

SABRAO Journal of Breeding and Genetics
 58 (5) 2338-2347, 2026
<http://doi.org/10.54910/sabrao2026.58.5.33>
<http://sabraojournal.org/>
 pISSN 1029-7073; eISSN 2224-8978



EARLY ANATOMICAL AND PHYSIOLOGICAL RESPONSES OF MAIZE TO GAMMA IRRADIATION AS A BASIS FOR SALINITY STRESS ADAPTATION BREEDING

N. RAHMAWATI^{1*}, A. LESTAMI¹, R. ALFI², and NURSA'ADAH¹

¹Department of Agrotechnology, Faculty of Agriculture, Universitas Sumatera Utara, Medan, Indonesia

²Department of Agrotechnology, Faculty of Agriculture, Universitas Riau, Pekanbaru, Indonesia

*Corresponding author's email: nini@usu.ac.id

Email addresses of co-authors: anggria@usu.ac.id, rahmatika.alfi@lecturer.unri.ac.id, nur.saadah@usu.ac.id

SUMMARY

Maize (*Zea mays* L.) production constraints increase from soil salinity, which interrupts plant growth through physiological and anatomical instability. Therefore, to develop stress-resilient cultivars, effective approaches are essential to generate adaptive variations in genetic material through mutation breeding using gamma irradiation. The concerned study aimed to evaluate the early anatomical and physiological responses of maize to gamma irradiation under non-stress conditions and identify the traits associated with salinity stress adaptation. Maize seeds received irradiation with Cobalt-60 (⁶⁰Co) gamma rays at doses of 0, 100, 200, and 300 Gy as they grew under field conditions with standard agronomic practices. The results showed gamma radiation induced dose-dependent anatomical and physiological responses in maize. A dose of 100 Gy tended to maintain the integrity of the anatomical structure and chlorophyll content. Meanwhile, a dose of 200–300 Gy caused considerable variations in the anatomical structure, particularly stomata size and tissue thickness, as well as a considerable decrease in chlorophyll b and total chlorophyll content in maize.

Keywords: Maize, induced mutation, dose response, salinity stress adaptation, leaf anatomy, chlorophyll pigments

Key findings: Gamma irradiation induced synchronized anatomical and physiological variations in maize, with an apparent dose-dependent response. The early responses highlighted the potential of anatomical and physiological traits as reliable indicators for selecting stress-adaptive genotypes through mutation breeding.

Communicating Editor: Dr. Tabyimbaeva Laila

Manuscript received: April 26, 2026; Accepted: June 28, 2026.

© Society for the Advancement of Breeding Research in Asia and Oceania (SABRAO) 2026

Citation: Rahmawati N, Lestami A, Alfi R, Nursa'Adah (2026). Early anatomical and physiological responses of maize to gamma irradiation as a basis for salinity stress adaptation breeding. *SABRAO J. Breed. Genet.* 58 (5) 2338-2347. <http://doi.org/10.54910/sabrao2026.58.5.33>.

INTRODUCTION

Maize is one of the most important cereal crops globally after wheat and rice, serving as a staple food and animal feed and providing raw materials for various industries (Tanumihardjo *et al.*, 2020). Global maize production reached approximately 1.22 gigatons in 2024 (FAO, 2024). The highest productivity potential and wide adaptability proved maize as a key donor to food security (Albahri *et al.*, 2023). However, larger demand driven by population growth and industrial utilization requires incessant improvement in both yield and stress resilience. Therefore, enhancing maize performance under suboptimal environmental conditions has become a major focus in crop improvement programs (Tiah *et al.*, 2026).

Maize production faces serious limitations when exposed to elevated soil salinity levels, particularly in arid and semi-arid regions where salt accumulation is increasingly widespread in the soil. According to the Food and Agriculture Organization (FAO, 2021), the global area of salt-affected soils covers 424 million hectares of topsoil and 833 million hectares of subsoil. Salinity stress disrupts plant growth through osmotic imbalance, ion toxicity, and oxidative stress conditions, which collectively impair water uptake, nutrient absorption, and metabolic activities (Pandit *et al.*, 2024). These disturbances have often shown an association with reductions in chlorophyll content and photosynthetic efficiency, as well as structural modifications in leaf tissues, including considerable variations in stomata and mesophyll characteristics (Mohamed *et al.*, 2020). Such physiological and anatomical responses reflect the complexity of plant adaptation to salinity stress at multiple levels, requiring strategies to generate adaptive variations (Wu *et al.*, 2026).

Mutation breeding through gamma irradiation has had wide usage to generate the genetic variability for crop improvement (Ntsomboh-Ntsefong *et al.*, 2023). This high-energy ionizing radiation induces the heritable variations at the DNA level, resulting in modifications in plant morphology, physiology, and anatomical structure, depending on the irradiation dose (Caplin and Willey, 2018).

