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Deciphering the genetic architecture of early flowering in the high yielding rice variety 'KAU Manu Ratna'

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Abstract

KAU Manu Ratna is a rice variety popular for its short duration and high yield. In the present study, the gene action of flowering genes of KAU Manu Ratna was studied in breeding populations obtained by crossing it with a long duration variety Swarna-Sub1. Studies in F_1, F_2, BC_1F_1, BC_1F_2 and BC_2F_1 populations revealed that the flowering duration in KAU Manu Ratna is controlled by two dominant genes with polymeric gene action. All the F_1, BC_1F_1 and BC_2F_1 plants flowered along with KAU Manu Ratna showed complete dominance for earliness, whereas F_2 plants segregated in a ratio of 9:6:1 for early, mid and late duration revealing its polymeric gene action. The segregation pattern of BC_1F_2 families also supports the polymeric gene action. In the F_2 population, days to flowering showed no strong correlation with yield-contributing traits. This suggests that the alleles responsible for earliness do not adversely impact the overall yield. Given these characteristics, KAU Manu Ratna is an ideal genetic resource for developing short duration climate-resilient rice varieties without compromising yield.

Keywords: KAU Manu Ratna, short-duration rice, early-flowering gene, polymeric gene action

INTRODUCTION

Rice is the staple food for approximately half of the world's population and it accounts for 76% of the calorific intake of South-East Asians (Zhao *et al.*, 2020). To meet global demand by 2050, rice production must increase by an estimated 75 million tons over 2020 levels (Pede *et al.*, 2025). However, rice cultivation is increasingly jeopardised by climatic instabilities, specifically erratic precipitation patterns, thermal stress from rising temperatures, escalating soil salinity, and prolonged moisture deficits (Jamal *et al.*, 2023). Developing varieties adaptable to the new situation is one of the most important mitigating strategies. While breeding for multi-stress tolerance is a complex and labour-intensive process, developing short-duration varieties offers a strategic "escape" mechanism that allows crops to adapt to diverse climatic challenges (Ashraf, 2010 and Liang *et al.*, 2024). According to Aditya *et al.* (2018) short-duration rice varieties carry significant advantages in the era of climate change.

Short duration varieties generally take 90-110 days, whereas medium duration varieties take 110-140 days and long duration varieties take more than 140 days to attain maturity. Generally, grain yield is positively correlated with growth duration of the genotype (Li *et al.*, 2019). It is hard to find genotypes combining high yield and short duration. Short duration varieties often suffer from a source-sink limitation. Because they spend less time in the vegetative and reproductive phases and often have lower biomass accumulation or produce fewer spikelets per panicle compared to long-duration genotypes (Won *et al.*, 2020). Rice is a short-day plant, flowering of rice is accelerated under short-day condition, while inhibited in long-day condition. With the development of new improved varieties adaptable to all seasons, rice appears to have weak or no photoperiod sensitivity. KAU Manu Ratna is a short duration (100 days) photo-insensitive rice variety with an average yield of 5600 kg ha^{-1}. This variety is an important genetic resource due to its comparatively high yield among the short duration varieties.

In rice, genetic regulation of flowering date is influenced by several major genes (Yamamoto *et al.*, 1998). So far, the genetics of flowering genes in KAU Manu Ratna

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remains unclear. Elucidating the genetic architecture and gene action governing flowering time in KAU Manu Ratna is fundamental to the breeding of high-yielding, early-maturing rice varieties. In this experiment, KAU Manu Ratna is crossed with Swarna-Sub1, a long duration (140-145 days) photo-insensitive high yielding variety with an average yield of 5500 kg ha^{-1} (Pradhan *et al.*, 2021), to study the gene action of flowering gene.

