



REVIEW

Nuclear Test Sites as Natural Experiments: Conceptual Perspectives on Plant Evolution from the New Mexico Desert

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ABSTRACT: The detonation of nuclear weapons, beginning with the Trinity test in New Mexico and followed by the bombings of Hiroshima and Nagasaki, created distinct environments of ionizing radiation exposure. While the ecological consequences of reactor accidents at Chernobyl and Fukushima have been extensively investigated, the potential evolutionary implications of historical weapons testing for plant communities remain comparatively underexplored, particularly in arid ecosystems. This review synthesizes available, yet fragmented, evidence to examine the hypothesis that residual radionuclides in arid test-site environments may have acted as potential selective pressures influencing plant persistence and stress-associated traits in native populations. We propose a comparative conceptual framework contrasting the exposure regimes of nuclear weapons testing with those of reactor accidents and acute detonations. Particular attention is given to the combined effects of initial high-dose exposure and subsequent chronic low-dose contamination, including the long-term persistence of high-linear energy transfer alpha-emitting radionuclides such as ²³⁹Pu in desert ecosystems. The analysis integrates current knowledge of radionuclide persistence, exposure pathways, and documented and inferred biological responses in local flora, including site-specific evidence of cytogenetic alterations in taxa such as *Machaeranthera* spp. alongside broader, largely indirect indications of physiological stress responses derived from comparable plant systems. Current evidence remains limited and uneven across taxa, with only a small number of species investigated directly under site-specific conditions. Given uncertainties in long-term dose reconstruction and environmental heterogeneity, adaptive evolution is considered here as a testable hypothesis rather than a demonstrated outcome. By situating New Mexico test sites within the broader context of radioecological research, this review outlines methodological approaches, including targeted field studies and multi-omics strategies, that may clarify whether sustained radiological exposure contributes to distinguishable ecological, physiological, and potentially evolutionary responses in plant populations.

KEYWORDS: Plant stress physiology; adaptive evolution; nuclear tests legacy; desert flora; environmental radiobiology

1 Introduction

The detonation of the first atomic bomb at the Trinity site in the New Mexico desert in July 1945 marked a pivotal moment in human history, irrevocably altering the global geopolitical landscape. Simultaneously,

it created a profound and localized environmental perturbation, subjecting a pristine desert ecosystem to an unprecedented combination of blast, thermal radiation, and ionizing radiation [1,2]. While the atomic bombings of Hiroshima and Nagasaki demonstrated the devastating effects of acute high dose radiation pulses on urban flora, the Trinity test, along with subsequent atmospheric nuclear tests, presents a distinct and critically understudied scenario [2,3]. This scenario involves the large-scale contamination of a natural ecosystem with a complex mixture of radionuclides, resulting in both acute and chronic exposure for resident biota [4,5].

In the decades since, the scientific understanding of ecological and evolutionary responses to radioactive contamination has been largely shaped by long term studies in the Exclusion Zones of Chernobyl and Fukushima [6–10]. These reactor accident sites have become natural laboratories for observing real time evolutionary processes under persistent low dose rate irradiation. The paradigm emerging from these studies is often interpreted as reflecting gradual adaptive or acclimatory responses, where chronic exposure may act as a selective pressure influencing genetic and epigenetic variation in plant populations over multiple generations [10–12]. However, this framework, centered on continuous contamination, does not fully encompass the diverse legacies of the nuclear age [3,10,13].

The historical nuclear testing in New Mexico represents a complementary yet a distinct, though partially overlapping, exposure context. The radiological footprint was characterized by the initial deposition of a diverse array of fission products and activation radionuclides, including long lived isotopes such as ^{239}Pu [14,15]. This created an environment of high initial dose rates, which decayed over time into a state of persistent low-level contamination, thereby exposing plant life to both an acute insult and a protracted chronic stressor. The unique selective pressures of this sequence, acting upon the resilient and often clonal native desert flora, may have contributed to distinct ecological and potentially evolutionary trajectories compared to those observed at reactor sites [14–16].

This review combines elements of a narrative synthesis and a conceptual perspective to evaluate the hypothesis that historical nuclear weapons testing in New Mexico may have acted as a potential selective pressure contributing to stress-associated and putative adaptive responses in native plant populations. We propose a comparative framework that juxtaposes the New Mexico case with the established models of Chernobyl and Fukushima, as well as the acute exposure event of Hiroshima and Nagasaki. By doing so, we seek to illuminate how differences in exposure regime, from acute versus chronic to pulse versus persistence, and ecosystem type, from arid desert to temperate forest, shape the trajectory of plant adaptation.

