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Radioecological and plant response patterns under chronic radiation exposure at former nuclear test sites

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ABSTRACT

Background: Atmospheric and underground nuclear weapons testing generated long-lasting radioactive contamination across multiple terrestrial and marine environments. Several former nuclear test sites still exhibit heterogeneous distributions of radionuclides in soils, groundwater, sediments, and biota decades after testing ceased.

Objective: This review critically examines radionuclide persistence, environmental transfer processes, and reported ecological and plant-related responses across major historical nuclear test regions, including the Nevada Test Site, Semipalatinsk, the Marshall Islands and French Polynesia.

Methods: A comparative literature-based analysis was conducted using radiological surveys, environmental monitoring reports, and peer-reviewed radioecological studies. The review evaluated contamination patterns, soil-to-biota transfer pathways, and documented ecological observations across chronically exposed environments.

Results: Persistent contamination involving radionuclides such as ^{137}Cs, ^{90}Sr, plutonium isotopes, americium, and tritium remain documented at several former testing areas. Monitoring programs consistently report strong spatial heterogeneity influenced by local geology, hydrology, atmospheric transport, and resuspension processes. Although some studies describe altered ecological dynamics and physiological stress responses in exposed organisms, evidence for consistent long-term ecosystem-scale effects or adaptive biological responses remains limited and site-dependent. Interpretation is further complicated by heterogeneous dosimetry, limited longitudinal datasets, and multiple environmental confounding factors.

Conclusions: Former nuclear test sites remain important environments for long-term radioecological investigation. Current evidence clearly supports persistent environmental contamination and ongoing radionuclide transfer processes, whereas broader ecological consequences remain incompletely resolved.

1. Introduction

Between 1945 and the late twentieth century, more than two thousand nuclear weapons tests were conducted worldwide, including both atmospheric and underground detonations (Prăvălie, 2014). These activities resulted in the dispersion of fission and activation products across terrestrial and marine environments, leading to persistent radiological contamination at numerous former test sites (Prăvălie, 2014). In this context, fallout refers to the deposition of radioactive particles produced during nuclear detonations, which are transported through the atmosphere and subsequently settle on terrestrial and aquatic surfaces, generating spatially heterogeneous contamination patterns influenced by detonation characteristics and meteorological conditions (Li et al., 2024; McGuffin et al., 2024). Although atmospheric fallout declined substantially following international test ban agreements, several regions remain characterized by heterogeneous

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radionuclide inventories, long-lived isotopes in soils, and spatially variable chronic exposure conditions (Prăvălie, 2014; Li et al., 2024).

Most investigations of nuclear test sites have focused on radiological characterization, dose reconstruction, and human health implications. Substantial data exists on radionuclide inventories, soil distribution patterns, and long-term decay processes (Prăvălie, 2014; Simon et al., 2022). However, biological investigations have often remained site specific and methodologically heterogeneous, limiting the development of a robust comparative ecological framework. Plant responses to chronic fallout exposure have been examined within individual geographic contexts, primarily through localized field observations and limited experimental studies, but a systematic cross-site synthesis integrating contamination profiles, plant physiology, and ecosystem dynamics remains limited (Pentreath and Woodhead, 2001; Bondarkov et al., 2011; Møller et al., 2012; Beresford et al., 2022; Oliver et al., 2024; Ludovici et al., 2026a).

Terrestrial vegetation plays a central role in contaminated ecosystems. Plants regulate primary productivity, influence soil structure and erosion processes, mediate radionuclide transfer within food webs, and contribute to long-term ecosystem recovery trajectories (Zhakypbek et al., 2024). Chronic exposure to ionizing radiation (IR) may affect plant metabolism, oxidative balance, genomic stability, reproduction, and competitive interactions, although the extent to which these responses scale to community or ecosystem-level processes remains incompletely resolved (Einor et al., 2016; Nybakken et al., 2023; Geras'kin, 2024).

Nuclear test sites therefore represent long-term environmental systems in which radiological gradients interact with climatic conditions, soil properties, and ecological processes. Comparative analysis across contrasting biomes allows evaluation of whether recurring physiological and ecological patterns emerge under chronic fallout exposure, or whether responses remain predominantly site dependent (Geras'kin and Volkova, 2014; Prăvălie, 2014; Ludovici et al., 2022; Yoschenko et al., 2025).

This review critically examines the environmental persistence of fallout contamination together with reported ecological and plant physiological responses across four major nuclear test regions: the Marshall Islands, Semipalatinsk in Kazakhstan, the Nevada Test Site in the United States, and French Polynesia. By integrating contamination characteristics, soil-to-plant transfer processes, physiological observations, and vegetation dynamics, we evaluate the extent to which common ecological patterns are supported across sites, assess current evidence for adaptive or long-term biological responses, and highlight research gaps relevant to environmental risk assessment in radiologically contaminated landscapes.

