



REVIEW ARTICLE

Space breeding: Principles, mechanisms, achievements and prospects for crop improvement

C S Shinde*, G R Andhale & V P Chimote

Department of Genetics and Plant Breeding, Mahatma Phule Krishi Vidyapeeth (MPKV), Rahuri, Ahilyanagar 413 722, Maharashtra, India

*Correspondence email - chetanshinde1135@gmail.com

Received: 22 October 2025; Accepted: 13 April 2026; Available online: Version 1.0: 20 June 2026

Cite this article: Shinde CS, Andhale GR, Chimote VP . Space breeding: Principles, mechanisms, achievements and prospects for crop improvement. Plant Science Today. 2026; 13(sp2): 1-13. <https://doi.org/10.14719/pst.12365>

Abstract

Space breeding is an emerging approach that integrates space science with plant breeding to generate novel genetic variation for crop improvement. It is a relatively novel agricultural frontier and technique, harnesses the unique conditions of the extra-terrestrial environment to accelerate crop improvement. This multidisciplinary approach exposes seeds to space conditions like microgravity, cosmic radiation and magnetic fields to induce higher mutation rates than terrestrial methods, creating useful genetic variation in plants. The implications of space breeding extend from improving agricultural productivity on Earth to ensuring the sustainability of long-term space missions and colonisation efforts on other celestial bodies. Space conditions such as microgravity, vacuum and high-energy radiation alter plant genetic structure. To fully realise the benefits of space breeding, a multidisciplinary approach is required, encompassing genetics, molecular biology, space technology and data science. Comprehensive studies on the effects of space radiation on plant genomes and transcriptome are essential to unravel the genetic basis of induced mutations. By combining this knowledge with advanced statistical modelling and simulation, researchers can accelerate the development of superior crop varieties and contribute to a sustainable future. Space breeding represents a promising approach for future crop improvement both on Earth and in space environments.

Keywords: cosmic radiation; crop improvement; genetic variation; microgravity; mutation breeding; space breeding

Introduction

Mutations are fundamental biological events that generate genetic variation in living organisms. Mutants arise due to mutation, which is a heritable change in genetic material and serves as a primary source of genetic diversity (1). Therefore, a mutation is defined as an abrupt, heritable change that occurs in an organism (2). In light of this, consider a scenario in which you travel into space and bring some crop seeds or germplasm with you. Seeds exposed to space conditions often exhibit genetic and phenotypic variations that can be exploited for crop improvement (1). This approach is known as space breeding.

Researchers have been examining the effects of cosmic radiation, microgravity and other elements of the space environment on plant growth and development since the commencement of space exploration. Numerous kinds of study have been carried out so far to produce better agricultural varieties and have some success in the space environment. China's space rice breeding operations are leading the world in scientific research (3). Due to the cosmic radiation and microgravity that space-grown plants have experienced, a variety of crop varieties with distinct genotypes and phenotypes resulting from cellular, subcellular, genomic, chromosomal and biochemical modifications have been produced. Genetic polymorphism and the development of crops with altered genetic combinations are mostly caused by DNA damage and chromosomal abnormalities brought on by cosmic

radiation. These modifications can be utilised to create crop types of the next generation that can endure a range of environmental circumstances (4).

In-depth space exploration has advanced significantly in recent years and space research is currently receiving a lot of attention (5–7). Space environments are characterised by microgravity, vacuum and high radiation levels (8). It consequently absorbs a significant amount of cosmic radiation, the effects of which are still poorly understood (9, 10). Furthermore, space is an extremely vacuum environment. Numerous laboratory and other studies have been carried out in an effort by certain scientists to establish life on Mars (11–13). Plant growth on Mars is challenging, nevertheless due to a few reasons, including the lack of a magnetic field (14, 15). The International Space Station (ISS), launched in 1998, serves as a platform for plant space biology research (16). In a microgravity setting, it has served as a research facility for astrobiology studies (17–21).

This review summarises the principles, mechanisms, achievements and future prospects of space breeding. It highlights the biological basis, applications and research progress in space breeding.

History of space breeding

Early observations of natural variation in plants were documented in ancient agricultural literature, although the scientific concept of mutation was established much later. Hugo de Vries, a Dutch

botanist, is credited with originating the concept of mutation when he saw changes in *Oenothera lamarckiana* Ser. (evening primrose) plants that were blossoming in Holland during the 1880s. As a result, he was named 'The Father of Mutation'. The term "mutation" was first used in 1900 by Hugo de Vries. The Latin word "mutare," which is its root, signifies "change" or "alteration."

The H J Muller received the Nobel Prize in 1946 for his demonstration in 1927 that is external application of X-ray mutagens can successfully generate a mutation in *Drosophila*. Eventually, in 1928, L J Stadler demonstrated that the physical mutagen X-ray was the cause of gene mutation in barley and maize. In India, mutation breeding research was led by scientists such as M S Swaminathan at Indian Agricultural Research Institute (IARI) and researchers at Bhabha Atomic Research Centre (BARC), Mumbai. Globally, more than 3300 mutant varieties from over 240 crop species have been released through mutation breeding programs coordinated by Food and Agriculture Organization (FAO) and International Atomic Energy Agency (IAEA) of United States.

Chinese scientists initially introduced space breeding, an innovative and successful method for agricultural mutational development, in 1987. Early studies reported increased mutation frequency in seeds exposed to spaceflight conditions compared to earth (1). In the early 1960s, researchers from the former Soviet Union (Russia) (Union of Soviet Socialist Republics (USSR)) conducted the first space breeding experiments on the plant wheat, peas and *Arabidopsis thaliana* (L.) Heynh. (22). China was the first country to send sweet pepper cultivar "Dragon Pepper 2" into space using high-altitude balloons (Fig. 1) in 1987. China started breeding space mutants after discovering a novel kind whose fruit weighed more than 250 kg and having risen in yield level up to 120 %. So the China is the first ever country to be successful in space breeding and designated as pioneer in space breeding work. On September 9, 2006, China launched Shijian-8, their first space breeding satellite (23). It included about 2020 plant accessions from 152 different plant species. With the ability to retrieve (recoverable) satellites, China is currently the third country in the world.

National Aeronautics and Space Administration (NASA) conducted plant experiments in 2014, 2015 and 2017 using systems such as the Vegetable Production System (VEGGIE) and Advanced Plant Habitat (APH) aboard spacecraft and the ISS

(International Space Station). Seeds of crops like lettuce, mustard, kale, radish, wheat and peppers were planted in growth media containing porous clay or arcillite with controlled-release fertilisers. Light emitting diode (LED) lighting, temperature, humidity and carbon dioxide were regulated automatically. Growth parameters, microbial populations, nutrient content and plant morphology were analysed (24). The China had launched 22 recoverable satellites thus far, with just one failure. By the end of 2017, China had conducted 13 experiments with recoverable satellites, several with high-altitude balloons and the Shenzhou spacecraft (Fig. 2), resulting in the launch of over 70 different crop kinds into orbit. In Shanxi Province, northwest China, a new space breeding research centre was opened in 2018. One of its goals is to grow superior tree seedlings for the Three-North Shelter Forest Program by using space technology.

Combined experiments by USA along with other countries in 2020 was launched on International Space Station (ISS). Experiments such as Plant Habitat-02 used growth chambers with controlled light, water and nutrients. Crops such as radish, lettuce, wheat and Chinese cabbage were cultivated. Ground control experiments were conducted simultaneously on earth under identical conditions for comparison. Growth parameters, gene expression, nutritional quality and plant physiology were evaluated (25).

Although the spacecraft's noise level is always high, space flight is not particularly silent. Furthermore, live cells may be discouraged or damaged by the increased sound frequency. China developed space-bred rice varieties (6). China's Chang'e-5 journey (mission) to lunar orbit lasted 183 days and 40 g of rice was dispatched with it (26). For the first time, a mature plant that produces new seeds at the end of its 120-day life cycle which starts with a seed hatching into seedlings from grains was finished in space. Rice seeds exposed to spaceflight showed genetic variation. The rice grains were first produced in a lab and subsequently in the field once the lunar mission was over and they returned to Earth and at Guangzhou's South China Agricultural University seeds were gathered. These experiments demonstrated the potential of space breeding for crop improvement (27–29).

In November 2022, the International Atomic Energy Agency (IAEA) and the Food and Agriculture Organization (FAO) of the United States sent seeds of two plant species-*Arabidopsis* and



A



B

Fig. 1. High altitude balloons (A = 28, B = 29).

