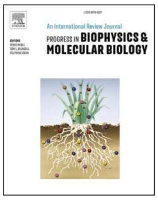
Progress in Biophysics and Molecular Biology 200 (2026) 1–5

Contents lists available at ScienceDirect

Progress in Biophysics and Molecular Biology

journal homepage: www.elsevier.com/locate/pbiomolbio



The phoenix flora: Plant survival, succession, and putative adaptation in the post-atomic landscapes of Hiroshima and Nagasaki

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ARTICLE INFO

Keywords:
Hiroshima
Nagasaki
Ionizing radiation
Higher plants
DNA damage

ABSTRACT

The atomic bombings of Hiroshima and Nagasaki in 1945 created a unique environment of acute, high-dose ionizing radiation, contrasting sharply with the chronic low-dose rate exposure in the Chernobyl and Fukushima Exclusion Zones. This stands in stark contrast to the chronic, low-dose rate contamination that defines the Chernobyl and Fukushima Exclusion Zones. While the long-term ecological effects of the latter are well-documented, a systematic synthesis of the floral response to the atomic bombings is lacking. This review integrates historical data with modern radio-ecological principles to analyze plant survival and succession. We document the remarkable recovery of vegetation, from the resprouting of survivor trees, the *hibakujumoku*, such as *Ginkgo biloba* trees, to the role of soil seed banks. We propose that this recovery was driven by constitutive resilience, relying on pre-existing traits such as robust DNA repair, antioxidant capacity, and protective morphology, rather than the multi-generational genetic adaptation observed in chronic exposure zones. By framing these events against the backdrop of Chernobyl and Fukushima, this review demonstrates how the nature of the radiological insult dictates fundamentally different ecological and evolutionary outcomes. The flora of Hiroshima and Nagasaki thus serves as a critical case study of extreme instantaneous stress tolerance. We conclude by proposing a future research agenda that employs advanced genomic tools on these living archives to uncover the mechanistic basis of their survival, thereby integrating a pivotal historical case into a holistic understanding of plant persistence in radically altered environments.

1. Introduction

The detonation of atomic bombs over Hiroshima and Nagasaki in 1945 created a unique and extreme environment, subjecting plant life to an unprecedented combination of instantaneous physical forces including a powerful blast, intense thermal radiation, and an acute, high-dose pulse of ionizing radiation (IR) (Douple et al., 2011; Ludovici et al., 2021; Xu and Dodt, 2023). In the decades, the scientific understanding of how ecosystems respond to radioactive contamination has been profoundly shaped by studies in the Exclusion Zones of Chernobyl and Fukushima (Ludovici et al., 2020, 2022; Mousseau and Møller, 2020). These sites have provided invaluable insights into the long-term effects of chronic, low dose rate exposure, revealing pathways for evolutionary adaptation in plants over multiple generations (Møller and Mousseau, 2011, 2015; Møller et al., 2012; Mousseau and Møller, 2020; Sakauchi and Otaki, 2024; Ludovici et al., 2026).

However, the scenario presented by the atomic bombings represents a fundamentally different paradigm. It was not a landscape of persistent contamination, but one of near total devastation followed by a rapid decline in radiation levels. The central question, therefore, shifts from

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https://doi.org/10.1016/j.pbiomolbio.2026.02.004
Received 11 December 2025; Received in revised form 28 December 2025; Accepted 9 February 2026
Available online 11 February 2026
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adaptation to chronic stress to one of immediate survival, resilience, and secondary succession following an acute insult (Geras'kin, 2016; Cannon and Kiang, 2022). Historical accounts document a remarkable phenomenon of relatively swift vegetation return, challenging initial assumptions of long-term sterility (Møller and Mousseau, 2016).

