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Germination and seedling growth of peanut mutants (*Arachis hypogaea* L.) under salt stress

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ABSTRACT

Peanut is an annual plant that self-pollinates. Because of its low genetic variability, it is vulnerable to biotic and abiotic constraints. Salinity is one of the major elements that create an adverse environment for the growth of most legumes, which influences plant development and production. To deal with this limitation, induced mutations have been used to improve tolerant plant varieties for the plants that are resistant and adaptable to changing environmental conditions. Consequently, this study aims to assess the germination, early seedling stage, and development stage along with morphological and physiological traits for three irradiated mutants at doses 100, 150, and 200Gy of two peanut varieties, Kp29 and Fleur11, under saline conditions. To test for salinity tolerance, the peanut plants were subjected to 0, 2.9, 5.8, 8.8 g/l NaCl. The obtained findings clearly show that the mutants irradiated at 150Gy and 200Gy were found to be the most salinity tolerant, having better performance and adaptation with significantly increased germination, plant growth aerial as well as root parts, chlorophyll content, and stomatal resistance, compared to unirradiated ones under salinity.

Keywords: peanut, mutant, salinity, tolerance, induced mutation.

INTRODUCTION

Peanut (*Arachis hypogaea* L.) is an economically important oilseed legume considered the 13th largest crop in the world due to its nutritional value. It grows in more than 100 countries and occupies third position after sunflower and canola with a cultivated area exceeding 15,000 hectares (USDA-IPAD., 2023). It has a particular interest in the concept of sustainable agriculture, as it plays an important role in maintaining soil fertility. However, the low genetic variability makes it sensitive to biotic and abiotic stress, which negatively affect plant development and production. The effects of climate change and the bad agronomic practices have increased the agricultural lands subjected to salinization (Ondrasek and Rengel, 2021). Due to high evaporation, poor rainfall, inadequate irrigation, and other unjust anthropogenic activities, the salt-affected land is growing at a pace of 10% per year (Abiala *et al.*, 2018). The salinized area will approach 50% of global arable land by 2050 (Sun *et al.*, 2018). The most threatened areas are mainly located in the South and East of the Mediterranean region and include Morocco, Algeria, Libya, Egypt, the State of Palestine as well as the Syrian Arab Republic (Satta *et al.*, 2015).

According to the 4th Report on the State of the Environment Morocco (REEM4) (ONEM, 2020), salinization has adversely affected more than 1.6 million hectares of soil; note that the areas most affected by salinity in Morocco are irrigated lands, making up about 1 million hectares, or 11% of useable agricultural area, resulting in major losses in agricultural productivity.

The harmful effect on plant performance depends on the stage of growth, plant species, salinity concentration, and duration (Hasanuzzaman *et al.*, 2014; Hessini *et al.*, 2015). Unfortunately, even a minimum quantity of salt in irrigation water can cause severe yield losses in most agricultural crops. Salinity has a dual impact on plant performance, acting either as an inhibitor of water uptake by roots, via osmotic stress affecting various downstream processes in plants within several hours; or as an accumulator of Na+ and Cl− ions, with subsequent toxic impacts via ionic stress (Flowers *et al.*, 2015; Acosta-Motos *et al.*, 2017; Carillo *et al.*, 2019; Zhao *et al.*, 2020). As a result, crop productivity is limited due to reduced growth and development rate, as well as changes in plant metabolic processes (photosynthesis, respiration, protein synthesis) by disturbing ions and water uptake, affecting nitrogen metabolism (Woodrow *et al.*, 2017; Hessini *et al.*, 2021).

Peanut represents one of the Fabaceae sensitive to salinity; their growth is generally reduced at concentrations of 50 mM NaCl (Zahran, 1991). The identification of salt-tolerant varieties and genotypes, capable of minimizing the depressive effects of salinity on yields, would certainly make it possible to improve agricultural production in the areas affected by salinity. Different approaches to induced mutations were used to improve the tolerant plant varieties to alleviate salinity stress in crops.

According to the cited research, gamma irradiation produces genetic variety in seeds, making it a natural way to contribute mutations for drought improvement in crops (Elsherbiny *et al.*, 2024). This method has been applied to induce mutagenesis in rice, soybean, chickpea, cowpea, and peanut crops, producing mutant lines with improved characteristics, such as increased yield and adaptable features (Akhar *et al.*, 2011; Shabani *et al.*, 2022; Saibari *et al.*, 2023b; Elsherbiny *et al.*, 2024). In addition to accelerating the development of desired features, gamma irradiation supports sustainable agriculture; yet, there are downsides, including the possibility of dangerous mutations and the need for radiation dosage optimization (Elsherbiny *et al.*, 2024). Further study on this method is essential to address food security in a changing environment. It is well known that wild peanut species have low genetic diversity (Ferguson *et al.*, 2004), also studies using simple sequence repeat (SSR) and single-nucleotide polymorphism (SNP) markers have revealed a lower level of genetic diversity in Chinese peanut cultivars compared to wild relatives or landraces, with average gene diversity indices around 0.11 to 0.15, which is considered low (Ren *et al.*, 2014).

Therefore, physical mutagenesis can be used to expand the genetic foundation for gamma radiation breeding (Thenuja, Sutharsan and Rifnas, 2024). Numerous cultivation plants now have innovative and valuable genetic variety, because of this quick and effective procedure (Di Pane *et al.*, 2018; Hanafy and Akladious, 2018; Darwesh and Elshahawy, 2021). In this context, the authors proceeded to evaluate the responses of peanut mutant lines to varying concentrations of NaCl at germination and seedling stages.

MATERIALS AND METHODS

Plant material

Mutant lines of three radiation gamma doses from two peanuts varieties Kp29 and Fleur 11 were used in this study. Non-irradiated seeds Kd0/Fd0, dose 100Gy: Kd1/Fd1, dose 150Gy: Kd2/Fd2, dose 200Gy: Kd3/Fd3. These mutants were recently developed and characterized as described by (Saibari *et al.*, 2023a).

Effect of salinity on the germination process and early seedling stage of peanut mutant

To evaluate the effect of salinity on the germination process, 108 peanut seeds for each variety were disinfected according to the method described by (Saibari *et al.*, 2023a), and allowed to germinate in sterile glass jars containing Joseph paper and moistened with 10 ml of saline solution at concentrations of 0, 2.9, 5.8, and 8.8 g/l. For control group (0 g/l), distilled water served to stimulate the absence of salt stress. Each treatment was replicated 3 times (9 seeds per treatment). The jars will then be kept at a temperature of 25±1 °C in the incubator and monitored every 24 hours for 10 days. A seed was considered germinated when the radical length was greater than 3 mm.