Reports often stated low doses stimulate growth and physiological activity, whereas higher doses tend to induce inhibitory effects due to cellular and DNA damage (Calabrese, 2014). In maize, irradiation doses ranging from 0 to 400 Gy have been effective to induce genetic variability (Afram *et al.*, 2024).

Gamma rays have shown an effective use to develop plant materials with improved adaptability, proving them as a valuable tool in breeding programs aimed at enhancing stress tolerance (Katiyar *et al.*, 2022). Gamma irradiation affects both the physiological and anatomical traits in maize (Yadav *et al.*, 2019) and winged bean (Samiyarsih *et al.*, 2020). Chlorophyll content and photosynthetic activity appeared to be particularly sensitive to irradiation, where low doses may stimulate metabolic processes, while higher gamma-ray doses often lead to chlorophyll degradation due to damage to chloroplast structures. Structural variations have also been in reports that include modifications in stomata size and density (Nilahayati *et al.*, 2024).

Gamma irradiation can be useful for modifying anatomical and physiological traits to develop desirable plant cultivars (Rosmala *et al.*, 2016). However, recent studies have focused on the effects of gamma irradiation in stress conditions (Atghaei *et al.*, 2023), whereas the early anatomical and physiological responses under non-stress environments remain less characterized. This baseline was evidently important for understanding irradiation-induced genetic variations and their potential relevance to abiotic stress adaptation. Therefore, the presented study aimed to evaluate the early anatomical and physiological responses of maize to gamma irradiation under non-stress conditions, providing a basis for identifying traits associated with salinity stress adaptation and supporting future selection strategies in breeding programs.

MATERIALS AND METHODS

Experimental site and procedure

This study commenced at the experimental plot of the Technical Implementation Units of

the Primary Crop Seeds, Deli Serdang District, North Sumatra, Medan, Indonesia, from September to November 2025. Anatomical and physiological analyses proceeded at the Biotechnology Laboratory, Faculty of Agriculture, Universitas Sumatera Utara, Medan, Indonesia. Maize cultivar Bisi-18 seeds (100 g per treatment) sustained irradiation with gamma rays from ^{60}Co using a Gamma Cell 220 irradiator at PAIR BATAN at doses of 100, 200, and 300 Gy. Determining the treatment doses was according to the previously obtained LD_{50} value of 379.164 Gy (Lestami *et al.*, 2026).

The completion of soil preparation transpired two weeks before planting. A total of 30 M1 seeds per dose entailed planting in rows at a distance of 70 cm $\times$ 20 cm, with one seed per planting hole. The plants received a basal fertilizer application of 300 kg/ha urea and a top-dressing (during the generative phase) of 100 kg/ha TSP and 100 kg/ha KCl. Plant maintenance continued manually and chemically according to the condition of the plants in the field.

Traits measurement

The recording of observations included the anatomical traits (cuticle thickness, upper epidermis, lower epidermis, mesophyll, the number of stomata, stomata length, stomata width, and stomata density) and physiological traits (chlorophyll a, chlorophyll b, and total chlorophyll). Anatomical and physiological observations on maize plants were at the vegetative stage (42 days after planting), with three plant samples randomly selected from each irradiation dose.

Leaf anatomy analysis

The study conducted leaf anatomical observations using the paraffin section method (Sass, 1951). The fixing of samples engaged FAA, formaldehyde: ethanol: acetic acid: aquades (5:50:10:35). The samples incurred dehydration through a graded ethanol series, embedded in paraffin, and sectioned using a rotary microtome. The sections' staining with safranin preceded their mounting on glass

slides for microscopic observation. The measurement of anatomical traits included cuticle thickness, upper epidermis, lower epidermis, and mesophyll, using a light microscope equipped with an ocular micrometer.

Stomata analysis

Stomata preparations ensued using the stomata printing method (Đlçđm *et al.*, 2010), wherein coating the abaxial (underside) surface of the leaf took place with a thin layer of clear nail polish containing acetone until dry and then covering with clear tape over the coated area. Afterward, carefully peeling the tape off ensured that the abaxial epidermal slice remained adhered to the tape. The tape containing the abaxial leaf slices entailed affixing to a glass slide. The stomata preparation, once secured to the slide, underwent examination under a microscope until a clear view of the stomata was visible for easy analysis. Stomata observations performed used a light microscope (ZEISS) at 40 $\times$ magnification with a field of view diameter of 2.8 units and an area of 0.5 mm².

