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# Morphological Variation and Yield-Determining Panicle Traits in M4 Red Rice (*Oryza sativa* L.) Mutant Lines Derived from 200 Gy Gamma Irradiation

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## ABSTRACT

Gamma irradiation is widely applied to induce genetic variability for crop improvement. This study evaluated morphological variation and identified key panicle traits determining yield in M4 mutant lines of red rice (*Oryza sativa* L.) derived from 200 Gy gamma irradiation. The experiment was arranged in an augmented randomized complete block design (augmented RCBD) involving mutant lines and control varieties. Observations included morphological traits and yield components, followed by analysis of variance, genetic coefficient of variation (GCV), correlation, and path analysis. The results showed that most traits were not significantly different among mutant genotypes ($p > 0.05$), whereas significant differences were mainly observed between mutant lines and control groups (C vs G). GCV ranged from 1.29% to 10.72%, indicating predominantly narrow to moderate genetic variability. Correlation analysis revealed a strong positive association between grain number per panicle and panicle density. The number of grains per panicle emerged as the most influential trait, showing a direct effect of 1.825 and a total effect of 0.871 on grain yield. These results underscore the importance of this trait as a selection criterion in red rice mutation breeding despite the presence of multicollinearity. Promising lines G12(18-10), G15(2-5), and G13(18-13) demonstrated superior performance. In conclusion, 200 Gy irradiation successfully induced phenotypic variation, yet genetic differentiation among mutants remains restricted. Grain number per panicle is the most effective selection trait, though multi-environment trials are essential to confirm stability.

## 1. INTRODUCTION

Rice (*Oryza sativa* L.) is the primary staple food for the majority of the Indonesian population, and its sustainable production remains a central challenge, particularly in regions characterized by dryland and marginal agroecosystems such as West Nusa Tenggara [1, 2]. In recent years, consumer demand has increased not only for high-yielding rice but also for nutritionally functional rice types, including red rice, which is rich in anthocyanins and other bioactive compounds with antioxidant properties [3, 4]. These attributes position red rice as an important component of sustainable food systems that integrate nutritional quality with agroecological resilience [5].

Despite its nutritional advantages, the productivity of local red rice cultivars remains relatively low compared to modern white rice varieties. This limitation is often associated with suboptimal yield components, particularly grain number per panicle and sink capacity [6, 7]. The G16 red rice genotype, developed from crosses between indica and javanica types, exhibits favorable grain quality and adaptability but is constrained by limited yield potential, necessitating targeted genetic improvement [8].

Induced mutation breeding using physical mutagens such as gamma rays offers a strategic approach to generate novel genetic variation while maintaining the desirable genetic background of elite local genotypes. Gamma irradiation has been widely applied in rice improvement programs to modify plant architecture, flowering behavior, yield components, and stress tolerance [9, 10]. The selection of a 200 Gy irradiation dose was informed by previous studies indicating that this level is close to the Lethal Dose 50 ($LD_{50}$) for rice plants, which typically ranges from 200 to 300 Gy [11, 12]. This dosage is considered optimal for inducing broad genetic diversity while maintaining a survival rate sufficient for the selection process in subsequent generations [13-15].

Evaluation of advanced mutant generations, such as M4, is particularly important because these populations tend to exhibit increased genetic stability while retaining sufficient variability for effective selection [16]. Character evaluation was conducted in the M4 generation, as genetic homozygosity reaches approximately 87.5% at this stage through natural selfing [12, 17]. The selection of the M4 generation ensures that the observed morphological traits and yield components have achieved sufficient stability, with genetic segregation significantly reduced compared to the M2 or M3 generations. This stability allows for higher accuracy in estimating genetic parameters and phenotypic characterization [13, 14].

Morphological and yield-related traits, especially those associated with panicle architecture, play a critical role in determining rice productivity. Panicle length, grain number, and panicle density have been consistently reported as major contributors to yield formation across diverse environments [18, 19]. Understanding the relationships among these traits through correlation and path coefficient analyses provides a quantitative basis for identifying key selection criteria and optimizing trait combinations under resource-limited conditions.

Therefore, this study aimed to (i) evaluate morphological and agronomic characteristics of M4 red rice mutant lines derived from 200 Gy gamma irradiation of the G16 genotype, (ii) estimate the extent of genetic variability among these mutant lines, and (iii) analyze the direct and indirect contributions of panicle-related traits to grain yield. The findings are expected to support the selection of superior mutant lines and contribute to the development of resilient red rice varieties adapted to sustainable agroecosystems.

## 2. MATERIALS AND METHODS

### 2.1 Study site and plant materials

The field experiment was conducted from May to November 2023 in Tatar Hamlet, Nyurlembang Village, Narmada District, West Lombok Regency, West Nusa Tenggara, Indonesia. The site represents a lowland rice-growing area with seasonal water availability. The plant materials consisted of 29 M4 mutant lines derived from gamma irradiation (200 Gy) of the G16 red rice genotype. Four rice varieties, namely G16, Inpari 32, IR64, and Ciliwung, were used as check varieties.

### 2.2 Experimental design and crop management

The experiment was arranged in an augmented randomized complete block design (augmented RCBD) with three blocks (r = 3). Each block contained all four check varieties (replicated across blocks = C) and a subset of unreplicated mutant lines (M), which were randomly assigned within each block. Each experimental plot measured 2 m × 1 m, with a planting distance of 20 cm × 20 cm, consisting of 4 rows per plot and 10 plants per row (Figure 1). One hill corresponded to a single transplanted seedling. Border rows were included to minimize edge effects. Standard agronomic practices for lowland rice cultivation were uniformly applied across all plots, including fertilization, irrigation, and pest management.

