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Heavy Metal-Induced Phyto-Hormetic Morpho-Physio-Biochemical Adjustments: A Critical Review

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Abstract

In the past, scientific communities obtained the dose–response only partially right. They correctly described responses at high heavy metal (HM) doses, but ignored and mischaracterized the crucial response at low HM doses. Lower dosages of non-essential heavy metals (HMs) in plants induced plant hormetic responses by triggering innocuous, beneficial, and growth-promoting morpho-physio-biochemical reactions. Instead of creating toxic symptoms in plants, these low amounts of non-essential HM or metalloid dosages improve or boost plants' metabolism at morphological, physiological, and biochemical levels. This review critically examines distinct non-essential HMs or metalloids-mediated hormetic effects inducing plant morpho-physio-biochemical response characteristics (end points) at specified exposure duration in diverse plant species. Additionally, the review highlights the details of hormesis inside the plant system along with non-essential heavy metal or metalloids-induced morphological, physiological, and biochemical hormetic responses that were clearly risk free, safe, and non-hazardous to plants' bodies. These responses further ensured the plant's fitness and long-term survival by strengthening the plant's immunity against subsequent future interactions with toxicants. The review study also looks over the potential working possible mechanisms behind non-essential HMs or metalloids-induced phyto-hormesis phenomena, such as activation of a variety of plant tolerance mechanisms like phytohormone defence pathways, antioxidant system, stress-related genes, and reactive oxygen species (ROS) homeostasis. All these all mechanisms and their cross talk might contribute to plant growth and developmental processes under modest HMs or metalloids stress.

Keywords Hormesis · Plants · Morpho-physio-biochemical · Heavy metals

Introduction

In the past, hormesis was one area where a toxicological community had a partial grasp of the dose–response relationship (Calabrese 2005a, b). The reason this occurred was because, in toxicology, the old way of thinking was based on a sigmoidal or S-shaped dose–response (Calabrese 2009). This means that as doses went down, responses would go back to "noise" levels and be similar to control values (Calabrese 2005a, b, 2009). Consequently, this interpretation led to the idea that there might be thresholds at low dosages, below which there would be no substantial effect (Calabrese 2005a, 2009). On the other hand, this perspective failed to take into account the hormetic dosage response, which can exhibit either a J-shaped curve or an inverted U-shaped curve, showing that beneficial effects can be achieved at low doses (Calabrese and Baldwin 1999). Therefore, such kind of historical perspective leads to the right and wrong interpretation of dose–response relationships under high and lower doses of various toxic substances (Calabrese 2005a, 2009). Consequences of` this interpretation further lead to the misconception of the hormesis phenomenon, research, and regulatory practices that mainly concentrated primarily on high doses and neglecting the benefits of lower doses (Calabrese 2005a, b, 2009). This had repercussions for the establishment of standards for the health of consumers, workers, and the environment, as well as for the administration of pharmacological substances (Calabrese 2005a, b, 2009). The significance of the statement about

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the scientific community's partial accuracy in understanding the dose–response relationship relies on the realization that traditional models, effective in high-dose scenarios, were useful for certain high-dose applications, but failed to recognize the complexity and potentially advantageous effects at lower doses (Calabrese 2005a, b, 2008, 2009). This finding has far-reaching consequences for the evaluation of hazards and the comprehension of the complete range of impacts that a toxic substance can have on biological systems (Calabrese 2003, 2005a, b; Calabrese and Baldwin 1999).

Due to this reason, non-essential elements for plant biological activities have long been recognized as extremely toxic and potentially harmful to plants, even in small amounts (Wu et al. 2010; Nagajyoti et al. 2010). However, hormesis occurrences were so frequent in stress-related studies that these have caused a quick comeback again in the planning and designing of stress-related research initiatives (Sun et al. 2020). Additionally, a rising number of recent investigatory studies have revealed that the response of plants to non-essential HMs or metalloids depends upon how much concentration of metal ion that plant is exposed to (Muszyńska and Labudda 2019). For many plant species, only very high concentrations of HMs or metalloids hinder plant development and cause damage, while at lower concentrations HMs or metalloids exposure does not harm plants and may even cause them to perform better by actually improving the plant functions (Arif et al. 2016). This phenomenon is called hormesis in which an organism's body reacts in two different ways to the same chemical, stressor, or drug (Calabrese and Baldwin 2002; Kitchin 2002; Mattson 2008; Kendig et al. 2010). The basic idea behind hormesis is that the reaction to a stimulus is non-linear and takes the form of a U-or J-shaped curve (Kitchin 2002). This means that the dose–response relationship is advantageous or stimulatory at low concentration levels, but has the opposite effect at larger or higher concentration levels (Mattson 2008; Kendig et al. 2010). Additionally, "Phytohormesis" is a plant-specific hormetic reactional response (Godínez-Mendoza et al. 2023; Shahid et al. 2020). This is the phenomenon in which plants respond positively to small amounts of chemicals or stressors that would normally be harmful in larger amounts (Godínez-Mendoza et al. 2023; Erofeeva 2022a, b, c; Shahid et al. 2020). This phenomenon holds true for a variety of plant species where the low concentration of HMs enhanced various growth metrics (root/shoot length, total biomass, fresh/dry weight, leaf area, etc.) (Liu et al. 2023; Oliverira et al. 2021; Malkowski et al. 2020; Li et al. 2019; Zhang et al. 2018; Miranda Pazcel et al. 2018), photosynthetic parameters [pigments (chlorophyll a, b, a+b, carotenoid) content, transpiration rate, stomatal conductance, photosynthetic rate, etc.] (Oliverira et al. 2021; Malkowski et al. 2020; Miranda Pazcel et al. 2018), phenolic compounds (Zhang et al. 2024; Malkowski et al. 2020), and various antioxidants (Yuebing et al. 2020). In addition to this, low concentrations of a variety of stressors (natural or anthropogenic) (Fig. 1) induce a favourable alteration in morphological, physiological, and biochemical parameters of several organisms (bacteria, algae, fungus, higher plants, or animals), which finally leads to generating benefiting responses in them (Camilo dos Santos et al. 2022; Agathokleous et al. 2019a, b, c; Pradhan et al. 2017; Calabrese and Baldwin 2000).

As a result of these factors, despite the fact that in the past certain non-essential HMs were considered to be harmful, they are now beginning to be recognized as beneficial and are now being considered within the group of beneficial elements (Carvalho et al. 2020). Not all plants need beneficial elements, but they can promote plant growth, and some plant taxa often need them (Carvalho et al. 2020). Earlier, the following elements were put into the categories of beneficial elements: aluminum (Al), cobalt (Co), cerium (Ce), iodine (I), lanthanum (La), selenium (Se), sodium (Na), silicon (Si), vanadium (V), and titanium (Ti), (Pilon-Smits et al. 2009). But presently, the following elements have been also identified as beneficial in specified lower dosages: arsenic (As), lead (Pb), mercury (Hg), cadmium (Cd), chromium (Cr), etc., by various researchers and scientists (Tables 1, 2, 3, 4, 5, 6, 7, 8). These heavy metals or metalloids are now relatively new to the list of beneficial elements. According to the various sources of databases (Scopus, Web of Sciences, Publons, Google Scholar, etc.), most of the research on various heavy metals or metalloids with a hormetic effect has been done and published in recent years with cadmium (Cd) (being the most studied), lead (Pb), zinc (Zn), chromium (Cr), arsenic (As), mercury (Hg), copper (Cu), manganese (Mn), platinum (Pt), tungstate (W), nickel (Ni), selenium (Se), lanthanum (La), tungstate (W), cerium (Ce), vanadium (V), samarium (Sm), etc. In fact, low to moderate amounts of heavy metal (Pb, Cd, Cr, Hg, Pt, W, Ni, Se, La, Ce, V, Sm, etc.) pollution is more likely to happen in nature than unrealistically high to excessively high amounts, which are often impossible. So, it is a significantly important research to know how plants react morphologically, physiologically, and biochemically to low levels of heavy metals (Pd, Cd, Cr, etc.), how these plants are able to maintain or even increase their performance under heavy metal exposure, and how the hormetic growth stimulatory mechanism actually works.

