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Identification of Promising Mutants in Gamma-Irradiated M_2 Generation of the Soybean Line based on Morpho-Agronomic Traits

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ABSTRACT

Background: Gamma irradiation is an effective physical mutagen used to induce genetic variation and support the development of improved soybean cultivars. This study aimed to evaluate the morphological changes and agronomic performance of the M.1.1.3 soybean line in the M, generation derived from seeds irradiated with different gamma-ray doses.

Methods: The field experiment was conducted from November 2024 to March 2025 using four gamma irradiation-derived populations (0, 150, 250 and 350 Gy). A total of 704 M, plants were assessed for morphological variations (leaf colour, stem morphology and sterility types) and eight agronomic traits, namely plant height, number of productive branches, flowering and maturity time, number of filled and empty pods, 100-seed weight and seed yield.

Result: Gamma irradiation induced a range of distinct morphological abnormalities, notably chlorophyll mutants such as xantha and viridis, along with stem swelling and multiple forms of reproductive sterility, including complete sterility, partial sterility and poorly developed racemes. Moderate doses of gamma irradiation (150-250 Gy) enhanced key agronomic traits, notably the number of productive branches, the number of filled pods and seed yield per plant. In contrast, higher doses (350 Gy) significantly reduced plant height, pod formation, seed set and overall yield. Flowering and maturity were progressively delayed with higher irradiation doses. These results provide essential information for advancing superior mutant lines in subsequent generations and support future soybean breeding efforts.

Key words: Agronomic traits, Chlorophyll mutants, M.1.1.3-Line, Process innovation, Sterility.

INTRODUCTION

Soybean (*Glycine max* L.) is one of the most important legume crops globally, serving as a primary source of protein, oil and essential nutrients for both human consumption and animal feed. De Wrachien *et al*.. (2021) stated that the current global population of 7.8 billion is predicted to increase to 9.7 billion by 2050 and 10.9 billion by the end of the century. This rapid population growth will substantially increase the global demand for food, protein and edible oil sources, making it essential to develop high-yielding and resilient new soybean varieties to ensure food security and achieve sustainable agricultural production.

Conventional breeding often faces limitations in generating sufficient genetic diversity to cope with emerging challenges such as climate change, soil degradation and increasing pest or disease pressures. To overcome these constraints, mutation breeding has been widely adopted as an alternative approach to create novel genetic variability.

Mutation induction can be achieved using chemical mutagens, such as ethyl methane sulfonate (Nilahayati *et al*., 2023) and colchicine (Zou *et al*., 2025), which are known to induce point mutations and chromosome doubling, respectively. In addition, physical mutagens, particularly gamma irradiation, have proven highly effective in inducing a broad spectrum of mutations. According to Beyaz and Yildiz (2017), gamma irradiation induces a wide range of genetic mutations, including single-base substitutions, deletions, insertions and chromosomal rearrangements, by causing DNA damage in plant cells. These mutations can result in new phenotypic traits, including improved yield,

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stress tolerance and disease resistance, which are often difficult to achieve through traditional breeding alone.

Gamma irradiation has successfully increased genetic and phenotypic diversity in crops such as rice (Li *et al.,* 2019), cowpea (Raina *et al*., 2022), grasspea (Singh *et al*., 2018) and groundnut (Nilahayati *et al*., 2024), enabling the selection of desirable traits for breeding programs. In soybeans, gamma irradiation has successfully induced desirable traits such as increased yield (Nilahayati *et al*., 2018; Nilahayati *et al*., 2022), improved disease resistance (Samudio-Oggero *et al*., 2025) and enhanced adaptability to abiotic stresses (Komatsu *et al*., 2023; Kang *et al*., 2024).

In the previous study, gamma irradiation was applied to the soybean line M.1.1.3 to induce genetic variation in the M_1 generation. The results show that gamma irradiation induced morphological and agronomic variation, including changes in leaf size, stem shape and sterility, while higher doses reduced seed viability, vegetative growth, yield components and delayed both flowering and harvesting times (Nilahayati *et al*., 2025). The M_2 generation, which follows the initial mutagenized (M_1) plants, is widely recognized as the key stage for observing and evaluating induced mutations. In the M_2 generation, most plants are genetic chimeras and only dominant mutations are typically expressed; recessive mutations remain masked and cannot be identified (Arisha *et al*., 2015).