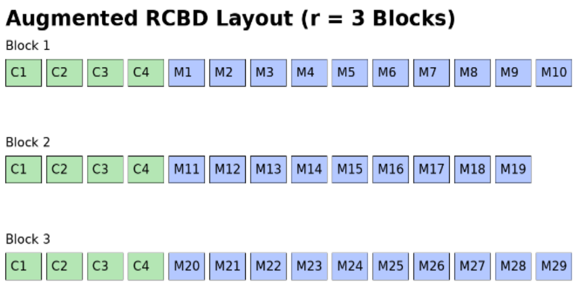


**Figure 1.** Layout of augmented randomized complete block design (Augmented RCBD) showing distribution of replicated check varieties and unreplicated mutant lines across blocks

### 2.3 Observed traits

Observations were recorded for agronomic, yield, and panicle-related traits, including: days to flowering, plant height, total tiller number, number of productive tillers, panicle length, longest panicle length, number of filled grains per panicle, number of unfilled grains per panicle, 100-grain weight, filled grain weight per hill, unfilled grain weight per hill, and total grain weight per hill. Grain weight measurements were recorded after drying to a standard moisture content of 14%, and observations were conducted on a per-hill basis. Panicle density was defined as the number of grains per unit length of panicle (grains cm$^{-1}$). Leaf and grain morphological traits were measured to support phenotypic characterization. For each genotype, five representative plants per plot were randomly selected. Leaf measurements (length, width, and angle) were taken at the maximum vegetative stage using the uppermost fully expanded leaf. Grain traits (length and width) were measured from 20 randomly selected filled grains per plant using a digital caliper.

### 2.4 Data analysis

Data were analyzed using analysis of variance based on the augmented RCBD model to test differences between mutant lines and check varieties (shown in Table 1). Mean comparisons were conducted using Tukey's honest significant difference test at a 5% significance level:

$$\text{BNJ}(\alpha) = \alpha,\ \text{dfp},\ \text{dfe} \times \sqrt{\frac{MSE}{r}}$$

where,

$\alpha$ = significance level, *dfp* = degrees of freedom for treatment, *dfe* = degrees of freedom for error, MSE = Mean Square Error, *r* = number of blocks (replications of check varieties).

Genetic variability was estimated using the genetic coefficient of variation (GCV), calculated as:

$$\text{GCV} = \frac{\sqrt{\sigma_g^2}}{\bar{x}} \times 100\%$$

where, $\sigma^2 g$ = genotypic variance, $\bar{x}$ = sample mean.

Genetic variance was estimated as:

$$\sigma_g^2 = \frac{MSG - MSE}{r}$$

where, MSG = Mean Square for Genotype, MSE = Mean Square Error.

In this study, *r* refers to the number of blocks (replications of check varieties) in the augmented design. Since mutant lines were unreplicated, variance components were estimated relative to replicated checks following standard procedures for augmented RCBD. Correlation and path coefficient analyses were performed to assess relationships among panicle traits and their direct and indirect effects on grain yield per hill.

To characterize the distribution and variability of key agronomic traits, graphical analyses were conducted using histograms and boxplots for TGW/hill (total grain weight per hill), FGP (number of filled grains per panicle), and PH (plant height). Histograms were employed to examine frequency distributions and identify potential skewness and outliers, whereas boxplots were used to summarize central tendency (median), dispersion (quartiles), and overall variability among mutant lines. In addition, comparisons between mutant lines and control plants were presented as bar plots, with error bars representing standard error (SE) or confidence intervals (CIs). The standard error was calculated as:

$$SE = \frac{SD}{\sqrt{n}}$$

where, *SD* denotes the standard deviation, and *n* represents the number of observations. All statistical analyses and graphical visualizations were carried out using Microsoft Excel.

**Table 1.** Analysis of variance for the augmented randomized complete block design (Augmented RCBD) model

| Sources | df | SS | MS | F-Value | Significance |
|---|---|---|---|---|---|
| Block | (r-1) | SSB | MSB | MSB/MS$_E$ | α(db b,dbe) |
| Treatment | ((g+c)-1) | SS$_P$ | MS$_P$ | MS$_P$/MS$_E$ | α(db p,dbe) |
| Checks (c) | (c-1) | SSC | MSC | MSC/MS$_E$ | α(db c,dbe) |
| Genotype (g) | (g-1) | SSG | MSG | MSG/MS$_E$ | α(db g,dbe) |
| C vs G | 1 | SSCG | MSCG | MSCG/MS$_E$ | α(db cg,dbe) |
| Error | ((g+rc)-1)-((g+c)-1)-(r-1)) | SS$_E$ | MS$_E$ | | |
| Total | ((g+rc)-1) | SST | | | |

Description: df = degree of freedom, SS = Sum Square, MS = Mean square, r = repeat, P = treatment, E = error.

## 3. RESULTS AND DISCUSSION

### 3.1 Results

3.1.1 Variation in agronomic and yield-related traits

Table 2 shows that the analysis of variance further indicated that most traits did not exhibit significant differences among mutant genotypes, suggesting relatively low genetic differentiation within the M4 population. In contrast, significant differences were detected between the mutant group and the check varieties (C vs G), indicating a clear shift in overall performance between these groups. This pattern is consistent with the characteristics of an augmented RCBD, where the absence of replication in mutant lines reduces the precision of variance estimation within the group, while the use of replicated checks enhances the ability to detect differences between groups.

Plant height, number of productive tillers, filled grain weight per hill, and total grain yield per hill differed significantly between mutant lines and the checks, indicating that gamma irradiation at a dose of 200 Gy successfully induced phenotypic variation at the M4 generation. In contrast, days to flowering and 100-grain weight showed non-significant differences, suggesting limited variation for these traits among the evaluated genotypes.

**Table 2.** Analysis of variance for morphological, growth, and yield-related traits of M4 red rice mutant lines

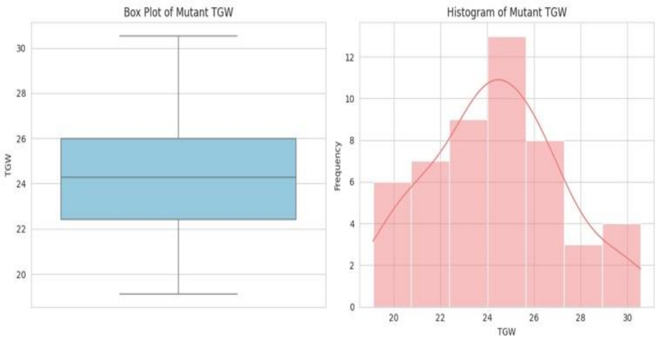
| No. | Morphological Characters | Genotype | C vs G |
|---|---|---|---|
| 1 | Days to flowering | ns | ns |
| 2 | Plant height | ns | * |
| 3 | Total tiller number | ns | * |
| 4 | Number of productive tillers | ns | * |
| 5 | Panicle length | ns | * |
| 6 | Longest panicle length | ns | ns |
| 7 | Number of unfilled grains per panicle | ns | * |
| 8 | Number of filled grains per panicle | ns | * |
| 9 | 100-grain weight | ns | ns |
| 10 | Filled grain weight per hill | * | * |
| 11 | Unfilled grain weight per hill | ns | * |
| 12 | Total grain weight per hill | ns | * |