The measured germination parameters were: Germination percentage (GP), germination speed (GS) and mean germination time (MGT). They were calculated according to the following formulas:

$$GP = \frac{Number\ of\ germinated\ seeds}{Total\ number\ of\ seeds} \times \quad (1)$$

(Hernández-Herrera *et al.*, 2014);

$$GS = \Sigma\frac{Gt}{Dt} \quad (2)$$

where: Gt is the number of seeds newly germinated on day t and Dt is the number of days (Batabyal, Dalal and Tah, 2014);

$$MGT = \frac{\Sigma(DXn)}{\Sigma n} \quad (3)$$

where: n is the number of seeds newly germinated on day and D is the number of days counted from the beginning of the test, and expressed as days (Hernández-Herrera *et al.*, 2014).

Several parameters were assessed during the early seedling stage, including the length, fresh and dry weight of hypocotyl, epicotyl and root. Length measurements were obtained by using a graduated ruler. Fresh weights were determined with an accurate scale. For the dry weight measurements, the hypocotyl, epicotyl, and root were subjected to an oven-drying process at a temperature of 70 °C for a period of 48 hours.

Effect of salinity on the development and plant physiology of seedlings

The study was conducted in a greenhouse at the Regional Center of Agricultural Research in Tangier. Sowing was carried out in plastic pots (22 cm wide and 20cm high). The soil used for sowing was collected from the surrounding area of the Regional Center of Agricultural Research in Larache, Morocco which had a pH of 5.5–6 and electrical conductivity of 40 mS/m (±25%), consisting of 80.5% sand, 11% silt, and 8.5% clay.

For each variety, four groups representing salinity concentrations were installed. Each group contains four lines presenting control seed line and three mutant seed lines. Each line contains three pots, each containing three seeds. The pots were irrigated regularly, every two days, with tap water for the control group, and with the three NaCl concentrations used to test peanut mutant's tolerance to salinity for the rest of the groups.

For saline treatment groups, water was used for irrigation in the first week of seedling, and then they were irrigated gently with saline solutions to avoid osmotic shock.

Several parameters were measured at the end of the flowering stage. The morphological traits including, number and surface of leaves, number of branches, number of nodules, length, fresh and dry weight of shoot and primary root. The physiological traits comprised chlorophyll content, and stomatal conductance. The chlorophyll content was measured using a SPAD-502 chlorophyll meter. The average surface measured was 6 mm², and the measurement has an accuracy of ±1 mg/cl. The stomatal conductance was measured using a "Leaf Porometer SC-1", the measurement obtained is the rate of CO_2 entering, or water vapor exiting through the stomata and expressed in Mmol/m².s. The physiological parameters were measured on the 3rd pair of leaves from the apex of the plants.

Statistical analysis

All the data were subjected to an analysis of variance (ANOVA), using IBM SPSS 26.0 software (Corp, 2019) and the difference between means were compared by Tukey's honestly significant difference (HSD) tests ($p < 0.05$).

RESULTS

Effect of NaCl on germination and early seedling stage of peanut mutants

The effect of various NaCl concentrations on the germination parameters shows that both varieties responded similarly to varying salt levels, as shown in Figure 1. However, unirradiated seeds reveal that with increasing salinity levels, there were corresponding declines in germination percentage (PG) and germination speed (GS) (Figure 1). In contrast, Fd2, Kd2, and Kd3 mutant exhibited a significant increase in PG at low and moderate concentrations (Fd2 at 2.9 g/l, and Kd2, Kd3 at 5.8 g/l). It was also noticed that the Kp29 mutants germinated significantly better than Fleur11 at high NaCl concentration (8.8 g/l).

In terms of mean germination time (GMT), both varieties showed an increase in salinity levels (Figure 1). Except for the Fd2 and Kd3 mutants, GMT decreased at high NaCl concentrations (8.8 g/l and 5.8 g/l, respectively). Furthermore, it was

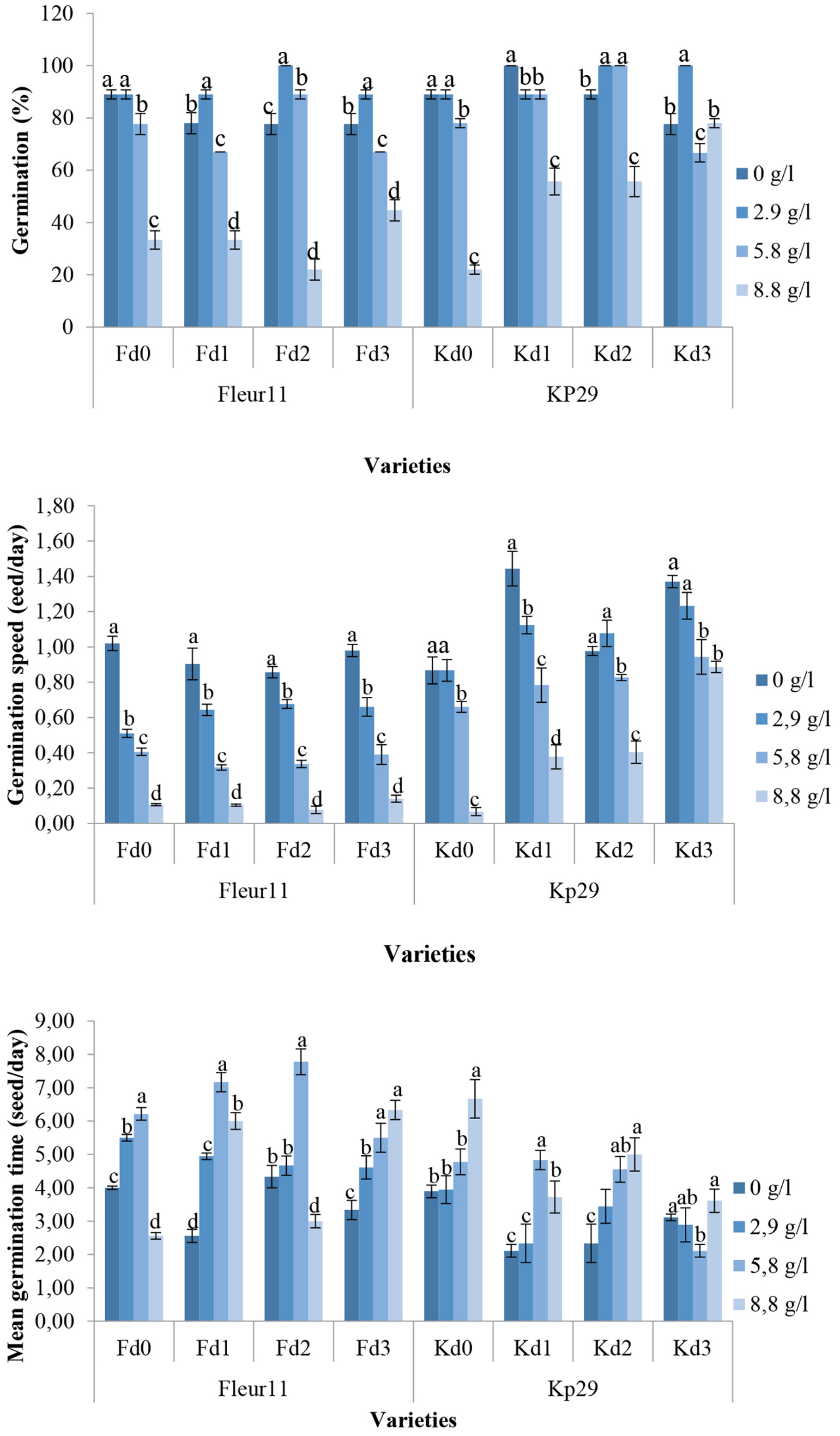

Figure 1. NaCl effect on germination (GP), germination speed (GS) and Mean germination time (MGT) of peanut mutants of both varieties

observed that the GMT of the Fleur11 mutants (2.5–8) was longer than the GMT of the Kp29 mutants (2–5 days).

