since characters showed high heritability and high genetic advance.

Fukrei *et al*. (2011) evaluated 21 upland rice genotypes for yield and yield components. All the traits studied were observed to have high genetic variability. The characters, plant height, flag leaf area, number of tillers per plant, number of ear bearing tillers, number of filled grains per panicle, root length, panicle weight, straw weight and grains yield recorded high GCV. Grain yield per plant and panicle weight had high broad sense heritability coupled with high genetic advance as per cent of mean. They concluded that this could be used as a selection criteria for improving upland rice grown in acid soils.

Singh *et al*. (2011) evaluated 81 rice genotypes for 13 quantitative traits to assess the genetic variability. A wide range of significant variation was observed in all characters except flag leaf width. The characters like number of spikelet per panicle, number of productive tillers per plant, grain yield per plant and harvest index exhibited high GCV and PCV. Biological yield per plant had high broad sense heritability and number of spikelet per panicle recorded high heritability with high genetic advance.

To study the genetic variability, heritability and genetic advance Yadav *et al*. (2011) evaluated 40 rice genotypes for harvest index, seed yield, number of spikelets per panicle, biological yield, plant height, flag leaf length, and number of tillers per plant. High heritability with high genetic advance was observed for Harvest index, seed yield, biological yield, number of spikelet per panicle and flag leaf length.

Dhanwani *et al*. (2013) evaluated rice genotypes for 19 qualitative traits and 13 quantitative traits for variability, heritability and genetic advance. Grain yield per plant, number of grains per panicle, gel consistency, alkali spreading value and water uptake recorded high GCV and PCV. Characters like kernel length, length of brown rice, L/B ratio of brown rice, paddy length, alkali spreading value, plant height, days to 50 per cent flowering, spikelet sterility percentage and grain yield per plant recorded high heritability. The character biological yield, grain yield per plant, alkali spreading value and gel consistency were observed to have high genetic advance.

Subudhi *et al*. (2013) analyzed 55 rice germplasm accessions collected from tribal dominated area of Orissa and Cuttack for 16 quantitative characters according to IRRI descriptor of rice. Significant variation was recorded for the characters evaluated. Leaf length varied from 30.7cm to 73.6 cm whereas 90.5cm to 184.4cm variation were reported for culm height, 8.9 to 20 in culm number and 22.2 to 32.06 cm in panicle length. The genotypes Chhotbasmati, Lajkuri, Pimpudibas, Kanika, Jaigundi and Bishnubhig were selected based on the results for further rice breeding programmes.

A wide range of variation was observed in rice genotypes for the characters; plant height, number of grains per panicle, days to 50 per cent flowering, 1000 grain weight, grain width and grain yield, in a study conducted by Islam *et al*. (2015). They evaluated 23 rice genotypes and studied genetic variability, heritability and genetic advance. They concluded that selection for the characters like number of grains per panicle, days to 50 per cent flowering and days to maturity could improve yield.

Mamata *et al.* (2018) evaluated F_2 populations of rice of the crosses Rajamudi X BR 2655 and Rathnachoodi X BR 2655 with 500 single plants. Grain yield per plant showed high PCV and GCV values whereas low PCV and GCV were observed in panicle length and 1000 grain weight. Characters such as spikelet fertility, plant height, and grain yield per plant and harvest index had high heritability with high genetic advance. Their findings revealed that additive genes controlled these characters and direct selection can improve the characters in rice.

Job (2018) studied variability among twenty five rice genotypes for yield and yield attributes. High heritability accompanied with high genetic advance as per cent of mean indicating the influence of additive gene action in the expression of trait were observed for days to fifty per cent flowering, flag leaf width, flag leaf length, panicle per plant, seed yield per plant and shattering per cent. Tillers per plant recorded moderate heritability coupled with high genetic gain implying the influence of both additive and non additive gene action in the expression of these characters.

2.3 Gene associated to grain shattering and character association

During the process of domestication non-shattering nature must have been unconsciously selected in rice. Using 125 recombinant inbred lines obtained from a cross between cultivated and wild rice strains Cai and Moroshima (2000) conducted a study to detect the genomic regions associated with shattering and dormancy. Simple interval mapping and composite interval mapping were used for QTL analysis and they mapped a total of 147 markers on 12 rice chromosomes. They concluded that the shattering QTLs and dormancy QTLs are linked in several chromosomal region.

Ishikawa *et al*. (2010) carried out a QTL analysis using BC2F1 backcross population between *O. sativa* CV Nipponbare (recurrent parent) and *O. rufipogan* acc W630 (donor parent) to understand the genetic control of shattering in rice. They could detect two strong QTLs on chromosome 1 and 4 which were identical to major seed shattering loci, qsH1 and sh4, respectively. Using BC_4F_2 and BC_4F_3 population the allelic interaction at these two loci were examined and they observed that the wild qsH1 allele has stronger effect on seed shattering than of sh4. They could also observed that backcross plants shed all the seeds, which having Nipponbare homozygous allele at shattering locus (qsH1, sh4). They concluded that , it's not a single mutation in the genetic background of wild rice that cause seed shattering and there are also some minor genes which are associated with formation of abscission layer there by enhance seed shattering.

Akasaka *et al*. (2011) conducted an experiment using weedy rice accessions and rice cultivars from Okayama, Japan. Their aim was to identify the molecular nature of seed shattering habit of weedy rice *Oryza sativa* L. in Okayama. They carried out time course change in seed shattering degree, histological analysis of pedicel structure and also genotyping of qsH1 and sh4 regions both in weedy rice and rice cultivars. Both weedy rice and cultivars showed decreased breaking tensile strength simultaneously at 21 days after heading. But complete loss of breaking tensile strength and grain dispersal were observed in weedy rice after 35 days after heading, whereas cultivars maintained the

BTS and didn't dispersed grains. They observed difference in pedicel structure between weedy and rice cultivars which affects BTS complete and cracked abscission layer was obtained in weedy rice and incomplete and uncracked in cultivars. But the grains qsH1 and sh4 which influenced the formation of abscission layer were identified in both weedy rice and cultivars. So they finalize that some unidentified shattering related genes also mediates the formation and degeneration of abscission layer in weedy rice from Okayama.

In order to establish the morphological basis of parallel evolution of seed shattering in weedy rice and wild rice Thurber *et al*., (2011) examined abscission layer at flower pedicel junction in weedy individuals in comparison with wild and cultivated relatives. A clear and well defined abscission layer was observed in shattering wild rice individuals whereas definite abscission layer was absent in non-shattering individuals. The abscission layer has formed prior to flowering in weedy rice and degrades at flowering stage. But abscission layer have been shown not to degrade after flowering in wild *O.rufipogan*. They suggested that unidentified regulatory genes may play a critical role in reacquisition of shattering in weedy rice.

Nunes *et al*. (2012) conducted an experiment using weedy rice accessions AV31 and AV60 and the rice cultivars Lacassije and Batatais to obtain gene expression related to seed shattering. Rice cultivars and weedy rice accessions didn't showed any difference in breaking tensile strength (BTS) at 10 days after pollination. But cultivated rice showed high BTS value at seed physiological maturity whereas weedy rice showed low BTS value. Nucleotide composition and gene expression studies 10 days after pollination revealed that the two major seed shattering genes qsH1 and sh4 were not important in weedy rice. They observed that seed shattering in weedy rice is positively associated with high expression of the gene OsCPL1. Further analysis reported that the genes OsXTH8 and OsCe19D which are related to cell wall synthesis/degradation plays an important role in seed shattering in rice.

Zhou *et al*. (2012) carried out an experiment with introgression lines in rice to study genetic control of seed shattering in rice. They introgressed chromosome 4 of shattering donor parent *O*. *rufipogan* W1943 into the reduced shattering recurrent parent *O*. *sativa* ssp *indica* cv GLA 4 in order to explore the seed shattering regulation pathway. The chromosome 4 substituted line SL4 showed very easy shattering. Analysis of seed shattering abortion mutants in wild rice introgression lines showed that an APETELA2 transcription factor encoded by SHAT1 gene is required for seed shattering in rice by the development of abscission zone. Genetic analysis reported that the SH4 gene positively regulates the expression of SHAT1 in AZ. They also noticed non-shattering feature in frame shift mutants in SH4. Their results revealed that active SHAT1 and SH4 is important in abscission zone development and seed shattering in rice.

Inoue *et al*. (2014) conducted on experiment to analyze seed shattering in rice using *Oryza sativa Nipponbare* and wild rice *Oryza rufipogan* W630 as parents. They observed that qsH3 locus is localized in an 850kb region on chromosome 3 through fine mapping of qsH3 region. Two types of introgression line independently carrying the *Nipponbare* homozygous alleles at sh4 or qsH3 in the genetic background of wild rice didn't show any change in seed shattering behaviour. But a reduction in the degree of seed shattering was reported in the introgression line having the *Nipponbare* homozygous allele at both qsH3 and sh4. Histological and scanning electron microscopy analysis in these lines revealed that abscission layer formation was inhibited around the vascular bundles. They concluded that the interaction of mutations at qsH3 region as well as sh4 region may have played a major role in domestication of rice with reduced seed shattering.

Kwon *et al*. (2015) developed twelve hybrid seeds by crossing *O*. *sativa* var. Iipoombyeo and *O*. *rufipogan* W259 in order to analysis seed shattering genes in rice. $F_{3:4}$ plants were analyzed to study seed shattering. Complete seed shattering was observed in wild species *O*. *rufipogan* whereas *O*. *sativa* showed resistance to seed shattering. Highly variable seed shattering degree were observed in 743 $F_{3:4}$ plants. Out of 743 plants 436 plants showed 0-5% shattering, 35 showed complete shattering and remaining were observed to have varying shattering from 5-95%. By genetic analysis of these $F_{3:4}$ population they reported that the sequence CACTA-AG 199 was associated with shattering trait CACTA-TD found in the qsH1 region of chromosome 1.

Yao *et al.*(2015) identified three QTLs, wd-qsh1, wd-qsh3 and wd-qsh5, when they analyzed F_2 population derived from cross between a strong seed shattering weedy rice accessions WD1292 with a non-shattering rice variety Minghui 86 (MH86). Based on microsatellite (SSR) variation pattern of the F2 individuals they could locate wd-qsh1, wd-qsh3 and wd-qsh5 on chromosome 1, 3 and 5 respectively. The same mutational seed persistent type of SH4 gene was detected in both the parental lines, which reveals that it has no role in seed shattering in weedy parent WD1292. Among three QTLs identified largest contribution to seed shattering was recorded for wd-qsh3. It contributes to 31.41% of total phenotypic variation. They also found that the three QTLs identified had no overlapping with major shattering loci, SH4, qSH1, sh-h, and SHAT 1, which were previously reported.

Sun *et al*. (2016) carried out an experiment with recombinant inbred line (RILs) and Near isogenic lines (NILs) population developed from the cross between cultivar R1126 (medium - grain) and CDL (big grain). They studied about grain shape, panicle length and seed shattering in rice. They reported a noval gene Panicle Traits 2 (PT2), from *Indica* rice Choundali (CDL). Cloning and functional analysis of PT2 showed that the gene is synonymous to a growth regulating factor 4 (OsGRF4) gene which encodes growth regulating factor. This factor positively regulates panicle length but negatively regulates seed shattering. Large grain, longer panicle and lower seed shattering were correlated with high expression OsGRF4 gene. It was also reported that OsGRF4 gene enhance increased cytokinin level since it regulates cytokinin dehydrogenase precursor genes. The detected high storage capacity associated with moderate seed shattering by OsGRF4 gene could be useful in rice breeding programme to reduce the yield loss.

Yoon *et al*. (2017) used T-DNA tagged Japonica rice Dongjin to study seed shattering. They determined that in addition to qsH1 and SH5 genes a Knox protein encoded by OSH-15 gene also regulate the grain shattering in rice. Also observed that osh-15 mutant showed reduced seed shattering phenotype. The high breaking tensile strength of the pedicel, which represents non seed shattering , were observed in mutant cultivar than Dongjin wild type. They generated transgenic plants expressing OSH-15 RNA interference (RNAi) in *Indica* CV Kasalath to confirm that the mutant phenotype was due to defect in OSH-15. All the transgenic plants showed reduced seed shattering than parental and segregating wild type plants. RNAi plants showed low abscission zone development when they observed longitudinal section of mature spikelets. The mutants also showed accumulation of lignin in internodes. Chromatin immune-precipitation assay demonstrated that CAD2 gene, which cause easy shattering by reducing lignin deposition in AZ, influenced both OSH-15 and SH5. They concluded that the dimer formed by OSH-15 and SH5 inhibit lignin biosynthesis genes and enhances seed shattering.

Job (2018) recorded highly significant correlation of seed yield per plant with number of tillers per plant, flag leaf width, number of panicles per plant and seeds per panicle and significant correlation with test weight. Shattering per cent recorded high significant inter correlation with panicle length and kernel length. Four selected shattering resistant rice genotypes were crossed in Line x Tester pattern with three shattering prone high yielding varieties. All the twelve hybrids were reported with high significant heterobeltiosis for plant height, flag leaf width, panicles per plant, panicle length, test weight, kernel width, kernel length and shattering per cent.

2.4 Mode of character inheritance

Nayak *et al*. (2007) carried out an experiment with four crosses between four scented (Basmati bahar, Kasturi, Muskbudhi and Kalimochi) and one non scented (Ratna) rice genotypes. They evaluated six populations (P_1, P_2, F_1, F_2, BC_1 and BC_2) to study the genetics of yield and yield components. Ten characters *viz*. days to 50 per cent flowering, plant height, panicle number per plant, panicle length, number of grains per panicle, 1000 grain weight, grain length, length by breadth ratio and grain yield per plant were evaluated. Ten plants randomly selected from P_1, P_2, F_1, F_2, BC_1 and BC_2 population and 30 plants of F_2 population of each cross were analyzed for ten characters. To test the adequacy of additive-dominance model they applied joint scaling test proposed by Caveli (1952). To know the adequacy of the model they carried three, five and six parameter model generation mean analysis. For analysis of days to 50 per cent flowering, panicle number per plant and grain length they reported that simple three parameter model was adequate. For almost all the characters five and six parameter model were fitted. In most of the crosses dominance effect were more important than the additive effect. With an exception of panicle length in cross Muskbudhi x Ratna, in which complementary type of epistasis and duplicate type of epistasis was observed. They suggested that to improve the grain yield and other attributes in scented rice recurrent selection or diallele selective mating seems to be the best method.

Roy and Senapati (2011) conducted an experiment with five diverse rice genotypes, IET6441, IET8002, Dudheswar, Basmati 385 and Sambamahsuri. Using these genotypes they evaluated three crosses namely IET6441 x Dudheswar, IET8002 x Basmati 385 and IET8002 x Sambamahsuri. Using six parameter model (Parents, F_1, F_2, BC_1 and BC_2) of generation mean analysis they studied nature of gene interaction in the inheritance of sixteen yield and seven grain quality traits. All the characters except florets per panicle, grain length, cooked kernel breadth and cooked kernel L/B ratio in IET6441 x Dudheswar, grain yield per plant in IET8002 x Basmati 385 and cooked kernel length in IET8002 x Sambamahsuri showed significance for additive gene effect whereas the characters except days to 50 per cent flowering, panicle length, florets per panicle and kernel length in IET6441 x Dudheswar showed dominance gene action. In the cross IET8002 x Basmati 385 dominant gene effect was observed in the characters except for total tillers per plant, productive tillers per plant, panicle length, florets per panicle, filled grains per panicle, floret fertility, 1000 grain weight, grain yield per plant, harvest index and cooked kernel L/B ratio. They also reported that duplicate epistasis plays an important role in the inheritance of almost all the yield and quality related traits in

IET6441 x Dudheswar, except for days to 50 per cent flowering, panicle length, florets per panicle and kernel length.

Srivastava *et al*. (2012) conducted an experiment to study the genetics of yield and yield components in aromatic rice. They evaluated parental, F_1, F_2, BC_1 and BC_2 generations of five crosses involving indigenous aromatic rice cultivar and subjected to generation mean analysis to study the gene actions of seven yield and its component traits. Dominance (h), additive x additive and dominance x dominance gene effect was significant for the entire yield traits studied. Dominant gene action was observed for 100 seed weight and additive x additive and dominance gene action for plant height and yield per plant. Plant height and panicle length was showed significant additive x dominance gene action. They reported additive and dominance gene action as well as epistatic interactions for all the yield traits which indicates the complex inheritance of the traits. Additive gene effect could be exploited using pedigree method of selection. They suggested diallel selective mating and reciprocal recurrent selection for simultaneous exploitation of both additive and non-additive gene effects for improving the traits.

Chamundeswari *et al*. (2013) made three crosses *viz*. BPT5204 x MTU1081, MTU1010 x TGL13595 and NLR34449 x MTU1075 with an aim to study non allelic components in rice. They evaluated six populations (P_1, P_2, F_1, F_2, B_1 and B_2) of the three crosses to understand the inheritance of seven yield and yield contributing characters. The seven characters were, days to 50 per cent flowering, plant height, number of tillers per plant, number of panicles per plant, panicle length, 1000 grain weight including grain yield per plant. Randomly selected 10 plants from parents (P_1 and P_2) and F1, 20 plants from backcrosses (BC_1 and BC_2) and 50 plants from F_2 were evaluated. Analysis was carried out by six parameter model of generation mean analysis suggested by Hayman (1958). The character days to 50 per cent flowering exhibited significant additive and additive x additive gene action in negative direction for all the three crosses. Plant height recorded significant additive and dominance gene action. The inheritance of tillers per plant were influenced by dominant gene action. In all crosses 1000 grain weight showed dominance and dominance x dominance gene action but in opposite direction. In the crosses MTU1010 x TGL13595 and NLR34449 x MTU1075 grain yield per plant recorded complementary epistasis while in the cross BPT5204 x MTU1081 it was found to be duplicate epistasis. Their results revealed that majority of yield contributing characters were significant for additive, dominance and epistatic interactions which indicates complex inheritance of the traits.

Savitha and Kumari (2014) carried out an experiment to study the mode of inheritance of yield and yield components in rice using generation mean analysis. They used six high yielding varieties as female parent and four traditional landraces as male parent. The F_1, F_2 and F_3 generations of six crosses *viz*. IR72 x Veeradagan, ADT39 x Kavuni, ADT 45 x Kavuni, ADT 43 x Navara, ASD16 x Navara and TPS4 x Kathanellu. Additive and dominance x dominance gene actions showed predominance for seven biometrical characters with duplicate gene action for the traits *viz*. plant height, number of productive tillers per plant, panicle length, number of filled grains per panicle and single plant yield. In most of the traits they observed highly significant additive x additive (i) and dominance x dominance (l) interactions. The sign of h and l were opposite in all the traits studied. They concluded that genetic variation in most studied traits was due to non-allelic gene interactions.

Bano *et al*. (2017) carried out generation mean analysis to study the mode of gene action for yield and quality traits in aromatic genotypes of rice. They followed six parameter model for parents (P_1 and P_2), F_1, F_2, BC_1 and BC_2 generations of three crosses *viz*. Pusa Sugandh 5 x Type 3, Ranbir Basmati x Pusa Basmati 1 and Kasturi Basmati x Type 3. The significant scaling test revealed existence of epistasis in the inheritance of characters under study. They reported significant mean values for all the crosses. They evaluated eight yield traits *viz*. days to 50 per cent flowering, days to maturity, plant height (cm), main panicle length (cm), effective tillers per plant, filled spikelet per panicle, 100 grain weight (g), and grain yield per plant and nine quality traits *viz*. kernel length, kernel breadth (both after and before cooking), kernel L/B ratio (both after and before cooking), kernel elongation ratio, alkali spreading value and amylose content. Except for days to maturity and main panicle length in the cross Pusa Sugandh 5 x Type 3 all the characters showed significant additive gene effect. Except panicle length and amylose content, in cross Kasturi Basmati x Type 3 exhibited significant dominance gene effect in all the characters for all the three crosses. For most of the characters, duplicate epistasis had a major contribution in inheritance in all the three crosses. They found highly significant positive dominant and dominant x dominant gene action in cross Pusa Sugandh 5 x Type 3 which indicates complementary epistasis and suggested that selection in early generation might be effective in improving the traits.

Kumar *et al*. (2017) carried out an experiment to study the genetics of yield and grain characters in rice using five parameter model generation mean analysis. They studied seven characters *viz*. grain length, grain breadth, grain L/B ratio, kernel length, kernel breadth, kernel L/B ratio and grain yield per plant. They observed P_1, P_2, F_1, F_2 and F_3 populations developed by two crosses, AURC22 x IR24 and AURC22 x TRY1. The analysis were carried out according to Mather (1949). Sixty (60) plants each from P_1, P_2 and F_1 population, 600 plants from F_2 and 300 plants from F_3 were observed. Grain length, grain breadth, kernel breadth and grain yield per plant in the cross AURC22 x TRY1 recorded additive gene effects. Positive and significant dominance gene effect were observed in the characters *viz*. grain length, kernel length, kernel breadth, kernel L/B ratio and grain yield per plant in the cross AURC22 x IR24. Kernel length in the cross AURC22 x TRY1 showed positive and significant dominance gene effect. Grain length, grain breadth, kernel breadth and grain yield per plant in both crosses reported positive and significant additive x additive effect. Negative and significant additive x additive effect was observed in grain L/B ratio and kernel L/B ratio in the cross AURC22 x IR24. But it recorded positive and significant dominance x dominance effect for grain breadth and kernel L/B ratio in same cross. They concluded that grain yield per plant and quality characters like grain length, grain breadth, kernel breadth follows additive gene action and additive x additive interaction. So for improvement of these traits simple pedigree breeding can be used.

Rao *et al*. (2017) conducted an experiment to study the mode of inheritance of yield and yield component traits in submergence rice. They carried out generation mean analysis using six basic generations *viz*. P_1, P_2, F_1, F_2, B_1 and B_2 of cross HUR-105 x Swarna Sub-1. The scales A, B, C and D were found significant for most of the traits under study, in both normal irrigated condition and submerged condition. These indicates the presence of epistatic interactions. Under irrigated condition plant height, panicle length, panicle weight, spikelet per panicle, test weight, yield per panicle and amylose content, h and l gene effect showed opposite sign, which indicates duplicate epistasis. Complementary epistasis were observed in the characters like productive tillers per plant, flowering time, maturity and gel consistency. Under normal irrigated condition characters except test weight showed predominant additive genetic variance.

Jondhale *et al*. (2018) conducted an experiment to study the inheritance pattern of quantitative traits in rice. They carried out generation mean analysis to study the mode of gene action for yield related traits. They studied characters like, days to 50 per cent flowering, plant height (cm), number of tillers per plant, length of panicle (cm), grain yield per plant (g), straw yield per plant (g), and harvest index (%). They evaluated different generations of the cross Karjat 2 x Mungo, both direct and reciprocal cross. Plant height, grain yield per plant and harvest index were found significant for additive x dominance model in reciprocal cross and days to 50 per cent flowering in both the crosses. The joint scaling test indicated that additive x additive and dominance x dominance interactions were more prominent and played a significant role in the inheritance of several traits. Additive x dominance gene action was found significant but having lesser effect in governing the traits. They found significant duplicate epistasis for days to 50 per cent flowering, grain yield per plant and straw yield per plant in both crosses, and number of tillers in direct cross. They concluded that more than one major gene group appeared to be involved for the expression of plant height and remaining traits observed the presence of at least one major gene group of genes controlling their inheritance.

Ganapati *et al*. (2020) carried out an experiment to study the gene action of yield and yield contributing traits in rice using six parameter model of generation mean analysis. They evaluated six populations P_1, P_2, F_1, F_2, BC_1 and BC_2 developed by crossing submergence tolerant FR13A (recurrent parent) and local variety Chamara (donor). They observed that characters, plant height, primary branches per panicle, secondary branches per panicle, number of unfilled grains per panicle and number of grains per panicle showed additive gene action. Days to heading also showed additive gene action but showed high negative significance. Primary branches per panicle, number of grains per panicle, secondary branches per panicle, yield per hill, yield per tiller and 1000 grain weight recorded positive significant for dominance component (h). Primary branches per panicle, secondary branches per panicle, number of grains per panicle, number of unfilled grains per panicle, yield per hill, yield per tiller and 1000 grain weight showed positive significant for additive x additive component (i). Plant height, primary branches per panicle, secondary branches per panicle and filled grains per panicle showed positive significant values for additive x dominance component (j). The characters, days to heading, days to maturity, plant height, inter nodal length, tillers per hill, primary branches per panicle, number of grains per panicle and number of unfilled grains per panicle were observed to have positive significant values for Dominance x dominance component (l). They also reported duplicate epistasis for the characters except panicle length. High heritability were observed in plant height, number of primary branches per panicle, and number of grains per panicle. The characters plant height, panicle length, number of filled grains per panicle and 1000 seed weight recorded with high genetic advance.