Note: ns = not significant; * = significant at $p \leq 0.05$

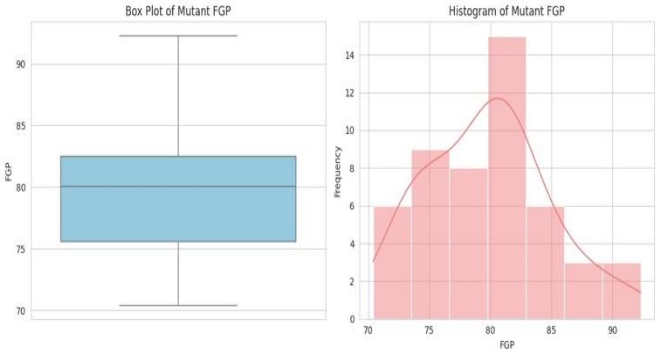
Mean comparisons revealed that several mutant lines exhibited shorter plant stature and higher grain yield per hill than the parental G16 line and local check varieties. Notably, mutant lines G12(18-10), G15(2-5), and G13(18-13) consistently showed favorable performance for yield-related traits, combining moderate plant height with higher filled grain weight per hill (Tables 3 and 4).

3.1.2 Panicle architecture and yield components

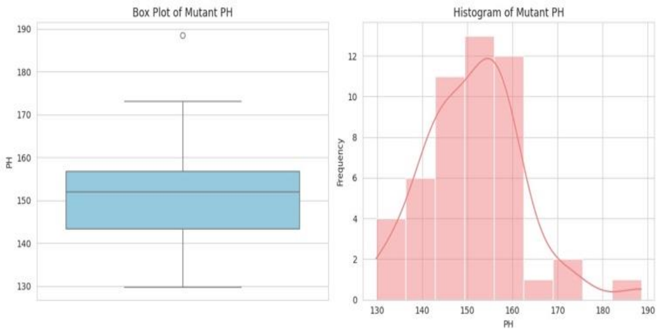
Significant variation was observed among mutant lines for panicle-related traits, including panicle length, number of filled grains per panicle, and number of unfilled grains per panicle. Mutant lines with longer panicles generally exhibited a higher number of filled grains per panicle, although this relationship was not absolute across all genotypes, as shown in Table 5. The number of filled grains per panicle emerged as a key yield component, contributing substantially to differences in total grain yield per hill among mutant lines.



(a)



(b)



(c)

**Figure 2.** (a) Visualization of TGW/hill (total grain weight per hill) distribution in mutant lines: histogram and boxplot, (b) Visualization of FGP (number of filled grains per panicle) distribution in mutant lines: histogram and boxplot, (c) Visualization of PH (plant height) distribution in mutant lines: histogram and boxplot

### 3.1.3 Distribution of key yield traits

Figure 2(a) showed that the TGW in mutant lines exhibited a median of approximately 24.3, with the central 50% of observations distributed within 22.4–26.0. Although the total range was relatively wide (11.5), dispersion within the core population remained constrained (IQR = 3.6). This pattern indicates good phenotypic stability, with variability maintained within normal limits and no evidence of extreme deviations, consistent with a quantitative trait under polygenic control with moderate variance.

Figure 2(b) showed the FGP in mutant lines exhibited a stable central tendency around 80, with moderate–high variability (IQR = 6.9). The distribution approximated normality with a slight positive (right) skew, indicating a marginal extension toward higher values. Overall, the data reflect good phenotypic homogeneity, although there is some expansion of variance toward the upper range, consistent with a quantitative trait under polygenic control with moderate dispersion.

Figure 2(c) showed that plant height (PH) in mutant lines was centered at ~152 cm, with high variability (IQR = 13.3) and a wide range (~59.3 cm). The distribution was near-normal but influenced by a high outlier (~188.8 cm), indicating elevated phenotypic variance. This suggests the presence of rare superior individuals, consistent with segregating polygenic effects producing extreme phenotypes.

**Table 3.** Tukey's honestly significant difference (HSD) test for growth and flowering traits of mutant lines and check varieties

| No. | Treatment | Growth | | | | | |
|---|---|---|---|---|---|---|---|
| | | PH (cm) | | TTN (stem) | | NPT (stem) | |
| 1 | G12(9-19) | 103.20 | c | 23.00 | ab | 21.20 | abc |
| 2 | G12(18-10) | 112.50 | cddef | 27.00 | ab | 23.10 | abc |
| 3 | G12(5-7) | 101.67 | bc | 26.00 | ab | 24.00 | abc |
| 4 | G12(7-10) | 109.00 | cddef | 22.33 | ab | 19.67 | abc |
| 5 | G12(2-4) | 105.20 | cddef | 20.78 | ab | 20.00 | abc |
| 6 | G15(2-5) | 109.67 | cddef | 23.40 | ab | 22.80 | abc |
| 7 | G15(4-20) | 119.90 | cdefg | 32.33 | ab | 27.44 | abc |
| 8 | G15(19-18) | 110.33 | cddef | 25.40 | ab | 19.50 | ab |
| 9 | G24(4-8) | 108.00 | cddef | 20.50 | ab | 17.50 | ab |
| 10 | G24(9-4) | 107.00 | cddef | 31.00 | ab | 29.00 | abc |
| 11 | G24(6-1) | 104.89 | cde | 23.22 | ab | 21.33 | abc |
| 12 | G24(17-2) | 113.38 | cddef | 17.63 | a | 15.25 | a |
| 13 | G24(10-1) | 104.86 | cde | 19.29 | ab | 17.71 | ab |
| 14 | G63(17-7) | 119.50 | cdefg | 24.60 | ab | 22.40 | abc |
| 15 | G63(9-5) | 113.67 | cdefg | 24.89 | ab | 23.56 | abc |
| 16 | G63(3-16) | 113.00 | cdefg | 23.50 | ab | 23.50 | abc |
| 17 | G63(6-11) | 119.10 | cdefg | 20.50 | ab | 19.50 | ab |
| 18 | G63(16-15) | 120.50 | cdefg | 24.10 | ab | 24.10 | abc |
| 19 | G63(5-14) | 132.90 | g | 25.40 | ab | 25.40 | abc |
| 20 | G63(19-9) | 124.50 | fg | 23.00 | ab | 19.30 | ab |
| 21 | G63(11-8) | 124.30 | efg | 23.10 | ab | 23.10 | abc |
| 22 | G63(15-18) | 116.50 | cdefg | 24.89 | ab | 21.60 | abc |
| 23 | G13(1-20) | 103.20 | c | 20.90 | ab | 20.90 | abc |
| 24 | G13(5-14) | 110.43 | cddef | 25.71 | ab | 25.71 | abc |
| 25 | G13(11-16) | 110.23 | cddef | 19.00 | ab | 18.86 | ab |
| 26 | G13(2-10) | 103.80 | cd | 25.50 | ab | 25.50 | abc |
| 27 | G13(12-2) | 109.60 | cddef | 21.70 | ab | 21.70 | abc |
| 28 | G13(17-19) | 107.50 | cddef | 28.60 | ab | 28.60 | abc |
| 29 | G13(18-13) | 110.40 | cddef | 26.56 | ab | 25.56 | abc |
| 30 | INPARI 32 | 82.57 | ab | 29.99 | ab | 27.29 | abc |
| 31 | IR64 | 74.10 | a | 33.69 | b | 34.43 | c |
| 32 | CILIWUNG | 83.47 | ab | 26.91 | ab | 24.90 | abc |
| 33 | G16 | 123.40 | defg | 24.33 | ab | 18.17 | ab |
| 34 | Tukey's HSD | 19.45 | | 14.81 | | 14.77 | - |

