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Essay

Mutagenesis by gamma radiation for genetic improvement of food-important plants

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Abstract

Mutagenesis induced by physical agents such as Co^{60} gamma radiation in plant cells or tissues generates structural changes in deoxyribonucleic acid and has increased genetic variability in crops of agricultural importance. Often, the starting material is plant species established in *in vitro* cultures, which facilitates the management and control of physicochemical conditions in addition to increasing the number of repetitions in a minimum space. As a product, it is expected to obtain improved varieties with tolerance to biotic or abiotic factors in addition to improving morphological and nutritional qualities. This review of the art study compiled information from the last 10 years to provide a current overview of the effect of gamma radiation on plant tissues *in vitro*, addressing from radiation sources, types of damage and repair mechanisms of deoxyribonucleic acid, in addition to the use of molecular markers to evidence variations at the genetic level. Success cases for crops of agro-industrial importance in Mexico will be analyzed, sharing the current expectations in the use of this technology.

Keywords:

ionizing radiation, plant breeding, plant tissue culture.

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Mutagenesis is a common technique for genetically improving crops of economic value, inducing changes in DNA sequence (Spencer *et al*., 2021). Mutagenesis can be induced by mutagenic agents such as gamma radiation (Mba, 2013). Gamma radiation-induced mutagenesis (GRIM) has been used in medicinal, ornamental, and fruit plants to improve characteristics such as nutritional content, shelf life, productivity, quality, and disease resistance (Mba, 2013; Udage, 2021). Currently, more than 40% of varieties obtained by mutagenesis have been developed through GRIM (IAEA, 2022b). Traditionally, the GRIM method has been applied to seeds; however, this process could take up to 9 years to obtain results, but in recent decades, it has been associated with the culture of plant tissues, allowing new varieties to be obtained in approximately 2 to 3 years (Mba, 2013; Spencer *et al*., 2021). This study provided an overview of the effects of gamma radiation on the improvement of nutritional and phytochemical characteristics in *in vitro* cultures of food importance.

Effect of gamma radiation and DNA repair in plant tissues

Gamma radiation is emitted by radioisotopes such as cobalt-60 (Co^{60}), cesium-137 (Cs^{137}) and to a lesser extent by plutonium-239 (Pu^{239}) (Mba, 2013; Udage, 2021). This radiation consists of electromagnetic waves with lengths less than $1x10^{-11}$ m and energy levels around 1.36 MeV (Spencer *et al*., 2021), capable of ionizing atoms by displacing electrons from their outer orbitals. Ionization of atoms can cause various effects on cells (Oladosu *et al*., 2016).

Radiation exerts its effect through two mechanisms: direct (physical) action, which is reflected in the damage of the molecule, and indirect (chemical) action of free radicals (Figure 1A) (Spencer *et al*., 2021; Riviello-Flores *et al*., 2022). The indirect action involves the absorption of energy by the water molecule, causing its dissociation (radiolysis). This absorption leads to the generation of H^+ ions and free radicals H• and OH•, causing chain reactions that produce secondary reactive oxygen species (ROS), such as hydrogen peroxide (H_2O_2), superoxide ($O_2•^{\#}$) and hydronium ion (H_2O^-) (Figure 1B) (Szwent, 2015; Puerta-Ortiz and Morales-Aramburo, 2020).

Free radical damage is concentrated in nitrogenous bases and sugars present in DNA, which cause base substitution, spontaneous depurination, generating structural alterations (Puerta-Ortiz and Morales-Aramburo, 2020). The direct damage resulting from radiation exposure involves structural changes in the nitrogenous bases of DNA, including the removal of bases (AP sites), hydrogen bond breaking, and single- and double-strand breaks (Figure 1C) (Szwent, 2015; Puerta-Ortiz and Morales-Aramburo, 2020). To counteract these effects, cells have evolved preventive mechanisms to protect and repair the affected DNA.