2.5 Methods to evaluate shattering

For evaluating seed shattering Gu *et al*. (2005a) bagged the panicle of each rice plant at the stage of heading. Shattering and non-shattering grains were obtained at maturity. The percentage of shattered seeds to the total seed weight was expressed as rate of seed shattering.

On the basis of air dried weight Gu *et al*. (2005b) quantified seed shattering in rice. Immediately after harvest panicle shaken gently for about 20s over a container to get shattered seeds and remaining seeds were collected by hand harvesting. The grains were dried in green house for 3 days after removing chaffy grains, plant particles and dirt. The rate of seed shattering was expressed as percentage of seeds that shattered to the total seed weight.

Akasaka *et al*. (2011) used breaking tensile strength, the force required to pull a grain from a pedicel, to evaluate seed shattering degree in rice. For this purpose they used shattering Habit Tester Model TR-II (Fuijiwara company, Japan) developed by Ishikawa *et al*. (1990). Shattering was estimated at an interval of three weeks from heading until harvest, which is normally 30 days after heading. For evaluating heads from seed shattering heads from primary tillers were used.

Htun *et al*. (2014) used a digital force gauge (FGP O.S, Nidei - Shimpo Co. Japan) to evaluate the shattering degree in F2 segregation population. They measured breaking tensile strength (BTS) that required to detach the seeds from pedicel to evaluate seed shattering. Seed shattering was measured after 35 days from planting. 25 plants were selected randomly and 5 panicles of each plant is evaluated (total 125 plants) and their average BTS values were calculated.

Inoue *et al*. (2014) analyzed seed shattering in rice by evaluating the breaking tensile strength required to detach the seeds from the pedicel using digital force gauge (FGP 0.5, Nidei- Shimpo, Japan). They measured BTS values of 10 spikelets per each plant. Three independent plants were used to calculate the average BTS value for a line. Based on flowering date each spikelet were coloured, since flowering date of spikelets were different within the panicle, and BTS values measured on the indicated date after flowering. Using unpaired students t- test they calculated the difference between the two genotypes of the progeny.

Kwon *et al*. (2015) grew rice plants in 5 inch pots in green house to evaluate seed shattering by reducing environmental effect. The plants to be evaluated were provided 10h light followed by 14h darkness for four weeks from 40 days after sowing. The panicle having highest number of florets were bagged to isolate auto shattered florets. Thirty days after flowering the two bagged heads are harvested. The head along with bags were placed in slanted (10 degree) wooden panel. A concrete roller of 1kg rolled twice over the head from top to bottom. The shattering percentage were measured by counting shattered grains.

Job (2018) measured seed shattering by Induced Random Impact (IRI) method, by using a force gauge apparatus. She collected ten panicles randomly from each line. Panicles were placed in force gauge apparatus after drying, along with 100 steel balls of 1 cm and rotated. Shattering resistance was measured as per cent grains shattered to that of total grains.

Materials and Methods

3. MATERIALS AND METHODS

The research on 'Genetics of shattering resistance in rice (*Oryza sativa* L.)' was conducted in the Department of Plant Breeding and Genetics, College of Horticulture, Kerala Agricultural University (KAU), from October, 2018 to June, 2020. The research work was subdivided into three experiments and carried out in two locations. Experiment I and II were conducted in the fields of Department of Plant Breeding and Genetics and Experiment III was conducted at Agronomy farm, Department of Agronomy, College of Horticulture. First two experiments were hybridization in pots and the progenies obtained in experiment I and II were raised along with parents in field for evaluation of seed shattering.

3.1 Materials

The experimental material comprised of two crosses between shattering prone rice variety Jyothi (PTB 39) and two shattering resistant rice varieties Triveni (PTB 38) and Aathira (PTB 51) to incorporate shattering resistance to variety Jyothi. Six generations (P_1, P_2, F_1, F_2, B_1 and B_2) were developed to study the mode of inheritance. The three varieties were procured from Regional Agricultural Research Station (RARS), Pattambi, Kerala. The salient features of the three rice varieties used in this study are presented in detail (Table 1).

3.2 Methods

The research work was divided in to three experiments

1. Hybridization of shattering prone high yielding variety Jyothi with shattering resistance varieties, Triveni and Aathira and development of F_1 population.

Table 1: Salient characteristics of the varieties used in the study

Sl. No.	Variety	Salient features	Source
1	Jyothi (PTB 39)	Moderately tolerant to brown plant hopper and blast but susceptible to sheath blight: suitable for direct sowing, transplanting and special systems of *kole* and Kuttanad. Highly shattering. 115-120 days.	RARS, Pattambi
2	Aathira (PTB 51)	Semi-tall, non-lodging, moderate resistance to blast and blight diseases and brown plant hopper. Suited for 1st and 2nd crop season and also for hilly area. Shattering resistant. 125-130 days.	RARS, Pattambi
3	Triveni (PTB 38)	Tolerant to brown plant hopper. Susceptible to blast and sheath blight. Shattering resistant. 105-110 days.	RARS, Pattambi

2. Back crossing F_1 progeny with both the parents and selfing of F_1

3. Field evaluation of six populations P_1, P_2, F_1, F_2, B_1 and B_2 of both the crosses

3.2.1 Experiment 1: Crossing of resistant genotype with shattering prone high yielding varieties

The two varieties Aathira and Triveni which were identified as resistant to shattering in previous studies conducted in the Department of Plant Breeding and Genetics were used as male parents in the hybridization programme to transfer the shattering resistance into shattering susceptible variety Jyothi. For hybridization purpose a non-replicated crossing block was laid down in field attached to Department of Plant Breeding and Genetics, College of Horticulture. Staggered sowing of parental lines was done at an interval of five days to ensure synchronization of flowering. The plants were raised in pots (2 seedlings per pot) and usual agronomical practices were provided to get healthy plants and good seed set. Two crosses were carried out *viz*. Jyothi x Triveni and Jyothi x Aathira. Clipping method was practiced for emasculation and followed by hand pollination to ensure fertilization.

3.2.1.1 Emasculation

Emasculation of female spikelet was done to ensure cross fertilization and F_1 development. Panicles that emerged more than 70 per cent out of flag leaf were used for emasculation. Emasculation was carried out during evening hours, after 5pm. About ten to fifteen florets which are likely to open the next day morning (Florets having anther height equal to half or more than half of the floret height) were selected for emasculation. The top one third portion of the panicles, which were already opened, and bottom one third, young/immature florets were removed. Emasculation was done by clipping off top one third of each selected florets using a clean scissors. The exposed anthers (six anthers) were removed one by one with the help of a needle/forceps. After emasculation of each floret the panicles were covered using a butter paper bag to avoid contamination. Immediately after emasculation, panicles were labeled and tagged

3.2.1.2 Pollination

Pollination of florets was carried out on the next day of emasculation. Pollen grains from the selected panicles, were collected in petri plates by shaking the male panicle. Pollination was carried out between 8am and 11am. Both wet method (pollen with water) and dry method was adopted to transfer the pollen to stigma. A camel brush was used to transfer the pollen to the stigmatic surface of female parent. After hand pollination the panicles were re-bagged to avoid contamination. The bags were removed one week after seed set.

Two F_1 hybrids were developed with Jyothi as female parent and Triveni and Aathira as male parents. Seeds were collected separately for the different crosses from female parent, Jyothi.

3.2.2 Experiment II: Backcrossing F_1 with both parents and selfing F_1

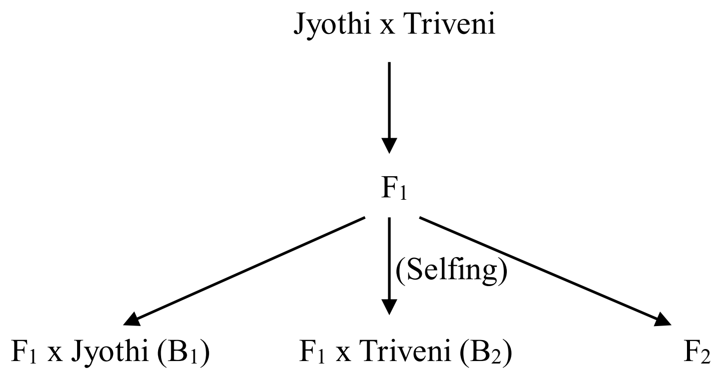
The F_1 progeny obtained from experiment I was backcrossed with both parents to obtain B_1 and B_2 populations. Selfing of F_1 was done to develop F_2 generations. The three parents (Jyothi, Triveni and Aathira) and progenies obtained from experiment I were sown in trays for nursery preparation. The seedlings were transplanted in pots, two seedlings per pots. Non-replicated crossing block was laid out for backcross programme. To ensure synchronized flowering of plants staggered sowing was practiced at an interval of five days. Usual agronomic practices were provided to get healthy plants and proper seed set. Selfing of F_1progeny was also carried out simultaneously to develop F_2 generations. Crossed seeds and selfed seeds were collected separately. Emasculation and crossing were done as described in experiment I.

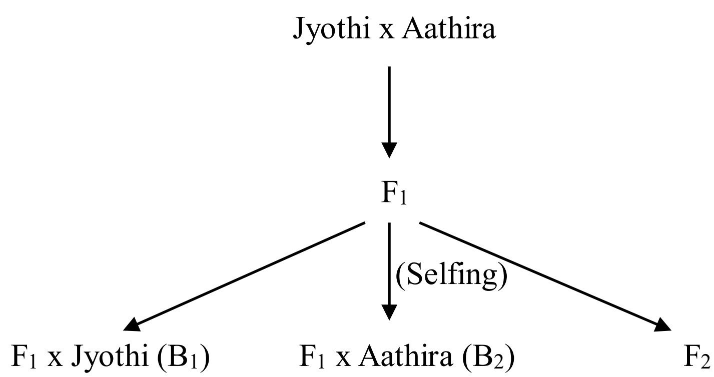
Emasculation

Pollination

Bagging

Plate I: Clipping method of hybridization





3.2.3 Experiment III: Evaluation of parents, F_1, F_2, B_1 andB_2 for shattering resistance

The data were analyzed using six parameter model of generation mean analysis proposed by Jinks and Jones, (1958). Progenies obtained from experiment I and experiment II (F1, F2, B1 and B2) were raised in the field along with parents for both the crosses and evaluated for shattering resistance.

The experiment was carried out at the farm of Department of Agronomy, College of Horticulture, Vellanikkara. Six generations (P_1, P_2, F_1, F_2, B_1 and B_2) developed from two crosses (Jyothi x Triveni and Jyothi x Aathira) were raised in a Randomized Block Design with three replications during February to June 2020. The seeds of each generations *viz*. parents (P1 and P2), F_1, B_1 and B_2 of each cross was sown in trays for nursery in an open condition and seedling of 22 days age were transplanted in randomized block design replicated three times. In case of F_2 seedlings were raised similar to other generations and 210 plants of each cross was raised in three rows with 70 plants in each row. The plants were transplanted at a spacing of 20cm between two rows and 15cm between plants. Recommended agronomic practices were followed to establish the crop. Twenty plants selected randomly from each parent, F_1, B_1 and B_2 and two hundred plants from F_2 were evaluated.

3.2.3.1 Observations recorded

Data were recorded on days to 50 per cent flowering, plant height (cm), panicles per plant (no.), panicle length (cm), spikelets per panicle (no.), seeds per panicle (no.), days to maturity, test weight (g), seed yield per panicle (g) and shattering (%) on single plant in each generations. Twenty plants selected randomly from each parent, F_1, B_1 and B_2 and two hundred plants from F_2 were evaluated. Observations were recorded as per "Standard Evaluation System of Rice" (IRRI, 1996) for following characters.

3.2.3.1.1 Days to 50 per cent flowering

The number of days taken from seedling to flowering of 50 per cent plants in each generation was counted.

3.2.3.1.2 Plant height (cm)

Height of the plant was measured from ground level to the tip of the flag leaf at maturity and expressed in centimetre.

Plate II: Hybrid seed

3.2.3.1.3 Number of tillers per plant

The total number of grains bearing and non-bearing tillers per plant were counted at maturity.

3.2.3.1.4 Number of panicles per plant

The total number of panicles per plant was counted.

3.2.3.1.5 Panicle length (cm)

At maturity length of main axis of panicle was measured from the base to the tip of panicle and recorded in centimetre.

3.2.3.1.6 Number of spikelets per panicle

Number of spikelets per panicle was counted at maturity from randomly selected three panicles of each plant and average number was recorded.

3.2.3.1.7 Number of seeds per panicle

Total number of seeds per panicle was recorded at maturity.

3.2.3.1.8 Days to maturity

Duration was recorded in days from seedling to 80 per cent of the grains on a panicle were fully ripened.

3.2.3.1.9 Test weight (g)

Random sample of 1000 well developed whole grains were taken at maturity after harvest and dried to optimum moisture level. Using an electronic balance this 1000 dried grains were weighed and expressed in grams.

3.2.3.1.10 Grain yield per plant (g)

All productive panicles at maturity were harvested and yield of individual plant was recorded in grams.

3.2.3.1.11 Seed shattering (%)

Shattering was measured by Induced Random Impact (IRI) method, by using a force gauge apparatus. For measuring the shattering percentage, panicles were harvested separately from each generation at physiological maturity and dried under shade in a paper bag for two to three days. Shattering percent was measured based on individual plants of each generations. Randomly selected five panicles were used to measure the shattering percent. After shade drying the panicles were placed in a force gauge apparatus along with 100 steel balls of 1 cm, rotated at 60rpm for 20 seconds and the number of shattered grains were counted. Shattering percent was calculated using the equation

Shattering per cent = (number of shattered grains/total number of grains) x 100

3.3. STATISTICAL ANALYSIS OF DATA

3.3.1 Generation mean analysis

The scaling tests A, B, C and D were computed and their variances were calculated to test the adequacy of the additive-dominance model in each case using formulae given by Mather (1949). When the interactions were confirmed then generation mean analysis was carried out following the methodology of Jinks and Jones (1958) using six generations and estimated the gene effects *viz*. M (mean), d (additive main effect), h (dominance main effect), i (additive x additive interaction effect), j (additive x dominance interaction effect), and l (dominance x dominance interaction effect).

Scaling test (Mather, 1949)

$$A = 2\bar{B}_1 - \bar{F}_1 - \bar{P}_1$$

$$B = 2\bar{B}_2 - \bar{F}_1 - \bar{P}_2$$

Field preparation and Lay out

Transplanting

30 DAS

Vegetative stage

Reproductive stage

Plate III: Experimental field

$C = 4\bar{F}_2 - 2\bar{F}_1 - \bar{P}_1 - \bar{P}_2$

$D = 4\bar{F}_3 - 2\bar{F}_2 - \bar{P}_1 - \bar{P}_2$

Six parameter model (Jinks and Jones, 1958)

m $= \frac{1}{2}\bar{P}_1 + \frac{1}{2}\bar{P}_2 + 4\bar{F}_2 - 2\bar{B}_1 - 2\bar{B}_2$

(d) $= \frac{1}{2}\bar{P}_1 - \frac{1}{2}\bar{P}_2$

(h) $= 6\bar{B}_1 + 6\bar{B}_2 + 8\bar{F}_2 - \bar{F}_1 - 3/2\bar{P}_1 - 3/2\,\bar{P}_2$

(i) $= 2\bar{B}_1 + 2\bar{B}_2 + 4\bar{F}_2$

(j) $= 2\bar{B}_1 - \bar{P}_1 - 2\bar{B}_2 + \bar{P}_2$

(l) $= \bar{P}_1 + \bar{P}_2 + 2\bar{F}_1 + 4\bar{F}_2 - 4\bar{B}_1 - 4\bar{B}_2$

3.3.2 Heterosis study

Relative Heterosis (RH) = MP – F_1 / MP x 100

Heterobeltiosis (HB) = BP – F_1 / BP x 100

Where, MP is mid parental value and BP is better parental value.

3.3.3 Variability study

3.3.3.1 Phenotypic Coefficient of Variance (PCV)

PCV = σp / Mean x 100

Where, σp is phenotypic standard deviation

3.3.3.2 Genotypic Coefficient of Variance (GCV)

GCV = σg / Mean x 100

Where, σg is genotypic standard deviation

Sivasubramaniam and Madhavamenon (1973) classified PCV and GCV into following classes.

0 – 10% - Low

10 – 20% - Medium

>20% - High

3.3.3.3 Heritability

Variance of phenotype (Vp), variance of genotype (Vg), environmental variance (Ve) and broad sense heritability (Hb) were calculated using the formula given by Kotecha and Zimmerman (1978).

$Hb = VF_2 - Ve/ VF_2$

Where,

$Ve = VP_1 + VP_2 + VF_1 / 3$

$Vp = VF_2$

$Vg = Vp – Ve$

Johnson *et al*. (1955) classified heritability values as follows:

Low - Less than 30%

Medium - 30 -60%

High - More than 60%

3.3.3.4 Genetic advance (GA)

$GA = σ^2g/σp \times k$

Where,

$σ^2g$ = Genotypic variance

$σp$ = Phenotypic standard deviation

k = Selection differential at a particular level of selection intensity

3.3.3.5 Genetic Gain (GG)

Genetic gain is the value of genetic advance expressed as percentage of mean.

GG = GA / mean x 100

The range of genetic advance as percent of mean is classified by Johnson *et al*. (1955)

Low - Less than 10%

Medium - 10 – 20%

High - More than 20%

Plate IV: Force gauge apparatus

Results

4. RESULTS

The research on 'Genetics of shattering resistance in rice (*Oryza sativa* L.)' was conducted in the Department of Plant Breeding and Genetics, College of Horticulture, Kerala Agricultural University (KAU), during the October, 2018 to June, 2020. Observations were recorded for shattering resistance and other ten quantitative characters. Observations were recorded for six generation (P_1, P_2, F_1, F_2, B_1 and B_2) developed from two different crosses. The results of scaling test and six parameter model generation mean analysis are presented in this chapter.

4.1 Average performance

4.1.1 Days to 50 per cent flowering

The mean performance for days to 50 per cent flowering varied across generations (Table 2). P_2 (Jyothi) recorded highest value for the character (88 days) while the lowest duration was recorded by B_2 population (77 days) in the cross Jyothi x Triveni. $F_1$was intermediate. The average time to flowering in both backcross population were found to be close to their respective male parents. The segregating population (F_2) recorded flowering from 78 days onwards up to 94 days after sowing with an average of 85 days which was slightly more than that of F_1 generation (82 days).

Average performance of the six generations derived from the cross Jyothi x Aathira is shown in table 3. Shortest duration for 50 per cent flowering was recorded for variety Jyothi (P_1) followed by B_1 generation while parent Aathira was late to reach 50 per cent flowering (P_2). F_1 generation was intermediate to both parents. The average duration for flowering in backcross populations were recorded close to their respective parental population. The average duration for flowering in backcross populations were recorded close to their respective male parental population. The F_2 population started flowering from 87 days and continued up to 106 days after sowing with an average of 96 days to 50 per cent flowering.

4.1.2 Plant height

Plant height recorded significant differences in six generation in both crosses. Average plant height for different generations obtained from the cross Jyothi x Triveni is presented in Table 2. Among the six populations, F_1 (98.50 cm) recorded highest value for plant height while parent Jyothi ($P_{1,}$ 85.70 cm) recorded the lowest value. The average height of the backcross populations were close to their respective male parents. Plant height of segregating population ranged from 72.3 cm to 115.7 cm with a mean of 95.21 cm.

In the cross Jyothi x Aathira the parent P_2 (Aathira, 121.7 cm) was the tallest while parent P_1 (Jyothi, 85.68 cm) recorded the least value (Table 3).F_1 population (100 cm) was intermediate. The average height of backcross populations was close to their respective male parents. The F_2 population expressed a range of plant height starting from 72.1 cm to 132.1 cm with an average height of 102.07 cm which was higher than plant height reported by F_1 population.

4.1.3 Tillers per plant

Mean values of number of tillers per plant varied among six generation in both the crosses under study. In the cross between Jyothi x Triveni highest tillers per plant was recorded for F_1 generation (31 nos.) followed by Jyothi (30 nos.) (Table 2). Lowest mean value for tillers per plant was recorded in B_1 generation (19 nos.). Backcross population B_2 (20 nos.) was observed to have mean value similar to P_2 (20 nos.) whereas B_1 generation showed relatively low tillers per plant compared to P_1. The F_2 population recorded a range of tillers from 6 tillers to 44 tillers per plant with an average of 23 tillers per plant in the cross Jyothi x Triveni.

Among six generations studied in the cross Jyothi x Aathira the highest mean value for tillers per plant obtained from was in F_2 population (31 nos.) followed by F_1(30.5 nos.) population (Table 3). B_1 (20 nos.) population recorded low tiller number compared to P_1 (30 nos.) whereas B_2 (30 nos.) generation showed slightly more tillers than P_2 (28 nos.).

The F_2 population exhibited a range of tillers from nine tillers to 69 tillers per plant with an average of 39 tillers per plant.

4.1.4 Panicles per plant

Six generations obtained from the cross between Jyothi x Triveni recorded different mean values (Table 2). F_1 generation (22 nos.) recorded higher number of panicles per plant. Lowest panicles per plant were noted for B_1 generation (11 nos.). B_2 generation (14 nos.) yielded mean panicle number close to P_2 (15 nos.). The F_2 population recorded a range of panicle number from 5 panicles to 35 panicles per plant with an average of 16 panicles per plant.

Among six generations derived from the cross Jyothi x Aathira, F_1 generation (23 nos.) recorded highest panicle number (Table 3). Backcross population (B_2, 20 nos.) recorded similar panicle number as of P_2 (21 nos.) whereas B_1 (13) showed slightly lower number of panicles per plant compared to P_1 (20 nos.). The F_2 population recorded a range of values from 6 panicles to 50 panicles per plant with an average of 21 panicles per plant in the population.

4.1.5 Panicle length

The variety Triveni (P_2, 24.6 cm) recorded highest average value for panicle length in the cross Jyothi x Triveni followed by F_1 (24.5 cm) population (Table 2). The average panicle length of backcross populations was recorded and was close to their respective male parental populations. The lowest average value for the character was observed in B_1 generation (21.83 cm). F_2 populations showed a range from 18.50 cm to 28.10 cm for panicle length with an average length of 23.5cm.

In the cross between Jyothi x Aathira, variety Aathira (27.84 cm) recorded the longest panicle followed by F_1 (27.02 cm) population (Table 3). The lowest panicle length was observed for B_1 (23.12 cm) generation. Average panicle length of backcross populations were recorded close to their respective male parents. Panicle length in F_2 populations varied from 20.35 cm to 29.95 cm with an average length of 24.49 cm.

4.1.6 Spikelets per panicle

Six generations obtained from the cross Jyothi x Triveni recorded different number of spikelet per panicle (Table 2). The F_1 population (145 no.) reported intermediate value of the parents. Triveni (P_2, 150 nos.) recorded highest spikelet per panicle whereas mean value for the character was lowest for B_1 population (107). B_1 generation showed very less number of spikelet compared to P_1. B_2 generation (142 nos.) was observed with a mean spikelet per panicle close to P_2 (132 nos.). The F_2segregants recorded a range from, 89.70 spikelets to 187.60 spikelets per panicle with an average of 132.12 spikelets per panicle.

Aathira (P_2, 186nos.) had high number of spikelet per panicle in the cross Jyothi x Aathira (Table 3). F_1 generation (151 nos.) recorded an intermediate value of parents. Both the backcross population yielded a mean spikelet number per panicle close to their respective male parents. Among six generations observed B_1 population (124 nos.) recorded lowest spikelet per panicle. F_2 population had a range of values varying from 107.50 to 212.70 with an average of 146.28 spikelets per panicle.

4.1.7 Seeds per panicle

Among six generations obtained from the cross between Jyothi x Triveni, Triveni (P_2, 130 nos.) recorded the highest value for seeds per panicle. F_1 population (124 nos.) recorded an intermediate value for the character between two parents. Backcross generations recorded lower mean value when compared to their respective male parents. F_2 population recorded a range of values for the character, 65.67 seeds to 149.20 seeds per panicle with an average of 105.14 seeds per panicle (Table 2).

Aathira (P_2, 152 nos.) recorded the highest number of seeds per panicle within different generations derived from the cross Jyothi x Aathira. F_1 (128 no.) showed an intermediate value between two parents for the character. Both the backcross populations recorded slightly lower seeds per panicle compared to respective male parents. B_1 generation (101 nos.) reported the lowest mean performance for the character. The F_2

population showed a range of values from, 88.65 seeds to 178.30 seeds per panicle with an average of 121.77 seeds per panicle (Table 3).