Concerning the influence of salinity on the early seedling stage (Table 1), it was found that salinity inhibits growth in seedlings of two varieties, which is represented by a decrease in epicotyl, hypocotyl and root with increasing NaCl concentration. However, several mutants of both varieties were able to develop hypocotyl and root under

Table 1. Effect of salinity levels on the epicotyl, hypocotyl, and root lengths of peanut mutants of both varieties, Kp29 and Fleur11

Parameter	Epicotyl Length (cm)		Hypocotyl Length (cm)		Root Length (cm)	
	Fleur11	Kp29	Fleur11	Kp29	Fleur11	Kp29
NaCl (g/l)	Fd0	Kd0	Fd0	Kd0	Fd0	Kd0
0	2.73^{a} ±0.03	0.00±0.00	2.64^{a} ±0.05	0.82^{a} ±0.02	2.89^{a} ±0.04	0.22^{c} ±0.02
2.9	0.00±0.00	0.00±0.00	0.77^{b} ±0.01	0.73^{b} ±0.03	0.37^{b} ±0.03	0.33^{a} ±0.02
5.8	0.00±0.00	0.00±0.00	0.4^{c} ±0.01	0.58^{c} ±0.03	0.22^{c} ±0.02	0.30^{b} ±0.02
8.8	0.00±0.00	0.00±0.00	0.16^{d} ±0.02	0.17^{d} ±0.02	0.20^{c} ±0.03	0.18^{d} ±0.03
NaCl (g/l)	Fd1	Kd1	Fd1	Kd1	Fd1	Kd1
0	2.51^{a} ±0.06	2.65^{a} ±0.02	2.43^{a} ±0.03	3.76^{a} ±0.58	1.06^{a} ±0.02	2.36^{a} ±0.03
2.9	0.00±0.00	0.33^{b} ±0.01	1.06^{b} ±0.02	2.00^{b} ±0.02	0.67^{b} ±0.02	1.16^{b} ±0.03
5.8	0.00±0.00	0.00±0.00	0.36^{c} ±0.02	0.63^{c} ±0.03	0.26^{c} ±0.02	0.31^{c} ±0.02
8.8	0.00±0.00	0.00±0.00	0.00±0.00	0.30^{c} ±0.03	0.14^{d} ±0.02	0.03^{d} ±0.01
NaCl (g/l)	Fd2	Kd2	Fd2	Kd2	Fd2	Kd2
0	3.40^{a} ±0.05	1.16^{a} ±0.02	3.98^{a} ±0.02	1.82^{a} ±0.03	4.39^{a} ±0.03	1.02^{b} ±0.03
2.9	0.00±0.00	1.11^{b} ±0.03	1.49^{b} ±0.03	2.21^{b} ±0.02	1.38^{b} ±0.03	1.17^{a} ±0.03
5.8	0.00±0.00	0.00±0.00	0.31^{c} ±0.02	0.36^{c} ±0.02	0.51^{c} ±0.03	0.19^{c} ±0.02
8.8	0.00±0.00	0.00±0.00	0.087^{d} ±0.01	0.27^{d} ±0.02	0.12^{d} ±0.03	0.04^{d} ±0.01
NaCl (g/l)	Fd3	Kd3	Fd3	Kd3	Fd3	Kd3
0	2.31^{a} ±0.04	0.92^{a} ±0.04	2.68^{a} ±0.02	2.74^{a} ±0.04	2.69^{a} ±0.02	2.32^{a} ±0.02
2.9	0.79^{ab} ±0.03	0.00±0.00	1.72^{b} ±0.03	0.98^{b} ±0.03	0.71^{b} ±0.03	0.67^{b} ±0.03
5.8	0.00±0.00	0.00±0.00	0.46^{c} ±0.02	0.57^{c} ±0.03	0.36^{c} ±0.03	0.41^{c} ±0.03
8.8	0.00±0.00	0.00±0.00	0.11^{d} ±0.01	0.42^{d} ±0.03	0.16^{d} ±0.02	0.39^{c} ±0.02

saline conditions at low concentrations better than unirradiated seeds. It was also observed that NaCl had an adverse effect on epicotyl growth, except the Fd3, Kd1, and Kd3 mutants growing at 2.9 g/l of NaCl.

When compared to the unirradiated seedling, Kd2 showed the greatest growth in epicotyl, hypocotyl, and root lengths (1.11, 2.21, and 1.16 cm, respectively) in the Kp29 variety, whereas the mutant Fd3 showed the greatest growth in epicotyl and hypocotyl lengths (0.79, 1.72 cm, respectively) in the Fleur11 variety. Similarly, the dry weight of the epicotyl, hypocotyl, and root were significantly affected by salinity levels. The dry weight of these traits was decreased significantly at the highest NaCl concentrations (Table 2). However, the inclusion of NaCl at the low concentration (2.9 g/l) significantly increased the hypocotyl and root dry matter of Kd2. It should be highlighted that the Kp29 mutants (Kd1, Kd2, and Kd3) exhibit better growth of these traits in the absence of salt than unirradiated plants (Kd0).

Effect of irrigation with saline water on the growth of peanut mutant

The growth parameters of peanut plants exhibited differential responses to the imposed salt stress and gamma irradiation. Based on the obtained results in unstressed condition (Figure 2), the mutants of the Fleur 11 variety subjected to high doses of radiation showed an increase in plant height and aerial dry weight with a decrease in the number of leaves and branches, while the Kp29 mutants showed a decrease in all these traits at high radiation doses.