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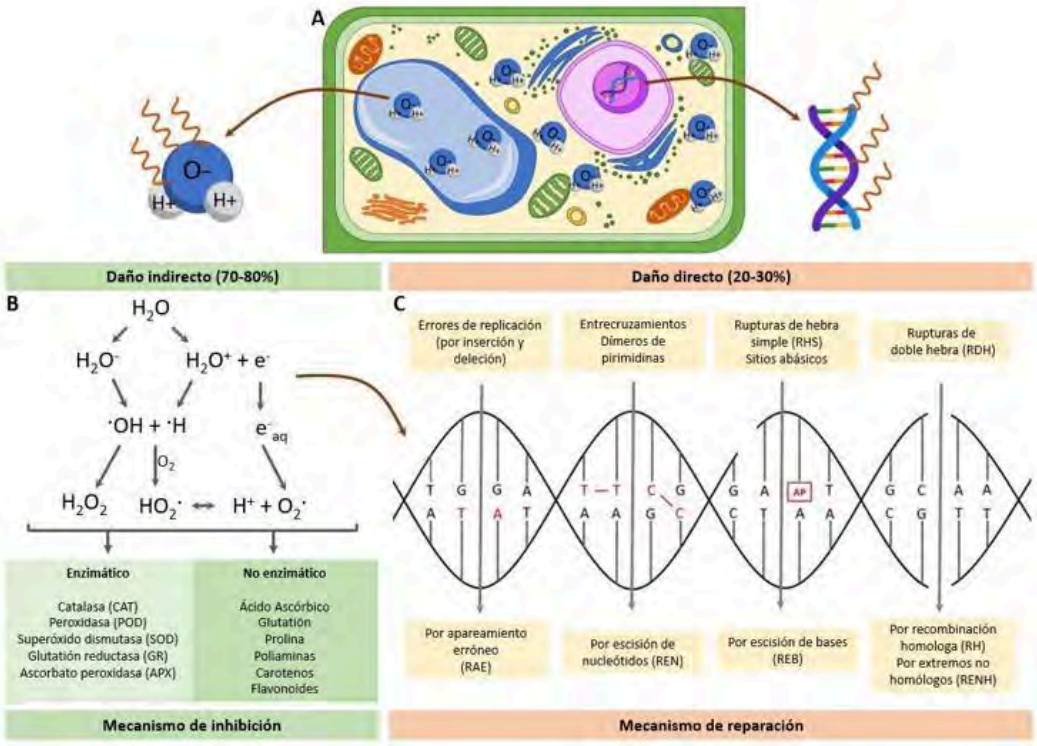
Figure 1. Damage caused by gamma radia on, main mechanisms of repair and inhibi on of free radicals. A) gamma radia on has the ability to generate ions, making it able to react directly with DNA or water molecules; B) indirect damage to DNA and free radical inhibition mechanisms; and C) direct damage to DNA and repair mechanisms.



Repair mechanisms include base excision repair (BER), which addresses single-strand breaks and AP sites, as well as nucleotide excision repair (REN), interstrand cross-links (Manova and Gruszka, 2015). In addition, mismatch repair (MMR) serves as the primary mechanism responsible for correcting changes induced by DNA insertions, deletions, and loops (Tafurt and Marin 2014; Manova and Gruszka, 2015).

In the case of double-strand break (DSB), it can be repaired by two mechanisms: homologous recombination (HR) and non-homologous end joining (NHEJ) (Kariuki *et al*., 2019). HR involves repairing broken ends of DNA using a homologous sequence as a template. On the other hand, non-homologous DNA end joining involves the direct binding of broken DNA strands without the requirement of a homologous sequence (Tafurt and Marin, 2014; Kariuki *et al*., 2019). In this sense, it has been found that the dose of gamma radiation in plants is related to the expression of DNA repair genes, such as pcna and fen1 (involved in base excision repair and mismatch repair), rad51 (associated with homologous recombination) and orc1 (involved in DNA replication) (Kariuki *et al*., 2019), suggesting a more effective repair process in newly formed tissues.

The response to ion-induced cell damage also involves increased enzyme activity of catalase (CAT), peroxidase (POD), superoxide dismutase (SOD), glutathione reductase (GR), and ascorbate peroxidase (APX) (Ali *et al*., 2015; Ludovici *et al*., 2020). In addition, non-enzymatic neutralizing molecules, such as ascorbic acid, glutathione, proline, polyamines, betalains, carotenes, and flavonoids, play a protective role against this type of stress (Demidchik, 2015; Ludovici *et al*., 2020), which has been widely documented in wheat (Hong *et al*., 2014) and rice (Kariuki *et al*., 2019). Therefore, increased accumulation of neutralizing enzymes and antioxidant molecules would prevent the detrimental effects of oxidative stress on plant tissues and inhibit DNA changes caused by free radicals.