Note: PH = plant height; TTN = total tiller number; NPT = number of productive tillers
Means followed by the same letter within a column are not significantly different at $p \leq 0.05$ according to Tukey's HSD test

Mutant lines G15(4-20) and G63(5-14) recorded among the highest values for filled grain weight and total grain yield per hill, although their performance was not always statistically distinct from other high-yielding mutant lines. Check varieties, particularly IR64, exhibited higher tiller numbers but did not consistently translate this advantage into higher grain yield per hill compared with selected mutant lines.

3.1.4 Comparison between mutant lines and control

Figure 3(a) showed that TGW in the control group (~30.0) was markedly higher than in mutant lines (~24.2), with an absolute difference of 5.8 units (~24%). The absence of overlap in the error intervals indicates a clear separation between groups, suggesting a strong and likely statistically significant difference, consistent with distinct expression of a quantitative trait under differing genetic backgrounds.

Figure 3(b) showed the FGP in the control group (~85.5) exceeded that of the mutant lines (~79.5) by 6.0 units (~7.5%). The absence of overlap between error bars indicates a clear separation of group means, suggesting a robust and likely statistically significant difference, consistent with differential expression of a quantitative trait governed by distinct genetic backgrounds.

Figure 3(c), Plant height (PH) in the control group (~160.0 cm) exceeded that of the mutant lines (~151.0 cm) by approximately 9.0 cm (~6%). The non-overlapping error intervals indicate a clear separation between group means, reflecting a pronounced difference that is likely statistically significant, consistent with differential expression of a quantitative trait under distinct genetic backgrounds.

3.1.5 Genetic variability of morphological traits

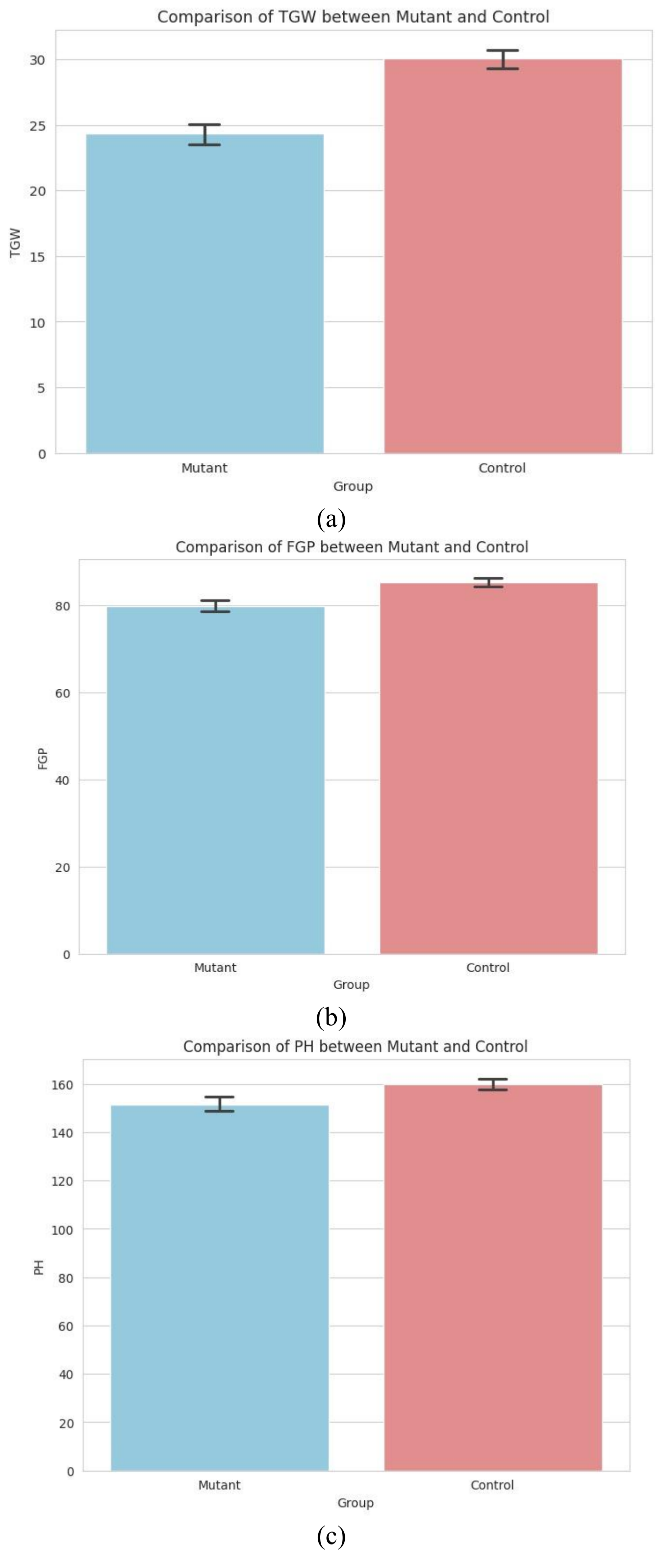
Table 5 shows the estimates of genetic variability, expressed as the GCV, ranged from narrow to moderate across the observed traits. Traits such as days to flowering, plant height, total tiller number, panicle length, longest panicle, number of filled grains per panicle, and 100-grain weight exhibited narrow genetic variability, indicating partial genetic fixation at the M4 generation. In contrast, the number of productive tillers, the number of unfilled grains per panicle, filled grain weight per hill, unfilled grain weight per hill, and total grain yield per hill displayed medium genetic variability.