4.1.8 Days to Maturity

Among six generations derived from the cross, Jyothi x Triveni shortest crop duration was recorded by B_2 generation (109 days) and longest duration was observed for Jyothi (P_1, 117 days). F_1 generation (113 days) resulted in intermediate duration between two parents. Backcross populations exhibited average duration close to their respective male parents. F_2 populations recorded maturity from 111 days onwards and continued up to 124 days with an average duration of 115 days (Table 2).

In the cross Jyothi x Aathira, Jyothi (P_1, 117 days) recorded the shortest maturity and B_2 generation (131 days) showed the longest duration. F_1 generation (124 days) showed intermediate maturity time between two parents. Mean duration of backcross populations were observed close to their parental (male parent) duration. The F_2 population matured from 117 days onwards and continued up to 136 days with an average of 125 days for maturation (Table 3).

4.1.9 Test weight

F_1 generation (29g) recorded higher test weight than both parents. The mean value of the test weight of backcross populations observed close to their respective male parents. B_1 generation (25.4g) recorded lowest test weight. F_2 population obtained a range of values varying from 20.10 g to 32.04 g with an average of 26.50 g in the cross Jyothi x Triveni (Table 2).

In the cross Jyothi x Aathira F_1 population (27.8g) recorded the highest test weight. Lowest test weight was recorded for Aathira (P_2, 23.8g). Both the backcross populations recorded test weight closer to their respective male parents. F_2 population recorded range of values from 19.65 g to 32.24 g with an average test weight of 25.35g (Table 3).

4.1.10 Grain yield per plant

Among the six-generations obtained from the cross between Jyothi x Triveni, F_1 population (62g) recorded the highest seed yield per plant. The lowest yield was recorded for the B_1 generation (20g). Yield per plant in B_1 generation was very low as compared to P_1 (50g) whereas B_2 generation (36.6g) yielded grain yield close to the grain yield of P_2 (43.8g). F_2 population recorded a range of grain yield from, 7.49 g to 91.62 g with an average yield of 36.50 g grain yield per plant (Table 2).

All the six-generation except B_1 generation (27g) exhibited good grain yield per plant in the cross Jyothi x Aathira. F_1 generation (62.5g) recorded high yield than two parents. B_1 generation recorded a comparatively low yield than P_1 (51g). B_2 (55g) obtained mean yield close to the yield of P_2 (56 g). F_2 population obtained a range of yield from 15.67 g to 131.77 g grain yield per plant with an average yield of 52 g per plant (Table 3).

4.1.11 Shattering (%)

The degree of shattering was observed high for Jyothi (P_1, 21.8 %) and lowest shattering was recorded by B_2 population (2.3 %) in the cross Jyothi x Triveni. F_1 showed (5 %) a moderate shattering percentage. B_1 generation (7.8 %) obtained moderate shattering value compared to P_1 which has a high degree of shattering. Both P_2 (2.7 %) and B_2 population exhibited low shattering value. F_2 population resulted in a range of shattering from 0.89 per cent to 16.49 per cent with an average shattering value of 6.11 per cent (Table 2).

Among six-generations derived from the cross Jyothi x Aathira, P_2 (Aathira, 2.04 %) recorded lowest shattering and P_1 (Jyothi, 21.8 %) recorded the highest shattering. B_1 generation (10.38 %) resulted in less shattering compared to the P_1 population. B_2 (3.9 %) and P_2 population exhibited almost similar value for shattering percentage. F_1 (3.8 %) showed a shattering value close to P_2. F_2 population recorded a range of shattering value, 0.86 per cent to 17.86 per cent with an average of 6.38 percent (Table 3).

Table 2: Average values of biometric characters in six generations developed from the cross Jyothi x Triveni

Character	P_1	P_2	F_1	F_2	B_1	B_2
DF	87.76	78.95	82.44	85.16	86.33	77.81
PH (cm)	85.69	98.10	98.53	95.21	86.76	96.32
TP (no.)	30.24	20.71	31.78	23.41	19.00	20.76
PP (no.)	19.71	15.71	22.39	16.12	11.52	14.24
PL (cm)	24.12	24.59	24.56	23.48	21.84	23.66
SPP (no.)	134.15	150.18	144.88	132.12	107.06	142.51
SDPP (no.)	118.39	130.44	124.82	105.14	84.80	117.35
DM	117.95	110.33	113.89	115.64	116.62	109.43
TW (g)	26.21	27.95	29.08	26.50	25.42	26.47
GYP (g)	50.32	43.87	62.15	36.51	20.94	36.65
SHAT (%)	21.82	2.74	4.59	6.11	7.87	2.31

DF: Days to 50 per cent flowering **PH**: Plant height **TP**: Tillers per plant **PP**: Panicles per plant **PL**: Panicle length

SPP: Spikelet per panicle **SDPP**: Seeds per panicle **DM**: Days to maturity **TW**: Test weight **GYP**: Grain yield per plant

SHAT: Shattering per cent

Table 3: Average values of biometrical characters in six generations obtained from the cross Jyothi x Aathira

Character	P_1	P_2	F_1	F_2	B_1	B_2
DF	87.07	100.93	94.17	95.57	90.40	100.64
PH (cm)	85.63	121.71	99.91	102.07	85.90	107.70
TP (no.)	30.40	27.93	30.42	31.61	20.90	30.09
PP (no.)	20.00	21.53	23.08	21.50	13.60	20.64
PL (cm)	24.02	27.84	27.02	24.50	23.12	25.07
SPP (no.)	134.24	186.07	151.81	146.28	124.23	157.77
SDPP (no.)	118.52	154.27	127.56	121.77	101.17	131.32
DM	117.33	130.93	124.17	125.57	120.40	131.09
TW (g)	26.25	23.84	27.79	25.35	24.89	24.93
GYP (g)	51.03	56.20	62.53	52.00	27.28	55.01
SHAT (%)	21.87	2.04	3.81	6.38	10.38	3.92

DF: Days to 50 per cent flowering **PH**: Plant height **TP**: Tillers per plant **PP**: Panicles per plant **PL**: Panicle length
SPP: Spikelet per panicle **SDPP**: Seeds per panicle **DM**: Days to maturity **TW**: Test weight **GYP**: Grain yield per plant
SHAT: Shattering per cent

4.2 Generation mean analysis

4.2.1 Days to 50 per cent flowering

4.2.1.1 Scaling test

Days to 50 per cent flowering showed significant and positive values for scale A, C and D and significant and negative value for scale B in the cross Jyothi x Triveni (Table 4). Days to 50 per cent flowering showed significant and positive values for scale B and C in the cross Jyothi x Aathira (Table 5).

4.2.1.2 Gene action

The mean effects (m) showed highly significant and positive value for days to 50 per cent flowering in the cross Jyothi x Triveni (Table 6). The additive component (d) was significant positive and the dominance component (h) was significant negative. The estimate of additive x additive (i) effect was observed to be significant and negative while additive x dominance (j) interaction and dominance x dominance (l) component was significant and positive. Degree of dominance was one for the character (Table 8).

The mean effects (m) showed highly significant and positive value for days to 50 per cent flowering in the cross Jyothi x Aathira (Table 7).The additive component (d) was significant and negative. The estimate of additive x additive (i) effect was observed to be significant and negative while additive x dominance (j) was significant and positive in the cross. Degree of dominance was less than one for the character in the cross Jyothi x Aathira (Table 9).

4.2.2 Plant height (cm)

4.2.2.1 Scaling test

The scale A was significant and negative and scale D was significant and positive in the cross Jyothi x Triveni (Table 4).

Plant height showed significant and positive scale D in the cross Jyothi x Aathira (Table 5).

4.2.2.2 Gene action

The mean effect (m) was significantly positive and the additive components (d) was significantly negative in the cross Jyothi x Triveni (Table 6). The dominance component (h) was observed to be significant and negative while the dominance x dominance component (l) showed significant positive effect. Degree of dominance was more than one in the cross (Table 8).

The mean effect (m) was significant and positive while the additive component was significant and negative in the cross Jyothi x Aathira (Table 7). The dominance component (h) was observed to be significant and negative while the dominance x dominance component (l) showed significant positive effect. The additive x additive (i) component was significant and negative in the cross. The degree of dominance was less than one for the character (Table 9).

4.2.3 Tillers per plant (No.)

4.2.3.1 Scaling test

The scale A, B and C were significant and negative whereas the scale D was significant and positive for tiller number in cross Jyothi x Triveni (Table 4).

The character showed significance for scale A for the character tillers per plant in the cross Jyothi x Aathira but in negative direction (Table 5).

4.2.3.2 Gene action

The character exhibited all the three type of gene action *viz.* additive, dominance and epistasis in the cross Jyothi x Triveni (Table 6). The mean effect (m) and additive component (d) were significant and positive. The dominance component (h), additive x additive component (i) and additive x dominance component (j) were significant and negative whereas dominance x dominance component (l) was significant and positive. Degree of dominance was more than one for the character (Table 8).

The mean effect (m) and additive component (d) were significant and positive in the cross Jyothi x Aathira (Table 7). Dominance gene effect and non-allelic interactions were non-significant for the inheritance of character in the cross.

4.2.4 Panicles per plant (No.)

4.2.4.1 Scaling test

The character showed significance for all the four scales. The character recorded significant and negative scale A, B, and C and significant positive scale D in the cross Jyothi x Triveni (Table 4).

In cross Jyothi x Aathira, only scale A was significant and negative (Table 5).

4.2.4.2 Gene action

The mean effect (m) was highly significant and positive whereas additive component (d) was significant and positive in the cross Jyothi x Triveni (Table 6). The dominance component (h) was significant and negative while the dominance x dominance component (l) was significant and positive. The additive x additive (i) and additive x dominance (j) components were significant and positive in the cross Jyothi x Triveni (Table 6). Degree of dominance was more than one for number of panicles (Table 8).

The mean effect (m) was highly significant and positive in the cross Jyothi x Aathira. Additive component (d) was significant and negative (Table 7). The dominance component (h) was significant and negative while the dominance x dominance component (l) was significant and positive. Degree of dominance was more than one for number of panicles in the cross (Table 9).

Table 4: Estimates of scaling test for biometrical characters in the cross Jyothi x Triveni

Scale	DF	PH	TP	PP	PL	SPP	SDPP	DM	TW	GYP	SHAT
A	2.46 ± 0.77**	-10.69 ±3.00**	-24.02 ±3.83**	-19.06±2.14**	-4.99±0.54**	-64.91 ±11.45**	-73.62±8.07**	1.39±0.69**	-4.44±1.04**	-70.59±5.01**	-10.67±2.59**
B	-5.78 ± .09**	-3.98±3.47	-10.97 ±2.64**	-9.63±2.71**	-1.83±0.44	-10.04±5.54	-20.57±6.22**	-5.37±1.01**	-4.09±0.59**	-32.72±8.19**	-2.71±0.31**
C	9.04 ± 1.29**	0.01±3.03	-20.87 ±2.99**	-15.71±2.02**	-3.89±0.49	-45.61±5.16**	-77.89±4.68**	6.51±1.05**	-6.30±0.79**	-72.43±5.05**	-9.29±0.97**
D	6.18 ± 0.67**	7.34±2.34**	7.06±2.49**	6.49±1.85**	1.46±0.45	14.67±6.69*	8.14±5.45	5.24±0.68**	1.12±0.71	15.44±5.21**	2.04±0.94*

*** Significance at 5 % level** **** Significance at 1% level**

DF: Days to 50 per cent flowering **PH**: Plant height **TP**: Tillers per plant **PP**: Panicles per plant **PL**: Panicle length

SPP: Spikelet per panicle **SDPP**: Seeds per panicle **DM**: Days to maturity **TW**: Test weight **GYP**: Grain yield per plant

SHAT: Shattering per cent

Table 5: Estimates of scaling test for biometrical characters in the cross Jyothi x Aathira

Scale	DF	PH	TP	PP	PL	SPP	SDPP	DM	TW	GYP	SHAT
A	-0.43 ± 1.62	-13.74±7.78	-19.02±5.62**	-15.88±3.86**	-4.79±1.45**	-37.59±12.00**	-43.74±9.05**	-0.70± 1.59	-4.27±0.28**	-59.00±6.99**	-4.92±1.93*
B	6.17 ±1.81**	-6.22±4.81	1.83±9.81	-3.34±7.38	-4.71±0.70**	-22.34±8.30*	-19.18±7.48*	7.08 ±1.30**	-1.78±0.64**	-8.71±19.90	1.99±1.08
C	5.95 ±2.27**	1.13±5.61	7.27±5.49	-1.72±3.75	-7.89±0.88**	-38.79±8.67**	-40.84±7.33**	5.69±2.25*	-4.25±1.09**	-24.30±9.44*	-6.02±1.59**
D	0.11 ±1.55	10.54±5.09*	12.23±6.19	8.75±4.49	0.80±0.88	10.57±8.35	11.04±6.73	-0.35± 1.42	0.89±0.63	21.70±11.46	-1.55±1.28

*** Significance at 5 % level** **** Significance at 1% level**

DF: Days to 50 per cent flowering **PH**: Plant height **TP**: Tillers per plant **PP**: Panicles per plant **PL**: Panicle length

SPP: Spikelet per panicle **SDPP**: Seeds per panicle **DM**: Days to maturity **TW**: Test weight **GYP**: Grain yield per plant

SHAT: Shattering per cent

4.2.5 Panicle length (cm)

4.2.5.1 Scaling test

Panicle length showed significant scale A, but in negative direction in the cross Jyothi x Triveni (Table 4).

The scale A was significant and negative in the cross Jyothi x Aathira. Scale B and C were significant and negative in the cross Jyothi x Aathira (Table 5).

4.2.5.2 Gene action

Mean effects (m) were significant and positive in the cross Jyothi x Triveni (Table 6). The additive component (d) was significant and negative for the character. The additive x additive (i) component and additive x dominance components (j) were significant and negative. Dominance component (h) was significant and negative while dominance x dominance (l) component was significant and positive in the cross. Degree of dominance was more than one for panicle length (Table 8).

Mean effect (m) was significant and positive in the cross Jyothi x Aathira (Table 7). The additive component (d) was significant and negative. Dominance component (h) was significant and negative and dominance x dominance component (l) was significant and positive. Degree of dominance was more than one for the character (Table 9).

4.2.6 Spikelet per panicle

4.1.6.2 Scaling test

The scale A and C were significant and negative for the character Jyothi x Triveni (Table 4). Scale D was significant and positive in the cross Jyothi x Triveni.

The scale A and C were significant and negative for the character in the cross Jyothi x Aathira while, scale B was significant and negative (Table 5).

4.1.6.3 Gene action

The character showed additive (d), dominance (h) and all the three types of epistatic gene effect in the cross Jyothi x Triveni (Table 6). The mean effects were significant and positive. Additive (d) and dominance components (h) were significant and negative. Additive x additive (i) and additive x dominance (j) components were significant but in negative direction. The dominance x dominance (l) component was significant and positive. Degree of dominance was more than one for spikelet per panicle in the cross Jyothi x Triveni (Table 8).

The character showed additive (d), dominance (h) and all types of epistatic gene effect except additive x additive (i) and additive x dominance (j) effects in the cross Jyothi x Aathira (Table 7). The mean effect was significant and positive. Additive (d) component and dominance components (h) were significant and negative. The dominance x dominance (l) component was significant and positive. Character recorded degree of dominance less than one in the cross (Table 9).

4.2.7 Seeds per panicle

4.2.7.1 Scaling test

The scale A, B and C were significant and negative for the character in the cross Jyothi x Triveni (Table 4).

Scale A, B and C were also significant and negative for the character in the cross Jyothi x Aathira (Table 5).

4.2.7.2 Gene action

All the components except additive x additive (i) component were significant in the cross Jyothi x Triveni (Table 6). The mean effects (m) and dominance x dominance (l) effects were significant and positive. The additive component (d), dominance component (h), additive x dominance (j) components was significant and negative. Degree of dominance was more than one for the character (Table 8).

Table 6: Estimate of genetic parameter for the eleven characters in the cross Jyothi x Triveni

Character	m	(d)	(h)	(i)	(j)	(l)
DF	95.72 ±1.36**	4.40 ±0.25**	-28.95 ±3.48**	-12.36 ±1.34**	8.24 ±1.05**	15.68 ±2.25**
PH	106.57±4.73**	-6.20±0.75**	-37.41±13.44**	-14.68±2.22	-6.72±4.44	29.36±8.90**
TP	39.59±5.00**	4.76±0.35**	-56.91±14.12**	-14.11±4.99**	-13.05±4.48**	49.10±9.35**
PP	30.69±3.71**	2.00±0.29**	-49.95±10.53**	-12.97±3.69**	-9.43±3.37**	41.65±6.94**
PL	27.28±0.09**	-0.24±0.11*	-12.47±2.58**	-2.93±0.89**	-3.17±0.84**	9.75±1.69**
SPP	171.50±13.39**	-8.01±0.67**	-130.90±38.87**	-29.33±13.38*	-54.87±12.64**	104.28±25.67**
SDPP	140.70±10.92**	-6.02±0.67**	-126.36±31.37**	-16.29±10.90	-53.05±10.13**	110.48±20.62**
DM	124.62±1.38**	3.81±0.29**	-25.17±3.72**	-10.48±1.36**	6.76±1.19**	14.44±2.39**
TW	29.31±1.41**	-0.87±0.06**	-10.99±3.88**	-2.23±1.41	-0.34±1.19	10.77±2.50**
GYP	77.97±10.45**	3.22±0.62**	-150.00±29.72**	-30.88±10.43**	-37.87±9.50**	134.18±19.51**
SHAT	16.37±1.89**	9.54±0.19**	-29.24±5.31**	-4.09±0.85**	-7.97±1.70**	17.47±3.45**

*** Significance at 5 % level** **** Significance at 1% level**

DF: Days to 50 per cent flowering **PH**: Plant height **TP**: Tillers per plant **PP**: Panicles per plant **PL**: Panicle length

SPP: Spikelet per panicle **SDPP**: Seeds per panicle **DM**: Days to maturity **TW**: Test weight **GYP**: Grain yield per plant

SHAT: Shattering per cent

Table 7: Estimate of genetic parameter for the biometrical characters in the cross Jyothi x Aathira

Character	m	(d)	(h)	(i)	(j)	(l)
DF	94.21 ±3.12**	-6.93 ±0.28**	5.48 ±8.13	-0.21 ±3.11**	-6.61 ±2.38**	-5.53 ±5.15
PH	124.76±10.21**	-18.04±0.72**	-65.90±28.57*	-21.09±10.18*	-7.51±9.01	41.05±18.66*
TP	53.62±12.39**	1.23±0.45*	-64.85±35.30	-24.46±12.39	-20.85±11.28	41.64±23.12
PP	38.27±8.98**	-0.77±0.37*	-51.93±25.78*	-17.51±8.97	-12.54±8.29	36.74±16.93*
PL	27.54±1.76**	-1.91±0.15**	-11.64±4.98*	-1.61±1.75	-0.08±1.60	11.12±3.26**
SPP	181.29±16.72**	-25.92±0.79**	-110.54±46.56*	-21.14±16.71	-15.26±14.55	81.07±30.19*
SDPP	158.48±13.49**	-17.87±0.91**	-115.93±37.41**	-22.08±13.46	-24.56±11.69*	85.01±24.23**
DM	123.44± 2.85**	-6.80± 0.25**	7.81± 7.18	0.70± 2.84	-7.78± 35.42	-7.08 ± 4.48
TW	26.84±1.26**	1.20±0.09**	-6.88±2.94*	-1.79±1.26	-2.49±0.69**	7.83±1.73**
GYP	97.02±22.93**	-2.58±0.62**	-145.61±65.67*	-43.41±22.92	-50.29±21.05*	111.12±43.07*
SHAT	8.85±2.58**	9.92±0.31**	-4.86±7.04	3.10±2.56	-6.91±2.21**	-0.18±4.52

*** Significance at 5 % level** **** Significance at 1% level**

DF: Days to 50 per cent flowering **PH**: Plant height **TP**: Tillers per plant **PP**: Panicles per plant **PL**: Panicle length

SPP: Spikelet per panicle **SDPP**: Seeds per panicle **DM**: Days to maturity **TW**: Test weight **GYP**: Grain yield per plant

SHAT: Shattering per cent

All the components except additive x additive (i) component were significant in the cross Jyothi x Aathira (Table 7). The mean effects (m) and dominance x dominance (l) effects were significant and positive. The additive component (d), dominance component (h), and additive x dominance (j) components were significant and negative. Degree of dominance was less than one for the character in the cross (Table 9).

4.2.8 Days to maturity

4.2.8.1 Scaling test

The scale A, C and D were significant and positive and scale B was significant and negative in the cross Jyothi x Triveni (Table 4).

The character days to maturity showed significant and positive scale B and C in the cross Jyothi x Aathira (Table 5).

4.2.8.2 Gene action

Mean effects (m) and the additive component (d) for days to maturity was significant and positive in the cross Jyothi x Triveni (Table 6).Dominance component (h) and additive x additive component (i) were significant and negative whereas additive x dominance (j) and dominance x dominance components (l) were significant and positive in the cross. Degree of dominance was less than one (Table 8).

Mean effects (m) for days to maturity was significant and positive in the cross Jyothi x Aathira (Table 7). The additive component (d) was significant and negative in the cross. Degree of dominance was less than one for days to maturity (Table 9).

4.2.9 Test weight

4.2.9.1 Scaling test

The scale A, B and C were significant and negative for the character in the cross Jyothi x Triveni (Table 4).

Scales A, B and C were also significant and negative for the character in the cross Jyothi x Aathira (Table 5).

4.2.9.2 Gene action

All the genetic components except additive x additive and additive x dominance effect were significant in the cross Jyothi x Triveni for the character. Mean effect (m) was significant and positive in the cross Jyothi x Triveni (Table 6) while, the additive (d) component was significant and negative. Dominance component (h) was significant and negative while dominance x dominance (l) effect was significant and positive. Degree of dominance was less than one for the character (Table 8).

The entire components except additive x additive effect were significant in the cross Jyothi x Aathira (Table 7). Mean effect (m), and additive (d) component was significant and positive. Dominance component (h) was significant and negative and dominance x dominance (l) effect was significant and positive. The additive x dominance component (j) was significant and negative. Degree of dominance was close to one for the character in the cross (Table 9).

4.2.10 Grain yield per plant (g)

4.1.10.2 Scaling test

Scale A, B and C were significantly negative and scale D was significant and positive for the character in the cross Jyothi x Triveni (Table 4).

The character showed significant and negative scale A and C in the cross Jyothi x Aathira (Table 5).

4.1.10.3 Gene action

All the six components were significant in the cross Jyothi x Triveni (Table 6). Mean effect (m) and additive component (d) was significant and positive in the cross Jyothi x Triveni (Table 6). The dominance component (h) was significant and negative while, dominance x dominance component (l) was significant and positive. Additive x additive

(i) gene effect was significant and negative but the additive x dominance (j) gene effect observed as significant and negative. Degree of dominance was more than one for the character (Table 8).

All the six components were significant except additive x additive component in the cross Jyothi x Aathira (Table 7). Mean effect (m) was significant and positive while additive component (d) was significant and negative. The dominance component (h) was significant and negative. Among interaction components, dominance x dominance (l) component was significant and positive whereas additive x dominance (j) gene effect observed as significant and negative. Degree of dominance was more than one for the character (Table 9).

4.2.11 Shattering (%)

4.2.11.1 Scaling test

Scale A, B and C were significant and negative and scale D was significant and positive in the cross Jyothi x Triveni (Table 4).

Shattering per cent showed significant and negative scale A and C in the cross Jyothi x Aathira (Table 5).

4.2.11.2 Gene action

Mean effect (m) and additive component (d) were significant and positive in the cross Jyothi x Triveni (Table 6). The dominance component (h) and additive x additive components (i) were significant and negative. The additive x dominance (j) component was significant and negative whereas dominance x dominance (l) component was significant and positive. Degree of dominance was one for the character (Table 8).

Mean effect (m) and additive component (d) were significant and positive for the character in the cross Jyothi x Aathira (Table 7). The additive x dominance (j) component was significant and negative in the cross. The degree of dominance was less than one for shattering per cent (Table 9).

