



## Review

## Complexity of responses to ionizing radiation in plants, and the impact on interacting biotic factors

Shubhi Mishra<sup>a,1</sup>, Gustavo Turqueto Duarte<sup>b,1</sup>, Nele Horemans<sup>b,c</sup>, Joske Ruytinx<sup>d</sup>, Dmitri Gudkov<sup>e</sup>, Maksym Danchenko<sup>a,\*</sup>

<sup>a</sup> Institute of Plant Genetics and Biotechnology, Plant Science and Biodiversity Centre, Slovak Academy of Sciences, 950 07 Nitra, Slovakia

<sup>b</sup> Unit for Biosphere Impact Studies, Belgian Nuclear Research Centre SCK CEN, 2400 Mol, Belgium

<sup>c</sup> Centre for Environmental Sciences, Hasselt University, 3590 Diepenbeek, Belgium

<sup>d</sup> Department of Bio-engineering Sciences, Vrije Universiteit Brussel, 1050 Brussels, Belgium

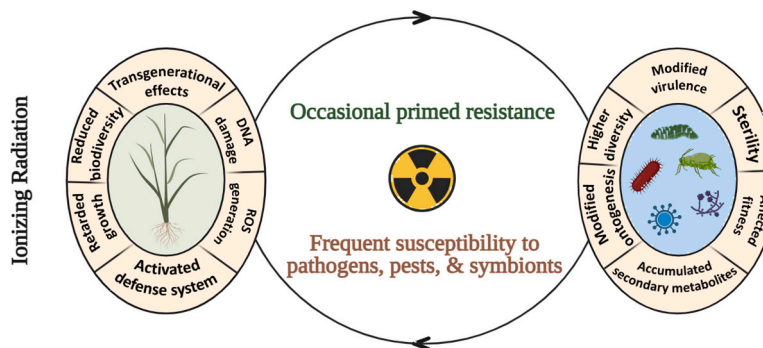
<sup>e</sup> Institute of Hydrobiology, National Academy of Sciences of Ukraine, 04210 Kyiv, Ukraine



## HIGHLIGHTS

- We summarized current knowledge on joint action of abiotic and biotic stressors.
- The combined effect of ionizing radiation and biotic factors in plants is unclear.
- Such interaction is essential for the risk assessment of nuclear technologies.
- Overall, the literature suggests that ionizing radiation compromises plant resistance.
- Specific laboratory and field research should enhance mechanistic understanding.

## GRAPHICAL ABSTRACT



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## ABSTRACT

In nature, plants are simultaneously exposed to different abiotic (e.g., heat, drought, and salinity) and biotic (e.g., bacteria, fungi, and insects) stresses. Climate change and anthropogenic pressure are expected to intensify the frequency of stress factors. Although plants are well equipped with unique and common defense systems protecting against stressors, they may compromise their growth and development for survival in such challenging environments. Ionizing radiation is a peculiar stress factor capable of causing clustered damage. Radionuclides are both naturally present on the planet and produced by human activities. Natural and artificial radioactivity

**Abbreviations:** AM, arbuscular mycorrhiza; APX, ascorbate peroxidase; AVR, avirulence; BER, base excision repair; CDPK, Ca<sup>2+</sup>-dependent protein kinase; CEZ, Chernobyl Exclusion Zone; ECM, ectomycorrhiza; ETI, effector-triggered immunity; GPX, glutathione peroxidase; GSH, glutathione; HR, homologous recombination; IAA, indole-3-acetic acid; IAEA, International Atomic Energy Agency; ICRP, International Commission on Radiological Protection; IR, ionizing radiation; LD<sub>50</sub>, median lethal dose; MAPK, mitogen-activated protein kinase; MMR, mismatch repair; NER, nucleotide excision repair; NHEJ, non-homologous end-joining; PR, pathogenesis-related; PRR, pattern recognition receptor; PTI, pattern-triggered immunity; R, resistance; ROS, reactive oxygen species; SOD, superoxide dismutase; TE, transposable element; UNSCEAR, United Nations Scientific Committee on the Effects of Atomic Radiation.

\* Corresponding author.

E-mail address: [maksym.danchenko@savba.sk](mailto:maksym.danchenko@savba.sk) (M. Danchenko).

<sup>1</sup> These authors contributed equally.

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Pathogens and symbionts  
Radionuclides

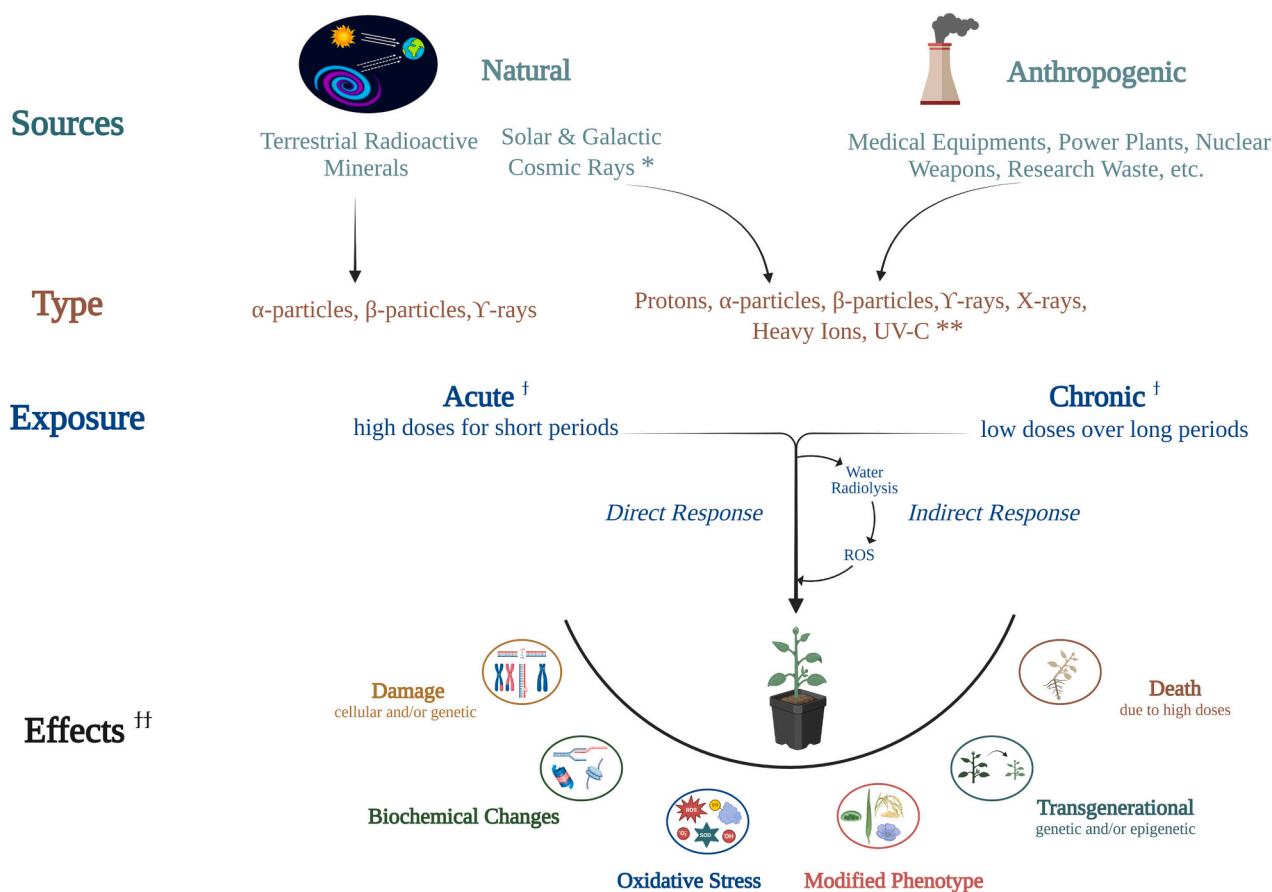
affects plants on molecular, biochemical, cellular, physiological, populational, and transgenerational levels. Moreover, the fitness of pests, pathogens, and symbionts is concomitantly challenged in radiologically contaminated areas. Plant responses to artificial acute ionizing radiation exposure and laboratory-simulated or field chronic exposure are often discordant. Acute or chronic ionizing radiation exposure may occasionally prime the defense system of plants to better tolerate the biotic stress or could often exhaust their metabolic reserves, making plants more susceptible to pests and pathogens. Currently, these alternatives are only marginally explored. Our review summarizes the available literature on the responses of host plants, biotic factors, and their interaction to ionizing radiation exposure. Such systematic analysis contributes to improved risk assessment in radiologically contaminated areas.

## 1. Scope of the story

Plants face multiple stresses in their natural habitats, which occur either individually or simultaneously. Although universal stress responses are often activated, unique ones may be required to cope with specific challenges. The interaction of stress factors can be synergistic, or antagonistic depending on the plant species and developmental stage, as well as the type and duration of the stress. The interaction of abiotic and biotic stresses, including mutualistic symbiotic interactions, so far has been explored only shallowly. The abiotic stress-primed defense system may be beneficial for plants fighting against pests and pathogens. Alternatively, prior exposure to abiotic stress can make the biotic factors more detrimental to plants due to resource exhaustion and compromised

physiology.

Ionizing radiation (IR) is among the abiotic stressors of plants. It affects plant growth, development, reproduction, morphology, and tolerance to other environmental stresses on molecular, biochemical, cellular, physiological, and populational levels. Radionuclides persistently influence plants in anthropogenically or naturally contaminated ecosystems. The interaction of irradiated plants with bio-aggressors is, however, poorly understood. Due to the insufficient information on these interactions, we lack appropriate management techniques to deal with unfavorable phenomena in nature and agriculture. Herein, in a pioneering attempt to comprehensively cover the topic, we collected, analyzed, and extracted available literature knowledge on the interplay between ionizing radiation exposure and interaction with biotic factors



**Fig. 1.** Overview of possible sources, types and effects of ionizing radiation exposure on plants. Notes: (\*) Solar and galactic cosmic rays are mostly composed by protons; (\*\*) UV-C is filtered by the atmosphere, and does not reach the surface of our planet; (†) the concepts of acute or chronic IR, and of low or high doses are species-specific, and should consider the lifespan and radiosensitivity of each organism (discussed in Section 3); (††) yet acute and chronic exposures might involve similar response pathways, the effects may not overlap (discussed in Section 3). Typical effects include: (i) genetic damage, which can be handled by an effective DNA repair system; (ii) normal biochemistry and metabolism are maintained through the synthesis of stress proteins, particularly chaperons and histones; (iii) oxidative stress in cells that is controlled by enzymatic and non-enzymatic antioxidants; (iv) phenotypes are modified either for damage avoidance (typical for acute exposure) or new homeostasis (characteristic for chronic irradiation); (v) inheritance is primarily mediated by epigenetic mechanisms. Abbreviations: ROS, reactive oxygen species; SOD, superoxide dismutase (created with BioRender).

in plants. Firstly, we defined the environmental factor—ionizing radiation. Secondly, we presented current consensus knowledge of plant reactions to acute and chronic exposures. Thirdly, we described paradigms of plant interactions with bio-aggressors and mycorrhiza symbionts in light of their radiosensitivity. Finally, we provided examples of currently scarce studies on the combined exposure of plants to biotic agents and ionizing radiation stress.

## 2. Ionizing radiation sources and exposure types

The emission of energy in the form of electromagnetic waves or particles is defined as radiation. It can be categorized as non-IR (e.g., ultraviolet A and B, visible light, microwaves, and radiowaves) and IR. Non-ionizing radiation can only move or oscillate the atom in a molecule but lacks the energy to detach electrons out of the atom. Conversely, IR is the form of energy released from an unstable nucleus to attain stability. It can be in the form of particles ( $\alpha$ - and  $\beta$ -particles, fast neutrons, and heavy ions) or electromagnetic waves (ultraviolet C and  $\gamma$ -/X-rays) (Fig. 1). As it will be discussed in Section 3, it is a harsh stressor for the plant if present above tolerance levels and causes many adverse consequences. Unlike other stressors, IR deposits energy along tracks, generating cytotoxic clustered damage, thereby forming multiple local DNA breakdown sites. Authors experimentally showed such phenomenon in vivo using X-rays and heavy ion beams in a human cell line (Nakano et al., 2022). Consequently, it produces clustered lesions that must be repaired, otherwise resulting in genetic and cellular instability. Depending on the radiation type, IR either has high penetration power or is capable of dense ionization. As such, it can generate super reactive hydroxyl radicals due to water radiolysis. These radicals interact with biopolymers and may lead to cell death if the damage outweighs the capacity of the protective system. Ionizing radiation exposure can be classified as acute or chronic, depending upon the intensity and duration of exposure. Ionizing radiation induces changes in plants on all levels of organization: From molecules to populations (Ludovici et al., 2020).