MATERIALS AND METHODS

Experiment site and design

The experiment was carried out in the Department of Plant Breeding and Genetics at College of Agriculture, Vellanikkara, Thrissur. KAU Manu Ratna, a high yielding short duration variety is taken as the female parent and Swarna-Sub1 as the male parent. Crossing of parents were done during the *Rabi,* 2023 season. The F_1 plants were raised in the net house during *Kharif,* 2024 along with both the parents. KAU Manu Ratna (female parent) was sown at five staggered intervals of seven days relative to the F_1 sowing date to ensure flowering synchronisation. Sowing occurred seven days before, simultaneously with, and at 7, 14, and 21 days after the F_1 sowing date. Seedlings of F_1s and parents were transplanted on 16th day to non-perforated plastic pots of diameter 30 cm. Each pot was planted with four seedlings. The design followed was completely randomised design with seven replications. In each replication, observations were taken from five plants.

DNA isolation and PCR analysis

Leaf samples were obtained from 45-day old seedlings for DNA extraction. Modified CTAB method was used for DNA extraction. Polymorphism between parents was checked using the specific markers for *Sub1* locus, ART5 and Sub1BC2. PCR was performed in 20 µl reactions containing 100 ng of DNA template, 2 µl of 10X Taq buffer A, 1 µl 2.5mM dNTP each, 1 µl each of forward and reverse markers and 0.13 µl of *Taq* DNA polymerase using a thermal cycler. After initial denaturation for 3 min at 95°C, each cycle comprised 50 sec denaturation at 94°C, 50 sec annealing at primer optimal temperature, and 1 min extension at 72°C with a final extension for 10 min at 72°C at the end of 35 cycles. The PCR products were mixed with bromophenol blue gel loading dye and were analyzed by electrophoresis on 2.5% agarose gel at 70V. The gels were stained in 0.5 mg/ml ethidium bromide and were documented using Molecular Imager Gel Doc XR+ (BIO-RAD).

Hybridity test and production of F_2 and backcross population

Hybridity of F_1s were checked using the polymorphic marker. Plants producing heterozygous bands for polymorphic markers were identified as true F_1s. The true F_1s were backcrossed with KAU Manu Ratna (female) as recipient parent to produce BC_1F_1 seeds. During *Rabi* 2024, 62 BC_1F_1's and 149 F_2s along with parents were grown in pots of diameter 30 cm in the net house. BC_1F_1's with *Sub1* locus were selected using specific marker for *Sub1* locus and again backcrossed with KAU Manu Ratna to produce BC_2F_1's. BC_2F_1's consisting of 283 plants and 139 BC_1F_2's from four BC_1F_1 families were grown in the wet land paddy field during *Kharif,* 2025 along with the parents. BC_1F_2's consists of 30 plants from B1-1 family, 36 plants from B1-3 family, 31 plants from B1-39 family, 42 plants from B1-50 family.

Relationships of days to flowering with yield contributing traits

In this experiment the influence of days to flowering on yield was studied through yield attributing traits *viz.,* panicle length, spikelet number per panicle, spikelet density and hundred seed weight on F_2 population. The observation on days to flowering was taken from the day of sowing to the first spikelet opening.

Statistical analysis

Statistical analysis was done with standard statistical procedures like ANOVA, descriptive statistics, normality test, Chi-square test and simple correlations using 'KAU GRAPES' statistical software (Gopinath *et al.*, 2020). The data on days to flowering for the F_1 generation were subjected to one-way Analysis of Variance (ANOVA) based on a Completely Randomized Design (CRD) with seven replications followed by Fisher's Least Significant Difference (LSD) test. Normality of the F_2 and BC_1F_2 population were tested using Shapiro-Wilk normality test. Chi-square (χ^2) goodness of fit test was performed to study the gene action of early flowering gene in the F_2 and BC_1F_2 population.

In the F_2 population, data on days to flowering, panicle length, spikelet number, spikelet density and hundred seed weight were subjected to normality test and linear relationship between days to flowering and other traits were studied using Pearsons two-tailed correlation test.

