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Mutation Breeding: A Tool for Crop Improvement and Agricultural Sustainability

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Summary

Mutation breeding has emerged as an efficient tool for crop improvement, providing an efficient way of improving characteristics like disease resistance, stress tolerance, and yield. With the use of physical and chemical mutagens to induce variations in genetics, scientists have developed high-performing crop varieties that support agricultural sustainability and food security. The approach has been immensely beneficial in producing crops that can tolerate severe environmental conditions, which lessens the need for traditional breeding techniques, which require longer to get the desired outcomes. However, advances in genome editing and molecular biology have increased the accuracy and efficiency of mutation breeding, despite some obstacles including random mutation effects and the requirement for stringent selection. Mutation breeding is still essential for producing durable and high-yielding crop varieties, which will ultimately promote sustainable farming methods and food production as agriculture meets increased global demands.

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1. Introduction

For over 10,000 years, plant cultivation and agriculture have been part of human evolution. As the global population grew, food security became a major concern because land and water became limited. The global population is projected to reach 9.7 billion by 2050, and with finite arable land and changing climate, the demand for more productive and resilient crops is crucial for ensuring food security (Paul et al., 2024). Conventional breeding techniques, such as cross-pollination and hybridization, have been instrumental in improving crop yields and adaptability over the past century (Altaf et al., 2024). However, these methods are often time-consuming, with the introduction of desirable traits taking 7 to 12 years to produce an improved variety. The genetic variability within major crop species has been greatly reduced due to years of directed breeding, limiting the potential for further improvements (Govindaraj et al., 2015).

To address these challenges, plant breeders and researchers are exploring alternative strategies, such as mutation breeding, which involves inducing random genetic changes in plants to create new variations. Freisleben and Lein in 1944, coined the term mutation breeding to refer the deliberate induction and mutant lines development for the purpose of crop improvement (Oladosu et al., 2016). Mutation breeding is a plant breeding technique that involves inducing genetic mutations in crops to create new variations with desirable traits. It is a powerful tool that can complement conventional breeding methods by generating a wide range of genetic diversity, potentially leading to the development of crops with improved traits, such as drought tolerance, disease resistance, and higher nutritional content (Sikora et al., 2011). This process is achieved using physical mutagens such as gamma rays, X-rays, or neutron radiation or chemical mutagens such as ethyl methanesulfonate (EMS) and sodium azide (Bado et al., 2023). The induced mutations can lead to beneficial traits, including improved yield, disease resistance, abiotic stress tolerance, and enhanced nutritional quality (Das et al., 2014). Unlike genetic modification, mutation breeding does not involve the insertion of foreign genes, instead, it accelerates natural genetic variation, which can be selected for crop improvement (Singer et al., 2021). This method has been widely used in agriculture to develop improved crop varieties with enhanced resilience and productivity.

Mutation breeding began when Lewis John Stadler in 1928 and 1930 started the use of mutation realizing that radiation-induced mutations could change plant traits (Kharkwal, 2023). Since then, this technique has been effectively used to develop an increasingly large number of crop varieties, greatly increasing the amount of food produced worldwide. High-yielding rice, wheat, and barley varieties that were essential to the Green Revolution are notable examples (Ahloowalia et al., 2004). Recent developments in genome sequencing and molecular biology have improved the accuracy and effectiveness of mutation breeding. Breeding has accelerated due to the identification and selection of advantageous mutations made easier by the combination of genetic markers and high-throughput screening techniques (Ahmar et al., 2020). Also, the potential of mutant breeding has been further enhanced by new technologies like Clustered Regularly Interspaced Short Palindromic Repeats-Cas9 (CRISPR-Cas9) genome editing, which allow for targeted alterations in plant genomes (Rasheed et al., 2021).

As agriculture faces increasing environmental pressures, including erratic weather patterns, soil degradation, and emerging plant diseases, mutation breeding remains a crucial tool for crop improvement. Its ability to generate novel genetic variations in a relatively short time makes it an invaluable strategy for enhancing crop resilience and productivity. With the integration of modern biotechnological advancements, mutation breeding is set to play a key role in ensuring sustainable agricultural production and global food security in the coming decades. This review provides an overview of mutation breeding, exploring its historical development, methodologies, and significant contributions to crop improvement. It delves into the different types of mutagens used, including physical and chemical agents, as well as emerging biotechnological approaches that enhance mutation efficiency. Furthermore, the review highlights the numerous benefits of mutation breeding, such as improved yield, stress tolerance, disease resistance, and biodiversity conservation. Additionally, it discusses the challenges associated with this technique and the potential future advancements that could further refine its applications.

2. History of mutation breeding

An overview of the key milestones in mutation breeding is represented in Table 1. The history of crop plant mutation dates back to 300 BC in China, first documented in the book Lula. The earliest natural cereal mutant was found about 2317 years ago (Solanki et al., 2011). From 1590 to 1868, various aberrant

Phase	Time Period	Key Events
Ancient beginnings	300 BC	First recorded natural mutant in cereals documented in Lüshi Chunqiu, China
Early observations	1590 – 1868	Discovery of diverse plant variations, laying the foundation for later studies on mutations
Discovery of mutagens	1895 – 1920	Discovery of X-rays and their effects on biological systems; Formulation of the "Law of Homologous Series" in genetics
Discovery phase	1920s –1930s	1927: Hermann J. Muller demonstrated X-ray-induced mutations in Drosophila; 1928: Lewis Stadler induced mutations in barley and maize using X-rays and UV radiation; First mutant crop variety, 'Vorsteland tobacco'
Experimental phase	1940s –1950s	Development of early mutagenesis methods using chemical mutagens (e.g., mustard gas); 1950: First mutant crop variety 'Pilsener' barley was released; Sweden funded research on multiple crops; Observations on varying crop resistance to radiationcv
Expansion phase	1960s – 1970s	FAO/IAEA initiated global mutation breeding programs; Several mutant crop varieties (e.g., rice, wheat, barley) were developed and commercialized; Mutation breeding expanded to Latin America and Asia; Pakistan released mutant wheat and rice varieties
Molecular phase	1980s – 1990s	Advances in molecular biology enabled DNA-level mutation analysis; Marker-Assisted Selection (MAS) integrated into mutation breeding; Space mutagenesis improved crop traits; FAO/IAEA recognized mutation breeding
Genomic phase	2000s – 2010s	TILLING (Targeting Induced Local Lesions in Genomes) developed for non-GMO mutation screening; 2010s: CRISPR-Cas9 revolutionized precision mutagenesis
Next-Gen phase	2020s – Present	Advanced techniques like base editing and prime editing applied for climate-resilient crops; Increased focus on sustainable and precision mutation breeding; China expanded space-based agricultural research

Table 1. Chronological overview of key milestones in mutation breeding history.

plants were identified. Mutation research advanced in 1895 with W.K. Rontgen's discovery of X-rays, leading to the first use of mutagens between 1897 and 1920 and N.I. Vavilov's "Law of Homologous Series of Variation" (Van Harten, 1998). Mutation breeding was pioneered in the 1920s by Lewis John Stadler, who utilized irradiation to induce genetic variation in crops. Around the same time, Hermann J. Muller conducted mutation experiments on fruit flies (Rouyan, 2019), while Stadler focused on barley, maize, and wheat, demonstrating that radiation could create genetic variability in crop plants (Rao et al., 2018).

Many geneticists regard mutation induction as a milestone in genetics. However, American researchers were initially skeptical about its significance in agricultural crops (Lindstrom, 1933; MacArthur, 1934). In the early years, chromosomal aberrations in Nicotiana were reported by Goodspeed and colleagues (Goodspeed and Thompson, 1959). The first-ever mutant crop variety, "Vorsteland" tobacco, with improved quality traits, was released in Indonesia in 1934. Russian scientists Delaunay and Sapehin identified the first wheat mutants of practical significance. The lecture on polymorphic factors in barley, delivered by Nilsson-Ehle in Halle in 1939, marked the beginning of a new era in the use of induced mutations in Germany. In the mid-1930s, mutants were developed, with one showing yield similar to the parent (Gustafsson, 1947). By the 1940s, research expanded with joint funding from Swedish institutions, leading to promising mutants in wheat, barley, oats, flax, soybeans, and lupine. Stadler's research focused on inducing single mutations and noting increased lethality from X-rays. Different crops responded differently to radiation: Cruciferae seeds tolerated up to 100,000 r, while pea plants were far more sensitive, with a limit of 10–20 r (Gustafsson, 1944). In 1942–1943, Eisleben Lien's model experiments on barley significantly advanced mutation research.