### 2.1. Acute exposure

When a high-dose IR is received during a short period (a few minutes to a few hours), it is referred to as acute exposure. It frequently leads to severe damage or even death of the organism, depending upon the treatment dose and life stage of the plant (Fig. 1). While for humans the borderline between high and low doses was estimated at 100 mSv, based on the risk of cancerogenic effect; this is not well defined for plants (UNSCEAR, 2008). The effects observed in organisms and populations immediately after a nuclear weapon test or accident at a nuclear facility (such as Chernobyl and Fukushima) are considered responses to acute high doses. Particularly, during Chernobyl and Fukushima accidents, 5300 PBq and 520 PBq of radioactive materials, respectively, were released into the environment (Steinhauser et al., 2014). Acute exposure does not naturally occur on our planet.

### 2.2. Laboratory-simulated and field chronic exposure

Continuous or irregular exposure to a low-dose IR for an extended duration is categorized as chronic irradiation. Of note, plants respond faster to acute IR than to chronic one, and promoter analysis revealed substantial differences in the specific regulatory elements of reactive genes (Kovalchuk et al., 2007). Chronic doses can be received due to the natural radiation in the environment, such as electromagnetic waves and particles released by decaying radium, thorium, uranium, and other radioactive minerals in the rocks, soil, vegetation, and groundwater (Fig. 1) (IAEA, 2003). Chronic environmental radioactivity is dependent on the presence of radionuclides with slow radioactive decay. Limited amounts of contaminating radionuclides are released during nuclear power production and fuel processing. Uranium ore deposits are among the dominating natural radiation sources. Some regions have

considerable natural radiation levels, for example, up to 30  $\mu\text{Gy/h}$  in Ramsar, Iran (Ghiassi-Nejad et al., 2002), 22  $\mu\text{Gy/h}$  in Morro do Ferro and Araxá, Minas Gerais, Brazil, 13  $\mu\text{Gy/h}$  in Meaípe, Espírito Santo, Brazil, and 4  $\mu\text{Gy/h}$  in Kerala, India (Sohrabi, 1998). Anthropogenic-caused nuclear contamination, such as due to accidents or bomb test sites, also results in chronically radioactive environments. According to the International Atomic Energy Agency (IAEA), Three Mile Island, United States in 1978, Chernobyl, Ukraine in 1986 (Beresford et al., 2016), and Fukushima Daiichi, Japan in 2011 (Ludovici et al., 2022) were the three major nuclear accidents in human history. Also, notable contamination remains in the Bikini Atoll of the Marshall Islands (hydrogen bomb test) (Hughes et al., 2019), Kyshtym in Russia (radiological accident) (Fesenko, 2019), and Perm in Russia (cobalt bomb test) (Ramzaev et al., 2011). The contaminating radionuclides persist in the areas surrounding these accident sites, affecting organisms and populations (Caplin and Willey, 2018; Jackson et al., 2022). The effects of chronic IR exposure are much less explored, particularly due to the massive challenge of arranging a proper experimental design in field conditions (Beresford et al., 2020a).

## 3. Plant responses to ionizing radiation

Ionizing radiation exposure may trigger beneficial hormetic effects on plant growth (Volkova et al., 2022), or it may be used for crop improvement by mutagenesis (Shu et al., 2012). In agriculture, an acute high-dose irradiation with X-rays,  $\gamma$ -rays, or heavy ions is used to develop different crop cultivars since they are effective in causing mutations (Nakano et al., 2010; Taheri et al., 2014). Facilities such as the  $\gamma$ -phytotron at the Korean Atomic Energy Research Institute (Kang et al., 2010), and the  $\gamma$ -greenhouse at the Malaysian Nuclear Agency (Ahmad et al., 2018), use chronic exposure for mutation breeding. For example, several horticulturally attractive variations (dwarfism, slender leaves, and large flowers) were reported in toad lily (*Tricyrtis hirta*) after the exposure of embryogenic calli to heavy ions (Nakano et al., 2010). Furthermore, vegetative (leaf length and width, number of shoots, and plant height) and reproductive (number of flowers) traits were efficiently modified in Siam tulip (*Curcuma alismatifolia*) (Taheri et al., 2014). The authors reported that a new amaranth cultivar, developed through mutation breeding, showed high seed weight and elevated folate content in a multiyear field experiment, thus is attractive for commercial growing (Hricová et al., 2021).

Nevertheless, IR also induces deleterious effects, which raise concerns for protecting the biota (ICRP, 2017; Beresford et al., 2020b; Duarte et al., 2023). According to the United Nations Scientific Committee on the Effects of Atomic Radiation (UNSCEAR) and the International Commission on Radiological Protection (ICRP), 100  $\mu\text{Gy/h}$  (400  $\mu\text{Gy/h}$  for aquatic organisms) and 300 mGy cumulative are the dose rate and dose thresholds for plant radioprotection (UNSCEAR, 2008; ICRP, 2008). Significant effects on plant populations are currently considered unlikely after acute exposures below 1 Gy (UNSCEAR, 2008). However, these values are based on a specific set of reference species, and mostly due to reproductive or morbidity consequences. Regardless, radiosensitivity is species-specific; thus, the low- or high-dose concept is relative. Plants can be as sensitive as mammals (e.g., some crop seedlings and Scots pine (*Pinus sylvestris*),  $\text{LD}_{50} < 4$  Gy), or as resistant as prokaryotes (e.g., white clover (*Trifolium repens*) seeds,  $\text{LD}_{50} \approx 1000$  Gy) (Harrison and Anderson, 1996; DiCarlo et al., 2011; Shu et al., 2012). Therefore, in an ecosystem dominated by conifers, such as the Northern forests, the postulate that plants are resistant to radiation is questionable, as exemplified by the Red Forest after the Chernobyl Nuclear Power Plant accident. Likewise, the characterization of a chronic exposure is also relative to the lifespan of the organism, and cannot be defined by a universal time and dose. For instance, for the same period, what may be considered an acute high-dose exposure to the radiosensitive Scots pine tree, would mean a chronic low-dose treatment to short-lived tiny aquatic plants like duckweeds (Lemnaceae). Several factors contribute

to plant radiosensitivity, including the developmental stage, genome size, and photosynthetic activity (Adam-Guillermín et al., 2018; Duarte et al., 2023). Furthermore, sensitivity also depends on the efficiency of the organism's defense mechanisms to counter the damage caused by IR. Although morphological evaluation of exposed organisms may not reveal the impact of IR exposure, molecular analyses highlight the presence of stress responses even at low doses, which may influence from short-term adaptive responses to long-term species evolution.

### 3.1. Direct and indirect effects of ionizing radiation exposure

Ionizing radiation can cause direct or indirect damage (Fig. 1). Direct damage is triggered by the deposition of radiation energy on cellular molecules, which leads to DNA base loss or substitution, disruption of its chains, and crosslinks (for review, see Duarte et al., 2023). Indirect damage is caused by the reactive oxygen species (ROS) produced during water radiolysis, which originates hydrated free electrons ( $e^-_{aq}$ ), free radicals ( $H^\bullet$ ,  $HO^\bullet$ ,  $HO_2^\bullet$ ), and their products ( $OH^-$ ,  $H_3O^+$ ,  $H_2$ ,  $H_2O_2$ ) (Le Caër, 2011). Reactive oxygen species accumulation to toxic levels results in oxidative damage, which includes modification of DNA bases and protein structure, DNA strand breaks, crosslinks, and lipid peroxidation, thus affecting the integrity of cellular membranes (Friso and van Wijk, 2015; Duarte et al., 2023). However, the input of ROS to the effects of IR exposure has not been fully explored under low water content conditions, such as in mature seeds of numerous plant species (Kauth and Biber, 2015; Leopold and Vertucci, 1989; Tangney et al., 2019). While ROS are naturally produced by organellar processes in the cells, they are also important cellular signaling molecules involved in hormone crosstalk, thus participating in stress responses and plant development (Das and Roychoudhury, 2014; Xia et al., 2015; Xie et al., 2019a; Choudhary et al., 2020). This observation implies that exposure to IR leads to ROS imbalance that affects cellular homeostasis (Duarte et al., 2023) and, as will be further discussed (Section 4), the interaction with biotic factors.

The first general trend that can be outlined during acute IR exposure is the activation of the DNA repair mechanisms (Fig. 1). DNA lesions are sensed by specific molecular machinery that can induce cell cycle arrest, programmed cell death (apoptosis), autophagy or, in plants, endoreplication (Adachi et al., 2011; Nisa et al., 2019; Wang et al., 2021; Duarte et al., 2023). The activation of the defense machinery upon acute IR exposure is a pattern that somewhat resembles the reaction to other stress conditions. Such crosstalk between stress response pathways was also reported for other eukaryotes, such as the tardigrades, whose radioresistance probably evolved as a byproduct of surviving desiccation (Bruckbauer and Cox, 2021). Reactive oxygen species accumulation due to heat, drought, or high light in plants may induce phosphorylation of Suppressor Of Gamma Response1 (SOG1), thus activating DNA damage repair (Nisa et al., 2019). Cell cycle arrest was promoted upon heat stress in *Arabidopsis thaliana* (hereafter referred as *Arabidopsis*), involving the activation of ANAC044 and ANAC085 transcription factors via SOG1 (Takahashi et al., 2019). Indeed, SOG1 is a hub integrating the Ataxia Telangiectasia Mutated (ATM) and ATM and Rad3-related (ATR) signaling pathways, which are primary DNA damage sensors for double- and single-strand breaks, respectively. ATM activation depends on the proteins of the MRN (MRE11, RAD50, and NBS1) complex, while ATR is recruited by ATRIP (ATR Interacting Protein) and activated by the 9-1-1 (RAD9, RAD1, and HUS1) complex (Amiard et al., 2010; Saldívar et al., 2017). DNA repair is also achieved independently from SOG1, via RAD51 and BRCA1 (Biedermann et al., 2017; Horváth et al., 2017). According to the damage, specific repair mechanisms are started, such as nucleotide excision repair (NER), base excision repair (BER), mismatch repair (MMR), homologous recombination (HR), non-homologous end-joining (NHEJ), and crosslinks repair, each of them depending on recruiting distinct sets of protein complexes that have been reviewed elsewhere (Manova and Gruszka, 2015; Kim et al., 2019; Nisa et al., 2019; Raina et al., 2021; Duarte et al., 2023). It has been recently shown that SOG1 can interact with RAD54 and BRCA1 for

regulating salinity-induced double-strand breaks via HR in *Arabidopsis* (Mahapatra and Roy, 2024). Because IR is an ancient stress factor for living organisms, and since the pathways involved in DNA repair also participate in error correction during the replication process, the proteins associated with the defense mechanisms are conserved across different life domains (Duarte et al., 2023).

A second trend during acute IR exposure responses is the activation of the enzymatic and non-enzymatic antioxidant mechanisms (Fig. 1). Ascorbate peroxidase (APX), catalase, glutathione peroxidase (GPX), superoxide dismutase (SOD), and thioredoxins are the primary enzymatic antioxidants, while ascorbate, glutathione (GSH), tocopherol, carotenoids, and proline are the main non-enzymatic ones (Choudhary et al., 2020; Huang et al., 2019; Sharma et al., 2012; Xia et al., 2015). The antioxidant system acts in a cellular compartment- and stress-specific way (Duarte et al., 2023; Sharma et al., 2012). There is an interesting overlap between the responses promoted by acute IR exposure and the fundamental role of the antioxidant system in generic environmental stress acclimation (Alscher et al., 2002; Falk and Munné-Bosch, 2010; Hasanuzzaman et al., 2019; Horemans et al., 2000; Kavi Kishor et al., 2022; Kocsy et al., 2005; Sadiq et al., 2019; Sofu et al., 2015). Symmetrical antioxidant complexes of manganese with metabolites might define cellular resistance to IR protecting the proteome from oxidative damage, thus authors suggested that radioresistance is predominantly a metabolic phenomenon (Sharma et al., 2017).

However, the aforementioned response patterns are less evident under chronic radiation exposure. For instance, transcriptome analysis of *P. sylvestris*, shepherd's purse (*Capsella bursa-pastoris*), and cow vetch (*Vicia cracca*) chronically exposed to a low-dose radiation in the Chernobyl Exclusion Zone (CEZ) suggested that the modulation of histones and chaperones and, to some extent ROS, antioxidants, and hormones is fundamental, but not DNA repair genes (Duarte et al., 2019; Volkova et al., 2021; Voronezhskaya et al., 2023). Histones are core elements of the nucleosome controlling the DNA packing, and chaperones assist protein folding. Although the increase in the expression of canonical histones is usually linked to the S phase of the cell cycle progression (Jiang and Berger, 2017), these proteins are also prone to IR-induced damage because of DNA-protein crosslinks (Dextraze et al., 2010; Enderle et al., 2019; Nakano et al., 2017).