RESULTS AND DISCUSSION

Hybridity test

Specific primers for *Sub1* locus, ART5 and Sub1BC2 **(Table 1)** were found to be polymorphic between the parents and ART5 was used to confirm the hybridity in the F_1 and BC_1F_1 plants. In the F_1 generation 36 plants were identified as true hybrids and used as male parent for backcrossing. Whereas, in BC_1F_1 generation, 27 plants with *Sub1* locus were selected for backcrossing.

Gene action for days to flowering

The days to flowering in F_1s ranged between 75 to 78 days whereas, it was 74 to 81 days in female parent KAU Manu Ratna and 104 to 108 days in male parent Swarna-Sub1. The average days to flowering was 76, 76, and 107 days in F_1, KAU Manu Ratna and Swarna-Sub1 respectively. One way analysis of variance done for days to flowering in F_1s and parents showed significant difference **(Table 2)**. Further, post-hoc analysis using Fisher's LSD test revealed that the mean of days to flowering in F_1

Table 1. Details of polymorphic markers

Marker	Forward sequence (5'-3')	Reverse sequence (3'-5')	Annealing temperature (ºC)
ART5	CAGGGAAAGAGATGGTGGA	TTGGCCCTAGGTTGTTTCAG	57.5
Sub1BC2	AAAACAATGGTTCCATACGAGAC	GCCTATCAATGCGTGCTCTT	55

Table 2. ANOVA table for days to flowering in F_1 and parents

Sources of variability	Degrees of freedom	Sums of squares	Mean Squares	F value	Probability of $F_{table} > F_{cal}$
Treatment	2	4313.672	2156.836	9384.025	0
Error	18	4.137	0.230	NA	NA

Table 3. Grouping for days to flowering based on Fisher's LSD test

Genotype	Mean value	Group
Swarna-Sub1	107	a
F_1	76	b
KAU Manu Ratna	76	b

plants did not differ significantly from the female parent, KAU Manu Ratna, but was significantly different from the male parent, Swarna-Sub1 **(Table 3)**. This showed that all F_1s flowered along with KAU Manu Ratna which reflects the dominant nature of flowering gene from KAU Manu Ratna.

In the 62 BC_1F_1 population the days to flowering ranged from 70 to 77 days. Whereas, the days to flowering of KAU Manu Ratna ranged between 74 to 82 days and that of Swarna-Sub1 ranged between 104 to 109 days. In the 283 BC_2F_1 population, the days to flowering ranged between 71 to 83 days and for KAU Manu Ratna it ranged between 73 to 83 days and that of Swarna-Sub1 ranged between 105 to 109. Days to flowering data from the BC_1F_1 and BC_2F_1 populations also confirms the dominant nature of early flowering allele in 'KAU Manu Ratna'. Earlier research has also identified dominant alleles responsible for early flowering in some rice cultivars. Doi *et al.* (1998) has reported a dominant allele (*Ehd1-gla*) of *Ehd1* gene, which confers early flowering under short day conditions in *Oryza glaberrima* by using a cross-combination between Taichung 65 and an accession of African rice (*Oryza glaberrima* Steud. accession no. IRGC104038). Conversely, there are cases where recessive inheritance pattern was observed for alleles that promote early flowering. In a population derived from the cross between Kasalath and Nipponbare rice cultivars by Yamamoto *et al.* (1998) Nipponbare allele at the *Hd1* (*Heading date1*) locus was found dominant to delay flowering, whereas the Kasalath allele for early flowering was found to be recessive.