The M4 mutant lines in Table 6 showed high variability in vegetative traits, particularly leaf angle (30.2° range) and leaf length (23.8 cm range), reflecting broad polygenic variation. In contrast, grain traits were highly stable, with minimal variation in grain length (0.11 mm) and width (0.04 mm), indicating strong genetic control and phenotypic canalization. This contrast suggests greater plasticity in vegetative traits, while several genotypes (notably the G63 group) displayed extreme values, consistent with transgressive expression and superior growth potential.

3.1.6 Correlation and path coefficient analysis

Table 7 shows the correlation analysis revealed both positive and negative associations among panicle traits and yield components. The number of filled grains per panicle showed a strong positive correlation with panicle density, indicating that denser panicles were associated with increased grain number. Conversely, 100-grain weight exhibited a weak negative correlation with panicle density and grain number, suggesting a trade-off between grain size and grain number.

Path coefficient analysis (Figure 4 and Table 8) revealed that the number of grains per panicle was the most influential trait affecting grain yield per hill, as indicated by its highest total effect value (0.871). Other traits, including panicle length, panicle density, and 100-grain weight, contributed to grain yield primarily through indirect effects mediated by grain number. These results indicate that the grain number per panicle is the highest.



(a)

(b)

(c)

**Figure 3.** (a) Visualization of TGW/hill (total grain weight per hill) comparison between mutant lines and control plants with standard error (SE), (b) Visualization of FGP (number of filled grains per panicle) comparison between mutant lines and control plants with standard error (SE), (c) Visualization of PH (plant height) comparison between mutant lines and control plants with standard error (SE)

**Table 4.** Tukey's honestly significant difference (HSD) test for yield and yield component traits of mutant lines and check varieties

| No. | Treatment | Yield Components | | | | | | | | | | Results | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | PL (cm) | | UGP (item) | | FGP (item) | | FGW (g) | | UGW (g) | | TGW (g hill$^{-1}$) | |
| 1 | G12(9-19) | 20.93 | abc | 9.61 | a | 84.72 | a | 37.32 | ab | 2.34 | ab | 42.94 | a |
| 2 | G12(18-10) | 23.13 | cde | 11.83 | ab | 123.77 | ab | 71.48 | ijkl | 1.93 | ab | 76.38 | fghi |
| 3 | G12(5-7) | 21.86 | abcde | 10.44 | a | 111.67 | ab | 46.73 | abcde | 2.33 | ab | 52.10 | abcd |
| 4 | G12(7-10) | 23.69 | e | 8.83 | a | 131.67 | ab | 56.85 | cdefghi | 1.96 | ab | 62.03 | bcdefg |
| 5 | G12(2-4) | 22.60 | bcde | 31.62 | b | 114.38 | ab | 60.06 | efghij | 1.52 | ab | 64.96 | cdefgh |
| 6 | G15(2-5) | 22.34 | bcde | 18.52 | ab | 107.24 | ab | 65.67 | ghijkl | 3.49 | b | 72.20 | efghi |
| 7 | G15(4-20) | 23.11 | bcde | 13.50 | ab | 142.07 | b | 81.35 | i | 2.99 | ab | 87.35 | i |
| 8 | G15(19-18) | 22.43 | bcde | 12.06 | ab | 116.78 | ab | 54.83 | cdefgh | 1.67 | ab | 59.62 | abcdef |
| 9 | G24(4-8) | 22.70 | bcde | 7.67 | a | 99.89 | ab | 48.25 | abcde | 1.40 | ab | 52.70 | abcd |
| 10 | G24(9-4) | 22.68 | bcde | 9.96 | a | 115.58 | ab | 60.39 | efghij | 3.43 | ab | 66.96 | defgh |
| 11 | G24(6-1) | 21.39 | abcd | 10.93 | a | 103.52 | ab | 51.62 | abcdefgh | 2.48 | ab | 57.39 | abcde |
| 12 | G24(1-2) | 22.68 | bcde | 10.33 | a | 124.21 | ab | 41.21 | abc | 1.33 | ab | 45.47 | ab |
| 13 | G24(10-1) | 22.43 | bcde | 7.38 | a | 99.88 | ab | 42.80 | abcd | 1.76 | ab | 47.64 | abc |
| 14 | G63(17-7) | 23.09 | bcde | 12.15 | ab | 131.45 | ab | 65.87 | hijkl | 2.23 | ab | 71.25 | efghi |
| 15 | G63(9-5) | 23.04 | bcde | 10.25 | a | 132.67 | ab | 62.70 | fghijk | 2.58 | ab | 68.38 | defgh |
| 16 | G63(3-16) | 23.08 | bcde | 11.78 | a | 130.67 | ab | 67.19 | hijkl | 1.68 | ab | 71.83 | efghi |
| 17 | G63(6-11) | 23.51 | de | 12.23 | ab | 128.93 | ab | 53.29 | bcdefgh | 1.26 | a | 57.56 | abcde |
| 18 | G63(16-15) | 23.15 | cde | 11.18 | a | 117.61 | ab | 64.90 | fghijk | 2.08 | ab | 70.04 | defgh |
| 19 | G63(5-14) | 23.74 | e | 17.86 | ab | 116.50 | ab | 72.41 | ijkl | 2.64 | ab | 77.96 | fghi |
| 20 | G63(19-9) | 23.59 | de | 10.07 | a | 143.70 | b | 62.14 | fghijk | 1.63 | ab | 66.92 | defgh |
| 21 | G63(11-8) | 23.59 | de | 14.39 | ab | 124.09 | ab | 74.18 | jkl | 1.77 | ab | 79.10 | ghi |
| 22 | G63(15-18) | 23.92 | e | 12.27 | ab | 123.23 | ab | 57.45 | cdefghi | 1.75 | ab | 62.50 | bcdefg |
| 23 | G13(1-20) | 22.13 | bcde | 12.00 | ab | 109.27 | ab | 49.51 | abcdefg | 1.83 | ab | 54.52 | abcde |
| 24 | G13(5-14) | 22.82 | bcde | 17.52 | ab | 113.33 | ab | 60.14 | efghij | 2.17 | ab | 65.37 | cdefgh |
| 25 | G13(11-16) | 22.54 | bcde | 8.83 | a | 111.11 | ab | 62.43 | fghijk | 2.09 | ab | 67.63 | cdefgh |
| 26 | G13(2-10) | 22.14 | bcde | 8.13 | a | 113.63 | ab | 60.34 | efghij | 1.39 | ab | 64.93 | cdefgh |
| 27 | G13(12-2) | 23.24 | de | 12.17 | ab | 121.20 | ab | 59.07 | defghij | 1.55 | ab | 63.66 | bcdefgh |
| 28 | G13(17-19) | 23.32 | de | 8.27 | a | 118.10 | ab | 59.11 | defghij | 1.41 | ab | 63.57 | bcdefgh |
| 29 | G13(18-13) | 22.70 | dcde | 10.93 | a | 133.33 | ab | 76.67 | kl | 1.84 | ab | 81.54 | hi |
| 30 | INPARI 32 | 19.73 | a | 20.10 | ab | 104.27 | ab | 45.68 | abcde | 3.19 | ab | 51.98 | abcd |
| 31 | IR64 | 20.83 | ab | 20.57 | ab | 107.13 | ab | 48.93 | abcdef | 3.28 | ab | 55.30 | abcde |
| 32 | CILIWUNG | 21.75 | abcde | 18.00 | ab | 100.13 | ab | 41.46 | abc | 3.20 | ab | 47.72 | abc |
| 33 | G16 | 23.24 | de | 17.17 | ab | 94.73 | ab | 35.32 | a | 2.66 | ab | 41.53 | a |
| 34 | Tukey's HSD | 2.28 | | 20.23 | | 57.04 | | 15.97 | | 2.16 | | 18.26 | |