Chlorophyll analysis

Maize leaves collected reached a weight of 1 g before grinding using a mortar. The ground material entailed extracting and dissolving in 10 mL of 96% ethanol with constant stirring. Next, filtering the extract through filter paper proceeded with the filtrate transferred to separate 2.5-mL cuvettes. The absorbance/optical density of each extract in the cuvettes incurred measurements at wavelengths of 649 and 665 nm using a spectrophotometer (LAMBDA 365 UV/Vis). The process continued with three repetitions for each sample. These chlorophyll calculations proceeded by following the procedure of Winternans and De-Mots (1965).

$$\text{Chlorophyll a} = (13.7 \times A_{665}) - (5.76 \times A_{649}),$$

$$\text{Chlorophyll b} = (25.8 \times A_{649}) - (7.60 \times A_{665}), \text{ and}$$

Total chlorophyll = Chlorophyll a + Chlorophyll b.

Statistical analysis

All the data gained analysis by calculating the treatment means for various quantitative traits. A t-test performed sought to compare the control treatment (0 Gy) with each gamma irradiation dose (100, 200, and 300 Gy) separately for all measured traits.

RESULTS AND DISCUSSION

Anatomical response

Microscopic examination of transverse leaf sections of maize revealed considerable variations in anatomical traits, including cuticle thickness, epidermal layers, mesophyll, and stomata traits across the different gamma irradiation doses (Table 1). Although most anatomical traits did not show significant differences compared with the control, the observable trends enunciated that gamma irradiation induced the slight structural modifications.

Leaf anatomical traits showed little variation among the irradiation treatments. The thickness of the cuticle, upper epidermis, lower epidermis, and mesophyll tended to increase at irradiation doses of 100–200 Gy, followed by a decrease at 300 Gy. According to Rosmala *et al.* (2016), radiation-induced variations in the leaf anatomy appeared to show an association with plant morphological adaptation to external turbulences. However,

the observed increase at low irradiation doses may reflect a mild adaptive response with enhanced protective and structural functions of leaf tissue (Erofeeva, 2024). Conversely, the decrease at higher irradiation doses suggests possible cellular degradation due to membrane damage, thereby inhibiting tissue development in the leaf structure (Choi *et al.*, 2021).

Increased cuticle and epidermis thickness serve as additional barriers against water loss and salt penetration, proving relevant in the context of adaptation to salinity stress conditions (Liu *et al.*, 2022). The cuticle plays a crucial role in minimizing non-stomata water loss and protecting leaf tissues from external stressors (Zhao *et al.*, 2025). Increased cuticle development improves water retention and surface protection and has an indicative association with greater tolerance to abiotic stress (Khan *et al.*, 2026). The anatomical structure of the leaves maintains the characteristic pattern of maize plants, with a single epidermal layer on the upper and lower surfaces, densely packed mesophyll tissue, and clearly visible stomatal guard cells. However, the different irradiation doses were evident with noticeable variations in tissue thickness and density in maize (Figure 1).

The upper and lower epidermis at the gamma ray dose of 0 Gy (control) were thin and uniform, with solid cell arrangements and thick mesophyll tissues. This structure reflects the normal physiological condition of maize plants without exposure to radiation. However, at a dose of 100 Gy, the thicknesses of the upper and lower epidermis increased slightly, and the mesophyll tissue appeared more developed, with a denser cell arrangement.

Table 1. Effect of gamma irradiation (0, 100, 200, and 300 Gy) on leaf anatomical traits of maize.

Traits	Irradiation Dose			
	0 Gy	100 Gy	200 Gy	300 Gy
Cuticle thickness (µm)	2.10±0.53	2.28±0.42	2.57±0.43	2.01±0.71
Upper epidermis (µm)	4.94±0.58	5.65±1.16	5.44±1.34	4.35±0.74
Lower epidermis (µm)	4.38±0.84	5.07±1.51	5.22±1.17	4.58±2.04
Mesophyll (µm)	30.74±5.78	31.17±4.55	33.92±11.82	30.57±5.69
Number of stomata (stomata)	7.33±0.58	6.44±0.77	6.33±0.88	7.00±0
Stomata length (µm)	45.06±43.65	43.07±2.38	42.67±3.06	36.19±2.75*
Stomata width (µm)	25.91±3.21	28.91±1.42	27.22±0.67	28.87±2.18
Stomata density (mm ⁻²)	123.89±9.75	108.88±13.01	107.00±14.90	118.26±0

(*) indicate significant differences compared to the control (0 Gy) at $P < 0.05$.