In the M_2 generation, segregation enables both recessive and dominant mutations to become homozygous and phenotypically expressed, making it ideal for mutation screening (Pramanik *et al*., 2023). Numerous mutation breeding studies compiled and summarized by Shu *et al*. (2012) have demonstrated that M_2 populations exhibit wide morphological and agronomic variation, including changes in plant height, leaf morphology, yield components and stress tolerance.

Therefore, this study was conducted to evaluate the phenotypic variability and agronomic performance of the M_2 soybean population derived from gamma-irradiated M.1.1.3 lines. The findings are expected to provide valuable information for selecting superior genotypes to be advanced in subsequent generations and to support future soybean breeding programs targeting productivity and resilience under water-limited conditions.

MATERIALS AND METHODS

Experimental site and materials

The field experiment was conducted in Meunasah Alue Village, Nisam District, North Aceh, Indonesia. Laboratory observations were carried out in the Agroecotechnology Laboratory, Faculty of Agriculture, Universitas Malikussaleh, Indonesia. The experiment was conducted from November 2024 to March 2025. Seeds of the soybean M.1.1.3-line (M, generation) were derived from M_1 plants previously irradiated with ^{60}Co gamma rays at doses of 0, 150, 250 and 350 Gy.

Experimental design and field management

The experiment comprised four radiation treatment levels: G_0 (0 Gy, control), G_1 (150 Gy), G_2 (250 Gy) and G_3 (350 Gy). Each treatment was grown in field plots (4 × 2.2 m for G_0 - G_1 and 1.6 × 2.2 m for G_3) with a spacing of 40 × 20 cm. A total of 704 plants were observed. Standard field management was followed, including organic fertilizer (10 t/ha manure) and inorganic fertilizer (50 kg/ha urea, 100 kg/ha SP-36 and 100 kg/ha KCl). Weeding, pest control and irrigation were carried out uniformly across treatments. Plants were harvested when approximately 95% of pods had turned brown and 90% of leaves had abscised.

Observations

Morphological traits observed included leaf colour, stem morphology and sterility types. These traits were recorded only when morphological changes were present in the plants. The observations were conducted by counting the number of plants exhibiting each type of morphological variation and documenting them through photographs. Agronomic traits evaluated comprised germination percentage (%), plant height (cm), number of productive branches (plant^{-1}), days to flowering (DAP), days to maturity (DAP), number of filled and empty pods (plant^{-1}), dry seed weight (g plant^{-1}), 100-seed weight (g) and estimated yield per hectare (kg ha^{-1}).

Data analysis

All data were statistically analyzed using paired t-tests in Minitab 14 software. Differences were considered significant at the 5% ($p<0.05$) and 1% ($p<0.01$) probability levels. Significant differences were interpreted as evidence of radiation-induced effects on agronomic traits.

RESULTS AND DISCUSSION

The results showed that among the plant populations treated with gamma radiation, noticeable changes were observed in most agronomic traits, including plant height, number of branches, pod formation, days to flowering and maturity and seed yield components. The agronomic performance of the M_2 soybean line M.1.1.3 derived from gamma-ray irradiation is presented in Table 1.

Gamma-ray treatment significantly affected plant height at 8 WAP (Weeks After Planting). The average height of control plants (0 Gy) was 75.19 cm, while the irradiated populations exhibited shorter plants. The mean heights were 73.33 cm, 69.82 cm and 70.10 cm for 150 Gy, 250 Gy and 350 Gy, respectively. The reductions at all irradiation doses were highly significant ($p<0.01$) compared to the control, indicating that gamma irradiation tends to suppress vegetative growth.

Gamma irradiation frequently leads to a reduction in plant height in the M_2 generation across a wide range of plant species, with the extent of reduction often depending on the radiation dose and plant genotype. In rice, gamma irradiation induces significant reductions in plant height in the M_2 generation, with reductions ranging from 11% to nearly 38% depending on the mutant line and dose (Sao *et al*., 2022). Similar reductions in plant height have been observed in safflower (Yaman and Bayraktar, 2023), okra

(Yakoro *et al*. 2023) and soybean (Addai *et al*., 2019). The reduction is generally dose-dependent, with higher doses causing greater stunting, though some low or moderate doses may have neutral or even stimulatory effects on growth in certain cases.

Moderate doses can sometimes promote mild physiological stress leading to compensatory growth responses, explaining why 150 Gy plants showed only a slight decrease. Valkova *et al*. (2022) stated that moderate doses of ionizing radiation (such as 150 Gy) can act as a mild stressor, activating plant defense and repair mechanisms without causing severe damage. This stress can stimulate antioxidant enzyme activity, enhance DNA repair and upregulate stress-response genes, leading to improved tolerance and, in some cases, even growth stimulation or only slight growth reduction compared to higher doses.