Note: PL = panicle length; UGP = number of unfilled grains per panicle; FGP = number of filled grains per panicle; FGW = filled grain weight per hill; UGW = unfilled grain weight per hill; TGW/hill = total grain weight per hill. Means followed by the same letter within a column are not significantly different according to Tukey's HSD test at $p \leq 0.05$

**Table 5.** Genetic coefficient of variation (GCV) of observed traits in M4 red rice mutant lines

| No. | Morphological Characters | $\sigma^2 g$ | GCV (%) | Criteria |
|---|---|---|---|---|
| 1 | Days to flowering | 1.56 | 1.64 | Narrow |
| 2 | Plant height | 13.35 | 3.26 | Narrow |
| 3 | Total tiller number | 0.57 | 3.15 | Narrow |
| 4 | Number of productive tillers | 0.55 | 3.13 | Narrow |
| 5 | Panicle length | 0.09 | 1.29 | Narrow |
| 6 | Longest panicle length | 1.08 | 4.13 | Narrow |
| 7 | Number of unfilled grains per panicle | 1.38 | 9.67 | Medium |
| 8 | Number of filled grains per panicle | 9.88 | 2.65 | Narrow |
| 9 | 100-grain weight | 0.00 | 1.65 | Narrow |
| 10 | Filled grain weight per hill | 33.30 | 9.70 | Medium |
| 11 | Unfilled grain weight per hill | 0.05 | 10.72 | Medium |
| 12 | Total grain weight per hill | 33.42 | 8.94 | Medium |

Note: $\sigma^2 g$ = Genotype variation, GCV = Genetic coefficient variation
The criteria for genetic coefficient variation were: broad (>14.5%), medium (5%–14.5%), narrow (<5%)

**Table 6.** Leaf and grain morphological characteristics of selected M4 red rice mutant lines

| No. | Treatment | Leaf Characteristics | | | Grain Characteristics | |
|---|---|---|---|---|---|---|
| | | Leaf Angle | Leaf Width | Leaf Length | Grain Length | Grain Width |
| 1 | G12(9-19) | 20.00 | 1.20 | 46.00 | 8.20 | 3.03 |
| 2 | G12(18-10) | 20.00 | 1.70 | 57.80 | 8.22 | 3.04 |
| 3 | G12(5-17) | 25.00 | 1.00 | 45.00 | 8.26 | 3.03 |
| 4 | G12(7-10) | 31.00 | 1.00 | 47.30 | 8.21 | 3.06 |
| 5 | G12(2-4) | 22.00 | 1.30 | 51.00 | 8.24 | 3.04 |

|  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|
| 6 | G15(2-5) | 26.00 | 1.20 | 55.20 | 8.22 | 3.05 |
| 7 | G15(4-20) | 27.50 | 1.50 | 61.20 | 8.22 | 3.06 |
| 8 | G15(19-18) | 28.00 | 1.00 | 63.40 | 8.19 | 3.04 |
| 9 | G24(4-8) | 28.00 | 1.00 | 60.30 | 8.23 | 3.05 |
| 10 | G24(9-4) | 18.00 | 1.50 | 58.20 | 8.24 | 3.04 |
| 11 | G24(6-1) | 29.00 | 1.20 | 48.00 | 8.24 | 3.05 |
| 12 | G24(17-2) | 34.00 | 1.50 | 62.80 | 8.23 | 3.05 |
| 13 | G24(16-1) | 19.00 | 1.00 | 61.40 | 8.18 | 3.02 |
| 14 | G63(17-7) | 45.00 | 1.50 | 55.00 | 8.19 | 3.05 |
| 15 | G63(9-5) | 33.40 | 1.50 | 54.50 | 8.24 | 3.05 |
| 16 | G63(3-16) | 25.50 | 1.50 | 47.40 | 8.18 | 3.05 |
| 17 | G63(6-11) | 46.40 | 1.50 | 56.20 | 8.23 | 3.05 |
| 18 | G63(16-15) | 30.60 | 1.40 | 59.60 | 8.23 | 3.03 |
| 19 | G63(5-14) | 48.20 | 1.10 | 68.40 | 8.26 | 3.05 |
| 20 | G63(19-9) | 19.20 | 1.00 | 63.20 | 8.26 | 3.04 |
| 21 | G63(11-8) | 37.40 | 1.00 | 61.00 | 8.21 | 3.04 |
| 22 | G63(15-18) | 23.00 | 1.00 | 67.00 | 8.21 | 3.04 |
| 23 | G13(1-20) | 40.20 | 1.00 | 44.60 | 8.24 | 3.04 |
| 24 | G13(5-14) | 35.00 | 1.50 | 53.00 | 8.16 | 3.06 |
| 25 | G13(11-16) | 24.00 | 1.30 | 51.10 | 8.21 | 3.05 |
| 26 | G13(2-10) | 38.00 | 1.00 | 57.40 | 8.21 | 3.04 |
| 27 | G13(12-2) | 39.80 | 1.40 | 52.10 | 8.22 | 3.04 |
| 28 | G13(17-19) | 23.00 | 1.00 | 48.90 | 8.18 | 3.03 |
| 29 | G13(18-13) | 29.00 | 1.30 | 59.60 | 8.27 | 3.06 |