Radiation-induced mutation breeding started in Latin America in the 1960s, beginning in six countries: Colombia, Peru, Brazil, Guatemala, Costa Rica, and Mexico (Moh, 1962). In China, rice breeding using induced mutation started in 1960 and has been continuously improving both conventional and hybrid varieties. The first mutant variety developed was from a series called '12 Zhefu.' Between 1986 and 1994, the most widely cultivated mutant variety was the Chinese 'Zhefu802,' which was evolved from 'Simei No. 2' (Moh, 1962). Radiation-induced biological effects were also observed in coffee breeding. In 1964, with the establishment of the joint FAO/IAEA Division of Nuclear

Techniques in Food and Agriculture, mutation breeding gained international recognition as a valuable tool for plant breeders (Shu et al., 2011). In 1979, Pakistan's Nuclear Institute of Agriculture released Jauhar-78, a salinity-tolerant wheat variety. Kiran-95 followed in 1996, offering improved grain quality and resistance to salinity and rust. Pakistan also released its first rice mutant, Kashmir Basmati, in 1977. Over the past 60 years, China, with IAEA and FAO, has developed over 1,000 mutant varieties across different crops. In 1987, China began using space mutagenesis for crop improvement, producing giant sweet peppers and enhancing wheat and rice traits through mutations induced by space radiation via satellites and high-altitude balloons (Wang and Hua, 2001). These mutations significantly boosted crop yields (Pathirana, 2021). To date, China has released around 741 mutant varieties across 45 crops and ornamental species (Mir et al., 2020). Recently, China launched a new satellite for agricultural and industrial applications (Anonymous, 2019).

3. Development of crop varieties through mutation breeding: a global overview

After Muller and Stadler discovered how to induce mutations, breeders from many countries began using mutation breeding to generate a wide range of genetic diversity through different mutagens. Radiation, especially gamma rays, became the most common and effective method due to its accessibility and safety, playing a key role in modern plant breeding. Most of the mutant varieties developed are food crops and ornamental plants. The FAO/IAEA maintains a comprehensive global database of these mutation-derived crop varieties (http://mvd.iaea.org). As of early 2022, over 3,365 mutant varieties from more than 240 plant species had been officially released. However, the IAEA's Mutant Variety Database (MVD) may not be regularly updated, as seen in the reported numbers for China (817), India (341), and Pakistan (56). In reality, China has already reported over 1,000 mutant varieties (Liu, 2021), India has reported 542, and Pakistan has released 79 (Figure 1). This suggests the total number of mutant varieties worldwide from more than 240 plant species likely exceeds 3,500. Most mutant varieties have been released over the past three decades. The cumulative number of officially released mutant varieties across six continents shows Asia leading with 2,052, followed by Europe with 960 and North America with 209.

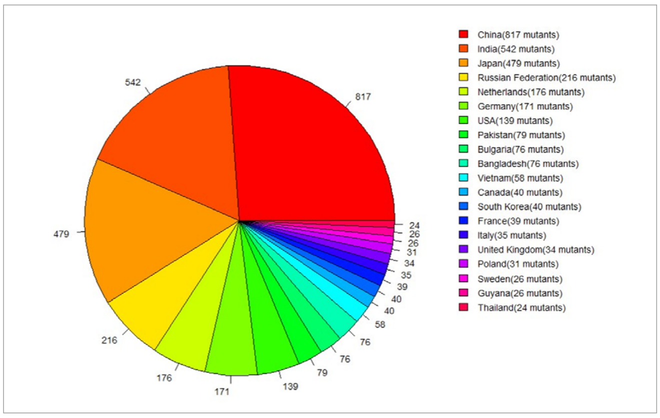

Figure 1. Number of mutant cultivars released in top 20 countries (Kharkwal, 2023).

Countries with over 100 released mutant varieties include China, India, Japan, the Russian Federation, the Netherlands, Germany, and the USA. Analyzing data on specific crops and the number of mutant varieties released worldwide (Figure 2) reveals that the top 20 positions are dominated by key food crops (cereals, pulses, oilseeds), as well as important fiber and ornamental plant species essential to global agriculture and economics. Over the past five decades, many countries have implemented extensive crop improvement programs using induced mutagenesis and mutation breeding, achieving remarkable success in developing numerous superior mutant varieties across key agricultural crops like cereals, pulses, oilseeds, vegetables, fruits, fibers, and ornamentals. These mutant varieties have been enhanced for traits such as yield, maturity, quality, and resistance to biotic and abiotic stresses. Although exact data on the total area cultivated with these commercially released mutant cultivars is not readily available, they are grown on millions of hectares and have made a significant global impact, contributing billions of dollars to agriculture and addressing food and nutritional security worldwide (Kharkwal, 2017). Most induced mutant varieties come from seed-propagated crops, with about 25% being ornamental plants. Most were developed directly through mutagenic treatment, while others came from cross-breeding with mutant varieties. Gamma radiation was the most commonly used mutagen.

Mutation breeding in rice has been highly successful, likely due to its diploid nature and self-fertilizing characteristics. Out of 1,616 mutant cereal varieties, rice accounts for 853. The first widely known rice mutant cultivar was Reimei, a short-straw (semi-dwarf) mutant from Fujiminori, released in Japan in 1966. Several important cultivars were developed later through cross-breeding with this cultivar (Nakagawa, 2021).

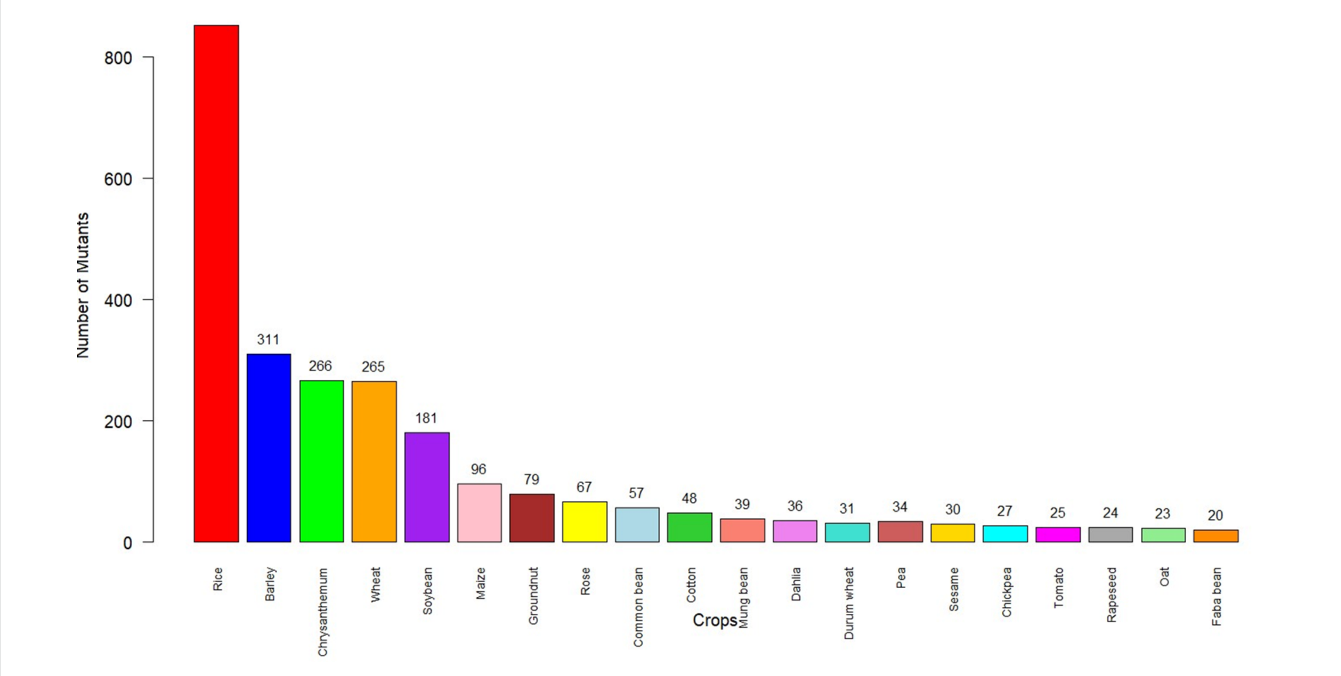

Figure 2. Number of mutant cultivars released in top 20 crops of the world (Kharkwal, 2023).