A central question concerns timescale. Approximately eight decades have elapsed since the Trinity detonation, raising the issue of whether this interval is sufficient for detectable evolutionary change in plant populations. While macroevolutionary processes unfold over much longer periods, microevolutionary shifts in allele frequencies can occur over relatively short timescales, particularly in species characterized by short generation times, high reproductive output, or clonal propagation. In desert ecosystems, several dominant taxa exhibit life-history traits that may permit measurable genetic or epigenetic shifts within tens of generations. In addition, desert plants are inherently exposed to multiple abiotic stressors, including high temperature, water limitation, and intense solar radiation [17]. These conditions involve well-characterized molecular pathways such as reactive oxygen species scavenging systems, heat shock proteins, and DNA repair mechanisms. The potential overlap between these stress-response pathways and those activated under ionizing radiation suggests that pre-existing stress tolerance may influence plant responses in contaminated environments, although this relationship remains to be empirically demonstrated [10,17,18]. Nevertheless, whether such changes have occurred in response to radiation exposure remains an empirical question that requires explicit testing rather than assumption.

At present, however, it remains difficult to disentangle the specific effects of ionizing radiation from those of co-occurring environmental stressors typical of desert ecosystems, including aridity, temperature variability, soil heterogeneity, and high solar radiation. This limitation highlights the need for carefully controlled experimental approaches in future studies aimed at isolating radiation-specific biological responses.

The following analysis will first delineate the specific radiological and ecological context of the New Mexico testing grounds. It will then critically assess the documented biological effects and potential adaptive responses in key desert plant species. This assessment will explore the molecular mechanisms, from enhanced DNA repair to oxidative stress management, that may underpin survival and fitness in this contaminated landscape. Finally, this review will identify critical knowledge gaps and outline a roadmap for future research. Understanding whether and how plant populations respond evolutionarily to persistent low-dose radiation has implications beyond historical interest. Such insights may inform ecological risk assessment at legacy nuclear sites, guide long-term land management strategies, and contribute to broader frameworks for forecasting ecosystem responses to chronic anthropogenic stressors. In this sense, the predictive value lies not in deterministic forecasting, but in refining the range of plausible ecological trajectories under sustained radiological exposure. We argue that the Trinity site and its surroundings constitute a scientifically valuable natural experiment for understanding the limits and mechanisms of plant evolution under anthropogenic extreme stress.

2 The New Mexico Test Site Environment: A Complex Radiological Legacy

The ecological context for potential plant adaptation in New Mexico is fundamentally shaped by the unique and complex radiological legacy of nuclear weapons testing [9,19,20]. Unlike the single reactor accidents at Chernobyl and Fukushima, or the acute aerial detonations over Hiroshima and Nagasaki, the scenario in New Mexico is characterized by a history of multiple tests, both atmospheric and underground, which deposited a diverse and persistent mixture of radionuclides into a fragile arid ecosystem [15,21].

The primary focus rests on the Trinity test of July 1945, the inaugural event that introduced fission products to the desert landscape. The radiological signature of this event and subsequent tests was distinct from that of reactor accidents [4,15]. While ^{137}Cs is a dominant contributor to long term dose in Chernobyl and Fukushima, the New Mexico site is notably characterized by a significant burden of transuranic elements, most notably ^{239}Pu [22–25]. This isotope, with a half-life of twenty-four thousand one hundred years, presents a long-term source of α radiation. α particles have a high linear energy transfer, causing dense ionization tracks and complex, difficult to repair DNA damage [26]. The relative biological effectiveness of α emitters like ^{239}Pu is considerably higher than that of γ or β emitters for the same absorbed dose. Consequently, the evolutionary pressure in this environment is not solely a function of total dose rate but is qualitatively shaped by the presence of these high linear energy transfer emitters [26,27].

It is important to recognize that Trinity-derived fallout does not represent the sole radiological input affecting ecosystems in New Mexico [15,22–25]. Subsequent atmospheric testing at the Nevada Test Site, as well as global fallout from worldwide nuclear detonations, contributed additional radionuclide deposition across the region. As a consequence, attributing contemporary soil inventories exclusively to Trinity may be challenging, particularly at broader spatial scales [23–25]. Rather than assuming singular causation, future investigations may benefit from gradient-based or spatially explicit designs that integrate cumulative radiological histories. Such approaches would also facilitate the separation of site-specific signals from regional or global fallout contributions, thereby reducing potential confounding effects in the interpretation of plant responses. Acknowledging these overlapping sources underscores the methodological complexity

of retrospective ecological analysis without negating the conceptual value of test-site landscapes as study systems [15,22–25].