2. Materials and methods

This review was conducted as a comparative narrative synthesis focused on four former nuclear weapons test regions: the Marshall Islands, the Semipalatinsk Test Site, the Nevada Test Site, and French Polynesia. Literature searches were performed using Scopus, Web of Science, and Google Scholar databases up to March 2026.

Search terms included combinations of: "nuclear test site", "fallout", "radioecology", "plant response", "soil-to-plant transfer", "chronic radiation", "vegetation", "Semipalatinsk", "Nevada Test Site", "Marshall Islands", and "French Polynesia".

Priority was given to peer-reviewed studies directly investigating radionuclide contamination, environmental transfer processes, vegetation dynamics, and plant physiological responses within the selected regions. Additional mechanistic studies from Chernobyl and Fukushima were included only when used to support broader conceptual interpretation of radiation-related biological processes and are explicitly distinguished from site-specific evidence.

Studies lacking sufficient methodological detail or unrelated to terrestrial ecological processes were not emphasized in the comparative analysis.

3. Radiological and environmental characterization of selected nuclear test regions

3.1. Historical testing patterns and deposition regimes

The four regions considered in this review differ substantially in the number, type, and temporal distribution of nuclear detonations, resulting in distinct contamination legacies. The Marshall Islands hosted 67 nuclear tests between 1946 and 1958, including several high-yield thermonuclear detonations that produced substantial fallout deposition across multiple atolls, with cumulative ^{137}Cs inventories ranging from a few kBq m−2 in southern atolls to >100 kBq m−2 in heavily affected northern locations such as Rongelap (Beck et al., 2010; Simon et al., 2010; Prăvălie, 2014). In contrast, the Semipalatinsk Test Site in Kazakhstan hosted 456 nuclear tests between 1949 and 1989, including both atmospheric and underground detonations, generating heterogeneous radionuclide deposition across steppe environments (Lukashenko et al., 2020). The Nevada Test Site was the location of 928 nuclear tests conducted between 1951 and 1992, including both atmospheric and underground detonations, with radionuclide redistribution strongly influenced by arid climatic conditions and episodic wind resuspension processes (Prăvălie, 2014; Simon et al., 2022). French Polynesia experienced 193 nuclear tests between 1966 and 1996, initially atmospheric and later underground, primarily affecting atoll environments characterized by complex marine-terrestrial radionuclide interactions (Drozdovitch et al., 2021).

These differing testing histories strongly influenced radionuclide composition, fallout deposition density, and subsequent environmental redistribution processes across terrestrial and marine environments. Atmospheric detonations generally produced broader and more heterogeneous fallout deposition patterns than underground tests, whereas underground detonations generated more spatially constrained contamination associated with venting events, subsidence, and localized radionuclide migration. Consequently, each region represents a distinct contamination regime shaped by explosive yield, detonation altitude or burial depth, atmospheric transport conditions, and long-term environmental redistribution processes (Beck et al., 2010; Prăvălie, 2014; McGuffin et al., 2024).

3.2. Radionuclide inventories and long-term persistence

Long-lived radionuclides including ^{137}Cs, ^{90}Sr, ^{239}Pu, ^{240}Pu and ^{241}Am remain major contributors to present-day radiological contamination and chronic exposure conditions across former nuclear test sites (Simon et al., 2010; Volkova et al., 2018; Lukashenko et al., 2020; Yoschenko et al., 2022; Ludovici et al., 2026b). However, radionuclide persistence and environmental mobility differ substantially among isotopes. While ^{137}Cs and ^{90}Sr, with half-lives of approximately 30 years, have undergone substantial decay since the period of active testing, plutonium isotopes and ^{241}Am remain environmentally persistent because of their substantially longer half-lives. These differences contribute to evolving radiological gradients over time, influencing external exposure conditions, radionuclide bioavailability, and long-term environmental transfer processes. Their environmental behavior is strongly influenced by soil composition, organic matter content, mineralogy, and hydrological dynamics, which collectively regulate radionuclide retention, mobility, and biological uptake (Simon et al., 2010; Møller and Mousseau, 2011; Payne and Edis, 2012; Lukashenko et al., 2020). In coral atoll systems such as the Marshall Islands and French Polynesia, carbonate-derived substrates and limited clay content strongly influence radionuclide retention, vertical migration, and soil-to-plant transfer dynamics. In contrast, the continental soils of Semipalatinsk and the arid terrains of the Nevada Test Site exhibit variable radionuclide sorption capacity and depth-distribution patterns influenced by erosion, precipitation regimes, wind redistribution, and bioturbation processes (Prăvălie, 2014; Lukashenko et al., 2020; Simon et al., 2022).