The mutant cultivar carried an allele similar to the well-known sd1 (semi-dwarf allele) found in Dee-geo-wu-gen (DGWG), a spontaneous dwarf mutant discovered by Chinese scientists. The DGWG mutant, with traits like dwarfness, stiff straw, fertilizer responsiveness, and daylength insensitivity, was a precursor to the Green Revolution. It was used in breeding programs to develop important varieties like Taichung Native-1 and IR8. In barley, 311 mutant varieties superior to the best control lines have been released by various countries, including Pallas (Sweden), Balder J (Finland), Diamant (Czech Republic), Trumpf (Germany), Goldspear (UK), Pennrad and Luther (USA), and Betina (France) (Van Harten, 1998).

4. Mutation concept and its importance

The term "mutation" was first introduced by Hugo de Vries in 1901 to describe a sudden, inheritable alteration in an organism's DNA. These changes can be induced by irradiation, chemicals, viruses, transposons, or chromosomal abnormalities during reproduction (Oladosu et al., 2016). Mutations, inheritable across generations, are classified into gene, chromosomal, and genomic types. Induced mutations have become a key method for developing improved crop germplasm (Suprasanna et al., 2015). Mutation breeding uses mutagens to modify plant cells, enhancing genetic variation which is essential for breeding and new trait development. By 1940, breeders adopted mutagenesis as a faster tool for creating plant mutations (Harwood, 2015), making it one of the most efficient techniques for global crop improvement. Mutations serve as the foundation for genetic variation, which is essential for genetic advancement and the process of genetic drift. Mutation breeding has been crucial in enhancing crop breeding, genetics, and genomic research by creating substantial genetic diversity. At the same time, global climate change poses a significant threat to the food supply chain, leading to the rapid loss of biodiversity in food and agriculture. Unpredictable climate changes threaten global crop yields, making the development of improved crop varieties crucial for sustainable agriculture. While natural mutations occur slowly, they enhance genetic diversity for breeding. Mutation breeding speeds up this process, enabling the creation of resilient varieties with multiple beneficial traits.

Mutagenesis is a powerful tool for inducing mutations, which can occur naturally or be artificially induced using mutagens. These mutagens are generally categorized into physical and chemical types (Chatterjee and Walker, 2017). Any living plant material can undergo physical and chemical mutagenesis, as long as it is capable of growth. This usually involves using meristematic tissues, such as apical and lateral meristems or embryos, or employing tissue culture techniques to cultivate cells, tissues, or organs. A summary of live plant materials used in plant mutation breeding is presented in Figure 3.

The use of mutagens increases the likelihood of obtaining desirable phenotypic traits and aids in the study of genetic variations, gene functions, and their association with phenotypes (Sharma et al., 2024). Different mutagenic agents like EMS, gamma rays, X-rays, and fast neutrons have been used worldwide to improve crop species (Pharmawati, 2024). Figures 4 and 5 illustrate the success of mutation breeding in various agricultural crops and major cereals (IAEA Mutant Database, 2021). In tomato breeding, whole-genome sequencing has helped identify millions of genetic variations, like SNPs and indels (Motolai, 2024). Advanced next-generation sequencing (NGS) techniques, such as MutMap and MutChromSeq, have made it easier to detect and identify useful mutations. These methods have been successfully applied in crops like wheat and barley (Jiang et al., 2024). Since 1963, the Nuclear Institute of Agriculture (NIA) in Tandojam, Pakistan, has used mutation breeding to develop improved crop varieties. NIA has released three mutant wheat varieties, seven rice varieties, and others like sugarcane, cotton, lentil, mungbean, and rapeseed. In 1978, NIA introduced the Shadab rice variety, derived from the IR6 variety using 0.5% EMS, with a high yield of 7 tons/ha and excellent grain quality (Bughio et al., 2007). In addition, the Nuclear Institute for Agriculture and Biology (NIAB) and other PAEC institutions have successfully developed mutant varieties of cotton, castor bean, sesame, and mandarin, significantly benefiting the farming community and improving their socio-economic conditions.

4.1 Spontaneous mutations

Spontaneous mutations occur naturally due to chromosomal abnormalities during biological processes. They serve as the foundation for evolutionary processes, driving genetic diversity in populations. These mutations often involve previously unknown genes, later identified and named based on their observable traits. Examples include the super-root (surl-7), maize bronze (bz), and carbohydrate accumulation mutant (caml) (Boerjan et al., 1995; Eimert et al., 1995). Spontaneous mutations occur at varying frequencies in different maize genotypes, with some exhibiting a high frequency in the pollen (Dooner et al., 2019). These mutations can be classified based on their inheritance patterns. Recessive mutations are expressed when two copies of the mutated allele are present, typically denoted by lowercase letters. In contrast, dominant mutations are expressed when a single mutated allele is present and are represented by capital letters. Partially-dominant mutations lead to an intermediate phenotype from a single mutated allele, and these are written with a capital letter followed by lowercase letters. Most spontaneous mutations are point mutations, which involve a change in a single base pair in the DNA sequence. The effects of these mutations vary depending on their context within the genome. The concept of dominance and recessiveness in genetic traits was first quantitatively explored by Gregor John Mendel in 1866, laying the foundation for the study of inheritance patterns in diploid organisms (Falk, 2001). These early observations helped establish the principles that guide our understanding of genetic variation and inheritance today.

4.2 Induced mutations

Apart from natural mutations, novel alleles can be generated in plants using chemical and physical mutagenesis, with the goal of introducing genetic variation while reducing negative outcomes such as chimeras, sterility, and lethality (Datta, 2014). This approach is valuable for enhancing one or two specific traits that influence crop productivity or quality. A key advantage of mutagenesis-based breeding is that it is not subject to the regulatory limitations associated with genetically modified organisms (GMOs) (Mir et al., 2024). In some crops, chemically induced mutagenesis has successfully led to the desired phenotype, although it may require screening thousands of lines. The use of advanced techniques such as high-throughput phenotyping (HTP) and NGS has significantly sped up the process of identifying mutants with beneficial traits. Furthermore, engineered nucleases have improved the precision of mutation breeding by allowing for targeted, gene-specific mutations. Both naturally occurring and induced allelic diversity offer a valuable genetic resource for breeding programs, facilitating the development of new agricultural traits (Xu et al., 2017). Table 2 shows some of the plant varieties developed using induced mutation.

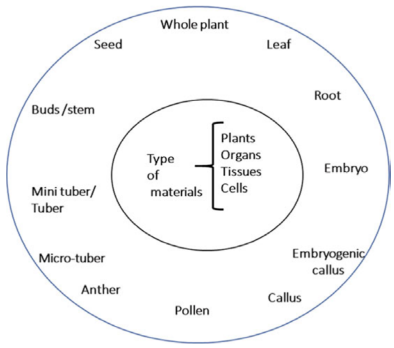

Figure 3. Plant materials used in mutation breeding include single cells and multi-cellular systems (Bado et al., 2023).

5. History of physical and chemical mutagens in plant breeding

Plant mutation breeding has a long history of technological development, optimization, and the successful release of mutant cultivars (Table 3). To date, more than 3,330 cultivars have been developed worldwide, with over 88% originating from physical and chemical mutagens (IAEA, 2020).

5.1 Physical mutagenesis

Physical mutagens have had the greatest impact on plant breeding (Table 4). They are classified into two groups: (1) Ionizing radiation and (2) Non-ionizing radiation. Ionizing radiation includes particulate radiation (alpha rays, beta rays, heavy-ion beams, and fast, slow, and thermal neutrons) and electromagnetic radiation (X-rays, gamma rays, cosmic rays, and electron beams). This classification is based on their ability to produce ions and their energy to alter the atomic structure of plant materials (Beyaz and Yildiz, 2017). In mutation breeding, ionizing radiation causes biological damage through two main interactions with DNA: physical and chemical. Physical damage happens when energy directly affects the DNA. Chemical damage occurs due to highly reactive free radicals (OH- and H+) that indirectly harm DNA (Reisz et al., 2014). Light of different wavelengths can also cause photochemical damage, like purine or pyrimidine dimers, leading to point mutations (Kurowska et al., 2012). In the presence of oxygen, radiation-induced free radicals form highly damaging peroxyradicals (Lagoda, 2012). Plant materials with high water content or specific biochemical compositions (e.g., oil) are more sensitive to radiation.