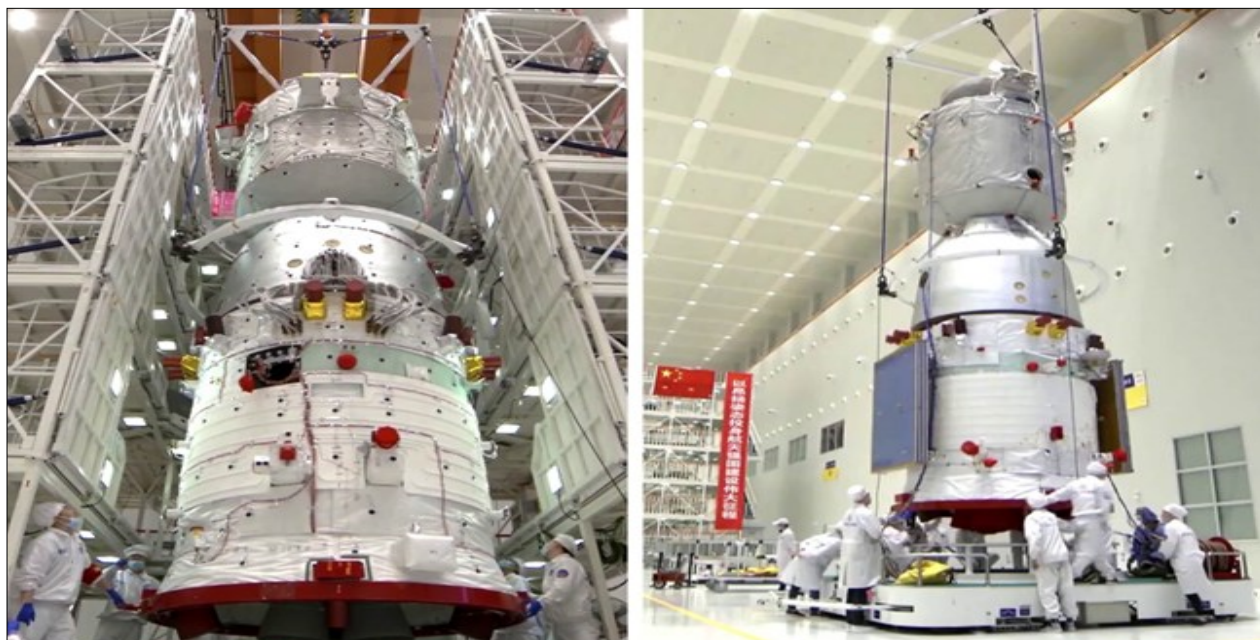


Fig. 2. Shenzhou spacecraft. Source : Image: Courtesy of China News Service, Courtesy of Wikimedia Commons (30).

Sorghum to the ISS, where they are subjected to cosmic radiation, extreme temperatures and microgravity. These seeds will be planted, nurtured and examined for favourable characteristics after they return. The purpose of these investigations is to better understand if crops grown under hard space settings, such as microgravity and extremely high temperatures, would become more adaptable to the harsh growth circumstances on Earth (3).

Recently India in 2024 through ISRO germinated cowpea seeds successfully in space within about 4 days. The experiment was conducted on the POEM-4 (PSLV orbital experiment module) platform in microgravity. The module acted like a mini greenhouse in space with controlled temperature and environment (31).

Space breeding

Cosmic radiation originating from outer space continuously reaches the Earth. Research indicates that plants exposed to zero gravity and cosmic radiation experience physical, physiological and genetic alterations (32, 33). Cosmic radiation can potentially be used for gene modification. Space crop projects have garnered global attention for many years and have successfully contributed a wealth of biological information (34, 35). This new scientific technique, called space breeding, merges space travel technology with farming. Space breeding involves exposing plant materials to cosmic radiation, microgravity and vacuum conditions to induce mutations. Space breeding refers to exposing seeds or strains to cosmic radiation and microgravity in space to mutate their genes, so as to create new species or varieties with greater performance. Space breeding also known as aviation breeding or space technology breeding or space mutagenesis. It is a relatively new development in breeding technology that combines biotechnology, modern agricultural technology and space technology with farming.

Plants exposed to space experience unique conditions unlike anything found on Earth. These conditions induce mutations and genetic variation. These variations are valuable resources for plant breeding. The main factors causing these mutations in space include high-energy radiation i.e. cosmic rays, weightlessness, unusual magnetic fields, near-perfect vacuum and other stresses. Cosmic rays are the primary mutagenic agents in space breeding.

The crops developed by space breeding also refer as cosmic crops or cosmic species. Such crops may also refer as next generation crops. These changes can affect how many seeds sprout (germination rate), their shape (morphology), the light-capturing pigments they contain (photosynthetic pigments), the structure of their energy-producing organelles (chloroplasts) and the activity of enzymes that help fight off damage (antioxidant enzyme activity). All of this translates to altered physiological (functional) and morphological (structural) characteristics in mature crops.

The crops have been developed by the technique of space breeding assumed to be safe comparatively than transgenic crops. No foreign genes are introduced during space breeding. These changes happen faster in space but are ultimately the same kind of thing that happens over time on Earth. Continuous and multi-step testing confirmed that the material did not contain any traces of space radiation; therefore, it does not pose any risk to Earth's biota and was subsequently released for cultivation (1).

The main objectives of space breeding are as follows

- **Boost crop resilience :** Increase resilience to harsh conditions such as biotic and abiotic stressors.
- **Boost yield :** Create high-yield crops to aid in space exploration.
- **Genetic variability :** Investigate novel genetic mutations and variants to promote genetic diversity.

Procedure to induce space breeding

The procedure of space breeding is illustrated in Fig. 3 and 4. Space breeding starts with subjecting the biological materials like seeds, cuttings or microbes or any biological material into the lower orbit of the Earth where the cosmic radiations are travelling. The subjection of biological materials is carried out by using the recoverable satellite, space aircraft or high-altitude balloons. In space, the materials are exposed to microgravity, cosmic radiation and vacuum conditions. These conditions induce genetic, physiological and biochemical mutations. Later on, the subjected materials bring back to the Earth for growing and analysis and test