This narrative of resilience is epitomized by the survival and resprouting of iconic survivor trees, the *hibakujumoku*, such as *Ginkgo biloba*. Their existence invites critical re-examination through a modern radio ecological lens (Tabassum et al., 2022). While the physical and radiological profiles of atomic bombings and nuclear accidents are distinct, the fundamental molecular challenges to plant life, namely DNA damage and oxidative stress, are universal (Mousseau and Møller, 2014; Ludovici et al., 2020). The sophisticated defense mechanisms identified in Chernobyl and Fukushima populations, such as enhanced DNA repair and antioxidant capacity, provide a useful comparative framework for generating hypotheses about how certain individuals in Hiroshima and Nagasaki may have withstood the initial radiation pulse (Bonisoli-Alquati et al., 2010; Møller and Mousseau, 2011; Obrador et al., 2022; Ludovici et al., 2026)

This review aims to synthesize the fragmented historical data on floral recovery in Hiroshima and Nagasaki within a modern radio ecological and evolutionary framework. By systematically comparing this acute exposure paradigm with the chronic models of Chernobyl and Fukushima, we explore the hypothesis that survival was driven by constitutive resilience, that is, preexisting physiological traits, rather than the multi-generational genetic adaptation observed in chronically contaminated sites. The following sections detail the atomic bomb environment, analyze successional patterns and survivor trees, known as *hibakujumoku*, and leverage molecular insights to propose mechanistic hypotheses for this resilience.

2. The atomic bomb environment: A tripartite stressor and its legacy

The environment created in the moments following the atomic detonations over Hiroshima and Nagasaki was unique in the annals of radioecology (Endo et al., 2007). Unlike the dispersal of radionuclides from reactor accidents, the primary agent of initial biological impact was the instantaneous release of prompt neutron and γ-radiation (Endo et al., 2007; Rojavin et al., 2011; Quaranta et al., 2023, 2024a,b). This acute pulse was accompanied by devastating physical forces, creating a tripartite stressor profile that defined the immediate survival challenge for flora (Oumeish and Oumeish, 2005; Boratyński et al., 2016).

2.1. The tripartite stressor profile

The first component was the blast wave, which physically uprooted, shattered, and stripped vegetation, creating a landscape of debris and broken timber. The second was thermal radiation, which generated surface temperatures sufficient to cause charring and combustion, leading to widespread fires. The third, and most distinctive from a radiobiological perspective, was the prompt IR (Douple et al., 2011; Shimizutani and Yamada, 2021). This consisted of an immense flux of neutrons and γ-rays delivered over a very short period, resulting in extremely high, localized absorbed doses (Sasaki et al., 2016).

Estimates suggest that doses in the immediate vicinity of the hypocenters could have reached several kGy, levels which are universally lethal to most plant life in controlled laboratory settings (Sasaki et al., 2016). This was followed by residual radiation from fallout, but the exposure profile remained fundamentally acute, with dose rates decaying rapidly over time, in stark contrast to the persistent contamination from ^{137}Cs and ^{90}Sr that characterizes Chernobyl and Fukushima (Ludovici et al., 2020, 2022, 2026; Malizia et al., 2021).

While direct experimental data from Hiroshima and Nagasaki are scarce, insights can be drawn from controlled acute irradiation studies. For instance, the large-scale ECOS-1 and ECOS-2 experiments, which examined the effects of acute, high-dose gamma irradiation on a mixed pine-birch forest in the Southern Urals, provide valuable benchmarks for understanding the threshold doses for morbidity and mortality, as well as patterns of early recovery in forest ecosystems following an acute radiological event (Fesenko et al., 2022).

A critical nuance in interpreting 'survival' in this context is the distinction between the immediate persistence of established organisms and the post-event regeneration from protected propagules. The *hibakujumoku* likely exemplify the former, where architectural features (e.g., thick bark, deep rooting) provided partial shielding from thermal and blast effects, allowing meristematic tissues to survive (Suzuki et al., 2020). In contrast, the rapid greening observed across the devastated landscapes was predominantly driven by the latter, facilitated by soil seed banks, rhizomes, and buried buds that escaped the direct brunt of the insult in micro-refugia. This distinction underscores that 'constitutive resilience' operates at multiple levels: within individuals (via robust physiology and morphology) and within populations (via persistent banks of propagules) (Cheng and McBride, 2006; Suzuki et al., 2020).