The environmental behavior of these radionuclides is further governed by local biogeochemistry. Arid conditions, alkaline soils, and sparse vegetation cover define the ecosystem. ^{239}Pu , being particle reactive, exhibits low mobility in such soil types, leading to highly heterogeneous contamination patterns [28]. However, this apparent immobility at the geochemical level does not necessarily preclude biological redistribution. Plant root systems and associated rhizosphere microorganisms may contribute to the mobilization or localized concentration of radionuclides, thereby influencing their bioavailability and uptake. When incorporated into dust, it can be redistributed by wind, creating a dynamic exposure scenario for plant life [28–30]. The uptake of radionuclides by plants is also influenced by these soil properties and by the specific physiology of desert flora. For instance, deep rooted perennial shrubs may access contaminated layers differently than shallow rooted annuals [30,31].

Further uncertainty concerns the magnitude and temporal evolution of absorbed dose rates experienced by plants in these environments. While dose reconstructions have been performed for human populations exposed to Trinity fallout, comparable long-term estimates for native flora remain limited. Spatial heterogeneity in soil contamination, vertical distribution of α -emitting radionuclides relative to root architecture, and intermittent exposure via resuspended dust introduce additional variability. Consequently, for most plant species in New Mexico, precise dose–response relationships cannot presently be established [20,25,32]. The evolutionary considerations discussed in this review should therefore be interpreted within a context of incomplete dosimetric resolution.

From a biological standpoint, the impact of α -emitting radionuclides depends critically on exposure pathways and internalization. External γ radiation may affect aerial tissues directly, whereas α particles exert meaningful biological effects primarily when radionuclides are incorporated into plant tissues through root uptake or when contaminated particles adhere to leaf surfaces [18,30,33]. In arid environments, wind-driven resuspension of fine particles may intermittently enhance foliar exposure. However, the micro-scale distribution of incorporated radionuclides within specific plant tissues remains poorly characterized, complicating attempts to infer cellular-level consequences from bulk soil measurements alone. Clarifying these pathways will be essential for linking environmental contamination to plausible mechanisms of biological response [34–36].

This combination of factors creates a multifaceted selective landscape. Plant populations have been exposed to an initial acute irradiation followed by decades of chronic, low dose rate exposure from a radionuclide mixture with high radiotoxicity. The exposure is further modulated by the abiotic stresses inherent to the desert environment, such as water scarcity and high temperatures [4,23,25]. This interplay between radiological and climatic stressors may be associated with the persistence of resilient plant phenotypes, although it cannot be assumed that adaptation to one stressor directly confers tolerance to another without shared underlying mechanisms [4,18,20,31,37].

Understanding this complex environment is a prerequisite for formulating sound hypotheses about plant adaptation. The following section will build upon this radiological and ecological foundation to analyze the specific biological responses and documented effects observed in the flora of the New Mexico test sites.

3 Documented Plant Responses and Potential Adaptive Traits in New Mexico Flora

Building upon the unique radiological context of the New Mexico test site, this section synthesizes the empirical evidence for biological effects and potential adaptive responses in native plant populations.

The documented responses range from immediate radiological damage to intriguing indications of long-term resilience, suggesting the possibility of sustained selective pressures operating over the decades since contamination, although the distinction between direct evidence and inferred responses remains critical [4,15,23,25,31].

Initial studies conducted in the aftermath of tests documented severe morphological abnormalities and population declines in sensitive species. However, a key observation, consistent with findings from Chernobyl, is that the exclusion zones are not barren wastelands. Instead, they host thriving plant communities, indicating that many species possess inherent tolerance or display persistence under chronic exposure, without necessarily implying evolutionary adaptation. Research has highlighted several native species that demonstrate notable persistence in contaminated areas [3,33]. These include hardy perennial shrubs such as *Gutierrezia sarothrae* (broom snakeweed) and *Yucca elata* (soap tree yucca), along with resilient grasses like *Sporobolus* species (dropseeds). Their persistence is consistent with pre-existing stress tolerance or stress-associated traits, while evidence for radiation-driven genetic adaptation in these taxa remains limited and largely indirect [20,31,38].

The proposed mechanisms for this resilience mirror the fundamental stress responses identified in other irradiated ecosystems. A critical line of evidence points to genetic and epigenetic alterations [39]. Studies on *Machaeranthera* species, a genus of desert asters, have revealed elevated frequencies of chromosomal aberrations in contaminated sites. This represents one of the few examples of site-specific cytogenetic evidence available for plant species in the New Mexico test sites [20,40,41] (Table 1). While this indicates ongoing genotoxic stress, it also implies strong selective pressure for enhanced DNA repair capacity. Furthermore, research on the native bunchgrass *Sporobolus airoides* has been interpreted as consistent with potential heritable genetic change, although this interpretation is primarily based on indirect evidence and broader plant radiation studies rather than site-specific molecular data. Alongside genetic changes, epigenetic modifications, such as differential DNA methylation patterns in plants from contaminated soils, offer a plausible mechanism for rapid, non-genetic adjustment to stress, potentially stabilizing over generations [20,31,37,40–42].