Description: Leaf angle (°) was measured as the inclination of the flag leaf relative to the vertical axis of the culm. Leaf width and leaf length were recorded in centimeters (cm), while grain length and grain width were measured in millimeters (mm) using a digital caliper. Reported values represent the mean of measurements obtained from sampled plants for each genotype.

**Table 7.** Correlation coefficients among rice panicle traits under gamma-ray irradiation (200 Gy)

| Panicle Trait Variables | X1 | X2 | X3 | X4 | X5 |
|---|---|---|---|---|---|
| X1 |  | 0.464** | 0.062 | 0.957** | -0.28** |
| X2 | 0.464** |  | 0.145 | 0.193 | -0.55 |
| X3 | 0.062 | 0.145 |  | 0.019 | 0.096 |
| X4 | 0.957** | 0.193 | 0.019 |  | -0.297** |
| X5 | -0.28** | -0.55 | 0.096 | -0.297** |  |

Description: X1 = Number of grains per panicle; X2 = Panicle length; X3 = Percentage of empty grains per panicle; X4 = Panicle density; X5 = Weight of 100 grains. ** = Significant correlation at the 5% level

**Table 8.** Direct and indirect effects of panicle traits on grain yield per hill based on path coefficient analysis

| Observation Variables | Direct Effect | Indirect Effect |  |  |  |  | Total Effect |
|---|---|---|---|---|---|---|---|
|  |  | X1 | X2 | X3 | X4 | X5 |  |
| X1 | 1.825 | 0 | -0.060 | 0.013 | -0.886 | -0.023 | 0.871 |
| X2 | 0.009 | -0.060 | 0 | -0.002 | 0.013 | 0.003 | -0.037 |
| X3 | 0.023 | 0.013 | -0.002 | 0 | -0.002 | 0.001 | 0.032 |
| X4 | 0.469 | -0.886 | 0.013 | -0.002 | 0 | 0.012* | -0.394 |
| X5 | 0.004 | -0.023 | 0.003 | 0.001 | 0.012* | 0 | -0.003 |

Description: X1 = number of grains per panicle; X2 = panicle length; X3 = percentage of empty grains per panicle; X4 = panicle density; X5 = weight of 100 grains; * = Significant based on the Sobel test

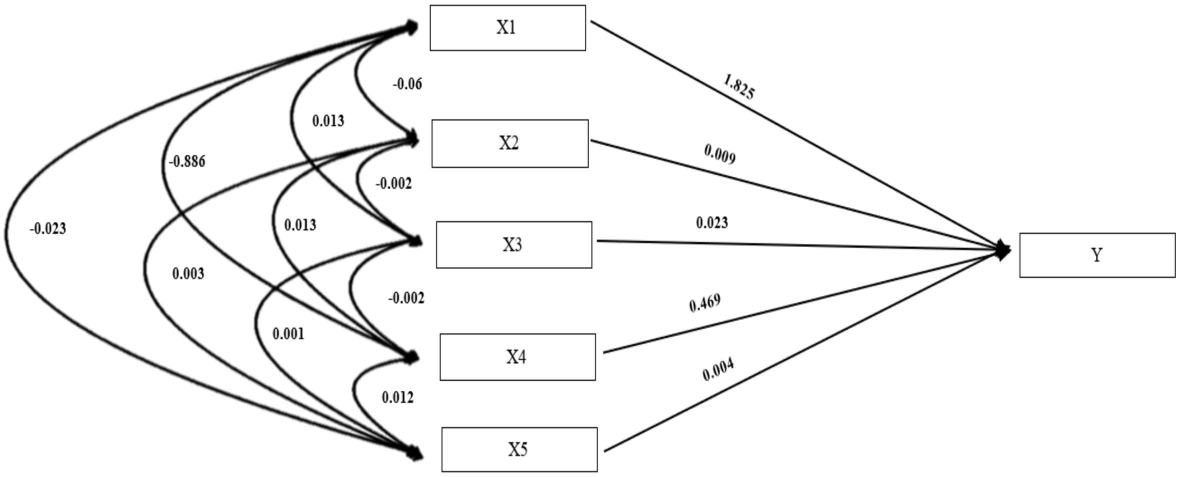


**Figure 4.** Path diagram illustrating direct and indirect effects of panicle traits on grain yield per hill
Description: X1: number of grain per panicle; X2: panicle length; X3 = percentage of empty grains per panicle; X4 = panicle density; X5 = weight of 100 grains ; Y = grain yield per hill

## 3.2 Discussion

### 3.2.1 Effectiveness of gamma irradiation in generating genetic variation

Gamma irradiation at a dose of 200 Gy demonstrated strong effectiveness in generating heritable genetic variation among M4 red rice mutant lines. Physical mutagens such as gamma rays are known to induce random point mutations and chromosomal alterations that can modify gene regulation associated with plant growth, development, and yield formation [20, 21]. The persistence of phenotypic differentiation at the M4 generation indicates that induced mutations were successfully fixed through successive selfing and selection cycles, while still retaining sufficient variability for meaningful genetic improvement. Similar trends have been reported in advanced mutant populations of rice, where exploitable variation remains detectable despite increasing homozygosity [22, 23].

The contrasting results between the non-significant Genotype effect and the significant C vs G comparison can be attributed to the structure of the augmented randomized complete block design (augmented RCBD). In this design, mutant lines are evaluated without replication, whereas check varieties are replicated across blocks, resulting in reduced sensitivity for detecting differences among mutant genotypes. Additionally, the relatively low GCV values suggest that many traits have approached genetic stabilization at the M4 generation following repeated selfing, a phenomenon commonly observed in advanced mutant populations where genetic segregation has been substantially reduced [13, 16, 17]. Consequently, the findings reflect limited variation within the mutant population but a distinct differentiation when compared to the control genotypes, which is consistent with the expected behavior of quantitative traits under selection and partial fixation [24, 25].