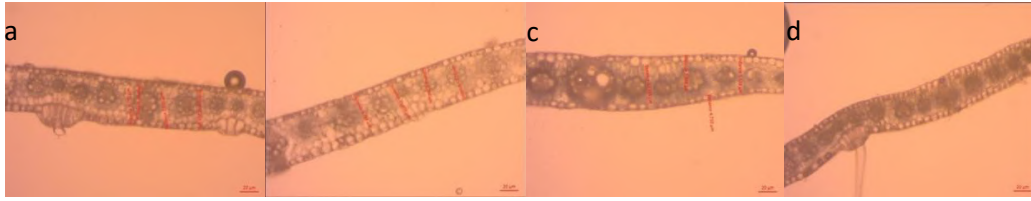


Figure 1. Microscopic observation of leaf epidermal structure in maize leaves with different irradiation doses: a) 0 Gy, b) 100 Gy, c) 200 Gy, and d) 300 Gy.

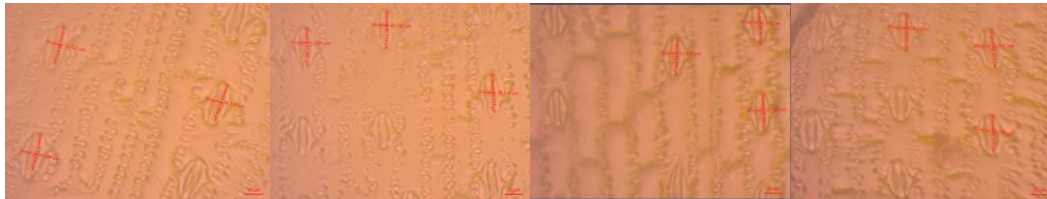


Figure 2. Microscopic observation of stomatal density in maize leaves with different irradiation doses: (a) 0 Gy, (b) 100 Gy, (c) 200 Gy, and (d) 300 Gy.

This tissue enhancement revealed low doses of gamma irradiation can stimulate tissue growth by the activation of metabolism and cell differentiation (Villegas *et al.*, 2023). The upper epidermis and mesophyll tissue were more noticeable at the dose of 200 Gy than in the control. In an adaptive response, the plant strengthens the tissue structure to increase protection against water loss and radiation damage (Lu *et al.*, 2025). In contrast, at the 300 Gy treatment, the epidermis and mesophyll tissue appeared to experience a decrease in thickness, with cells arranged irregularly and some showing signs of vacuolization and cell wall degradation in maize. Higher radiation doses have exceeded the tolerance threshold of plant tissues, causing cellular disorganization due to the accumulation of free radicals that damage the plasma membrane and organelle structure (Choi *et al.*, 2021).

Stomata characteristics showed a more diverse response to irradiation. At the 300 Gy treatment, a significant reduction in stomata length was evident, indicating that stomata morphology was predominantly sensitive to high radiation doses. According to Haworth *et al.* (2023), the reduction in stomata size may influence the gas exchange capacity and

transpiration efficiency, eventually affecting physiological performance. The number and density of stomata exhibited slight fluctuations with nonsignificant differences, suggesting that stomata distribution remains relatively stable under non-stress conditions. However, in the leaves of maize plants in the control, stomatal density was higher than in plants treated with doses of 100–300 Gy. A considerable decrease in stomatal density can reduce the rate of transpiration and water loss, which may considerably be an important adaptation to environmental conditions that cause physiological stress, such as irradiation and salinity (Hasanuzzaman *et al.*, 2023).

Based on the study observations, in all irradiation treatments, the stomata still showed an elliptical structure with paired guard cells. However, the size and density of stomata varied across the different irradiation doses (Figure 2). Control maize plants (0 Gy) exhibited relatively large stomata with even distribution and a fairly high density. Stomata at a dose of 100 Gy gave a structure similar to the control, although the guard cells appeared slightly shorter and the stomata openings were somewhat narrower. This structure indicated that low-dose irradiation has not caused significant anatomical damage and may even

activate an adaptive response to mild stress. Stomata at a dose of 200 Gy tended to be smaller and have slightly narrower openings. The number of stomata per unit area also decreased compared with the control. This may be because of the plants' physiological response to reduce transpiration rate, as well as maintain the water balance in response to oxidative stress (Kardiman and Ræbild, 2018). According to Chua and Lau (2024), reduction in stomatal size and density is one of the plant adaptation mechanisms to environmental stress conditions, including ionization stress conditions. However, at the dose of 300 Gy, stomata showed the most obvious narrowing, with irregularly shaped openings and some guard cells even showing signs of morphological damage. The reduction in stomata opening area at this dose revealed that the radiation has exceeded the physiological tolerance threshold of the plant, thus interrupting the normal function of guard cells (Araújo *et al.*, 2011).