### 3.2. Discordant effects of acute and chronic radiation exposure

Most of our knowledge about the effects of IR exposure derives from short-term experiments involving high doses (Fig. 2, Table S1, and references therein). Overall, these studies helped to unravel the immediate impacts (beneficial or harmful) of IR exposure and the mechanisms involved in these responses. However, given the nature of the radionuclides, the contaminated environment represents a chronic stress for the biota, covering from the life cycle to generations of local species. They include plants inhabiting naturally radioactive environments, or contaminated areas created due to anthropogenic activity. Simulating long-term exposures in controlled laboratory conditions is technically challenging, and although some progress has been recently made, these experiments are often limited to several days/weeks (sub-chronic exposures) or involve short-lived organisms (Fig. 3, Table S2, and references therein). Indeed, the complexity of the radioecological field data can hardly be simulated in the sense of species interactions, ecosystem uniqueness, heterogeneity of the contamination, and duration of actual chronic exposures. These factors highlight the importance of the data from the natural environment (Fig. 4, Table S3, and references therein). Of note, proper experimental designs in field conditions are super challenging because of numerous confounding factors.

Historically, morphological analyses have been used as standard criteria for evaluating the impact of IR exposure, which includes the effects on viability, growth, and development. Although the adverse effects on morphological traits are apparent at acute high doses, the lack of phenotypic differences under chronic low-dose conditions has been

Development stage				Irradiation			Analysis											Reference								
Species	Exposure	Sample	Source	Type	Dose	Dose rate, energy or activity	Antioxidants	Biotoxic interactions	Damage (DNA or cytogenetic)	Chronic counterpart	Gene Expression	Growth/Development	Hormesis	Hormone levels	Metabolites	Methylation status	Mutation		Oxidative stress	Photosynthesis parameters	Protein content	Repair	ROS/free radicals	Transgenerational effects	Transposable elements	
<i>Allium cepa</i>	Seedling **	Seedling roots	<sup>60</sup> Co	γ	**	0.411 Gy/s	●	●																Saghizadeh et al., 2008		
	Seedling	Seedling roots	<sup>241</sup> Am	α	0.02–0.2 Gy	7.92 mGy/min	●															●		Xavier et al., 2021		
	Seedling	Seedling roots	<sup>90</sup> Sr/ <sup>60</sup> Co	β	0.04–1.44 Gy	63.1 mGy/min	●																		Xavier et al., 2023	
<i>Arabidopsis thaliana</i>	Seed	Seeds to juvenile shoots	Accelerator	Protons	**	1.1–6.5 MeV																			Qin et al., 2007	
	Seed and seedling	Seeds and seedlings	C ions	Heavy ion	20–175 Gy	17.3 MeV/u **																			Hase et al., 2018	
	Seed	Seeds to adult shoots**	<sup>60</sup> Co	γ	500–2250 Gy	8.33–37.5 Gy/min *																			Hase et al., 2020	
	Seed	Seeds and juvenile plants	<sup>60</sup> Co	γ	50–150 Gy	463 Gy/h	●																			Babina et al., 2020
	Seed from CEZ	Seeds and juvenile shoots	<sup>60</sup> Co	γ	150 Gy	460 Gy/h																				Podluskii et al., 2022
	Juvenile	Juvenile shoots	<sup>60</sup> Co	γ	1 Gy	0.025 Gy/s																				Kovalchuk et al., 2007
	Seedling	Adult shoots	**	γ	200 Gy	8.3 or 200 Gy/h	●																			Goh et al., 2014
	Juvenile	Adult shoots	<sup>60</sup> Co	γ	100–2000 Gy	4.17–83.33 Gy/h *																				Kim et al., 2014
Adult	Adult rosettes	<sup>137</sup> Cs	X-ray	15 Gy	89 cGy/s																				Kryvokhyzha et al., 2019	
<i>Bromus inermis</i>	Seed from EURT	Seeds to juvenile shoots and roots	<sup>137</sup> Cs	γ	250 Gy	38–41 Gy/s																			Antonova et al., 2015	
	Seed	Seeds to juvenile shoots	<sup>60</sup> Co	γ	15–150 Gy	0.18 Gy/s	●																		Tilaki et al., 2015	
<i>Glycine max</i>	Seed	Seeds to seedlings	<sup>60</sup> Co	γ	50–250 Gy	0.312 kGy/h																			Nobre et al., 2022	
	Seed	Seed to juvenile shoots	*	γ	100–400 Gy	*	●																		Im et al., 2018	
	Seed	Seeds to adult shoots	Carbon-ion <sup>137</sup> Cs	Heavy ion	γ: 100–400 Gy Ion: 40–180 Gy	**																				Feng et al., 2023
	Seed	Juvenile shoots	<sup>137</sup> Cs	γ	300 Gy	10 Gy/min	●																			Çelik et al., 2014
	Seed	Juvenile leaves	Accelerator	Proton	50–400 Gy	57 MeV **	●																			Im et al., 2017
<i>Hordeum vulgare</i>	Seeds	Seeds to seedlings	*	γ	200, 200 or 1200 Gy	*																			Sarduie-Nasab et al., 2010	
	Seeds	Seeds to seedlings	<sup>60</sup> Co	γ	2–50 Gy	20–350 Gy/h	●																			Geras'kin et al., 2017
	Seeds	Seeds to seedlings	<sup>60</sup> Co	γ	15–100 Gy	60 Gy/h																				Volkova et al., 2019
	Seed	Seeds to seedlings	<sup>60</sup> Co	γ	20 Gy	60 Gy/h																				Gorbatova et al., 2020
	Seed	Seeds to seedlings	<sup>60</sup> Co	γ	20 Gy	60 Gy/h																				Pishenin et al., 2021
	Seed	Seeds to seedlings	<sup>137</sup> Cs	γ	50, 100 or 200 Gy	0.74 R/min																				Antonova et al., 2022
	Seed	Seeds to adult plants	<sup>60</sup> Co	γ	5, 10 or 20 Gy	*	●																			Hussein, 2022
	Seed	Seeds to adult plants	<sup>60</sup> Co	γ	20 Gy	60 Gy/h																				Kazakova et al., 2024
	Germinating seed	Seedling roots	<sup>137</sup> Cs	γ	10–1000 mGy	0.5 Gy/h	●																			Geras'kin et al., 2007
	Seedling to juvenile	Seedling to juvenile shoots and roots	Tomography	X-ray	4.2 or 7.8 Gy	4.2 Gy/h **																				Blaser et al., 2018
<i>Lemna minor</i>	Seed	Seedlings	Accelerator	Proton	3 or 5 Gy	150 MeV	●																		Oprica et al., 2020	
<i>Oryza sativa</i>	Plant **	Plants **	<sup>137</sup> Cs	γ	18, 42, 63 Gy	0.74 Gy/min																			Bodnar and Cheban, 2023	
	Seed	Embryos	C ion	Heavy ion	15 Gy	**																			Ishii et al., 2016	
	Seed	Seed to adult plants	Ar ion C ion Ne ion	Heavy ion	50–300 Gy	7.1 Gy/min 7.7 Gy/min 5.5 Gy/min																				Zheng et al., 2020
	Seedling	Seedling shoots	C ion	Heavy ion	9–270 Gy	2.3 Gy/min																				Rakwal et al., 2008
	Seedling	Seedling leaves	CEZ soil <sup>137</sup> Cs	Mixed γ	**	5.34 μGy/day 13–380 μGy/day																				Rakwal et al., 2009
	Seed	Seedlings	<sup>60</sup> Co Earth's orbit Cyclotron	cosmic rays heavy ion	γ: 200 Gy cosmic: 15 days Ion: 40 Gy	**																				Hwang et al., 2014
	Seed	Seedlings root and shoot	*	γ	50–500 Gy	*	●																			Zhang et al., 2019
	Seed	Seedlings	N ion	Heavy ion	**	**																				Huang et al., 2022
	Seed	Seedling to adult leaves	C ion	Heavy ion	25–300 Gy	60 Gy/min																				Ren et al., 2023
	Seed	Juvenile to adult shoots	C ion	Heavy ion	0.01–20 Gy	0.5 Gy/min.																				Zhao et al., 2018
Juvenile	Juvenile to adult shoots	<sup>60</sup> Co	γ	100, 200, 300 Gy	12.5–37.5 Gy/h	●																			Choi et al., 2021	
Seed	Adult plants*	<sup>60</sup> Co	γ	50–350 Gy	120 Gy/h																				Maity et al., 2005	
<i>Pinus sylvestris</i>	Adult	Seeds	CEZ	Mixed	0.5–15 Gy	**																			Fedotov et al., 2006	
	Seed	Seedlings	<sup>60</sup> Co	γ	15 Gy	0.6 Gy/min																				Geras'kin et al., 2011
	Adult	Adult plants**	CEZ	Mixed	0.1–60 Gy **	**																				Arkhipov et al., 1994
	Adult	Adult tree cores	EURT	Mixed	10.9–133.3 Gy	109–1333 mGy/day																				Kukarskih et al., 2021
<i>Triticum aestivum</i>	Seed	Seed to seedling	<sup>60</sup> Co	γ	100, 300 or 500 Gy	12.5–62.5 Gy/h	●																			Hong et al., 2018
	Seed	Seed to seedling	<sup>60</sup> Co	γ	100, 300 or 500 Gy	12.5–62.5 Gy/h	●																			Hong et al., 2022
	Seed	Seed to seedling	<sup>60</sup> Co	γ	100–400 Gy	0.864 kGy/h	●																			Kiani et al., 2022
	Seed	Seedling leaves	*	γ	100, 150 or 250 Gy	7 Gy/min	●																			Han et al., 2016
<i>Vicia faba</i>	Root **	Root	<sup>60</sup> Co	γ	0.01–0.30 Gy	0.09 Gy/min																				Kuglik et al., 1990
	Seed	Seedlings	<sup>60</sup> Co	γ	2–100 Gy	0.54 Gy/min	●																			Moussa, 2008
	Seedling to juvenile	Seedling to juvenile shoots and roots	Tomography	X-rays	4.2 or 7.8 Gy	4.2 Gy/h **																				Blaser et al., 2018

**Fig. 2.** Graphical representation of studied plant responses to acute irradiation. The data comprise the species that have been studied under both acute and chronic conditions. Black marks indicate the performed analysis. The summary of key results of each cited work is presented in Table S1. Notes: (\*) data unavailable, the information was inferred whenever possible; (\*\*) please refer to the publication for more details; (†) converted for standardization purposes, 1 Gy = 100 rad = 1 Sv. Life cycle refers to continuous exposure over multiple generations; mixed refers to irradiation by different radionuclides and their decay over the years. Abbreviations: CEZ, Chornobyl Exclusion Zone; Cont., contamination; EURT, East Ural Radioactive Trace; FEZ, Fukushima Exclusion Zone; Gen., generation. The following studies are cited: Antonova et al., 2015; Antonova et al., 2022; Arkhipov et al., 1994; Babina et al., 2020; Blaser et al., 2018; Bodnar and Cheban, 2023; Çelik et al., 2014; Choi et al., 2021; Fedotov et al., 2006; Feng et al., 2023; Geras'kin et al., 2007; Geras'kin et al., 2011; Geras'kin et al., 2017; Goh et al., 2014; Gorbatova et al., 2020; Han et al., 2016; Hase et al., 2018; Hase et al., 2020; Hong et al., 2018; Hong et al., 2022; Huang et al., 2022; Hussein, 2022; Hwang et al., 2014; Im et al., 2017; Im et al., 2018; Ishii et al., 2016; Kazakova et al., 2024; Kiani et al., 2022; Kim et al., 2014; Kovalchuk et al., 2007; Kryvokhyzha et al., 2019; Kuglik et al., 1990; Kukarskih et al., 2021; Maity et al., 2005; Moussa, 2008; Nobre et al., 2022; Oprica et al., 2020; Pishenin et al., 2021; Podluskii et al., 2022; Qin et al., 2007; Rakwal et al., 2008; Rakwal et al., 2009; Ren et al., 2023; Saghizadeh et al., 2008; Sarduie-Nasab et al., 2010; Tilaki et al., 2015; Volkova et al., 2019; Xavier et al., 2021; Xavier et al., 2023; Zhang et al., 2019; Zhao et al., 2018; Zheng et al., 2020.