2.2. Documented survival and the hibakujumoku

Against this backdrop of near-total devastation, the survival and subsequent recovery of certain plant individuals and propagules became a subject of scientific and symbolic interest (Geras'kin, 2016; Suzuki et al., 2020). The most compelling evidence comes from the *hibakujumoku* (survivor trees), which were located close enough to the hypocenters to endure the initial cataclysm yet managed to resprout. These trees are not merely historical relics; they are biological archives holding potential information on extreme radio-tolerance (Suzuki et al., 2020). It is important to acknowledge, however, the inherent survivorship bias in studying these individuals. They represent an extremely small fraction of the pre-existing population that, by a combination of fortunate location, genetic predisposition, or protective microenvironment, withstood the cataclysm (Cheng and McBride, 2006; Suzuki et al., 2020). While their specific traits may not be statistically representative of the original forest, their existence provides a unique, albeit exceptional, window into the upper limits of physiological and morphological tolerance that were present within the species' gene pool (Suzuki et al., 2020). Their survival suggests the existence of pre-adaptive traits, such as profound seed or bud protection, robust enzymatic DNA repair systems that could be rapidly activated, or substantial non-enzymatic antioxidant reserves capable of mitigating the initial oxidative burst (Table 1) (Mousseau et al., 2013; Yoschenko et al., 2016; Volkova et al., 2018; Ludovici et al., 2022; Tabassum et al., 2022; Ludovici et al., 2026).

2.3. A framework for analysis

The existence of these survivors, coupled with the documented patterns of rapid succession, allows us to move from mere observation to a mechanistic hypothesis. The acute radiation pulse, while distinct from chronic exposure, acts upon the same fundamental cellular targets: nuclear DNA and the redox balance of the cell (Esnault et al., 2010; Caplin and Willey, 2018; Ludovici et al., 2020, 2022, 2026; Duarte et al., 2023). Therefore, the molecular strategies for survival in Hiroshima and Nagasaki are likely to share commonalities with those being actively selected for in Chernobyl and Fukushima. These include the efficient sensing of DNA double-strand breaks (DSBs) via the Ataxia-Telangiectasia Mutated(ATM)/ATM and Rad3-Related (ATR) kinases, the rapid deployment of homologous recombination repair, and the upregulation of antioxidant enzymes like superoxide dismutase (SOD) and peroxidases (Esnault et al., 2010; Møller and Mousseau, 2011, 2015; Caplin and Willey, 2018; Ludovici et al., 2020, 2022, 2026; Mousseau and Møller, 2020; Duarte et al., 2023).

The unique aspect of the atomic bomb case is that these systems had to be constitutively present or inducible within a single individual's lifetime to confer survival, rather than being selected over multiple

Table 1
Documented *Hibakujumoku* and other resilient plant species in Hiroshima and nagasaki.

Species	Common Name	Location(s)	Documented Evidence/Notable Traits	References
Ginkgo biloba	Ginkgo	Hiroshima (e.g., Hosen-ji Temple)	Iconic survivor; resprouted from buds shortly after the event; known for high levels of antioxidant flavonoids and robust stress resistance.	(Mousseau et al., 2013; Yoschenko et al., 2016; Volkova et al., 2018; Ludovici et al., 2022; Tabassum et al., 2022; Ludovici et al., 2026)
Ilex rotunda	Kurogane Holly	Hiroshima	Several surviving individuals; species is known for its hard wood and general resilience to environmental stress.	
Salix babylonica	Weeping Willow	Hiroshima	Observed resprouting from surviving root systems; willows are known for high growth rates and phenotypic plasticity.	
Celtis sinensis	Japanese Hackberry	Hiroshima	Documented survivor trees; species is hardy and tolerant of urban conditions.	
Eurya emarginata	Emarginata Japanese Holly	Hiroshima	Surviving shrubs noted; part of the early successional flora in the region.	
Miscanthus sinensis	Japanese Silver Grass	Hiroshima & Nagasaki	A pioneering grass species; likely one of the first to recolonize open areas due to its wind-dispersed seeds and vigorous rhizomatous growth.	
Pinus densiflora	Japanese Red Pine	General Area	While many perished, the species played a role in secondary succession; studies from Fukushima show mechanisms for coping with radiation stress.	

generations (Socol and Dobrzyński, 2015). The following section will delve into the successional patterns that emerged from the resilience of these initial survivors and the dormant seed bank.