Hormesis in Plants: Occurrence

The hormesis phenomenon has been increasingly proven and observed across a wide range of biological organization levels (i.e. cell, tissue, organism, or species, population and communities) in various categories of organisms (like bacteria, animals, and plants) (Erofeeva 2022b). This

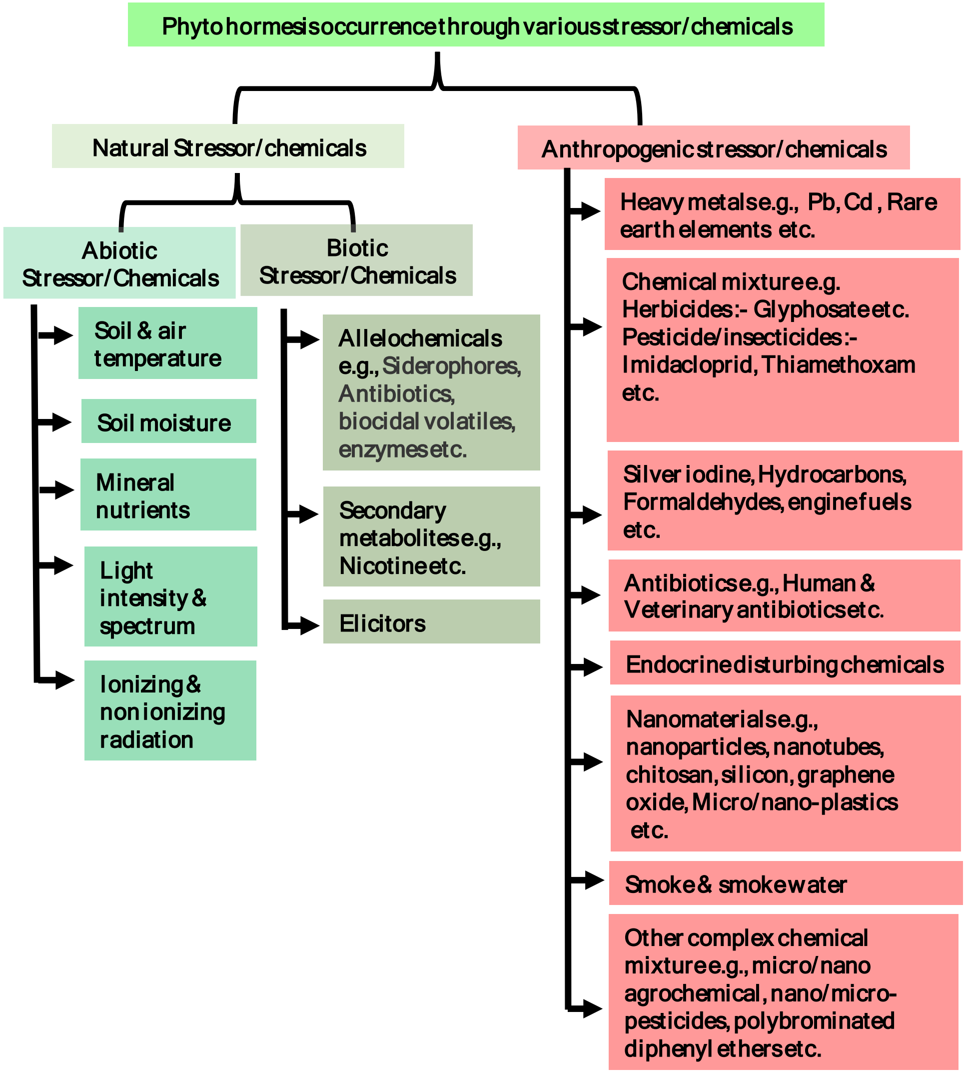


Fig. 1 General illustration of phytohormesis occurrences through various stressors (adapted from source: Erofeeva 2022c)

phenomenon has also been reported with various kinds of toxicants (non-essential heavy metals, pesticides, herbicides, fungicides, chemical mixtures, advanced new emerging environmental pollutants like micro/nanomaterials, etc.) and with various living organisms (bacteria, fungus, animals, and plants) (Camilo dos Santos et al. 2022; Agathokleous et al. 2019a, b, c; Pradhan et al. 2017; Calabrese 2004; Calabrese and Baldwin 2000).

Inside plants, the hormesis phenomenon is found in diverse groups ranging from lower plants algae to higher herbaceous/woody plants angiosperm and also has been found in all phases of plant growth ranging from seed, seedling, vegetative, and flowering to ripening plants (Erofeeva 2021, 2022b). Moreover, hormesis inside the plant system is caused by a variety of low doses of stressors that could be of natural or anthropogenic origin (also shown in Fig. 1), including newly emerging micro/nano stressors such as nanoparticles, nanotubes, and various other chemical mixtures. Phyto-hormesis occurs through natural stressors including both abiotic (soil temperature/moisture, air temperature, mineral nutrients, light intensity, ionizing/non-ionizing radiation, etc.) and biotic stressors (allelochemicals, secondary metabolites, elicitor, etc.) (Erofeeva 2022c). Also, phyto-hormesis occursg through anthropogenic stressors including heavy metals, rare earth metals, herbicides, pesticides, insecticides, fungicides, silver iodine, organic acids, hydrocarbons, formaldehyde, engine fuels, antibiotics, endocrine-disturbing chemicals, nanomaterials, micro/nano-plastic, smoke/smoke water, chemical mixtures, etc. (also shown in Fig. 1) (Erofeeva 2022c). All the aforementioned variables (natural and anthropogenic) affect plant metabolism in unique ways. However, they all have the ability to induce phyto-hormesis in some way or other.

Table 1 Hormetic morphological responses of various plants species under low doses of heavy metal

S. no.	Plant species (belong to family)	Heavy metal (HMs)	Hormesis doses	Exposure time	End point evaluated	Stimulatory response	References
1.	*Lonchocarpuscultratus* (Fabaceae)	Pb	56 mg kg^{-1} of Pb	6 months	Leaf area	24.7% increase in leaf area in comparison to the untreated control	Oliveira et al. (2021)
2.	*Lonchocarpuscultratus* (Fabaceae)	Pb	56 and 292 mg kg^{-1} of Pb	6 months	Root length	Increment in the root length up to 66.7% as compared to the control	Oliveira et al. (2021)
3.	*Zea mays* (Poaceae)	Pb	1000 µM Pb	24 h	Shoot elongation	A twofold increase in corn coleoptile section	Małkowski et al. (2020)
4.	*Zea mays* (Poaceae)	Pb	5 µM Pb	4 days	Corn shoot elongations	Significant increase in the corn shoot elongations	Małkowski et al. (2020)
5.	*Suaeda salsa* (Amranthaceae)	Pb	800 mg kg^{-1} Pb in combination with 0.25% $Na^{+}$and Ca^{+} ions	90 days	Plant Fresh weight and height	23% and 14% increase in plant height and Fresh weight, respectively, as compared to plants treated with 800 mg kg^{-1}Pb without any saline ions	Li et al. (2019)
6.	*Brassica juncea*(Brassicaceae)	Pb	125 and 250 mg kg^{-1}	60 days	Root or shoot length, root or shoot dry weight, leaf dry weight and area	Increase in the root or shoot length, root or shoot dry weight, leaf dry weight and area in comparison to untreated control	Naaz and Chauhan (2019)
7.	*Anthyllisvulneraria* (Fabaceae)	Pb	0.5 and 1.5 mM	8 weeks (56 days)	root length, root and shoot dry weight	0.5 mMPb causes the increase in root length while 1.5 mMPb increases root and shoot dry weight	Piwowarczyk et al. (2018)
8.	*Arabidopsis thaliana* (Brassicaceae)	Pb	100 mg kg^{-1} Pbbioaugmentedwith *Mucorcircinelloides* and *Trichodermaasperellum*	Data not provided	Root length and shoot FW	Enhanced root length and shoot fresh weight as compared to control	Zhang et al. (2018)
9.	*Tagetesminuta*L. (Asteraceae)	Pb	Used Pb pollutant soil from battery recycling smelter area	*Tagetesminuta* L. was only grown in Pb pollutant soil till blooming, then harvested	Arial biomass (leaves and stem)	Significant increase in aerial biomass of *Tagetesminuta* L. grown in Pb-pollutant soil	Miranda Pazcel et al. (2018)