In rice, *Hd1* and *Ehd1* are two key flowering time genes influenced by photoperiod. In the current experiment both the parents involved are photo-insensitive. The mean days to flowering of KAU Manu Ratna and Swarna-Sub1 in *Kharif* 2024 (F_1), *Rabi* 2024 (F_2) and *Kharif* 2025 (BC_1F_2) was 76, 78, 77 days and 107, 106,108 days respectively. This proves that the influence of photoperiod on flowering of parents was negligible. In the course of rice domestication and breeding, photoperiod-insensitive rice evolved as a result of several kinds of loss-of-function alleles at the photoperiod-sensitive gene loci (Zhu *et al*., 2017). For example, a missense mutation in a photoperiod sensitivity gene *OsPRR37* causes extreme early flowering in the accession H143 (subsp. *japonica*) under different day lengths (Koo *et al*., 2013) and overexpression of this gene has caused late flowering and mis-regulation of several flowering related genes (Liu *et al*., 2018). Similarly, Kitaake, an extreme early flowering variety poses defective alleles for *Ghd7* and *OsPRR37* gene resulting in its photo-insensitive nature (Kim *et al*., 2013). The photoperiod insensitivity of KAU Manu Ratna likely results from natural allelic variation, specifically loss- or gain-of-function mutations in key photoperiod-sensitive genes.

The gene action of the early flowering allele in KAU Manu Ratna was further studied using the F_2 and BC_1F_2 populations. In the F_2 plant, flowering days ranged between 73 to 108 days **(Fig.1)** with an average of 87 days and flowering of KAU Manu Ratna ranged from 75 to 84 days with an average of 78 days and that of Swarna-Sub1 ranged from 104 to 109 days with an average of 106 days. Descriptive statistics for days to flowering are shown in **Table 4**. Normality test for data distribution showed p-value < 0.05. According to Shapiro-Wilk normality test, If the p-value > 0.05 we can assume the normality. In other words, the distribution of the data is not significantly different from normal distribution. Here the results of Shapiro-Wilk normality test indicate non-

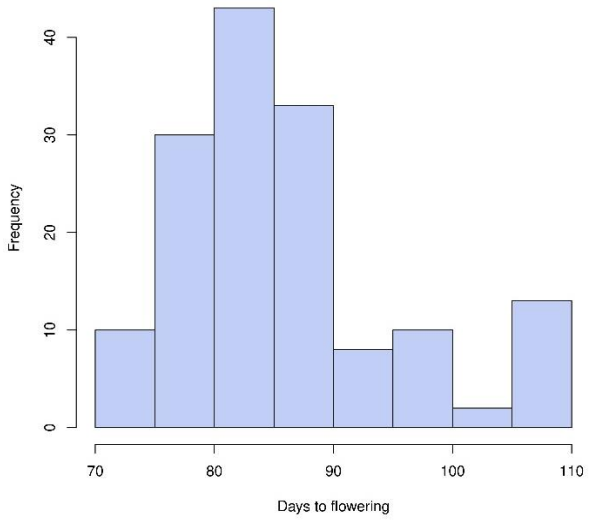

Fig.1. Histogram of days to flowering in F_2 population of cross between KAU Manu Ratna and Swarna Sub1

normal distribution for days to flowering in F_2 population and it follows a positive skewness. Which means greater proportion of individuals have lower value for days to flowering. This indicates that majority plants in F_2 population was early flowering in nature.

Since the population did not follow normal distribution, a non-parametric χ^2 test was done. F_2 plants were grouped into three classes based on flowering days of parents. Plants showing flowering upto 84 days were classified as early group, those flowered between 85-98 days were classified as mid and those between 104-108 were classified as late group. Assuming that short duration in KAU Manu Ratna is governed by two dominant gene action the goodness of fit was tested using Chi-square test **(Table 5)** for polymeric gene action. No significant difference between observed and expected value (9:6:1) was found. This showed that the flowering days in KAU Manu Ratna is the result of two dominant gene action. Whenever at least a single copy of dominant alleles from two genes is present the plants flower early; when dominant allele of only one gene is present it produces mid-flowering plants and; whenever dominant alleles from both gene are absent, that is in double recessive condition late flowering happens.