3. Mechanisms of survival: from molecular resilience to ecological succession

The following discussion on molecular mechanisms is necessarily inferential and hypothetical, as direct molecular studies on the *hibakujumoku* are, to our knowledge, non-existent. We draw upon the well-established principles of plant radiobiology and insights from chronic exposure studies to propose plausible mechanisms that could underpin the observed constitutive resilience. It is crucial to distinguish between mechanisms demonstrated in laboratory or chronic-field settings and those postulated for the unique acute event discussed here.

The documented recovery of plant life in Hiroshima and Nagasaki invites an exploration of plausible mechanisms that could have enabled both immediate survival and subsequent regrowth (Suzuki et al., 2020). In the following section, we propose a hypothetical, multi-layered model that bridges intrinsic molecular defenses to broader ecological strategies. It is crucial to note that this discussion is necessarily inferential; direct molecular evidence from the *hibakujumoku* is lacking. Therefore, we draw upon well-established principles of plant radiobiology and insights from chronic exposure studies to generate testable hypotheses about the basis of constitutive resilience in this unique acute exposure context.

The first putative mechanism involves a constitutive capacity for DNA repair. Species such as *Ginkgo biloba* may possess inherently robust DNA Damage Response pathways (Tabassum et al., 2022). The rapid activation of sensor kinases like ATM and ATR, coupled with efficient repair processes such as homologous recombination, is hypothesized to have been crucial for restoring genomic integrity following the initial radiation pulse (Esanult et al., 2010; Caplin and Willey, 2018; Ludovici et al., 2020; Ludovici et al., 2022; Duarte et al., 2023; Ludovici et al., 2026). This cellular survival would have been a prerequisite for the subsequent resprouting from protected buds. A second, interrelated mechanism is a significant antioxidant buffering capacity. The acute radiolysis of water generated a massive burst of reactive oxygen species (Esnault et al., 2010; Ludovici et al., 2020). Therefore, it is plausible that survivor species maintained high baseline levels of non-enzymatic antioxidants, including flavonoids, ascorbate, and glutathione, or possessed the ability to rapidly upregulate antioxidant enzymes like SOD and catalase (Esnault et al., 2010; Møller et al., 2016; Caplin and Willey, 2018; Duarte et al., 2023). The well-documented high flavonoid content in Ginkgo could be a prime candidate contributing to its notable resilience (Suzuki et al., 2020). Furthermore, morphological and architectural shielding played an undeniable role. Protected meristems buried within bark or below the soil surface, along with persistent seed banks possessing robust protective coats, were physically shielded from the direct thermal and blast effects. This architectural buffering allowed for regeneration from undamaged tissues even when the above-ground structure was completely destroyed (Suzuki et al., 2020).

Beyond the individual survivor trees, the rapid greening of the landscape was largely driven by classic ecological mechanisms. The soil seed bank served as a critical reservoir of life (Sakauchi and Otaki, 2024). Seeds, by virtue of being compact and often buried, were effectively shielded from the initial devastation. The creation of vast, open, and disturbed areas created ideal conditions for pioneer species with ruderal strategies. Grasses such as *Miscanthus sinensis* and various fast-growing herbs were able to germinate and dominate the early successional stages, a process analogous to primary succession on volcanic terrains or after severe wildfires (Suzuki et al., 2020).