The observed anatomical responses may have a linkage to radiation-induced cellular and structural changes. Physiologically, exposure to gamma radiation leads to the production of reactive oxygen species (ROS), which can cause structural variations in the epidermis and surrounding tissues

(Nuszkiewicz *et al.*, 2020). Plants capable of efficiently regulating stomata morphology will have an adaptive advantage in coping with stress conditions, including salinity stress (Matkowski and Daszkowska-Golec, 2023). Therefore, the stomata observations supported the possibility of variations in leaf anatomy as an initial adaptive mechanism in response to irradiation-induced stress conditions.

Physiological response

The physiological response of maize to gamma irradiation acquired evaluation based on chlorophyll content. Variations in chlorophyll a, chlorophyll b, and total chlorophyll across the different irradiation doses are visible in Figure 3. The differential response of chlorophyll components to gamma irradiation evinced a selective sensitivity of photosynthetic pigments. Chlorophyll a showed a slight increase with moderate irradiation doses compared with the control, whereas chlorophyll b and total chlorophyll revealed a declining trend with increasing radiation levels. This pattern suggested that chlorophyll a could be relatively more stable, enabling stimulation under mild irradiation stress, while chlorophyll b appeared to be more vulnerable to radiation-induced damage.

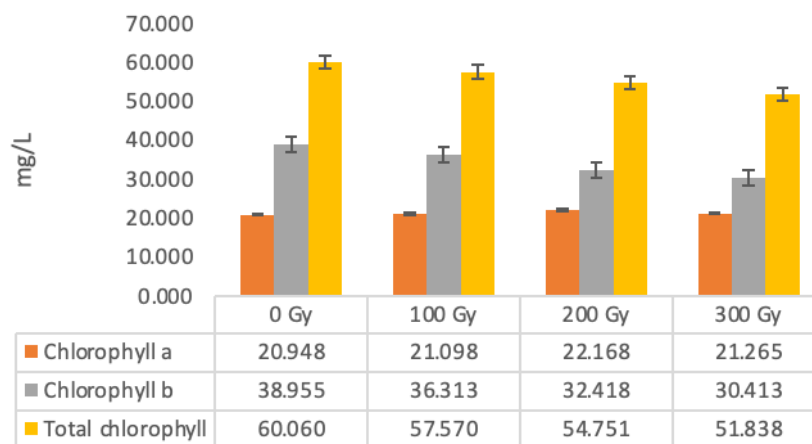


Figure 3. Effect of gamma irradiation (0, 100, 200, and 300 Gy) on chlorophyll content (a, b, and total) in maize leaves.

The chlorophyll a enhancement can mean an association with a stimulatory effect of low-to-moderate gamma irradiation on photosynthetic metabolism. Such responses were often in association with hormesis, where sub-lethal stress conditions enhanced the metabolic activity, including pigment and chloroplast synthesis and their functions (Agathokleous *et al.*, 2020). Chlorophyll a, being a primary photosynthetic pigment, expressed direct involvement in photochemical reactions, which could undergo preferential synthesis to sustain core photosynthetic processes under mild stress conditions (Tamiaki and Kichishima, 2025). The chlorophyll b reduction revealed the higher sensitivity of accessory pigments to irradiation stress. Chlorophyll b plays a crucial role in light-harvesting complexes (LHC), extending the range of light absorption and transferring excitation energy to chlorophyll a (Kume *et al.*, 2018). However, the damage to chlorophyll b can result from the degradation of light-harvesting complexes and oxidative damage induced by ROS generated under higher irradiation doses. Klavins *et al.* (2026) also reported the selective degradation, where accessory pigments proved more vulnerable to environmental stress than to primary pigments.

Gamma irradiation resulted in a general reduction in chlorophyll b and total chlorophyll content in maize plants. However, at 100 Gy the reduction in these pigments was considerably lower than at higher doses (200 and 300 Gy). This pattern revealed an obvious dose-dependent response. The comparatively small reduction at 100 Gy suggested that plant cells were still capable of maintaining chlorophyll stability under moderate irradiation stress. At this dose, cellular repair mechanisms and antioxidant systems may remain functional, thereby minimizing oxidative damage to chloroplast structures (Caplin and Willey, 2018). The ROS generated by irradiation can reach effective scavenging at lower radiation doses, preventing significant degradation of photosynthetic pigments. As a result, the integrity of light-harvesting complexes had the chlorophyll b slightly affected (Tan *et al.*, 2023). In contrast, the

significant decline in chlorophyll b and total chlorophyll at 200 and 300 Gy indicates increasing radiation-induced stress, where higher irradiation doses progressively disrupt chlorophyll biosynthesis and enhance chlorophyll degradation. Higher irradiation doses occurred to enhance the ROS production, which resulted in lipid peroxidation, protein denaturation, and disruption of chloroplast membranes, particularly the thylakoid system (Hasanuzzaman *et al.*, 2020).