Development stage			Irradiation				Analysis													Reference							
Species	Exposure	Sample	Source	Type	Dose	Dose rate, energy or activity	Duration	Acute counterpart	Antioxidants	Biotic interactions	Damage (DNA or cytogenetic)	Gene Expression	Growth/Development	Hormesis	Hormone levels	Metabolites	Methylation status	Mutation	Oxidative stress		Photosynthesis parameters	Protein content	Repair	ROS/free radicals	Transpositional effects	Transposable elements	
<i>Allium cepa</i>	Seedling	Roots	Ramsar soil	Mixed	*	0.08–100 µGy/h	5 days	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Saghizadeh et al., 2008	
	Juvenile *	Shoots *	<sup>137</sup> Cs (soil)	γ	1 Gy	34 MBq/kg	21 days	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Kovalchuk et al., 2007	
<i>Arabidopsis thaliana</i>	Juvenile to adult	Adult shoots	*	γ	200 Gy	1.33, 2 or 4 Gy/h	5, 10, 15 days	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Goh et al., 2014	
	Seedling	Shoots	<sup>137</sup> Cs	γ	10.9–18.4 Gy	113 mGy/h	4 or 7 days	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Biermans et al., 2015a	
	Seedling	Juvenile shoots	<sup>241</sup> Am	α	0.4–3.3 Gy	1–35,000 µGy/h	4 or 7 days	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Biermans et al., 2015b	
	Seedling	Juvenile roots and shoots	<sup>137</sup> Cs	γ	7–156 Gy	22–457 mGy/h	14 days	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	van de Walle et al., 2016
	Seedling	Seedling to adult roots and shoots	<sup>60</sup> Co	γ	0.14–194.4 Gy **	1–540 mGy/h	6 or 15 days	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Blagojevic et al., 2019	
	Seed to adult	Adult rosette	<sup>137</sup> Cs	β + γ	3 or 17 cGy	10 <sup>-7</sup> or 6.8 × 10 <sup>-8</sup> cGy/s	6 weeks	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Kryvokhyzha et al., 2019
	Juvenile	Seeds to adult shoots	<sup>60</sup> Co	γ	2.5–916 Gy	0.6–500 mGy/h *	2 weeks	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Hase et al., 2020
	Seedling to juvenile	Juvenile rosettes	<sup>137</sup> Cs	γ	7–156 Gy	30–430 mGy/h	2 weeks	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Laanen et al., 2021
<i>Bromus inermis</i>	Seeds from EURT	Seed to juvenile roots and shoots	EURT	Mixed	0.40–4.19 mGy (seed) 0.55–6.95 mGy (plant)	**	**	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Antonova et al., 2015	
<i>Hordeum vulgare</i>	Life cycle	Apical tillers and seeds	*	γ	16.5–2240 R	0.17–23.2 R/day	1 gen.	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Conger et al., 1974	
	Seed to adult	Pollen	U mineral	γ	11.5 or 20 mGy <sup>†</sup>	7–15 µGy/h <sup>†</sup>	68 days *	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Faure 1977	
<i>Lemna minor</i>	Seed	Leaves	<sup>137</sup> Cs (cont.)	β + γ	0.48–4.8 mGy	4.92–49.2 kBq/kg	23 days	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Geras'kin et al., 2005	
	Juvenile and adult **	Seedlings to adult plants	<sup>90</sup> Sr (cont)	β	**	25–25000 kBq/L	3 gen. **	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	van Hoeck et al., 2015	
	Juvenile and adult **	Seedlings to adult plants	<sup>90</sup> Sr (cont) <sup>137</sup> Cs	β γ	**	β: 25–25000 kBq/L γ: 27–1500 mGy/h	3 gen. **	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	van Hoeck et al., 2017	
<i>Oryza sativa</i>	Juvenile and adult **	Seedlings to adult plants	<sup>60</sup> Co	γ	0.16–11.84 Gy	1–70 mGy/h	3 gen. **	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Xie et al., 2019b	
	Seedling	Seedling to juvenile shoots	<sup>137</sup> Cs	γ	9–134 Gy	27–400 mGy/h	2 weeks	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Kariuki et al., 2019	
<i>Pinus sylvestris</i>	Juvenile	Juvenile to adult shoots	<sup>60</sup> Co	γ	100, 200, 300 Gy	0.42–1.25 Gy/h **	10 days	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Choi et al., 2021	
	Seedling	Seedling to juvenile roots and shoots	<sup>60</sup> Co	γ	0.14–194.4 Gy **	1–540 mGy/h	6 or 15 days	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Blagojevic et al., 2019	
<i>Triticum aestivum</i>	Seed	Seed to seedling	<sup>60</sup> Co	γ	100, 300 or 500 Gy	0.298–1.488 Gy/h	2 weeks	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Hong et al., 2018	
	Seed	Seed to seedling	<sup>60</sup> Co	γ	100, 300 or 500 Gy	0.298–1.488 Gy/h	2 weeks	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Hong et al., 2022	
	Seedling	Seedling to juvenile shoots	<sup>60</sup> Co	γ	50 Gy	0.166–0.5 Gy/h	2, 4 or 6 weeks	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Hong et al., 2014	
<i>Vicia faba</i>	Seed	Seeds to juvenile shoots and roots	<sup>137</sup> Cs	γ	16.2–1070 mGy	0.015–0.9 mGy/h	45 days	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	Atteh and Adeyeye, 2022	

**Fig. 3.** Graphical representation of studied plant responses to laboratory-simulated chronic irradiation. The data comprise the species that have been studied under both acute and chronic conditions. Black marks indicate the performed analysis. The summary of the essential results of each referenced study is presented in Table S2. Notes: (\*) data unavailable, the information was inferred whenever possible; (\*\*) please refer to the publication for more details; converted for standardization purposes, 1 Gy = 100 rad = 1 Sv. Life cycle refers to continuous exposure over multiple generations; mixed refers to irradiation by different radionuclides and their decay over the years. Abbreviations: CEZ, Chernobyl Exclusion Zone; Cont., contamination; EURT, East Ural Radioactive Trace; FEZ, Fukushima Exclusion Zone; Gen., generation. The following studies are cited: Antonova et al., 2015; Atteh and Adeyeye, 2022; Biermans et al., 2015a; Biermans et al., 2015b; Blagojevic et al., 2019; Choi et al., 2021; Conger et al., 1974; Faure, 1977; Geras'kin et al., 2005; Goh et al., 2014; Hase et al., 2020; Hong et al., 2014; Hong et al., 2018; Hong et al., 2022; Kariuki et al., 2019; Kovalchuk et al., 2007; Kryvokhyzha et al., 2019; Laanen et al., 2021; Saghizadeh et al., 2008; van de Walle et al., 2016; van Hoeck et al., 2015; Volkova et al., 2017; Xie et al., 2019b.

used for setting up higher safety limits for the biota (UNSCEAR, 2008). In recent years, more sensitive molecular analyses started to reveal that chronically exposed organisms, even at low doses, do show stress response profiles. A few species have been studied under both acute and chronic conditions (Figs. 2–4; Tables S1–3), and not surprisingly, the response patterns adopted by plants to counter acute or chronic IR exposure are dissimilar; in fact, often contrasting. Under acute exposure, the organism focuses its energy on avoiding damage at the cost of growth and development. However, the defense mechanisms are energetically demanding, and they may have detrimental effects on cellular development and plant growth if sustained over long periods (Duarte et al., 2023). Such phenomenon is reflected, for instance, even in the modulation of stable traits, such as flowering time (Kryvokhyzha et al., 2019; Laanen et al., 2023). That means trade-offs might exist for plant responses and adaptation to chronic radiation exposure (Duarte et al., 2023). As a matter of fact, nearly absent induction of DNA repair genes has been reported for plants under chronic radiation exposure in natural environments (Fig. 4). In such a long-term stress condition, it seems that the organisms aim at controlling ROS-generating processes (energy- and signaling-related), specific non-enzymatic antioxidants, the concentration of ions, and the integrity of membranes. Indeed, although being damaging byproducts from water radiolysis, ROS are essential plant signaling molecules. They are involved in biotic (Section 4) and abiotic stress responses, in crosstalk with hormone pathways, as well as in growth and development from seed germination to senescence (Choudhary et al., 2020; Gudkov et al., 2019; Sharma et al., 2012; Xia et al., 2015; Xie et al., 2019a). This means that when exposed to IR, plants experience ROS homeostasis imbalance, which can lead to cell death (Choudhary et al., 2020; Das and Roychoudhury, 2014; Duarte et al., 2023; Sharma et al., 2012). Although quenching ROS levels by

increasing the activity and concentration of enzymatic and non-enzymatic antioxidants is commonly observed during acute exposure responses (Fig. 2), this is only occasionally noticed under chronic ones (Figs. 3–4). In such conditions, plants probably attempt to establish a new homeostasis for coping with the chronic stress without dampening the ROS-dependent systems to save (or alleviate) signaling and cross-talks with hormone pathways. This strategy may explain, for instance, a higher mutation accumulation in chronically exposed plants compared to their acutely irradiated counterparts (Hase et al., 2020).

As the importance of environmental conservation becomes more recognized, the radioprotection of plants comes into focus. Compelling evidence from contaminated areas suggests that organisms exposed to a chronic low-dose IR (even earlier considered safe) trigger molecular stress responses that impact the plant's homeostasis, even though they might not be morphologically evident (Kashparova et al., 2020; Sakauchi et al., 2021; Volkova et al., 2021; Makarenko et al., 2023). These findings have been facilitated by the development of new techniques, which allow the analysis of non-model organisms on the omics scale (Volkova and Geras'kin, 2018). Yet, it is still difficult to establish the acute or chronic response standards because they depend on many different factors, including the radiosensitivity of each specific species, dose rate and total dose, ontogenesis stage of the organism, and confounding factors in natural environments. Furthermore, the lack of data overlap, and not seldom the lack of a detailed description of methodology in literature, hamper linking the information derived from acute and chronic exposures. The impact of environmental contamination by radionuclides on biodiversity, and how it would affect the interactions across organisms with different radiosensitivities still remains to be investigated.

Development stage			Irradiation					Analysis											Reference								
Species	Exposure	Sample	Source	Type	Dose	Dose rate, energy or activity	Duration	Acute counterpart	Antioxidants	Biotic interactions	Damage (DNA or cytogenetic)	Gene Expression	Growth/Development	Hormesis	Hormone levels	Metabolites	Methylation status	Mutation		Oxidative stress	Photosynthesis parameters	Protein content	Repair	ROS/free radicals	Transgenerational effects	Transposable elements	
<i>Arabidopsis thaliana</i>	Life cycle	Embryos **	CEZ	Mixed	0.151–3179.5 cGy **	0.0002–2.4 R/h	6 years																			Abramov et al., 2005	
	Life cycle	Embryos **	CEZ	Mixed	0.151–3179.5 cGy **	0.0002–2.4 R/h	6 years																				Shuryak and Brenner., 2021
	Life cycle	Seedlings **	CEZ	Mixed	**	1–370 µGy/h	30 years																				Horemans et al., 2018
	Life cycle	Seedlings **	CEZ	Mixed	**	0.33 - 3.76 µGy/h	30 years **																				Podlutskii et al., 2022
<i>Glycine max</i>	Life cycle	Seeds	CEZ	Mixed	**	**	1 gen. **																			Danchenko et al., 2009	
	Life cycle	Seeds	CEZ	Mixed	**	**	1 gen. **																			Clubicová et al., 2012	
	Life cycle	Seeds and adult leaves	CEZ	Mixed	**	30.31 µGy/h	8 gen.																			Pernis et al., 2020	
	Life cycle	Seedlings	CEZ	Mixed	13.23 cGy <sup>†</sup>	**	6 gen.																				Georgieva et al., 2017
<i>Oryza sativa</i>	Seedling	Seedlings	FEZ	γ **	**	1.6–4.2 µGy/h <sup>†</sup>	6–72h																			Hayashi et al., 2014	
	Seedling	Seedlings	FEZ	γ **	**	2.6–5 µGy/h <sup>†</sup>	72h																			Hayashi et al., 2015	
<i>Pinus sylvestris</i>	Adult	Endosperm and embryo	CEZ	Mixed	7–130 mGy/y	0.8–14.8 µGy/h	Aprox. 25 years																			Geras'kin and Volkova, 2014	
	Adult **	Seeds	CEZ	Mixed	**	0.37–1.21 µGy/h	20–26 years																			Geras'kin et al., 2011	
	Adult **	Seeds	CEZ	Mixed	0.5–20 Gy	0.01–0.25 mGy/h	18 years																			Fedotov et al. 2006	
	Adult	Seeds and needles	CEZ	Mixed	10–66 mGy/year	**	> 25 years																				Volkova et al. 2017
	Adult	Needles	CEZ	Mixed	**	**	3 years																				Kal'chenko and Fedotov, 2001
	Adult **	Needles	CEZ	Mixed	**	*	10 years **																				Kovalchuk et al., 2003
	Adult	Needles	CEZ	Mixed	5.7–10.6 Gy/year	0.006–0.044 µGy/h <sup>†</sup>	> 20 years																				Kuchma et al., 2011
	Adult	Needles	CEZ	Mixed	0.23–128.5 mGy/year	**	20–25 years																				Duarte et al., 2019
	Adult	Needles	CEZ	Mixed	**	0.22–286 µGy/h	Aprox. 25 years **																				Kashparova et al., 2020
	Adult	Needles	CEZ	Mixed	0.23–128.5 mGy/year	**	29 years																				
<i>Triticum aestivum</i>	Life cycle	Shoot tips and needles	CEZ	Mixed	**	0.2–220 µGy/h	**																				Nybakken et al., 2023
<i>Vicia cracca</i>	Life cycle	Seeds to adult plants	CEZ	Mixed	0.1, 0.8 or 2.7 Gy	1–37 mR/h	3 gen.																				Dmitriev et al., 2009
	Life cycle	Adult leaves	CEZ	Mixed	1.13–51.57 mGy/year	**	35 years																				Voronezhskaya et al., 2023