This framework underscores a fundamental dichotomy in plant responses to radiological stress (Ludovici et al., 2026). The atomic bombings imposed an acute selection filter, where survival depended on constitutive traits immediately available within individuals (e.g., pre-existing robust DNA repair, antioxidants, or shielded meristems) (Endo et al., 2007; Douple et al., 2011; Xu and Dodt, 2023; Sakauchi and Otaki, 2024). In stark contrast, the chronic, low-dose rate exposure in Chernobyl and Fukushima acts as a gradual selective pressure, shaping populations over generations through the differential success of heritable genetic variants (Table 2) (Mousseau et al., 2013; Geras'kin, 2016; Volkova et al., 2018; Ludovici et al., 2020; Ludovici et al., 2022; Ludovici et al., 2026). Thus, while both scenarios involve IR, they engage different evolutionary processes: one testing the limits of standing variation and phenotypic robustness, the other driving population-level genetic change (Esnault et al., 2010; Socol and Dobrzyński, 2015; Møller et al., 2016; Møller and Mousseau, 2017; Caplin and Willey, 2018; Ludovici et al., 2020, 2022, 2026; Suzuki et al., 2020; Duarte et al., 2023).

4. Future implications and research directions: predicting ecosystem trajectories

The synthesis presented in this review, while drawing a coherent narrative from fragmented data, ultimately highlights the significant knowledge gaps that remain regarding the botanical legacy of the atomic bombings (Suzuki et al., 2020). The hypotheses on molecular resilience we have proposed require empirical validation. Therefore, the future of this research lies in leveraging advanced technologies to interrogate these living archives, the *hibakujumoku*, and their descendant populations.

Table 2
Key molecular pathways in acute survival and chronic adaptation to IR.

Gene/Pathway Name	Function/Role in Stress Response	Hypothesized Role in Acute Survival (*Hibakujumoku* – Hiroshima & Nagasaki)	Documented Role in Chronic Adaptation (Chernobyl/ Fukushima)	References
ATM/ATR kinases	DNA damage sensing; initiation of the DNA Damage Response (DDR).	Critical for immediate sensing of massive DNA damage, triggering cell cycle arrest and repair in meristematic cells.	Selected for efficient signaling under continuous stress; populations show genetic signatures of selection in DDR pathways.	(Esnault et al., 2010; Socol and Dobrzyński, 2015; Møller et al., 2016; Møller and Mousseau, 2017; Caplin and Willey, 2018; Ludovici et al., 2020, 2022, 2026; Fesenko et al., 2022; Duarte et al., 2023)
RAD51	Key mediator of Homologous Recombination (HR), a high-fidelity DNA repair pathway.	Essential for the accurate repair of complex double-strand breaks induced by the acute radiation pulse, preserving genomic integrity in survivors.	Upregulated in chronically exposed populations; increased recombination frequency is a potential adaptive trait.	
KU70/KU80	Core components of Non-Homologous End Joining (NHEJ), an error-prone DNA repair pathway.	Likely activated for rapid, initial repair to ensure short-term survival, potentially at the cost of increased local mutation rates.	May be favored for immediate survival in high-dose microsites, contributing to a higher mutational load in populations.	
Superoxide Dismutase (SOD)	Primary antioxidant defense; converts superoxide radicals into hydrogen peroxide.	High constitutive activity would be vital to scavenge the initial burst of superoxide radicals from prompt radiation.	Upregulation or selection for more stable isoforms is observed, enhancing long-term management of oxidative stress.	
Pathway: Phenylpropanoids	Synthesis of flavonoids and other phenolic compounds with potent antioxidant properties.	High constitutive levels in species like *Ginkgo biloba* provided a pre-formed chemical shield against the acute oxidative burst.	Induction of this pathway is a common response; selection may favor genotypes with enhanced flavonoid biosynthesis capacity.	
Glutathione S-Transferase (GST)	Detoxification of oxidative stress products and xenobiotics.	Rapid induction would be necessary to manage the plethora of toxic, radiation-derived compounds within cells.	Consistently upregulated in exposed populations, contributing to metabolic resilience and radionuclide chelation.	

Note: The molecular roles hypothesized for the Hiroshima and Nagasaki context are extrapolations based on fundamental radiobiological principles and observations from other irradiation studies (e.g., chronic low-dose rate, laboratory acute exposures). They remain to be empirically tested in the *hibakujumoku* or their descendants.