Table 1 (continued)

S. no.	Plant species (belong to family)	Heavy metal (HMs)	Hormesis doses	Exposure time	End point evaluated	Stimulatory response	References
10.	*Viciafaba* (Fabaceae)	Pb	250 mgkg^{-1}	20 days	Plant height	Increase in plant height as compared to untreated plants	Wang et al. (2010)
11.	*Jatropha curcas* (Euphorbiaceae)	Pb and Cr	1.0 mM Cr and 3.0 mMPb	30 Days	Biomass	Increase in biomass	Bernabé-Antonio et al. (2015)
12.	Triticumaestivum (Poaceae)	Pb and Cu	0.04, 0.08,0.16 g L^{-1} Pband 0.05 × 10^{-1} g L^{-1} Cu	8 days	Root and shoot length	0.04, 0.08, 0.16 g L^{-1}Pb increase in shoot length, 0.16 g L^{-1}Pb stimulated the increase in root length whereas 0.05 × 10^{-1} g L^{-1} Cu stimulated both root and shoot length of the Wheat plant as compared to control	Erofeeva (2014)
13.	*Menthapiperita* (Lamiaceae)	Pb and Cr	30 and 60 mg kg^{-1}	102 days	Fresh biomass, root dry weight	Significant enhancement in fresh biomass, root dry weight of mint species in both Cr- and Pb-treated plants as compared to untreated plants samples	Prasad et al. (2010)
14.	*Arabis paniculata* Franch (Brassicaceae)	Pb, Zn, Cd	48 µM Pb, 306 µM Zn and 44 µM Cd	18 days	Root and shoot growth	48 µM Pb induced 17.1% shoot growth, 43.2% root growth, 306 µM Zn induced 40.5% shoot growth, 43.6% root growth and 44 µM Cd-induced 41.3% shoot growth, and 38.8% root growth as compared to the control	Tang et al. (2009)
15.	*Brassica oleracea* (cultivar "Youxiu") (Brassicaceae)	Cd	2.5 mg kg^{-1} Cd	14 days	Leaf area and fresh weight	In comparison to the control (0 mg kg^{-1} Cd), there was an increase in leaf area and fresh weight of the shoot, root, and entire seedling by 23, 17, and 19%, respectively	Ma et al. (2022)

Table 1 (continued)

S. no.	Plant species (belong to family)	Heavy metal (HMs)	Hormesis doses	Exposure time	End point evaluated	Stimulatory response	References
16.	*Brassica napus L. var. Es Astrid (Euralissemences, France)* (Brassiceae)	Cd	5 µM	28 days	Root–shoot biomass	Root- shoot biomass enhancement as compared to control	Durenne et al. (2018)
17.	*MalvaCrispa*, *Malvarotundifolia*, *Sidarhombifolia* (Malvaceae) and *Celosia cristata*, *Celosia argentea*(Amaranthaceae)	Cd	5 mg kg^{-1}	60 days	Shoot biomass	Significant increase in shoot biomass of all the plant species as compared to the control	Wu et al. (2018)
18.	*Lonicera japonica* Thunb. (Caprifoliaceae)	Cd	2.5 and 5 mg L^{-1}	28 days	Plant height and dry weight	Significant increase in plant height (11.9% and 12.8%) and dry weight as compared to untreated plants	Liu et al. (2015)
19.	*Lonicera japonica* Thunb. (Caprifoliaceae)	Cd	0.5 and 2.5 mg L^{-1}	28 days	Root length	Significant increase in root length	Liu et al. (2015)
20.	*Lonicera japonica* Thunb. (Caprifoliaceae)	Cd	10 mg kg^{-1}	90 days	Dry weight	Increase in root shoot dry weight	Liu et al. (2013a)
21.	*Lonicera japonica* Thunb. (Caprifoliaceae)	Cd	5 and 25 µM L^{-1}	2 weeks (14 days)	Root elongation	Enhancement in root length as compared to untreated plants	Lian et al. (2012)
22.	*Lonicera japonica* Thunb. (Caprifoliaceae)	Cd	5 mg L^{-1}	28 days	Dry leaves or root, plant biomass, and plant height	Stimulation in dry leaves or root, plant biomass, and plant height as compared to the control	Zhouli et al. (2011)
23.	*Vetiveriazizanioides* (L.) Nash (Poaceae)	Cd	1 mg L^{-1} Cd	15 days	Plant biomass (Root and shoot biomass)	Slight increase in root and shoot biomass	Aibibu et al. (2010)
24.	*Solanumtuberosum* L. cv. Macaca (Solanaceae)	Cd	100 µM	22 days	Root dry weight	Increase in root dry weight	Gonçalves et al. (2009)
25.	*Solanumtuberosum* L. cv. Asterix and Macaca (Solanaceae)	Cd	100 µM Cd and 200 µM Cd	22 days	Shoot dry weight	The potato cultivar Asterix shoot dry weight increased at 100 µM Cd, whereas the potato cultivar Macaca shoot dry weight increased at both 100 µM and 200 µM Cd exposure	Gonçalves et al. (2009)

Table 1 (continued)

S. no.	Plant species (belong to family)	Heavy metal (HMs)	Hormesis doses	Exposure time	End point evaluated	Stimulatory response	References
26.	*Brassica juncea*(Brassicaceae)	Cd	20 µM	14 days	Dry biomass (root and shoot)	28% increases in dry biomass of root and 38% increases in dry biomass of shoot as compared to the control	Seth et al. (2008)
27.	*Spirodelapolyrrhiza*(Araceae)	Cd	0.1 µM	4 days	Plant biomass (fresh biomass)	Enhancement in plant biomass with respect to control	Seth et al. (2007)
28.	*Salsola kali* (Amaranthaceae)	Cd	20 mg L^{-1}	15 days	Root dry weight	67% root mass enhancement as compared to untreated plants	de la Rosa et al. (2004)
29.	*Thlaspicaerulescens* (Brassicaceae)	Cd	3 µM L^{-1}	14 and 31 days	Total plant biomass	Under 14 days of Cd exposure, 37% rise in total plant biomass and under 31 days of Cd exposure, 75% rise in total plant biomass in comparison to control	Roosens et al. (2003)
30.	*Spirodelapolyrrhiza* (Araceae)	Cd and As	1 µM Cd (II) and 20 µM As (V)	1 day	Plant biomass (fresh biomass)	25% enhancement in plant biomass under 1 µM Cd (II) exposure and 30% enhancement in plant biomass under 20 µM As (V) exposure	Seth et al. (2007)
31.	*Solanumnigrum* (Solanaceae)	Cr	0.5 and 1 mM	21 days (3 weeks)	shoot fresh and dry weight of root and shoot	Increase in shoot fresh and root shoot dry weight with maximum increase at 1 mM Cr as comparison to control	UdDin et al. (2015)
32.	*Allium cepa* L. (Liliaceae)	Cr	6.25, 12.5, 25, 50, 100, 200 µM	3,6,12,24 h	Root length	Cr treatments for 3, 6, 12, and 24 h stimulate root length in a concentration-dependent manner	Patnaik et al. (2013)
33.	*Allium cepa* L. (Liliaceae)	Cr	6.25, 12.5, 25, 50, 100, 200 µM	1 day	Root length	Stimulate root length in a concentration-dependent manner	Patnaik et al. (2013)
34.	*Allium cepa* L. (Liliaceae)	Cr	12.5 µM	5 days	Root length	Stimulate root length as compared to control	Patnaik et al. (2013)

Table 1 (continued)