The use of gamma irradiation on M.1.1.3 soybean lines at M_2 generation showed that the number of productive branches varied significantly among treatments. The control plants produced 6.83±1.12 branches, whereas populations exposed to 150 Gy and 250 Gy produced slightly more branches (8.00±2.24 and 7.40±1.21, respectively), both of which were significantly higher than the control. However, the 350 Gy population had fewer branches (5.33±1.53; $p<0.05$).

Gamma irradiation at moderate doses has been shown to induce mutations that affect plant growth regulators, particularly auxins and cytokinins, which are central to apical dominance and lateral bud development (Li *et al.*, 2024). This finding agrees with Mohsen *et al*. (2023) and Mehetre and Kshirsagar (2022), who reported that gamma irradiation significantly increases the number of productive branches in the M_2 generation, especially at low to moderate doses (100-300 Gy). Optimal results depend heavily on the dosage and variety used. Excessive dosages can damage plants and reduce productivity.

A consistent delay in flowering with increasing irradiation doses. The control plants flowered at 36.57±1.01 days, whereas irradiated populations required 43.38±1.50, 48.56±1.82 and 54.66±0.57 days at 150, 250 and 350 Gy, respectively, showing highly significant differences ($p<0.01$) from the control. The pattern of maturity followed a similar trend to flowering time. The control population reached maturity as early as 85.23±1.01 days, whereas irradiated plants matured later, 91.38±1.98, 92.89±2.50 and 97.66±0.57 days for 150, 250 and 350 Gy, respectively. These differences were highly significant ($p<0.01$). A similar report by El-Khateeb *et al*. (2023) reported that gamma irradiation in *Gaillardia pulchella* seed induced sufficient genetic variability, with low doses promoting early flowering and increased flower number, while high doses delayed flowering.

Gamma irradiation influenced pod development significantly. The number of filled pods increased from

Table 1: Mean values of agronomic characteristics of the M_2 soybean population M.1.1.3 derived from gamma-ray irradiation in the second-generation planting.

Agronomic characteristic	Population (P)			
	P 0 Gy	P 150 Gy	P 250 Gy	P 350 Gy
Plant height (8 WAP)	75.19±2.05	73.33**±1.56	69.82**±2.73	70.10**±8.11
Number of productive branches	6.83±1.12	8.00**±2.24	7.40*±1.21	5.33*±1,53
Number of filled pods	115±25.5	152.1** ±48.9	141.6**±40.2	61.3**±21.7
Number of empty pods	1.83±1.34	6.67** ±4.55	12.93**±6.63	16.33**±5.13
Days to flowering	36.57±1.01	43.38**±1.50	48.56**±1.82	54.66**±0.57
Days to maturity	85.23±1.01	91.38**±1.98	92.89**±2.50	97.66**±0.57
Seed weight per plant (g)	32.36±8.75	39.9**±12.1	37.3*±11.8	9.99**±5.39
100-seed weight (g)	14.52±0.85	14.60^{ns}±1.38	14.4^{ns}±1.02	9.88**±5.41

Note : * = Significantly different from control population (0 Gy) at 5% level based on t-test.
** = Highly significant difference from control population (0 Gy) at 1% level based on t-test.
Ns = Not significantly different from control population (0 Gy) based on t-test.

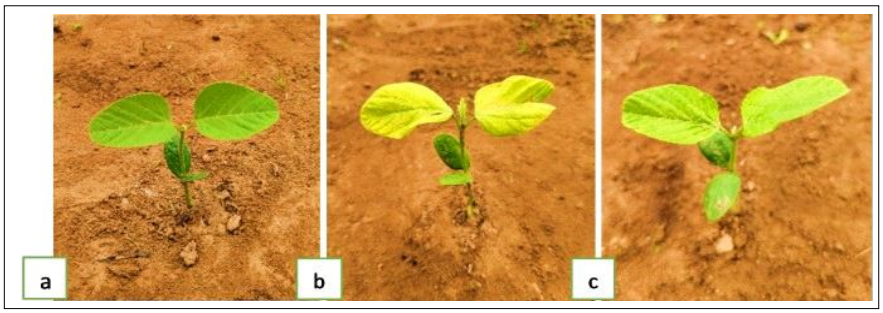


Fig 1: Leaf color changes (a. Normal soybean leaf, b. Xantha, c. Viridis).