Table 8: Components of genetic variances for biometrical characters in the cross Jyothi x Triveni

Character	E	D	H	Degree of dominance
DF	2.42	40.01	-40.73	-1.01
PH	19.54	42.29	63.42	1.22
TP	8.27	72.24	100.44	1.18
PP	4.12	24.02	75.19	1.77
PL	0.42	0.29	5.00	4.14
SPP	18.38	-562.23	2148.16	-1.95
SDPP	15.66	-115.64	1111.99	-3.10
DM	2.09	23.32	-19.47	-0.91
TW	0.12	15.87	-1.53	-0.31
GYP	16.66	116.16	749.40	2.54
SHAT	1.12	11.60	12.75	1.04

DF: Days to 50 per cent flowering **PH**: Plant height **TP**: Tillers per plant **PP**: Panicles per plant **PL**: Panicle length

SPP: Spikelet per panicle **SDPP**: Seeds per panicle **DM**: Days to maturity **TW**: Test weight **GYP**: Grain yield per plant

SHAT: Shattering per cent

Table 9: Components of genetic variances for biometrical characters in the cross Jyothi x Aathira

Character	E	D	H	Degree of dominance
DF	2.15	84.91	-65.36	-0.88
PH	15.18	235.86	109.62	0.68
TP	6.09	40.86	612.82	3.87
PP	3.92	-42.93	394.95	-3.03
PL	0.55	2.93	7.45	1.59
SPP	15.19	757.71	260.26	0.59
SDPP	18.99	563.51	54.31	0.31
DM	1.73	93.64	-81.14	-0.93
TW	0.19	27.46	-25.82	-0.97
GYP	11.55	-208.37	2566.94	-3.51
SHAT	1.99	32.10	-17.14	0.73

DF: Days to 50 per cent flowering **PH**: Plant height **TP**: Tillers per plant **PP**: Panicles per plant **PL**: Panicle length

SPP: Spikelet per panicle **SDPP**: Seeds per panicle **DM**: Days to maturity **TW**: Test weight **GYP**: Grain yield per plant

SHAT: Shattering per cent

4.2 Heterosis

Jyothi x Triveni

Significant and positive relative heterosis was recorded for the characters, plant height (7.22%), tillers per plant (24.74%), panicles per plant (26.39%), spikelet per panicle (1.91%), test weight (7.38%) and grain yield per plant (31.97%) while the characters, days to 50 per cent flowering (1.09%) and shattering per cent (62.61%) recorded significant and negative value for relative heterosis in the cross (Table 10).

Characters like panicles per plant (13.57%), test weight (4.03%) and grain yield per plant (23.52%) e recorded significant and positive value for heterobeltiosis whereas characters *viz*. days to 50 per cent flowering (6.06%), spikelet per panicle (3.53%), seeds per panicle (4.30%), days to maturity (3.45%) and shattering per cent (78.96%) recorded significant and negative value for heterobeltiosis (Table 10).

Jyothi x Aathira,

Significant and positive value for relative heterosis was obtained for the characters, panicles per plant (11.16%), panicle length (4.17%), test weight (10.95%) and grain yield per plant (16.64%). The characters *viz*. plant height (3.63%), spikelet per panicle (5.21%), seeds per panicle (6.48%) and shattering per cent (68.14%) recorded significant and negative value for relative heterosis in the cross (Table 11).

Panicles per plant (7.19%), test weight (5.87%) and grain yield per plant (11.27%) recorded significant and positive value for heterobeltiosis whereas characters *viz*. plant height (14.82%), panicle length (2.98%), spikelets per panicle (18.41%), seeds per panicle (17.31%), days to maturity (5.17%) and shattering per cent (82.58%) recorded significant and negative value for heterobeltiosis in the cross Jyothi x Aathira (Table 11).

Table 10: Heterosis effect of eleven characters in the cross Jyothi x Triveni

Character	P_1	P_2	F_1	RH (%)	HB (%)
DF	87.76	78.95	82.44	-1.09*	-6.06**
PH (cm)	85.69	98.10	98.53	7.22**	0.44
TP (no.)	30.24	20.71	31.78	24.74**	5.09
PP (no.)	19.71	15.71	22.39	26.39**	13.57*
PL (cm)	24.12	24.59	24.56	0.83	-0.15
SPP (no.)	134.15	150.18	144.88	1.91**	-3.53**
SDPP (no.)	118.39	130.44	124.82	0.33	-4.30**
DM	117.95	110.33	113.89	-0.22	-3.45**
TW (g)	26.21	27.95	29.08	7.38**	4.03**
GYP (g)	50.32	43.87	62.15	31.97**	23.52**
SHAT (%)	21.82	2.74	4.59	-62.61**	-78.96**

*** Significance at 5 % level** **** Significance at 1% level**

DF: Days to 50 per cent flowering **PH**: Plant height **TP**: Tillers per plant **PP**: Panicles per plant **PL**: Panicle length
SPP: Spikelet per panicle **SDPP**: Seeds per panicle **DM**: Days to maturity **TW**: Test weight **GYP**: Grain yield per plant
SHAT: Shattering per cent

Table 11: Heterosis effect of eleven characters in the cross Jyothi x Aathira

Character	P_1	P_2	F_1	RH (%)	HB (%)
DF	87.07	100.93	94.17	0.18	-6.87
PH (cm)	85.63	121.71	99.91	-3.63**	-14.82**
TP (no.)	30.40	27.93	30.42	4.29	0.06
PP (no.)	20.00	21.53	23.08	11.16*	7.19*
PL (cm)	24.02	27.84	27.02	4.17**	-2.98**
SPP (no.)	134.24	186.07	151.81	-5.21**	-18.41**
SDPP (no.)	118.52	154.27	127.56	-6.48**	-17.31**
DM	117.33	130.93	124.17	0.03	-5.17**
TW (g)	26.25	23.84	27.79	10.95**	5.87**
GYP (g)	51.03	56.20	62.53	16.64**	11.27**
SHAT (%)	21.87	2.04	3.81	-68.14**	-82.58**

*** Significance at 5 % level** **** Significance at 1% level**

DF: Days to 50 per cent flowering **PH**: Plant height **TP**: Tillers per plant **PP**: Panicles per plant **PL**: Panicle length

SPP: Spikelet per panicle **SDPP**: Seeds per panicle **DM**: Days to maturity **TW**: Test weight **GYP**: Grain yield per plant

SHAT: Shattering per cent

4.3 Variability studies

4.3.1 Phenotypic and genotypic coefficient of variation (F_2 Generation)

Coefficient of variation provides a relative measure of variance among different traits under study. In general, the estimates phenotypic coefficient of variation (PCV) were higher than the genotypic coefficient of variation (GCV) indicating the effect of environment on expression of genotype.

The phenotypic coefficient of variation (PCV) ranged from 2.58 per cent for days to maturity to 52.01 per cent for shattering per cent. The characters *viz*. days to 50 per cent flowering (4.11%), plant height (7.90%), panicle length (5.74%) and days to maturity (2.58%) recorded low PCV. The characters, spikelet per panicle (12.54%), seeds per panicle (14.61%), and test weight (10.45%) recorded moderate value for PCV whereas tillers per plant (35.61%), panicles per panicle (36.66%), grain yield per plant (44.34%) and shattering per cent (52.01%) recorded high PCV in F_2 population obtained from the cross Jyothi x Triveni(Table 12).

The genotypic coefficient of variation (GCV) showed a range from 2.25 per cent for days to maturity to 49.05 per cent for shattering per cent. The characters *viz*. days to 50 per cent flowering (3.68%), plant height (6.39%), panicle length (5.03%) and days to maturity (2.25%) recorded low GCV. The characters, spikelet per panicle (12.11%), seeds per panicle (14.11%), and test weight (10.37%) recorded moderate value for GCV whereas tillers per plant (33.43%), panicles per panicle (34.42%), grain yield per plant (42.34%) and shattering per cent (49.05%) recorded high GCV in F_2 population obtained from the cross Jyothi x Triveni (Table 12).

The phenotypic coefficient of variation (PCV) showed a range from 4.23 per cent for days to maturity to 58.17 per cent for shattering per cent. The characters *viz*. days to 50 per cent flowering (5.56%), panicle length (8.04%) and days to maturity (4.23%) recorded low PCV. The characters, plant height (12.41%), spikelet per panicle (14.65%), seeds per panicle (14.56%), and test weight (10.78%) recorded moderate value for PCV whereas tillers per plant (42.41%), panicles per panicle (41.92%), grain yield per plant (45.06%) and shattering per cent (58.17%) recorded high PCV in F_2 population obtained from the cross Jyothi x Aathira (Table 13).

The genotypic coefficient of variation (GCV) showed a range from 4.10 per cent for days to maturity to 53.80 per cent for shattering per cent. The characters *viz*. days to 50 per cent flowering (5.35%), panicle length (7.45%) and days to maturity (4.10%) recorded low GCV. The characters, plant height (11.81%), spikelet per panicle (14.40%), seeds per panicle (14.11%), and test weight (10.64%) recorded moderate value for GCV whereas tillers per plant (41.69%), panicles per panicle (40.90%), grain yield per plant (44.59%) and shattering per cent (53.80%) recorded high GCV in F_2 population obtained from the cross Jyothi x Aathira (Table 13).

4.3.2 Heritability and genetic advance

The amount of genetic variation in a population alone will not be of much use to the breeder unless it is supplemented with the information on heritability estimate which is a measure of the heritable portion of the total variation. Heritability plays an important role in deciding the strategy for selection of a character since high heritability indicates high scope of genetic improvement of the character through selection.

Out of eleven characters studied in F_2 population obtained from the cross Jyothi x Triveni, tillers per plant, panicles per plant, spikelet per panicle, seeds per panicle, test weight, grain yield per plant and shattering per cent recorded high broad sense heritability accompanied with high genetic advance. The characters plant height recorded high heritability followed by moderate genetic advance whereas characters like, days to 50 per cent, panicle length and days to maturity recorded high heritability along with low genetic advance (Table 12).

Characters *viz*. plant height, tillers per plant, panicles per plant, spikelet per panicle, seeds per panicle, test weight, grain yield per plant and shattering per cent recorded high broad sense heritability accompanied with high genetic advance in F_2 population obtained from Jyothi x Aathira. The characters days to 50 per cent flowering and panicle length recorded high heritability followed by moderate genetic advance whereas character days to maturity recorded high heritability along with low genetic advance in the population (Table 13).

Table 12: Variability studies in F_2 population of the cross Jyothi x Triveni

Characters	Range		Mean	Coefficient of variation (%)		Heritability broad sense (%)	Genetic advance (%)
	Minimum	Maximum		GCV	PCV		
Days to 50 per cent flowering	78	94	85.16	5.35	5.56	80.19	6.79
Plant height (cm)	72.3	115.7	95.21	11.81	12.41	65.44	10.65
Tillers per plant (no.)	6	44	23.41	41.69	42.41	88.10	64.63
Panicles per plant (no.)	5	35	16.12	40.90	41.92	88.18	66.58
Panicle length (cm)	18.50	28.01	23.48	7.45	8.04	77.02	9.10
Spikelets per panicle (no.)	89.70	187.60	132.12	14.40	14.65	93.30	24.09
Seeds per panicle (no.)	65.67	149.20	105.14	14.11	14.56	93.36	28.09
Days to maturity	111	124	115.64	4.10	4.23	76.45	4.06
Test weight (g)	20.10	32.04	26.50	10.64	10.78	98.45	21.19
Grain yield per plant (g)	7.49	91.62	36.51	44.59	45.06	93.64	85.53
Shattering per cent	0.89	16.50	6.11	53.80	58.17	88.95	95.30

Table 13: Variability studies in F_2 population of the cross Jyothi x Aathira

Characters	Range		Mean	Coefficient of variation (%)		Heritability broad sense (%)	Genetic advance (%)
	Minimum	Maximum		GCV	PCV		
Days to 50 per cent flowering	87	106	95.57	5.35	5.56	92.39	10.59
Plant height (cm)	72.1	132.1	102.07	11.81	12.41	90.54	23.15
Tillers per plant (no.)	9	69	31.61	41.69	42.41	96.61	84.41
Panicles per plant(no.)	6	50	21.50	40.90	41.92	95.17	82.18
Panicle length (cm)	20.35	29.95	24.50	7.45	8.04	85.89	14.22
Spikelets per panicle (no.)	107.50	212.70	146.28	14.40	14.65	96.69	29.18
Seeds per panicle (no.)	88.65	178.30	121.77	14.11	14.56	93.96	28.18
Days to maturity	117	136	125.57	4.10	4.23	93.87	8.19
Test weight (g)	19.65	32.24	25.35	10.64	10.78	97.39	21.63
Grain yield per plant (g)	15.67	131.77	52.00	44.59	45.06	97.90	90.88
Shattering per cent	0.86	17.86	6.38	53.80	58.17	85.53	96.49

Discussion

5. DISCUSSION

5.1: Generation mean analysis

5.1.1 Days to 50 per cent flowering

Significant scale A and B in the cross Jyothi x Triveni indicates the presence of additive x dominance interaction in the inheritance of the character. Significant scale C reveals the presence of dominance x dominance interaction whereas the significant scale D indicates the presence of additive x additive interaction in inheritance of days to 50 per cent flowering in the cross Jyothi x Triveni

Significant scale B indicates the presence of additive x dominance interaction in inheritance of the character. Significant scale C reveals the presence of dominance x dominance interaction in inheritance of the character in the cross Jyothi x Aathira.

Both the crosses recorded significance for the scales which indicates the presence of non-allelic interaction in inheritance of the character days to 50 per cent flowering. The findings of this study are in conformity to the reports of Savitha and Kumari (2015).

Mean (m) effect was significant and positive for days to 50 per cent flowering in both crosses (fig.3). This was in agreement with the findings of Chamundeswari *et al*. (2013) and Ganapati *et al*. (2020). The significant and positive additive component (d) in the cross Jyothi x Triveni indicates that more genes are contributed by the maternal parent (Jyothi) which flowered late (fig.1).

The significant and negative dominance component (h) (fig.3) in the cross Jyothi x Triveni indicates higher contribution from the early flowering parent (Triveni). This is in agreement with the results of Chamundeswari *et al*. (2013).The significant and opposite sign for dominance component (h) and dominance x dominance (l) component (fig.3) indicates the presence of duplicate gene action in the expression of character. Similar results were obtained by Srivastava *et al*. (2012), and Savitha and Kumari (2015)

Fig. 1: Days to 50 per cent flowering in six generations (Jyothi x Triveni)

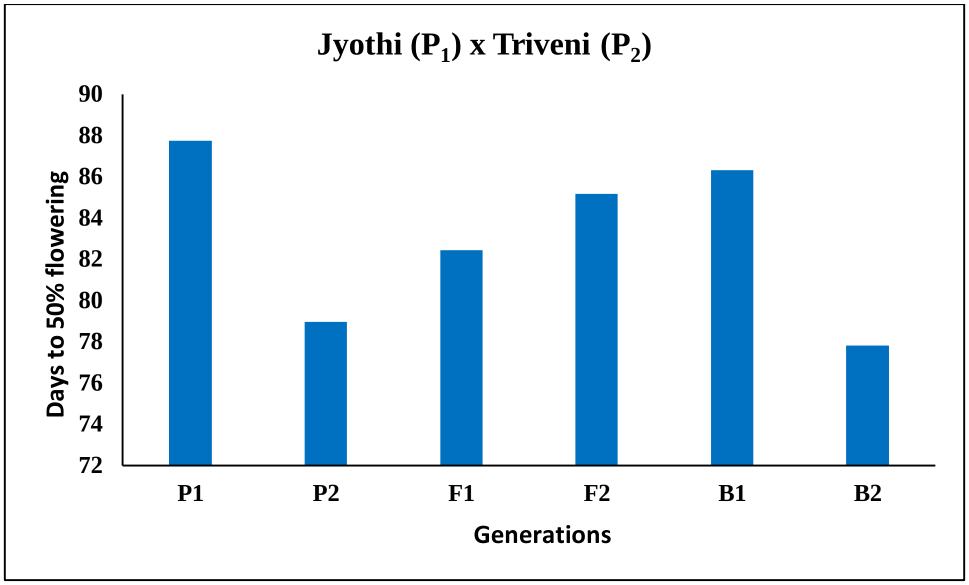


Fig. 2: Days to 50 per cent flowering in six generations (Jyothi x Aathira)

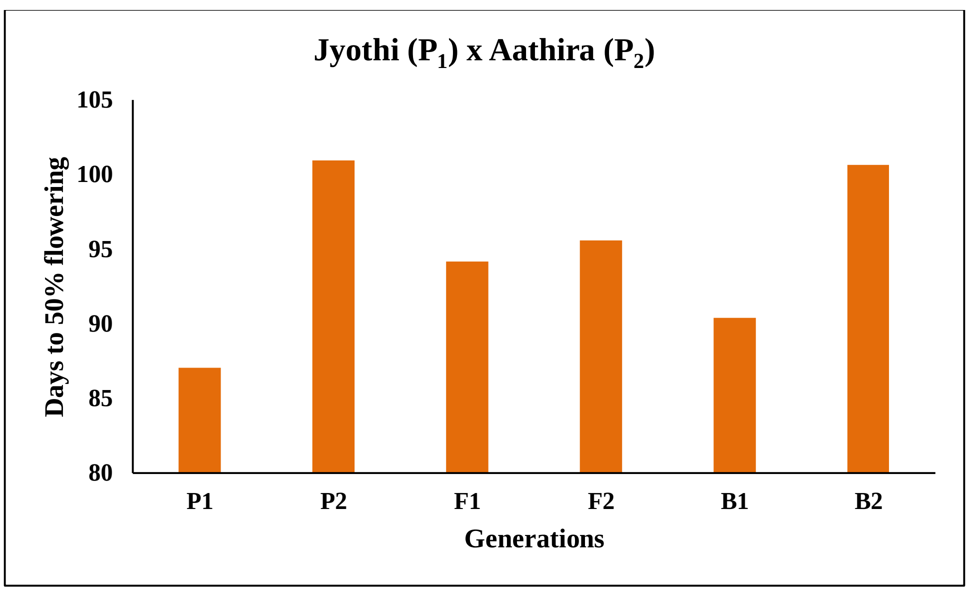
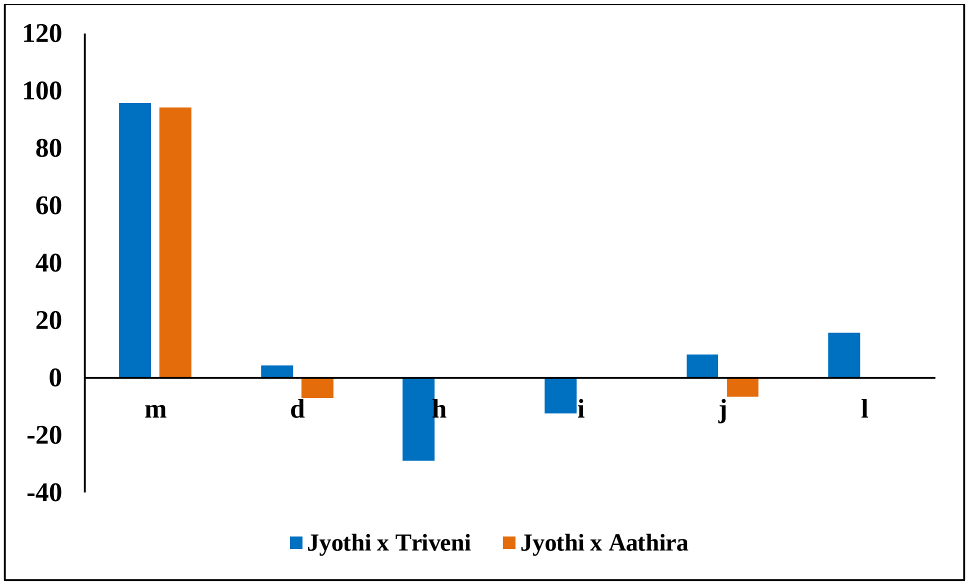


Fig.3: Six parameter model for days to 50 per cent flowering



The significant and relatively high magnitude for dominance (h) component (fig.3) in the cross Jyothi x Triveni shows predominance of dominance gene effects for the expression of days to 50 per cent flowering in the cross. This is in conformity with findings by Liang *et al*. (1996).

The character exhibits both additive and non-additive gene action along with epistatic interactions which shows the complex inheritance of the character in the cross Jyothi x Triveni. Hence simple selection may not yield desirable recombinants.

The significant and negative additive component (d) (fig.3) in the cross Jyothi x Aathira indicates that parent which flowers early (Jyothi, fig.2) contributes more for the inheritance of character. This finding is in confirmation with the studies of Jondhale *et al*. (2018) and Ganapati *et al*. (2020). Significant and major influence of additive (d) and additive x additive (i) gene effects for the character in the cross Jyothi x Aathira can be utilized for further improvement through direct selection.

5.1.2 Plant height (cm)

Significant scale A indicates the presence of additive x dominance interaction whereas significant scale D indicates the presence of dominance x dominance interaction for the inheritance of plant height in the cross Jyothi x Triveni.

Significant scale D reveals the presence of additive x additive interaction for inheritance of plant height in the cross.

In general significant scaling test reveals the presence of non-allelic interaction for inheritance of plant height in both crosses. This is in agreement with Srivastava *et al*. (2012), Savitha and Kumari (2015) and Ganapati *et al*. (2020).

Mean (m) effect was significant and positive (fig.6) for plant height in both crosses. Verma *et al*. (2006), Chamundeswari *et al*. (2013) and Nayak *et al*. (2017) also obtained similar results.

Significant and negative additive component (d and dominance component) (fig.6) in the cross Jyothi x Triveni indicates major contribution from the short parent (fig.4). The significant and negative dominance component (h) coupled with significant positive dominance x dominance (l) interaction (fig.6) indicates the presence of duplicate type of epistasis in the inheritance of the character. Duplicate epistasis for plant height was earlier reported by Hasib *et al*. (2002) and Nayak *et al*. (2007). Relatively high magnitude of dominance gene effect (fig.6) over additive gene effect that indicates dominance gene effect plays a larger role of inheritance of plant height in this cross.

Significant and negative additive (d) component (fig.6) in the cross Jyothi x Aathira indicates the major contribution of genes from the short parent (fig.5). Significant and negative dominance component (h) indicates dominance gene action towards short parent (fig.5).The dominance component (h) was observed to be significant and negative and the dominance x dominance component (l) showed significant positive effect (fig.6).