The relatively stable condition at 100 Gy, followed by significant decline at higher doses, suggested this threshold may represent a shift between the tolerable stress and damaging stress in maize plants. Accordingly, 100 Gy can tend to be a more optimal dose in maintaining physiological balance while still inducing variation. Therefore, the gradual reduction pattern across increasing irradiation doses also highlighted the sensitivity of chlorophyll b as an early indicator of stress intensity (Petjukevics and Skute, 2022).

The maize plant responses to gamma irradiation enunciated a close relationship between the anatomical adjustments and physiological regulation. In leaf tissues, the structural modifications, particularly in the epidermis, mesophyll, and stomata, appeared to be in close association with variations in chlorophyll composition (Bak, 2026). Such integration suggested that anatomical traits play a crucial role in modulating physiological responses under irradiation-induced stress and imitate plant's capacity to uphold the functional stability (Katiyar *et al.*, 2022). Therefore, the combined evaluation of anatomical and physiological traits provides a robust basis for identifying early-response traits that can be useful to support selection strategies aimed at improving salinity stress adaptation.

CONCLUSIONS

Gamma radiation induced dose-dependent responses in maize plants, affecting both anatomical and physiological traits. A radiation dose of 100 Gy tends to maintain the reliability of anatomical structures and chlorophyll content. Meanwhile, higher doses (200–300

Gy) cause variations in anatomical structures, particularly stomatal size and tissue thickness, as well as a decrease in chlorophyll b and total chlorophyll content. The results provided basic information on radiation-induced variations and also highlighted the potential of integrating anatomical and physiological traits for early selection in mutation breeding programs aimed at improving salinity stress adaptation.

ACKNOWLEDGMENTS

The authors would like to thank the Universitas Sumatera Utara, Indonesia, for funding this research through the Applied Research Scheme (TALENTA) with Research Contract Number: 13452/UN5.1.R/PT.01.03/2025, dated June 25, 2025.

REFERENCES

- Afram Y, Amenorpe G, Bediako EA, Darkwa AA, Shandu SF, Labuschagne MT, Amegbor IK (2024). Induction of genetic variability of maize genotypes through radiation revealed mutants resistant to maize streak disease. Applied radiation and isotopes: Including data, instrumentation and methods for use in agriculture, industry and medicine, 207, 111279. <https://doi.org/10.1016/j.apradiso.2024.111279>.
- Agathokleous E, Feng Z, Peñuelas J (2020). Chlorophyll hormesis: Are chlorophylls major components of stress biology in higher plants?. *Sci. Total Environ.* 726: 138637. <https://doi.org/10.1016/j.scitotenv.2020.138637>.
- Albahri G, Alyamani AA, Badran A, Hijazi A, Nasser M, Maresca M, Baydoun E (2023). Enhancing essential grains yield for sustainable food security and bio-safe agriculture through latest innovative approaches. *Agronomy* 13(7): 1709. <https://doi.org/10.3390/agronomy13071709>.
- Atghaei M, Rezaie MR, Baghizadeh A, Mirshekarpour H (2023). Investigation of gamma-ray effect on physiological and biochemical traits of triticale plant under salinity stress. *Chem. Methodol.* 7(6): 447-459. <https://doi.org/10.22034/chemm.2023.389655.1659>.
- Araújo WL, Fernie AR, Nunes-Nesi A (2011). Control of stomatal aperture: A renaissance of the old guard. *Plant Signal. Behav.* 6(9): 1305-1311. <https://doi.org/10.4161/psb.6.9.16425>.
- Bak T (2026). Changes in stomata and chlorophyll content with leaf growth in cherry laurel. *ISPEC J. Agric. Sci.* 10(1): 73-80. <https://doi.org/10.5281/zenodo.18171645>.
- Calabrese EJ (2014). Hormesis: A fundamental concept in biology. *Microbial cell*, 1(5): 145-149. <https://doi.org/10.15698/mic2014.05.145>.
- Caplin N, Willey N (2018). Ionizing radiation, higher plants, and radioprotection: From acute high doses to chronic low doses. *Front. Plant Sci.* 9: 847. <https://doi.org/10.3389/fpls.2018.00847>.
- Choi HI, Han SM, Jo YD, Hong MJ, Kim SH, Kim JB (2021). Effects of acute and chronic gamma irradiation on the cell biology and physiology of rice plants. *Plants* 10(3): 439. <https://doi.org/10.3390/plants10030439>.
- Chua LC, Lau OS (2024). Stomatal development in the changing climate. *Development* 151(20): dev202681. <https://doi.org/10.1242/dev.202681>.
- Đilçdm A, Özay SG, Kökddl G (2010). Exomorphic seed characters and anatomy of leaf and stem of some *Vincetoxicum* (Asclepiadaceae/Apocynaceae) species from Turkey. *J. Fac. Pharm. Ankara.* 39(1): 1-16. https://doi.org/10.1501/Eczfak_00000000550.
- Erofeeva EA (2024). Plant hormesis: The energy aspect of low and high-dose stresses. *Plant Stress* 14: 100628. <https://doi.org/10.1016/j.stress.2024.100628>.
- FAO (2021). Global Map of Salt Affected Soils Version 1.0. <https://www.fao.org/soils-portal/data-hub/soil-maps-and-databases/global-map-of-salt-affected-soils/en/>.
- FAO (2024). World Food and Agriculture – Statistical Yearbook 2024. Rome. <https://doi.org/10.4060/cd2971en>.
- Hasanuzzaman M, Bhuyan MHMB, Parvin K, Bhuiyan TF, Anee TI, Nahar K, Hossen MS, Zulfiqar F, Alam MM, Fujita M (2020). Regulation of ROS metabolism in plants under environmental stress: A review of recent experimental evidence. *Int. J. Mol. Sci.* 21(22): 8695. <https://doi.org/10.3390/ijms21228695>.
- Hasanuzzaman M, Zhou M, Shabala S (2023). How does stomatal density and residual transpiration contribute to osmotic stress tolerance?. *Plants* 12(3): 494. <https://doi.org/10.3390/plants12030494>.
- Haworth M, Marino G, Materassi A, Raschi A, Scutt CP, Centritto M (2023). The functional significance of the stomatal size to density relationship: Interaction with atmospheric