S. no.	Plant species (belong to family)	Heavy metal (HMs)	Hormesis doses	Exposure time	End point evaluated	Stimulatory response	References
35.	*Allium cepa* L. (Liliaceae)	Cr	12.5 µM	1 day, then a 4-day recovery period with tap water	Root growth	Significant enhancement in the root growth	Patnaik et al. (2013)
36.	*Panicumvirgatum*L (Poaceae)	Cr	10 µM	30 days	Dry weight	50% stimulation in dry weight in comparison to control	Chen et al. (2012)
37.	*Arabidopsis thaliana* (Brassicaceae)	Cr	100 µM	8 days (germination percentage) 5 days (root length) 10 days (fresh weight)	Germination percentage, root length and fresh weight	Increase in germination percentage, root length and fresh weight in comparison to control	Castro et al. (2007)
38.	*Arabidopsis thaliana* (Brassicaceae)	Pt	2.5 µM	14 days (2 Weeks)	Fresh or dry weight, root length, and leaf area	2.5 µM Cd increased fresh weight (12.5% rosette + 44% roots + 16.5% whole plant), dry weight (9% rosette + 44% root + 12% whole plant), 23% leaf area and 3.5% root length as compared to control plants	Gawrońska et al. (2018)
39.	*Brassica oleracea* var. *italica* L. (Brassicaceae)	W	1,5,10 mg kg^{-1}	30 days	Root and shoot length, fresh and dry weight	Rise in the root or shoot length, fresh and dry weight of 30 days old plant	Dawood, and Azooz (2019)
40.	*Symplocospaniculate*(Symplocaceae)	Al	1 mM L^{-1}	2 weeks (14 days)	Total plant biomass	Increase in plant biomass and root–shoot ratio as compared to control	Schmitt et al. (2016
41.	*Glycine max* (Fabaceae)	La	5 µM	28 days	Root length	Rise in root length as compared to untreated plants sample	de Oliveira et al. (2015)
42.	*Oryzasativa*(Poaceae)	La	0.05 mmol L^{-1}	13 days	Length and fresh weight of root	Increased length and fresh weight of root as compared to control	Liu et al. (2013b)
43.	*Triticum durum* (Poaceae)	La	0.01 mM	9 days	Root length	Increased root length	d’Aquino et al. (2009)
44.	*Oryzasativa*(Poaceae)	La	30 mg kg^{-1}	30 days	Plant height	Increased plant height	Zeng et al. (2006)
45.	*Cistanchedeserticola*(Orobanchaceae)	La	0.01 mmol l^{-1}	30 days	Cell growth	Increased cell growth as compared to control	Ouyang et al. (2003)
46.	*Taxusyunnanensis*(Taxaceae)	La	2.3 and 5.8 µM	32 days	Cell growth	Increased growth of cells as compared to control	Wu et al. (2001)

Table 1 (continued)

S. no.	Plant species (belong to family)	Heavy metal (HMs)	Hormesis doses	Exposure time	End point evaluated	Stimulatory response	References
47.	*Triticumastivum*(cv. Arta &Bahara) (Poaceae)	Sm and Ce	2500 µM	21 days	Root or shoot length, fresh or dry plant weight and plant height	Rise in the root or shoot length, fresh or dry plant weight and plant height as compared to the control	Haghighi et al. (2023)

Hormesis: General Principles or Universal Characteristics

Hormesis is regarded as a universal phenomenon that is widespread in nature, which occurs regardless of stressor type, the organism in which it happens, or what kind of physiological processes that organism undergoes (Shahid et al. 2020; Agathokleous et al. 2019a). This is because hormesis is prevalent in nature and does not depend on these factors. In addition to this, one of the most important fundamental adaptations in the organism (plant, animals, fungi, bacteria, etc.) during the low amount of (biotic or abiotic) stressor are biological plasticity (Calabrese and Mattson 2011), specificity, super-compensation, secondary adaptation, intermittency, and stress oscillation (detail shown in Fig. 2) (Calabrese 2008; Shi et al. 2016). It is revealed that a plant or any other organism must experience some level of stress to achieve optimal fitness through these universal biological principles.

Furthermore, hormesis is often observed and widely represented when the study design meets the predetermined conditions, i.e. a clearly defined NOAEL (no observed adverse effect level), second dosage below NOAEL, exposure time, parameter end point, and statistical analysis techniques (Calabrese and Baldwin 2001). Additionally, hormesis is also thought to have common global quantitative characteristics (a thorough explanation may be seen in Fig. 3) that can lead to hormetic pre-conditioning (Erofeeva 2022c). Hormetic pre-conditioning is a process that occurs when low-dose exposures build organism resistance to later high-dose exposures (Erofeeva 2022a). Hormetic conditioning (pre-conditioning (especially in the case of plants) or post-conditioning) is thoroughly researched and well studied at the organism level (plant or animals) in response to low doses of the stressor (Erofeeva 2022c; Agathokleous and Calabrese 2020). In agriculture, pre-conditioning (also called priming) is used to boost plant yield and resilience to environmental stresses (Wiszniewska 2021). Hormesis includes different positive responses at a dose below the NOAEL and negative effects at a dose greater than the NOAEL (Agathokleous et al. 2022). This indicates that stress-induced inhibition and hormetic stimulation are both global adaptive responses in plants (Agathokleous and Calabrese 2020). The hormesis phenomenon is thought to be the reason why it is so common among plants because of its capacity to overcompensate for plant characteristics and hence induce pre-conditioning and hormetic adaptive responses (Poschenrieder et al. 2013). Because of these general characteristics, stressed plants are better equipped to deal with unstable environmental changes, uncertainty, and future challenges.

Table 2 Plant photosynthetic hormesis responses of various plants species under low doses of heavy metal

S. no.	Plant species (belong to family)	Heavy metal (HMs)	Hormesis doses	Exposure time	Endpoint evaluated	Photosynthetic stimulatory response	References
	Lonchocarpuscultratus (Fabaceae)	Pb	180 mg kg^{-1} of Pb	6 months	Stomatal conductance (mol H2O m-2 s-1)	Enhancement in stomatal conductance as compared to control	Oliveira et al. (2021)
	Lonchocarpuscultratus (Fabaceae)	Pb	180 mg kg^{-1} of Pb	6 months	Transpiration rate (mol H2O m-2 s-1)	Enhancement in transpiration rate as compared to control	Oliveira et al. (2021)
	Zea mays L. cv. KOSMO 230 (Poaceae)	Pb	0.5, 1, 5 and 10 µM Pb	14 days old seedling treated with Pb for last 4 days	Chlorophyll content	Significant increase in Chlorophyll content with the maximum increase in 10 µM Pb (approx. 45 r.u.)	Małkowski et al. (2020)
	Zea mays L. cv. KOSMO 230 (Poaceae)	Pb	0.5, 1, 5 and 10 µM Pb	14 days old seedling treated with Pb for last 4 days	Photosynthetic rate	Significant increase in photosynthetic rate with maximum increase in 1 µM Pb (26 µmol CO_2m^{-2} s^{-1})	Małkowski et al. (2020)
	Zea mays L. cv. KOSMO 230 (Poaceae)	Pb	0.5, 1, 5 and 10 µM Pb	14 days old seedling treated with Pb for the last 4 days	Transpiration rate	Significant increase in transpiration rate with maximum increase in 0.5 and 1 µM Pb (approx. 1.7 and 1.6 mmol H_2Om^{-2} s^{-1})	Małkowski et al. (2020)
	Zea mays L. cv. KOSMO 230 (Poaceae)	Pb	0.5, 1, 5 and 10 µM Pb	14 days old seedling treated with Pb for the last 4 days	Stomatal conductance	No significant increase in stomatal conductance as compared to control. Moreover, a slight decrease in the stomatal conductance as compared to control 0.5, 1,5,10 (approx. 81, 79, 78,77 respectively)	Małkowski et al. (2020)
7. **s**	*Tagetesminuta*L. (Asteraceae)	Pb	Used Pb pollutant soil from battery recycling smelter area	*Tagetesminuta* L. was only grown in Pb pollutant soil till blooming, then harvested for further analysis	Chlorophyll and carotenoid content	Increase in Chl a, Chl b, total chlorophyll and carotenoid content of *Tagetesminuta*L. grown in Pb-pollutant soil	Miranda Pazcel et al. (2018)
	Triticumaestivum (Poaceae)	Pb	1.25×10^{-3} and 0.01 g L^{-1} Pb	8 days	Chlorophyll a,b	1.25×10^{-3} g L^{-1}Pb increased chlorophyll a whereas 0.01 g L^{-1}Pb increased chlorophyll b in the Wheat plant as compared to the control	Erofeeva (2014)