115±25.5 in the control to 152.1±48.9 at 150 Gy and 141.6±40.2 at 250 Gy ($p<0.01$). However, a drastic reduction was observed at 350 Gy (61.3±21.7). In contrast, the number of empty pods increased markedly with radiation intensity from 1.83 ± 1.34 (control) to 6.67±4.55, 12.93±6.63 and 16.33±5.13 for 150, 250 and 350 Gy, respectively.

Seed yield per plant was strongly affected by irradiation dose. The control population produced 32.36±8.75 g of seeds per plant, which increased significantly to 39.9±12.1 g at 100 Gy and 37.3±11.8 g at 250 Gy, but dropped sharply to 9.99±5.39 g at 300 Gy ($p<0.01$). The 100-seed weight remained relatively stable across lower doses but declined significantly at higher irradiation levels. The control population recorded a mean value of 14.52±0.85 g, while the 150 Gy and 250 Gy treatments produced comparable values of 14.60±1.38 g and 14.40±1.02 g, respectively (P = NS; α = 0.01). In contrast, a significant reduction was observed at 350 Gy, with a mean of 9.88±5.41 g.

Seed yield in the M_2 generation is strongly influenced by the irradiation dose. Moderate doses (typically 50-200 Gy, depending on species) can enhance yield or maintain it at control levels, but higher doses (e”300 Gy) generally cause a significant reduction in seed yield due to increased physiological and genetic damage (Addai, 2019). At lower irradiation doses, the 100-seed weight often remains stable or may even increase slightly, reflecting beneficial mutagenic effects. However, with increasing radiation dose-particularly beyond 200-300 Gy-a pronounced decline in 100-seed weight was evident, with the greatest reductions occurring at 350 Gy and higher doses. This pattern is consistent across multiple crops, such as soybean (Badr *et al*., 2018) and corn (Kikakedimau *et al*., 2022).

In this study, we further found morphological diversity in leaf colour. There are two types of chlorophyll mutants, namely the *xantha* and *viridis*. Both types began to appear when the plants were 7 days after planting (DAP). In the *xantha* type mutants, when the plants reached 6 months, expressed symptoms of wilting in all parts of the plant and then slowly died. The *viridis* type mutants experienced a change in leaf colour to normal when the plants were 4 weeks after planting. The gamma-irradiation–induced change in leaf colour in the soybean line M.1.1.3, observed in the M, generation, is illustrated in Fig 1.

Leaf colour changes were noted at a dose of 150 Gy, with 3 viridis mutants identified among 224 plants observed. At a population dose of 250 Gy, there were 2 xantha mutants and 8 viridis mutants found out of 201 plants observed. Additionally, at 350 Gy, 2 xantha mutants were observed among 3 plants. Overall, 15 out of 518 plants exhibited changes in leaf colour across all doses.

The colour of *xantha* soybean leaves is characterised by bright yellow to pale yellow due to low chlorophyll content in the leaves, making the green colour of chlorophyll invisible. Vasudevan *et al*. (2023) stated that *xantha* mutans exhibit a yellowish color because of a severe reduction or absence of chlorophyll, with carotenoids remaining visible. *Xantha* mutants typically survive only a few leaf stages due to their inability to perform efficient photosynthesis. *Viridis* mutants display light yellowish-green (viridine green) leaves at early growth stages, reflecting a moderate reduction in chlorophyll. *Viridis* mutants are viable and can survive to maturity, with leaf colour gradually shifting to normal green as chlorophyll content increases during development. This transition is due to the progressive accumulation of chlorophyll as the plant matures. Nilahayati *et al*. (2016) revealed that chlorophyll mutations are often used to assess the genetic impact of various mutagens because they are easier to detect. Similarly, Vasudevan *et al.* (2023) emphasized that across many plant species and mutagens, chlorophyll mutations are consistently used as the primary, most dependable index for mutagen sensitivity and mutagenic efficiency, even though the mutants themselves are rarely of direct economic value.