Over time, radioactive decay has reduced overall activity levels; however, redistribution processes including resuspension, downward migration, root uptake, and lateral transport continue to maintain heterogeneous exposure conditions across contaminated landscapes (Beck et al., 2010; Simon et al., 2010). The persistence of long-lived actinides contributes to continued chronic contamination, even in areas where external dose rates have declined substantially relative to the immediate post-detonation period (Simon et al., 2010; Prăvălie, 2014; Mishra et al., 2024). Although radionuclide inventories and activity levels vary substantially among sites, isotope-specific half-lives together with ongoing redistribution processes continue to sustain measurable environmental contamination decades after nuclear testing activities ceased.

3.3. Environmental context and soil properties

Climatic and edaphic conditions strongly influence radionuclide bioavailability, environmental mobility, and soil-to-plant transfer processes across contaminated ecosystems. Tropical atoll environments are characterized by high rainfall, rapid organic matter turnover, carbonate-derived soils, and relatively simple vegetation assemblages adapted to nutrient-poor substrates. These factors influence both radionuclide cycling, leaching dynamics and vegetation recovery patterns (Corcho-Alvarado et al., 2021; Drozdovitch et al., 2021). In contrast, the continental steppe of Semipalatinsk experiences marked seasonal variation, with freeze-thaw cycles and variable precipitation affecting soil structure and contaminant mobility (Lukashenko et al., 2020). The Nevada Test Site represents an arid system with low precipitation, sparse vegetation cover, and high potential for wind-driven resuspension of contaminated particles (Prăvălie, 2014; Kaminski et al., 2024).

Such environmental differences contribute to substantial variability in soil-to-plant transfer processes, with transfer factors differing according to radionuclide chemistry, soil composition, vegetation type, and local hydrological conditions (Velasco et al., 2008; Møller et al., 2016; Geras'kin et al., 2017; Yoschenko et al., 2016; Fesenko et al., 2022). Extensive datasets on soil-to-plant transfer factors have been reported for the Semipalatinsk Test Site, providing valuable quantitative insight into radionuclide transfer and environmental mobility under continental conditions (Larionova et al., 2018, 2021; Krivitskiy et al., 2026). Additional investigations conducted on vegetation growing around contaminated nuclear fuel cycle facilities in Kazakhstan further highlight the complexity of artificial radionuclide accumulation under different environmental settings (Larionova et al., 2024). Studies across different contaminated sectors of the Semipalatinsk Test Site have documented substantial differences in radionuclide accumulation among plant communities, reflecting variation in soil properties, contamination histories, and local ecological conditions (Larionova et al., 2018, 2021; Krivitskiy et al., 2026). Consequently, chronic exposure conditions cannot be interpreted independently of local climatic constraints and soil chemistry (Thiry et al., 2009; Geras'kin, 2016; Yoschenko et al., 2018).

3.4. Spatial heterogeneity and radiological gradients

A defining feature of former nuclear test sites is the presence of pronounced small-scale and landscape-level radiological gradients. In this context, radiological gradients refer to spatial and temporal variations in radionuclide activity concentrations and associated dose rates, occurring across both localized and broader landscape-scale environments. Patchy deposition, topographic variation, and differential soil retention generate heterogeneous exposure mosaics that may vary over short distances. These gradients represent persistent environmental variables that may contribute to localized differences in plant establishment, competitive interactions, and vegetation distribution patterns under chronic exposure conditions (Prăvălie, 2014).

Understanding plant responses therefore requires integration of contamination gradients with ecological context (Yoschenko et al., 2011; Oudalova and Geras'kin, 2012; Yoschenko et al., 2017; Duarte et al., 2023). Dose rate alone is insufficient to predict biological responses without consideration of radionuclide speciation, soil binding dynamics, and plant functional traits (Ansoborlo et al., 2007). Comparative analysis across regions characterized by contrasting environmental constraints may help identify recurring radioecological patterns while acknowledging substantial site-specific variability and methodological limitations (Simon et al., 2010; Prăvălie, 2014; Lukashenko et al., 2020; Mousseau and Møller, 2020; Corcho-Alvarado et al., 2021).

A comparative summary of the main radiological and environmental characteristics of the four selected nuclear test regions is provided in Table 1.