Table 2 (continued)

S. no.	Plant species (belong to family)	Heavy metal (HMs)	Hormesis doses	Exposure time	Endpoint evaluated	Photosynthetic stimulatory response	References
	Arabis paniculata Franch (Brassicaceae)	Pb, Zn, Cd	97 µM Pb, 306 µM and 9 µM Cd	18 days	Chlorophyll (a,b, a + b) content	Enhancement in chlorophyll content as compared to control	Tang et al. (2009)
	Dianthus carthusianorum (Caryophyllaceae)	Cd	1 µM	24 weeks (168 days)	Chlorophyll (a,b) and carotenoid content	Enhanced chlorophyll and carotenoid content	Muszyńska et al. (2018)
	Miscanthussacchariflorus and *Miscanthussinensis*	Cd	2 mg kg^{-1}	40 days	Chlorophyll content	Increased chlorophyll content	Jiang et al. (2018)
	Lonicera japonica Thunb. (Caprifoliaceae)	Cd	0.5, 2.5 and 5 mg L^{-1}	28 days	Chlorophyll (a,b) and carotenoid content	Enhancement in chlorophyll and carotenoid content as compared to untreated plant samples	Liu et al. (2015)
	Lonicera japonica Thunb. (Caprifoliaceae)	Cd	2.5 mg kg^{-1}	30 and 90 days	Stomatal conductance and transpiration rate	Enhancement in stomatal conductance and transpiration rate as compared to control	Jia et al. (2015)
	Lonicera japonica Thunb. (Caprifoliaceae)	Cd	2.5 mg kg^{-1}	90 days	Photosynthetic rate	Enhancement in photosynthetic rate	Jia et al. (2015)
	Lonicera japonica Thunb. (Caprifoliaceae)	Cd	10 mg kg^{-1}	30 days	Photosynthetic rate	Enhancement in photosynthetic rate	Jia et al. (2015)
	Lonicera japonica Thunb. (Caprifoliaceae)	Cd	2.5, 5, 10, 25 mg kg^{-1}	30 and 90 days	Chlorophyll Fluorescence traits	Rise in photochemical quenching coefficient (q_p) from 2.5–25 mg kg^{-1}	Jia et al. (2015)
		Cd	2.5 and 5 mg kg^{-1}	90 days	Chlorophyll Fluorescence traits	Rise in PSII quantum yield (ϕPSII)	Jia et al. (2015)
		Cd	2.5, 5, 10, 25 mg kg^{-1}	30 days	Chlorophyll Fluorescence traits	Rise in PSII quantum yield (ϕPSII) from 2.5–25 mg kg^{-1} Cd	Jia et al. (2015)
		Cd	2.5 and 5 mg kg^{-1}	30 and 90 days	Chlorophyll Fluorescence traits	Rise in PSII photochemical efficiency (Fv/Fm)	Jia et al. (2015)
		Cd	2.5, 5 and 10 mg kg^{-1}	30 and 90 days	Chlorophyll Fluorescence traits	Rise in PSII photochemistry maximum efficiency (Fv/Fo)	Jia et al. (2015)
		Cd	2.5 mg kg^{-1}	90 days	Chlorophyll a, b, a + b and carotenoids content	The maximum rise in Chlorophyll a, b, a + b and carotenoids content	Jia et al. (2015)

Table 2 (continued)

S. no.	Plant species (belong to family)	Heavy metal (HMs)	Hormesis doses	Exposure time	Endpoint evaluated	Photosynthetic stimulatory response	References
	Lonicera japonica Thunb. (Caprifoliaceae)	Cd	10 mg kg^{-1}	30 days	Photosynthetic rate and transpiration rate	Significant increase in photosynthetic rate and transpiration rate	Liu et al. (2013a)
	Lonicera japonica Thunb. (Caprifoliaceae)	Cd	5 and 25 μM L^{-1}	2 weeks (14 days)	Chlorophyll a and b content	Slight rise in chlorophyll content in comparison to the control	Lian et al. (2012)
	Lonicera japonica Thunb. (Caprifoliaceae)	Cd	25 and 50 μM L^{-1}	2 weeks (14 days)	Carotenoid content	Significant enhancement in carotenoid content as compared to control	Lian et al. (2012)
	Lonicera japonica Thunb. (Caprifoliaceae)	Cd	5, 10 and 25 mg L^{-1}	28 days	Total chlorophyll and carotenoid content	Slight increase in chlorophyll and carotenoid content	Zhouli et al. (2011)
	Vetiveriazizanioides (L.) Nash (Poaceae)	Cd	1 mg L^{-1} Cd	15 days	Chlorophyll a and b content	Rise in chlorophyll content in comparison to untreated plant leaves samples	Aibibu et al. (2010)
	Brassica juncea(Brassicaceae)	Cd	20 μM	14 days	Chlorophyll (a,b, total)	42% total Chlorophyll, 25% Chl a and 16% Chl b rise as compared to the control	Seth et al. (2008)
	Brassica juncea (Brassicaceae)	Cd	160 μM	14 days	Carotenoid content	Gradual increase upto 160 μM Cd with a maximum increase of 21% at 160 μM Cd	Seth et al. (2008)
	Spirodelapolyrrhiza(Araceae)	Cd and As	2 μM Cd (II) and 20 μM As(V)	1 day	Photosynthetic pigment (chlorophyll content and carotenoid content)	Enhancement in chlorophyll and carotenoid content as compared to control	Seth et al. (2007)
	Spirodelapolyrrhiza(Araceae)	Cd and As	0.5 μM Cd (II) and 10 μM As(V)	4 days	Chlorophyll and carotenoid content	Enhancement in chlorophyll and carotenoid content as compared to control	Seth et al. (2007)

Table 2 (continued)

S. no.	Plant species (belong to family)	Heavy metal (HMs)	Hormesis doses	Exposure time	Endpoint evaluated	Photosynthetic stimulatory response	References
	Spirodelapolyrhiza (Giant duckweed) *Lemnaceae*	Ni andNaCl stress	0.039–0.625 mgL^{-1} of Ni 3.2–4.6 gL^{-1} of NaCl	72 h exposure	Chlorophyll Fluorescence imaging attributes	Found to have a stimulatory effect on chlorophyll fluorescence parameters of the efficiency of the water-splitting complex on the donor side of PSII (Fv/Fo), the maximum efficiency of PSII photochemistry (Fv/Fm), the electron transport rate (ETR), the effective quantum yield of PSII photochemistry (FPSII), the redox state of quinone A (QA) and representing the fraction of open PSII RCs (qp)	Oláh et al. (2021)
	Brassica oleracea var. *italica* L. (Brassicaceae)	W	1,5,10 mg kg^{-1}	30 days	Chlorophyll (a,b) and Carotenoids	Significant increase in the Chlorophyll and Carotenoids contents in 30 days old plant	Dawood, and Azooz (2019)
	Arabidopsis thaliana (Brassicaceae)	Pt	2.5 and 5 µM	14 days (2 Weeks)	Total chlorophyll and net photosynthesis rate	11–20% rise in net photosynthesis rate and 4–13% rise in total chlorophyll content as compared to control	Gawrońska et al. (2018)
	Theobroma cacao (Malvaceae)	Cr (III)	100 mg kg^{-1} soil	1,15,21 and 28 days	Photosynthetic rate (P_N), stomatal conductance (gs) and transpiration rate (E)	Significant rise in Photosynthetic rate (P_N), stomatal conductance (gs) and transpiration rate (E)	do Nascimento et al. (2018)
	Camellia sinensis (Theaceae)	Al	300 µM	8 weeks (56 days)	Chlorophyll a, b, carotenoid content, photosynthetic rate, transpiration rate and stomatal conductance	Rise in chlorophyll a, b, carotenoid content, photosynthetic rate, transpiration rate and stomatal conductance	Hajiboland et al. (2013)

Table 2 (continued)

S. no.	Plant species (belong to family)	Heavy metal (HMs)	Hormesis doses	Exposure time	Endpoint evaluated	Photosynthetic stimulatory response	References
	Camellia sinensis (Theaceae)	Al	300 µM	8 weeks (56 days)	Chlorophyll Fluorescence traits	Rise in Fv/Fm (PSII photochemical potential, F′v/F′m (open PSII excitation-capture efficency) and PSII quantum yield as compared to control in younger leaves	Hajiboland et al. (2013)