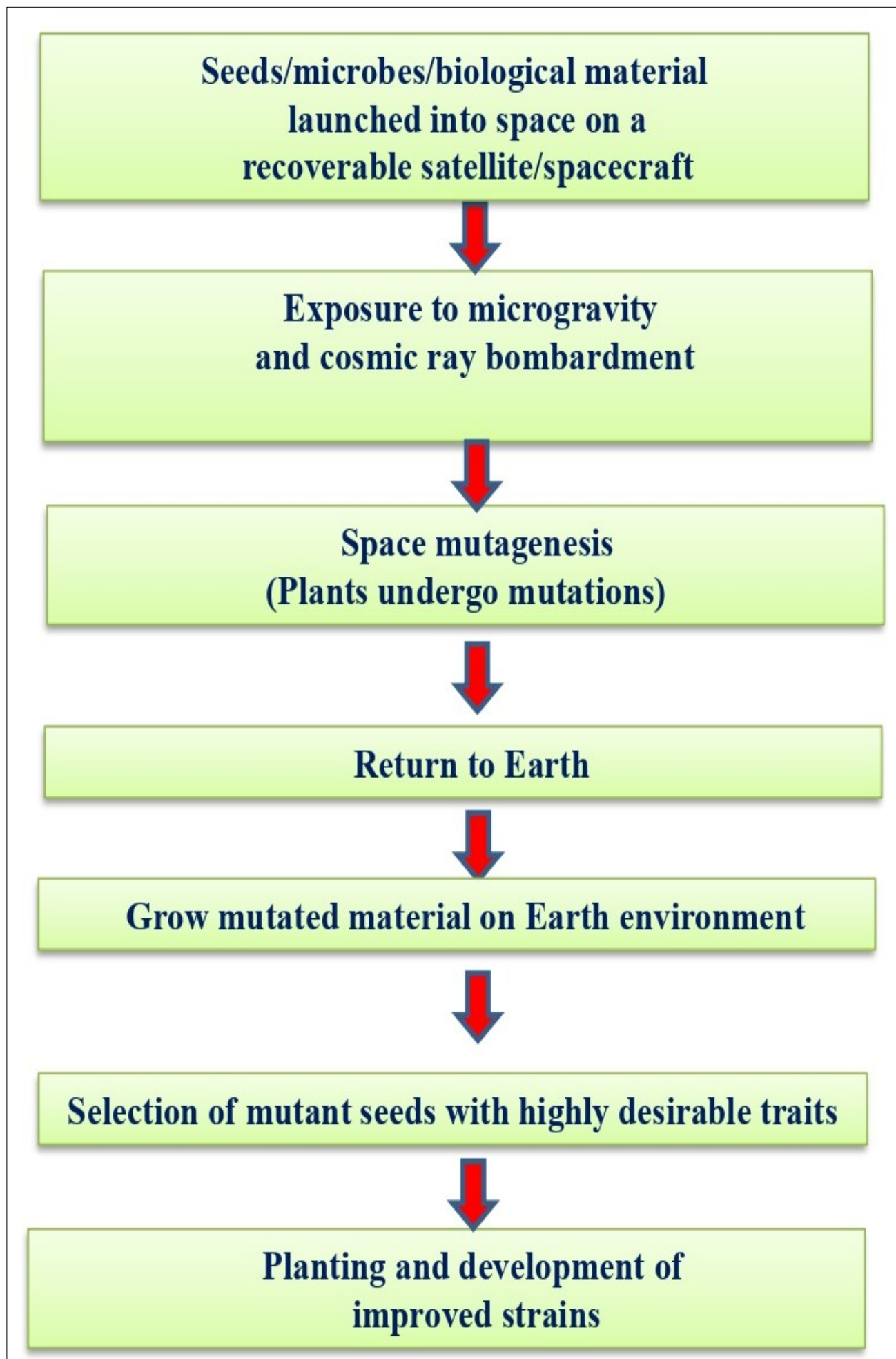


Fig. 3. Procedure of space breeding showing exposure, mutation induction and selection.

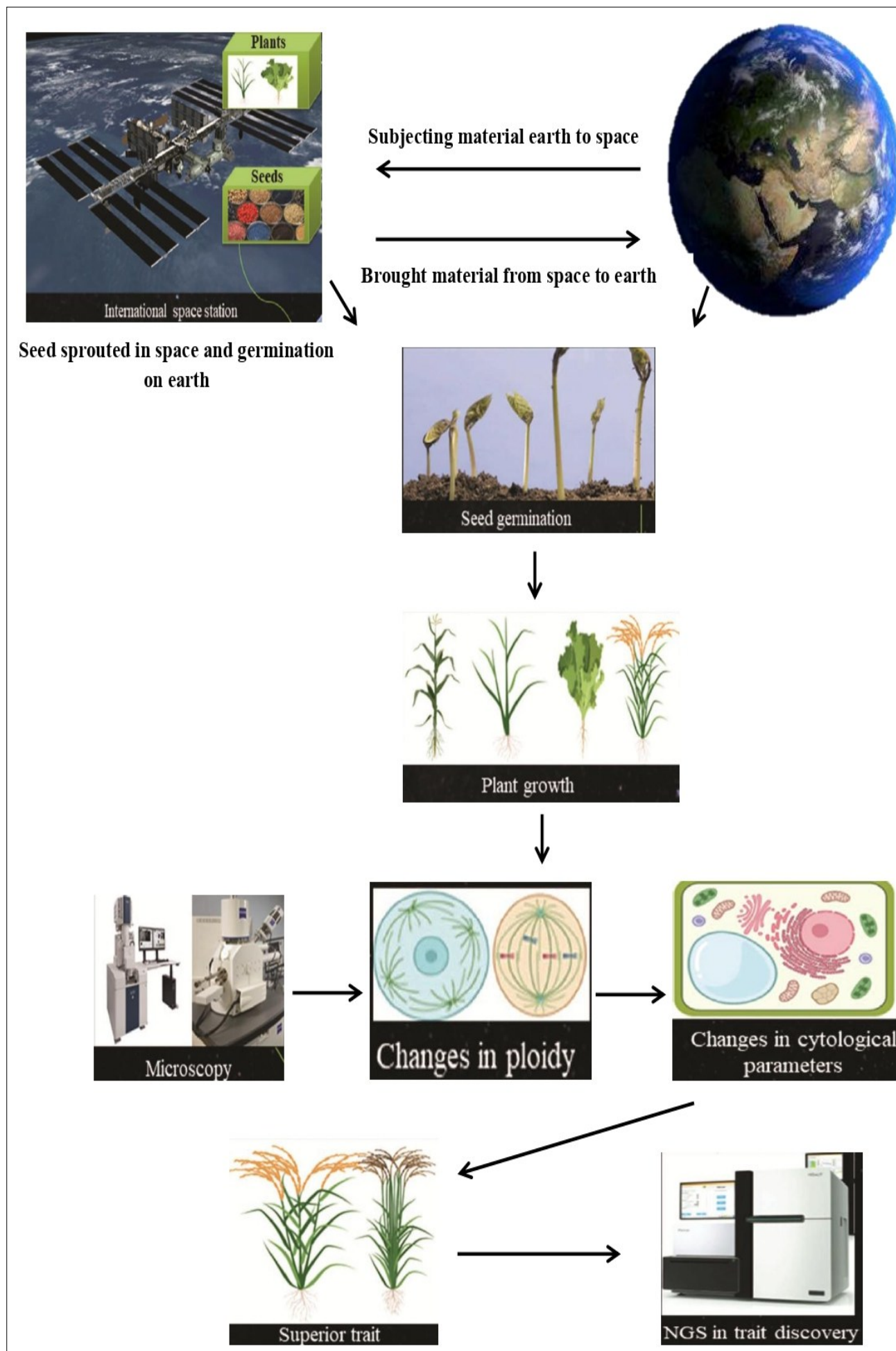


Fig. 4. Schematic representation of mutation induction and selection in space breeding (4).

for traces of radiation as well as any mutant. Alternatively, another scenario also like seeds can be sprouted in space and the resulting plants brought back to Earth for analysis. The testing will result in identification of mutant with desirable characters. Scientists use various tools to identify plant materials with promising mutations caused by space travel. Molecular markers such as Amplified Fragment Length Polymorphism (AFLP), Random Amplified Polymorphic DNA (RAPD) and Simple Sequence Repeats (SSR) are used to detect genetic variation. Once a plant shows desirable traits, advanced DNA sequencing can pinpoint the genes likely influenced by the space environment. With this knowledge, scientists can employ molecular breeding techniques to create crops with these beneficial traits. Selected mutants are evaluated and released as improved varieties.

Modifications brought about by biological materials being exposed to space environment

Exposure to space environments induces several cellular, physiological and genetic changes in plants, as described below.

Cell shape

Space exposure alters cell structure and morphology. For instance, in case of pine tree cotyledon shows round shape cell also the in meristematic tissues of roots of *Crepis* and maize shows same. It is possible that the increased surface tension combined with lower mechanical pressure in microgravity is responsible for the observed decrease in cell attachment (36). *Funaria hygrometrica* moss cultivated in space for 96 days exhibited a higher frequency of pear-shaped and dumbbell-shaped cells in comparison to identical moss grown under terrestrial conditions in space for 96 days had more pear- and dumbbell-shaped cells (37).

Size of cell and proliferation/differentiation pattern

Space exposure affects cell size and structure (37). The roots of *Crepis*, maize, peas and wheat were shown to have bigger cells (38–40). Wheat and maize seedlings have been shown to exhibit increased cell elongation (36, 40). Anise (*Illicium verum* - Chakraphul) seeds were cultivated for somatic embryogenesis on shuttle flight D-1 and it was discovered that the somatic embryo cells differentiated more quickly in space. This suggests that whereas differentiation on Earth takes 6 days, it occurred in 4 days in space.

It has been observed that orchid plants grow and develop more slowly in space. The flowers experienced serious damage stopped growing and eventually died once the space mission began (41). Even after 6 months, the orchid plants' roots, stems and leaves did not show any signs of blossoming (42). The growth of *Arabidopsis* plants was markedly delayed in space compared to the control group. It took twice as long for these plants to reach the rosette stage and 8 days longer to begin flowering (43). Carrot somatic embryos were shown to have a wider differentiation zone, which led to longer roots (36). It is possible that the space-grown plants produced chlorophyll prior than the ground-grown plants because they received more sunshine (44). Early root hairs formed close to the tips of the roots as a result of the cells' early differentiation due to abnormal elongation (43). Growing oat seedlings in the SL-2 spacecraft revealed more lateral roots, possibly as a result of the root tips exhibit slower rate of cell division causing growing lateral roots. When compared to the control, the internode of pea seedlings cultivated in space was seen to be incredibly extended (41).