4. Radionuclide dynamics and soil-to-plant transfer processes

Radionuclide behavior in former nuclear test sites is governed by physicochemical interactions among deposited fallout particles, soil matrices, hydrological conditions, and plant uptake processes (Salbu et al., 2004; Payne and Edis, 2012; Mohammad et al., 2025). Long-lived isotopes such as ^{137}Cs and ^{90}Sr exhibit distinct mobility patterns depending on mineral composition, cation exchange capacity, organic matter content and soil moisture conditions. ^{137}Cs is often strongly adsorbed to clay minerals in continental soils, reducing immediate bioavailability but permitting gradual root uptake over extended periods (Payne and Edis, 2012; Malizia et al., 2021; Bituh et al., 2025). In contrast, ^{90}Sr may display greater mobility in certain substrates due to its chemical similarity to calcium, promoting incorporation into plant tissues via calcium transport pathways (Bituh et al., 2025; Mohammad et al., 2025).

In coral atoll environments, limited clay content and carbonate-dominated substrates can influence radionuclide retention and mobility differently from silicate-based continental soils. Variability in leaching, vertical migration, and surface redistribution contributes to heterogeneous radionuclide activity profiles in soils (Corcho-Alvarado et al., 2021; Drozdovitch et al., 2021). Arid environments such as the Nevada Test Site present additional complexity due to low precipitation, limited organic matter accumulation, and episodic wind-driven resuspension, potentially reintroducing radionuclides onto plant surfaces (Prăvălie, 2014).

Reported soil-to-plant transfer factors vary substantially across sites and radionuclides, reflecting differences in species traits, rooting depth, soil chemistry, hydrological conditions, and local microtopography.

Reported transfer factors for ^{137}Cs and ^{90}Sr may vary by several orders of magnitude across contaminated systems, depending on radionuclide chemistry, vegetation type, soil mineralogy, and local hydrological conditions (Velasco et al., 2008; Parvin et al., 2025).

Chronic exposure conditions therefore result from interactions among external dose rates, internal radionuclide incorporation, and site-specific environmental modifiers (Velasco et al., 2008; Møller and Mousseau, 2017; Parvin et al., 2025).

Understanding these transfer dynamics is essential for interpreting observed plant physiological responses. Without integration of contamination intensity, radionuclide speciation, and soil properties, biological endpoints cannot be reliably compared across regions. Consequently, comparative ecological assessment must explicitly consider both contamination profiles and environmental context when evaluating long-term vegetation responses (Salbu et al., 2004; Payne and Edis, 2012; Bituh et al., 2025; Parvin et al., 2025).

Table 1
Comparative radiological and environmental characteristics of selected former nuclear test regions.

Region	Testing period	Dominant test type	Approximate number of tests	Principal long-lived radionuclides	Dominant environmental characteristics	Vegetation context	Main environmental redistribution processes	Current contamination profile	References
Marshall Islands	1946–1958	Atmospheric thermonuclear	67	^{137}Cs, ^{90}Sr, ^{239}Pu, ^{240}Pu, ^{241}Am	Tropical coral atolls; carbonate-derived soils; low clay content; high rainfall	Coconut-dominated atoll vegetation and low-diversity tropical assemblages	Leaching, vertical migration, marine-terrestrial redistribution, resuspension	Persistent heterogeneous contamination with localized high-activity zones in northern atolls, including Bikini and Rongelap	Beck et al. (2010); Simon et al. (2010); Corcho-Alvarado et al. (2021)
Semipalatinsk Test Site, Kazakhstan	1949–1989	Atmospheric and underground	456	^{137}Cs, ^{90}Sr, Pu isotopes	Continental steppe; silicate soils; seasonal freeze-thaw cycles; variable precipitation	Grassland-steppe vegetation with mixed herbaceous communities	Wind redistribution, soil migration, erosion, bioturbation	Strongly heterogeneous contamination near test epicenters and fallout traces	Prăvălie (2014); Larionova et al. (2018); Lukashenko et al. (2020)
Nevada Test Site, USA	1951–1992	Atmospheric and underground	928	^{137}Cs, ^{90}Sr, Pu isotopes, ^{241}Am, tritium	Arid desert environment; coarse-textured soils; low organic matter; limited precipitation	Sparse xerophytic desert vegetation	Wind-driven resuspension, episodic surface redistribution, limited downward migration	Patchy contamination with persistent actinide redistribution in surface soils	Simon et al. (2022); Prăvălie (2014); Kaminski et al. (2024)
French Polynesia	1966–1996	Atmospheric and underground	193	^{137}Cs, Pu isotopes	Tropical atoll systems with strong marine-terrestrial interactions and shallow carbonate soils	Tropical coastal vegetation and atoll-associated plant communities	Marine aerosol deposition, leaching, sediment redistribution	Residual site-dependent contamination influenced by atmospheric fallout and oceanic transport processes	Drozdovitch et al. (2021); Prăvălie (2014)