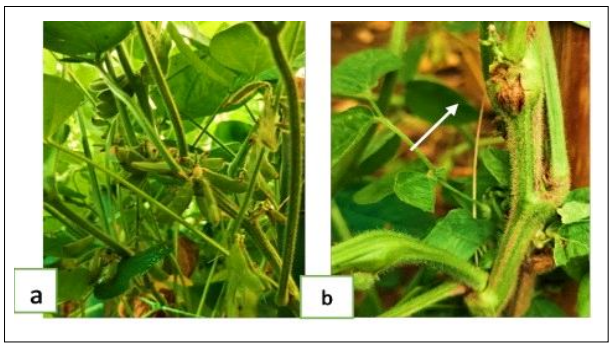
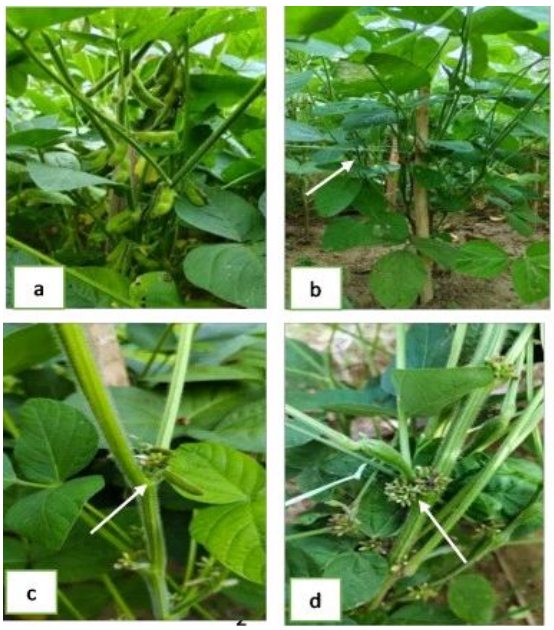


Fig 2: Stem morphology types in the soybean plant (a. Normal soybean plant, b. Plant showing swelling at the stem nodes).



(a) Normal soybean (b) Full sterility (c) Partial sterility (d) Undeveloped raceme flower.

Fig 3: Sterility variation.

The results of this study demonstrated morphological diversity in the stem shape of soybean line M.1.1.3 resulting from gamma irradiation in the M_2 generation. There is swelling in the stem nodes of the plants. Stem swelling occurred only in the 250 Gy gamma-irradiated population, observed in 8 plants out of 199 individuals. Variations in stem morphology of the soybean line M.1.1.3, induced by gamma irradiation and observed in the M_2 generation, are shown in Fig 2. Multiple studies confirmed that gamma irradiation causes substantial variation in morphological traits such as stem shape. Similar findings are reported across other soybean lines, where gamma irradiation in the M_2 generation resulted in a spectrum of morphological mutants, including altered stem shapes (Nobre *et al*., 2019; Mehetre *et al*., 2022b).

The results of this study also showed a gradation of sterility in the M.1.1.3 soybean line of the M_2 generation caused by gamma irradiation. The observed sterility variations were categorized into three types: fully sterile, partially sterile and undeveloped racemes. The sterility variation of the M.1.1.3 soybean line in the M_2 generation caused by gamma irradiation is shown in Fig 3.

A fully sterile variation was clearly identified in the 250 Gy population, with 3 out of 199 plants affected. Additionally, 5 plants in the same population exhibited partial sterility. In the 150 Gy population, 6 out of 224 plants displayed poorly developed racemes, while 15 out of 199 in the 250 Gy population did as well. Normal soybean plants are expected to produce both flowers and pods. Full sterility results in the complete absence of flowers and pods, whereas partial sterility allows 5 to 10 pods, each containing just one seed. Poorly developed racemes produce flower buds that fail to open (do not bloom).

As described by Choi *et al*. (2021), gamma radiation induces DNA damage through direct strand breaks and reactive oxygen species generation, leading to chromosomal aberrations, gene mutations and impaired DNA repair mechanisms. In line with Kumar and Dwivedi (2012), this damage disrupts key cellular processes, including meiosis and mitosis, resulting in abnormal chromosomal segregation, fragmentation during meiosis and other cytological abnormalities, leading to defective pollen mother cells and reduced pollen fertility. Furthermore, Priyanka *et al*. (2021) reported that high doses of gamma rays inhibit flower formation, reduce the number of petals and cause malformed or undeveloped flowers, contributing to partial or complete sterility.

CONCLUSION

Gamma irradiation induced morphological and agronomic variation in the M.1.1.3 soybean line at the M, generation. Moderate radiation doses (150-250 Gy) enhanced branching, pod formation, seed weight and yield, whereas high doses (350 Gy) were detrimental to plant growth and reproduction. Therefore, doses between 150-250 Gy are recommended for mutation breeding and selection of superior soybean lines in subsequent generations. Further evaluation should focus on heritability and stability of desirable traits.

Conflict of interest

On behalf of all authors, I would like to declare that there is no conflict of interest regarding the publication of our manuscript.

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