Division of cell

Space environment has been found to induce a universal mutagenic response in plants, characterised by rising chromosomal abnormalities and a subsequent decline in mitotic cell division when compared to terrestrial conditions (45).

Plants grown in Biosatellite II have been exhibit declined in cell division (46, 47). Cell division rates were lower in pea (*Pisum sativum* L.) and hawkweed (*Crepis capillaris* (L.) Wallr.) seedlings cultivated aboard spacecraft during Soviet space flights (40, 41, 48) 10 % less dividing cells were found in *Helianthus annuus* L. plants cultivated on Shuttle missions SL-2 and STS-3 and in oat seedlings grown on SL-2 than in ground-control plants (43, 49). Sunflowers, mung beans and oats exhibited decreased mitotic cell division during the anaphase and telophase stages. Since the cell cycle was predominantly halted at metaphase, prolonged space travel might have led to a more significant reduction in cell division (41). On the other hand, the majority of lettuce cells were halted in the telophase when cell division was inhibited.

Changes in chromosome number and arrangement (Chromosomal aberration)

Space radiation attacks cellular DNA, inducing damage that manifests as single nucleotide errors, single-strand fractures or brake and double-strand fracture (50). Double-stranded DNA breaks are a primary and severe form of DNA damage. To maintain genomic integrity, cells activate various repair mechanisms. However, if these breaks are not repaired accurately, it can lead to cell death or premature aging (50). Due to the severity of DNA damage inflicted by alpha rays and other high-energy radiation, the non-homologous end joining pathway is insufficient for repair (51).

To address DNA damage in these situations, the cell employs the homologous recombination machinery. As previously stated, space-based plant cultivation is often associated with the development of chromosomal anomalies. The unstable chromosomal abnormalities categorized as ring, rearranged acentric and multicentric chromosomes, which they found to be consistently unrepaired (50). Unstable chromosomal abnormalities, characterised by broken DNA ends, missing telomeres and faulty distribution mechanisms, are usually lost in the process of cell division. The presence of 2 centromeres makes dicentric chromosomes, the most frequent type of unstable chromosomal aberration and it is easily distinguishable (50–53). Monocentric chromosomes, indicative of stable chromosomal aberrations, can be inherited by daughter cells and serve as a reliable indicator of previous exposure to cosmic radiation.

Seedlings of *Crepis* and *P. sativum* from Soviet Union space missions have been observed to contain multiple nuclei and aneuploidy ($2n-1=33$) in root cells was found in a sample of sunflowers cultivated on STS-2 spacecraft (54). The microspores of *Tradescantia paludosa* E.S. Anderson & Woodson were similarly shown to exhibit mitotic abnormalities, including aberrant nucleus movement (55, 56). On a similar vein, chromosomes were grouped during metaphase rather than found on the equatorial plate. The abnormal cellular behaviour in *T. paludosa*, including irregular chromosome distribution, incomplete chromatid separation and atypical mitotic spindle (55).

This kind of misaligned chromatid separation may result in the aneuploid genome seen in sunflowers. Studies on *Tradescantia* have revealed fused embryo sacs in plants with either clumped or dispersed nuclear configurations. One possible reason for this could be a spindle organisation issue. Moreover, *Tradescantia* root tips were characterised by the presence of cells with multiple nuclei, abnormal nuclear structures and disturbed spindle organisation (57). Root tip cells were more susceptible to chromosomal abnormalities. These abnormalities were exacerbated in *C. capillaris*, while *A. thaliana* experienced a significant decline in seed quality and germination. Spaceflight conditions induced abnormal reproductive development and seed formation in *Arabidopsis*, leading to reduced germination, survival and fertility (41).

Chromosomal abnormalities in meristematic stem cells were identified as the root cause of the observed occurrences. These cells, unlike dormant seeds are metabolically active and thus more susceptible to the damaging effects of cosmic radiation encountered during space travel. *Crepis* seeds exposed to space radiation for 3 to 234 days exhibited a higher frequency of chromosomal aberrations compared to those germinated on Earth after similar radiation exposure (58). Despite the application of radioprotective agents like 5-methoxytryptamine, aminoethyl isothiurea and cysteine, chromosomal abnormalities caused by space radiation in barley have persisted (59, 60).

Changes occur in cellular components level

The plants cultivated in weightlessness experienced significant cell wall alterations (61, 62). Compared to ground-based controls, these cell walls were reduced by approximately two-thirds in thickness. Mung bean seedlings grown in space for 24 days showed an 18 % decrease in lignin content, while their cell walls contained 54 % less cellulose (41). Previous research has indicated that space-grown seedlings exhibit lower protein and enzyme levels (63). Furthermore, while we have observed reduced chromosomal abnormalities and mitotic activity in space-grown plants, these organisms also display altered cellular structures. Specifically, *Arabidopsis* and pea plants cultivated in space have shown condensed chromatin within statenchyma cells and irregular nuclear placement in their root systems (64). Pine cells cultivated in space exhibited a reduction in nucleoli count, contrasting with wheat seedlings that demonstrated a significant increase in nuclear volume. Seven-day-old seedlings showed diminished starch granules and plastid reticulum within the amyloplast, accompanied by a more defined stroma. In contrast, space-grown cells displayed a haphazard arrangement of amyloplasts in the root cap. After 18 days, most plastids contained a single central starch granule, although some had minimal or no starch granules (65). Maize seedlings exhibited reduced starch levels in columella cells at the age of 4.8 days compared to control plants on Earth. Pea plants grown in space showed signs of chloroplast damage after 29 days, including disrupted grana structures, swollen intergrana regions and condensed grana stacks. Additionally, the formation of electron transport vesicles was observed (41).

The endoplasmic reticulum (ER) cisternae in columella cells of space-grown *Arabidopsis*, cucumber and pea seedlings exhibited decreased electron density (41). In contrast to the complete disappearance of rough ER and ribosomes reported in *Funaria protonema*, other cases have demonstrated a shrinkage

and rounding of the ER cisternae (65). Space-grown maize seedlings displayed abnormal ER morphology, characterised by spherical and elliptical ER structures clustered at the cell periphery. In contrast, maize seedlings germinated on Earth and subsequently grown in space exhibited normal ER distribution within columella cells (66). This illustrates how gravity affects the ER's distribution and integrity. Root cap cells of *Arabidopsis*, maize and pea seedlings exhibited swollen mitochondria with dense internal structures and disorganised membranes under microgravity conditions, (36, 67). In pea root meristems, weightlessness induced structural changes in Golgi apparatus (dictyosomes), leading to a significant reduction in their size within the root cap's protective layers (calyptragen, columella and peripheral cells) compared to ground controls (68). Concurrently, mucilage secretion was markedly decreased in pea and maize seedlings grown in space (68, 69). Interestingly, peroxidase activity was elevated by 18 % in space-grown lucerne seedlings relative to their terrestrial counterparts (70).

Changes occur in mineral element composition

Space environments induce multifaceted changes in plants, affecting their molecular, cellular, genomic and physiological processes. Consequently, the elemental composition of plant cells can be significantly altered. For instance, pea plants grown in the unique conditions of the Salyut space station displayed marked variations in mineral content, with decreases in calcium, iron, magnesium, manganese and zinc, but increases in phosphorus and potassium within their shoot systems (61). Reduced root growth is likely linked to deficiencies in essential elements. The decline in calcium levels, a crucial signalling molecule, may account for decreased metabolic, cellular and physiological functions within the plant (71–75). Manganese deficiency directly correlates with impaired photosynthesis due to its essential role in the water-splitting process. Furthermore, a decrease in calcium, magnesium and potassium levels in 5-day-old pea seedlings under microgravity conditions led to reduced ATPase activity. Consequently, inhibited ATPase function in plasmodesmata resulted in diminished protein content. The primary cause of ATPase dysfunction is likely a substantial decline in calcium-dependent ATPases. While calcium was present in plasmodesmata and the plasma membrane of control plants, it was redistributed to the plastid, endoplasmic reticulum, Golgi apparatus and nuclear membrane in the experimental group (76). The results imply an increased propensity for cellular calcium to bind to membranes under low-gravity conditions. Moreover, membrane phospholipases are regulated by alterations in calcium ion concentration. Therefore, the diminished ability of the calcium pump to utilise ATP results in disturbances to both active and passive calcium transport processes (76).