This sensitivity can lead to a range of mutations, from point mutations to deletions, strand breaks, and chromosomal rearrangements. Physical mutagens have been used on various plant materials, from whole plants (in gamma fields) to single cells (in gamma cells). Gamma rays have been used extensively, leading to the development of 1,604 mutants, while X-rays resulted in 561 mutants (Mir et al., 2020). The exposure of plants to X-rays provided the first clear evidence that phenotypic variability could be artificially induced. Gamma irradiation is known to produce significant genetic mutations, often causing large chromosomal deletions and chromosome rearrangements. It has been applied to induce mutations in various plant tissues, including seeds, cuttings, pollens, and calli (Rafi et al., 2023).

Since the 1960s, gamma irradiation has become the most commonly used mutagen in crop improvement due to its efficiency in generating mutations. This radiation-based mutagenesis technique has been particularly favored over other methods like acclimatization, selection, and hybridization, as it offers faster results with higher genetic variation, though the latter methods are more time-consuming and labor-intensive (Gao, 2003). Fast neutron-induced mutagenesis is a powerful technique that can cause significant genetic changes, including deletions ranging from a few bases to millions (Kumawat et al., 2019). While not widely used in the past, its ability to induce large-scale genetic changes has made fast neutrons an increasingly valuable tool in modern crop science (Amiteye, 2023a).

5.2 Chemical mutagenesis

Chemical mutagenesis is one of the most effective and rapid methods for inducing mutations in a wide range of plant species. Among the most commonly used chemical mutagens are ethyl methane sulfonate (EMS) and sodium azide, which have been applied to various crops such as tomatoes (Mistry et al., 2022). Other chemical mutagens used in mutation breeding include hydroxylamine, methyl methane sulfonate (MMS), hydrogen fluoride (HF), and N-methyl-N-nitrosourea (MNU) (Amiteye, 2023b). Of these, EMS is the most frequently utilized due to its high efficiency in inducing point mutations (single nucleotide changes) and chromosomal deletions (loss of chromosomal segments). Chemical mutagens have been employed to develop mutant populations in numerous cereal crops, including maize (Roychowdhury and Tah, 2013), barley (Talamè et al., 2008), rice (Serrat et al., 2014), sorghum (Kalpande et al., 2022), as well as both hexaploid bread wheat (Hussain et al., 2021) and durum wheat (Colasuonno et al., 2016). One of the notable applications of EMS is in the enhancement of potyvirus resistance in tomatoes (Akhtar and Shahid, 2025). This widespread use of chemical mutagens has proven to be a valuable tool for crop improvement, facilitating the development of novel traits and increased genetic diversity in plant populations. The choice of chemical mutagen depends on the objective and all have advantages and disadvantages (Table 5).

5.3 Space mutagenesis

Space-induced mutation breeding, or space mutagenesis, uses cosmic rays and space radiation to induce mutations in seeds. These experiments, conducted aboard satellites, space shuttles, and high-altitude balloons, offer advantages over traditional methods like gamma radiation (Mohanta et al., 2021). Space radiation has a lower impact on plant tissues than gamma rays on Earth, making it a more controlled and potentially safer option for inducing genetic changes. It allows for the development of mutations that might not occur as readily with other mutagenesis techniques, resulting in novel traits that could significantly enhance crop productivity, disease resistance, or environmental adaptability (Pathirana, 2021; Chakraborty et al., 2024). China achieved the first major success in space-induced mutation breeding, developing 41 crop varieties using this technique. These include widely grown crops like rice, wheat, cotton, sesame, pepper, tomato, and alfalfa, which have improved traits such as higher yields, better quality, and increased resilience to environmental stresses (Liu et al., 2008). Beyond crop improvement, space mutagenesis is also considered a potential solution to climate change challenges, such as unpredictable weather patterns and soil degradation. By inducing mutations that improve plant resilience and growth in adverse conditions, space-induced mutation breeding may become a critical tool in ensuring food security in the face of global environmental challenges (Mazhar et al., 2024).

Mutagens	Advantages	Disadvantages
Chemical	- Tested, proven, robust - Point mutation predominant - Relatively less chromosomal damage - High mutation rates and densities are useful for gene-phenotype association studies - Different mutation spectra - Identification of multiple mutant alleles	- Mutagenesis is random and widespread - Chemicals are very hazardous, non-environmentally friendly and regulated - Penetration difficulties in multi-cellular plant parts - Difficulties in reproducibility - Sensitivity of some target tissues and organs - Difficult to assess effective dose and reproducibility - The dose rate needs to be determined for each genotype - Stability of the mutagen

Table 6. Advantages and disadvantages of chemical mutagens.

5.4 Ion beam mutagenesis

Heavy-ion beam mutagenesis is an advanced and powerful tool in mutation breeding, offering a unique advantage by inducing high mutation rates with lower radiation doses (Bradshaw and Bradshaw, 2016). This technique creates a localized effect on DNA, allowing specific traits to be altered in irradiated cultivars without causing widespread damage. This precision has made the technique popular in countries like China and Japan, where it has successfully produced many mutant plant varieties (Liu et al., 2021; Nakagawa, 2023).

In Japan, high-energy ion beam irradiation has led to the development of ornamental plants such as carnations, chrysanthemums, and verbena, as well as color and shape variations in petunias, dahlias, and torenias (Okamura et al., 2006; Ibrahim et al., 2018). In China, low-energy ion beams have been used to improve both ornamental and agricultural crops, including salt-tolerant rice, mutant muskmelons, blast-resistant rice, and rice varieties that require less fertilizer (Zhang et al., 2022; Mingli and Zengliang, 2007; Ma et al., 2021). Additionally, coniferous trees and citrus fruits have also benefited from ion beam mutagenesis, highlighting the versatility of this technique in improving various plant species (Bado et al., 2018). Ion beam mutagenesis has proven valuable in improving environmental stress tolerance, disease resistance, and reducing input requirements, making it a key tool in modern crop improvement and agricultural sustainability (Roychowdhury and Tah, 2013; Khah et al., 2024). This approach is set to play a crucial role in tackling future challenges in crop breeding, including climate change and the demand for more sustainable agricultural practices.

5.5 High hydrostatic pressure

High hydrostatic pressure (HHP) is an extreme thermo-physical factor that influences various cellular processes, including the synthesis of DNA, RNA, and proteins, as well as cell survival (Ishii et al., 2004). This method has proven highly effective in inducing mutagenesis in microorganisms. In recent years, HHP has gained recognition as a cost-effective approach in mutation breeding for developing new mutant varieties. One notable example is its application in creating mutant rice varieties (Zhang et al., 2013).

5.6 Targeting induced local lesions in genomes

TILLING is a technique used for the precise identification of mutations within specific genes. It is a high-throughput, non-transgenic reverse genetics approach that integrates mutagenesis with a sensitive DNA screening method, enabling the detection of allelic variants in target genes (Sato et al., 2006). This method serves as an effective early-screening tool for identifying point mutations in genes of interest from small populations, allowing geneticists to study gene function and link genotypes to phenotypes. By combining traditional mutagenesis with advanced high-throughput mutation discovery, TILLING enhances the efficiency of utilizing induced mutations and detecting nucleotide polymorphisms. As a cost-effective and widely applicable reverse genetics strategy, it has significant potential to accelerate the development of crop varieties with improved traits in the coming years (Till et al., 2009).

5.7 Biotechnological mutagenesis

Recent advancements in biotechnology have significantly enhanced mutation breeding by improving the precision and efficiency of genetic modifications. Figure 4 provides us an overview of the advanced biotechnological approaches in mutation breeding. Recent advancements in biotechnology have significantly enhanced mutation breeding by improving the precision and efficiency of genetic modifications. Among these, genome editing technologies such as genome editing technologies like CRISPR-Cas9, (Transcription Activator-Like Effector Nucleases) TALENs, and Zinc Finger Nucleases (ZFNs), allow for targeted genetic modifications, enhancing the effectiveness of mutation breeding (Wani et al., 2023). CRISPR-Cas9 has become the most widely used genome editing tool due to its precision in targeting specific DNA sequences for modification. It has been successfully applied to improve traits like drought and salinity resistance, disease resistance, and nutritional enhancement in crops such as rice, wheat, and tomatoes (Sami et al., 2021). Unlike conventional mutagenesis, which can cause unintended genetic changes, CRISPR-Cas9 enables controlled alterations, making it a preferred method for speeding up crop improvement. Other genome editing techniques, such as TALENs and ZFNs, also enable targeted mutagenesis, but their complexity and higher costs have led to the dominance of CRISPR-based technologies, which are simpler and more cost-effective (Nagar et al., 2021; Khan et al., 2022).