5. Plant physiological responses to chronic ionizing radiation

Chronic exposure to IR represents a persistent abiotic stress condition that may influence physiological, biochemical, and molecular processes in plants (Beresford et al., 2020; Ludovici et al., 2020; Dowlath et al., 2021; Kukarskih et al., 2021; Nguyen Phuong et al., 2021). Unlike acute high-dose exposure, the radiological environments of former nuclear test sites are characterized by prolonged low to moderate dose rates, frequently spatially heterogeneous and modulated by soil properties and plant functional traits. In practical terms, this generally corresponds to dose rates ranging from near-background conditions to several tens of μGy h−1, depending on the site, radionuclide distribution, and local environmental conditions. Under such conditions, plant responses are influenced by interactions between external radiation fields, internal radionuclide incorporation, and local environmental constraints (Beresford et al., 2020; Geras'kin, 2024).

One of the most consistently reported effects of chronic radiation exposure in plants is the modulation of oxidative balance (Esnault et al., 2010; Ludovici et al., 2020). IR promotes the formation of reactive oxygen species through radiolysis of cellular water and secondary metabolic reactions (Jernfors et al., 2017; Geras'kin et al., 2019; Holiaka et al., 2020). Elevated levels of reactive oxygen species (ROS) may contribute to alterations in membrane integrity, protein structure, and nucleic acid stability if antioxidant defenses are insufficient (Esnault et al., 2010; Caplin and Willey, 2018; Ludovici et al., 2026b). Several studies conducted in contaminated environments have reported alterations in antioxidant enzyme activities, including superoxide dismutase, catalase, and peroxidases, consistent with activation of physiological stress-response pathways under chronic exposure conditions. However, reported responses are not uniform across species or regions, reflecting differences in baseline stress tolerance and environmental context (Esnault et al., 2010; Caplin and Willey, 2018; Geras'kin et al., 2018; Ludovici et al., 2020; Duarte et al., 2022; Ludovici et al., 2026b).

At the genomic level, chronic radiation exposure may contribute to DNA damage through strand breaks, base modifications, and chromosomal aberrations (Ludovici et al., 2021). Activation of DNA repair pathways, including homologous recombination and non-homologous end joining mechanisms, has been proposed as a key component of plant resilience under radiological stress (Nickoloff et al., 2023). Yet, evidence linking molecular damage markers to long-term fitness consequences in field conditions remains limited. Many investigations rely on short-term assays or controlled experiments, while in situ studies across test sites are comparatively scarce (Ludovici et al., 2021; Nickoloff et al., 2023; Tan et al., 2023).

Photosynthetic performance represents another sensitive endpoint. Alterations in chlorophyll content, photosystem efficiency, and carbon assimilation have been observed in some contaminated environments, particularly under localized higher-dose conditions. Nonetheless, other studies report minimal or transient effects, suggesting that physiological acclimation may mitigate sustained functional impairment in certain species (Li et al., 2023).

Reproductive processes may also be influenced under chronic exposure conditions. Reduced seed viability, altered pollen morphology and changes in germination rates have been described in specific contexts. However, the consistency of these findings across different test regions remains uncertain, partly due to methodological heterogeneity and variable exposure assessment (Møller et al., 2016; Geras'kin et al., 2017; Møller and Mousseau, 2017; Parousis-Paraskevas et al., 2025).

Overall, current evidence suggests that chronic fallout exposure may influence oxidative regulation, genomic integrity, and metabolic performance in plants (Ludovici et al., 2026a). Yet, the magnitude and ecological significance of these effects appear strongly influenced by site-specific environmental conditions, species traits, and contamination gradients. A comparative framework is therefore essential to distinguish generalized physiological patterns from localized responses (Murphy et al., 2023).

6. Vegetation structure and ecological succession under chronic fallout exposure

Beyond individual physiological responses, chronic radiological contamination may contribute to localized variation in vegetation structure and ecological trajectories under long-term exposure conditions (Yoschenko et al., 2011; Oudalova and Geras'kin, 2012; Yoschenko et al., 2017; Duarte et al., 2023). Nuclear test sites provide heterogeneous environmental conditions in which soil contamination, climatic constraints, and disturbance history interact to shape plant community dynamics. However, evidence for consistent radiation-driven restructuring of plant communities remains limited and region dependent (Simon et al., 2010; Prăvălie, 2014; Mishra et al., 2024).