**Fig. 4.** Graphical representation of studied plant responses to chronic irradiation in natural environments. The data comprise the species that have been studied under both acute and chronic conditions. Black marks indicate the performed analysis. The summary of the major results of each cited work is presented in Table S3. Notes: (\*) data unavailable, the information was inferred whenever possible; (\*\*) please refer to the publication for more details; (†) converted for standardization purposes, 1 Gy = 100 rad = 1 Sv. Life cycle refers to continuous exposure over multiple generations; mixed refers to irradiation by different radionuclides and their decay over the years. Abbreviations: CEZ, Chornobyl Exclusion Zone; Cont., contamination; EURT, East Ural Radioactive Trace; FEZ, Fukushima Exclusion Zone; Gen., generation. The following studies are cited: Abramov et al., 2005; Danchenko et al., 2009; Dmitriev et al., 2009; Duarte et al., 2019; Fedotov et al., 2006; Georgieva et al., 2017; Geras'kin and Volkova, 2014; Geras'kin et al., 2011; Hayashi et al., 2014; Hayashi et al., 2015; Horemans et al., 2018; Kal'chenko and Fedotov, 2001; Kashparova et al., 2020; Klubicova et al., 2012; Kovalchuk et al., 2003; Kuchma et al., 2011; Nybakken et al., 2023; Pernis et al., 2020; Podlutskii et al., 2022; Shuryak and Brenner, 2021; Volkova et al., 2017; Volkova et al., 2018; Voronezhskaya et al., 2023.

### 3.3. Transgenerational effects of ionizing radiation on plants

One of the most critical questions regarding exposure to IR is the occurrence of heritable consequences, as even low doses in field conditions can cause effects across multiple generations (Adam-Guillermin et al., 2018; Belli and Tabocchini, 2020; Garnier-Laplace et al., 2015; Horemans et al., 2019; Omar-Nazir et al., 2018; Pernis et al., 2020; Volkova and Geras'kin, 2018; Volkova et al., 2021). Although different studies have compared the impact of IR on fitness and mutation accumulation over generations (Abramov et al., 1992; Abramov et al., 2005; Antonova et al., 2015; Antonova and Pozolotina, 2020; Nobre et al., 2022; Ellegren et al., 1997; Hase et al., 2020; Shimalina et al., 2023; Shuryak and Brenner, 2021), with a particular interest for plant breeding programs (Shu et al., 2012), our knowledge regarding the mechanisms underlying the transgenerational effects of IR is still limited to plants with short life cycles. In simulated laboratory conditions, the researchers studied inherited traits in *Arabidopsis* (Hase et al., 2020; Laanen et al., 2021; Podlutskii et al., 2022; van de Walle et al., 2016; van de Walle et al., 2016), smooth brome (*Bromus inermis*) (Antonova et al., 2015), soybean (*Glycine max*) (Nobre et al., 2022; Feng et al., 2023), common duckweed (*Lemna minor*) (van Hoek et al., 2017, 2015; Xie et al., 2019b), and rice (*Oryza sativa*) (Choi et al., 2021; Ren et al., 2023; Zheng et al., 2020), and the long-lived species *P. sylvestris* that survived the acute doses of the accident in Chornobyl (Fedotov et al., 2006; Geras'kin et al., 2011). In natural environments, studies with *Arabidopsis* (Abramov et al., 2005; Horemans et al., 2018), silver birch (*Betula verrucosa*) tree (Boubriak et al., 2008), *G. max* (Danchenko et al., 2009; Georgieva et al., 2017; Klubicova et al., 2012; Pernis et al., 2020), flax (*Linum usitatissimum*) (Ziarovská et al., 2022), *P. sylvestris* (Fedotov et al.,

2006; Geras'kin et al., 2011; Geras'kin and Volkova, 2014; Kovalchuk et al., 2003), and *V. cracca* (Voronezhskaya et al., 2023) have been performed in the CEZ, while one study reported the effects on *C. bursa-pastoris* from Fukushima (Horemans et al., 2018). In summary, the evaluation of the mechanisms underlying the transgenerational effects indicated that epigenetic modifications are dominant.

Classically, mutations in DNA sequence were considered the source of heritable phenotypes, which, under the pressure of selection, would outline evolution (Miryeganeh and Saze, 2019; Wendel et al., 2016). However, epigenetic changes also can be the source of inherited phenotypic variability over multiple generations. Broadly speaking, epigenetics is defined as chemical modifications of the chromatin that control gene expression in response to environmental cues, which may be inherited (Bird, 2007; Jones, 2012; Miryeganeh and Saze, 2019; Richards, 2011). They include DNA methylation, histone modifications, and the activity of small non-coding RNAs involved in RNA interference (Eichten et al., 2014; Horemans et al., 2019; Kim et al., 2015; Matzke and Mosher, 2014; Miryeganeh and Saze, 2019). These pathways are in crosstalk (Du et al., 2015; Wu et al., 2010). Different histone modifications can alter the accessibility of the DNA sequence, controlling chromatin and gene activities. They include methylation, acetylation, ubiquitination, and phosphorylation (Zhao et al., 2019). As discussed above (Section 3.1), the modulation of histones seems to be a trend among chronically exposed organisms. Considering that histone H3/H4 acetylation, H3 Lysine 4 and H3 Lysine 9 methylation (H3K4me and H3K9me, respectively) are conserved among eukaryotes, it is logical to propose that the control of histone activity/status could be a general pattern during chronic IR responses across plants.

Epigenetic mechanisms are also involved in silencing repetitive

sequences that can damage the integrity of the genome, such as transposable elements (TEs), thus probably impacting plant fitness (Mhiri et al., 2022; Slotkin and Martienssen, 2007). Transposable elements silencing may occur by DNA methylation at CG and non-CG (CXG or CXX, where X stands for A, C or T) contexts, while the former is also linked to gene transcription by RNA polymerase II (Mhiri et al., 2022; Miryeganeh and Saze, 2019). Interestingly, TEs can be activated by stress (Mhiri et al., 2022), and IR exposure triggers the modulation of TEs and related gene activities (Duarte et al., 2019; Kim et al., 2014; Laanen et al., 2021; Žiarovská et al., 2022), which seems crucial for organisms living under chronic IR exposure (Duarte et al., 2019; Volkova et al., 2021). Indeed, if a TE inserts near a functional genomic sequence, the DNA methylation that follows, may change the expression of genes in the vicinity, thus leading to phenotypic modifications. Accordingly, genomic DNA hypermethylation after IR exposure has been reported for the radiosensitive *P. sylvestris* in the CEZ (Bondarenko et al., 2023; Kovalchuk et al., 2003; Volkova et al., 2018), and for the radioresistant *Arabidopsis* under simulated chronic exposure (Laanen et al., 2021). Such a pattern may occur as a protective measure for increasing the genome stability (Horemans et al., 2018; Kovalchuk et al., 2003; Volkova et al., 2018). Yet, whole genome hypomethylation was observed in *Arabidopsis* populations originating from the CEZ (Horemans et al., 2018). Although the reason why both chronically exposed *Arabidopsis* and *P. sylvestris* from CEZ would show inverse methylation status remains elusive, they may represent specific cases of adaptation and acclimation, respectively. Long-lived trees, Scots pines, have been experiencing a low-dose IR exposure for 20–30 years (Kovalchuk et al., 2003; Volkova et al., 2018). Furthermore, conifers have large genomes (up to 40 Gb), mostly composed of repetitive regions (Duarte et al., 2022). *Arabidopsis*, on the other hand, is an annual plant, meaning that the evaluated samples belong roughly to the 30<sup>th</sup> generation exposed to a low-dose IR (Horemans et al., 2018). Reduced DNA methylation could promote genetic variation by increasing the activity of TEs (Richards et al., 2017), and it has been suggested that differential methylation could be related to local adaptation (Dubin et al., 2015). As a matter of fact, the contribution of IR-dependent epigenetic changes to the evolution of species may have been underestimated in general. For example, Kronholm and Collins (2016) proposed that evolutionarily important traits may first appear by epigenetic alteration, which could later become genetically encoded by spontaneous mutations. Epigenetic mutations occur at a much higher rate than genetic ones (Ossowski et al., 2010; van der Graaf et al., 2015), although the frequency of epigenetic inheritance is still debated (Hofmeister et al., 2017; Kronholm and Collins, 2016; Miryeganeh and Saze, 2019; Verhoeven et al., 2016). Overall, it would be interesting to consider the impact of epigenetic factors on species evolutionary rates from the perspective of the evolution on Earth, given that the surface IR levels changed across the Eons, and for billions of years, they were considerably higher than at present times (Duarte et al., 2023).

Finally, the importance of epigenetic studies involving species in their natural environments has been highlighted, which often show a higher degree of epigenetic rather than genetic diversity (Alvarez et al., 2015; Miryeganeh and Saze, 2019; Narum et al., 2013). The effects of epigenetic variations seem especially important for adapting populations with limited genetic diversity, such as clonal or inbred populations (Latzel et al., 2016). In this regard, an excellent model for IR transgenerational studies is *L. minor*, an aquatic species naturally inhabiting contaminated areas, whose reproduction is primarily vegetative and occurs within a couple of days (~2.5 days).

#### 4. Plant biotic stress and symbiotic interactions in light of radioresistance of pathogens, pests, and symbionts

Multiple pests and pathogens, such as bacteria, fungi, viruses, and arthropods, attack plants, endangering the sustainable yield of crops. Plants resist attacks through their physical barriers, particularly cuticle,

wax, and trichomes, serving as their first defense line (Iqbal et al., 2021; Rejeb et al., 2014) (Fig. 5). The intensity of infection and the response of plants varies with plant species, biotic factors involved, and environmental conditions (Kushalappa and Gunnaiah, 2013). On the other hand, mutualistic microbes often enhance the fitness of host plants. Exposure of plant pathogens, pests, and symbionts to IR may significantly impact their fitness, life cycle, diversity, virulence, and eventually interaction with the host (Fig. 5). However, some biotic factors are naturally resistant to IR due to either their peculiar genetic background or the history of growth in the IR-exposed environment (Ragon et al., 2011).