RNA interference (RNAi) is another promising approach in biotechnological mutagenesis, focusing on gene silencing rather than altering DNA sequences. RNAi has been used to reduce allergenic proteins in peanuts and improve fungal resistance in wheat by suppressing susceptibility genes (Biswal et al., 2024). Unlike permanent genome edits, RNAi modifications are reversible, offering flexibility for crop improvement.

In addition to gene-editing methods, somaclonal variation and in vitro mutagenesis have also played key roles in mutation breeding. Somaclonal variation, which occurs during plant tissue culture, has helped develop disease-resistant sugarcane and high-yielding banana varieties (Altaf et al., 2024). In vitro mutagenesis, involving exposure to mutagenic agents in controlled conditions, allows for the rapid selection of mutant lines with desired traits (Penna et al., 2012). As technology advances, emerging genome-editing tools such as prime editing and base editing are expected to further refine mutation breeding by allowing for more precise and predictable modifications (Caso and Davies, 2022). Additionally, integrating omics technologies, including genomics, transcriptomics, and proteomics, will enhance our ability to understand mutation effects at the molecular level, optimizing breeding strategies for future crop improvement (Yang et al., 2021).

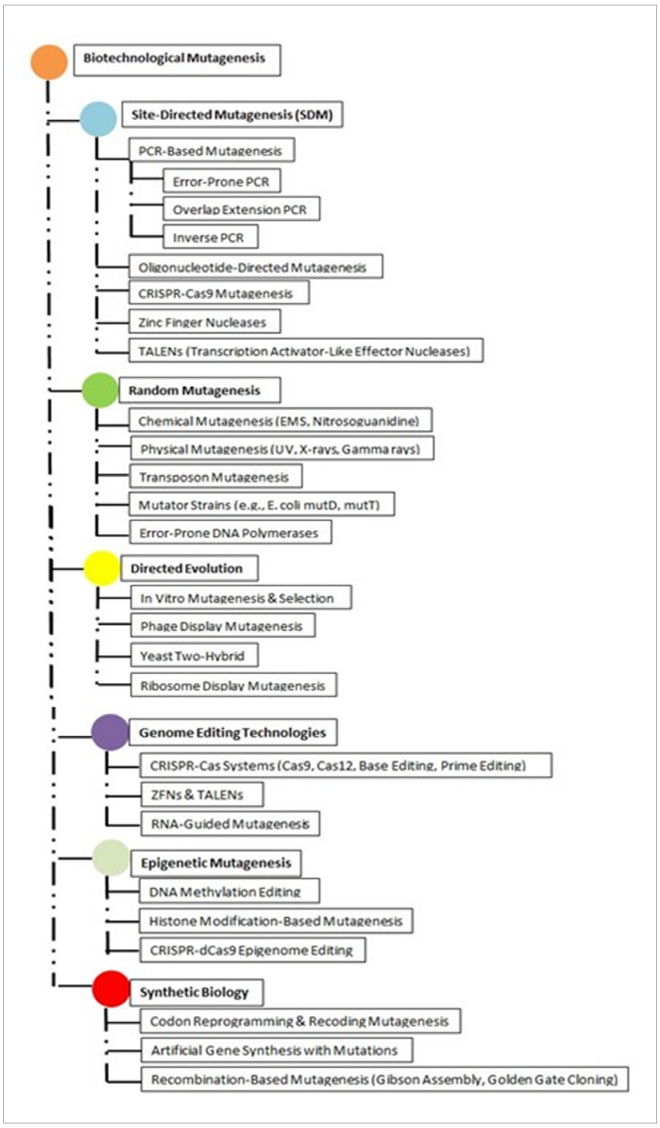

Figure 4. Advances in biotechnological mutagenesis: techniques

Mutagen	Advantages	Disadvantages	Comments
Gamma rays	- Low LET radiation - Optimal procedures published and available - Regional, national and international services available - Highly reproducibility - Deep penetration in multi-cellular systems - Choice of high or low DNA damage - Cause single nucleotide substitution, inversion and deletion	- Requires a radioactive source - Many restrictions for new source and refurbished sources - Problem of high dose rate of new (highly reactive) sources - Requires specialized physical structure/ laboratories and technicians	- Most successful, has resulted in 66.91% of officially released mutant cultivars
X-rays	- Non-radioactive - Low LET radiation - Easy accessibility - Penetrates tissues from a few millimetres to a few centimetres	- Requires optimal settings for uniform irradiation - Optimized procedures are generally not available	- Second most popular physical mutagen with 21.89% of officially released mutant cultivars
Neutron rays (fast, slow, thermal)	- High LET radiation - Penetrates tissues from a few millimetres to a few centimetres - Saturate genome for genetic studies - Cause point mutation, A/T to G/C transition, insertion, inversion, translocations tandem duplication and deletion - Gene knock-outs	- Requires nuclear reactor or accelerator - Relative high cost - Can create large deletions (>1Mb) - Can delete multiple genes at a time - Difficulty of absorbed dosage estimation due to surface contamination	- Third most popular physical mutagen with over 5.23% of officially released mutant cultivars
UV light	- Very low LET radiation - Available - Activation of transposable elements (indirect genemutation) - Effective in pollen and fungal mycelium - Relative low cost	- Low penetration - Limited to single cell layer or sensitive material	- Very limited effectiveness and use in plant mutation breeding
Ion beam	- High LET radiation - Large biological effects - High mutation rates - High survival rates of M1/M1V1 - Wide and new phenotypic variation	- Deposit high energy/damage - Not tested on a large number of species - Laborious sample preparation - Low accessibility of ion beam irradiators/ facilities - Anatomy of seed and meristematic tissue can be limiting	- High installation cost of the accelerator - Highly effectiveness in ornamental - Good for genetics studies
Cosmic rays	- High-energy ion radiation - High LET radiation - Tested on various plant species	- Requires space flight - Massive investment costs and intensive technological support - Very limited accessibility - Mechanism of space-induced mutation not fully understood - Limited to plant materials in dormant state (not actively growing)	- Access to space programme - Possibility to induce novel variation - Possibility to obtain rare mutants - Effective ground simulation of space environment factors may increase this approach

Table 4. Comparison of various physical mutagens in plant breeding and genetics- advantages and disadvantages.

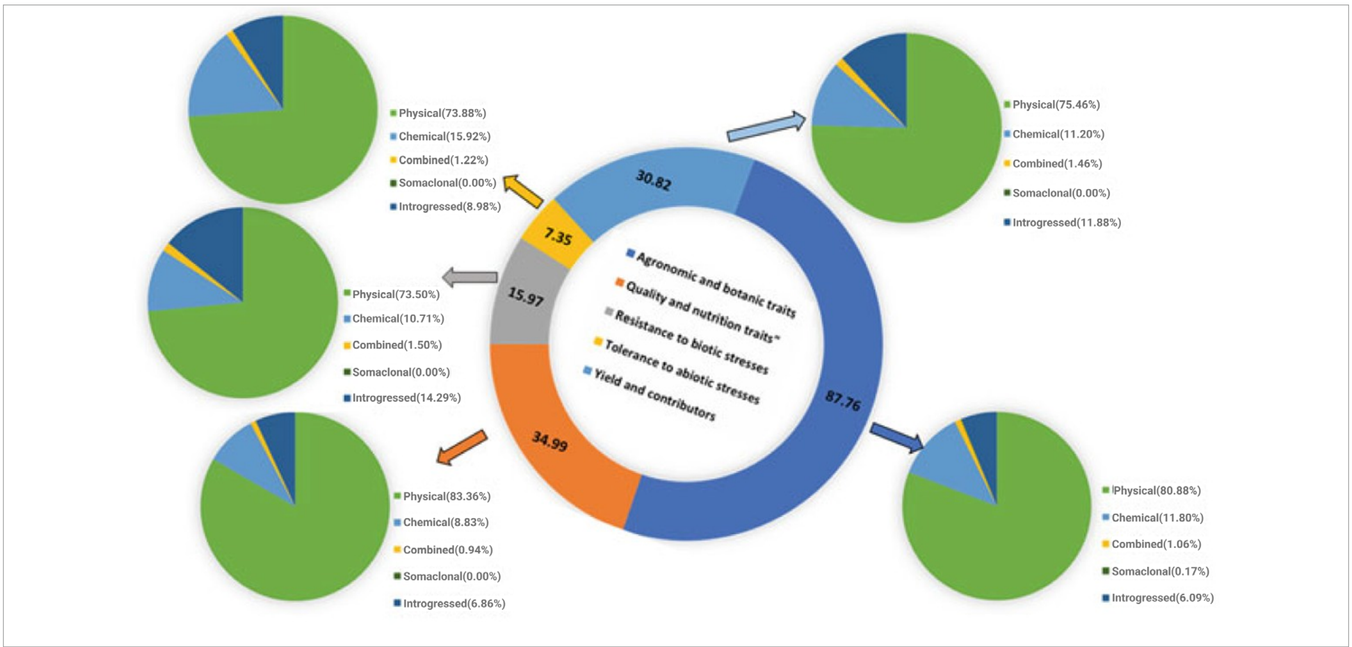

Figure 5. Benefits of mutagens in inducing crop traits(IAEA, 2020).