Fig. 4: Plant height for six generations (Jyothi x Triveni)

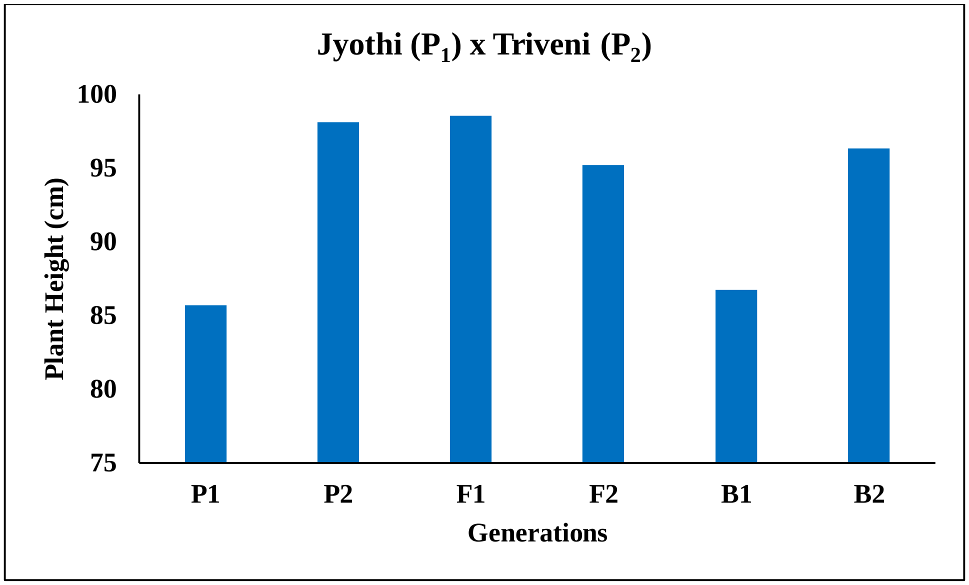
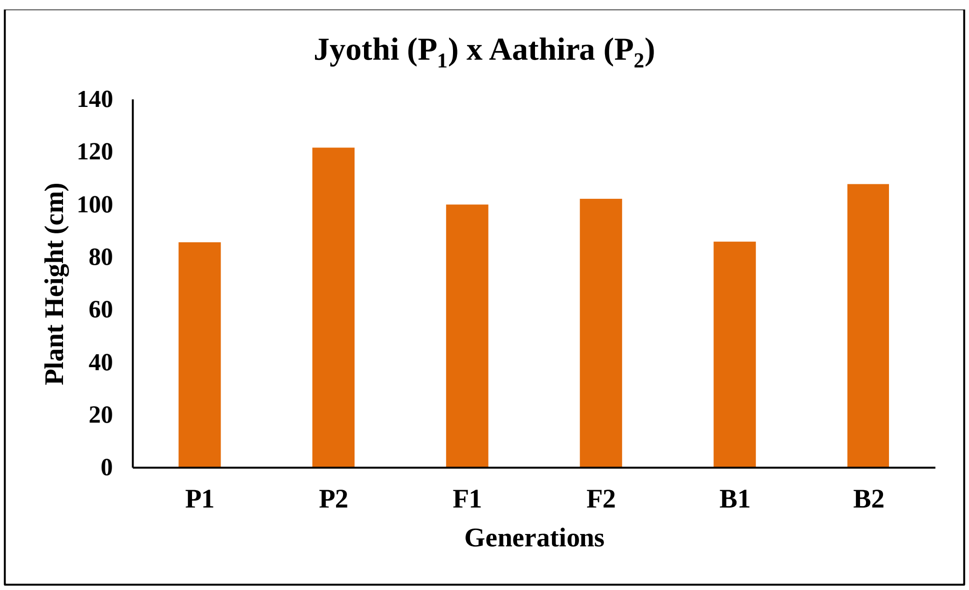


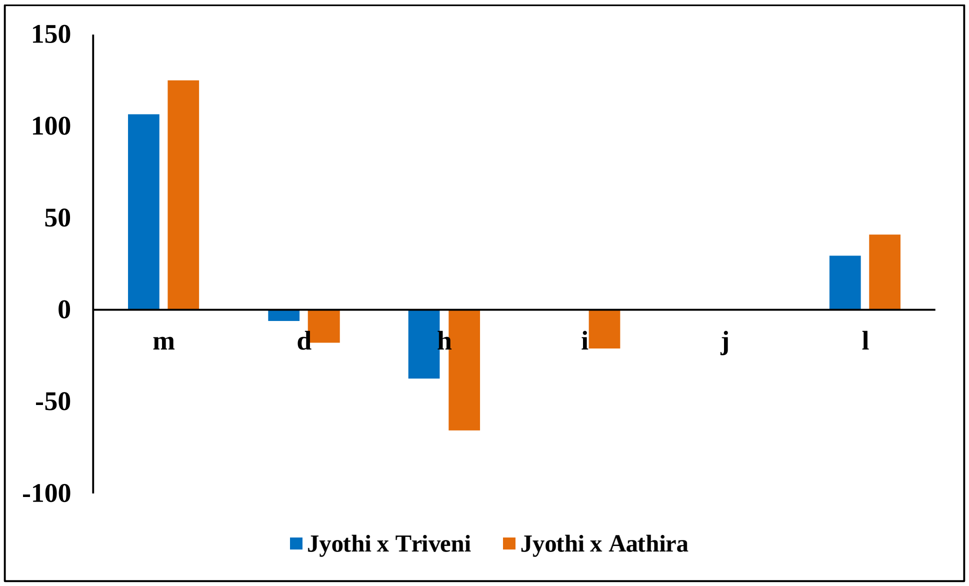
Fig. 5: Plant height for six generations in the cross Jyothi x Aathira



These results indicate the presence of duplicate type of epistasis for the character which is in conformity with the results of Divya *et al*. (2014) and Rao *et al*. (2017)

Plant height was observed to be having significant and negative additive component in both crosses. Ganapati *et al*. (2020) reported significant and positive additive gene effect for plant height indicating the major influence of tall parent in inheritance of plant height.

Fig.6: Six parameter model for plant height



The predominant additive gene action with duplicate gene interaction indicates that segregants with desirable plant stature of either of the parent could be selected through direct selection to improve the character. Higher magnitude of dominance component may interfere with improvement by direct selection in early segregation population. It may be overcome by random mating among F_2 segregants. As rice is a self-pollinated crop selection at later generations may yield desirable recombinants with reduced height.

5.1.3 Tillers per plant (nos.)

Significant scaling test reveals the presence of non-allelic interaction in the inheritance of tillers per plant in both crosses which is in accordance with the findings of Bano *et al*. (2017) and Jondhale *et al*. (2018).

Significant scale A and B indicates the presence of additive x dominance interaction. Significant scale C reveals the presence of dominance x dominance interaction whereas the significant scale D indicates the presence of additive x additive interaction for inheritance of number of tillers in the cross Jyothi x Triveni.

Significant scale A indicates the presence of additive x dominance interaction in inheritance of the character in the cross Jyothi x Aathira.

Mean (m) effect was significant and positive for tillers per plant in both the crosses (fig.9). Significant mean effect is supported by the findings of Roy and Senapati (2011), Divya*et al*. (2014), Bano *et al*. (2017) and Jondhale *et al*. (2018).

Significant and positive additive (d) component (fig.9) reveals the major contribution of parent with high tillers to increase the character in the cross Jyothi x Triveni (fig.7).The negative sign for dominance component indicates the dominance towards the parent with lower tillers per plant (fig.7). Significant and negative dominance (h) gene effect (fig.9) for the character is in agreement with the results of Roy and Senapati (2011), Divya *et al*. (2014), Bano *et al.* (2017) and Jondhale *et al.* (2018). The opposite direction of the dominance component (h) and dominance x dominance (l) component (fig.9) indicates the presence of duplicate gene action in inheritance of character. Presence of duplicate gene action for number of tillers per plant is in conformity with the results of Bano *et al*. (2017) and Jondhale *et al*. (2018).

Fig. 7: Number of tillers for six generations in the cross Jyothi x Triveni

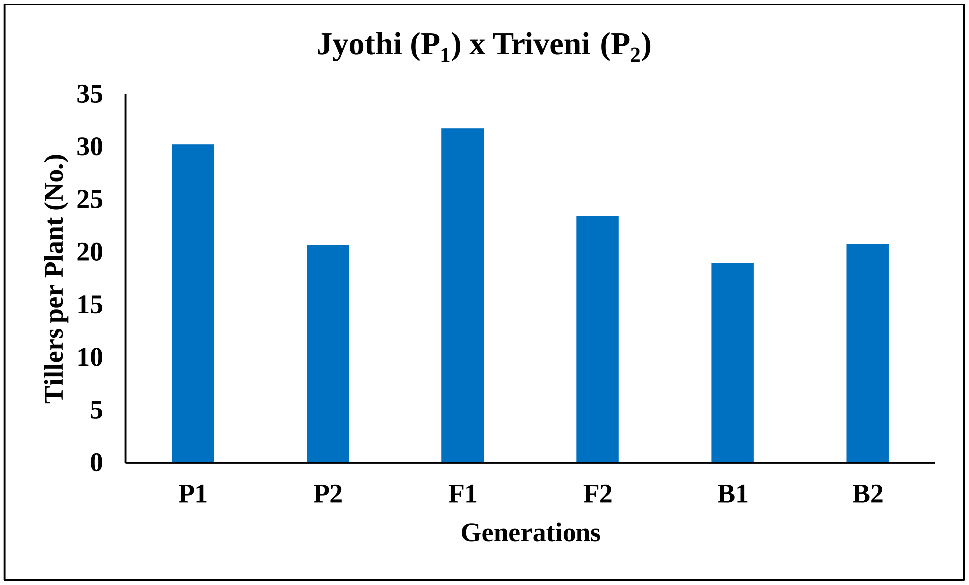
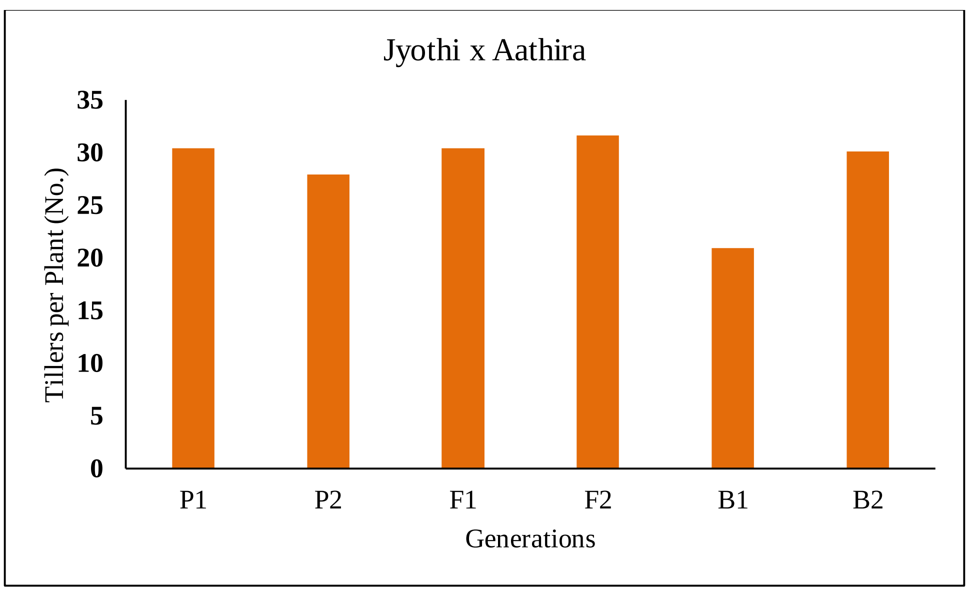
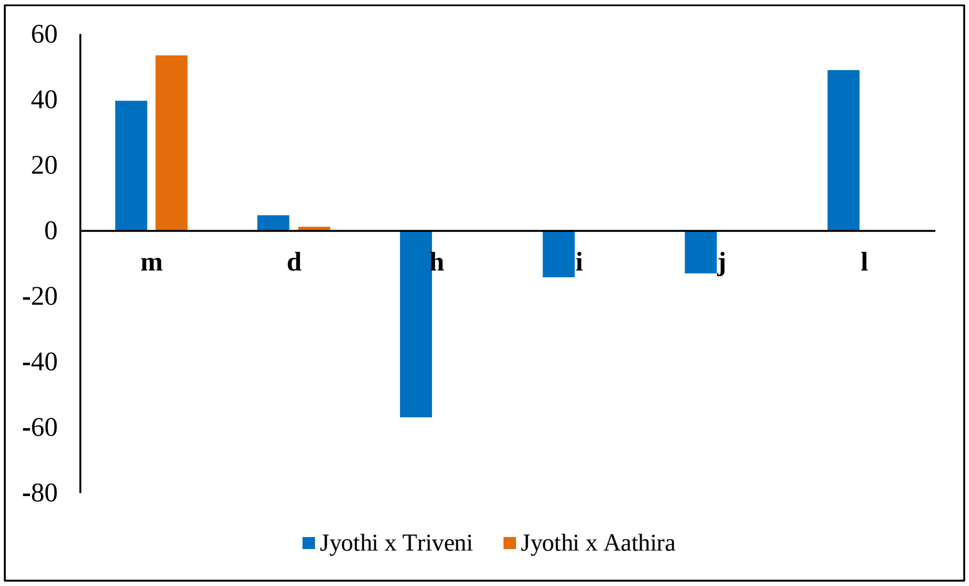


Fig. 8: Number of tillers for six generations in the cross Jyothi x Aathira



Relatively high magnitude for dominance (h) component over additive (d) component (fig.9) reveals the predominant dominant gene effect for inheritance of number of tillers in the cross Jyothi x Triveni.

Fig.9: Six parameter model for tillers per plant



The character exhibited all the three type of gene action *viz*. additive, dominance and epistasis in the cross Jyothi x Triveni. This shows the complex inheritance of the character in the cross. Hence simple selection may not be effective for the improvement of the character. Jondhale *et al*. (2018) also reported the importance of both additive and dominance gene effects in the inheritance of tillers per plant. Significant and positive additive (d) component (fig.9) reveals the major contribution of genes from the parent with high tillers (fig.8) for inheritance of tillers per plant in the cross Jyothi x Aathira. It was observed that the character is influenced by additive gene effect in the cross Jyothi x Aathira. Direct selection will be rewarding characters with predominant additive gene action.

Additive gene effect was reported positive for the character in both crosses (Fig. 9). This is supported by the findings of Divya *et al*. (2014).

Inheritance of tillers per plant is influenced by additive gene effect in the cross Jyothi x Aathira. Additive gene effect can be effectively utilized by direct selection or by pedigree method to improve the character. The character shows complex inheritance pattern in the cross Jyothi x Triveni since the character is influenced by additive, dominance and all the three types of non-allelic interaction. Hence selection at early segregating generations may not be rewarding. Selection at later generations might be helpful not only avoid dominance gene effect but also to obtain superior genotype. Intermating among selected genotype from F_2 can also be adopted to improve the character. This help to remove the dominance gene effect and to break undesirable linkages.

5.1.4 Panicles per plant (nos.)

Both the crosses recorded significance for the scales which indicates the presence of non-allelic interaction in the expression of the character. These results were in agreement with the findings of Chamundeswari *et al*. (2013) and Savitha and Kumari (2015). Significant scaling test reveals that epistatic interaction model is adequate to explain the gene action for the character.

Significant scale A and B indicates the presence of additive x dominance interaction for inheritance of character. Significant scale C reveals the presence of dominance x dominance interaction whereas the significant scale D indicates the presence of additive x additive interaction for inheritance of character in the cross Jyothi x Triveni.

The significant scale A reveals the presence of additive x dominance interaction for the inheritance of panicles per plant in the cross Jyothi x Aathira.

Mean (m) effect was significant and positive for panicles per plant in both the crosses (fig.12) which is in accordance with the findings of Nayak *et al*. (2007), Savitha and Kumari (2015) and Rao *et al*. (2017).

Significant and positive additive (d) component (fig.12) in the cross Jyothi x Triveni reveals that the character is mostly controlled by genes carried from the parent having higher panicles per plant (fig.10). Significant and negative dominance (h) gene effect (fig.12) indicates dominance effect towards the parent having lower panicle number per plant (fig.10). Significant and opposite sign for the dominance (h) component and dominance x dominance (l) components (fig.12) reveals the presence of duplicate epistasis in the expression of the character in the cross. The relatively high magnitude of dominance component over additive component (fig.12) indicates the importance of dominance gene effect in inheritance of the character.

Significant and negative additive (d) component (fig.12) in the cross Jyothi x Aathira indicates that the parent having lower panicles per plant (fig.11) contributes more genes for the expression of the character. Significant and negative dominance gene effect (fig.12) indicates the dominance effect towards parent having lower panicle number per plant (fig.11). Significant and opposite sign for the dominance (h) component and dominance x dominance (l) components (fig.12) reveals the presence of duplicate epistasis in expression of the character in the cross. The relatively high magnitude of dominance component over additive component (fig.12) indicates the importance of dominance gene effect in inheritance of panicles per plant.

The presence of duplicate gene action in the expression of the character are in conformity with the studies of Hasib *et al*. (2002), Divya *et al*. (2014) and Rao *et al*. (2017). Nayak *et al*. (2007) observed similar sign for dominance (h) component and dominance x dominance (l) component which reveals the presence of complementary epistasis. Rao *et al*. (2017) also reported complementary epistasis for the character under irrigated condition. Srivastava *et al*. (2012) reported significant additive (d) and dominance x dominance (l) gene effect with duplicate type of epistasis.

Fig. 10: Panicles in six generations in the cross Jyothi x Triveni

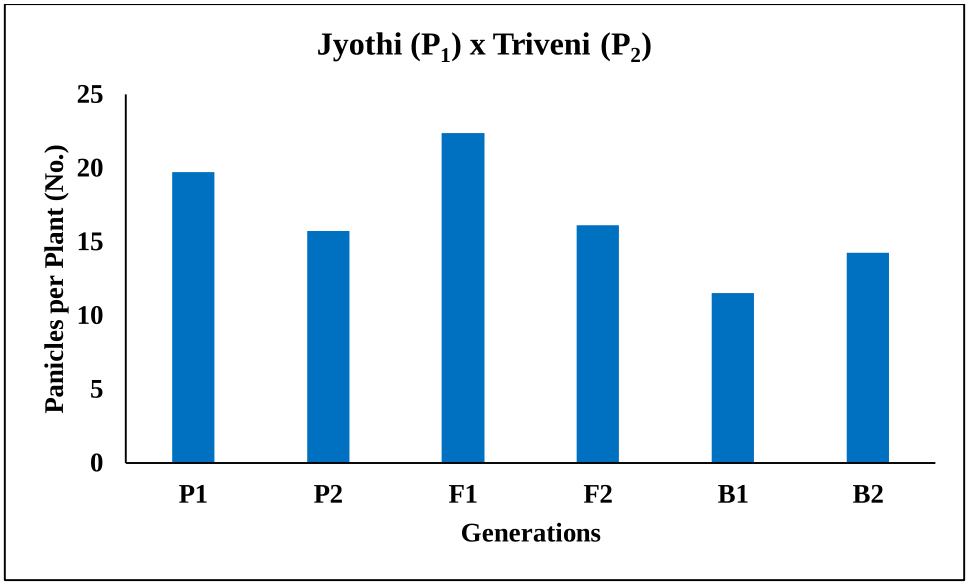


Fig. 11: Panicles in six generations in the cross Jyothi x Aathira

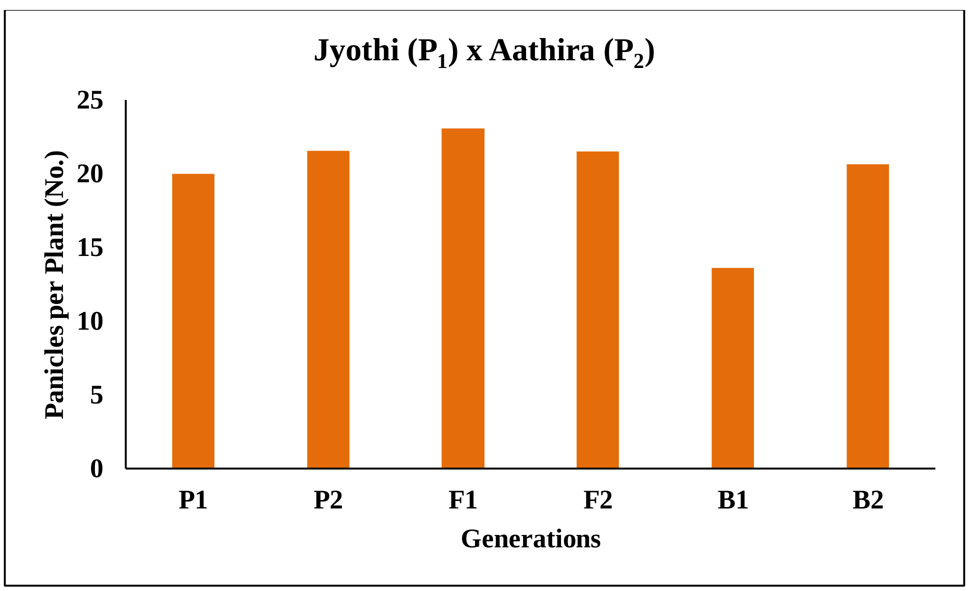
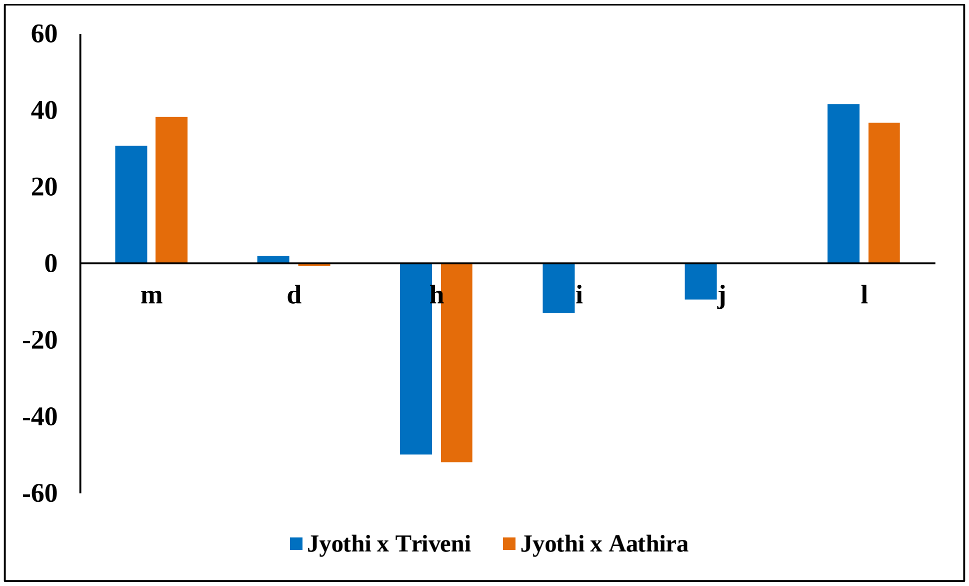


Fig.12: Six parameter model for panicles per plant



Subbulakshmi (2013) reported additive, dominance x dominance and duplicate gene action for panicles per plant whereas Patil *et al*. (2003) reported predominant additive gene effect in regulating the character. Preponderance of dominant additive gene effects indicates that direct election maybe in the improvement of the character.

The estimation of genetic components of variances resulted with degree of dominance more than one for number of panicles in both the crosses that reveals the major role of dominance in the expression of the character. High degree of dominance, more than one, was observed for the character by Rao *et al*. (2017).

The character recorded the influence of additive and non-additive gene effects with dominant epistasis for inheritance. These results indicate that the character can be improved by selection at later generations. Since dominance gene effect is predominant with duplicate gene effects selection in early segregating generations might not yield superior recombinants. Delaying selection to later generations could help avoid the effect of dominance gene effect. Intermating of F_2 segregants could help not only to harness the dominance gene action but also to break undesirable linkages present.

5.1.5 Panicle length (cm)

Significant scaling test reveals the presence of non-allelic interaction in the inheritance of character in both crosses. This reveals that epistatic interaction model is adequate to explain the gene action for panicle length. This is in agreement with results of Jondhale *et al*. (2018).

Significant scale A indicates the presence of additive x dominance interaction in the inheritance of the character in the cross Jyothi x Triveni. Significant scale A and B indicates the presence of additive x dominance interaction in the inheritance of panicle length in the cross Jyothi x Aathira. Significant scale C indicates the presence of dominance x dominance interaction for inheritance of character.

Mean (m) effect was significant and positive for panicle length in both the crosses (fig.15). The results are in conformity to the findings of Verma *et al*. (2006) and Nayak *et al*. (2007).

Significant negative additive (d) component (fig.15) in the cross Jyothi x Triveni component reveals that the major genes for expression of the character were contributed by the parent having lower panicle length (fig.13).Significant and negative dominance (h)component (fig.15)indicates that the character shows dominance towards the parent having short panicle length (fig.13).The significant and opposite sign of the dominance component (h) and dominance x dominance (l) component(fig.15) indicates the presence of duplicate gene action for governing the character. High magnitude of dominance component (fig.15) was also recorded than additive component which shows the major role of dominance gene action in expression of the character in the cross Jyothi x Triveni.