##### 4.1. Plant-pathogen interaction and mechanisms of infectious agents resistance to irradiation

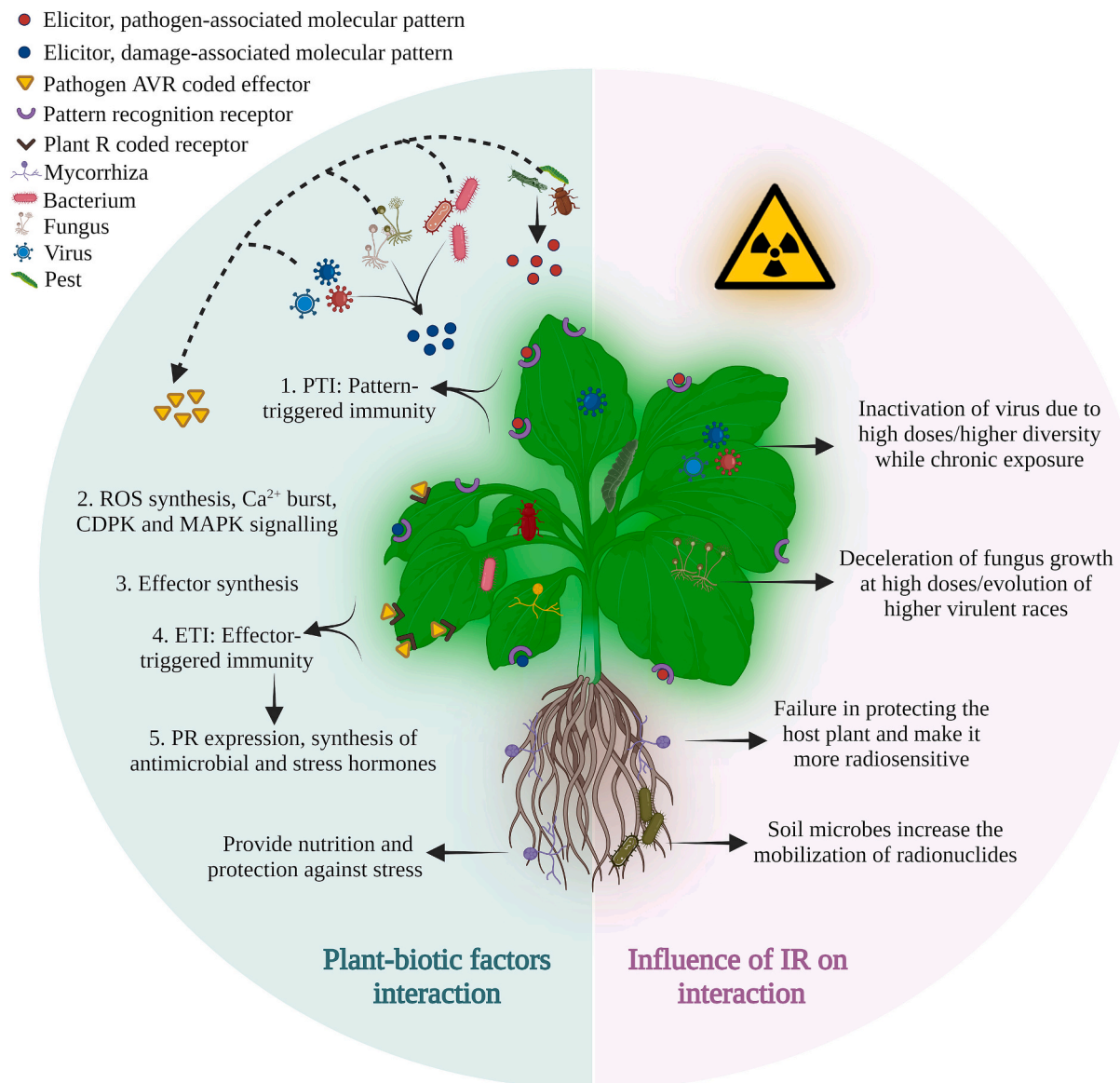
Pests and pathogens influence the metabolic activity of plants to facilitate infection. In response, plants often compromise their growth and development, reallocating resources for the synthesis of various defense compounds in order to deter, eliminate, or at least contain the invaders. The cell wall and plasma membrane are the first line of defense, independent of the type of biotic factor (Hematy et al., 2009; Zebelo, 2020). Pattern recognition receptors (PRRs), present on the plasma membrane, recognize the elicitors produced by the pathogens (Hematy et al., 2009). Consequently, pattern-triggered immunity (PTI) is activated. It initiates several cellular responses, such as ROS synthesis, calcium burst, Ca<sup>2+</sup>-dependent protein kinases (CDPKs) and mitogen-activated protein kinases (MAPKs) signaling (Fig. 5). Pathogen-produced elicitors, peptides, metabolites, cell wall components, enzymes, and toxins inhibit the plant immune system (Carere et al., 2016).

Some pathogens contain specific avirulence (AVR) genes, which synthesize race-specific effectors that target host resistance genes and increase virulence (Kushalappa et al., 2016). The plant genome has resistance (R) genes coding receptors that recognize these effectors (Zhang et al., 2015). The effectors induce effector-triggered immunity (ETI), the second line of defense response of plants (Fig. 5). It initiates a race-specific hypersensitive response, including localized cell death. Effector-triggered immunity activates the transcription of pathogenesis-related (PR) genes, and the synthesis of versatile defense compounds such as salicylic acid, ethylene, jasmonic acid, different antimicrobials, along with lignification and strengthening of the cell wall.

Viruses show higher resistance to irradiation than other pathogens (Jeong and Jeong, 2018). Nonetheless,  $\gamma$ -rays can be used to sterilize viruses (Lowy et al., 2001). In fact,  $\gamma$ -radiation slowly inactivated *Cucumber green mottle mosaic virus* on tobacco (*Nicotiana tabacum*) plants with a terminal effect at doses higher than 40 kGy. Ionizing radiation disturbed the structure of viral particles, breaking down their proteins and nucleic acids (Jin-Sung et al., 2017). Of note, chronic exposure could increase the occurrence and diversity of viruses in contaminated areas, threatening biosafety (Boubriak et al., 2016). Plants in a contaminated environment are prone to viral infection due to the increased virulence of circulating strains (Dmitriev et al., 2009).

Chronic exposure to IR affects the genetic diversity of bacteria. Previously, Zavilgelsky et al. (1998) reported that the isolates of soil bacteria collected from sites near the Chernobyl Nuclear Power Plant and the *Escherichia coli* mutant SA236, serving as a positive control, had a higher resistance to the X-rays, ultraviolet C, and mutagen than microorganisms collected from a clean area. Three decades after the accident, the Chernobyl region has a rich microbiome diversity with multiple taxonomic groups. The structure of microbial communities in wetlands was shaped by the radiation level in soil, bottom sediment, and water (Videvall et al., 2023; Theodorakopoulos et al., 2017). Ionizing radiation also affects endophytic bacteria. Zhu et al. (2021) studied the genetic diversity of endophytic bacteria of the halophytic shrub *Kalidium schrenkianum* in Northwest China, contaminated with <sup>137</sup>Cs. They reported that the IR exposure increased the genetic diversity of their bacterial population and the community diversity in roots compared to





**Fig. 5.** Overview of plant-biotic factors interactions (left panel) and possible changes due to ionizing radiation exposure (right panel). Plants evolved diverse mechanisms to resist or tolerate pathogens and pests, frequently at the cost of slower growth and development. Existing physical barriers, such as cuticle, wax, and trichomes, hamper the progress of infection. The plasma membrane contains pattern recognition receptors, which recognize elicitors produced by biotic factors and activate pattern-triggered immunity, causing an oxidative burst. Pathogens and pests synthesize race-specific effectors recognized by plant resistance genes. Consequently, effector-triggered immunity is activated and plants synthesize versatile defense compounds. Ionizing radiation exposure might unbalance these responses, and depending on the radiosensitivity of organisms, it may impact the coevolution of plant-biotic factors interactions. Abbreviations: AVR, avirulence gene; CDPK, Ca<sup>2+</sup>-dependent protein kinase; MAPK, mitogen-activated protein kinase; R, resistance gene; ROS, reactive oxygen species; PR, pathogenesis-related gene (created with BioRender).

shoots. The nitrogen-fixing bacteria associated with legumes *Medicago* spp. in the CEZ secreted a profuse amount of versatile exopolysaccharides that could be relevant for radioadaptation (Pawlicki-Jullian et al., 2010). Despite living in an ecological niche without IR exposure, several genera of bacteria, such as *Methylobacterium*, *Deinococcus*, *Bacillus*, and some Archaea, are resistant to extreme levels of  $\gamma$ -radiation. Such tolerance may be explained by their efficient DNA repair system (Pawlicki-Jullian et al., 2010). Of note, *Deinococcus radiodurans* has a rare genetic code for *ddrA* (DNA damage response), *ddrB*, *ddrC*, *ddrD*, and *pprA* (pleiotropic protein promoting DNA repair) genes. The encoded set of proteins enables robust RecA-independent (DNA recombination and repair) DNA repair in a harsh environment (Tanaka et al., 2004). Microorganisms from distant taxa can resist irradiation several orders of magnitude above the natural background. Resistance to chronic IR is not limited to strains from extreme environments but

occurs among many common microbes. Reduction of growth rate and metabolic flexibility is a characteristic feature of stress-resistant genotypes. Radioresistance may be associated with non-enzymatic antioxidants (Shuryak, 2019), and may also depend on the overall activity of the damage repair machinery (Duarte et al., 2023).

Fungi are more resistant to IR than other eukaryotes (Sharma et al., 2017; Shuryak et al., 2017). Fungal strains collected from Chernobyl Nuclear Power Plant showed higher genetic homogeneity and resistance to IR compared with relatives from control sampling sites (Mironenko et al., 2000). According to the study of *Puccinia graminis* genotypes from the CEZ, new races of the stem rust-causing fungus with higher virulence appeared; moreover, plants had a weakened defense system (Dmitriev et al., 2009). Conversely, the study of *Microbotryum lychnidis-dioicae*, responsible for anther smut disease, from the same area showed no signs of genomic evolution, while its prevalence was reduced in Chernobyl

environment (Aguileta et al., 2016). According to the microarray analysis of *Saccharomyces cerevisiae* yeast (Kimura et al., 2006), genes involved in the cell cycle, DNA processing, defense mechanism, protein and cell fate, and metabolism were quickly upregulated by acute radiation exposure. Ionizing radiation delays the germination and growth of fungal spores in a dose-dependent manner. Particularly, 5 kGy of  $\gamma$ -radiation decelerated the growth of *Alternaria alternata*, causing leaf spot disease, and 10 kGy completely halted it (Braghini et al., 2009). Maity et al. (2008) reported that 1–2 kGy of  $\gamma$ -radiation is an optimal dose for eradicating seed-borne fungi yet not damaging seed viability.

The characteristics and developmental pace of fungi are affected by IR (Tugay et al., 2011). Some fungal genera contain pigment melanin having antioxidant properties and protecting against IR as well as other stressors, including ultraviolet and toxic metals (Dadachova and Casadevall, 2008; Pacelli et al., 2017). The fungal colony collected from the damaged reactor of the Chernobyl Nuclear Power Plant was dominated by melanized species of fungi (Dadachova and Casadevall, 2008). These species had high catalase and nuclease activities. Interestingly, fungi can even bioremediate radionuclides. The insoluble radionuclides are converted into ions and enter the food chain, thereby increasing human health risks (Zhdanova et al., 2004). The non-melanized fungi have other pigments enabling radiation tolerance; for example, the red pigment in *M. lychnidis-dioicae* protects from ultraviolet light (Aguileta et al., 2016).

#### 4.2. Mutualistic relationships with fungi

Virtually all plants are involved in mutualistic relationships with fungi. Mycorrhizal symbiosis, the association between plant roots and soil fungi that facilitated the conquest of land by plants around 450 million years ago, is most likely the most widespread in the terrestrial environment (Tedersoo et al., 2020; Rich et al., 2021; Strullu-Derrien et al., 2018). Today, 90 % of land plants are estimated to engage with hyphal fungi to result in some type of mycorrhiza. Mycorrhiza can be extracellular, intracellular or both (Genre et al., 2020). The most common and well-studied types are arbuscular mycorrhiza (AM) and ectomycorrhiza (ECM). Arbuscular mycorrhiza fungi penetrate plant cell walls and form tree-like structures (arbuscules) in root cortex cells, whereas hyphae from ECM fungi remain in the apoplastic space between epidermis and cortex cells and form a mantle around root tips (Genre et al., 2020). Irrespective of their morphology, all these symbioses with the plant are mutually beneficial, providing carbon assimilates to the fungus in exchange for mineral nutrients and water. Eventually, both partners may be relieved from abiotic stress. Evidence for mycorrhizal fungi enhancing plant performance in stressful conditions is overwhelming and includes studies both on AM and ECM. Benefits of mycorrhizal fungi that impact plant performance in stressful environments consist of an improved nutrient supply, limited transfer of pollutants, modification of the immune system, and priming of the antioxidant machinery (Branco et al., 2022).

All AM plants are characterized by a core set of genes to establish symbiosis. These genes are conserved across plant lineages and include members of the common symbiotic signaling pathway that are shared with the establishment of nitrogen fixation in legumes and actinorhizal plants together with transcription factors controlling specific symbiotic functions, such as phosphate and lipid transport (Genre et al., 2020). In ECM plants, no specific marker genes have been identified yet. Regardless of the initial signaling mechanisms and partner recognition, lateral roots are the preferred infection sites and eventually, lateral root formation is stimulated by the fungal partner. It was shown that the mycelium of ECM fungus *Laccaria bicolor* produces massive amounts of auxin indole-3 acetic acid (IAA), thus modifying the auxin metabolism of plants and altering root architecture through enhancement of a number of short lateral roots (Felten et al., 2009; Vayssières et al., 2015). Also, in AM plants, auxin seems to be involved in symbiosis development, activating auxin-inducible promoters in colonized roots (Ludwig-Müller and

Güther, 2007). The sub-apical root zone is the most common target for fungal colonization. In this zone, colonization relies on the degradation of middle lamella pectins and the mechanical forces posed by hyphal tip growth. Recently, the authors showed that a pectin methylesterase of the ECM fungus *L. bicolor* participated in mycorrhizal development in poplar (Chowdhury et al., 2022) next to other cell wall-modifying enzymes, such as endoglucanases and polygalacturonases (Zhang et al., 2018 and 2021). Besides, mycorrhizal fungi deploy hundreds of secreted effector proteins to modify the plant immune system and allow for massive hyphal proliferation in the apoplastic space (Aparicio Chacón et al., 2023; Plett et al., 2020; Zeng et al., 2019).