Under salinity stress conditions (Figure 2), the stem length of all mutant plant varieties was reduced. Except for Kd2, Kd3, and Fd3 which showed a considerable increase in stem length at 8.8 g/l of NaCl for Kd2, Fd3 and at 2.9, 5.8 g/l for Kd3. Under high concentrations of salinity, plants of both varieties exhibited a significant increment in various growth parameters, as compared with control (Figure 2). The mutants exhibit a range of values for aerial dry matter (Figure 2); Fd2 achieves the greatest value at 2.9 g/l and Fd3, Kd3 at 8.8 g/l of NaCl. Similarly, the number of

Table 2. Effect of salinity levels on the epicotyl, hypocotyl, and root dry weight of peanut mutants of both varieties, Kp29 and Fleur11

Parameter	Epicotyl dry weight (g)		Hypocotyl dry weight (g)		Root dry weight (g)	
	Fleur11	Kp29	Fleur11	Kp29	Fleur11	Kp29
NaCl (g/l)	Fd0	Kd0	Fd0	Kd0	Fd0	Kd0
0	0.0311^{a}±0.0018	0.0000±0.0000	0.0600^{a}±0.0019	0.0127^{a}±0.0006	0.0169^{a}±0.0008	0.0012^{a}±0.0007
2.9	0.0000±0.0000	0.0000±0.0000	0.0115^{b}±0.0004	0.0097^{b}±0.0006	0.0029^{b}±0.0004	0.002^{a} ±0.0009
5.8	0.0000±0.0000	0.0000±0.0000	0.0075^{c}±0.0005	0.0081^{c}±0.0002	0.0017^{b}±0.0006	0.0018^{a}±0.0002
8.8	0.0000±0.0000	0.0000±0.0000	0.0022^{d}±0.0002	0.0019^{d}±0.0002	0.0015^{b}±0.0005	0.0014^{a}±0.0006
NaCl (g/l)	Fd1	Kd1	Fd1	Kd1	Fd1	Kd1
0	0.0221^{a}±0.0001	0.0237^{a}±0.0008	0.0444^{a}±0.0005	0.0482^{a}±0.0009	0.0061^{a}±0.0004	0.0138^{a}±0.0005
2.9	0.0000±0.0000	0.0018^{b}±0.0002	0.0157^{b}±0.0009	0.0231^{b}±0.0010	0.0021^{b}±0.0005	0.0044^{b}±0.0010
5.8	0.0000±0.0000	0.0000±0.0000	0.0058^{c}±0.0003	0.0092^{c}±0.0004	0.0021^{b}±0.0004	0.0008^{c}±0.0003
8.8	0.0000±0.0000	0.0000±0.0000	0.0000±0.0000	0.0037^{d}±0.0001	0.0016^{b}±0.0005	0.0001^{c}±0.0001
NaCl (g/l)	Fd2	Kd2	Fd2	Kd2	Fd2	Kd2
0	0.0287^{a}±0.0059	0.0108^{a}±0.0001	0.0625^{a}±0.0013	0.0202^{b}±0.0019	0.0114^{a}±0.0004	0.0045^{b}±0.0005
2.9	0.0000±0.0000	0.0045^{b}±0.0002	0.0288^{b}±0.0004	0.0431^{a}±0.0007	0.0049^{b}±0.0004	0.0081^{a}±0.0003
5.8	0.0000±0.0000	0.0000±0.0000	0.0050^{c}±0.0004	0.0068^{c}±0.0003	0.0033^{c}±0.0008	0.0014^{c}±0.0005
8.8	0.0000±0.0000	0.0000±0.0000	0.0009^{d}±0.0001	0.0061^{c}±0.0002	0.0012^{d}±0.0007	0.0003^{d}±0.0001
NaCl (g/l)	Fd3	Kd3	Fd3	Kd3	Fd3	Kd3
0	0.0199^{a}±0.0003	0.0142^{a}±0.0006	0.0554^{a}±0.0015	0.0757^{a}±0.0015	0.0117^{a}±0.0004	0.0114^{a}±0.0004
2.9	0.0076^{b}±0.0003	0.0000±0.0000	0.0284^{b}±0.0021	0.0146^{b}±0.0004	0.0047^{b}±0.0002	0.0026^{b}±0.0005
5.8	0.0000±0.0000	0.0000±0.0000	0.0080^{c}±0.0005	0.0094^{c}±0.0002	0.0027^{c}±0.0006	0.0023^{b}±0.0006
8.8	0.0000±0.0000	0.0000±0.0000	0.0013^{d}±0.0001	0.0068^{d}±0.0004	0.0015^{d}±0.0005	0.0016^{b}±0.0005

branches (Figure 2) was also increased significantly in mutant plants, particularly in Kd2 and Fd3 at 2.9 and 8.8 g/l of NaCl. The number of leaves per plant was also increased in the mutants grown under saline conditions (Figure 2,3). The highest values were recorded by Fd2 and Kd3 at 2.9 g/l, Kd2 at 5.8 g/l and Fd3 at 8.8 g/l of NaCl. Concerning the foliar surface, the mutants Kd1, Kd2, and Kd3 show a considerable expansion at 2.9 and 8.8 g/l. These findings are consistent with those of 30, who found that salinity stress had a substantial effect on plant growth components such as shoot and root lengths, as well as fresh and dry weights of rice seedlings. However, the surface of the leaves decreased significantly (Figures 2,3) with increasing NaCl concentrations. Except for the Fd2 plants, which increased significantly, this parameter compared to the control.

On the basis of these findings, it was concluded that the mutants irradiated at 150Gy and 200Gy of both varieties evolved resistance to different concentrations of NaCl, which was reflected in an increase in their aerial part.

Salinity had a strong inhibitory effect on root development in both peanut varieties, with significant reductions in root length, root dry weight, and nodule number as NaCl concentration increased. However, the magnitude of reduction varied among the genotypes. The 150 Gy mutant of Kp29 (Kd2) maintained the longest roots and highest root biomass at moderate salinity (2.9 and 5.8 g/L), while the 200 Gy mutant of Fleur11 (Fd3) showed superior root length and nodulation compared to its respective control. In contrast, the non-irradiated lines (Kd0 and Fd0) were the most sensitive, with pronounced decreases in all root traits under 8.8 g/L NaCl. These observations highlight that induced mutants, particularly Kd2 and Fd3, retained more robust root growth and symbiotic potential under saline conditions (Figure 4).