Physiological adaptations are equally critical for survival. The combination of radiological and desert aridity stresses necessitates efficient management of oxidative stress [21]. It is hypothesized, based largely on general plant stress biology and studies from other irradiated systems, that successful resident species may upregulate antioxidant defense systems, including enzymes like superoxide dismutase and peroxidases, to mitigate radiation-induced reactive oxygen species [18,20,31,33]. The synthesis of protective secondary metabolites, such as flavonoids and other phenolic compounds, likely provides an additional layer of antioxidant protection [43]. These physiological buffering capacities may confer a fitness advantage under combined radiological and environmental stress, although their specific contribution in the New Mexico context remains to be directly demonstrated. To improve clarity, it is essential to distinguish between site-specific observations and broader inferences derived from general plant radiation biology. The evidence summarized below should therefore be interpreted within this context [20,23,25,33].

Table 1: Documented plant species and responses at the New Mexico nuclear test sites.

Species	Common Name	Documented Evidence/Notable Traits	References
<i>Machaeranthera</i> spp.	Desert Aster	Elevated frequencies of chromosomal aberrations reported in contaminated sites; represents one of the few examples of site-specific cytogenetic evidence in New Mexico flora.	
<i>Sporobolus airoides</i>	Alkali Sacaton	Evidence consistent with potential radiation-associated genetic or physiological responses based on broader grass and plant radiation literature; site-specific molecular data currently lacking.	
<i>Yucca elata</i>	Soap Tree Yucca	Long-lived perennial; persistence in contaminated areas suggests ecological resilience, but no direct evidence of radiation-associated genetic or molecular changes is currently available.	[3,21,23,25,41]
<i>Gutierrezia sarothrae</i>	Broom Snakeweed	Widespread perennial shrub; persistence in contaminated areas indicates tolerance to environmental stress, without direct evidence linking this to radiation-specific effects.	
<i>Sporobolus</i> spp.	Dropseeds	Resilient grasses; epigenetic or physiological responses to environmental stress are plausible based on analogous studies but remain unconfirmed for New Mexico populations.	

In summary, the flora of the New Mexico test sites exhibits indications of radiological impact, although the strength of evidence varies considerably among species and is often indirect. The persistence of resilient species is consistent with the possibility of selective pressures operating in these environments, but it does not by itself distinguish between inherent tolerance, phenotypic plasticity and adaptive evolutionary change [15,21,23]. The molecular targets and pathways summarized in Table 2 represent candidate mechanisms that could underpin the biological patterns described above and serve as focal points for future hypothesis-driven investigations.

It is important to emphasize that the molecular pathways and gene candidates listed in Table 2 are proposed as hypotheses derived from general plant biology and radiation studies and have not yet been validated in the specific context of New Mexico test-site flora.

The following section will explore the future research directions required to move from observing these correlations to conclusively demonstrating adaptive evolution.

Table 2: Hypothesized candidate genes and molecular pathways for plant species in New Mexico test-site environments.

Species	Exposure Context (qualitative)	Candidate Genes/Regulators	Pathways/Processes	Evidence Level	Dose-Response Pattern (Qualitative)	References
<i>Machaeranthera</i> spp. (Desert aster)	Mixed: historical pulse + chronic low-dose	ATM, ATR, SOG1, RAD51, XRCC family, PARP; DNMTs (maintenance methylation)	DNA damage response (DSB sensing and repair: HR/NHEJ), DDR signaling, epigenetic regulation (DNA methylation)	Direct (cytogenetic aberrations reported); candidate molecular pathways inferred from general plant radiation studies	Acute: rapid activation of DDR; chronic: selection for efficient repair, possible stable epigenetic shifts (hypothesized)	
<i>Sporobolus airoides</i> (Alkali sacaton)	Chronic soil-borne/particle exposure	SOD, CAT, APX, GST; GSH-metabolism genes; RAD51, XRCC	Antioxidant systems (ROS detoxification), redox homeostasis, DNA repair	Indirect (based on broader grass and plant radiation studies; no species-specific molecular data available)	Chronic low-dose: sustained antioxidant up-regulation; potential trade-offs in growth/reproduction (hypothesized)	
<i>Yucca elata</i> (Soap tree yucca)	Long-lived perennial; mixed exposure (intermittent foliar + root)	PAL, CHS, other phenylpropanoid enzymes; HSPs; ATR; transcription factors (WRKY, NAC)	Secondary metabolism (flavonoid/phenylpropanoid biosynthesis), proteostasis, stress signaling	Inferred (ecological persistence observed; no direct species-specific molecular or genetic data available)	Chronic: enhanced secondary metabolite biosynthesis and protective physiologies; intermittent acute responses possible (hypothesized)	[15,21,23–25]
<i>Gutierrezia sarothrae</i> (Broom snakeweed)	Patchy chronic contamination; resilient perennial	MAPK cascade components; ABA-pathway genes; antioxidant enzymes (SOD/CAT/APX); epigenetic modulators (HMTs/DNMTs)	Stress signaling networks (hormonal regulation), redox balance, epigenetic regulation of stress responses	Inferred (ecological persistence observed; no direct evidence linking responses to radiation-specific effects)	Chronic: modulation of signaling pathways and antioxidant defenses; epigenetic regulation plausible (hypothesized)	
<i>Sporobolus</i> spp. (other dropseeds)	Mixed/gradient-dependent exposures	SOG1, RAD51, XRCC; DNMTs; SOD/CAT; transcriptional regulators of stress (bZIP, AP2/ERF)	DDR, epigenetic modification, ROS detoxification, transcriptional reprogramming	Indirect (based on analogous grass studies; no species-specific data available for New Mexico populations)	Dose-dependent DDR activation; chronic exposures favor epigenetic and metabolic adjustments (hypothesized)	