- [CO₂] and role in plant physiological behaviour. *Sci. Total Environ.* 863: 160908. <https://doi.org/10.1016/j.scitotenv.2022.160908>.
- Kardiman R, Ræbild A (2018). Relationship between stomatal density, size and speed of opening in Sumatran rainforest species. *Tree Physiol.* 38(5): 696–705. <https://doi.org/10.1093/treephys/tpx149>.
- Katiyar P, Pandey N, Keshavkan S (2022). Gamma radiation: A potential tool for abiotic stress mitigation and management of agroecosystem. *Plant Stress* 5: 100089. <https://doi.org/10.1016/j.stress.2022.100089>.
- Khan AB, Iqbal B, Akbar R, Du D, Wang YF (2026). From molecules to field: Integrated insights into cuticle-mediated drought tolerance in plants. *Biotechnol. Adv.* 89: 108877. <https://doi.org/10.1016/j.biotechadv.2026.108877>.
- Klavins L, Zommere A, Gricenko T, Klavins M (2026). The multifunctionality of plant pigments: Roles, recovery from by-products, and stability challenges. *J. Agric. Food Res.* 26: 102748. <https://doi.org/10.1016/j.jafr.2026.102748>.
- Kume A, Akitsu T, Nasahara KN (2018). Why is chlorophyll b only used in light-harvesting systems?. *J. Plant Res.* 131(6): 961–972. <https://doi.org/10.1007/s10265-018-1052-7>.
- Lestami A, Maysaroh U, Alfi R, Wahyuni H (2026). Determination of radiosensitivity and growth response of maize seedlings to gamma ray irradiation. *IOP Conf. Ser.: Earth Environ. Sci.* 1583: 012013. <https://doi.org/10.1088/1755-1315/1583/1/012013>.
- Liu L, Wang X, Chang C (2022). Toward a smart skin: Harnessing cuticle biosynthesis for crop adaptation to drought, salinity, temperature, and ultraviolet stress. *Front. Plant Sci.* 13: 961829. <https://doi.org/10.3389/fpls.2022.961829>.
- Lu C, Li W, Feng X, Chen J, Hu S, Tan Y, Wu L (2025). The dynamic remodeling of plant cell wall in response to heat stress. *Genes* 16(6): 628. <https://doi.org/10.3390/genes16060628>.
- Matkowski H, Daszkowska-Golec A (2023). Update on stomata development and action under abiotic stress. *Front. Plant Sci.* 14: 1270180. <https://doi.org/10.3389/fpls.2023.1270180>.
- Mohamed IAA, Shalby N, Bai C, Qin M, Agami RA, Jie K, Wang B, Zhou G (2020). Stomatal and photosynthetic traits are associated with investigating sodium chloride tolerance of *Brassica napus* L. cultivars. *Plants* 9(1): 1–19. <https://doi.org/10.3390/plants9010062>.
- Nilahayati, Handayani RS, Nazimah, Neni, Saputra D (2024). Gamma-ray irradiation alters the morphology, anatomy and agronomic characters of the groundnut (*Arachis hypogaea* L.) bison cultivar in M1 generation. *Biodiversitas.* 25(11): 4179–4189. <https://doi.org/10.13057/biodiv/d251117>.
- Ntsomboh-Ntsefong G, Paul Ernest F, Benoit Constant LLN, Mbi Kinsley T, Alain Hervé Z, Hortense Noelle M, Joseph Martin B (2023). Gamma ray induced mutagenesis for crop improvement: Applications, advancements, and challenges. In: Gamma Rays - Current Insights. *Intech Open.* <https://doi.org/10.5772/intechopen.1002997>.
- Nuszkiewicz J, Woźniak A, Szewczyk-Golec K (2020). Ionizing radiation as a source of oxidative stress-the protective role of melatonin and vitamin D. *Int. J. Mol. Sci.* 21(16): 5804. <https://doi.org/10.3390/ijms21165804>.
- Pandit K, Chandni, Kaur S, Kumar M, Bhardwaj R, Kaur S (2024). Salinity stress: Impact on plant growth. *Adv. Food Secur. Sustain.* 9: 145–160. <https://doi.org/10.1016/bs.af2s.2024.07.002>.
- Petjukevics A, Skute N (2022). Chlorophyll fluorescence changes as plant early state indicator under different water salinity regimes on the invasive macrophyte *Elodea canadensis* (Michx., 1803). *One Ecosyst.* 7: e82389. <https://doi.org/10.3897/oneeco.7.e82389>.
- Rosmala A, Khumaida N, Sukma D (2016). Alteration of leaf anatomy of handeuleum (*Graptophyllum pictum* L. Griff) due to gamma irradiation. *Hayati J. Biosci.* 23(3): 138–142. <https://doi.org/10.1016/j.hjb.2016.12.003>.
- Samiyarsih S, Palupi D, Fitrianto N, Naipospos N (2020). The effect of cobalt 60 gamma rays irradiation on anatomical characters and chlorophyll content of winged-bean (*Psophocarpus tetragonolobus* [L.] DC). *IOP Conf. Ser.: Earth Environ. Sci.* 593, 012028. <https://doi.org/10.1088/1755-1315/593/1/012028>.
- Sass JE (1951). Botanical Microtechnique. 2nd edition. The Iowa State College Press. Ames. pp. 228.
- Tamiaki H, Kichishima S (2025). Chlorophyll pigments and their synthetic analogs. *Plant Cell Physiol.* 66(2): 153–167. <https://doi.org/10.1093/pcp/pcae094>.
- Tan Y, Duan Y, Chi Q, Wang R, Yin Y, Cui D, Li S, Wang A, Ma R, Li B, Jiao Z, Sun H (2023). The role of reactive oxygen species in plant response to radiation. *Int. J. Mol. Sci.*