A primary and promising direction involves the application of multi-omics approaches. Genomic sequencing of survivor trees could reveal signatures of selection in genes related to DNA repair and oxidative stress management, potentially identifying constitutive genetic advantages that pre-dated the 1945 event (Fan et al., 2025). Comparative transcriptomics and metabolomics of these individuals, alongside conspecifics from control areas, could illuminate the persistent molecular footprint of the extreme stress event, even decades later. Furthermore, the potential role of epigenetic regulation (e.g., stress-induced DNA methylation) in the response and potential memory of such an event is a compelling but highly speculative avenue (Ludovici et al., 2020, 2022). To date, no epigenetic studies have been conducted on *hibakujumoku* or their progeny. Therefore, investigating whether descendants of survivor trees carry heritable epigenetic marks represents a pure hypothesis that would provide profound insights into the possibility of transgenerational acclimation to extreme acute stress, framing a clear objective for future research (Bilichak and Kovalchuk, 2016; Fan et al., 2025).

Another critical avenue is the explicit testing of radio-tolerance. Controlled laboratory experiments, exposing progeny from *hibakujumoku* and control populations to acute and chronic gamma radiation, could quantitatively test for heritable differences in resilience. This would directly address the question of whether the survivor trees represent merely fortunate individuals or genotypes with a truly adaptive, heritable advantage (Suzuki et al., 2020).

In conclusion, the flora of Hiroshima and Nagasaki represents an unparalleled case study in the limits of plant resilience. This review has argued that these landscapes are not merely historical monuments but are, in fact, a unique natural laboratory. They provide a critical counterpoint to the chronic exposure scenarios of Chernobyl and Fukushima, illustrating how life can persist through a singular, catastrophic event driven by pre-existing constitutive defenses and robust ecological strategies. The survival and resurgence of plant life in these cities stand as a powerful testament to the remarkable resilience inherent in the plant kingdom. By moving from historical observation to a hypothesis-driven research paradigm, we can transform these survivor trees from symbols of destruction into keystones for understanding the fundamental mechanisms of life under the most extreme duress. The continued scientific exploration of this phoenix flora will undoubtedly yield universal insights into the interplay between rapid resilience and long-term adaptation in a world facing increasingly intense anthropogenic stressors.

5. Conclusion

The 1945 atomic bombings of Hiroshima and Nagasaki created a natural experiment of unparalleled severity, offering a distinct lens through which to view plant stress tolerance. This review has argued that the recovery of flora in these cities is best explained by a model of constitutive resilience, where survival and regrowth relied on preexisting physiological, morphological, and ecological buffers. This model stands in complementary opposition to the paradigm of gradual genetic adaptation emerging from sites of chronic contamination like Chernobyl and Fukushima. Together, these case studies illustrate that the trajectory of life in radiologically altered environments is not singular but is fundamentally prescribed by the temporal nature of the insult itself, whether instantaneous or persistent.

The legacy of the *hibakujumoku* transcends symbolism; they represent unique biological archives whose study has been largely confined to historical observation. The future research agenda we propose, employing advanced genomics, transcriptomics, and controlled phenotypic assays, aims to transform these survivors from monuments into model systems. By doing so, we can move from plausible hypothesis to mechanistic understanding, uncovering the genetic and epigenetic foundations of extreme stress tolerance. In an era of increasing anthropogenic pressure, integrating this pivotal historical case into the broader framework of environmental science provides not only a clearer understanding of the past but also critical insights for predicting and fostering resilience in the future.

CRediT authorship contribution statement

Gian Marco Ludovici: Writing – review & editing, Visualization, Resources, Investigation, Data curation, Conceptualization. **Paola Amelia Tassi:** Writing – original draft, Investigation, Formal analysis. **Alba Iannotti:** Writing – review & editing, Validation, Project administration. **Colomba Russo:** Writing – review & editing, Validation, Project administration. **Fausto D'Agostino:** Writing – review & editing, Formal analysis. **Matilde Neble Segade:** Writing – review & editing, Methodology. **Timothy Alexander Mousseau:** Writing – review & editing, Resources, Methodology, Data curation. **Andrea Malizia:** Writing – review & editing, Visualization, Validation, Supervision, Project administration, Data curation.

Ethics Approval and consent to participate

The informed consent was waived because of the retrospective nature of this study.

Funding

None.

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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