4 Future Research Directions: A Roadmap for a Pioneering Field

The synthesis presented in this review underscores that the New Mexico test sites constitute a critical yet underexplored natural laboratory for plant radioecology. The limited and fragmented nature of the existing literature necessitates a coordinated and innovative research agenda to transform preliminary observations into a mechanistic understanding of evolutionary adaptation. Future investigations should leverage advanced technologies and hypothesis driven experimental designs to address several key frontiers. In particular, addressing the current limitations in dosimetric reconstruction will be essential. Retrospective approaches such as optically stimulated luminescence (OSL) or electron paramagnetic resonance (EPR) applied to soil minerals or long-lived plant structures could provide valuable constraints on historical dose exposure [44,45].

A primary and imperative direction involves the explicit testing of local adaptation through reciprocal transplant experiments and common garden studies. Establishing common gardens where populations from contaminated sites are grown alongside control populations in non-contaminated soils would allow researchers to disentangle genetic adaptation from phenotypic plasticity. In addition, the use of standardized or sterilized substrates in controlled conditions will be important to minimize variability in soil chemistry and isolate the specific contribution of radiological exposure. Observing whether putatively tolerant traits, such as enhanced growth or reduced cytogenetic damage, persist in a common environment would provide conclusive evidence for evolutionary change. Complementarily, reciprocal transplants would test the fitness consequences of these adaptations in the native environment [46].

The application of multi omics technologies represents another essential frontier. Integrating genomics, transcriptomics, proteomics, and metabolomics on the same plant individuals from contamination gradients could provide a systems-level view of plant responses, although such approaches have not yet been widely applied to New Mexico test-site flora [47]. Genomic sequencing could reveal signatures of selection in genes related to DNA damage response, chromatin remodeling, and antioxidant defense. Transcriptomic and metabolomic profiling could identify the key regulatory networks and crucial metabolic pathways, such as the phenylpropanoid pathway for flavonoid biosynthesis, that are actively deployed for survival in the field [48–50].

Metagenomic analyses of the rhizosphere soil of resilient species such as *Yucca elata* or *Gutierrezia sarothrae* could help characterize associated microbial communities; however, controlled experimental approaches, including synthetic microbial communities or targeted inoculation studies, will be necessary to determine whether these microbes actively contribute to plant radiotolerance rather than simply co-occurring with host plants in contaminated soils [21,51,52].

Finally, research must explore the potential evolutionary tradeoffs associated with radiation tolerance. A critical question is whether enhanced resilience to radiation comes at a cost to other fitness components. Controlled experiments are needed to determine if tolerant genotypes exhibit reduced competitiveness, decreased resistance to biotic stressors like pathogens, or lower reproductive output in benign environments. Understanding these potential trade-offs will be important for accurately modelling the long-term ecological trajectories of these systems under combined environmental and radiological stress [53]. The logistical and regulatory constraints associated with access to nuclear test sites, often located within restricted governmental or military areas, should also be considered. Progress in this field will likely require coordinated interdisciplinary efforts involving ecologists, radiobiologists, physicists, and relevant regulatory agencies [23–25,53].

5 Conclusion

This review situates the New Mexico nuclear test sites within the broader context of plant radioecology, highlighting their potential as a distinctive, yet underexplored, system for investigating plant responses to ionizing radiation. The radiological legacy of these sites, characterized by a complex mixture of long-lived radionuclides within an arid ecosystem, may have contributed to the establishment of a unique environmental context in which both acute and chronic stressors interact.

The persistence of native plant communities in these environments, together with limited and often indirect evidence of genetic and epigenetic alterations, provides a preliminary basis for considering the potential role of radiation as a selective factor. However, current knowledge remains insufficient to determine whether observed patterns reflect radiation-driven adaptive processes, phenotypic plasticity, or the expression of pre-existing stress tolerance typical of desert flora.