Hormesis Curves for Different Morpho-Physio-Biochemical Parameter Measures in Plants

In plants, the hormesis phenomenon displays various types of curves for different parameters measured like inverted U- or J-shape, U- or J-shape, non-monotonic types of curves (Erofeeva 2014), and two dents hormesis curve (Shahid et al. 2020; Jia et al. 2015; Tang et al. 2009) (as shown in the Figs. 4, 5, and 6). Generally, an inverted U- or J-shape curve is the most common type of hormesis curve (Calabrese 2004; Kendig et al. 2010), which has been observed in all the plant growth indicators like root or shoot length, fresh or dry weight, total biomass, plant height, leaves area/number, pigment (chlorophyll (a,b,a+b), carotenoids), and various other photosynthetic parameters (Calabrese and Blain 2009; Shahid et al. 2020). Moreover, U- or J-shaped hormesis curves have been observed for plant defence mechanisms, such as the surplus production of reactive radicals (i.e. hydroxyl radical, hydrogen peroxide, superoxide anion content, lipid peroxidation, and electrolyte leakage) and the activation of various antioxidants (enzymatic and non-enzymatic) (Shahid et al. 2020) (Fig. 4). In addition to this, the two dent hormesis curve is observed for various plant growth parameters such as total biomass, root biomass, chlorophyll, and stomatal conductance (Shahid et al. 2020; Jia et al. 2015; Tang et al. 2009) (Fig. 5), while non-monotonic types of the curve are observed for plant parameters such as fresh/dry weight, root/shoot length, photosynthetic pigments, and lipid peroxidation (Erofeeva 2014) (Fig. 6).

Impact of Different Factors on Phyto-Hormesis (Concentration, Time, Species Type, or End Point)

Hormesis's presence and magnitude (observable effect) depend on numerous factors. These factors serve as a potential source of variation. Hormesis responses in plants induced through various natural or anthropogenic stressors are species dependent, time dependent as well as concentration dependent (as shown in Figs. 7, 8, and 9). Hormesis response in plants is species dependent, meaning depending on the type of plant species, stressor dosages may either stimulate or hinder growth (Fig. 9) (Agathokleous et al. 2020a; Belz and Sinkkonen 2021). Thus, these responses vary among different plant species. Time-dependent hormetic response, referred to as the hormesis response measured minutes after the stressor dosage exposure, noticeably differs from that measured

Table 3 Oxidative stress markers induced hormesis responses of various plants species under low doses of heavy metals stress

S. no.	Plant species (belong to family)	Heavy metal (HMs)	Hormesis doses	Exposure time	End point evaluated	Hormetic response in plants	References
	Zea mays L. cv. KOSMO 230 (Poaceae)	Pb	1000 µM Pb 0.11 µmol g^{-1} FW	24 h	Hydrogen peroxide (H_2O_2) content	The non-significant increase indicates the maintenance of the almost same level of hydrogen peroxide as the control plants	Małkowski et al. (2020)
	Zea mays L. cv. KOSMO 230 (Poaceae)	Pb	5 and 10 µM Pb	14 days old seedlings expose to Pb for the last 4 days	H_2O_2 content	A slight decreased indicates the maintenance of the almost same level of hydrogen peroxide as the control plants	Małkowski et al. (2020)
	Suaeda salsa (Amranthaceae)	Pb	800 mg kg^{-1} Pb in combination with 0.25% $Na^+$and Ca^+ ions	90 Day old plants	MDA (malondialdehyde) content	47% decrease in the MDA content	Li et al. (2019)
	Anthyllisvulneraria (Fabaceae)	Pb	0.5 mM	4 Weeks (28 days)	MDA content	Decreased in MDA content	Piwowarczyk et al. (2018)
	Viciafaba (Fabaceae)	Pb	6.25 and 12.5 $mgkg^{-1}$	20 Days	Superoxide (O_2^-) anion content and lipid peroxidation	Decreased in superoxide anion and MDA content in comparison to control	Wang et al. (2010)
	Brassica oleracea var. *italica* L. (Brassicaceae)	W	1, 5, 10 mg kg^{-1}	30 days	Electrolyte leakage, lipid peroxidation, hydroxyl radical and superoxide anion	Significant reduction up to a concentration 10 mg Tungstate per kg of soil in 30 days old plants as compared to control	Dawood and Azooz (2019)
	Brassica oleracea var. *italica* L. (Brassicaceae)	W	1, 5, 10 mg kg^{-1}	30 days	H_2O_2 content	A very slow rise in H_2O_2 content at a concentration 1-10 mg Tungstate per kg soil was observed as compared to the control	Dawood and Azooz (2019)
	Triticumaestivum (Poaceae)	Mn and Cd	1.25×10^{-3}, 0.05×10^{-1} g L^{-1}Mn and 0.01 g L^{-1} Cd	8 days	MDA content	Significant decrease in MDA content as compared to untreated plant sample	Erofeeva (2014)
	Medicagosativa(Fabaceae)	Cr	0.5 mg L^{-1}	59 days	MDA and H_2O_2 content	A slight decrease in MDA and H_2O_2 content as compared to the untreated control	Christou et al. (2020)

Table 3 (continued)

S. no.	Plant species (belong to family)	Heavy metal (HMs)	Hormesis doses	Exposure time	End point evaluated	Hormetic response in plants	References
	*Allium cepa*L. (Liliaceae)	Cr	6.25, 12.5, 25, 50, 100, 200 µM	1 Day	MDA content	Concentration-dependent manner decreased in MDA content	Patnaik et al. (2013)
	*Allium cepa*L. (Liliaceae)	Cr	6.25 and 12.5 µM	5 Day	MDA content	MDA content decreased as compared to the untreated control	Patnaik et al. (2013)
	*Allium cepa*L. (Liliaceae)	Cr	6.25, 12.5, 25, 50, 100, 200 µM	1 Day	Hydrogen peroxide content	Hydrogen peroxide content decreased in a concentration-dependent manner with a maximum decrease at 50 µM	Patnaik et al. (2013)
	*Allium cepa*L. (Liliaceae)	Cr	6.25, 12.5, 25, 50, 100, 200 µM	1 Day	Superoxide anion content	Superoxide anion content decreased in a concentration-dependent manner	Patnaik et al. (2013)
	*Allium cepa*L. (Liliaceae)	Cr	6.25 and 12.5 µM	5 Day	Superoxide anion content	Significant reduction in superoxide anion content as compared to control	Patnaik et al. (2013)
	Camellia sinensis (Theaceae)	Al	300 µM	8 weeks (56 days)	MDA and H_2O_2 Content	Significantly decreased in MDA and H_2O_2 content	Hajiboland et al. (2013)
	Lonicera japonica Thunb. (Caprifoliaceae)	Cd	2.5 mg L^{-1}	14 days	MDA content	Decrease in MDA content as compared to the untreated control	Jia et al. (2013)
	Lonicera japonica Thunb. (Caprifoliaceae)	Cd	5 and 25 µM L^{-1}	2 weeks (14 days)	MDA content	A slight decrease in MDA content as compared to the untreated control group	Lian et al. (2012)
	Lonicera japonica Thunb. (Caprifoliaceae)	Cd	5, 25 and 50 µM L^{-1}	2 weeks (14 days)	Superoxide anion radical (O_2^-) Content	5, 25 and 50 µM L^{-1} Cd doses showed 21.39, 10.89 and 2.56% decreases in superoxide anion content as compared to untreated control group	Lian et al. (2012)
	Lonicera japonica Thunb. (Caprifoliaceae)	La(III)	30 mg L^{-1}	2 days	MDA and H_2O_2 content	Significant decrease in MDA and H_2O_2 content as compared to control	Guo et al. (2014)

Table 3 (continued)