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Dosimetry and radiosensitivity in genetic improvement

The efficiency of obtaining mutants by gamma radiation depends on the determination of an optimal radiation dose. Since the frequency of mutations is influenced by dose, exposure rate, and tissue tolerance (Oladosu *et al*., 2016), the evaluation of radiosensitivity and dosimetry in improvement programs with mutagenic agents becomes crucial. Radiation dosimetry determines the amount or dose absorbed by biological material, expressed in Gray units (1Gy = 1 J kg^{-1} = 100 R) (Spencer *et al*., 2021). The relationship between the absorbed dose and the deleterious effects of the tissues is evidenced in the reduction of germination rate, seedling height, survival rate, biomass accumulation, among others (Mba, 2013).

Assessing the radiosensitivity of biological material involves determining a lethality metric when increasing radiation dose (Oladosu *et al*., 2016). This allows the calculation of lethal doses that affect specific percentages (eg., LD_{30}, LD_{40}, LD_{50}, and LD_{60}) of the irradiated sample or that reduce tissue growth (GR_{30}, GR_{40}, GR_{50}, and GR_{60}), facilitating the identification of mutations in the surviving population (Mba, 2013; Riviello-Flores *et al*., 2022). LD_{50} and GR_{50} are used as a reference when irradiating large populations (greater than 400 individuals), increasing the probability of obtaining materials of interest (Penna and Bhagwat, 2023). However, questions persist about the arbitrariness of these values due to the risk of missing desirable mutations that can appear at low doses of radiation (Mba, 2013).

Therefore, it is important to balance effective doses to generate variations in DNA sequences, without leading to harmful mutations or considerable reductions in population size. Recent radiosensitivity studies have shown that undifferentiated tissues such as calluses and somatic embryos are more sensitive to gamma radiation (12-60 Gy) due to their high water content, in contrast to seeds (38-184 Gy) or lignified tissues such as shoots, seedlings, roots, and buds (23-250 Gy) (Abdelnour-Esquivel *et al*., 2020; Pérez-Jiménez *et al*., 2020; Royani *et al*., 2021; Huerta-Olalde *et al*., 2022).

For example, Royani *et al*. (2021) studied Zollinger's indigo (*Indigofera zollingeriana*) crops and found greater sensitivity in seeds with an LD_{50} of 184 Gy, while more lignified tissues (seedlings) exhibited greater tolerance (254 Gy). In contrast, Pérez *et al*. (2020) studied *Citrus* spp. plants and observed that the seeds were more resistant to gamma radiation, with LD_{50} values of 127 Gy in Alemow and 156 Gy in sour orange, compared to the buds of lemon crops (LD_{50} of 25-26 Gy). Thus, the loss of explants and seedling regeneration capacity depends on the species, physiology, genetics, and stage of development during the GRIM processes.

Improved characteristics in *in vitro* cultures exposed to gamma radiation

Natural mutations are recognized for their ability to induce genetic variability with low frequency (10^{-5} and 10^{-8}) in cultivated plants (Spencer *et al*., 2021). To overcome this limitation, GRIM emerges as a valuable tool by increasing the frequency of mutations and facilitating the selection of desirable agronomic traits.

Table 1 illustrates the benefits of GRIM in crop improvement. One of the main advantages is the ability to induce mutations that increase the tolerance of crops to biotic stress, such as diseases, and abiotic stress, including water, salt, and cold stress. It also significantly increases productivity and improves the nutritional content of crops without compromising their yield. This offers the potential to develop improved varieties with higher nutritional value, addressing nutritional deficiencies and improving the overall quality of agricultural products.

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Table 1. Determination of LD_{50} to obtain presumed mutant lines *in vitro* in food value crops in the last three years (2019-2022).