Fig. 13: Panicle length for six generation in the cross Jyothi x Triveni

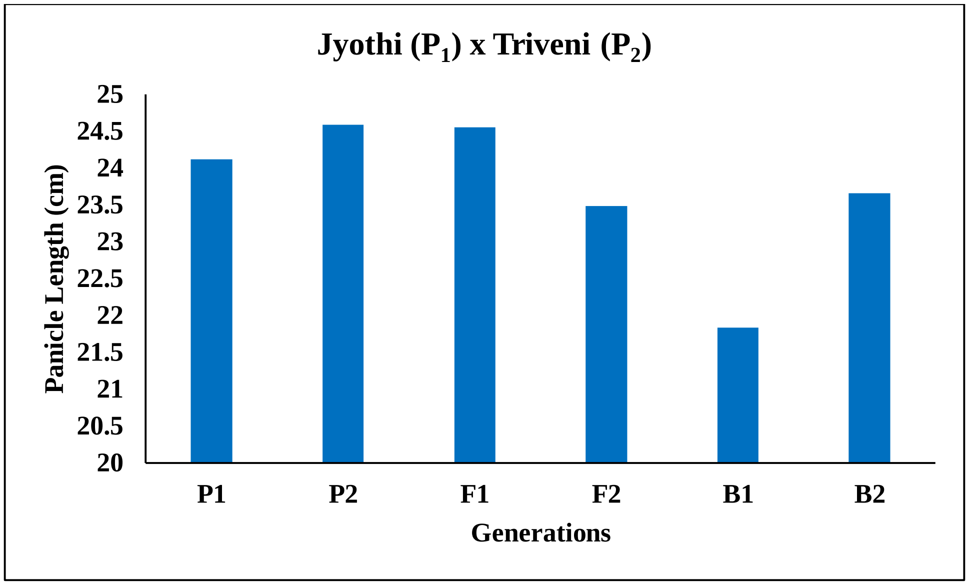
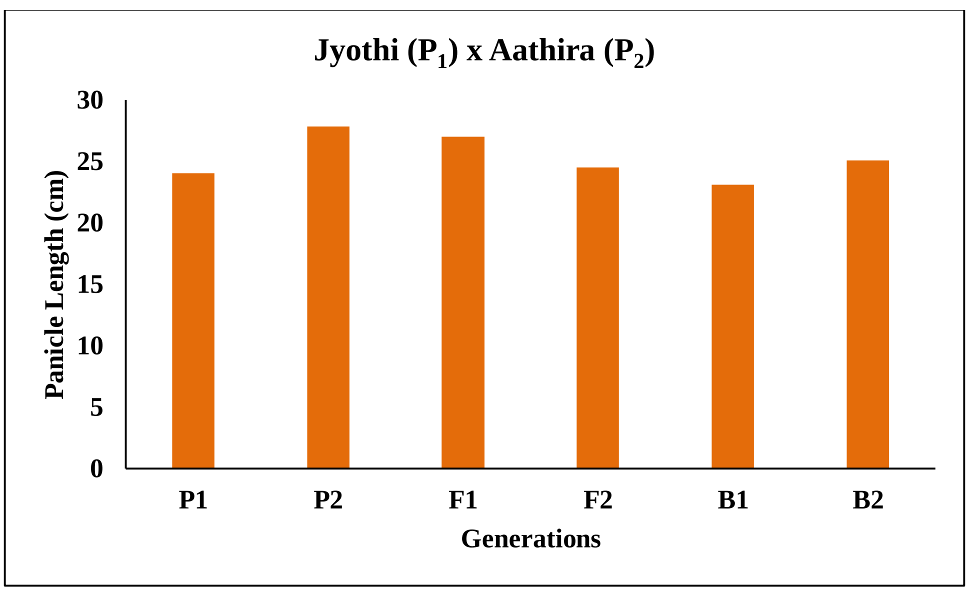


Fig. 14: Panicle length for six generation in the cross Jyothi x Aathira

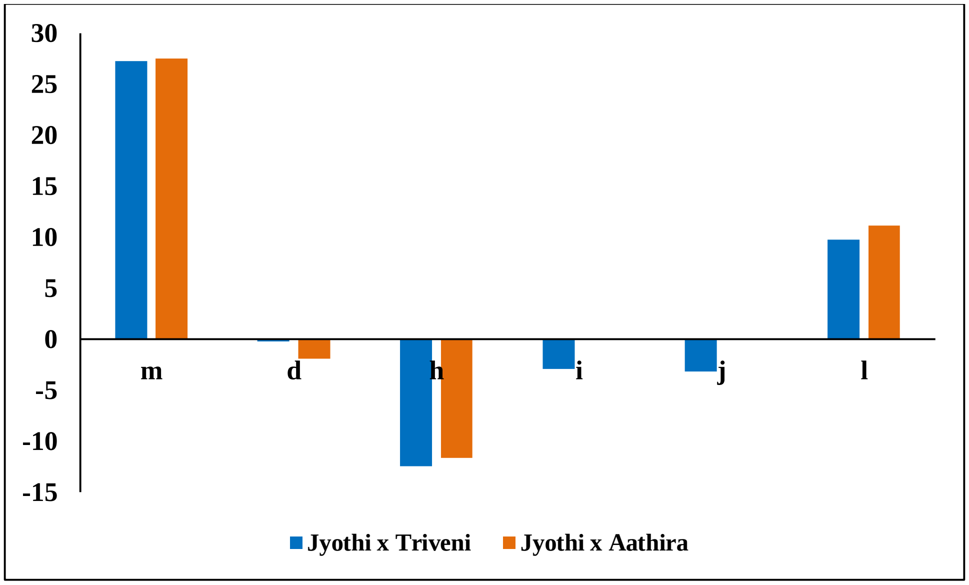


Significant and negative additive (d) component (fig.15) reveals that the major genes for expression of character were contributed by the parent with lower panicle length (fig.14) in the cross Jyothi x Aathira. Significant and negative dominance (h) component (fig.15) indicates that the character shows dominance towards the parent having short panicle length (fig.14). The significant and opposite sign of the dominance (h) component and dominance x dominance (l) component (fig.15) indicates the presence of duplicate gene action for governing the character. High magnitude of dominance component than additive component (fig.15) shows the major role of dominance gene action in the expression of character.

Both the crosses reported significant and negative additive (d) component (Fig. 15). Negative sign reveals that the major genes for expression of character were contributed by the parent having lower panicle length. The findings are in conformity to the reports of Chamundeswari *et al*. (2013) and Rao *et al*. (2017).

Dominance component (h) was negative in both crosses (Fig. 15). Rao *et al*. (2017) reported significant and positive dominance component (h) under normal irrigated condition.

Fig.15: Six parameter model for panicle length



Significant and negative dominance component (h) along with significant and positive dominance x dominance (l) component indicates the presence of duplicate type of epistasis in the inheritance of panicle length in both the cross. These findings are in agreement with the results of Nayak *et al*. (2007), Divya *et al*. (2014) and Rao *et al*. (2017).

Higher magnitude for dominance gene action and more than one degree of dominance indicates the major role of dominance gene action in the expression of character. Rao *et al*. (2017) have reported similar results.

The inheritance of panicle length is influenced by additive and dominance gene effect with duplicate type of epistasis; hence selection maybe postponed to later generations. Pedigree method followed by delayed selection at later generations can also be adopted to improve the character. Intermating among F_2 segregants or multiple cross programme with selected segregants can be adopted to avoid the effect of dominance in the character there by obtaining desirable recombinants.

5.1.6 Spikelets per panicle (no.)

Significant scaling test reveals that epistatic interaction model is adequate to explain the gene action for spikelets per panicle. Findings of Roy and Senapati (2011) and Rao *et al*. (2017) are in agreement with the results of the present study.

Significant scale A indicates the presence of additive x dominance interaction in the cross Jyothi x Triveni. Significant scale C indicates the presence of dominance x dominance interaction. Significant scale D reveals the presence of additive x additive interaction in inheritance of spikelets per panicle in the cross Jyothi x Triveni.

Significant scale A and B indicates the presence of additive x dominance interaction in the cross Jyothi x Aathira. Significant scale C indicates the presence of dominance x dominance interaction for inheritance of spikelets per panicle.

Mean (m) effect was significant and positive for spikelets per panicle in both the crosses (fig.18). This is conformity with the findings of Divya *et al*. (2014) and Rao *et al*. (2017).

Significant and negative additive (d) component (fig.18) in the cross Jyothi x Triveni reveals that the major contribution in inheritance was from the parent with less number of spikelet per panicle (fig.16). Negative sign for dominance (h) component (fig.18) indicates that the parent having less number of spikelet played a larger role in the inheritance (fig.16). Significant and opposite sign of the dominance (h) component and dominance x dominance (l) component (fig.18) indicates the presence of duplicate gene action in the expression of the character. Higher magnitude for dominance (h) component than the additive component (fig.18) indicating the predominant role of dominance gene effect in inheritance of character in the cross Jyothi x Triveni.

Additive (d) component and dominance (h) components were significant and negative in the cross Jyothi x Aathira (fig.18). The negative sign for the additive (d) component reveals the major contribution of the parent with less number of spikelet per panicle (fig.17) in the inheritance of character. Negative sign of dominance component indicates the dominance effect towards the parent having lowest spikelets per panicle (fig.17). The significant and opposite sign of the dominance (h) component and dominance x dominance (l) component (fig.18) indicates the presence of duplicate gene action in the expression of the character. The relatively high magnitude for dominance component was observed than the additive component (fig.18) which shows the predominant role of dominance gene effect in the inheritance of character.

Additive component (d) was significant and negative for the character in both the crosses (Fig 18) which is supported by the findings of Rao *et al*. (2017),

Fig. 16: Spikelet number for six generation in the cross Jyothi x Triveni

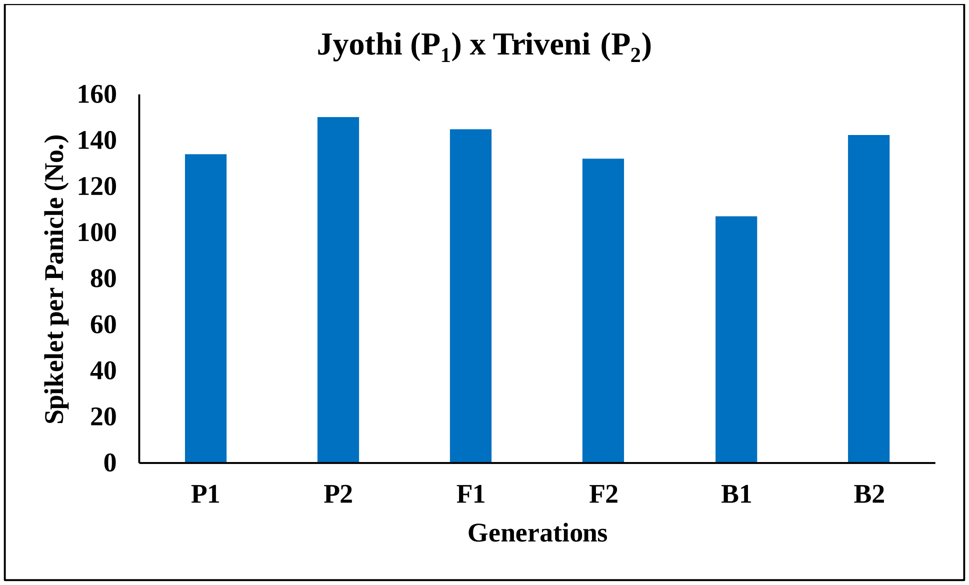


Fig. 17: Spikelet number for six generation in the cross Jyothi x Aathira

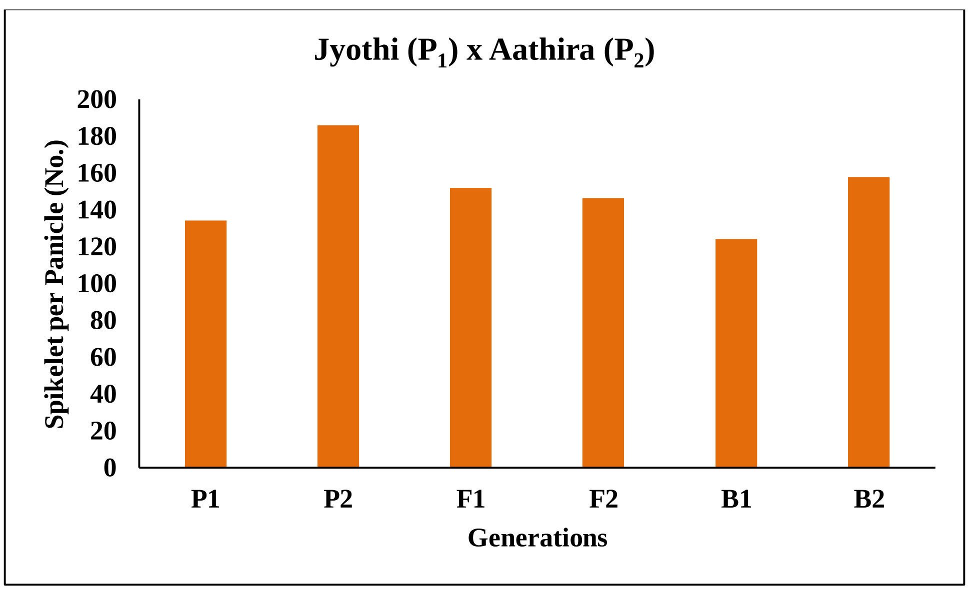
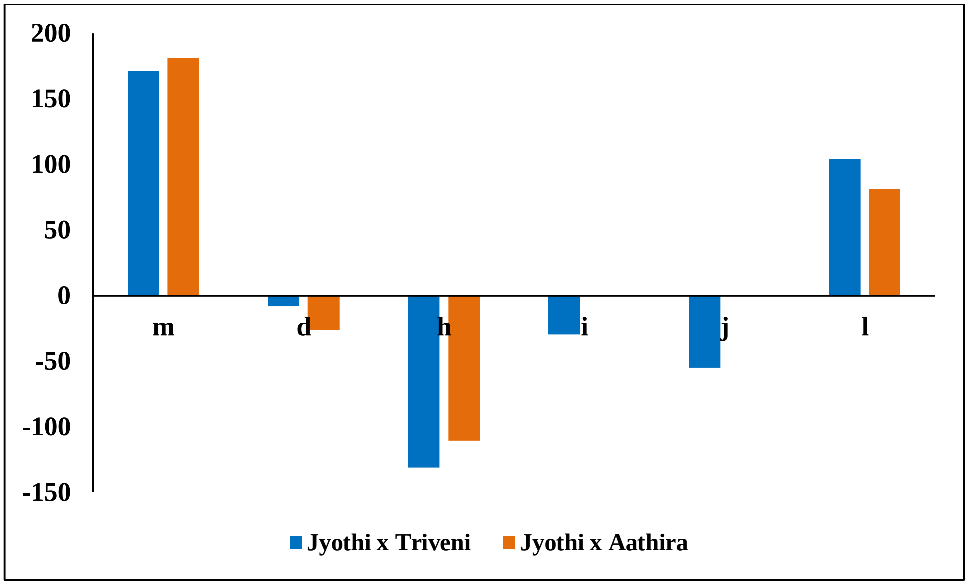


Fig.18: Six parameter model for spikelet per panicle



Dominance component (h) was significant and negative in both crosses (Fig. 18). This is in accordance with the results of Rao *et al.* (2017). Presence of duplicate type of epistasis in the inheritance of spikelets per panicle is supported by Hasib *et al*. (2002), Divya *et al*. (2014) and Rao *et al*. (2017).

The character number of spikelet per panicle is influenced by additive and dominance gene effect with duplicate epistasis in both the cross. Predominant additive gene effect with duplicate epistasis can be exploited by the pedigree method of breeding. Since dominance gene playing a major role in the inheritance of character selection at early segregating generation might not yield desirable recombinants. Delaying selection process to later generation could help to avoid the dominance gene effect.

5.1.7 Seeds per panicle (no.)

Significant scaling test reveals the presence of non-allelic interaction in the inheritance of seeds per panicle in both the crosses. This also reveals that epistatic interaction model is adequate to explain the gene action for seeds per panicle. This is in conformity with the studies of Nayak *et al*. (2007) and Divya *et al*. (2014).

Significant scale A and B indicates the presence of additive x dominance interaction for the inheritance of seeds per panicle in the cross Jyothi x Triveni and Jyothi x Aathira. Significant scale C reveals the presence of dominance x dominance interaction in both the cross.

Mean (m) effect was significant and positive for seeds per panicle in both the cross (fig.21).This was supported by the results of Divya *et al*. (2014), Savitha and Kumari (2015) and Bano *et al*. (2017).

Significant and negative additive (d) component (fig.21) in the cross Jyothi x Triveni indicates that the character is mostly contributed by the genes carried from the parent having less number of seeds per panicle (fig.19). Negative sign for dominance (h) component (fig.21) reveals that dominance effect towards the parent with lower seeds per panicle (fig.19). Significant and opposite sign for dominant (h) component and dominance x dominance component (l) component (fig.21) indicates the presence of duplicate gene action in expression of character. The high magnitude for dominance component over the additive component (fig.21) for the character indicates the major role of dominance gene effect in the inheritance of character.

Significant and negative additive (d) component (fig.21) in the cross Jyothi x Aathira indicate that the character is mostly contributed by the genes from the parent having less number of seeds per panicle (fig.20). The negative sign for dominance (h) component (fig.21) reveals that dominance of the character towards the parent with lower seeds per panicle (fig.20). Significant and opposite sign for dominant (h) component and dominance x dominance (l) component (fig.21) indicates the presence of duplicate gene action in expression of seeds per panicle in the cross Jyothi x Aathira. High magnitude for dominance component over additive component (fig.21) for the character indicates the major role of dominance gene effect in inheritance of character.

Fig. 19: Number of seeds per panicle in six generation in Jyothi x Triveni

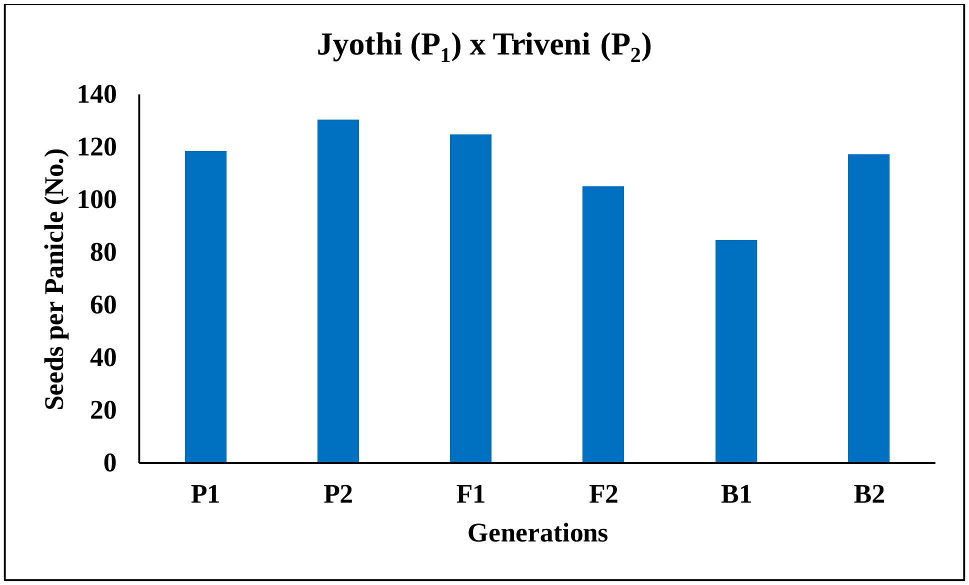


Fig. 20: Number of seeds per panicle in six generation in Jyothi x Aathira

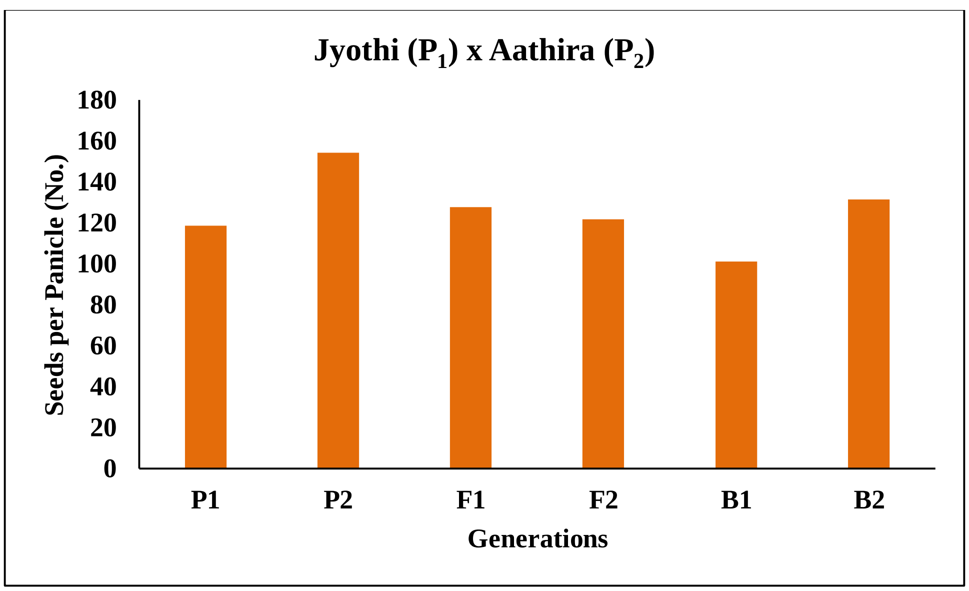
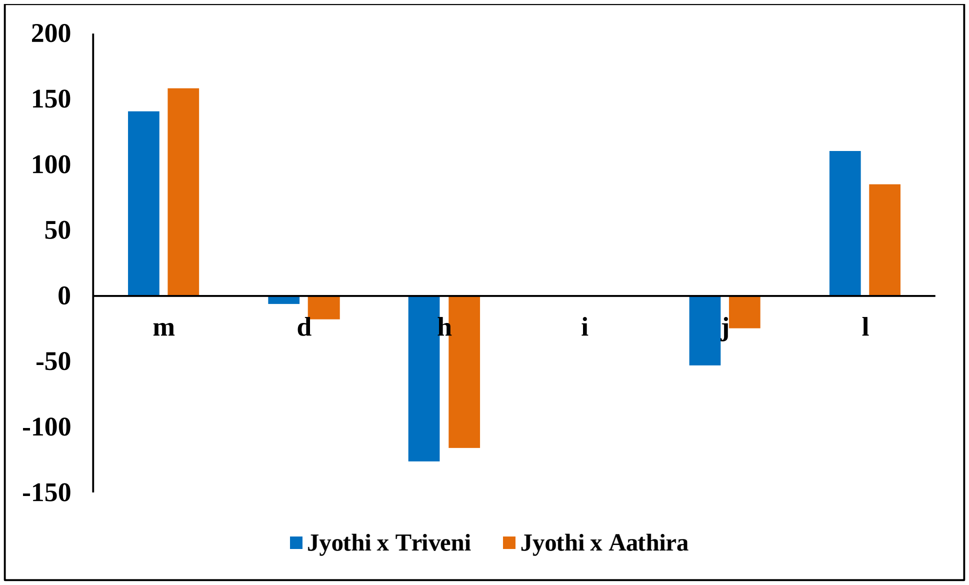


Fig.21: Six parameter model for seeds per panicle



Additive component was significant and negative for seeds per panicle in both the crosses. Divya *et al*. (2014) and Savitha and Kumari (2015) reported significant and positive additive gene effect for the character, which shows the major contribution of the gene from the parent having more number of seeds per panicle.

Dominance component (h) was recorded significant and negative in both the crosses (Fig. 21).This was supported by the results of Divya *et al*. (2014), Savitha and Kumari (2015) and Bano *et al*. (2017). Dominance gene effect and dominance x dominance gene interactions were in opposite direction which shows the presence of duplicate type of epistasis in the inheritance of character in both the cross. This was in agreement with the findings of Divya *et al*. (2014). Bano *et al*. (2017) reported significant and similar sign for dominance (h) component and dominance x dominance (l) component that indicates the presence of complementary gene action for inheritance of the character.

The high magnitude for the dominance component over the additive component was observed for seeds per panicle in both the cross. Gomez *et al*. (2003) observed predominant additive (d) gene effect for the character whereas the studies by Anbumalarmathi *et al*. (2005) revealed the presence of both additive and non-additive gene effects in the inheritance of character.

Nayak *et al*. (2007) reported the importance of additive (d), dominance and all the three types of non-allelic interaction in controlling the character. Bano *et al*. (2017) also reported significance for all six parameters *viz*. m, (d), (h), (i), (j), and (l) for seeds per panicle.

The seeds per panicle were influenced by additive, dominance gene effect and epistatic interactions with duplicate type of epistasis. This indicates the complex inheritance of the character. Direct selection will not yield desirable recombinants. Hence intermating among selected F_2 genotypes or recurrent selection may help to obtain good recombinants by avoiding the dominance gene effect. Pedigree method followed by delayed selection can also be adopted to improve the character.

5.1.8 Days to maturity

Significant scaling test for days to maturity was similar to the results of Bano *et al*. (2017) and Ganapati *et al*. (2020).

Significant scale A and B indicates the presence of additive x dominance interaction in the cross Jyothi x Aathira. Significant scale C reveals the presence of dominance x dominance interaction whereas the significant scale D indicates the presence of additive x additive interaction for the inheritance of days to maturity in the cross.

Significant scale B indicates the presence of additive x dominance interaction for inheritance of days to maturity in the cross Jyothi x Aathira. Significant scale C reveals the presence of dominance x dominance interaction in expression of the character.