Morphological variation

Spaceflight environments can significantly impact plant growth and development. In a study involving *Arabidopsis* plants, cotyledon-stage seedlings were successfully launched into space and reached the flowering stage. However, despite normal external appearance, the reproductive organs, the androecium and gynoecium, were infertile and degraded. These findings suggest that the unique lighting conditions in space induced sterility in the reproductive structures without affecting overall plant morphology (58, 61, 67, 77). Upon return to Earth, the

plants completed their flowering cycle. However, their subsequent offspring exhibited reduced germination rates, a higher incidence of genetic mutations and lower reproductive capacity (77, 78). Despite being grown to maturity under space conditions, *Arabidopsis* plants showed growth abnormalities such as shortened stature, fewer leaves and a decreased number of smaller siliques (41). The F₁ seeds produced in space exhibited reduced seedling vigour, as evidenced by smaller hypocotyls and cotyledons, which negatively impacted their germination success. Despite these challenges, 42 % of these seeds developed into mature plants. However, the subsequent F₂ generation displayed normal growth patterns, indistinguishable from ground-based controls (41, 79).

Genetic variation

Space travel can induce genetic alterations in crop plants. So, the depiction of such genetic variation is necessary to evaluate new diverse genetic loci. To uncover these changes, researchers analysed 201 rice varieties grown from seeds exposed to spaceflight conditions using RAPD markers. These analyses revealed a significant 30.2 % increase in genetic variation compared to ground-based controls, suggesting that the space environment can induce substantial genetic mutations in rice. Despite the challenges of spaceflight, all plant specimens returned to Earth exhibited normal growth and reproductive capabilities. Ground-based control plants maintained their typical growth patterns. Genetic analysis using 24 random primers identified a total of 189 genetic markers, with each primer revealing between 4–15 loci. There were 400–2000 base pair fragments in the amplicon reported (80).

Genetic analysis of rice seeds I-B11 using the OPS-19 primer identified at least 12 single nucleotide polymorphisms (SNPs) compared to control samples. Previous research also reported SNPs in other rice varieties (80). To further investigate genetic changes across generations, I-B11 and I-B15 rice seeds were examined using 29 random primers. A total of 121 polymorphic loci were detected. Comparative analysis revealed significant genetic differences between space-grown rice, their offspring and ground-based controls. Specifically, 9 new polymorphic loci appeared in the first generation of I-B11, with an additional 9 identified in subsequent generations (80). Plants with space-bound seeds grew shorter than their wild type counterparts, QHZ, according to the field study. On the other hand, the second-generation progeny of I-B11 headed 8–10 days ahead of the control QHZ.

Analysis of 3 *Oryza sativa* L. restorer lines (R998, Gui99 and Hanghui No. 7) exposed to spaceflight conditions identified at least 2538 polymorphic loci using 104 pairs of SSR primers. Small-scale DNA mutations, such as deletions or insertions, accounted for 9.85 % of the observed genetic variations (81). Among 56 primer pairs used for AFLP analysis, 32 combinations produced amplifiable fragments. Sequencing of these fragments revealed a similarity to the expressed sequence tag gi33771201 from a maize sperm library (81). The third chromosome contains the DNA sequence AC187265 (81). Lucerne seedlings cultivated in space exhibited an 18 % increase in peroxidase activity compared to ground-based controls. This elevated enzyme activity might be attributed to the accumulation of reactive oxygen species induced by spaceflight conditions. Additionally,

peroxidase gel electrophoresis revealed distinct band patterns in space-grown seedlings, indicating altered protein profiles (70).

Achievements

China, the United States and Russia are the leading countries in space breeding research, with China developing more than 741 mutant crop varieties. More than 741 mutant varieties of crops such as rice, wheat, cotton, tomato, sesame and pepper have been developed and released in China through space breeding programs. The mutants were high-yield, high-quality and multi-resistant crop varieties (82). Several countries have successfully developed superior crop varieties, as presented in Table 1. For example, A high-yielding and stress-tolerant rice variety (Fig. 5) developed through space breeding by China, demonstrating enhanced productivity and adaptability. Also, super hybrid giant pumpkin (Fig. 6) with exceptionally large fruit size was successfully developed through space breeding, demonstrating enhanced growth potential and yield (1).

Russia experiments concluded that wheat (*Triticum aestivum* L.), peas and *Arabidopsis* successfully germinated and grew in microgravity conditions. However, growth abnormalities such as reduced biomass, disoriented root growth and delayed reproductive development were observed. In one experiment with Super dwarf wheat, plants grew for about 90 days but did not produce grain due to limited light and environmental stress. These experiments demonstrated that plant growth in space is possible but requires optimised environmental control (22). The NASA demonstrated that several crops including romaine lettuce, mustard greens, kale, radish and chilli peppers were successfully grown in space. Some vegetables were harvested and consumed by astronauts and microbial tests showed that the produce was safe for human consumption (24). The ISS mission said that radish and leafy vegetables successfully completed their growth cycles in microgravity (25). The ISRO studies showed that exposure to space conditions can alter seed germination, growth rate and genetic variability in cowpea (31, 83).

Institutions involved in space breeding research

Several leading Chinese institutes are actively engaged in the field of space breeding, contributing significantly to the development of novel crop varieties and the advancement of agricultural biotechnology. The Space Breeding Research Centre of China serves as a central hub for coordinating and implementing experiments related to crop mutation and genetic improvement under spaceflight conditions. The Chinese Academy of Agricultural Sciences (CAAS), through its specialised divisions such as the Institute of Crop Sciences, plays a pivotal role in studying genetic variations induced by space environments and translating them into practical breeding outcomes. Furthermore, the Innovation in Space Breeding Technology and Development of New Crop Varieties Program focuses on integrating space-induced mutations with modern genomic tools to enhance crop productivity, stress tolerance and nutritional quality. Complementing these efforts, regional institutions like the South China Agricultural University and the Fujian Academy of Agricultural Sciences are also contributing to applied research, germplasm improvement and field evaluation of space-bred cultivars. Collectively, these institutions underscore China's strategic commitment to utilising space biotechnology for sustainable agricultural innovation.

Table 1. Space-Bred crop varieties developed by different countries

Sl. No	Crop	Variety	Developed characteristics	Country
		Luyuan 502		
		SP 8581, SP 0225 and SP 798	High yield (11 % more than local variety), Highly stable, Tolerant to drought and key diseases.	
1	Wheat	SP 8724 and SP 2290	Early maturity, disease resistance and strong gluten	
			Large spike dwarf wheat with spike lengths over 15 cm	
		Tian Kong 5, Tian Kong 6, Long Fu Mai 15, Long Fu Mai 17 and Hang Mai 96		
2	Rice	Space rice (Rice from heaven)	Resilient to diseases and climate change	China
3	Rice	Te You Hang 1, Il You Hang 1, Hua Hang 1, Il You Hang 148, Il You Hang 2, Liang You Hang 2, Pei Za Tai Feng, Pei Za Hang 7, Sheng Ba Si Miao, Jin Hang Si Miao, Hua Hang Si Miao, Yue Hang 1, Zhe 101, Zhong Zao 21, Zhong Zhe You 1, Hang Hui 8, R8007 and Hang Tian 36	Restorer lines with broad compatibility, strong restorative ability, high combining ability, good blast resistance and excellent grain quality	
4	Giant pumpkin	Giant pumpkin super hybrid	Large size fruit	
5	Mushroom (Edible)	Nongtou-1	Stronger fragrance and higher yield than local mushrooms	
6	Cotton	Zhong Mian 42 and Zhong Mian 50	-	
7	Sesame	Zhongzhi 11 and Zhongzhi 13	-	
		Yu Jiao 1, Yu Jiao 2, Yu Jiao 3, Yu Jiao 4 and Longjiao 9		
8	Green pepper		-	
9	Tomato	Yu fan 1 and Yu fan 2	-	
10	Alfalfa	Nong Jing 11	High-yielding, cold-tolerant alfalfa variety	

Characteristics of some mutant cultivars not disclosed yet (82).