Specie	Tissue	Source	Results		Authors
			Medium lethal dose (LD_{50})	Outstanding lines	
* *R. fruticosus* 'Tupy' (blackberry)	Shoots	Co^{60}	30.8 Gy	Resistant to *B. cinerea*	Huerta-Olalde *et al.* (2022)
* *O. sativa* L. (rice)	Seeds Embryogenic callus	Co^{60}	SD (seed) 60 Gy (callus)	Tolerance to salt stress and sorbitol	Abdelnour-Esquivel *et al.* (2020)
*** *A. tequilana* cv. Azul (agave)	Seedlings	Co^{60}	ND	Increase in fructose and sucrose	Ángeles-Espino *et al.* (2020)
* *** *Z. officinale Rosc.* (ginger)	Shoots	Co^{60}	56 Gy	Increase in gingerol resistant to *F. oxysporum f.sp. zingiberi*	Sharma *et al.* (2020)
*** *P. ginseng* Mayer (ginseng)	Callus y roots	Co^{60}	20-75 Gy (Callus) 23.7-52.3 Gy (Root)	Increase in ginsenosides	Le *et al.* (2019)
*** *V. mungo* L. Hepper (black beans)	Seeds	Co^{60}	ND	Increase in reducing sugars, starch, amino acids, and proteins	Yasmin *et al.* (2019)

ND= no data available; Gy= grays; *= materials with tolerance to biotic and abiotic stress; **= materials with morphological improvements; ***materials with nutritional and phytochemical improvements.

Tolerance to abiotic and biotic stress

The use of gamma radiation has been shown to be effective in the development of *in vitro* plants with desirable characteristics, such as tolerance to abiotic stress. In this sense, promising varieties with resistance to high salt content have been generated (Table 1). Such is the case of what was reported by Abdelnour-Esquivel *et al*. (2020), who obtained rice (*O. sativa* L.) lines with greater resistance to sodium chloride (NaCl) at a concentration of 200 mM.

These mutant plants showed a 75% higher resistance to NaCl and two times more resistance to sorbitol content (10% w/v) compared to the reference material. Similarly, Nikam *et al*. (2015) reported positive results in sugarcane (*Saccharum officinarum* L.) plants regenerated from irradiated calluses kept under salt stress (100 mM NaCl). They identified 18 mutant materials that exhibited higher total production of sugarcane (25%), commercial sugarcane (12%), degrees Brix (6%), and sucrose (10%), in contrast to their control.

The effect of GRIM *in vitro* on the generation of heavy metal-resistant plants has not been comprehensively studied. However, Qi *et al*. (2015) exposed *Arabidopsis thaliana* seeds to different doses of radiation (0 to 150 Gy), which were germinated *in vitro* in the presence of $CdCl_2$ and/or $Pb(NO_3)_2$. The results showed significant increases in germination rate (25 and 32%) and root length (20 and 42%) in plants exposed to Cd and Pb.

In addition, there were increases in the enzymatic activity of SOD (50% and 70%), POD (22% and 52%) and CAT (139% and 112%). The exposure of plants to heavy metals triggers an imbalance in the formation of ROS, which leads to oxidative stress, putting the survival of the crop at risk. This leads to an increase in free radical neutralizing enzymes to mitigate detrimental effects and preserve cellular homeostasis.

On the other hand, GRIM offers a valuable approach to obtaining disease-resistant plants, with *in vitro* culture being a frequent tool during selection, as it allows the pathogen itself, metabolites,

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toxins, or microorganism filtrates to be included in the culture medium (Penna and Bhagwat, 2023), facilitating the identification and selection of elite lines (Table 1). Sharma *et al*. (2020) conducted a study on ginger (*Zingiber officinale* Rosc.) shoots exposed to fungal culture filtrates (FCF) of *Fusarium oxysporum* f. sp. *zingiberi*., in which it was possible to obtain materials tolerant in 15 and 17.5% of FCF, *in vivo* evaluations confirmed a significant improvement in the resistance of these materials (46.4 and 52%, respectively).

Similar results were published by Huerta-Olalde *et al*. (2022), who evaluated the effect of *Botrytis cinerea* mycelium filtrates on *in vitro* blackberry (*Rubus fruticosus* 'Tupy) shoots irradiated with gamma rays. They identified ten lines that exceeded 50% survival in terms of chlorotic and necrotic tissues, only two materials (rfgum5 and rfgum6) with signs of infection such as leaf detachment or mycelium growth, and no phenotypic changes were reported during their multiplication and development.