In tropical atoll systems such as the Marshall Islands and parts of French Polynesia, vegetation recovery following intensive atmospheric testing has been influenced by both mechanical disturbance and radiological contamination (Simon et al., 2010; Prăvălie, 2014; Drozdovitch et al., 2021).

Early post-detonation phases were characterized by severe disturbance of vegetation cover and soil structure, followed by progressive recolonization processes (Ludovici et al., 2026b). Long-term observations indicate that community composition often reflects a combination of natural successional processes and site-specific contamination patterns. In several cases, dominant species appear capable of persisting under residual contamination levels, although localized changes in species abundance have been reported in areas with higher radionuclide inventories (Geras'kin, 2024; Yoschenko et al., 2025).

In continental steppe environments such as Semipalatinsk, chronic exposure is superimposed on ecosystems adapted to strong seasonal variability and climatic stress (Lukashenko et al., 2020; Fesenko et al., 2022). Vegetation patterns in contaminated zones have shown spatial heterogeneity, sometimes corresponding to radiological gradients, but disentangling radiation effects from soil properties, grazing pressure, and microtopography remains challenging. Similar complexities arise in the arid landscapes of the Nevada Test Site, where low productivity, sparse vegetation cover, and wind redistribution of contaminated particles contribute to patchy community responses (Simon et al., 2010; Lukashenko et al., 2020).

Functional trait analysis may provide a useful framework for interpreting vegetation patterns under chronic radiation exposure. Traits related to stress tolerance, resource allocation, and reproductive strategy may influence species persistence in contaminated soils. Nevertheless, direct evidence linking specific functional traits to radiological tolerance in field conditions is limited. Most available data derive from localized surveys rather than standardized cross-site comparisons.

Importantly, long-term ecological trajectories in former nuclear test sites are shaped not only by contamination intensity but also by land use restrictions, absence of anthropogenic disturbance, and natural recovery processes over decades. In some regions, exclusion of human activities has allowed relatively undisturbed ecological succession, complicating attribution of vegetation patterns solely to radiological factors (Simon et al., 2010; Lukashenko et al., 2020).

Overall, current evidence suggests that although chronic fallout exposure may contribute to spatial heterogeneity in vegetation structure, consistent radiation-driven successional patterns have not been consistently demonstrated across all sites. Comparative assessment across distinct biomes highlights the importance of integrating contamination data with climatic, edaphic, and disturbance variables when evaluating ecosystem resilience in radiologically affected landscapes (Egorov et al., 2017).

A structured comparison of reported physiological and ecological responses across the four regions is summarized in Table 2.

7. Phenotypic plasticity and potential adaptive responses under chronic exposure

A central question in the study of vegetation inhabiting former nuclear test sites concerns the extent to which observed responses reflect phenotypic plasticity rather than heritable adaptive change (Geras'kin, 2024). Chronic exposure to low or moderate dose rates may represent a persistent environmental stressor; however, demonstrating adaptive evolution in natural populations requires robust genetic evidence together with demonstrable fitness advantages under contaminated conditions (Ludovici et al., 2020; Geras'kin, 2024; Ludovici et al., 2026a).

Many reported plant responses in radiologically affected areas, including modulation of antioxidant activity, alterations in growth patterns, and changes in reproductive output, can be interpreted within the framework of physiological acclimation (Velasco et al., 2008; Møller and Mousseau, 2017; Parvin et al., 2025). Plants possess inherent capacity to adjust metabolic pathways and stress response networks in response to environmental variability. In ecosystems already characterized by climatic stress, distinguishing radiation-specific responses from broader stress acclimation mechanisms is particularly challenging (Esnault et al., 2010; Caplin and Willey, 2018).

Evidence supporting potential adaptive responses remains limited and often indirect. Some studies have described changes in cytogenetic markers, mutation frequencies, or shifts in allele distributions within contaminated zones (Yoschenko et al., 2011; Xavier et al., 2023). However, linking such observations to increased fitness or stable transgenerational inheritance under natural field conditions remains methodologically challenging. Confounding factors such as spatial heterogeneity, small population sizes, and historical disturbance further complicate interpretation (Bilichak and Kovalchuk, 2016; Faraji and Metz, 2026).

Transgenerational effects have been proposed in certain contexts, including altered germination patterns or reproductive performance in progeny from contaminated sites. Yet, consistent demonstration of heritable radiation-associated traits across multiple generations under natural conditions is scarce. Controlled experimental validation is often lacking, and few studies integrate genomic, physiological, and ecological endpoints within the same populations (Herman and Sultan, 2011).