The descriptive statistics results **(Table 4)** for days to flowering in BC_1F_2 population showed non-normal distribution and positively skewed values, indicating the abundance of early flowering plants. The BC_1F_2 population of 139 plants from four BC_1F_1 families were classified into different classes based on the flowering duration of parents. The flowering days in KAU Manu Ratna ranged between 73-83 days and that of Swarna sub1 was 101-108 days. Accordingly, plants that flowered between 73-83 days were classified as early, those between 84-100 days as mid, and those between 101-108 days were classified as late. The hypothetical segregation pattern in case of polymeric gene action in BC_1F_2 plant is shown in **Fig.2**.

All BC_1F_2's from B1-1 and B1-39 family showed similar flowering pattern as that of KAU Manu Ratna. Flowering days of B1-1 family and B1-39 family ranged between 73-83 days. This suggests that B1-1 and B1-39 BC_1F_1 plants have two dominant genes in homozygous condition for flowering as in KAU Manu Ratna. Flowering days of B1-3 family ranged between 73-100 days and for B1-50 family 76-94 days. Flowering days of plants in B1-3 and B1-50 family showed 3: 1 segregation ratio for early and mid-duration and this was confirmed using Chi-square test **(Table 6 & 7)**. This suggests that B1-3 and B1-50 BC_1F_1 plants have one dominant gene in homozygous condition and other in heterozygous condition. The segregation

Table 4. Descriptive statistics for days to flowering in F_2 and BC_1F_2 population

Generation	Mean ± SD	Min.	Max.	Shapiro-Wilk (W) statistic		Skewness	SE Skewness
				W	p-value		
F_2	86.55 ± 8.79	73	108	0.90627	3.30E-08	0.91	0.2
BC_1F_2	80.13 ± 5.51	73	100	0.87918	2.92E-09	1.26	0.21

Table 5. Goodness of fit Chi-square test for a 9:6:1 ratio for early, mid and late flowering plants in F_2

Class in days	Observed value (O)	Expected value (E)	O-E	$(O-E)^2$	$(O-E)^2/E$
73-84	82	83.8125	-1.8125	3.285	0.0392
85-98	52	55.875	-3.875	15.015	0.2687
104-108	15	9.3125	5.6875	32.347	3.4735
Total	145		df = (3-1) = 2		χ^2 value = 3.7814

Significance value @ 0.05 = 5.99; 0.01 = 9.21

pattern in BC_1F_2 also support the polymeric gene action for flowering duration in the population derived by the cross between KAU Manu Ratna and Swarna-Sub1, where early flowering occurs when at least one dominant allele is present at both loci ($E_{1_}\backslash_E_{2_}$). The presence of dominant alleles in either the homozygous or heterozygous state for both genes triggers the earliest phenotypic expression. Mid-flowering occurs when one gene is in the double recessive state while the other gene possesses at least one dominant allele ($e_1e_1\backslash E_{2_}$ or $E_{1_}\backslash e_2e_2$). Late flowering occurs only in the double homozygous recessive condition ($e_1e_1e_2e_2$). Gu and Foley (2007) have reported epistatic interaction of three loci to regulate flowering in photoperiod sensitive rice in a backcross population.

Relationships of days to flowering with yield contributing traits

Yield is a very complex trait contributed by several component traits. Many previous workers have established the direct and indirect effect of different component traits on yield. Li *et al.* (2019) has reported that the grain yield of indica varieties is highly influenced by traits like filled grain number per panicle, 1000-grain-weight, plant height, panicle length, grains per panicle, seed setting rate, long growth period, low panicle number per unit area, and low seed length-width ratio. Sampath *et al.* (1989) reported significant positive correlation of grain yield with panicle length, grains per panicle and hundred grain weight. Selvarani *et al.* (2022) also reported significant positive