S. no.	Plant species (belong to family)	Heavy metal (HMs)	Hormesis doses	Exposure time	End point evaluated	Hormetic response in plants	References
	Triticum astivum (cv. Arta) (Poaceae)	Ce	15,000 μM	21 days	H_2O_2 content	The maximum decrease in H_2O_2 content at 15,000 μM Ce	Haghighi et al. (2023)
	Triticum astivum (cv. Bahara) (Poaceae)	Ce	10,000 μM	21 days	H_2O_2 content	The maximum decrease in H_2O_2 content at 10,000 μM Ce	Haghighi et al. (2023)
	Triticum astivum (cv. Arta &Bahara) (Poaceae)	Sm	15,000 μM	21 days	H_2O_2 content	The maximum decrease in H_2O_2 content at 15,000 μM Sm	Haghighi et al. (2023)

after hours, days, or even weeks (Fig. 8) (Zulfiqar et al. 2019). In addition to this, inside plants, the MAX (maximum stimulation) produced by some contaminants (trace elements, nanomaterials, chemical mixtures, ozone, and lanthanum) rises after a few hours to around 140–150% of the untreated control and then reduces after a month to 120–130% of the control (Agathokleous et al. 2020a; Li et al. 2022; Erofeeva 2022b). The gap between the MAX dosage and the NOAEL is also expected to expand with time (Agathokleous et al. 2020a). Moreover, different plant growth stages, such as seedling, vegetative, or fully adult flowering stages, are thought to have different responding abilities when it comes to hormesis due to variate differences in stress resilience (Erofeeva 2021). For instance, exposure to the herbicide 2,4-D choline salt at stage B4 (flower bud development) results in an increase in cotton output, whereas exposure at stage V4 (vegetative stage) results in a loss in yield and exposure at stage C4 (box cracking stage) and has no effect on this parameter (Marques et al. 2021). Also, the hormetic phenomenon is concentration dependent simply means that the toxicity of a natural or anthropogenic stressor depends on the exposure's dosage (Fig. 7) (Poschenrieder et al. 2013). Paracelsus (1493–1541) also stated that 'The poison is in the dose'. According to him, the correct dosage is what distinguishes a poison from a curative treatment (Poschenrieder et al. 2013). In addition to these dependent factors, hormesis is also influenced by various other factors. One of these is the parameter end point calculated (that means the end point that is measured for the different parameters within the same plant species); for example, the same quantity of phytotoxin dosage may have no effect on root growth while promoting shoot growth (Velini et al. 2008; Belz and Duke 2017). According to Velini et al. (2008) the optimal hormetic dose of glyphosate to stimulate root growth of *Pinus caribaea Morelet* was 2 g ha^{-1}, while the optimal hormetic dose for stimulating leaf growth was 20 g ha^{-1}. Therefore, the hormetic dosage can change depending on several parameters within the same plant species.

In summary, heavy metal exposure in plants may offer certain advantages, notably in the realm of environmental remediation, occurrences of phytohormesis phenomenon in plants, etc. However, the drawbacks are also substantial, especially when the plants are exposed to higher amounts of heavy metals for a longer duration of time. Therefore, the exact effects of heavy metals on plants rely on many factors, such as the type and amount of metal present, the length of exposure, the type of plant involved, the plant developmental stage, and the various other conditions in the environment.

Table 4 Hormesis effects on proteins stimulation in various plants species under low doses of heavy metals stress

S. no.	Plant species (belong to family)	Heavy metal (HMs)	Hormesis doses	Exposure time	Endpoint evaluated	Stimulatory response	References
	Viciafaba (Fabaceae)	Pb	250 mg kg^{-1}	20 days	Heat shock protein 70 (HSP70)	Heat shock protein 70 (HSP70) increase in the roots of *viciafaba* seedlings to the maximum in comparison to control and other treatments	Wang et al. (2010)
	Arabidopsis thaliana (Brassicaceae)	Cd	100 mM L^{-1}	46 days	Protein content	Slight increase in protein content as compared to the control	Carneiroe et al. (2017)
	Vetiveriazizanioides (L.) Nash (Poaceae)	Cd	1 mg L^{-1} Cd	15 days	Protein content	The rise in protein content in leaves as compared to the control	Aibibu et al. (2010)
	Brassica juncea (Brassicaceae)	Cd	20 µM	14 days	Protein content	45% increase at 20 µM Cd	Seth et al. (2008)
	Spirodelapolyrrhiza(Araceae)	Cd and As	2 µM Cd (II) and 20 µM As (V)	1 day	Total protein content	76% enhancement in total protein content under 2 µM Cd (II) exposure and 40% enhancement in total protein content under 20 µM As (V) exposure	Seth et al. (2007)
	Triticum astivum (Poaceae)	Zn	50 µM	14 days	Soluble proteins	Maximum enhancement in soluble protein as compared to control	Wei et al. (2022)
	Brassica oleracea var. *italica* L. (Brassicaceae)	W	1,5,10 mg kg^{-1}	30 days	Soluble protein	Significant increase in the soluble protein contents in 30 days old plant	Dawood and Azooz (2019)
	Glycine max (Fabaceae)	La	0.08 mM	7 days	Soluble protein	Increased in soluble protein content as compared to control	Zhang et al. (2017)
	Vicia faba (Fabaceae)	La, Cd	6 µM Cd, 8 µM La	15 days	Heat shock protein 70 (HSP70)	Combine treatment of 6 µM Cd and 8 µM La revealed a significant increase in HSP70	Wang et al. (2012a)
	Vicia faba (Fabaceae)	La, Cd	6 µM Cd, 30–240 µM La	15 days	Heat shock protein 70 (HSP70)	Combine treatment of 6 µM Cd and 30–240 µM La revealed significant hormetic responses, with the significant increase in HSP70 content in the low dosage area in 30–240 mg L^{-1} La with 6 µM Cd	Wang et al. (2012b)

Table 4 (continued)

S. no.	Plant species (belong to family)	Heavy metal (HMs)	Hormesis doses	Exposure time	Endpoint evaluated	Stimulatory response	References
	Triticum astivum (cv. Arta andBahara) (Poaceae)	Ce	2500 and 5000 µM	21 days	Protein content	The maximum increase in protein content at 5000 µM Ce in both the wheat plant cultivars	Haghighi et al. (2023)
	Triticum astivum (cv. Arta &Bahara) (Poaceae)	Sm	2500 and 5000 µM	21 days	Protein content	5000 µM Sm increased protein content to the maximum in Arta wheat cultivar, while 2500 µM Sm increased protein content to the maximum in Bahara wheat cultivar	Haghighi et al. (2023)

Heavy Metal-Induced Hormetic Effects on Plants' Morpho-Physio-Biochemical and Molecular Parameters

Recent experimental studies have shed a great amount of light on the phenomena of hormesis. According to these experimental studies, there is a lot of significant data showing that the hormesis phenomenon induced by a different kind of mild stressors (heavy metal and other toxic chemicals) has been responsible for improving integral end points (i.e. morphological, physiological, and molecular parameters) of the organisms (bacteria, plants, or animal) that describe essential biological processes (growth, development, reproduction, and resistance to stressors) (Calabrese and Baldwin 2000) (Tables 1, 2, 3, 4, 5, 6, 7, 8). Researchers believe that when plants are subjected to hormetic stimulation, a low level of HMs activates non-specific defence mechanisms that protect plants from severe stresses (Agathokleous et al. 2020a). These non-specific defence systems include biochemical or bioactive chemical compounds, stress hormones, enzymatic or non-enzymatic antioxidant defences, various secondary metabolites, osmolytes, and stress protein synthesis. Furthermore, scientists who are genuinely interested in hormesis inside plant systems have most frequently studied the morpho-physiological markers such as growth, photosynthesis-related parameters, and oxidative stress markers (Oliveira et al. 2021; Malkowski et al. 2020; Li et al. 2019).

Technological advancements in the field of omics, including genomics, miRNAomics, transcriptomics, proteomics, metabolomics, and phenomics, have considerably contributed to deepening our understanding of these hormetic responses (Raza et al. 2023; Rico-Chávez et al. 2022). These technologies reveal the complex networks and mechanistic processes by which an organism controls and regulates their response to minor stimuli by diving deeper into hormesis' cellular and molecular basis (Raza et al. 2023; Rico-Chávez et al. 2022). This multifaceted approach highlights the potential applicability of these discoveries to agricultural and environmental management, while also highlighting the unique nature of hormetic responses. Omics-based exploration of hormesis in plants has the potential to change the face of sustainable agriculture by helping scientists find ways to make plants more resilient and productive (Raza et al. 2023; Rico-Chávez et al. 2022). Thus, integrating omics technologies into the morpho-physio-biochemical studies in plant hormesis is a major step towards understanding the complex relationship between organisms and mild environmental stressors, which could be used to improve plant health and growth in changing environments.