**Fig. 5.** Space rice (Chinese rice from heaven), (1).**Fig. 6.** Super hybrid of giant pumpkin having large size, (1).

The NASA and its research facility Kennedy Space Centre have played an important role in space breeding by conducting plant growth and genetic studies under microgravity conditions using plant growth systems on the ISS. In Russia, the Russian Academy of Sciences and the Institute of Biomedical Problems have carried out pioneering experiments on seed germination, plant physiology and mutation induction in space. In Europe, the European Space Agency along with the German Aerospace Centre conducts several plant biology and space agriculture experiments. Similarly, the Japan Aerospace Exploration Agency performs plant cultivation and genetic research in the Kibo laboratory module of the ISS.

In India, crop improvement via non-conventional mutation and space-biology pathways is gaining traction through collaborative efforts between the ISRO and agricultural research bodies such as the Indian Council of Agricultural Research (ICAR). The ISRO's modular experiment called the Compact Research Module for Orbital Plant Studies demonstrated the germination of black-eyed pea (cowpea) seeds in orbit, indicating the viability of plant life cycles under micro-gravity and controlled environmental conditions (83).

Together, these agencies contribute significantly to the advancement of space breeding and the development of crops suitable for long-term space missions and future space agriculture.

Advantages

1. Improves the quality of agriculture products in less time.
2. Produced some mutations with potentially breakthrough impacts on important economic traits such as crop yield and quality.
3. Leads to producing new types, traits and genes that are rare in nature or difficult to obtain by conventional methods.
4. It produces numerous high-quality sources, effectively addresses the issue of food scarcity and offers unlimited benefits to the world.

Disadvantages/Limitation

1. The chance of detrimental mutation in an organism's DNA which could negatively affect other cultivated plant varieties.
2. Implementation of programme is very costly.
3. Require high technological assistance that many other nations are either unable or unwilling to provide.
4. Some peoples having ethical concern about product generated by space breeding like transgenic crops.
5. Long distance may create communication problems.

Objective of space breeding

Space breeding accelerates mutation frequency by exposing plant materials to cosmic radiation and microgravity. This technique relies on natural cosmic rays instead of human-made radiation like X-rays or ionic beams. Usually, Earth's atmosphere is a protective covering to the living things, but seeds in space are constantly bombarded by such high-energy rays. This can sometimes lead to beneficial changes, like plants that grow faster, need less water, or resist harsh conditions. Scientists are looking for these rare gems - mutations that make crops stronger, more productive or hardier. Harness the much more and other maximum potential of space by merging advance

technology in agriculture advancement. While creating plants that can flourish in space is a valuable scientific pursuit, there's a risk of unintended consequences.

Challenges in space breeding

Maintaining optimal environmental conditions such as temperature, humidity, light intensity, carbon dioxide concentration and nutrient availability in spacecraft is technically challenging and directly influences plant growth, development and mutation stability. Microgravity alters plant physiological processes such as water uptake, root orientation, cell division and hormone signalling, making normal growth difficult. Space-induced mutations caused by cosmic radiation and microgravity may be unstable across generations, therefore multi-generation screening and molecular characterisation are required to ensure genetic stability and heritability of desirable traits (4). Limited spacecraft space, strict payload capacity and the high cost of launching biological materials restrict the scale of crop experiments. Space experiments are also constrained by restricted availability of water, nutrients and energy resources, as well as limited experimental duration. Operational challenges include maintaining sterile conditions, preventing microbial contamination and ensuring reliable automated monitoring systems. Furthermore, most mutations induced by space exposure are neutral or deleterious, making the identification, isolation and stabilisation of beneficial mutants through phenotypic screening and genomic analysis extremely difficult. Addressing these technical, genetic and operational challenges is essential to improve the efficiency and reliability of crop space breeding programs (57).

Conclusion

Space breeding represents an important approach in modern crop improvement. It enables the generation of novel genetic variation useful for crop improvement that wouldn't be possible on Earth. Advances in space technology have supported mutation breeding under extra-terrestrial conditions. This is a giant leap forward for humanity's future in space agriculture and it will significantly improve traditional farming practices. But space breeding not only just about practical applications but also incredibly important for scientific understanding of how space affects living things. We need to delve deeper into the practical uses of space-induced mutations, even though it requires significant funding and advanced technology. To understand the genetic changes caused by space radiation, we should sequence both the genome and transcriptome (the set of RNA molecules). Additionally, studying SNPs (single nucleotide polymorphisms) and conducting genome-wide association studies can help identify genetic markers linked to successful space breeding programs. The successful seed breeding of plants and their generation alternation in space are essential to ensure that human beings have the ability to survive in extra-terrestrial space for a long time.

Thus, it is unclear how society might respond to genetically modified crops grown in space. To comprehend the genetic alterations brought about by space radiation, scientists ought to examine these crops transcriptome and genome. The impact of space on the crop's protein and metabolite composition requires more research. Scientists can expedite space breeding projects by finding genetic markers linked to desired qualities using genome-

wide association and SNP research. Once a useful gene has been identified, other crop kinds can benefit from its application. This information can be used to model and forecast the consequences of space breeding on various crops, along with information on mutations and chromosomal alterations.

For better understanding of how genes interact with the environment, large amounts of environmental data can be analysed with the aid of sophisticated statistical algorithms. Space breeding tactics can be optimised by the integration of genetic, phenotypic and environmental data. Researchers can select for desired features and increase crop yields by modelling the impact of space on crop genetics. To find advantageous features, a complex statistical model might integrate genetic data from several crop species. This strategy can hasten the creation of novel crop varieties with enhanced traits. This work essentially emphasises the potential of space breeding as a tool for agricultural improvement, but in order to fully realise its benefits, extensive research and sophisticated statistical techniques are required.

Future perspectives of space breeding

Scientists have been working to emulate space settings on Earth to reproduce the fast mutations seen there. Ground-based efforts to create "space simulation" breeding methods have been on-going for some time. Only microgravity, though, has been effectively replicated and experiments in this area have been carried out. Space simulation breeding methods are still under development. Advances in space technology are expanding opportunities for plant research and space agriculture. Space breeding has potential to improve crop productivity and agricultural sustainability. Space breeding may contribute to future crop improvement programs.

Acknowledgements

Special thanks to the all-field workers as well as lab workers for necessary help.

Authors' contributions

CSS and GRA contributed to manuscript writing and drafting. VPC was responsible for reviewing, checking and finalizing the manuscript. All authors have read and approved the final version of manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