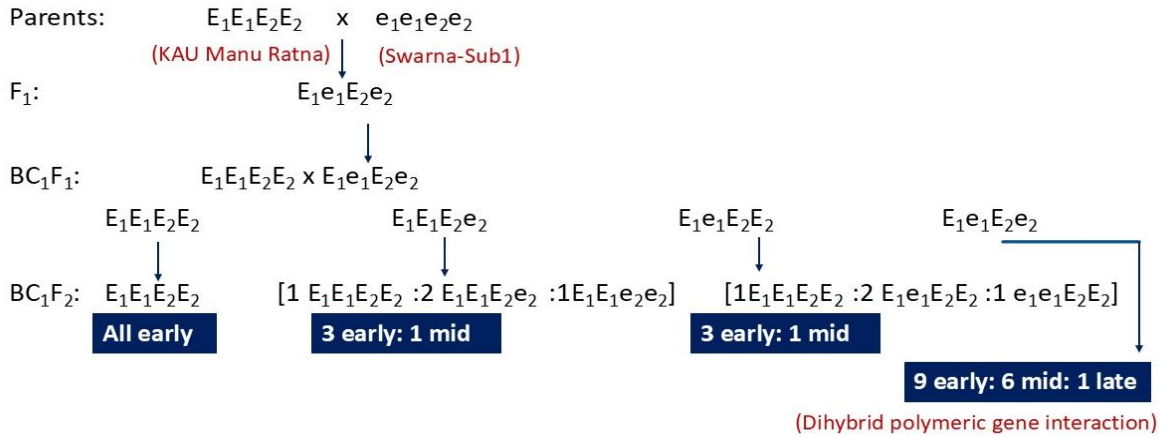

Fig.2. Hypothetical segregation ratio for polymeric gene interaction in a BC_1F_2 backcross population. Consider E_1 and E_2 as dominant alleles for early flowering from two different genes and e_1 and e_2 are their respective recessive counterparts. Here the early flowering parent, KAU Manu Ratna (recurrent parent) possesses both dominant alleles in homozygous condition and the late flowering parent Swarna-Sub1 possesses double recessive alleles.

Table 6. Goodness of fit Chi-square test for a 3:1 ratio for early and mid-flowering plants in BC_1F_2 population (B1-3 family)

Class in days	Observed	Expected	O-E	$(O-E)^2$	$(O-E)^2/E$
73-83 (early)	25	27	-2	4	0.1481
84-100 (mid)	11	9	2	4	0.4444
Total	36		df = (2-1) = 1		χ^2 value = 0.5925

Significance value @ 0.05 = 3.841; 0.01 = 6.635

Table 7. Goodness of fit Chi-square test for a 3:1 ratio for early and mid-flowering plants in BC_1F_2 population (B1-50 family)

Class in days	Observed	Expected	O-E	$(O-E)^2$	$(O-E)^2/E$
73-83 (early)	29	31.5	-2.5	6.25	0.1984
84-100 (mid)	13	10.5	2.5	6.25	0.5952
Total	42		df = (2-1) = 1		χ^2 value = 0.7936

Significance value @ 0.05 = 3.841; 0.01 = 6.635

correlation of per plant yield with number of spikelets per panicle and panicle length in rice. Spikelet number per unit area is another important yield component of rice (Okamura *et al*., 2026). In this experiment, descriptive statistics obtained for the yield contributing traits *viz.,* hundred seed weight, panicle length, spikelet density and spikelet number in F_2 population is given in **Table 8**. Result of Shapiro-Wilk normality test showed normal distribution for hundred seed weight, panicle length and spikelet density, whereas, spikelet number doesn't follow normal distribution.

Correlation studies of days to flowering with different yield attributing traits like panicle length, spikelet number, spikelet density and hundred seed weight shows that the days to flowering in the F_2 population derived from the cross between KAU Manu Ratna and Swarna-Sub1 has very weak or no correlation with the major yield contributing traits **(Fig.3)**, only panicle length showed significant positive correlation (0.21. This showed that early flowering gene in KAU Manu Ratna may not significantly influence the yield. Many previous works have observed disadvantageous positive correlation between days to flowering and yield component traits (Kalyan *et al*., 2017; Mishra *et al*., 2017). Mahalakshmi *et al.* (2024) has reported direct positive associations between grain yield and days to 50% flowering, ear-bearing tillers per square meter, panicle length, grains per panicle and test weight. Since allele for earliness in KAU Manu Ratna does not significantly influence the yield, this variety can be used for developing high yielding short duration varieties.