In this context, the New Mexico test sites may be conceptualized as occupying an intermediate position between the acute exposure scenarios of Hiroshima and Nagasaki and the long-term chronic contamination observed in Chernobyl and Fukushima. This framework should be regarded as a working hypothesis, rather than a defined radiological category, requiring further empirical validation.

A central challenge remains the limited availability of site-specific data and the difficulty of disentangling the effects of ionizing radiation from those of co-occurring environmental stressors, including aridity, temperature variability, and soil heterogeneity. Addressing these limitations will require integrative and carefully controlled experimental approaches, combining field-based studies with advanced molecular and ecological methods.

Future research should prioritize the development of robust experimental designs capable of distinguishing between ecological persistence, physiological acclimation, and adaptive evolutionary change. In particular, the integration of multi-omics approaches, controlled common garden experiments, and improved dosimetric reconstruction will be essential for establishing clearer links between environmental exposure and biological response.

Overall, the study of plant communities in New Mexico test-site environments offers a valuable opportunity to advance our understanding of plant responses to chronic radiological exposure. Such insights may contribute not only to fundamental questions in evolutionary and stress biology, but also to the refinement of ecological risk assessment models for environments impacted by long-lived radionuclides.

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References

1. Hanson SK, Oldham WJ. Weapons radiochemistry: Trinity and beyond. *Nucl Technol.* 2021;207(sup1):S295–308. [[CrossRef](#)].
2. Carr AB. Thirty minutes before the dawn. *Nucl Technol.* 2021;207(sup1):S1–S23. [[CrossRef](#)].
3. Ludovici GM, Tassi PA, Iannotti A, Russo C, D’Agostino F, Neble Segade M, et al. The *Phoenix flora*: Plant survival, succession, and putative adaptation in the post-atomic landscapes of Hiroshima and Nagasaki. *Prog Biophys Mol Biol.* 2026;200:1–5. [[CrossRef](#)].
4. Práválie R. Nuclear weapons tests and environmental consequences: A global perspective. *AMBIO.* 2014;43(6):729–44. [[CrossRef](#)].
5. Saravanan P, Anjan DK, Vharshini S, Sowmya B, López-Maldonado EA, Saravanan V, et al. A comprehensive review of eco toxicity of Cesium 137 deterioration of radionuclides pollution. *Environ Sci Pollut Res.* 2025;32(26):15518–45. [[CrossRef](#)].
6. Ludovici GM, Chierici A, de Souza SO, D’Errico F, Iannotti A, Malizia A. Effects of ionizing radiation on flora ten years after the Fukushima Dai-ichi disaster. *Plants.* 2022;11(2):222. [[CrossRef](#)].
7. Yildiz Deniz G. Chernobyl as a natural laboratory: Genetic instability, adaptation, and ecological recovery in flora and fauna under chronic radiation. *Mutat Res Genet Toxicol Environ Mutagen.* 2025;907:503898. [[CrossRef](#)].
8. Ajanaku O, Ilori AO, Ediagbonya TF. Dynamics of radionuclide movement in forests: A review of Chernobyl and Fukushima impact studies. *J Environ Radioact.* 2025;287:107723. [[CrossRef](#)].
9. Mousseau TA. The biology of Chernobyl. *Annu Rev Ecol Evol Syst.* 2021;52:87–109. [[CrossRef](#)].
10. Ludovici GM, Tassi PA, Iannotti A, Russo C, Giorgio SM, Malizia A. The unnatural selection: Plant evolution and adaptation in the Chernobyl and Fukushima Exclusion Zones. *J Environ Radioact.* 2026;291:107850. [[CrossRef](#)].
11. Konoplev A. Fukushima and Chernobyl: Similarities and differences of radiocesium behavior in the soil-water environment. *Toxics.* 2022;10(10):578. [[CrossRef](#)].
12. Pareniuk O, Yasuda N. Chornobyl exclusion zone: Current status and challenges. *Ann ICRP.* 2021;50(1_suppl):201–8. [[CrossRef](#)].
13. Ajah SA, Akanji L, Gomes J. Recent trends in nuclear accident events prediction: A review. *Nucl Technol.* 2025;211(11):2668–98. [[CrossRef](#)].
14. Smith MBR, Collins ED, DePaoli DW, Gallego NC, Heilbronn LH, Jensen CL, et al. Nuclear physics, radioisotope fuels, and protective components. In: Woerner DF, editor. *The technology of discovery.* Hoboken, NJ, USA: John Wiley & Sons, Inc.; 2023. p. 85–132. [[CrossRef](#)].
15. Simon SL, Bouville A, Beck HL, Melo DR. Estimated radiation doses received by new Mexico residents from the 1945 trinity nuclear test. *Health Phys.* 2020;119(4):428–77. [[CrossRef](#)].
16. Dorhout JM, Wilkerson MP. A review of nuclear forensics: 2016–2020. Los Alamos, NM, USA: Los Alamos National Laboratory; 2021. 27 p. Report No.: LA-UR-21-28895.
17. Jiang Z, van Zanten M, Sasidharan R. Mechanisms of plant acclimation to multiple abiotic stresses. *Commun Biol.* 2025;8:655. [[CrossRef](#)].
18. Ludovici GM, Oliveira de Souza S, Chierici A, Cascone MG, D’Errico F, Malizia A. Adaptation to ionizing radiation of higher plants: From environmental radioactivity to Chernobyl disaster. *J Environ Radioact.* 2020;222:106375. [[CrossRef](#)].
19. Turnbull J. Making sense of nuclear natures: Ecologies, expertise, aesthetics. *Prog Environ Geogr.* 2025;4(4):436–64. [[CrossRef](#)].
20. Geras’kin S. Plant adaptation to ionizing radiation: Mechanisms and patterns. *Sci Total Environ.* 2024;916:170201. [[CrossRef](#)].
21. Rehman A, Memon RA, Hameed M, Naz N, Ali Shah A, Moussa IM, et al. Exploring the adaptive mechanisms and strategies of various populations of *Sporobolus ioclados* in response to arid conditions in Cholistan desert. *BMC Plant Biol.* 2024;24(1):947. [[CrossRef](#)].
22. Ivanov MM, Fominykh P, Ivanova N, Krasnov S, Golosov V. The long-term dynamics of the particulate ¹³⁷Cs supply from eroded arable slopes during the post-Chernobyl period. *Toxics.* 2026;14(4):344. [[CrossRef](#)].