Chlorophyll content (SPAD values) and stomatal conductance also declined progressively with increasing salt concentration, indicating reduced photosynthetic capacity and gas exchange. Among the genotypes, the 150 Gy and 200 Gy mutants consistently maintained higher chlorophyll levels than their corresponding controls, especially under moderate stress (5.8 g/L). Similarly, stomatal conductance was least affected in Kd2 and Fd3, suggesting a better capacity to

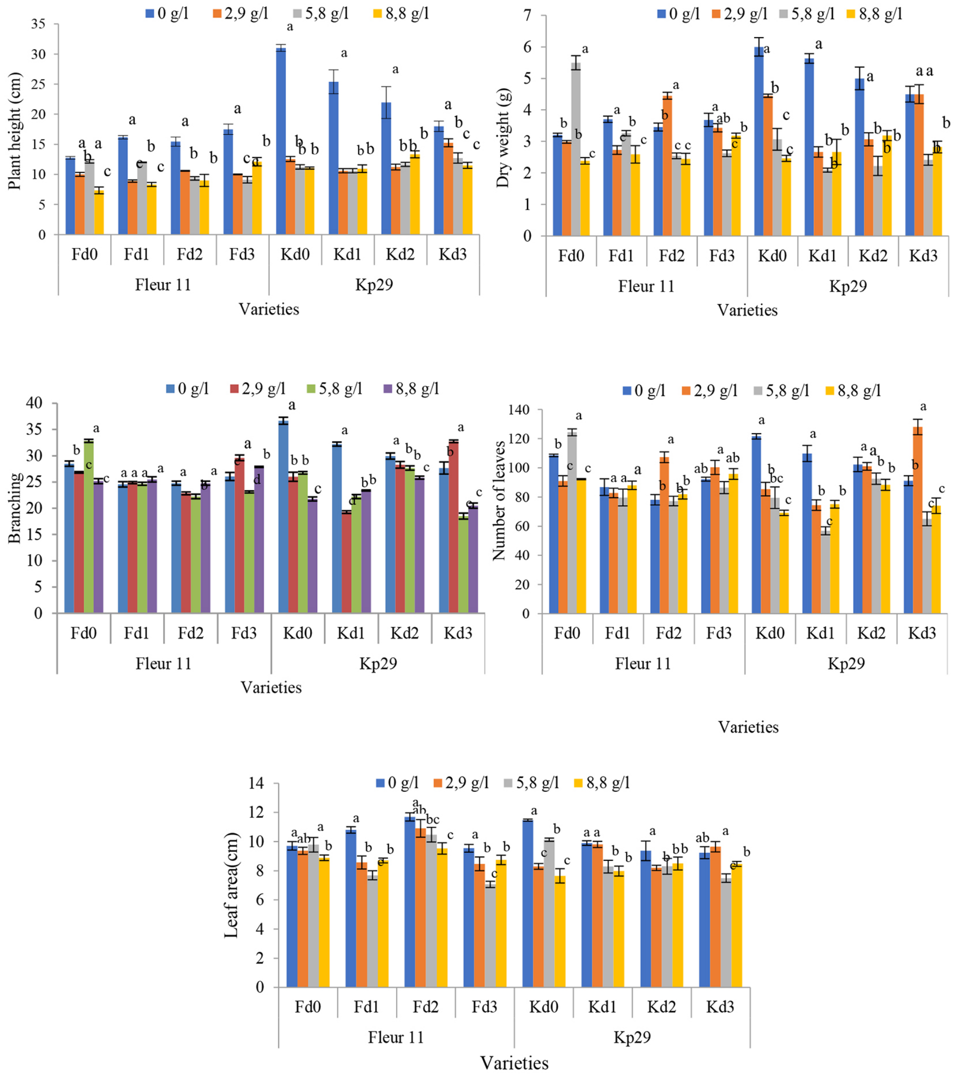

Figure 2. The influence of salinity on the growth of peanut mutants aerial parts. Plant height (A), dry weight (B), branching (C), number of leaves (D), leaf area (E). All data represent means ± SD. Treatments with letter differences present significant differences at 5%

regulate water use efficiency under salt stress. The control lines (Kd0 and Fd0) showed the sharpest reductions, particularly at 8.8 g/L NaCl. These physiological results support the morphological findings, confirming that the mutants derived from higher irradiation doses displayed enhanced tolerance to salinity (Figure 5).

DISCUSSION

Salinity is one of the major abiotic stresses limiting crop productivity worldwide, and its impact is particularly severe in legumes, such as peanut, which are sensitive to osmotic and ionic imbalances. In the present study, the germination, seedling growth, morphological, and physiological responses of gamma-irradiated peanut mutants were evaluated under increasing levels of NaCl stress. The obtained findings confirm that salt stress significantly reduces germination percentage, seedling vigor, biomass accumulation, and physiological performance, but also demonstrate that certain mutant lines, especially those derived from 150 and 200 Gy irradiation, retain superior tolerance compared to their non-irradiated controls.

Salt stress reduced germination percentage (GP), germination speed (GS), and increased mean germination time (MGT), in agreement with the reports in peanut and other legumes (Desheva, Desheva and Stamatov, 2020; Parmar *et al.*, 2024) and as deduced in the study of Panuccio et al., the higher coefficient of velocity of germination

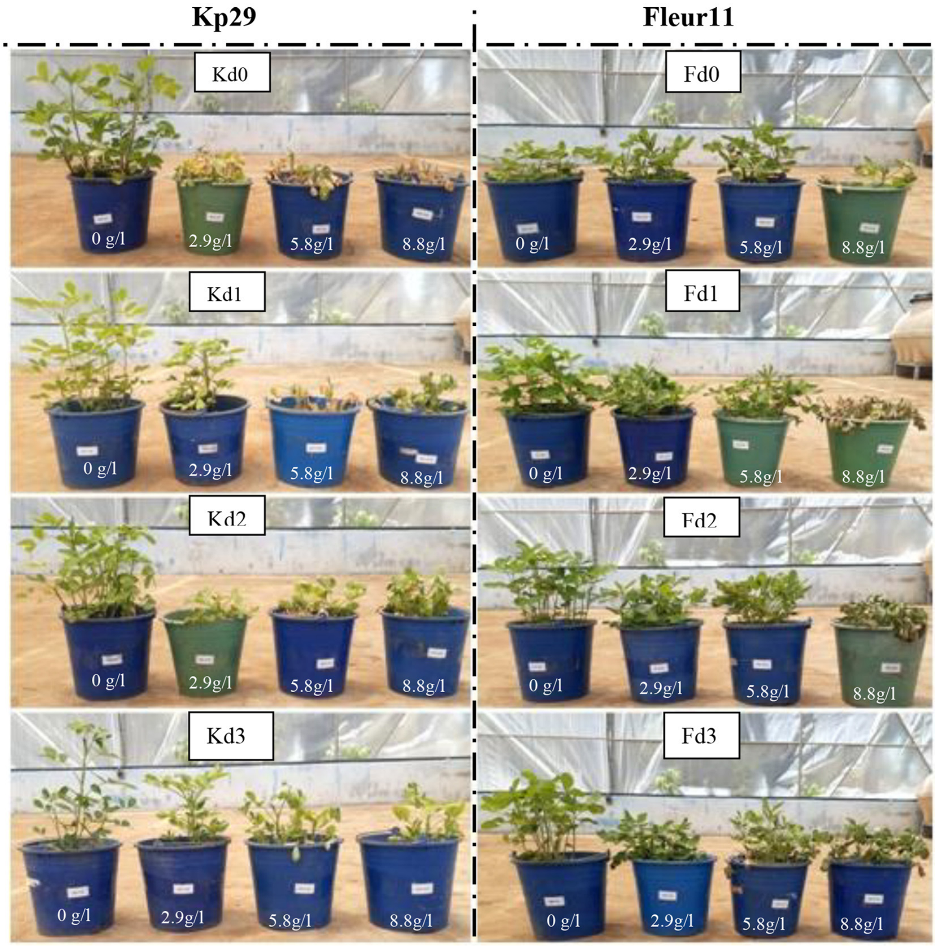

Figure 3. Effect of NaCl on the growth of peanut mutants of both varieties after 30 days of germination