In this experiment, panicle length and spikelet number showed highly significant positive correlation with spikelet density. This result showed that lengthy panicles can accommodate more spikelets and panicles with more spikelets per unit area will increase the spikelet density. Panda *et al*. (2015), has also reported that the increase in the number of spikelets on a panicle generally leads to a decrease in the inter-grain space, resulting in compactness of the panicle.

Table 8. Descriptive statistics for yield contributing traits in F_2 population

Trait	Mean ± SD	Min.	Max.	Shapiro-Wilk (W) statistic		Skew-ness	SE Skew-ness
				W	p-value		
Hundred seed weight (g)	2.7 ± 0.33	1.89	3.42	0.9911	0.4736	-0.14	0.2
Panicle length (cm)	25.5 ± 2.54	20.1	32.1	0.98773	0.2137	0.26	0.2
Spikelet density (No./cm)	6.26 ± 1.27	3.62	9.62	0.98725	0.1892	0.19	0.2
Spikelet number	161.35 ± 43.79	73	287	0.98154	0.04276	0.46	0.2

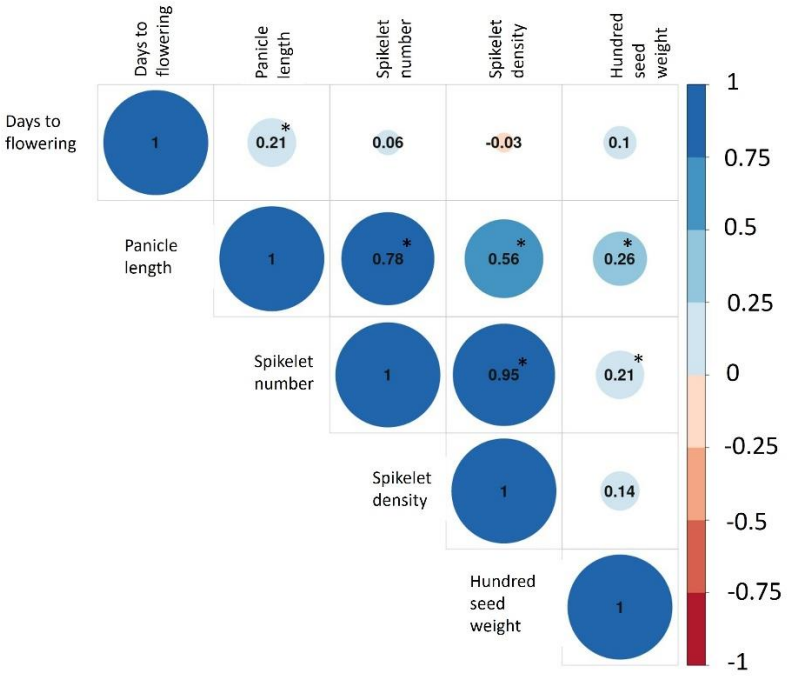

Fig.3. Correlogram of days to flowering with yield component traits
* Significant at 0.05 level

This study represents the first investigation into the genetic basis of days to flowering in KAU Manu Ratna rice, a short rice variety. This study result indicates that the early flowering trait in KAU Manu Ratna is governed by dominant alleles with polymeric gene action. KAU Manu Ratna carries dominant alleles for both governing genes in a homozygous state ($E_1E_1E_2E_2$). This simplifies the transfer of early maturity into elite breeding lines through hybridization. The lack of a strong correlation between days to flowering and yield-contributing traits indicates that the early flowering alleles in KAU Manu Ratna do not negatively impact yield. Consequently, KAU Manu Ratna serves as a valuable genotype for developing high yielding short duration rice varieties without the typical "yield penalty" associated with early maturity. While this study establishes the inheritance pattern, further research should focus on specific genes and molecular markers associated with earliness in KAU Manu Ratna.

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