- 24(4): 3346. <https://doi.org/10.3390/ijms24043346>.
- Tanumihardjo SA, McCulley L, Roh R, Lopez-Ridaura S, Palacios-Rojas N, Gunaratna NS (2020). Maize agro-food systems to ensure food and nutrition security in reference to the sustainable development goals. *Global Food Secur.* 25: 100327, <https://doi.org/10.1016/j.gfs.2019.100327>.
- Tiah FS, Msuya DG, Nassary EK, Tryphone GM (2026). Maize seed quality attributes: Exploring genetic, agronomic, and environmental factors for sustainable improvement – A systematic review. *J. Agric. Food Res.* 25: 102623. <https://doi.org/10.1016/j.jafr.2025.102623>.
- Villegas D, Sepúlveda C, Ly D (2023). Use of low-dose gamma radiation to promote the germination and early development in seeds. In: *Seed Biology - New advances. Intech Open.* <https://doi.org/10.5772/intechopen.1003137>.
- Yadav A, Singh B, Singh SD (2019). Impact of gamma irradiation on growth, yield and physiological attributes of maize. *Indian J. Exp. Biol.* 57: 116–122.
- Wintermans JFGM, De-Mots A (1965). Spectrophotometric characteristics of Chlorophylls a and b and their pheophytins in ethanol. *Biochim. Biophys. Acta Bioenerg.* 109(2): 448–453. [https://doi.org/10.1016/0926-6585\(65\)90170-6](https://doi.org/10.1016/0926-6585(65)90170-6).
- Wu Y, Liu J, Zhao L, Wu H, Zhu Y, Ahmad I, Zhou G (2026). Abiotic stress responses in crop plants: A multi-scale approach. *J. Integr. Agric.* 25(1): 1–15. <https://doi.org/10.1016/j.jia.2024.09.003>.
- Zhao P, Li Q, Lei Y, Zou J, Li Q (2025). Adaptation of cuticle metabolism to abiotic stress in plants. *Crop Environ.* 4(1): 38–44. <https://doi.org/10.1016/j.crope.2025.01.001>.