Mean (m) effect was significant and positive for days to maturity in both the crosses (fig.24). It is in conformity with the findings of Srivastava *et al*. (2012) and Bano *et al*. (2017)

Fig. 22: Days to maturity for six generation in the cross Jyothi x Triveni

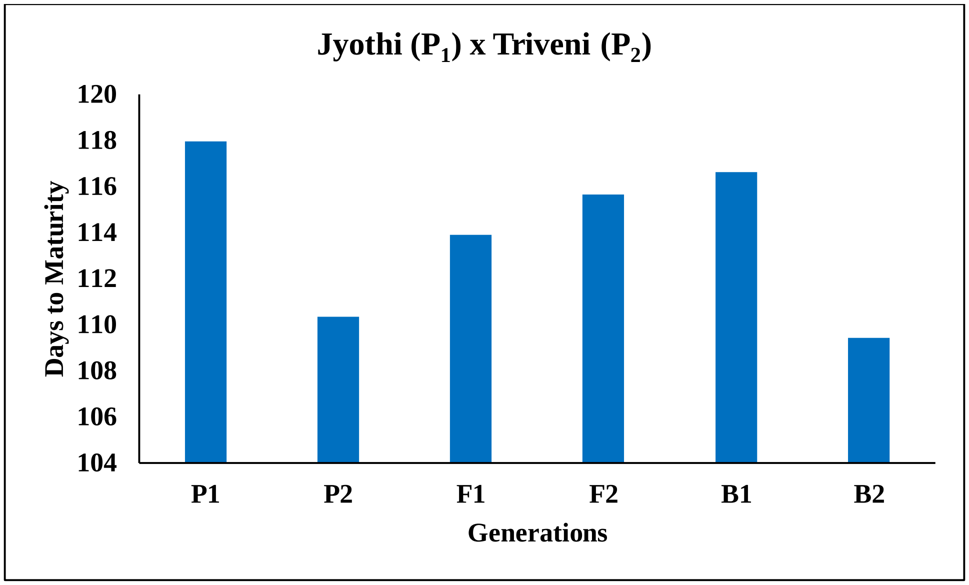
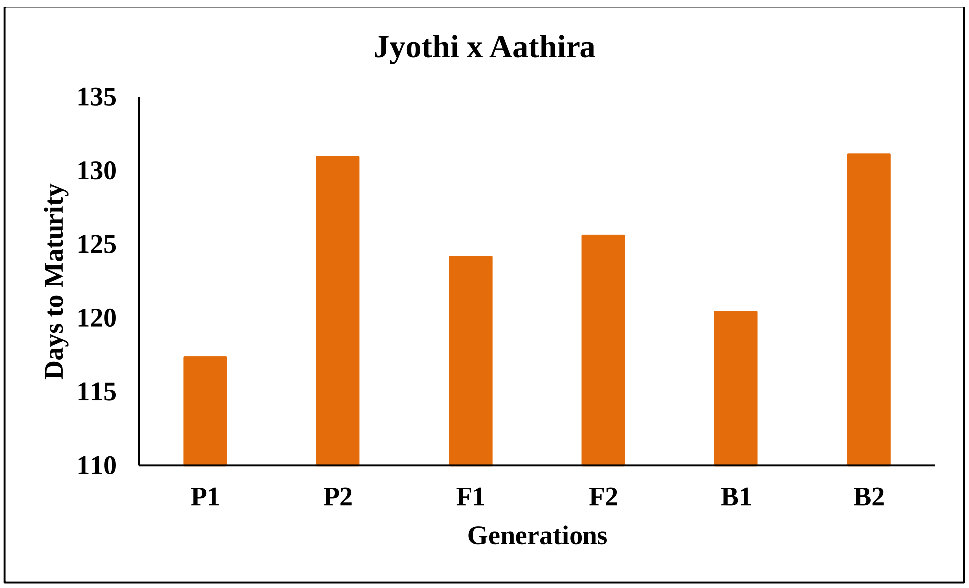


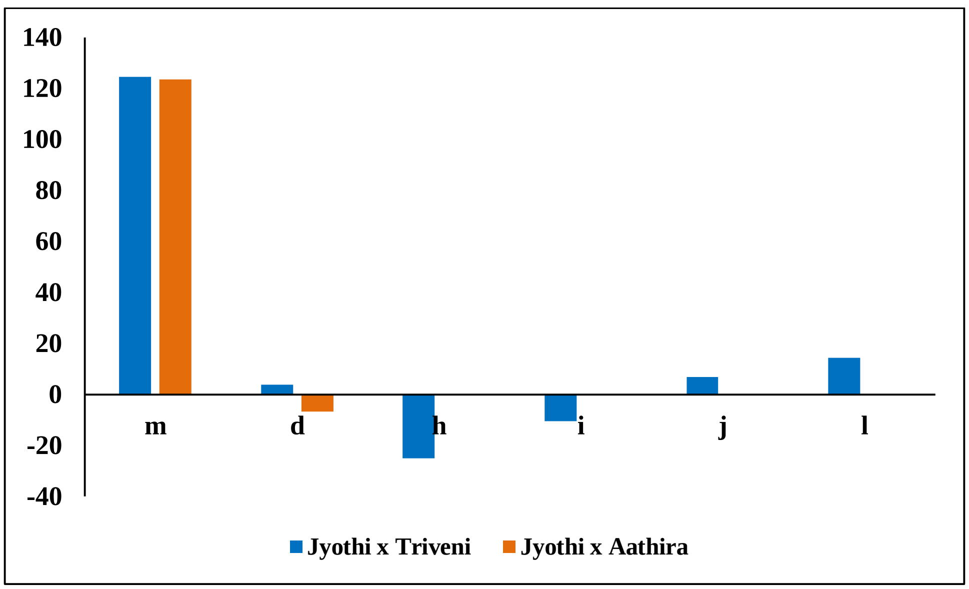
Fig. 23: Days to maturity for six generation in the cross Jyothi x Aathira



Significant and positive additive (d) component (fig.24) indicates that late maturing parent (fig.22) contributes more gene for the character in the cross Jyothi x Triveni. The significant and negative dominance (h) component (fig.24) reveals that dominance towards the parent having the shortest duration (fig.22). This was supported by Srivastava *et al*. (2012). Bano *et al*. (2017) reported significant and positive dominance gene effect which shows the dominance towards the parent having longer duration.

Significant and opposite sign for the dominance components (h) and dominance x dominance component (l) indicates the presence of duplicate gene action in governing the character in Jyothi x Triveni. This was supported by Srivastava *et al*. (2012), Bano *et al*. (2017) and Ganapati *et al*. (2020).

Fig.24: Six parameter model for days to maturity



Dominance (d) component (fig.24) showed relatively high magnitude than additive component in the cross Jyothi x Triveni which reveals the preponderance of dominance gene action in the inheritance of character which are in conformity with the reports of Srivastava *et al*. (2012) and Bano *et al*. (2017).

Significant and negative additive (d) component (fig.24) indicates higher contribution of the short duration parent (fig.23) in the cross Jyothi x Aathira. Srivastava *et al*. (2012) and Bano *et al*. (2017) have reported significant and negative additive gene effects. The predominant additive effect can be exploited by direct selection to yield early duration genotypes in this cross.

Inheritance of days to maturity was influenced by additive and non-additive gene actions with the duplicate type of epistasis in the cross Jyothi x Triveni. This indicates the complex nature of inheritance governing the character. Since additive and dominance gene plays a major role in the inheritance of character simple selection might not help to identify the desired recombinants. To overcome the dominance gene effect, biparental mating, mating between selected individual from F_2 generation or recurrent selection might be helpful. Since rice is a self-pollinated crop pedigree method followed by delaying selection to later generations may be effective in isolating early duration genotypes. Days to maturity recorded significant additive gene effect in the cross Jyothi x Aathira. Direct selection to yield in early duration genotypes will be rewarding.

5.1.9 Test weight (g)

Significant scaling test is supported by the findings of Kumar *et al*. (2007) and Chamundeswari *et al*. (2013).

Significant scale A and B indicates the presence of additive x dominance interaction for the inheritance of character in the cross Jyothi x Triveni. Significant scale C reveals the presence of dominance x dominance interaction in the expression of the character.

Significant scale A and B in the cross Jyothi x Aathira indicates the presence of additive x dominance interaction and significant scale C reveals the presence of dominance x dominance interaction for the character.

Fig. 25: Test weight for six generations in the cross Jyothi x Triveni

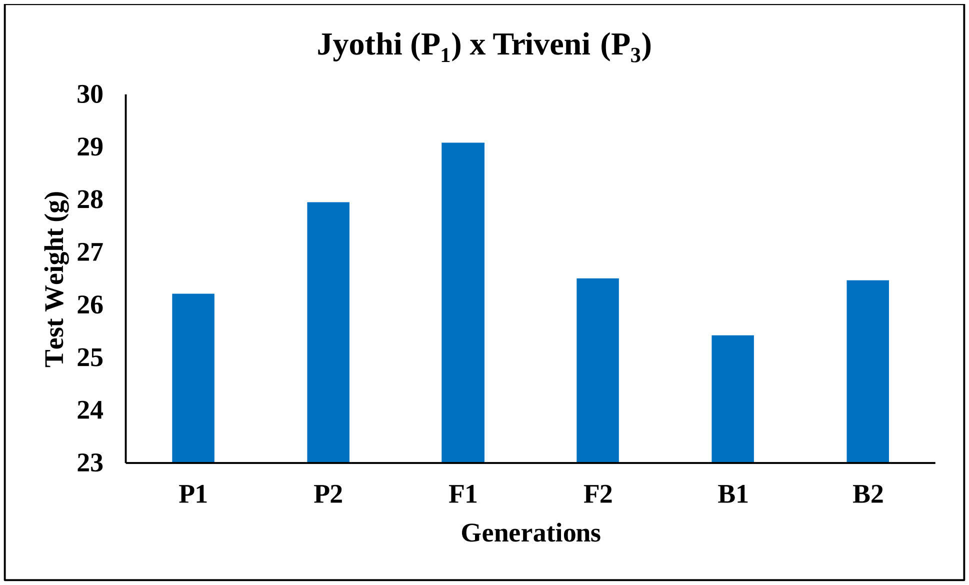
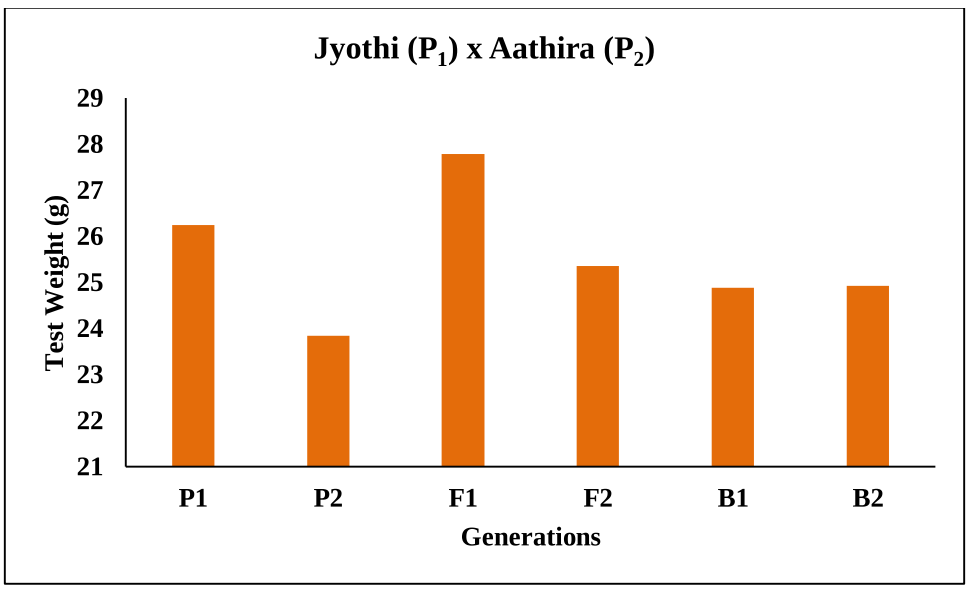


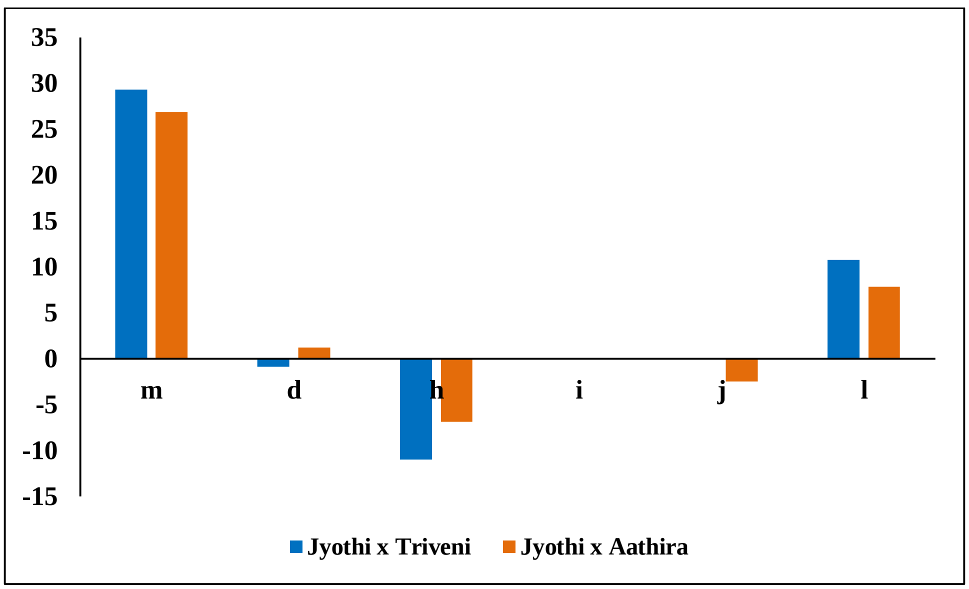
Fig. 26: Test weight for six generations in the cross Jyothi x Aathira



Mean (m) effect was significant and positive for test weight in both the crosses (fig.27). This is in agreement with the findings of Verma *et al*. (2006) and Nayak *et al*. (2007).

Significant and negative additive (d) component (fig.27) in the cross Jyothi x Triveni indicates the major contribution of the parent with lower test weight (fig.25) in the inheritance of the character. This was supported by Nayak *et* al. (2007) and Chamundeswari *et al*. (2013). The negative sign for dominance (h) component (fig.27) indicates the dominance of the character towards parent having lower test weight (fig.25).The opposite sign of dominance (h) component and dominance x dominance (l) component (fig.27) indicates the presence of duplicate type of epistasis for the character.

Fig.27: Six parameter model for test weight



Significant and positive additive (d) component (fig.27) shows the predominant contribution of the parent with high test weight (fig.26) in the inheritance of the character in the cross Jyothi x Aathira. Chamundeswari *et al*. (2013) reported significant and positive additive component. The negative sign for dominance (h) component (fig.27) indicates the dominance of the character towards parent having lower test weight (fig.26).The opposite sign of dominance component (h) and dominance x dominance (l) component (fig.27) indicates the presence of duplicate type of epistasis for the character.

Dominance component (h) was significant and negative in both the crosses (fig. 27). This is supported by the findings of Nayak *et* al. (2007), and Chamundeswari *et al*. (2013). Chamundeswari *et al*. (2013), Divya *et al*. (2014) and Rao *et al*. (2017) have observed duplicate epistasis for inheritance of test weight.

Higher magnitude of dominance gene effect than additive gene effect observed in both the cross indicating the major role of dominance gene effect in expression of test weight.

The presence of significant dominance effect coupled with duplicate epistasis restricts the scope of simple selection for improvement of the character. Non-allelic interactions with duplicate type of epistasis can be utilized effectively in the pedigree method of breeding by delaying selection to later generations. Biparental mating in early segregating population or recurrent selection may be adopted, which help to exploit both additive and dominance gene effect simultaneously.

5.1.10 Grain yield per plant (g)

Significant scaling tests are supported by Verma *et al*. (2006) and Chamundeswari *et al*. (2013).Significant scale A and B indicates the presence of additive x dominance interaction for inheritance of the character in the cross Jyothi x Triveni. Significant scale C reveals the presence of dominance x dominance interaction whereas the significant scale D indicates the presence of additive x additive interaction for the inheritance of character in the cross.

Significant scale A indicates the presence of additive x dominance interaction for the inheritance of the character in the cross Jyothi x Aathira. Significant scale C reveals the presence of dominance x dominance interaction in the inheritance of grain yield per plant in the cross.

Fig. 28: Seed yield for six generations in the cross Jyothi x Triveni

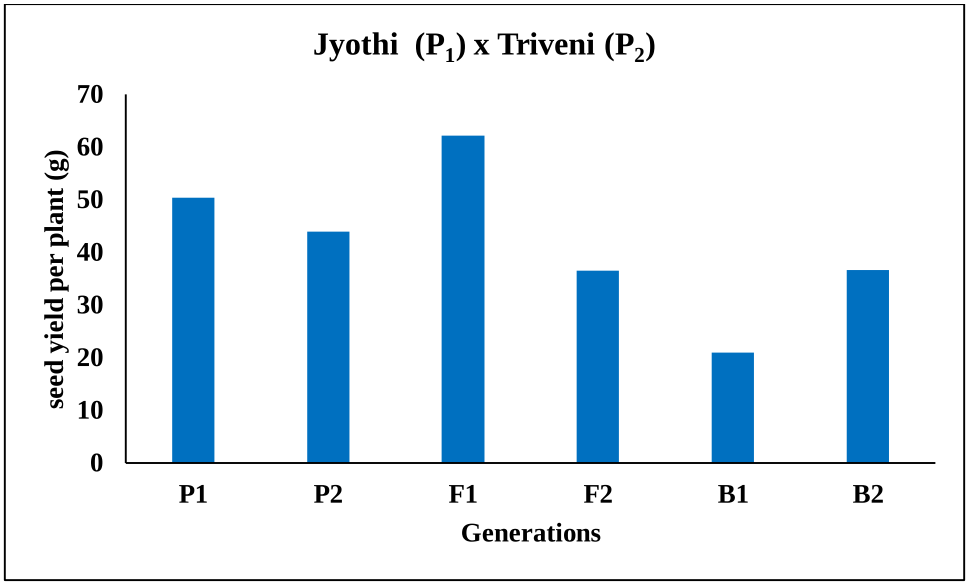
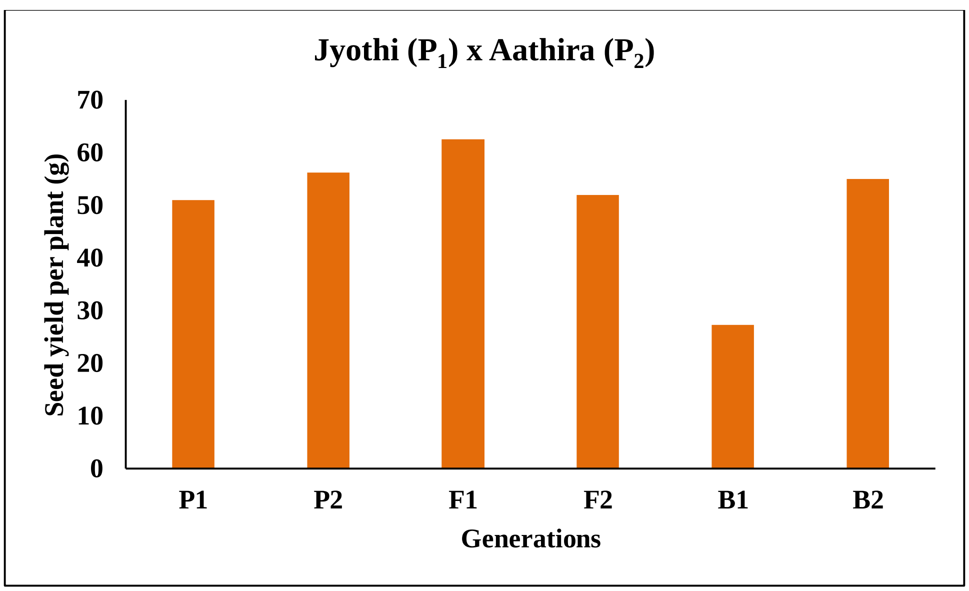


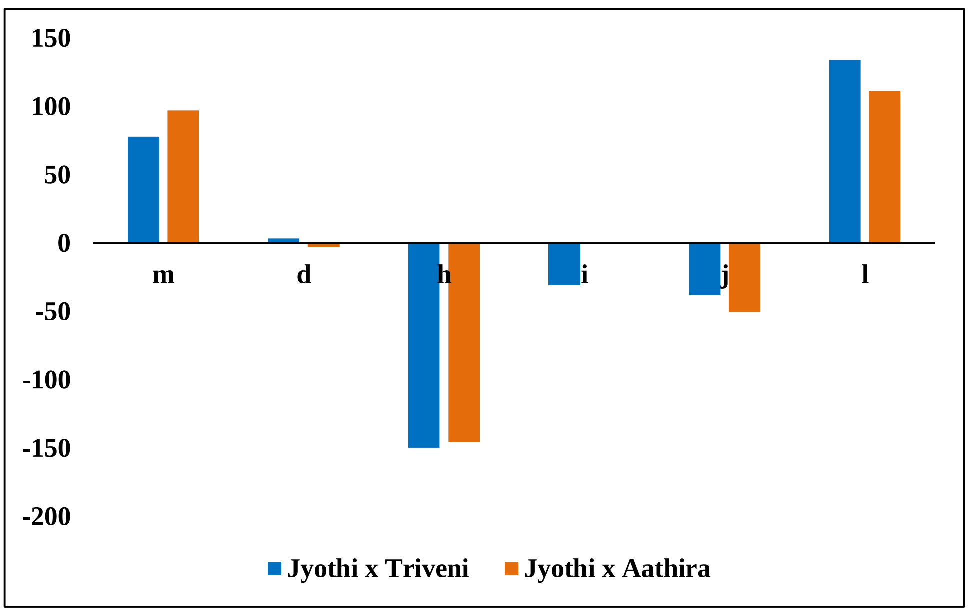
Fig. 29: Seed yield for six generations in the cross Jyothi x Aathira



Mean (m) effect was significant and positive for grain yield per plant in both the cross (fig.30). A significant mean effect for the character is supported by Hasib *et* al. (2002), Divya *et al*. (2014) and Rao *et al.* (2017).

Significant and positive additive (d) component (fig.30) in the cross Jyothi x Triveni reveals that the parent with high grain yield (fig.28) contributes more genes for increasing the character. This was supported by Jondhale *et al*. (2018). Negative sign for dominance (h) component (fig.30) indicates the dominance of the character towards parent having lower grain yield (fig.28). The dominance (h) component was significant and negative and dominance x dominance (l) component (fig.30) was significant and positive. This indicates the presence of duplicate epistasis in the expression of grain yield in the cross. Dominance component (h) was recorded high magnitude than the additive component (d). This indicates the major role of dominance gene in the inheritance of character.

Fig.30: Six parameter model for grain yield per plant



Additive component (d) was significant and negative (fig.30) in the cross Jyothi x Aathira, which shows higher contribution of parent with less grain yield in the expression of the character (fig.29). This was supported by Chamundeswari *et al*. (2013) and Srivastava *et al*. (2012). Negative sign for dominance (h) component (fig.30) indicates dominance effect of character towards the parent having lower grain yield (fig.29).The dominance (h) component was significant and negative and dominance x dominance (l) component (fig.30) was significant and positive. This indicates the presence of duplicate epistasis for the character. Dominance component (h) recorded higher magnitude than the additive component (d). This indicates the major role of dominance gene effect in inheritance of grain yield.

Dominance component (h) was reported significant and negative in both the crosses (fig.30). This was supported by Chamundeswari *et al.* (2013). Whereas Srivastava *et al.* (2012) and Jondhale *et al*. (2018) reported significant positive dominance component which indicate the dominance of the character towards the parent having higher yield per plant. Dominance component (h) was recorded high magnitude than the additive component (d). This was supported by Bano *et al*. (2017) and Nayak *et al*. (2007). Srivastava *et al*. (2012) and Venkatesan *et al*. (2007) also observed relatively high magnitude for dominance component (h) over additive component (d).

The present study recorded significant negative dominance component and significant positive dominance x dominance component in both crosses. This indicates the presence of duplicate type of epistasis in the inheritance of character. This was in agreement with the findings of Babu and Reddy (2002), Kumar *et al.* (2004) and Savitha and Kumari (2015).

Predominant additive and additive x additive gene effects can be exploited by direct selection or by pedigree method followed by selection to obtain desirable recombinants. In the present study the character is influenced by both additive and non-additive genes with duplicate gene effects; hence selection in the early segregating generation may not be useful to obtain desirable recombinants. Rice is a self-pollinated crop so delaying the selection process to later generations may help to overcome the effects of dominance gene effect and to obtain superior recombinants.

5.1.11 Shattering (%)

Significant scale A and B indicates the presence of additive x dominance interaction for inheritance of shattering resistance in Jyothi x Triveni. Significant scale C reveals the presence of dominance x dominance interaction whereas the significant scale D indicates the presence of additive x additive interaction in the inheritance of the character in the cross.

Significant scale A indicates the presence of additive x dominance (j) interaction for the inheritance of shattering resistance in the cross Jyothi x Aathira. Significant scale C reveals the presence of dominance x dominance (l) interaction for inheritance of shattering resistance in the cross Jyothi x Aathira.

Mean (m) effect was significant and positive for shattering per cent in both the cross (fig.33).Significant and positive additive (d) component (fig.33) reveals that the parent with high shattering value (fig.31) contribute more genes for expressing the character in the cross Jyothi x Triveni. Significant and negative dominance (h) component (fig.33) indicates the dominance effect towards the parent having low shattering value (fig.31). The present study recorded significant and negative dominance component (h) with significant positive dominance x dominance (l) component (fig.33) in the cross Jyothi x Triveni. This indicates the presence of duplicate type of epistasis in inheritance of the character. Dominance component (h) recorded high magnitude (fig.33) compared to additive component (i) in the cross Jyothi x Triveni. This indicates the importance of dominance gene action in the inheritance of character.