6. Benefits of mutation breeding

Mutation breeding has significantly contributed to crop improvement in various ways, enhancing productivity, resilience, and genetic diversity. Physical mutagens have proven to be the most effective in generating new traits, with chemical mutagens, combined treatments, and somaclonal variation following in effectiveness (Figure 5). By inducing specific genetic changes, this technique allows breeders to develop improved crop varieties with desirable traits that may not be easily obtained through conventional breeding methods. Over the years, mutation breeding has played a crucial role in addressing global food security challenges by increasing yield potential, enhancing crop quality, and improving resistance to environmental and biological stresses.

6.1. Enhanced yield and quality

Mutation breeding has successfully improved crop yield and quality traits, such as grain size, nutritional content, shelf life, and processing characteristics. For example, semi-dwarf rice varieties like IR8, developed through mutation and selective breeding, were key to the Green Revolution, boosting rice production globally (Gopala Krishnan et al., 2022). Mutant wheat varieties, such as Sharbati Sonora, offer improved grain quality, higher protein content, and better milling properties (Saini et al., 2020). In legumes, mutation breeding has produced high-yielding, protein-rich varieties, such as mung bean and soybean, with better resistance to environmental stress (Pataczek et al., 2018). Mutation breeding has also improved fruit crops like bananas and citrus, enhancing sweetness, reducing seed content, and increasing resistance to post-harvest diseases (Mathiazhagan et al., 2021). In tomatoes, mutant lines with improved firmness, higher lycopene content, and extended shelf life benefit both fresh-market and processing industries (Nie et al., 2024). Additionally, mutation breeding has produced high-yielding cassava varieties resistant to Cassava Mosaic Disease (CMD), ensuring stable production in Africa and Asia (Ntui et al., 2024). In sweet potatoes, gamma irradiation has led to mutant varieties with higher beta-carotene content, addressing vitamin A deficiency in many developing regions (Islam, 2024).

6.2. Improved stress tolerance

Climate resilience is a fundamental pillar of sustainable agriculture, encompassing both anticipation and preparedness to enhance adaptability in the face of climate change. Within an ecosystem, resilience can be strengthened by assessing vulnerabilities related to exposure and the responses of organisms. This process often involves strategic approaches to climate mitigation and adaptation (Figure 6). Mutation breeding has an important role in enhancing crop resilience to various abiotic stresses, including drought, salinity, extreme temperatures, and soil nutrient deficiencies (KhokharVoytas et al., 2023). One of the most critical applications of mutation breeding has been the development of drought-tolerant crops, which are essential for sustaining agricultural productivity in arid and semi-arid regions. For example, mutant wheat varieties like Pallas and drought-resistant barley strains, created through gamma radiation, show improved root systems and better water-use efficiency (Banerjee et al., 2008). Rice mutants such as IRRI 154, produced with chemical mutagens, exhibit enhanced root growth and delayed leaf rolling, making them more resilient to dry spells (ABD Elmajid, 2018).

Mutation breeding has also enhanced salinity tolerance, with salt-tolerant rice varieties like Pokkali and FL530 Mutant showing improved sodium exclusion and root architecture under saline conditions (Baadu et al., 2023). Additionally, sorghum and tomato mutant lines have improved salt tolerance by regulating ion uptake and increasing proline accumulation, helping them maintain health and productivity (de Oliveira et al., 2020; Pan et al., 2010). In addition to water-related stresses, mutation breeding has been instrumental in developing crop varieties that can withstand extreme temperatures. Heat-tolerant maize varieties, such as HQPM-7, maintain pollen viability and kernel filling even under high-temperature conditions, ensuring stable grain production (Dwivedi et al., 2016). Cotton varieties bred through chemical mutagenesis exhibit improved fiber quality and boll retention despite high-temperature exposure (Majeed et al., 2021).

Mutation breeding has also improved nutrient deficiency tolerance in crops grown in poor soils. For example, rice varieties with mutations in the OsPSTOL1 gene show enhanced phosphorus uptake, making them suitable for phosphorus-deficient soils (Navea et al., 2024). Similarly, pearl millet mutants with improved nitrogen-use efficiency help farmers achieve higher yields with less fertilizer application (Daduwal et al., 2024).

6.3. Disease and pest resistance

Mutation breeding has been important in developing crop varieties with enhanced resistance to various fungal, bacterial, and viral pathogens, as well as insect pests (Figure 6). These genetic improvements play a crucial role in reducing yield losses, minimizing the need for chemical pesticides, and promoting sustainable agricultural practices. One of the most notable successes of mutation breeding is the development

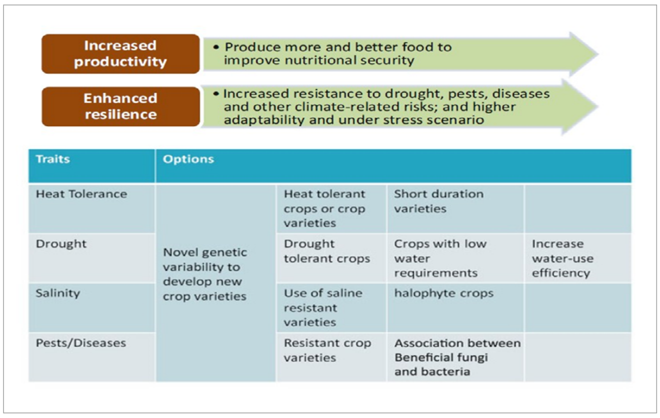

Figure 6. Climate-resilient mutation crop breeding (Kumar et al., 2023).

of rust-resistant wheat varieties, which have helped mitigate the devastating effects of fungal pathogens such as Puccinia spp.. Mutant wheat lines with resistance to stem rust (Puccinia graminis f. sp. tritici), stripe rust (Puccinia striiformis), and leaf rust (Puccinia triticina) have been developed through gamma irradiation and chemical mutagenesis. For instance, the wheat variety Sharbati Sonora, developed through induced mutations, shows strong resistance to leaf rust, ensuring stable yields in rust-prone areas (Babu et al., 2020). Similarly, wheat cultivars like HD 2967 exhibit broad-spectrum resistance to rust diseases, reducing disease-related losses (Joshi et al., 2017). In legumes, mutation breeding has produced groundnut varieties resistant to leaf spots and other fungal infections. Mutant groundnut cultivars such as TG-26 and ICGV 87165 exhibit strong resistance to early and late leaf spots caused by Cercospora spp., reducing yield losses and improving seed quality (Bhat et al., 2022). In chickpeas, induced mutations have led to resistance against Ascochyta blight (Ascochyta rabiei), a major fungal disease affecting production in temperate regions (Pande et al., 2005).

Mutation breeding has also enhanced resistance to bacterial diseases in crops like rice and tomato. For example, rice mutants developed through gamma-ray mutagenesis, such as IRBB21, show improved resistance to bacterial leaf blight (Xanthomonas oryzae pv. oryzae), reducing the disease's impact (Tu et al., 2000). In tomatoes, mutation breeding has produced resistant lines against bacterial wilt (Ralstonia solanacearum), a common disease in tropical and subtropical regions (Singh et al., 2015).