So far, it is unclear how radionuclides impact the establishment and maintenance of mycorrhizal symbiosis. *Rhizophagus irregularis* spores can germinate and establish AM symbiosis with *Plantago lanceolata* after exposure to chronic doses of up to 30 Gy  $\gamma$ -irradiation at a rate 109 mGy/h (Kothamasi et al., 2016), at higher doses (113 Gy at rate 404 mGy/h) colonization was impaired. Exposure of the same fungal species to Cs (applied as a mix of stable and radioactive isotopes), on the other hand, inhibited colonization of barrel medic (*Medicago truncatula*) roots (Wiesel et al., 2015). Nevertheless, mycorrhizal fungi are abundantly present in radiocaesium-contaminated environments of Chernobyl and Fukushima areas (Higo et al., 2019). These fungi display a set of species-/strain-specific detoxification mechanisms, including melanin accumulation and activation of ROS decomposing enzymes upon chronic IR exposure with cumulative doses 8–55 Gy (Kothamasi et al., 2019). Particular interest went (and still goes) towards monitoring radionuclides, mostly  $^{137}\text{Cs}$ , accumulation in edible mushrooms, including ECM-forming species. Macrofungi tend to accumulate  $^{137}\text{Cs}$  in their fruiting bodies at concentrations several times exceeding the measured soil concentration (Orita et al., 2018). Transfer factors and magnitude by which fungi accumulate  $^{137}\text{Cs}$  in their fruiting bodies depend on the species and strains (Ohnuki et al., 2019; Vinichuk et al., 2010). Overall, fungi are a sink for  $^{137}\text{Cs}$  in soil and, in particular, for mycorrhizal fungi; this trait raises questions regarding its effect on radionuclide translocation towards the host plant. Pine seedlings colonized by ECM fungus *Astraeus hygrometricus* showed an increased Cs concentration but enhanced growth compared to non-inoculated trees (Ogo et al., 2018). Similar results were obtained after establishing symbiosis with *Rhizopogon roseolus* (Ogo et al., 2018; Ladeyn et al., 2008). On the other hand, ECM fungus *Hebeloma crustuliniforme* reduced radiocaesium uptake into seedlings of Norway spruce (*Picea abies*) (Brunner et al., 1996). The same inconsistency is present in results reported for AM symbiosis. Some AM fungi may enhance the uptake of Cs by their host plant, whereas others decrease it (Rosén et al., 2005; Takenaka et al., 2021). Consequently, the translocation effect is dependent on the fungal-plant combination. All these laboratory experiments to investigate Cs translocation and tolerance towards irradiation are examples of a short-term acute stress assessment and might differ from responses observed after chronic exposure in nature. Besides, neither fungal strains nor plant seeds included in the experiments originated from radionuclide-contaminated environments. Despite being very informative for assessing radionuclide dynamics, they will not shed light on local adaptation and might not entirely reflect the full protective potential of fungal ecotypes in exclusion zones.

#### 4.3. Interaction between plants and frequently radiosensitive pests

Plants synthesize chemical compounds to avoid pest attacks by creating toxicity or decreasing the digestibility and nutritious value of their tissues (Mello and Silva-Filho, 2002). Plant pests use different feeding strategies—leaf chewing and phloem sap sucking—to satisfy their nutritional requirements. Beetles, as well as larvae of butterflies and grasshoppers (Acrididae), are chewers (Clissold, 2007). Examples of sap-sucking pests include aphids, whiteflies, and planthoppers (Jain et al., 2021). During both types of interactions, pests release oral secretions as well as regurgitate from the foregut and the midgut

containing elicitors at the site of the attack (Chung et al., 2013; Mori et al., 2003) (Fig. 5). Elicitor molecules activate a cascade of biochemical reactions that trigger the plant defense system and interact with receptors changing the transmembrane potential of the cellular plasma membrane, followed by an influx of  $\text{Ca}^{2+}$  inside the cell, triggering downstream network of protein kinases (Maffei et al., 2007). Simultaneous synthesis of ROS activates the defense genes via the jasmonic acid signaling pathway, further boosting the plant antioxidant system (Sharma et al., 2012). Furthermore, cell wall thickening starts at the attack site, trichomes and root density increase for strengthening barriers against further invasion (Brian Traw and Dawson, 2002). Plants also synthesize specific protective proteins, such as amylases, chitinases, proteinase inhibitors, and lectins (Mello and Silva-Filho, 2002; Rajniece et al., 2020). Some chemical compounds, pre-stored in tissues, such as polyphenol oxidase and variable phenolics, are toxic to insects, decreasing the digestibility or nutritious value of plants (Bhonwong et al., 2009). Pests evolved different mechanisms to overcome the constitutive and induced plant reactions, nullifying the effect of plant-secreted secondary metabolites and toxins (Nishida, 2002). Pests enzymatically transform them into non-toxic products through oxidation, reduction, hydrolysis, or conjugation of molecules, sometimes with the help of symbiotic microbes (Jeschke et al., 2016). The presence of the bacterium *Candidatus* Ishikawaella capsulate in the beetle *Megacopta cribraria* is an example of microbial symbiosis (Couret et al., 2019), facilitating the feeding of the pest.

The tolerance of pests to IR varies with species, such as butterflies and moths (Lepidoptera) have a higher tolerance than beetles and weevils (Coleoptera), true bugs (Hemiptera), as well as flies and mosquitoes (Diptera) (Follett and Griffin, 2012). Pests are more susceptible to IR during earlier stages of their life cycle (Hallman et al., 2010). Specifically, chronic exposure of developing *Tetraneura* gall-making aphids nearby Fukushima Daiichi caused morphological abnormalities and mortality. Researchers showed that the first stage of development of aphid galls in the contaminated zone suffered more than juveniles in a controlled clean environment (Akimoto, 2014). Ionizing radiation also affected the expression of male-specific proteins, reducing insect competence for finding and mating females (Chang et al., 2016). Acute irradiation may influence the gender determination of insect pests. For example, the endosymbiotic relationship between the mite *Brevipalpus phoenicis* and the bacteria of the genus *Cardinium* defines the emergence of haploid females.  $\gamma$ -Radiation exposure of mites eliminated bacteria from them and increased the proportion of hatched males (Novelli et al., 2008). Summarizing, morphological abnormalities, higher mortality, lower mating frequency, and unnatural gender balance negatively influence pest populations, apparently lowering their pressure on host plants. Acute IR can sterilize insects in a dose-dependent manner (Zhang et al., 2023). Irrespective of species and life stage, IR affects the immune response of insects (Gabarty et al., 2013; Gómez-Alonso et al., 2022). It modulates redox metabolism and inhibits some enzyme activities, such as phenol oxidase and lysozyme (Kheirallah and El-Samad, 2016). Researchers reported that the second-generation larvae did not inherit abnormalities (Akimoto, 2014).

Pollinators, such as bumblebees (*Bombus terrestris*), substantially affect plant populations in radiologically contaminated zones. Model laboratory experiment showed that *B. terrestris* queen fecundity was impaired already at  $50\mu\text{Gy/h}$ , delaying colony growth (Raines et al., 2020). Moreover, another study with the same insect demonstrated that at field-realistic  $200\mu\text{Gy/h}$ , feeding and metabolic rate were elevated relative to controls (Burrows et al., 2022). These changes could drive significant ecological consequences—impaired pollination services for plants. Somewhat contradictory, another study showed that the number of carpenter bee (*Xylocopa appendiculata*) individuals around Fukushima dropped while other bee species (*Ceratina flavipes*) increased population size, concluding that pollination services were largely unaffected (Yoshioka et al., 2015).

## 5. Interplay between ionizing radiation, host plants, and biotic factors

In nature, plants face multiple stressors simultaneously, while hosting diverse pathogenic and mutualistic organisms. In this respect, environmental impact assessment focusing on only one stressor at a time can lead to biased or wrong conclusions (Salbu et al., 2019). Simultaneous action of abiotic and biotic stresses triggers a complex adaptive response, including crosstalk of signaling pathways, and the abiotic environment impacts disease severity (Zandalinas et al., 2020). Currently, researchers focus on elucidating the molecular interplay and regulatory principles of combined responses (Saijo and Loo, 2020). Accumulation of specific compounds may lead to cross-tolerance, such as genetic manipulation of polyamine synthesis, improved tolerance to multiple stress factors (Hussain et al., 2011).

### 5.1. Positive, neutral, and negative relations between stresses

Some molecular and physiological reactions are common in plants responding to the combined action of challenging factors, such as the decrease in growth rate, the accumulation of ROS, and the activation of antioxidant machinery (Antonioni et al., 2018; Zhang et al., 2020). However, other reactions are unique to the specific stress combinations, which may be seriously more damaging than individual challenges (Zandalinas et al., 2021). Exposure of plants to abiotic stress conditions modulates their resistance to pests and pathogens in a synergistic, neutral, or antagonistic manner, depending upon the type and duration of the stress condition (Ramegowda and Senthil-Kumar, 2015; Suzuki et al., 2014), the genotype of the plant and pathogen, their age/developmental stage, and infection mode (Bostock et al., 2014) (Table 1). Mechanisms behind compromised immunity include hormonal imbalance (particularly accumulation of abscisic acid), repressed metabolism, and expression of stress genes (Mohr and Cahill, 2003; Prash and Sonnewald, 2013). Contrarily, exposure to some abiotic stresses primed the defense system of plants and improved their resistance to pests and pathogens (Suzuki et al., 2014), though examples are more scarce.

In most cases, attacking bacteria thrive in abiotic stress scenarios as was shown for heat leading to compromised resistance against the bacterial pathogen *Pseudomonas syringae* in Arabidopsis (Wang et al., 2009; Huot et al., 2017) and for salt stress promoting the growth of the same pathogen and intensified the disease symptoms in cucumber (*Cucumis sativus*). Among other effects combined stress caused changes in phytohormone homeostasis and signaling as well as more substantial  $\text{H}_2\text{O}_2$  accumulation and Fe SOD activation (Wang et al., 2009; Huot et al., 2017; Chojak-Koźniewska et al., 2017). Crosstalk between stress response pathways might minimize a fitness cost. Salinity and drought inhibited immune responses to the bacterium *P. syringae* in old Arabidopsis leaves through abscisic acid; however, younger leaves remedied signaling through PBS3 involved in salicylic acid response (Berens et al., 2019). Another study reported that Pierce's disease symptoms were enhanced in bacterium *Xylella fastidiosa*-infected, water-stressed grape (*Vitis vinifera*) plants (Choi et al., 2013). Global warming modeling suggested that rice disease—bacterial panicle blight caused by *Burkholderia glumae*—might cause additional substantial loss in production (Shew et al., 2019). On the other hand, the multiplication of the bacterial pathogen *P. syringae* was inhibited by drought stress in Arabidopsis. Combined stressed plants displayed reduced ROS generation and declined cell death, which could be attributed to the effective basal defense responses (Gupta et al., 2016).