The presence of significant dominance effect coupled with the duplicate type of epistasis restricts the scope of simple selection for the inheritance of character in the cross

Fig. 31: Shattering percentage for six generation in cross Jyothi x Triveni

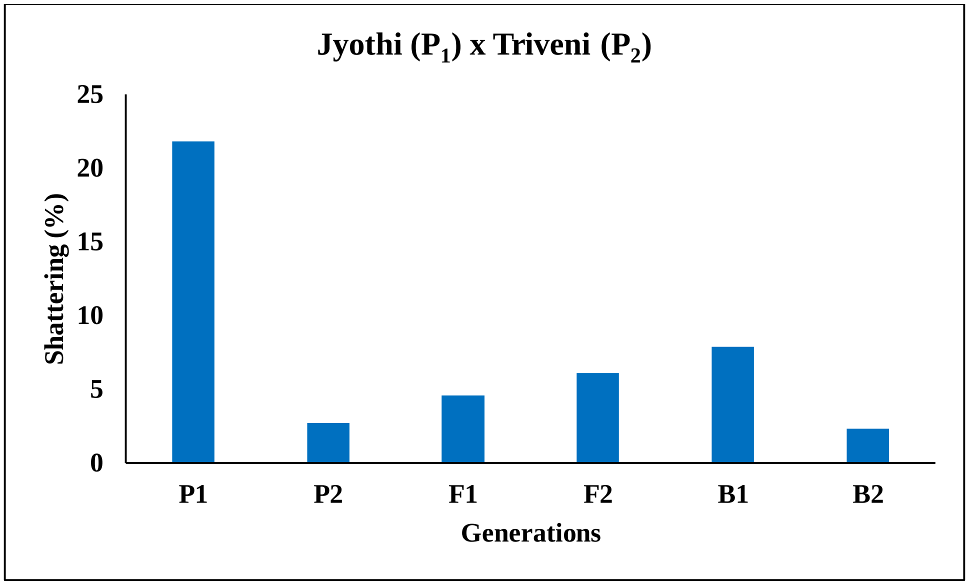
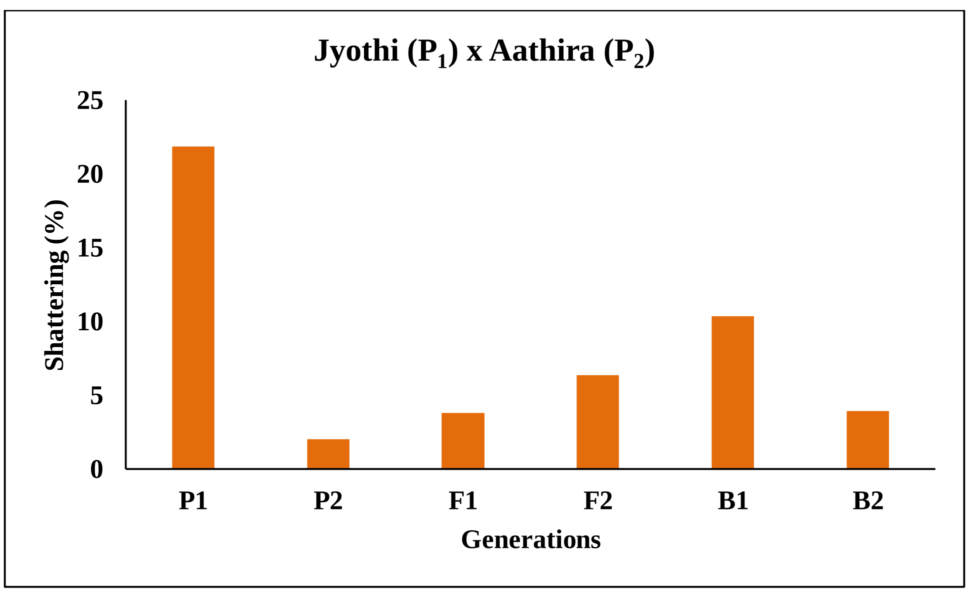


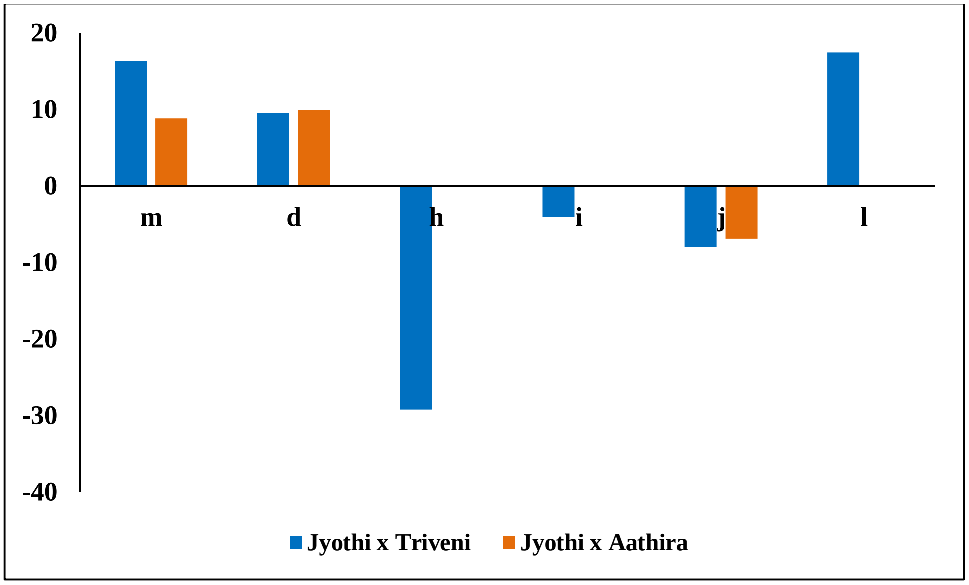
Fig. 32: Shattering percentage for six generation in cross Jyothi x Aathira



Jyothi x Triveni. Non-allelic interactions with duplicate type of epistasis can be utilized effectively in the pedigree method of breeding by delaying selection to a later generation.

Significant and positive additive (d) component (fig.33) in the cross Jyothi x Aathira reveals that the parents with high shattering value contribute more genes for expressing the character (fig.32). The character recorded predominant additive gene effect in the cross Jyothi x Aathira.

Fig.33: Six parameter model for shattering per cent



The presence of significant dominance effect coupled with the duplicate type of epistasis restricts the scope of simple selection for the inheritance of character. Non-allelic interactions with duplicate type of epistasis can be utilized effectively in the pedigree method of breeding by delaying selection to later generations. Biparental mating in early segregating population or recurrent selection may help in exploiting both additive and dominance gene effect simultaneously. In the cross Jyothi x Aathira the character has recorded additive gene effect. Hence simple selection or pedigree method can be utilized to obtain superior genotypes with moderate shattering, from the segregating population derived from the cross Jyothi x Aathira.

In general, dominance gene effect played a major role in controlling the genetic variance in most of the traits studied. Presence of additive and non-additive along with epistatic interaction shows the complex inheritance of the characters. Predominant dominant gene effect along with duplicate epistasis limits the scope of direct selection. The characters *viz*. days to 50 per cent flowering, tillers per plant, days to maturity and shattering per cent in the cross Jyothi x Aathira showed predominant role of additive gene effect in inheritance. These characters can be improved by direct selection. Non allelic interaction with duplicate type of epistasis can be utilized effectively in pedigree breeding by delaying selection to a later generation. Use of bi parental mating in early segregating generation helps to exploit both additive and dominance gene effect there by obtaining superior recombinants having good yield with moderate seed shattering.

5.2 Heterosis

Job (2018) reported significant and negative relative heterosis and heterobeltiosis for days to 50 per cent flowering and days to maturity. Similar results were also obtained in the present study. Significant negative heterosis for plant height in the cross Jyothi x Aathira is in conformity with the results of Alam *et al* (2003) and Job (2018) whereas the character exhibited positive relative heterosis in the cross Jyothi x Triveni. Sarkar *et al* (2002) reported significant and positive heterobeltiosis for plant height.

Tillers per plant recorded significant and positive relative heterosis in the cross Jyothi x Triveni whereas Job (2018) reported significant and negative relative heterosis for the character. Sarkar *et al* (2002) reported significant and negative heterobeltiosis for tillers per plant. Job (2018) also reported significant and negative relative heterosis for panicle length whereas panicle length exhibited positive relative heterosis in the cross Jyothi x Aathira. Significant and negative heterosis for spikelets per panicle is in conformity with the findings of Faiz *et al*. (2006).

Significant and positive heterosis for test weight and days to maturity are in agreement with Alam *et al* (2003) and Job (2018). Significant and positive heterosis for grain yield per plant is in agreement with the results of Faiz *et al* (2006) and Job (2018). Job (2018) also supported with significant and negative heterosis for seed shattering per cent, which is in desirable direction.

Days to 50 per cent flowering, panicles per plant, test weight, grain yield per plant and shattering per cent recorded significant heterosis in desirable direction in the both cross. Plant height showed significant heterosis in desirable direction in the cross Jyothi x Aathira.

5.3 Variability studies

5.3.1 Phenotypic and genotypic coefficient of variation

The difference between phenotypic and genotypic coefficient of variation indicates the influence of environment in each character. Higher the difference between PCV and GCV higher will be the environmental influence on the character and lower the difference, character is less influenced by environment.

Low PCV and GCV values for days to 50 per cent flowering and days to maturity was observed in both the crosses whereas moderate value of PCV and GCV were reported for the character by Karthikeyan *et al*. (2010) and Job (2018). Low PCV and GCV values for plant height in F_2 population obtained from the cross Jyothi x Triveni is in conformity with the findings of Borkakati *et al*. (2005) and Job (2018).

Tillers per plant were recorded high PCV and GCV while Job (2018) reported moderate GCV and high PCV for the character. Panicle length was observed to be having low PCV and GCV in both the crosses. This is in agreement with the results of Karthikeyan *et al*. (2010). Sabesan *et al*. (2009), Jayasudha and Sharma (2010), Fiyaz *et al*. (2011), and Job (2018) also reported high level of GCV and PCV for grain yield per plant. Seeds per panicle and test weight recorded moderate value for PCV and GCV whereas Job (2018) reported low PCV and GCV for the characters.

High GCV and PCV values for shattering per cent in the present study are in conformity with the findings of Job (2018). Higher values of PCV and GCV for shattering per cent and grain yield per plant reveals the presence of large variation for character in the population. Improvement of such character is possible through selection.

5.3.2 Heritability and genetic advance

High heritability for a character indicates the effectiveness of selection based on phenotype. High heritability followed by high genetic advance indicates that the character is controlled by additive genes and selection for such characters will be effective. High heritability followed by low genetic advance shows the presence of dominance gene effect in controlling the character and selection may not be effective for such characters.

Singh *et al*., (2011) reported high heritability for days to 50 per cent flowering. Quatadah *et al*. (2012) and Job (2018) reported high heritability for grain yield per plant. Akhtar *et al*. (2011), Fiyaz *et al*. (2011) and Job (2018) reported high heritability for plant height in rice similar to the present study. Kumar *et al*. (2012) and Job (2018) also reported high heritability value for panicle length and grains per panicle. High broad sense heritability observed in characters, plant height, days to 50 per cent flowering, days to maturity, grain yield per plant, test weight and spikelet per panicle are in conformity with the results of Yadav *et al*. (2011).

The characters, tillers per plant, panicles per plant, spikelets per panicle, seeds per panicle, test weight, grain yield per plant and shattering per cent recorded high heritability accompanied by high genetic advance. Yadav *et al*. (2011) reported that for effective selection for a character, it is necessary to consider genetic advance along with heritability. Since these characters shows high genetic advance, selection might be effective in character improvement.

Table 14: Breeding strategies for improving different characters in cross I

Character	Cross I : Jyothi x Triveni										Breeding strategy suggested
	A	B	C	D	m	d	h	i	j	l	
Days to 50 per cent flowering	+	-	+	+	+	+	-	-	+	+	Bi parental mating in early segregating generation, pedigree breeding by selection at later generation
Plant height (cm)	-			+	+	-	-			+	Bi parental mating in early segregating generation, pedigree breeding by selection at later generation
Tillers per plant (no.)	-	-	-	+	+	+	-	-	-	+	Bi parental mating in early segregating generation, pedigree breeding by selection at later generation
Panicles per plant (no.)	-	-	-	+	+	+	-	-	-	+	Bi parental mating in early segregating generation, pedigree breeding by selection at later generation
Panicle length (cm)	-				+	-	-	-	-	+	Bi parental mating in early segregating generation, pedigree breeding by selection at later generation
Spikelets per panicle (no.)	-		-	+	+	-	-	-	-	+	Bi parental mating in early segregating generation, pedigree breeding by selection at later generation
Seeds per panicle (no.)	-	-	-		+	-	-		-	+	Bi parental mating in early segregating generation, pedigree breeding by selection at later generation
Days to maturity	+	-	-	-	+	+	-	-	+	+	Bi parental mating in early segregating generation, pedigree breeding by selection at later generation
Test weight (g)	-	-	-		+	-	-	-	-	+	Bi parental mating in early segregating generation, pedigree breeding by selection at later generation
Grain yield per plant (g)	-	-	-	+	+	+	-	-	-	+	Bi parental mating in early segregating generation, pedigree breeding by selection at later generation
Shattering per cent	-	-	-	+	+	+	-	-	-	+	Bi parental mating in early segregating generation, pedigree breeding by selection at later generation

Significant and positive: **+ve** sign Significant and negative: **-ve** sign

Table 15: Breeding strategies for improving different characters in cross II

Character	Cross II : Jyothi x Aathira										Breeding strategy suggested
	A	B	C	D	m	d	h	i	j	l	
Days to 50 per cent flowering		+	+		+	-		-	-		Direct or Pedigree selection
Plant height (cm)				+	+	-	-	-		+	Bi parental mating in early segregating generation, pedigree breeding by selection at later generation
Tillers per plant (no.)	-				+	+					Direct or Pedigree selection
Panicles per plant (no.)	-				+	-	-			+	Bi parental mating in early segregating generation, pedigree breeding by selection at later generation
Panicle length (cm)	-	-	-		+	-	-			+	Bi parental mating in early segregating generation, pedigree breeding by selection at later generation
Spikelets per panicle (no.)	-	-	-		+	-	-			+	Bi parental mating in early segregating generation, pedigree breeding by selection at later generation
Seeds per panicle (no.)	-	-	-		+	-	-		-	+	Bi parental mating in early segregating generation, pedigree breeding by selection at later generation
Days to maturity		+	+		+	-					Direct or Pedigree selection
Test weight (g)	-	-	-		+	+	-		-	+	Bi parental mating in early segregating generation, pedigree breeding by selection at later generation
Grain yield per plant (g)	-		-	+	+	+	-	-	-	+	Bi parental mating in early segregating generation, pedigree breeding by selection at later generation
Shattering per cent	-		-		+	+			-		Direct or Pedigree selection

Significant and positive: **+ve** sign Significant and negative: **-ve** sign

Summary

6. SUMMARY

The research on ‘Genetics of shattering resistance in rice (*Oryza sativa* L.)’ was conducted in the Department of Plant Breeding and Genetics, College of Horticulture, Kerala Agricultural University (KAU), during the October, 2018 to June, 2020. The research work was subdivided into three experiments and carried out in two locations. Experiment I was hybridization of easy shattering high yielding rice variety (Jyothi) with shattering resistant varieties (Aathira and Triveni). Experiment II was backcrossing of F_1 with both the parents and selfing of F_1. During experiment III progenies obtained from experiment I and II were planted in field along with parents to evaluate shattering resistance and other yield characters.

Six generations (P_1, P_2, F_1, F_2, B_1 and B_2) obtained from both the cross combinations were evaluated for eleven quantitative characters and generation mean analysis was carried out to study the mode of inheritance pattern of each character. Heterosis for eleven characters in two crosses were also studied. In addition to generation mean analysis and heterosis variability was also studied.

Salient findings of the research work are summarized below:

Generation mean analysis

- All the eleven characters showed significance for scaling test. Epistatic and epistatic interaction model was adequate to explain the gene action for the all the characters.
- The mean effects (m) were significant and positive for all the characters studied in both the crosses.
- Significant and positive value for additive (d) component were recorded for characters *viz.* days to 50 per cent flowering, tillers per plant, panicles per plant, days to maturity, grain yield per plant and shattering per cent, whereas plant height, panicle length, spikelets per panicle, seeds per panicle and test weight recorded significant and negative additive (d) component in the cross Jyothi x Triveni.

- Additive (d) component was significant and positive for the characters, tillers per plant, test weight and shattering per cent. While the characters days to 50 per cent flowering, plant height, panicles per plant, panicle length, spikelets per panicle, seeds per panicle, days to maturity, and grain yield per plant recorded significant and negative additive gene effect in the cross Jyothi x Aathira.
- All the characters exhibited significant and negative value for dominance (h) gene effect in the cross Jyothi x Triveni.
- The characters except days to 50 per cent flowering, tillers per plant, days to maturity and shattering per cent exhibited significant and negative dominance (h) gene effect in the cross Jyothi x Aathira.
- Among interaction components additive x additive (i) component was significant and negative for all the characters except plant height, seeds per panicle and test weight in the cross Jyothi x Triveni. Additive x dominance (j) component was significant and positive for the characters, days to 50 per cent flowering and days to maturity while the characters tillers per plant, panicles per plant, spikelets per plant, seeds per panicle, grain yield per plant and shattering per cent recorded significant and negative additive x dominance (j) effect. Dominance x dominance (l) was significant and positive for all the characters in the cross.
- Additive x additive (i) component was significant only for days to 50 per cent flowering and plant height but in negative direction. The characters days to 50 per cent flowering, seeds per panicle, test weight, grain yield per plant and shattering per cent exhibited significant and negative additive x dominance (l) interaction for inheritance in the cross Jyothi x Aathira. The characters except days to 50 per cent flowering, tillers per plant, days to maturity and shattering per cent exhibited significant and positive dominance x dominance (l) interaction effect in inheritance.
- All the characters in the cross Jyothi x Triveni exhibited duplicate gene action.

- The characters except days to 50 per cent flowering, tillers per plant, days to maturity and shattering per cent exhibited duplicate gene action in in the cross Jyothi x Aathira.
- Dominant gene effect was found to have major role than additive gene effect in inheritance of most of the characters in both the cross.
- Inheritance of days to 50 per cent flowering, tillers per plant, days to maturity and shattering per cent in the cross Jyothi x Aathira were influenced predominantly by additive gene effect.
- Most of the characters exhibited degree of dominance more than one in both the cross.
- Presence of additive and non-additive gene action along with epistatic interaction shows the complex inheritance of the characters. Predominant dominant gene effect along with duplicate epistasis limits the scope of direct selection.
- Predominant role of additive gene effect in inheritance can be improved by direct selection.
- Non allelic interaction with duplicate type of epistasis can be utilized effectively in pedigree breeding by delaying selection to a later generation. Use of bi parental mating in early segregating generation helps to exploit both additive and dominance gene effect there by obtaining superior recombinants having good yield with moderate seed shattering.

Heterosis

- Characters except panicle length and days to maturity showed relative heterosis in the cross Jyothi x Triveni. Characters *viz*. days to 50 per cent flowering, panicles per plant, spikelets per panicle, seeds per panicle, days to maturity, test weight, grain yield per plant and shattering per cent exhibited heterobeltiosis in the cross.
- Days to 50 per cent flowering, tillers per plant, panicle per plant, test weight, grain yield per plant and shattering per cent recorded significant heterosis in desirable direction. While the characters days to 50 per cent flowering, panicles

per plant, test weight, grain yield per plant, and shattering per cent recorded desirable heterobeltiosis in the cross Jyothi x Triveni.

- Characters except days to 50 per cent flowering, tillers per plant and days to maturity showed significant relative heterosis in the cross Jyothi x Aathira. The characters except days to 50 per cent flowering and tillers per plant recorded significant heterobeltiosis.
- Plant height, panicles per plant, test weight, grain yield per plant and shattering per cent showed significant heterosis in desirable direction. Plant height, days to maturity, test weight, grain yield per plant and shattering per cent showed heterobeltiosis in desirable direction.

Variability study

- Days to 50 per cent flowering, plant height, panicle length and days to maturity showed low GCV and PCV values advance in F_2 population derived from the cross Jyothi x Triveni. Spikelets per panicle, seeds per panicle, test weight recorded moderate value for GCV and PCV and other characters exhibited high GCV and PCV value. Test weight was least influenced by environment and shattering per cent was most influenced by environment in the population.
- Days to 50 per cent flowering, panicle length and days to maturity recorded low GCV and PCV values in F_2 population derived from the cross Jyothi x Aathira. Plant height, spikelets per panicle, seeds per panicle and test weight showed moderate value for GCV and PCV whereas all the other characters exhibited high GCV and PCV value. Days to maturity and test weight were least influenced by environment and shattering per cent was most influenced by environment in the population.
- All the characters showed high heritability in both the populations studied.
- Plant height, panicle length and days to maturity showed low genetic advance. Plant height was recorded with moderate genetic advance while, other characters exhibited high genetic advance in F_2 population derived from the cross Jyothi x Triveni.

- Days to maturity showed low genetic advance. Days to 50 per cent flowering and panicle length recorded moderate genetic advance and other characters recorded high genetic advance in F_2 population derived from the cross Jyothi x Aathira.

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GENETICS OF SHATTERING RESISTANCE IN RICE (*Oryza sativa* L.)

By

AKHIL K. P.

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ABSTRACT OF THE THESIS

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Department of Plant Breeding and Genetics

COLLEGE OF HORTICULTURE

VELLANIKKARA, THRISSUR – 680656

KERALA, INDIA

ABSTRACT

Rice is the staple food crop of Kerala. Among the plethora of rice varieties available Jyothi is by far the most popular in the state owing to its consumer preference. Easy seed shattering leads to significant loss in Jyothi which can be overcome by transferring shattering resistance to it. Screening of genotypes for shattering resistance identified donors like Athira and Triveni with good combining ability. The present experiment was thus envisaged to transfer shattering resistance to Jyothi from the donors and to study the nature of inheritance of seed shattering trait using six parameter model of generation mean analysis. Observations were recorded in the two crosses viz., Jyothi x Aathira and Jyothi x Triveni for eleven quantitative characters *viz*. days to 50 per cent flowering, plant height, tillers per plant, panicles per plant, panicle length, spikelets per panicle, seeds per panicle, days to maturity, test weight, grain yield per plant and shattering per cent in six generation (P_1, P_2, F_1, F_2, B_1 and B_2) obtained from the two crosses.

Panicle per plant, test weight, grain yield per plant and shattering per cent recorded significant heterosis in the desirable direction in both the crosses.

Mean effect (m) was significant and positive for all the characters studied in both the crosses. The additive component (d) was significant and positive for days to 50 per cent flowering, tillers per plant, panicles per plant, days to maturity, grain yield per plant and shattering per cent in the cross Jyothi x Triveni while the other characters recorded significant and negative additive gene effect. The characters tillers per plant, test weight and shattering per cent showed significant positive additive gene effect in the cross Jyothi x Aathira and rest of the characters showed significant and negative additive component. Dominance gene effect was observed to be significant and negative for most of the characters studied in both the crosses.

Non-allelic interactions were observed to be significant in most of the characters except days to 50 per cent flowering, tillers per plant, days to maturity and shattering per cent in the cross Jyothi x Aathira. The epistatic interaction model of generation mean

analysis was found adequate for obtaining gene actions for all the characters. Among the three type of interactions dominance x dominance interaction was found to be more important for all the characters. Additive x additive and additive x dominance gene interactions were found to be equally important for most of the characters studied in both the crosses.

Dominance gene effect was observed controlling the genetic variance in most of the traits studied. Presence of additive and non-additive along with epistatic interaction revealed the complex nature of inheritance of the characters. Predominant dominant gene effect along with duplicate epistasis limits the scope of direct selection.

In the F_2 populations characters showed high heritability in both the populations studied. Plant height, panicle length and days to maturity were found to have low genetic advance. Plant height recorded moderate genetic advance, whereas, other characters exhibited high genetic advance in F_2 population derived from the cross Jyothi x Triveni. Days to maturity showed low genetic advance, days to 50 per cent flowering and panicle length recorded moderate genetic advance and other characters recorded high genetic advance in F_2 population derived from the cross Jyothi x Aathira.

As shattering resistance is governed predominantly by additive gene effects selection in the early segregating generations will be highly rewarding. The selected lines may be advanced to further generations to identify lines with high yield coupled with shattering resistance and can be forwarded to develop high yielding varieties with low shattering or bi-parental mating among the selected lines may be undertaken to recover superior recombinants with high yield and shattering resistance.