Comparative analysis across the four regions considered in this review suggests that while chronic fallout exposure may contribute to localized variation in plant traits, current evidence does not support generalized adaptive evolution driven exclusively by radiological factors. Instead, responses appear to reflect a combination of phenotypic plasticity, pre-existing stress tolerance, and site-specific environmental constraints (Simon et al., 2010; Lukashenko et al., 2020).

Future research integrating genomic approaches, common garden experiments, and long-term field monitoring will be essential to clarify whether chronic radiological gradients act primarily as selective agents or as modulators of existing stress response capacity in terrestrial vegetation.

8. Implications for environmental risk assessment and long-term monitoring

Although the nuclear test sites examined in this review represent historical legacies, they remain highly relevant for contemporary environmental risk assessment. These regions provide rare long-term field systems in which chronic radiological exposure has interacted with natural ecosystems for decades. As such, they offer empirical insight into the ecological responses associated with persistent low to moderate dose rates, complementing short-term laboratory and post-accident investigations (Simon et al., 2010; Prăvălie, 2014; Drozdovitch et al., 2021).

Table 2
Reported plant physiological and ecological responses under chronic fallout exposure.

Region	Exposure characteristics	Reported physiological observations	Reported reproductive observations	Reported community-level patterns	Current evidence interpretation	Main knowledge gaps	References
Marshall Islands	Chronic heterogeneous fallout contamination in tropical atoll systems	Reported modulation of oxidative balance and physiological stress markers under localized contamination conditions	Variable observations on germination and reproductive performance	Vegetation recovery influenced by disturbance history and residual contamination	Limited direct evidence for long-term adaptive responses	Scarcity of long-term plant physiological and genetic studies	Simon et al. (2010); Corcho-Alvarado et al. (2021); Drozdovitch et al. (2021)
Semipalatinsk Test Site	Spatially heterogeneous chronic exposure under continental steppe conditions	Cytogenetic alterations and oxidative stress responses reported in localized studies	Variable reproductive responses under chronic exposure conditions	Patchy vegetation patterns associated with heterogeneous contamination gradients	Evidence remains site-specific and methodologically heterogeneous	Limited standardized cross-site comparisons	Larionova et al. (2018); Larionova et al. (2021); Fesenko et al. (2022); Krivitskiy et al. (2026)
Nevada Test Site	Arid low-productivity environment with episodic radionuclide resuspension	Limited field-based physiological datasets currently available	Reproductive effects poorly documented	Spatial heterogeneity in vegetation distribution near contaminated zones	Insufficient evidence for generalized long-term ecological responses	Lack of integrated physiological and ecological investigations	Simon et al. (2022); Kaminski et al. (2024)
French Polynesia	Tropical atoll systems with marine-terrestrial radionuclide interactions	Plant physiological datasets remain limited	Reproductive effects insufficiently documented	Recovery trajectories influenced by both fallout deposition and environmental disturbance	Evidence remains fragmentary and site dependent	Limited recent terrestrial plant-focused studies	Prăvălie (2014); Drozdovitch et al. (2021)

Environmental risk frameworks for radiological contamination often rely on controlled exposure experiments, modeling approaches, or data derived from limited time frames. In contrast, former test sites allow evaluation of vegetation dynamics under prolonged and spatially heterogeneous exposure conditions (Egorov et al., 2017). Integrating soil characteristics, radionuclide inventories, and plant functional responses from these systems can improve parameterization of dose–effect relationships under realistic environmental conditions (Murphy et al., 2023).

Comparative assessment across distinct climatic zones also highlights the importance of context-dependent risk interpretation. Identical radionuclide inventories may lead to different ecological outcomes depending on soil composition, hydrology, and baseline stress levels. Consequently, generalized risk coefficients may not fully capture site-specific ecological responses (Geras'kin et al., 2019; Chandra et al., 2023).

Long-term monitoring strategies should therefore incorporate not only external dose measurements but also soil-to-plant transfer dynamics, species composition changes, and functional trait indicators. Vegetation surveys, coupled with radionuclide speciation analysis and physiological biomarkers, can enhance early detection of ecological shifts in contaminated landscapes (Guillén et al., 2018).

Insights derived from nuclear test regions may also inform preparedness and response strategies for future radiological contamination events (Simon et al., 2010; Prăvălie, 2014; Corcho-Alvarado et al., 2021; Drozdovitch et al., 2021; McGuffin et al., 2024). Understanding the range of vegetation responses under chronic exposure conditions may contribute to more realistic predictions of ecosystem recovery trajectories and support evidence-based remediation planning.