References

- Bhanu AN. Space breeding: space inspired mutation breeding for crop improvement. *Biol Bull.* 2022;22:13–20.
- Singh BD. Principles of plant breeding. Kalyani Publ. 2020:286–311.
- International Atomic Energy Agency. Cosmic crops. English newsletter. 2024.
- Mohanta TK, Mishra AK, Mohanta YK, Al-Harrasi A. Space breeding: the next-generation crops. *Front Plant Sci.* 2022;12:771985. <https://doi.org/10.3389/fpls.2021.771985>
- Frisbee RH. Advanced space propulsion for the 21st century. *J Propuls Power.* 2003;19(6):1129–54. <https://doi.org/10.2514/2.6948>
- Anqi F. China's first "space rice" that made round trip to moon yields grain. *Glob Times.* 2021.
- Young L, Sutton J. Handbook of bioastronautics. Springer; 2021:3–19. https://doi.org/10.1007/978-3-319-12191-8_88
- Eichinger R, Garny H, Šácha P, Danker J, Dietmüller S, Oberländer-Hayn S. Effects of missing gravity waves on stratospheric dynamics; part 1: climatology. *Clim Dyn.* 2020;54:3165–83. <https://doi.org/10.1007/s00382-020-05166-w>
- Bagshaw M. Cosmic radiation in commercial aviation. *Travel Med Infect Dis.* 2008;6(3):125–7. <https://doi.org/10.1016/j.tmaid.2007.10.003>
- Zhang SN, Adriani O, Albergo S, Ambrosi G, An Q, Bao TW, et al. The high energy cosmic-radiation detection (HERD) facility onboard China's space station. In: Space telescopes and instrumentation. 2014.
- McKay CP. Past, present and future life on Mars. *Gravit Space Biol Bull.* 1998;11(1):41–50.
- Simoneit BR, Summons RE, Jahnke LL. Biomarkers as tracers for life on early earth and Mars. *Orig Life Evol Biosph.* 1998;28:475–83. <https://doi.org/10.1023/A:1006508012904>
- Westall F, Loizeau D, Foucher F, Bost N, Bertrand M, Vago J. Habitability on Mars from a microbial point of view. *Astrobiology.* 2013;13(9):887–97. <https://doi.org/10.1089/ast.2013.1000>
- Acuña MH, Connerney JEP, Wasilewski P, Lin RP, Mitchell D anderson KA, et al. Magnetic field of Mars: summary of results from the aerobraking and mapping orbits. *J Geophys Res Planets.* 2001;106(E10):23403–17. <https://doi.org/10.1029/2000JE001404>
- Connerney JEP, Acuña MH, Wasilewski PJ, Kletetschka G, Ness NF, Rème H. The global magnetic field of Mars and implications for crustal evolution. *Geophys Res Lett.* 2001;28(21):4015–8. <https://doi.org/10.1029/2001GL013619>
- Thirsk R, Kuipers A, Mukai C, Williams D. The space-flight environment: the international space station and beyond. *Can Med Assoc J.* 2009;180(12):1216–20. <https://doi.org/10.1503/cmaj.081125>
- Penley NJ, Schafer CP, Bartoe JDF. The international space station as a microgravity research platform. *Acta Astronaut.* 2002;50(11):691–6. [https://doi.org/10.1016/S0094-5765\(02\)00003-6](https://doi.org/10.1016/S0094-5765(02)00003-6)
- Jules K, McPherson K, Hrovat K, Kelly E, Reckart T. A status report on the characterization of the microgravity environment of the international space station. *Acta Astronaut.* 2004;55(3-9):335–64. <https://doi.org/10.1016/j.actaastro.2004.05.057>
- Rabbow E, Horneck G, Rettberg P, Schott JU, Panitz C, L'Afflito A. EXPOSE, an astrobiological exposure facility on the international space station—from proposal to flight. *Orig Life Evol Biosph.* 2009;39:581–98. <https://doi.org/10.1007/s1084-009-9173-6>
- Rabbow E, Rettberg P, Barczyk S, Bohmeier M, Parpart A, Panitz C, et al. EXPOSE-E: an ESA astrobiology mission 1.5 years in space. *Astrobiology.* 2012;12(5):374–86. <https://doi.org/10.1089/ast.2011.0760>
- Rabbow E, Rettberg P, Barczyk S, Bohmeier M, Parpart A, Panitz C, et al. The astrobiological mission EXPOSE-R on board of the international space station. *Int J Astrobiol.* 2015;14(1):3–16. <https://doi.org/10.1017/S1473550414000202>
- Salisbury FB, Campbell WF, Carman JG, Bingham GE, Bubenheim DL, Yendler B, et al. Plant growth during the greenhouse II experiment on the Mir orbital station. *Adv Space Res.* 2003;31(1):221–7. [https://doi.org/10.1016/S0273-1177\(02\)00744-5](https://doi.org/10.1016/S0273-1177(02)00744-5)
- Chen S. Countdown starts for China's big mutant crop space mission in race for food security. *South China Morning Post.* 2019.
- Khodadad CLM, Hummerick ME, Spencer LE, Dixit AR, Richards JT, Romeyn MW, et al. Microbial and nutritional analysis of lettuce crops grown on the international space station. *Front Plant Sci.*

- 2020;11(199):1–15. <https://doi.org/10.3389/fpls.2020.00199>
25. Danielle S. Astronauts harvest radish crop on the international space station. NASA. 2020.
26. Ghosh P. What is space rice? China harvests 1st batch of seeds that travelled around moon. Hindustan Times. 2021.
27. Resende RT, Piepho HP, Rosa GJM, Silva-Junior OB, Silva FF, de Resende MDV, et al. Enviromics in breeding: applications and perspectives on envirotypic-assisted selection. Theor Appl Genet. 2021;134:95–112. <https://doi.org/10.1007/s00122-020-03684-z>
28. Grush L. New company space perspective wants to take you to the stratosphere via high-altitude balloon. The Verge. 2020.
29. Tingle A. When the balloon goes up: high-altitude for military application. Mil Rev. 2020;100(4):68–73.
30. Mohnty S. Shenzhou: the star of China's human space program. Stir World. 2022.
31. The Times of India. Life sprouts in space; ISRO successfully germinates cowpea seeds in just four days under microgravity conditions. 2025.
32. Krikorian AD, Steward FC. Morphogenetic responses of cultured totipotent cells of carrot (*Daucus carota* var. *carota*) at zero gravity. Science. 1978;200(4337):67–8. <https://doi.org/10.1126/science.200.4337.67>
33. Böhmer M, Schleiff E. Microgravity research in plants. EMBO Rep. 2019;20(9):e48541. <https://doi.org/10.15252/embr.201948541>
34. Ferl R, Wheeler R, Levine HG, Paul AL. Plants in space. Curr Opin Plant Biol. 2002;5(3):258–63. [https://doi.org/10.1016/S1369-5266\(02\)00254-6](https://doi.org/10.1016/S1369-5266(02)00254-6)
35. Wolverton C, Kiss JZ. An update on plant space biology. Gravit Space Biol Bull. 2009;22(2):13–20.
36. Il'ne Y, Parfenov G. Biologicheskoye issledovaniya na biosputnikakh. Moscow: Nauka; 1979.
37. Kordyum EL, Nedukha EM, Stynik KM, Mashinsky AL. Optical and electron-microscopic studies of the *Funaria hygrometrica* protonema after cultivation for 96 days in space. Adv Space Res. 1981;1(14):159–62. [https://doi.org/10.1016/0273-1177\(81\)90257-X](https://doi.org/10.1016/0273-1177(81)90257-X)
38. Merkys AJ, Mashinsky AL, Laurinavichius RS, Nechitailo GS, Yaroshius AV, Izupak EA, et al. The development of seedling shoots under space flight conditions. Life Sci Space Res. 1975;13:53–7. <https://doi.org/10.1515/9783112482247-010>
39. Merkys A, Laurinavichius R, Mashinsky A, Yaroshius A, Savichene E. Effect of weightlessness and its simulation on the growth and morphology of cells and tissues of pea and lettuce seedlings. In: Merkys AJ, editor. Organizmy i sila tyazhesti. 1976:238–46.
40. Halstead TW, Dutcher FR. Plants in space. Annu Rev Plant Physiol. 1987;38:317–45. <https://doi.org/10.1146/annurev.pp.38.060187.001533>
41. Gorkin Y, Mashinsky A, Yazdovskiy V. Birthday flowers: "Salyut-6", our commentary. Pravda. 1980;3.
42. Merkys A, Laurinavichius R. Complete cycle of individual development of *Arabidopsis thaliana* (L.) Heynh. plants on board the "Salyut-T" orbital station. Dokl Akad Nauk SSSR. 1983;271(2):509–12.
43. Theimer RR, Kudielka RA, Rosch I. Induction of somatic embryogenesis in anise in microgravity. Naturwissenschaften. 1986;73(7):442–3. <https://doi.org/10.1007/BF00367292>
44. Liu L, Guo H, Zhao L, Wang J, Gu Y, Zhao S, et al. Achievements and perspective of crop space breeding in China. In: Shu QY, editor. Induced plant mutation in the genomics era. Rome: FAO; 2009:213–5.
45. Thimann KV. Biosatellite II experiments: preliminary results. Proc Natl Acad Sci U S A. 1968;60(2):347–61. <https://doi.org/10.1073/pnas.60.2.347>
46. Dubinin NP, Glembofsky YL, Vaulina EN, Merks AI, Laurinavichius RS, Palmbakh LR, et al. Biological experiments on the orbital station Salyut 4. Life Sci Space Res. 1977;15:267–72.
47. Tairbekov M, Parfenov G, Platonova R, Zhvalikovskaya V. Study of plant cells using the Biofiksator-L instrument. 1979:161–9.
48. Sytnik KM, Kordyum EL, Belyavskaya NA, Nedukha EM, Tarasenko VA. Biological effects of weightlessness and clinostatic conditions registered in cells of root meristem and cap of higher plants. Adv Space Res. 1983;3(9):251–5. [https://doi.org/10.1016/0273-1177\(83\)90065-0](https://doi.org/10.1016/0273-1177(83)90065-0)
49. Furukawa S, Nagamatsu A, Neno M, Fujimori A, Kakinuma S, Katsube T, et al. Space radiation biology for "living in space." Biomed Res Int. 2020;4703286. <https://doi.org/10.1155/2020/4703286>
50. Mohanta TK, Bashir T, Hashem A, Abd Allah EF, Bae H. Genome editing tools in plants. Gene. 2017;8:399. <https://doi.org/10.3390/genes8120399>
51. MacKinnon RN, Campbell LJ. The role of dicentric chromosome formation and secondary centromere deletion in the evolution of myeloid malignancy. Genet Res Int. 2011;2011:643628. <https://doi.org/10.4061/2011/643628>
52. Stimpson KM, Matheny JE, Sullivan BA. Dicentric chromosomes: unique models to study centromere function and inactivation. Chromosome Res. 2012;20(5):595–605. <https://doi.org/10.1007/s10577-012-9302-3>
53. Krikorian A, O'Connor S. Experiments on plants grown in space: karyological observation. Ann Bot. 1984;54(3):49–63. <https://doi.org/10.1093/oxfordjournals.aob.a086866>
54. Delone N, Bykovskii V, Antipov V, Parfenov G, Vysotskii V. Effect of space-flight factors on *Tradescantia paludosa* microspores on board the satellite spaceships Vostok 5 and 6. Cosm Res. 1964;2:268–27.
55. Delone N, Egorov B, Antipov V. Effect of the factors of cosmic flight of the satellite ship Voskhod on the microspore *Tradescantia paludosa*. Cosm Res. 1966;4:139–43.
56. Saunders J. The experiments of Biosatellite II. NASA SP204. Washington, DC: NASA; 1971:352.
57. Kostina L, Anikeeva I, Vaulina E. The influence of space flight factors on viability and mutability of plants. Adv Space Res. 1984;4(10):65–70. [https://doi.org/10.1016/0273-1177\(84\)90225-4](https://doi.org/10.1016/0273-1177(84)90225-4)
58. Nuzhdin N, Dozotseva R. Genetic changes induced by space flight factors in barley seeds on "Soyuz-5" and "Soyuz-9" craft. Zh Obshch Biol. 1972;33:336–46.
59. Nuzhdin N, Dozotseva R, Samokhvalova N, Nechaev I, Petrova L. Genetic damages of seeds caused by their two-stage stay in space. Zh Obshch Biol. 1975;36:332–40.
60. Dubinin N. Biologicheskoye issledovaniya na orbital'nykh stantsiyakh "Salyut". Moscow: Nauka; 1984:248.
61. Laurinavichius R, Marchyukaytis A, Shvegzhedene DV, Mashinsky A. Metabolism of pea plants grown under space flight conditions. Moscow: Nauka; 198:96–102.
62. Cowles JR, Scheld HW, Lemay R, Peterson C. Growth and lignification in seedlings exposed to eight days of microgravity. Ann Bot. 1984;54(3):33–48. <https://doi.org/10.1093/oxfordjournals.aob.a086865>
63. Kordyum E, Sytnik K. Biological effects of weightlessness at cellular and subcellular levels. Physiologist. 1983;26(1):S141–S142.
64. Sytnik K, Kordyum E, Nedukha E, Sidorenko P, Fomicheva V. Rastitel'naya kletka pri izmenenii geofizicheskikh faktorov. Kiev: Naukova Dumka; 1984:135.
65. Moore R, McClelen C, Fondren W, Wang C. The influence of microgravity on root-cap regeneration and the structure of columella cells in *Zea mays*. Am J Bot. 1987;74(2):216–21. <https://doi.org/10.1093/oxfordjournals.aob.a086865>