Additionally, it has led to the development of viral-resistant crop varieties, decreasing the need for chemical control measures. In cassava, induced mutations have resulted in resistance to cassava mosaic virus (CMV), a major threat to food security in Africa. Similarly, mung bean mutants with resistance to mung bean yellow mosaic virus (MYMV) have been developed, improving yield stability in virus-prone areas (B. Sai et al., 2017). In papaya, mutagenesis has produced strains resistant to papaya ringspot virus (PRSV), ensuring continued production in affected regions (Fitch, 2010).

6.4. Shortened breeding cycle

Mutation breeding speeds up crop improvement compared to traditional breeding, which relies on natural genetic variation and takes multiple generations to introduce desired traits. By directly inducing specific mutations, mutation breeding allows for faster development of new cultivars with enhanced traits (Ahmar et al., 2020), shortening the breeding cycle and generating beneficial mutations that could take decades to occur naturally. For instance, semi-dwarf rice varieties such as IR8, developed through induced mutagenesis, contributed to the Green Revolution by significantly increasing yields while reducing the time needed for variety development (Gaur et al., 2020). Similarly, mutant barley cultivars like Diamant were developed much faster than conventionally bred counterparts, demonstrating early maturity and improved grain yield (Suprasanna et al., 2015).

Mutation breeding not only accelerates the development of high-yielding varieties but also improves specific agronomic traits without altering the overall genetics of elite cultivars. It is especially beneficial for crops with long reproductive cycles, such as bananas, sugarcane, and cassava, which traditionally have slow breeding processes. For example, early-maturing sugarcane mutants with higher sucrose content and cassava mutants with reduced growth duration and improved yield stability have been developed, improving food security and reducing time to commercial production (Swapna et al., 2012; Rahmawati et al., 2024). In vitro mutagenesis combined with tissue culture techniques has significantly accelerated the breeding process. This approach has been used in crops like potato and banana, where disease-resistant mutant lines, such as those resistant to Fusarium wilt and bacterial wilt, were developed within a few years instead of decades (Sharma et al., 2024; El Hadrami et al., 2005). These advancements demonstrate how mutation breeding offers a time-efficient and cost-effective alternative to traditional methods.

6.5. Application in orphan crops

Mutation breeding has significantly improved orphan crops, which are crucial for food security, nutrition, and resilience in developing countries. These crops, often grown in marginal environments, are typically overlooked in mainstream breeding programs, making mutation breeding an essential tool for enhancing their performance and stress tolerance (Santhoshini et al., 2025). A key example is cassava (Manihot esculenta), where mutation breeding has led to the development of high-yielding, early-maturing, and disease-resistant varieties, including those resistant to Cassava Mosaic Disease (CMD) and cassava brown streak disease (CBSD) in Ghana (Elegba, 2018). Similarly, induced mutations have improved sorghum varieties, making them more resilient and productive. For example, gamma-ray-induced mutants of sorghum have shown resistance to Striga hermonthica, a parasitic weed that severely affects yields in sub-Saharan Africa (Mohinuddin et al., 2023). Additionally, mutant lines with enhanced starch and protein content have improved the nutritional value of sorghum (Elkonin et al., 2023).

Mutation breeding has also significantly improved other orphan crops such as millet, pigeon pea, cowpea, and sesame. Mutant pearl millet lines show better drought and heat tolerance, larger grain size, and higher protein content, making them suitable for extreme climates (Tara Satyavathi et al., 2021). Pigeon pea mutants with shorter maturity periods and resistance to fusarium wilt have reduced production constraints in smallholder farming systems (Ravikumara, 2015). Cowpea mutants demonstrate improved resistance to aphids and drought, enhancing adaptability to climate change (Sindhu et al., 2019). In addition, mutation breeding has been successfully applied to orphan oilseed crops such as sesame (Sesamum indicum), which is cultivated in low-input farming systems. Mutant sesame lines with higher oil content, increased yield, and resistance to bacterial blight have provided significant benefits for small-scale farmers in Asia and Africa (Weldemichael et al., 2023).

7. Mutation breeding in Fiji

Fiji started its first experiments using mutation breeding in the year 2020 to identify anthracnose tolerant varieties in chillies. Anthracnose disease, caused by the fungus Colletotrichum spp., significantly impacts chilli production in Fiji, resulting in the destruction of approximately 50% of crops on registered export farms. The red fire chilli variety is the primary export variety and which is most vulnerable to this disease. The Ministry of Agriculture has documented that this disease was initially reported in Fiji in the year 2010. Over the years, Fiji has been evaluating fungicides and varieties against anthracnose in chilli and other Solanaceae crops with little success. The red fire chilli variety seeds have been imported from Fiji, subjected to radiation treatment (0 Gy, 60 Gy, 80 Gy, 120 Gy), and subsequently returned to Fiji for screening purposes. The experiments are currently underway in its M3 stage and will continue to identify tolerant lines. Efforts are currently underway to induce mutation breeding in other crops such as rice, ginger, banana and kava to improve productivity and disease tolerance.

8. Challenges and future prospects

Despite its many advantages, mutation breeding faces several challenges that must be overcome to fully harness its potential for crop improvement. A major drawback is the random nature of mutations, especially when using physical and chemical mutagens. Unlike genome editing, which allows for precise modifications, traditional mutation breeding induces changes at unpredictable genomic locations, leading to a high occurrence of undesirable mutations that may negatively impact plant growth, yield, or quality. This necessitates extensive screening and selection, making the process labor-intensive and time-consuming. Another significant challenge is the potential negative effects of mutagenesis. Some mutations may cause reduced fertility, developmental abnormalities, or compromised stress tolerance, limiting their use in large-scale agriculture.

The application of chemical mutagens such as EMS and NaN_3 raises concerns about genotoxicity and environmental safety, requiring strict handling protocols. Similarly, radiation-induced mutagenesis, including gamma irradiation, can result in extensive chromosomal rearrangements, leading to genetic instability. Furthermore, the efficiency of mutation breeding depends on advanced phenotyping and genotyping techniques for rapid screening and characterization of mutants. Traditional selection methods based on phenotypic traits can be slow and influenced by environmental variability. While molecular markers have improved the identification of desirable mutations at the DNA level, integrating these tools into conventional mutation breeding remains challenging, particularly in resource-limited settings where access to modern sequencing and lab infrastructure is limited.

Mutation breeding holds great promise for crop improvement, particularly with the integration of genomics, molecular biology, and advanced breeding technologies. One of the most significant advancements is the use of molecular markers, such as SNPs and simple sequence repeats (SSRs), which facilitate marker-assisted selection (MAS) in mutant populations. By directly linking specific mutations to desirable traits, MAS significantly reduces breeding time and enhances selection efficiency. The application of omics technologies including genomics, transcriptomics, proteomics, and metabolomics is expected to revolutionize mutation breeding. These approaches provide deep insights into gene expression, protein interactions, and metabolic pathways influenced by induced mutations.

A major breakthrough in mutation breeding is the integration of genome editing tools such as CRISPR-Cas9, TALENs, and base editing, which allow for precise, targeted mutagenesis. Unlike conventional mutagenesis, which introduces random genetic changes, CRISPR-based techniques mimic beneficial natural variations, significantly accelerating the development of improved crop varieties. This approach, often termed "speed breeding", has the potential to rapidly enhance climate resilience, pest resistance, and nutritional quality without requiring lengthy screening processes. Additionally, HTP technologies, including drones, spectral imaging, and AI-driven data analysis, are transforming mutant selection by enabling real-time, large-scale field assessments of plant traits. These innovations enhance breeding efficiency by quickly identifying high-performing mutant lines based on growth, stress response, and productivity.

As global food security concerns continue to grow, mutation breeding will remain a key tool in developing resilient, high-yielding, and nutritionally enriched crops. The combination of NGS, bioinformatics, and predictive breeding models will further enhance our ability to design climate-adaptive crops capable of withstanding extreme environmental conditions. Future research should also prioritize optimizing mutagenesis protocols, refining screening techniques, and leveraging biotechnology to maximize the benefits of mutation breeding in sustainable agriculture.

9. Conclusion

Mutation breeding remains a crucial approach in crop improvement, enabling the development of high-yielding, stress-resistant, and nutritionally superior plant varieties. While challenges such as random mutations, labor-intensive selection, and potential adverse effects persist, advancements in genomic technologies, molecular markers, and genome editing are addressing these limitations. The incorporation of CRISPR-Cas9, MAS, omics approaches, and HTP has significantly enhanced the accuracy, efficiency, and overall impact of mutation breeding. Moving forward, the future of mutation breeding depends on its integration with modern biotechnological innovations, AI, and digital agriculture. These advancements will accelerate the breeding process, facilitating the development of climate-resilient and resource-efficient crops to meet global food security challenges. By harnessing cutting-edge technologies, mutation breeding will continue to drive agricultural advancements, ensuring sustainable food production and supporting global food systems in an era of environmental change.