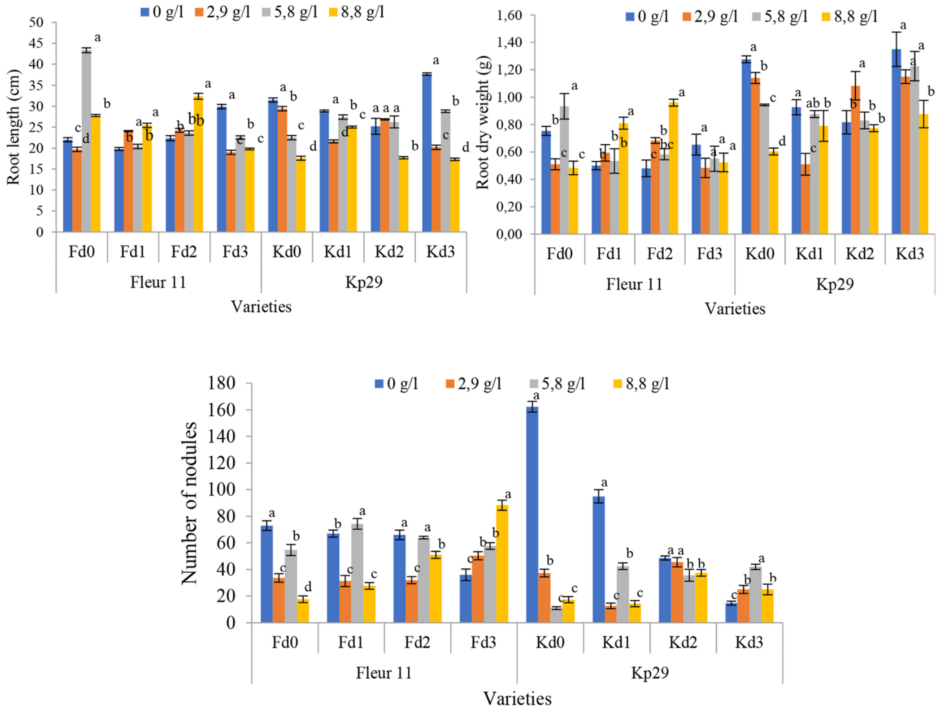

Figure 4. The influence of salinity on the growth of peanut mutants root parts. Root length (A), root dry weight (B), number of nodules (C). All data represent means ± SD. Treatments with letter differences present significant differences at 5%

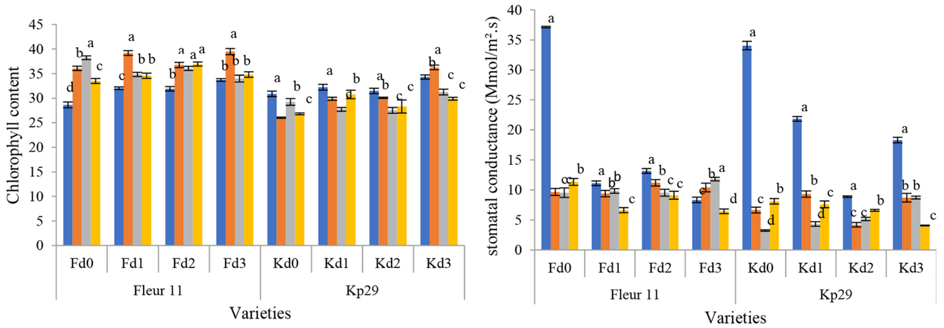

Figure 5. The influence of salinity on chlorophyll content (A) and stomatal conductance (B). All data represent means ± SD. Treatments with letter differences present significant differences at 5%

(CVG) and the lower TMG indicate faster and more vigorous seed germination (Panuccio *et al.*, 2014). The higher sensitivity of non-irradiated controls (Kd0 and Fd0) reflects the inhibitory effects of NaCl on water uptake and enzyme activity, which delay radicle protrusion. In contrast, the 150 Gy (Kd2) and 200 Gy (Fd3) mutants maintained better germination performance, suggesting that induced mutagenesis may have enhanced osmotic adjustment or membrane stability during imbibition. Similar positive effects of irradiation on stress tolerance at the germination stage have been reported in chickpea (Abdoun *et al.*, 2022) and cowpea (Deme *et al.*, 2022). The findings on beans by (Haleem, 2012), showed that the seeds exposed to gamma radiation enhanced germination and vigor, while alleviating the negative effects of salt stress, compared to unirradiated seeds. Also, (Qi *et al.*, 2014), reported that the germination potential of irradiated *Arabidopsis* seeds under salt stress, was higher than that control seeds. Several previous studies have noted that gamma irradiation improves plant growth in response to salt stress (Chakravarty and Sen, 2001; El-Beltagi, Ahmed and El-Desouky, 2011; El-Beltagi *et al.*, 2013). In fact, it was reported that irradiated plants have higher levels of proline synthesis than non-irradiated plants, which is part of the salt tolerance mechanism in crops (Al-Rumaih and Al-Rumaih, 2008). Proline accumulation is considered a defense mechanism against salt stress, because it prevents degradation of enzymes and maintains their structural as well as functional activity. (Kishor *et al.*, 2005) established *in vitro* the role of proline in protection against radiation as well as various abiotic stresses, including high and low temperatures, salinity, etc.

According to these results, the plants exposed to gamma rays at doses of 150Gy and 200Gy exhibit the highest levels of salt tolerance during the early growth stage. The obtained findings are consistent with those of (Qi *et al.*, 2014) who found that gamma irradiation could obviously alleviate the adverse effect of salt stress on growth by improving the antioxidant enzyme system, reducing oxidative stress, encouraging proline accumulation, and stimulating salt stress signal transduction. Similar studies by (Meena, Meena and Yadav, 2016; Satu and Ahmad, 2019) show that high salinity levels prevents seed germination and extends the time required for unirradiated peanuts to germinate.