9. Research gaps and future directions

Despite decades of investigation, significant knowledge gaps remain in the study of vegetation exposed to chronic fallout contamination. One major limitation is the scarcity of standardized cross-site comparisons using harmonized methodologies. Differences in sampling design, exposure assessment, and biological endpoints complicate direct evaluation of ecological patterns across regions (Simon et al., 2010; Prăvălie, 2014; Lukashenko et al., 2020; Corcho-Alvarado et al., 2021; Drozdovitch et al., 2021; McGuffin et al., 2024; Ludovici et al., 2026a).

Future research would benefit from integrated approaches combining radiological characterization, soil chemistry, plant physiology, and population-level analyses within the same study systems. Application of genomic and transcriptomic tools in field populations may help clarify whether chronic exposure is associated primarily with transient stress responses or more persistent biological modifications. However, such analyses must be coupled with ecological performance metrics to establish functional relevance (Chandra et al., 2023; Murphy et al., 2023; Parousis-Paraskevas et al., 2025).

Functional trait-based frameworks may also warrant further development. Linking contamination gradients to measurable traits related to stress tolerance, resource allocation, and reproduction could improve predictive understanding of vegetation dynamics in contaminated areas (Díaz et al., 2013; Murphy et al., 2023; Parousis-Paraskevas et al., 2025).

Long-term datasets remain particularly valuable. Continuous monitoring across decades is essential to detect subtle shifts in community composition and to distinguish transient fluctuations from directional change. Former nuclear test sites, where access restrictions have limited additional disturbance, offer unique opportunities for such longitudinal investigations (Simon et al., 2010; Prăvălie, 2014; Lukashenko et al., 2020; Corcho-Alvarado et al., 2021; Drozdovitch et al., 2021; McGuffin et al., 2024; Ludovici et al., 2026a).

Finally, improved integration between radioecology, plant physiology, and environmental risk science is needed. Bridging disciplinary boundaries may strengthen interpretation of chronic exposure effects and support development of more refined ecological risk models applicable to both legacy and potential future radiological contamination scenarios (Rhodes et al., 2020; Geras'kin, 2024; Ludovici et al., 2026b).

10. Conclusions

Former nuclear test sites remain environmentally significant systems for investigating the long-term behavior of radionuclides and their interactions with terrestrial ecosystems under chronic exposure conditions. Comparative analysis across the Marshall Islands, Semipalatinsk, the Nevada Test Site, and French Polynesia demonstrates that persistent contamination patterns are strongly shaped by radionuclide composition, climatic variability, soil properties, and environmental redistribution processes.

Across these regions, current evidence supports the persistence of heterogeneous radiological gradients and ongoing soil-to-plant transfer processes decades after nuclear testing activities ceased. Reported plant responses include alterations in oxidative balance, physiological stress regulation, reproductive performance, and vegetation dynamics under specific environmental conditions. However, the magnitude, consistency, and ecological significance of these responses remain highly site dependent and are often complicated by methodological variability, heterogeneous dosimetry, and multiple environmental confounding factors.

Evidence supporting generalized adaptive evolution or stable transgenerational responses driven exclusively by chronic radiation exposure remains limited. In most cases, observed patterns are more consistently interpreted within the framework of phenotypic plasticity, stress acclimation, and interactions with pre-existing environmental constraints.

This review highlights the importance of integrating radiological characterization, soil chemistry, transfer dynamics, plant physiology, and ecological context when interpreting long-term responses in contaminated landscapes. Former nuclear test regions continue to provide valuable field systems for improving environmental risk assessment frameworks, refining long-term monitoring strategies, and advancing understanding of ecosystem responses under chronic radiological exposure.

Future progress will depend on standardized cross-site methodologies, long-term ecological monitoring, and interdisciplinary approaches capable of linking environmental radioactivity with functional biological and ecological endpoints under realistic field conditions.

CRediT authorship contribution statement

Gian Marco Ludovici: Conceptualization, Data curation, Investigation, Resources, Visualization, Writing – original draft, Writing – review & editing. **Paola Amelia Tassi:** Formal analysis, Investigation, Writing – review & editing. **Alba Iannotti:** Supervision, Validation, Writing – review & editing. **Colomba Russo:** Project administration, Supervision, Validation, Writing – review & editing. **Francesco Gargallo di Castel Lentini:** Funding acquisition, Writing – review & editing. **Timothy Alexander Mousseau:** Data curation, Methodology, Resources, Writing – review & editing. **Andrea Malizia:** Data curation, Funding acquisition, Project administration, Supervision, Validation, Visualization, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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