A vast majority of published literature argues for enhanced susceptibility to fungal infections under environmental stress. Drought has been reported to increase the susceptibility to fungal infection in peanuts (*Arachis hypogaea*), wheat (*Triticum aestivum*), common bean (*Phaseolus vulgaris*), and chickpeas (*Cicer arietinum*) (Luo et al., 2005; Lastochkina et al., 2020; Mayek-Pérez et al., 2002; Sinha et al., 2019). Similarly, salt stress facilitated the fungal infection of *Phytophthora*

**Table 1**  
Type of plant response to a combination of biotic and abiotic stresses.

Group	Biotic stressor	Abiotic factor	Interaction type	Plant host	Reference	
Bacteria	<i>Pseudomonas syringae</i>	Drought	Synergistic	Arabidopsis	Mohr and Cahill, 2003	
	<i>Xylella fastidiosa</i>	Drought	Synergistic	Grape	Choi et al., 2013	
	<i>Burkholderia glumae</i>	Global warming	Synergistic	Rice	Shew et al., 2019	
	<i>P. syringae</i>	Heat	Synergistic	Arabidopsis	Huot et al., 2017; Wang et al., 2009	
	<i>P. syringae</i>	Salinity	Synergistic	Cucumber	Chojak-Koźniewska et al., 2017	
	<i>P. syringae</i>	Salinity, Drought	Synergistic	Arabidopsis	Berens et al., 2019	
	<i>P. syringae</i>	Drought	Antagonistic	Arabidopsis, Tobacco	Gupta et al., 2016; Ramegowda et al., 2013	
	Fungi	<i>Macrophomina phaseolina</i>	Drought	Synergistic	Common bean	Mayek-Pérez et al., 2002
		<i>Rhizoctonia bataticola</i> , <i>Fusarium solani</i>	Drought	Synergistic	Chickpea	Sinha et al., 2019
		<i>Aspergillus parasiticus</i>	Drought	Synergistic	Peanut	Luo et al., 2005
<i>Fusarium culmorum</i>		Drought	Synergistic	Wheat	Lastochkina et al., 2020	
<i>Puccinia triticana</i>		Ionizing radiation	Synergistic	Wheat	Dmitriev et al., 2011	
<i>Phytophthora capsici</i>		Salinity	Synergistic	Tomato	Pye et al., 2018	
<i>Oidium neolyopersici</i>		Mild/Severe Salinity	Synergistic/ Antagonistic	Tomato	Kissoudis et al., 2016	
<i>Verticillium longisporum</i>		Drought	Antagonistic	Arabidopsis	Reusche et al., 2012	
<i>Sclerotinia sclerotiorum</i>		Drought	Antagonistic	Tobacco	Ramegowda et al., 2013	
<i>O. neolyopersici</i>		Drought, Salinity	Antagonistic	Tomato	Achuo et al., 2006	
<i>Fusarium solani</i>		Ionizing radiation	Antagonistic	Sunflower	Abu-Tahon et al., 2021	
<i>Magnaporthe oryza</i>		Ionizing radiation + Plant extract	Antagonistic	Rice	Gajbar et al., 2021	
Viruses		<i>Tobacco mosaic virus</i>	Heat	Synergistic	Tobacco	Király et al., 2008
	<i>Turnip mosaic virus</i>	Heat + Drought	Synergistic	Arabidopsis	Prasch and Sonnnewald, 2013	
	<i>Brome mosaic virus</i> , <i>Cucumber mosaic virus</i> , <i>Tobacco mosaic virus</i> , <i>Tobacco rattle virus</i>	Drought	Antagonistic	Multiple plants	Xu et al., 2008	
	<i>Tomato yellow leaf curl virus</i>	Ionizing radiation	Antagonistic	Tomato	Zhou et al., 2019	
	Pests	<i>Pieris rapae</i>	Drought	Synergistic	Arabidopsis	Davila Olivas et al., 2016
<i>Steneotarsonemus phragmitidis</i>		Ionizing radiation	Synergistic	Reed	Gudkov et al., 2006	
<i>Pieris brassicae/Spodoptera littoralis</i>		Drought	Synergistic/ Antagonistic	Garlic mustard	Gutbrodt et al., 2011	
<i>Tetranychus urticae</i>		Drought	Neutral	Barrel medic	Antoniou et al., 2018	
<i>Trialeurodes vaporariorum</i>		Drought	Neutral, Antagonistic	Tomato	González-Klenner et al., 2022	
Symbionts	<i>Bradyrhizobium japonicum</i> + <i>Azospirillum brasilense</i>	Drought	Synergistic	Soybean	Silva et al., 2019	
	<i>Epichloe coenophiala</i>	Ionizing radiation	Synergistic	Tall fescue	Amirikhah et al., 2021	
	<i>Bacillus subtilis</i>	Drought	Antagonistic	Fenugreek	Barnawal et al., 2013	

*capsici*, causing root and crown rot in tomato plants (*Solanum lycopersicum*) (Pye et al., 2018) and affected powdery mildew resistance in tomatoes in a genotype- and stress intensity-dependent manner (Kissoudis et al., 2016). On the other hand, adult spring wheat plants, tolerant to heat, resisted the fungus *Puccinia striiformis*, causing stripe rust (Carter et al., 2009). Interestingly, Arabidopsis showed drought stress tolerance upon infection with soilborne fungal pathogen *Verticillium longisporum* that displayed conditionally mutualistic features (Reusche et al., 2012). Plant responses also depend on whether the pathogens are necrotrophic or biotrophic (Achuo et al., 2006; Sinha et al., 2019) and on the complex regulation of hormonal crosstalk, which are crucial for the adaptation to the combined stress (Bai et al., 2018).

Contradictory findings were reported for plant-virus and plant-pest interactions during abiotic challenge. High temperature inhibited *Tobacco mosaic virus* (TMV)-induced hypersensitive-type necrotization in tobacco due to the lower NADPH oxidase activity and depletion of superoxide radicals, thus allowing the disease to spread (Király et al., 2008). Vice versa, exploring the interaction of several viruses with multiple plants, the authors concluded that infection improved plant tolerance to drought, which correlated with increased osmoprotectant and antioxidant levels in infected plants (Xu et al., 2008). Drought stress was irrelevant to the dynamics of mite *Tetranychus urticae* infestation in *M. truncatula* (Antoniou et al., 2018).

The performance of tomatoes challenged by combined drought and greenhouse whitefly (*Trialeurodes vaporariorum*) was similar to the condition with chewing pests along (González-Klenner et al., 2022). A combination of drought and caterpillars *Pieris rapae* induced an extensive downregulation of Arabidopsis genes involved in defense against pathogens and a more substantial growth reduction (Davila Olivas et al.,

2016). Specialist leaf-chewing herbivore *Pieris brassicae* developed faster on drought-stressed garlic mustard (*Alliaria petiolata*), while generalist *Spodoptera littoralis* showed retarded development (Gutbrodt et al., 2011).

Several reports showed the protective role of symbionts under environmental stress. Soybean plants co-inoculated with growth-promoting rhizobacteria *Bradyrhizobium japonicum* and *Azospirillum brasilense* improved the root nodulation under severe drought conditions or, in other words, stress facilitated colonization by symbionts (Silva et al., 2019). A plant growth-promoting rhizobacterium *Bacillus subtilis* strain possessing high activity of 1-aminocyclopropane-1-carboxylic acid deaminase, which cleaves ethylene precursor, considerably protected fenugreek (*Trigonella foenum-graecum*) plants under severe drought stress conditions (Barnawal et al., 2013).

## 5.2. Crosstalk of ionizing radiation with biotic agents

Only a few studies focused on deciphering complex interacting networks that function if IR exposure coincides with a pathogen attack on the plant. In other words, the response of the irradiated plants to the biotic stress conditions has not yet been widely explored. The role of a primed defense system during the crosstalk with biotic stress is not yet mechanistically clear. Ionizing radiation affects both the morphology (e.g., leaf area and size) and the anatomy/biochemistry (e.g., the lipid composition of the cell membrane) of plants (Boratynski et al., 2016; Hinton et al., 2007). Assuming that the first line of defense is weakened, it is plausible that plants may become more susceptible to biotic stress (Dmitriev et al., 2011). Pests inhabiting the chronically affected area interact with host plant populations. Gudkov et al. (2006) analyzed the

productivity and pest resistance of common reed (*Phragmites australis*) in the CEZ. His group reported more massive damage from gall-producing mites (*Steneotarsonemus phragmitidis*) in substantially contaminated ponds, along with vegetative phenotype and seed morphology defects (Table 1). Recently, we confirmed higher susceptibility to pathogenic fungus in common reed leaves collected from heavily contaminated lakes compared to the samples from control ponds. Of note, we detected only minor changes in proteome; furthermore, the sampling site more strongly affected it than radionuclide contamination (unpublished data). We earlier suggested compromised plant immunity based on differentially abundant proteins in soybean seeds grown for multiple generations in the Chernobyl region (Pernis et al., 2020).

A high-dose  $\gamma$ -radiation (> 100 Gy) compromised seed germination, early growth, and antioxidant system (especially activities of catalase and SOD) in tall fescue (*Festuca arundinaceae*) inoculated with beneficial endophytic fungus *Epichloe coenophiala*. The presence of the endophyte failed to protect host plants, vice versa; they became more radiosensitive (Amirikhah et al., 2021). A field trial in the CEZ showed lower resistance of wheat to the fungal disease brown rust (*Puccinia triticana*). Specifically, the disease symptoms were enhanced on plots with higher IR intensity. Authors suggested that the reduced activity of proteinase inhibitors was at least partially responsible for lower phytoimmunity (Dmitriev et al., 2011). Pre-treatment of sunflower (*Helianthus annuus*) seeds with 6 % aqueous extract of fat hen (*Chenopodium album*) and 6 Gy  $\gamma$ -radiation reduced the incidence of fungal disease caused by *F. solani* from 51 to 28 %. Authors claimed an increased content of non-enzymatic antioxidants and nucleic acids due to the combined pre-treatment of inoculated plants (Abu-Tahon et al., 2021). Rice grown from seeds soaked in methanolic extracts (150  $\mu$ g/mL) of *T. foenum-graecum* seeds treated by 20 Gy of  $\gamma$ -rays were 56 % protected from fungal disease rice blast (*Magnaporthe oryza*), coincided with an early increase in peroxidase activity. Of note, this report contained occasional non-coherent descriptions of experimental design (Gajjar et al., 2021). Resistance to viruses may be primed in irradiated crops. Zhou et al. (2019) reported that neutron radiation-induced tomatoes were less susceptible to *Tomato yellow leaf curl virus*. Transcriptome changes in plants were more pronounced than phenotypic changes. The presence of soil microbes influences the mobilization of radionuclides by plants. For example, inoculation of the substrate with *Burkholderia* sp. decreased the uptake of  $^{137}\text{Cs}$  by rapeseeds (*Brassica napus*), and vice versa; the addition of *Bacillus megaterium* culture to soil caused a higher accumulation of radionuclide in the vegetative part, opening a perspective for phytoremediation (Pareniuk et al., 2015).

Multiple bacterial and fungal plant pathogens induce double-strand breaks in the genomes of infected host plants. Plant defense systems suppress such damage. Thus, in essence, plant immune and DNA damage repair responses are interconnected (Song and Bent, 2014). Interestingly, compelling evidence suggests that the activation of DNA damage response is essential for plant immunity (Nisa et al., 2019). DNA damage and salicylic acid synergistically induce the expression of defense genes. Curiously, the authors demonstrated that salicylic acid can trigger DNA damage even without genotoxic stress. Moreover, the DNA damage sensor proteins RAD17 and ATR are required for effective immune responses (Yan et al., 2013). Poly (ADP-ribose) polymerases (PARPs) catalyze the transfer of poly(ADP-ribose) units onto target proteins, and autoactivation of PARPs has a prominent role in DNA damage repair. PARP2 is a major active enzyme in Arabidopsis, ensuring the viability of plants challenged by IR. In parallel, it restricts the growth of phytopathogenic bacteria (Song et al., 2015). Transcription factor SOG1 regulates the majority of the genes induced by  $\gamma$ -rays and promotes DNA repair. The authors showed that defense-related genes were among enriched SOG1 targets. Furthermore, they proved that this transcription factor is required for resistance against fungal infection, yet it was irrelevant in the context of bacterial one (Ogita et al., 2018).

## 6. Key concepts and open questions

Ionizing radiation affects virtually all aspects of plants' life. It causes DNA breaks, gene mutations, chromosomal aberrations, generates excessive ROS, changes transcriptomic, proteomic (including landscape of post-translational modifications of the proteins), and metabolomic profiles. The effects on molecular and biochemical levels may modify ontogenesis, expand to plant populations, or even persist in subsequent generations due to genetic and epigenetic heritable mechanisms. Moreover, plants face the complexity of other environmental challenges, including pathogens/pests attacks or mutually beneficial symbiotic interactions with microorganisms. The borderline between acute and chronic exposure is blurred for plants. Under acute exposure, organisms focus their energy on avoiding damage at the cost of growth and development. On the other hand, plants probably attempt to establish a new homeostasis for coping with chronic stress without dampening the ROS-dependent systems to save (or alleviate) signaling and crosstalks with hormone pathways. The complexity of the radioecological field data can hardly be simulated in the sense of species interactions, ecosystems uniqueness, heterogeneity of the contamination, and duration of actual chronic exposures. The response of irradiated plants to biotic stress factors is only marginally explored. Shared damage/protection mechanisms among stress conditions may explain an occasionally primed defense system by IR, improving plant resistance to biotic challenges. Contrary, detoxifying a harmful action of radionuclides often exhausts energy reserves, making plants more vulnerable to biotic threats. Plausibly, these scenarios are specific for taxonomic groups or developmental stages. On the other side, plants, pests, pathogens, and symbionts living in a contaminated zone may adapt, modifying their virulence. Understanding the relationship between plants and biotic factors upon exposure to IR can improve the management of contaminated areas.

### CRedit authorship contribution statement

**Shubhi Mishra:** Writing – original draft, Visualization, Conceptualization. **Gustavo Turqueto Duarte:** Writing – original draft. **Nele Horemans:** Writing – review & editing, Funding acquisition. **Joske Ruytinx:** Writing – review & editing. **Dmitri Gudkov:** Writing – review & editing. **Maksym Danchenko:** Writing – original draft, Funding acquisition, Conceptualization.

### 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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### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2024.171567>.

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