Concerning GS, particularly the mutants Kd1 and Kd3 displayed the highest value when NaCl was absent; however the rate of germination slowed down considerably as salinity levels increased. The discovery in the study of Meena et al., found that epicotyl is more sensitive to salinity than roots. This response is induced by the toxic effects of salt which limit the contribution of metabolism to early emerging tissues, as metabolic production is considerably altered under high salt stress, as reported by (Taffouo *et al.*, 2009). Additionally, according to Ashraf and Harri and Khayatnezhad and Gholamin, the increase in external osmotic pressure affects the ability of a seed to absorb water and causes an accumulation of Na^+ and Cl^- inside the embryo, which affects the metabolic processes of germination and results in the death of embryonic cell tissue (Ashraf and Harris, 2004; Khayatnezhad and Gholamin, 2011).

Not only GS but salt stress markedly reduced plant height, dry weight, number of branches and leaves, and leaf area, consistent with the general growth suppression observed in glycophytes under salinity (Gupta and Huang, 2014). However, the extent of reduction varied across genotypes. The 150 Gy mutant of Kp29 (Kd2) and the 200 Gy mutant of Fleur11 (Fd3) maintained significantly higher shoot biomass as well as leaf area under moderate and high salinity. Similar genotype-dependent responses have been noted in groundnut cultivars differing in salt sensitivity (Singh *et al.*, 2010; Nithila *et al.*, 2013). The enhanced performance of mutant lines suggests an improved capacity for osmotic regulation and photosynthetic maintenance under stress; it is translated by the accumulation of osmolytes or activation of membrane transporters that help retain water and essential solutes. Meanwhile, photosynthetic maintenance indicates the mutants can sustain chlorophyll function, electron transport, and carbon fixation despite the adverse stress, which sustains growth and productivity (Zhao *et al.*, 2017; Sharma *et al.*, 2019; Nazari *et al.*, 2024).

Roots are the first plant organ to detect saltwater in the rhizosphere and the first to suffer from salt stress. However, the highest root growth of peanuts observed under salinity conditions must have occurred as a response of the plant to adverse conditions of the environment. Plants respond to abiotic stresses in many ways, at the molecular, cellular, and whole plants levels. These responses include physiological, morphological, and developmental changes, such as inhibition of shoot growth and the stimulation of root growth, as well as modifications in the metabolic pathway, such as the synthesis of osmolytes and antioxidant enzyme, protein localization and degradation (Roychoudhury and Tripathi, 2019). In the presented study, root traits were also strongly affected by salinity, with clear reductions in length, biomass, and nodulation. Nevertheless, mutants Kd2 and Fd3 sustained relatively higher root length and nodule numbers compared with their controls. In terms of plant roots, unirradiated plants responded to moderate and high NaCl concentrations by increasing root length in the Fleur11 variety. In contrast, when the NaCl concentration increased, there was a significant decrease in the Kp29 variety. This is explained by un unbalance where increasing salinity leads to a high concentration of rhizospheric ions (mainly Na+ and Cl-), thus causing a significant depletion in water potential (Flowers *et al.*, 2015; Carillo *et al.*, 2019).

Root system robustness is a critical determinant of salt tolerance, as deeper or longer roots facilitate water acquisition and ion compartmentalization, in fact, root architecture remodeling under salt stress involves increased main root length and lateral root development, helping plants access water as well as regulate ion balance and ion compartmentalization within roots and tissues is fundamental for salt tolerance, preventing toxic salt accumulation in sensitive shoot tissues (Peng *et al.*, 2016; Julkowska *et al.*, 2017; Fan *et al.*, 2023). Previous reports have highlighted that root length was reduced by 35–58% when peanut plants were subjected to saline stress (Steiner *et al.*, 2019). Comparable findings have been reported in salt-tolerant groundnut varieties (Satu and Ahmad, 2019) and in gamma-irradiated cowpea mutants (Deme *et al.*, 2022), highlighting the value of mutagenesis in improving root plasticity under stress. Because mutagenesis generates mutants with altered root system architecture, such as longer primary roots, increased lateral root formation, and deeper rooting. These changes improve water and nutrient acquisition under stress conditions, this is one explanation behind this observation (Justamante *et al.*, 2025) and Qi *et al.*, has also shown that irradiation improves the root length of Arabidopsis under salt stress (Qi *et al.*, 2014), but this time another aspect behind it was revealed and it is due to the fact that proline synthesis, which is involved in salt tolerance mechanisms across crops, was shown to be higher in irradiated plants than in unirradiated plants, as reported by (Al-Rumaih and Al-Rumaih, 2008; Esfandiari *et al.*, 2008).

The number of nodules in the unirradiated plants of both varieties was also affected by salt. As the salt level increases, the number of nodules on the roots reduces. Similarly, for many peanut cultivars, a considerable reduction in nodule number under salt stress has been previously reported for different peanut cultivars (Vadez *et al.*, 2005; Dardanelli *et al.*, 2009). Also, (Alfarraji *et al.*, 2022) revealed that the number of root nodules reduced by 27% to 49% when soil salinity increased in cowpea plants. This is due to the effect of salt, which prevents the absorption of Ca, affecting the growth of roots and root hair, giving an additional mechanism to inhibit nodule formation as reported by (Bouhmouch *et al.*, 2005) and also salt stress inhibits multiple phases of nodule development in legumes by reducing rhizobial colonization and impairing root hair formation, essential for nodule initiation. This results in fewer nodules as salinity increases; also, salinity-induced reduction in nodulation can also be linked to decreased rhizobial survival and infection sites, and to stress-driven ethylene accumulation in plants, which negatively impacts nodulation (Win *et al.*, 2023). However, in this study, mutants of the two varieties at varying NaCl concentrations showed an increase in this trait. The highest values were recorded in Fd3 and Kd2 at the concentrations of 8.8 g/l and 2.9 g/l of NaCl, respectively. These results are in accordance with those of El-Beltagi et al., who revealed that irradiating seeds significantly boosted the number of nodules of cowpea plants. On the basis of these results, the mutants of both peanut varieties proved resistant to the different salinity concentrations studied, which was reflected in the development of the root part (El-Beltagi *et al.*, 2013). Chlorophyll content (SPAD index) and stomatal conductance decreased progressively with salinity confirming that photosynthesis is one of the primary processes impaired under salt stress. Yet, the mutants irradiated at 150 and 200 Gy consistently retained higher chlorophyll levels and better stomatal regulation. This suggests improved photoprotection and water use efficiency, which are key adaptive traits under saline conditions. Similar physiological resilience has been observed in salt-tolerant peanut genotypes (Wen *et al.*, 2021) and in irradiated rice mutants (Abdelnour-Esquivel *et al.*, 2020). The maintenance of chlorophyll under stress could be related to reduced Na^+ toxicity in chloroplasts and more efficient antioxidative defense systems, though further biochemical validation would be required, and chloroplasts produce reactive oxygen species (ROS) under salt stress, causing oxidative damage that contributes to chlorophyll degradation. However, salt-tolerant plants have more active antioxidative enzymes, such as SOD, ascorbate peroxidase and non-enzymatic antioxidants to scavenge ROS and protect chloroplast integrity (Lu *et al.*, 2023). The results of stomatal conductance showed a significant decrease in the leaves of two peanut varieties under salt stress, which was particularly apparent at the highest concentration of NaCl (8.8g/l) in all mutants. However, all the plants irrigated with well water exhibited higher stomatal conductance except for Fd3. Soil salinity levels frequently have a negative impact on stomatal conductance as reported by (Rasouli *et al.*, 2021; Soltabayeva *et al.*, 2021). Salinity disturbs the equilibrium between roots moisture supply and the atmospheric evaporative demand, causing osmotic stress to reduce leaf water potential which is one of the most important salinity tolerance mechanisms in plants, and as a result, stomatal conductance reduces rapidly to maintain water (Munns, biology and 2008, 2008; Tardieu, Simonneau and Muller, 2018; Buckley, 2019). Salinity affected the germination phase and later plant development through distinct physiological processes. During germination, the main constraint was osmotic stress, which limited water uptake and slowed radicle emergence. However, at the seedling and vegetative stages, plants were additionally exposed to the ionic stress caused by Na^+ and Cl^- accumulation, leading to reduced cell expansion, chlorophyll loss, impaired stomatal functioning, and inhibition of root and nodule formation. These combined stresses explain why germination was only moderately affected, whereas plant growth and biomass were significantly reduced at higher salinity levels.