Panicle architecture emerged as a central determinant of grain yield formation in the evaluated mutant lines. The number of filled grains per panicle showed the strongest influence on yield expression, confirming that grain number constitutes the primary sink component governing rice productivity. Classical yield physiology studies emphasize that improvements in sink size are generally more effective for yield enhancement than increases in individual grain weight, particularly under environments with limited resources [26, 27]. The hierarchical relationship among yield components indicates that traits such as panicle length and panicle density contribute to yield mainly through their effects on grain number. This pattern is consistent with path analysis results reported by studies [7, 28], which identified panicle traits as key indirect drivers of yield across diverse rice genotypes.

The observed range of genetic variability has important implications for selection strategies in mutation breeding programs. Narrow variability detected for certain morphological traits suggests that these characters are approaching genetic stabilization, a common feature of advanced mutant generations subjected to directional selection [11, 29]. In contrast, traits related to yield formation, particularly productive tiller number and grain yield per hill, still exhibited sufficient variability to allow further genetic gain. According to quantitative genetic theory, traits combining moderate variability with strong associations to yield are optimal targets for selection, as they offer a balance between stability and improvement potential [24]. These findings support the prioritization of panicle-related traits as selection criteria in subsequent breeding stages.

From an agroecological perspective, the identification of mutant lines with moderate plant height, efficient panicle architecture, and stable yield performance is highly relevant for sustainable rice production systems. Reduced plant stature contributes to lodging resistance, while enhanced grain number per panicle increases yield efficiency without necessitating higher external inputs. Mutation breeding thus complements conventional breeding approaches by enabling the development of rice ideotypes adapted to marginal and dryland agroecosystems, where resilience and input-use efficiency are critical [16, 30]. The mutant lines evaluated in this study, therefore, represent valuable genetic resources for the development of resilient red rice varieties that integrate productivity, adaptability, and nutritional quality.

The variability in TGW/plant reflects differences in assimilate partitioning among mutant lines, with high-value outliers indicating the emergence of elite genotypes for selection. The wide distribution further highlights the importance of selection intensity in breeding programs [24]. FGP, as an indicator of sink strength, showed increased mean values and upper outliers, suggesting improved grain filling efficiency; such variability provides a broader selection base for yield improvement [7, 25]. Variation in plant height reflects differences in plant architecture, where dwarf types may enhance lodging resistance and taller types contribute to biomass production, supporting strategic selection under breeding objectives [24].

### 3.2.2 Genetic variability of morphological traits

The magnitude of genetic variability observed among morphological and agronomic traits provides important insights into the selection potential of the evaluated M4 mutant population. Traits exhibiting narrow genetic variability, such as days to flowering, plant height, and 100-grain weight, indicate a high degree of genetic stabilization resulting from successive selfing and selection cycles. Such stabilization is characteristic of advanced mutant generations and suggests that further improvement for these traits through simple selection may be limited [13, 31]. Nevertheless, genetic uniformity for these characters can be advantageous for varietal development, as it contributes to phenotypic consistency and agronomic predictability.

In contrast, moderate genetic variability was detected for traits directly associated with yield formation, including productive tiller number and grain yield per hill, which indicates that these characters remain responsive to selection. According to [25, 32], traits with moderate variability offer optimal opportunities for genetic gain because they balance stability with improvement potential. The persistence of variability in yield-related traits at the M4 generation suggests that induced mutations affecting complex quantitative traits are not fully fixed, thereby allowing continued selection in subsequent generations.

### 3.2.3 Correlation and path coefficient analysis

Correlation analysis revealed meaningful associations among panicle traits and yield components, highlighting the interconnected nature of yield formation in rice. Positive associations between panicle density and the number of filled grains per panicle indicate that denser panicles generally support higher grain numbers, thereby enhancing sink capacity. Conversely, weak or negative associations between 100-grain weight and grain number suggest a trade-off between grain size and grain number, a phenomenon commonly reported in rice yield physiology [18, 33].

Path coefficient analysis provided a more refined understanding of these relationships by partitioning correlation coefficients into direct and indirect effects. The number of filled grains per panicle exerted the strongest direct effect on grain yield per hill, confirming its role as the principal determinant of yield variation. Other traits, such as panicle length and panicle density, influenced yield primarily through indirect pathways mediated by grain number. Similar patterns have been documented by studies [6, 28], which emphasized that path analysis is a powerful tool for identifying key selection criteria by distinguishing true causal effects from spurious correlations. These findings reinforce the strategic importance of focusing selection on panicle traits that directly enhance sink size in mutation-based rice improvement programs.

According to Olivoto et al. [34], standardized path coefficients exceeding unity (>1.0) are not statistical errors but rather a mathematical manifestation of a data structure characterized by high multicollinearity. In this study, the direct effect of the number of grains per panicle (X1) was found to be 1.825, which exceeds unity. This phenomenon is attributed to the strong intercorrelations among the panicle traits evaluated. As standardized path coefficients are partial regression coefficients, they can exceed 1.0 when predictor variables are highly correlated, potentially making the estimations sensitive to minor data variations. Therefore, these results should be interpreted with caution; while X1 exerts a substantial direct positive influence, it is partially offset by negative indirect effects through other traits, resulting in a lower yet consistent total effect of 0.871.

## 4. CONCLUSIONS

This study demonstrates that gamma irradiation at a dose of 200 Gy is an effective tool for inducing phenotypic variation in G16 red rice, as evidenced by the significant differences observed between the mutant population and the control varieties. However, by the M4 generation, genetic differentiation among the individual mutant lines remains relatively narrow for most agronomic traits, showing low to moderate genotypic GCV. This suggests that the population is approaching genetic homogenization following successive generations of selection and selfing.

Path analysis identified grain number per panicle as the most critical yield determinant, exhibiting the highest total effect (0.871) on grain weight per hill, while its direct effect (1.825) was influenced by multicollinearity among panicle traits on grain weight per hill. Consequently, this trait is recommended as the primary selection criterion for the continued improvement of these red rice lines. While several promising lines—specifically G12(18-10), G15(2-5), and G13(18-13)—exhibited superior yield performance, their stability and adaptability must be validated through multi-environment trials before they can be considered for formal varietal release.

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