23. Bouville A, Beck HL, Thiessen KM, Hoffman FO, Potischman N, Simon SL. The methodology used to assess doses from the first nuclear weapons test (trinity) to the populations of new Mexico. *Health Phys.* 2020;119(4):400–27. [[CrossRef](#)].
24. Beck HL, Simon SL, Bouville A, Romanyukha A. Accounting for unfissioned *Plutonium* from the trinity atomic bomb test. *Health Phys.* 2020;119(4):504–16. [[CrossRef](#)].
25. Simon SL, Bouville A, Beck HL, Anspaugh LR, Thiessen KM, Hoffman FO, et al. Dose estimation for exposure to radioactive fallout from nuclear detonations. *Health Phys.* 2022;122(1):1–20. [[CrossRef](#)].
26. Miederer M, Benešová-Schäfer M, Mamat C, Kästner D, Pretze M, Michler E, et al. Alpha-emitting radionuclides: Current status and future perspectives. *Pharmaceutics.* 2024;17(1):76. [[CrossRef](#)].
27. Cruz-Nova P, Trujillo-Nolasco M, Aranda-Lara L, Ferro-Flores G, Ocampo-García B. Radiobiological effect of alpha particles. The scientific basis of targeted alpha-particle therapy. *Nucl Med Biol.* 2025;146:109044. [[CrossRef](#)].
28. Mohammad REA, Veerasingam S, Suresh G, Rajendran S, Sadasivuni KK, Ghani S, et al. Tackling environmental radionuclides contamination: A systematic review of chemical, biological, and physical remediation strategies. *Chem Eng J Adv.* 2025;23:100802. [[CrossRef](#)].
29. Deblonde GJP, Kersting AB, Zavarin M. Open questions on the environmental chemistry of radionuclides. *Commun Chem.* 2020;3:167. [[CrossRef](#)].
30. Li H, Wang Q, Zhang C, Su W, Ma Y, Zhong Q, et al. Geochemical distribution and environmental risks of radionuclides in soils and sediments runoff of a uranium mining area in South China. *Toxics.* 2024;12(1):95. [[CrossRef](#)].
31. Duarte GT, Volkova PY, Fiengo Perez F, Horemans N. Chronic ionizing radiation of plants: An evolutionary factor from direct damage to non-target effects. *Plants.* 2023;12(5):1178. [[CrossRef](#)].
32. Veresoglou SD, Begum N. Dose-response curves: The next frontier in plant ecology. *Trends Plant Sci.* 2024;29(9):971–7. [[CrossRef](#)].
33. Yoschenko V, Nanba K, Orosun MM, Zhang J, Johnson TE. Assessing the quasi-equilibrium distribution of Fukushima-derived radiocesium in a typical Japanese cedar forest using an isotopic approach. *J Environ Radioact.* 2025;288:107742. [[CrossRef](#)].
34. Semioshkina N, Voigt G. Soil–Plant transfer of radionuclides in arid environments. *J Environ Radioact.* 2021;237:106692. [[CrossRef](#)].
35. Brown J, Teien HC, Thørring H, Skipperud L, Hosseini A, Lind OC, et al. Transfer of radionuclides through ecological systems: Lessons learned from 10 years of research within CERAD CoE. *Sci Total Environ.* 2024;940:173503. [[CrossRef](#)].
36. Makki AA, Hajjar D, Bagais O, Soliman M. Soil-to-plant transfer factor of natural radionuclides and associated health risk in some vegetable species in arid area. *J Radioanal Nucl Chem.* 2024;333(8):3947–54. [[CrossRef](#)].
37. Zhang H, Zhao Y, Zhu JK. Thriving under stress: How plants balance growth and the stress response. *Dev Cell.* 2020;55(5):529–43. [[CrossRef](#)].
38. Mishra S, Duarte GT, Horemans N, Ruytinx J, Gudkov D, Danchenko M. Complexity of responses to ionizing radiation in plants, and the impact on interacting biotic factors. *Sci Total Environ.* 2024;924:171567. [[CrossRef](#)].
39. Wu T, Liu Y, Wang Z, Yao Y, Cheng X, Zhao Y. A systematic review of terrestrial ecosystem resilience: Trends and adaptations over the past 50 years. *Geogr Sustain.* 2026;7(1):100410. [[CrossRef](#)].
40. Morgan DR, Hartman RL. A synopsis of *Machaeranthera* (Asteraceae: Astereae), with recognition of segregate Genera. *SIDA Contrib Bot.* 2003;20(4):1387–416.
41. Varney DM, Rhoads WA. Chronic radiation induced chromosomal aberrations in native shrubs at Nevada Test Site. In: *Proceedings of the Symposium on dynamics of transuranics in terrestrial and aquatic environments*; 1976 Oct 5–7; Gatlinburg, TN, USA. p. 351–78.
42. Lodhi N, Srivastava R. Dynamics and malleability of plant DNA methylation during abiotic stresses. *Epigenomes.* 2025;9(3):31. [[CrossRef](#)].
43. Kuljarusnont S, Iwakami S, Iwashina T, Tungmunthum D. Flavonoids and other phenolic compounds for physiological roles, plant species delimitation, and medical benefits: A promising view. *Molecules.* 2024;29(22):5351. [[CrossRef](#)].
44. Ainsbury EA. Networking in biological and physical retrospective dosimetry in Europe and beyond. *J Radiat Res.* 2024;65(Supplement_1):i2–5. [[CrossRef](#)].