Improvement of nutritional and phytochemical quality

Elite varieties obtained by GRIM frequently exhibit metabolic, phytochemical, and nutritional alterations. An important example is the study conducted by Yasmin *et al*. (2019) on black beans (*Vigna mung* L.) exposed to 800 Gy of gamma radiation, they showed increases in the content of reducing sugars, starch, proteins, and amino acids by 26, 32, 28, and 21%, respectively. These findings suggest that GRIM has the potential to be a tool for improving nutritional content.

GRIM has not only improved the nutrient content of crops, but also optimized the phytochemical content, enhancing bioactive properties and providing high-value food. Le *et al*. (2019) generated four mutant lines (1G-20-12, 1G-20-16, 1G-20-19, and 1G-20-20) of ginseng (*P. ginseng* Mayer) roots, with increases in number (up to four times), length (up to nine times), and dry weight (up to six times). In addition, the content of ginsenosides, such as protopanaxatriol and protopanaxadiol, increased by six to ten times. Similar results were reported by Sharman and Tjarkur (2021), where irradiated ginger (*Z. officinale* Rosc.) shoots showed changes in the accumulation of essential oils, oleoresins, and 6-gingerol by 56% more compared to non-irradiated ones.

Similarly, Ángeles-Espino *et al*. (2020) generated mutant lines of *Agave tequilana* after two irradiation cycles (0 and 25 Gy). These mutant plants doubled the glucose, fructose, and sucrose contents, there was also increased accumulation of neokestose, kestotetrose, and ketopentose, which are high-value fructooligosaccharides in the family Agavaceae.

Molecular evidence in the evaluation of mutagenesis

Molecular DNA analysis encompasses a variety of techniques essential to GRIM programs as they validate the presence of mutant and epimutant materials among groups of irradiated materials (Riviello-Flores *et al*., 2022; Bhat *et al*., 2023). Polymerase chain reaction (PCR)-based molecular markers, such as SSR and ISSR, are frequently used (Due *et al*., 2019; Bhat *et al*., 2023) in mutagenesis improvement programs.

For example, ISSR markers have shown efficient results for identifying polymorphic DNA in mutants derived from banana (*M. paradisiaca* cv. sapientum), a study in which the authors managed to obtain nine bands, eight of them polymorphic. This showed a high level of genetic variation (90%) and coefficient of similarity (47%) between the materials with outstanding morphological changes and the reference material (Due *et al*., 2019).

Currently, methods with advanced markers (SRAP, SCoT, DArT, QTL) have been developed and successfully applied in research works, such as El-Fiki *et al*. (2021), by using ten SCoT and ISSR markers in tomato (*L. esculentum* Mill.), they identified 114 and 101 bands, respectively, where the average percentage of polymorphic bands of ISSR markers was lower than SCoT (40% and 65%, respectively). This reflected the average of the highest marker index for SCoT (0.34) compared to the ISSR markers (0.15). Although the values of the polymorphism information content (PIC)

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in both techniques were highly informative (0.429 and 0.347), the SCoT markers provided more information about the polymorphic variation detected.

Although any group of molecular markers provides information on genetic variations, their selection is essential to achieve the objectives set, considering factors such as previous sequencing, reproducibility, polymorphism, mechanism of gene action, quality and quantity of DNA required, marker index and cost (Nadeem *et al*., 2018; Bhat *et al*., 2023). Therefore, the use of new markers, such as SCoT, SNP, QTL, SRAP, DArT and RBIP, has shown greater control over some of these factors (Nadeem *et al*., 2018; El-Fiki *et al*., 2021; Bali, 2023; Bhat *et al*., 2023).

Conclusions

Gamma radiation-induced mutagenesis (GRIM) has been highlighted as a valuable tool for the genetic improvement of *in vitro* cultures of food value plants. Although it has generated disease-resistant, salt-tolerant varieties and increases in metabolites of interest, there is limited information on tolerance to water stress, temperature, pH, heavy metals, and nutritional improvements.

In addition, most of the programs have focused on fast-growing crops, leaving crops with longer cycles (grapes, avocados, guavas, and nopal) uncovered. Based on he findings of this review, there is a promising opportunity to use GRIM in slow-growing, *in vitro*-established crops, thereby extending the benefits for sustainable agriculture and high-value food production.

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