doi.org/10.2307/2444023

66. Kordyum EL, Sytnik KM, Chernyaeva II. Peculiarities of genital organ formation in *Arabidopsis thaliana* (L.) Heynh. under spaceflight conditions. *Adv Space Res.* 1983;3(9):247–50. [https://doi.org/10.1016/0273-1177\(83\)90064-9](https://doi.org/10.1016/0273-1177(83)90064-9)
67. Moore R, Fondren WM, McClelen CE, Wang CL. Influence of microgravity on cellular differentiation in root caps of *Zea mays*. *Am J Bot.* 1987;74(7):1006–12. <https://doi.org/10.1002/j.1537-2197.1987.tb08710.x>
68. Tairbekov M, Grif V, Barmicheva E, Valovich E. Cytomorphology and ultrastructure of the root of the maize meristem in weightlessness. *Izv Akad Nauk SSSR Ser Biol.* 1986;(5):680–87.
69. Li J, Ren WB, Guo HQ, Liu YX, Cheng LB, WJ Z, et al. Effect of space flight factors on the peroxidase polymorphism and its activity of alfalfa. *Seed.* 2004;04.
70. Mohanta TK, Occhipinti A, Atsbaha Zebelo S, Foti M, Fliegmann J, Bossi S, et al. *Ginkgo biloba* responds to herbivory by activating early signaling and direct defenses. *PLoS One.* 2012;7(3):e32822. <https://doi.org/10.1371/journal.pone.0032822>
71. Mohanta TK, Mohanta N, Mohanta YK, Bae H. Genome-wide identification of calcium dependent protein kinase gene family in plant lineage shows presence of novel D-x-D and D-E-L motifs in EF-hand domain. *Front Plant Sci.* 2015;6:1146. <https://doi.org/10.3389/fpls.2015.01146>
72. Mohanta T, Kumar P, Bae H. Genomics and evolutionary aspect of calcium signaling event in calmodulin and calmodulin-like proteins in plants. *BMC Plant Biol.* 2017;17:38. <https://doi.org/10.1186/s12870-017-0989-3>
73. Mohanta TK, Yadav D, Khan AL, Hashem A, Abd Allah EF, Al-Harrasi A, et al. Molecular players of EF-hand containing calcium signaling event in plants. *Int J Mol Sci.* 2019;20(6):1476. <https://doi.org/10.3390/ijms20061476>
74. Mohanta TK, Sinha AK. Role of calcium-dependent protein kinases during abiotic stress tolerance. In: *Abiotic stress response in plants.* 2016:185–206. <https://doi.org/10.1002/9783527694570.ch9>
75. Palladina T, Kordyum E, Bilyavs'ka N. Activity and localization of transport adenosine triphosphatases in cells of pea seedling root cells in hypogravity conditions. *Ukr Bot Zh.* 1984;41:54–7.
76. Kordyum E, Chernyaeva I. Peculiarities in formation of *Arabidopsis thaliana* (L.) Heynh. generative organs under space flight conditions. *Dopov Akad Nauk Ukr RSR Ser B.* 1982;(8):67–70.
77. Kostina L, Anikeeva I, Vaulina E. Experiments with developing plants aboard Salyut-6 orbital stations. *Space Biol Aerosp Med.* 1986;20:73–78.
78. Parfenov G, Abramova V. Flowering and maturing of *Arabidopsis* seeds in weightlessness: experiment on the biosatellite "Kosmos-1." 1981;129:254–6.
79. Luo Y, Wang X, Mei M, Zhuang C, Feng Z, Zengquan W, et al. Genomic polymorphism in consecutive generation rice plants from seeds on board a spaceship and their relationship with space HZE particles. *Front Biol China.* 2007;2(3):297–302. <https://doi.org/10.1007/s11515-007-0043-1>
80. Wu D, Liu Y, Guo T, Zhang J, Chen Z, Wang H, et al. Variation of restoring ability and analysis of genetic polymorphism in posterity of restorer lines by space mutagenesis. *J South China Agric Univ.* 2011;32(1):1–5.
81. Zhang L, Niu X, Dai Y, Cao M. Amplified fragment length polymorphism analysis of male sterile mutant induced by space flight in maize. *J Maize Sci.* 2012;20(2):50–3.
82. Liu L, Guo H, Zhao L, Gu J, Zhao S, et al. The basic achievements and prospects of 20 years of space breeding in China. *J Nucl Agric Sci.* 2007;21(6):589–92.
83. CROPS (compact research module for orbital plant studies): a leap in space biological experiments. 2025.

Additional information

Peer review: Publisher thanks Sectional Editor and the other anonymous reviewers for their contribution to the peer review of this work.

Reprints & permissions information is available at https://horizonpublishing.com/journals/index.php/PST/open_access_policy

Publisher's Note: Horizon e-Publishing Group remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Indexing: Plant Science Today, published by Horizon e-Publishing Group, is covered by Scopus, Web of Science, BIOSIS Previews, Clarivate Analytics, NAAS, UGC Care, etc
See https://horizonpublishing.com/journals/index.php/PST/indexing_abstracting

Copyright: © The Author(s). This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution and reproduction in any medium, provided the original author and source are credited (<https://creativecommons.org/licenses/by/4.0/>)

Publisher information: Plant Science Today is published by HORIZON e-Publishing Group with support from Empirion Publishers Private Limited, Thiruvananthapuram, India.