45. Fattibene P, Trompier F, Bassinet C, Ciesielski B, Discher M, Eakins J, et al. Reflections on the future developments of research in retrospective physical dosimetry. *Phys Open*. 2023;14:100132. [[CrossRef](#)].
46. Zuma MC, Burgess TI, Sapsford SJ. Addressing variability and advancing methodological clarity in plant-soil feedback experiments. *J Plant Interact*. 2025;20(1):2529228. [[CrossRef](#)].
47. Li L, Ge Z, Liu S, Zheng K, Li Y, Chen K, et al. Multi-omics landscape and molecular basis of radiation tolerance in a tardigrade. *Science*. 2024;386(6720):eadl0799. [[CrossRef](#)].
48. Wang Y, Zhang J, Wang P, Li Y, Wang Y, Yan Y, et al. Integrated transcriptomic and metabolomic analysis reveals tissue-specific flavonoid biosynthesis and MYB-mediated regulation of UGT71A1 in *Panax quinquefolius*. *Int J Mol Sci*. 2025;26(6):2669. [[CrossRef](#)].
49. Khan A, Tian R, Bean SR, Yerka M, Jiao Y. Transcriptome and metabolome analyses reveal regulatory networks associated with nutrition synthesis in sorghum seeds. *Commun Biol*. 2024;7:841. [[CrossRef](#)].
50. Wang H, Gang H, Chen J, Liu J, Zhang X, Fu C, et al. Transcriptomic and metabolomic analyses reveal molecular and metabolic regulation of anthocyanin biosynthesis in three varieties of currant. *Food Res Int*. 2024;196:115056. [[CrossRef](#)].
51. Peng M, Jiang M, Wang C, Yang ZA, He H. Metagenomic insights into the influence of soil habitat on rhizosphere microbial function and element cycling in ephemeral plants. *Appl Soil Ecol*. 2026;219:106700. [[CrossRef](#)].
52. Alharbi SM, Al-Sulami N, Al-Amrah H, Anwar Y, Gadah OA, Bahamdain LA, et al. Metagenomic characterization of the *Maerua crassifolia* soil rhizosphere: Uncovering microbial networks for nutrient acquisition and plant resilience in arid ecosystems. *Genes*. 2025;16(3):285. [[CrossRef](#)].
53. Schuwirth N, Borgwardt F, Domisch S, Friedrichs M, Kattwinkel M, Kneis D, et al. How to make ecological models useful for environmental management. *Ecol Model*. 2019;411:108784. [[CrossRef](#)].