Appendix

Variety name	Latin name	Common name	Country	Registration
IIyou 623 and IIyou 673	Oryza sativa L.	Rice	China	2007 and 2008, respectively
ABHIMANYU	Bougainvillea sp.	Paper flower	India	2010
AL-BEELY	Musa sp.	Banana	Sudan	2007
ALDAMLA	Prunus avium L	Cherry	Turkey	2014
Albisoara	Glycine max L.	Soybean	Republic of Moldova	2010
Ana Delia	Hibiscus sp.	Hibiscus	Cuba	2013
ARTIpurple and ARTIqueen	Dendrarithema grandiflorum (Ramat.) Kitamura	Chrysanthemum	Republic of Korea	2011
Beinong 103	Glycine max L.	Soybean	China	2009
Binadhan-19	Oryza sativa L.	Rice	Bangladesh	2017
Binachinabadam-7	Arachis hypogaea L.	Groundnut	Bangladesh	2014
Binamasur-11	Lens culinaris Medik.	Lentil	Bangladesh	2017
Binagom-1	Triticum aestivum L.	Wheat	Bangladesh	2016
Binasarisha-9	Brassica napus L.	Rapeseed	Bangladesh	2013
Binamoog-9	Vigna radiate (L.) Wil.	Mung bean	Bangladesh	2017
Binapiaz-1 and 2	Allium cepa L.	Onion	Bangladesh	2018
Binatomato-13	Lycopersicon esculenta M.	Tomato	Bangladesh	2018
Binatil-4	Sesamum indicum L.	Sesame	Bangladesh	2016
Binasola-10	Cicer arietinum L.	Chickpea	Bangladesh	2016
BURAK	Prunus avium L.	Sweet cherry	Turkey	2014

Table 2. Some of the major plant varieties developed through induced mutations (FAO-IAEA, 2020).

Date	Milestone		References
	Physical mutagenesis	Chemical mutagenesis	
1838–1839	Description of the cell theory and suggestion of totipotency of cells		Scheiden (1838)
1868	Introduction of the ‘histogen theory’ to explain shoot apex behavior in plants		Darwin (1868), Van Harten (1998)
1895–1900	The discovery of various kinds of radiation		Forster and Shu (2012)
1901–1905	Suggestions and promotion of radiation in plant and animal mutation breeding		de Vries (1901, 1903, 1905)
1907	Proposition of the word ‘chimera’		Cramer (1907)
1907	Dendrarithema grandiflorum (Ramat.) Kitamura		Republic of Korea
1927	Attempts of induced mutations in seed propagated crops using gamma and X-rays		Gager and Blakeslee (1927), Muller (1927), Von Sengbush (1927)

Date	Milestone		References
	Physical mutagenesis	Chemical mutagenesis	
1928	Successful mutation induction and discovery of mutagenic effects of X-rays in barley and maize		Stadler (1928a, b)
1930s	Continued of deliberated mutation in plants The first official mutation breeding programmes: in Sweden, Germany, United States		Stadler (1929), Goodspeed (1929), Kharkwal (2012)
1931	Deliberate mutation induction on potato		Asseyeva (1931)
1932		Attempts to induce mutations using chemicals	Sakharov (1932), Klein (1932)
1934	Release of physically (X-rays) improved cultivar tabak 'Chlorina' cv. (Indonesia)		Rana (1965)
1941–1943		Description of the ability of chemicals to induce mutations, i.e. mustard gas	Auerbach and Robson (1942), Oehlkers (1943)
1942	Report of induced disease resistance in a crop plant; X-ray-induced powdery mildew resistance in barley		Freislebe and Lein (1942)
1944		First report on the deliberate use of chemical mutagens	Auerbach and Robson (1944)
1944–1946		Continuation of the demonstration of the mutagenic effects of chemicals	Auerbach and Robson (1946), Oehlkers (1946), Rapoport (1946)
1949	Start of the gamma irradiation in plant mutation breeding Released of mutant in vegetatively propagated crop by X-rays: Tulipcv. 'Faraday' in Netherlands		Sparrow and Singleton (1953) https://mvd.iaea.org/
1954	Officially improved food crop plant by X-rays, pea mutant 'Stral-art' cv.		https://mvd.iaea.org/
1961	Officially released introgressed mutant cultivar Antirrhinumcv. 'Juliva'		https://mvd.iaea.org/
1963	Release of mutant from gamma ray: mutant variety 'Mori-hou-fu3A' cv. of apple		https://mvd.iaea.org/
1964	Release of mutant cultivar in sweet cherry cv. 'Compact Lambert' in Canada		Sigurbjornsson and Micke (1974)
1964	Setup of the FAO/IAEA Joint Division with a mandate to support the production of induced mutations for food security issues in developing countries		Forster and Shu (2012)
1966	UN Geneva Conference on 'Peaceful Application of Atomic Energy'		Donini and Sonnino (1998)
1966		Official release of the chemically (diethylsulphate, dES) improved cultivar of barley, cv. Luther in the United States	Nilan and Muir (1967)

Date	Milestone		References
	Physical mutagenesis	Chemical mutagenesis	
1968	Release of the mutant cultivar (X-ray) potato cv. ‘Mariline 2’ in Belgium		Van Harten (1989)
1969–1970	The first FAO/IAEA international training course on crop mutation breeding Pullman Symposium on plant mutation breeding - Publication of first classified list of mutant cultivars - Publication of the first Manual on Mutation Breeding		IAEA (1970), Kharkwal (2012)
1972	Start of ‘Mutation Breeding Newsletter’ published by FAO/IAEA		Forster and Shu (2012)
1975	Initiation of coordination research programme organized by FAO and IAEA on ‘Improvement of vegetatively propagated plants through induced mutations’		FAO/IAEA (1975)
1977	Publication of the second edition of Manual on Mutation Breeding		IAEA (1977)
1978	Start of space mutation breeding in China		Xianfang et al., (2004)
1980–1981	- Introduction of tissue culture (biotechnology) for invitro mutation induction - First mutation breeding report on VPCs - FAO/IAEA first symposium on ‘Use of induced mutations as a tool in plant research’ in Vienna, Austria		Broertjes (1982), Kharkwal (2012)
1989–1990	Use of RIKEN RI-Beam Factory (ion beam) for radiation biology research and plant breeding		Abe et al., (2012)
1993	FAO/IAEA Mutant Variety Database (https://mvd.iaea.org/)		Forster and Shu (2012)
1998	Release of the rice mutant cv. ‘Hangyu’ 1 from cosmic irradiation		https://mvd.iaea.org/
2000–2005	TILLING (Targeting Induced Local Lesion in Genome) to induce and study mutation-phenotype association		McCallum et al., (2000), Colbert et al., (2001)
2002	Release of ion beam commercial mutant cv. ‘Temari Bright Pink’		Abe et al., (2012)
2005–2010	Biotechnologies for targeted mutation discovery and wide spectrum establishment: - Direct genomics election (DGS) method - Exome capture sequencing for mutation screening and functional genomic analysis - High-throughput sequencing and mutation discovery methods based on massive parallel sequencing - Using next-generation sequencing (NGS) for rapid detection of rare mutation in targeted gene		Basiardes et al., (2005), Okou et al., (2007), Mamanova et al., (2010), Gilchrist and Haughn (2010), Tsai et al., (2011)
2008	International Symposium on Induced Mutation in Plants in Vienna, Austria. Induced Plant Mutation in the Genomics Era.		Shu (2009)
2018	- IAEA/FAO International Symposium on Plant Mutation Breeding and Biotechnology - Publication of the third edition of the Manual on Mutation Breeding - New breeding techniques (e.g. genome editing) are not exempted from the current EUGMO legislation - Physical or chemical treatments are explicitly exempted from the EUGMO legislation		FAO/IAEA (2018), Court-of-Justice-of-the-European-Union (2018), Holme et al., (2019)
2020	Emmanuelle Charpentier and Jennifer A. Doudna won the 2020 Nobel Prize in Chemistry for the development of a method for genome editing (CRISPR/Cas)		Wu et al., (2020)

Table 3. Historical milestones in physical and chemical mutagenesis in plant breeding.

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