The physiological measurement revealed that exposing peanut plants to salt stress interestingly resulted in higher chlorophyll content than the control, in both unirradiated and mutant plants of the Fleur11 variety. This stimulating impact is in line with previous reports (Liu, 2003; Redondo-Gómez *et al.*, 2007; Qados, 2011; Orzechowska *et al.*, 2021), which revealed the positive effects of salinity on several physiological processes, including osmoregulation, photosynthetic activity, and enzyme activity. It may be due to improved performance of the positive interaction between Cl− and the Mn_4O_5Ca cluster of the oxygen-evolving complex (Popelková and Yocum, 2007). Also, Cl- has been shown to stimulate various enzymes, including ATPase and alpha-amylase, which hydrolyze amidon into sugars and require chloride for activation, according to (Critchley, 1983). Beyond these physiological mechanisms, the superior performance of the 150 Gy and 200 Gy mutants also carries important practical implications for peanut cultivation in saline environments. Their ability to maintain higher germination, biomass production, and physiological stability under moderate to high NaCl levels suggests that these lines could be directly exploited in the agricultural systems where soil salinity restricts productivity (Ondrasek and Rengel, 2021; ONEM, 2020). Mutants such as Kd2 and Fd3, which sustained more robust root growth and nodulation, may offer additional advantages in restoring soil fertility through improved biological nitrogen fixation under stress (Bouhmouch et al., 2005). These traits make them suitable candidates for cultivation in coastal zones, arid regions, and the areas irrigated with brackish water, where traditional peanut cultivars often fail to establish. Furthermore, these mutants represent valuable genetic resources for breeding programs aiming to introgress salt-tolerance traits such as osmotic adjustment, antioxidative capacity, and root architectural plasticity into elite groundnut varieties, thereby supporting the long-term strategies for enhancing resilience in salinity-affected agricultural systems.

Taken together, the obtained results highlight that gamma irradiation can generate genetic variability that enhances salinity tolerance in peanut. In particular, the Kp29-Kd2 (150 Gy) and Fleur11-Fd3 (200 Gy) mutants exhibited superior performance at multiple levels from germination to root/shoot growth and physiological maintenance. This indicates that mutagenesis can be a valuable breeding tool for improving peanut resilience to salinity. It represents a practical and accessible tool for crop improvement, as it is widely recognized as a safe, non-transgenic method that has been used for decades in plant breeding programs. The technique requires only a single irradiation event, after which mutant lines follow standard agronomic evaluation, making it cost-effective compared with more technologically demanding approaches. Its extensive regulatory acceptance and successful use in releasing numerous crop varieties worldwide further support the suitability of gamma mutagenesis for developing salt-tolerant peanut lines and the consistency of the obtained results with previous studies in legumes and cereals strengthens the case for integrating mutagenized lines into breeding programs targeting salt-affected environments. These trends can be observed under controlled greenhouse conditions and they seem promising, but the expression of salinity tolerance may vary under field environments where temperature, humidity, and soil salinity fluctuate over time. These additional stresses can influence osmotic balance, transpiration, and ion accumulation, making multi-location field trials essential to confirm the stability and agronomic relevance of the mutants identified as tolerant. Future research should focus on physiological mechanisms, such as ion homeostasis, antioxidant activity, and gene expression, underlying the improved tolerance observed in these mutants. Also, additional molecular and agronomic investigations remain necessary. DNA-level analyses such as SSR, SNP profiling, or whole-genome approaches would help determine whether key genes involved in osmotic adjustment, ion transport, and antioxidative protection were modified during mutagenesis, as previously demonstrated in peanut and other irradiated crops (Ferguson, Bramel and Chandra, 2004; Ren *et al*., 2014; Abdelnour-Esquivel *et al*., 2020). Complementary gene expression studies under NaCl stress would further clarify whether pathways related to proline biosynthesis, ROS detoxification, or membrane stability are differentially activated in the most tolerant mutants, in line with the findings from *Arabidopsis* and cereals subjected to gamma irradiation (Qi *et al*., 2014). Biochemical assays measuring Na^+/K^+ accumulation, proline content, and antioxidant enzyme activity would also provide functional validation of the physiological mechanisms inferred from this study (Al-Rumaih and Al-Rumaih, 2008; El-Beltagi *et al*., 2013). Moreover, detailed characterization of root system architecture using rhizotrons or soil imaging techniques would help confirm the enhanced root plasticity observed in Kd2 and Fd3 under salinity (Julkowska *et al*., 2017; Fan *et al*., 2023). Finally, multi-location field trials in naturally saline soils are essential to determine whether the tolerance expressed under controlled conditions is stable and agronomically relevant, given that greenhouse performance does not always fully predict field behavior in peanut or other legumes (Vadez *et al*., 2005; Satu and Ahmad, 2019). Such complementary investigations would provide the necessary validation to integrate these mutants into large-scale breeding programs targeted at salinity-affected regions.

CONCLUSIONS

Compared to the unirradiated plants, the mutants were found salinity-tolerant during germination, early growth stage, and the development stage. Considering all the parameters studied, the mutants irradiated at 150Gy and 200Gy showed to be more tolerant to salinity than the unirradiated plants of two peanut varieties, and 8.8 g/l of NaCl solution was proved to be ineffective to suppress seed germination but was strongly inhibitory during early seedling growth. It also turns out that the two varieties of peanut studied are more resilient to salt stress when exposed to gamma radiation, these mutants have the performance and are, thus, promising for salinity-tolerance breeding. This study clearly showed that gamma irradiation can be used to generate genetic diversity among the segregating population to improve salt tolerant plants.

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