Table 5 Antioxidative defence response in various plants species under low doses of heavy metals stress

S. no.	Plant species (belong to family)	Heavy metal (HMs)	Hormesis doses	Exposure time	Endpoint evaluated	Antioxidative defence response	References
	Suaeda salsa (Amranthaceae)	Pb	800 mg kg^{-1} Pb in combination with 0.25% $Na^+$and Ca^+ ions	90 Day old plants	Peroxidase (POD) activity	8% lower POD activity as compared to the control plant	Li et al. (2019)
	No data provided	Pb	500 mg kg^{-1} Pb Phaeozem soil sample	No data provided	Catalase (CAT) activity	Approximately 72.9% enhancement in soil catalase activity in Pb-treated Phaeozem soil sample (1.10 ml g^{-1}) as compared to control (0.62 ml g^{-1})	Yuebing et al. (2020)
	Lonicera japonica Thunb. (Caprifoliaceae)	Cd	5 and 25 μM L^{-1}	2 weeks (14 days)	Catalase (CAT)	Increase in CAT activity (21.10 and 25.88%) under low doses of Cd (5 and 25 μM L^{-1}), respectively	Lian et al. (2012)
	Lonicera japonica Thunb. (Caprifoliaceae)	Cd	5, 25 and 50 μM L^{-1}	2 weeks (14 days)	Peroxidase (POD)	No significant alteration under low doses of Cd	Lian et al. (2012)
	Lonicera japonica Thunb. (Caprifoliaceae)	Cd	10 mg L^{-1}	14 days	Superoxide dismutase (SOD)	Maximum enhancement in SOD activity in leaves in comparison to untreated control group	Liu et al. (2009)
	Lonicera japonica Thunb. (Caprifoliaceae)	Cd	10, 25, 50 mg L^{-1}	7 days	Catalase (CAT)	Leaves showed increase in catalase activity with maximum increase at 25 mg L^{-1} as compared to untreated control group	Liu et al. (2009)
	Lonicera japonica Thunb. (Caprifoliaceae)	Cd	5 mg L^{-1}	7 days	Catalase (CAT)	Threefold enhancement in catalase enzyme in root as compared to control and other treatment	Liu et al. (2009)
	Brassica juncea (Brassicaceae)	Cd	20 μM	14 days	Glutathione content	At 20 μM Cd show a maximum increase of 3.3 folds as compared to the control treatment	Seth et al. (2008)
	Miscanthussinensis (Poaceae)	Cd	2.2 and 4.4 μM	1 month	Peroxidase (POD)	Showed a decrease in POD activities compared to the control group	Scebba et al. (2006)
	Miscanthus sinensis (Poaceae)	Cd	2.2 μM	3 months	Catalase (CAT), peroxidase (POD), ascorbate peroxidase (APX)	Showed the maximum increase in all tested enzyme (CAT, POD, APX) activities in comparison to the control group	Scebba et al. (2006)

Table 5 (continued)

S. no.	Plant species (belong to family)	Heavy metal (HMs)	Hormesis doses	Exposure time	Endpoint evaluated	Antioxidative defence response	References
	Allium cepa L. (Liliaceae)	Cr	6.25, 12.5, 25, 50, 100, 200 µM	1 Day	Catalase (CAT)	Concentration-dependent increase in catalase activity	Patnaik et al. (2013)
	Allium cepa L. (Liliaceae)	Cr	12.5 µM	5 Day	Catalase (CAT)	The maximum increased at 12.5 µM Cr in comparison to the untreated control and other treatments	Patnaik et al. (2013)
	Allium cepa L. (Liliaceae)	Cr	12.5 µM	5 Day	Ascorbate peroxidase (APX)	The maximum increased at 12.5 µM Cr as compared to untreated control	Patnaik et al. (2013)
	Brassica oleracea var. *italica* L. (Brassicaceae)	W	1,5,10 mg kg^{-1}	30 days	Superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APOX), glutathione peroxidase (GPOX)	Significant increase in Superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APOX) and glutathione peroxidase (GPOX) activity under low doses of tungstate (1–5 mg kg^{-1})	Dawood and Azooz (2019)
	Brassica oleracea var. *italica* L. (Brassicaceae)	W	1,5,10 mg kg^{-1}	30 days	Glutathione S- transferase (GST)	Decrease in the activity of glutathione S- transferase (GST) under low doses of tungstate (1–5 mg kg^{-1})	Dawood and Azooz (2019
	Brassica oleracea var. *italica* L. (Brassicaceae)	W	1,5,10 mg kg^{-1}	30 days	Reduced glutathione, ascorbic acid, α-tocopherol	Significant increase in ascorbic acid, reduced glutathione, and α-tocopherol contents in 30 days old plants as compared to control	Dawood and Azooz (2019)
	Miscanthus sinensis (Poaceae)	Hg	62.1 mg kg^{-1}	30 days	Superoxide dismutase (SOD)	The maximum increase in SOD activity as compared to control and other treatments	Zhao et al. (2019)
	Miscanthus sinensis (Poaceae)	Hg	183 mg kg^{-1}	60 days	Superoxide dismutase (SOD)	The maximum increase in SOD activity as compared to control and other treatments	Zhao et al. (2019)
	Miscanthus sinensis (Poaceae)	Hg	493 mg kg^{-1}	90 days	Superoxide dismutase (SOD)	The maximum increase in SOD activity as compared to control and other treatments	Zhao et al. (2019)

Table 5 (continued)

S. no.	Plant species (belong to family)	Heavy metal (HMs)	Hormesis doses	Exposure time	Endpoint evaluated	Antioxidative defence response	References
	Triticum astivum (Poaceae)	Zn	100 and 300 μML^{-1}	14 days	CAT and POD	The maximum increase in CAT and POD activity as compared to control and other treatments	Wei et al. (2022)
	Triticum astivum (Poaceae)	Zn	100 μML^{-1}	14 days	SOD and APX	The maximum increase in SOD and APX activity as compared to control and other treatments	Wei et al. (2022)
	Oryza sativa (Poaceae)	La	0.05 mM	13 days	Catalase (CAT)	The maximum increase in CAT activity at lower La concentration	Liu et al. (2016)
	Vicia faba (Fabaceae)	La	108 $\mu g\ g^{-1}$	15 days	Guaiacol peroxidase (GPX)	GPX activity displays a U-shape response curve with a maximum decrease at 108 $\mu g\ g^{-1}$ La content in the roots of a plant	Wang et al. (2011)
	Vicia faba (Fabaceae)	La, Cd	6 μM Cd, 8 and 30 μM La	15 days	Catalase (CAT) and superoxide dismutase (SOD)	Combined treatment of 6 μM Cd and 8 μM La enhanced CAT activity to a maximum, while 6 μM Cd in combination with 30 μM La stimulated SOD activity to the maximum as compared to control and other treatments	Wang et al. (2012a)
	Vicia faba (Fabaceae)	La, Cd	6 μM Cd, 8–120 μM La	15 days	Ascorbate peroxidase (APX)	Combined treatment of 6 μM Cd and 8–120 μM La revealed significant hormetic responses, with significant effects being shown in the low dosage area in 8–120 μM La with 6 μM Cd	Wang et al. (2012b)
	Camellia sinensis (Theaceae)	Al	300 μM	8 weeks (56 days)	Catalase (CAT), ascorbate peroxidase (APX), superoxide dismutase (SOD), and glutathione reductase (GR) activity	Increased in catalase (CAT), ascorbate peroxidase (APX), superoxide dismutase (SOD), and glutathione reductase (GR) activity as compared to untreated control	Hajiboland et al. (2013)

Table 6 Hormesis effects on phenolic compounds of various plants species under low doses of heavy metals stress

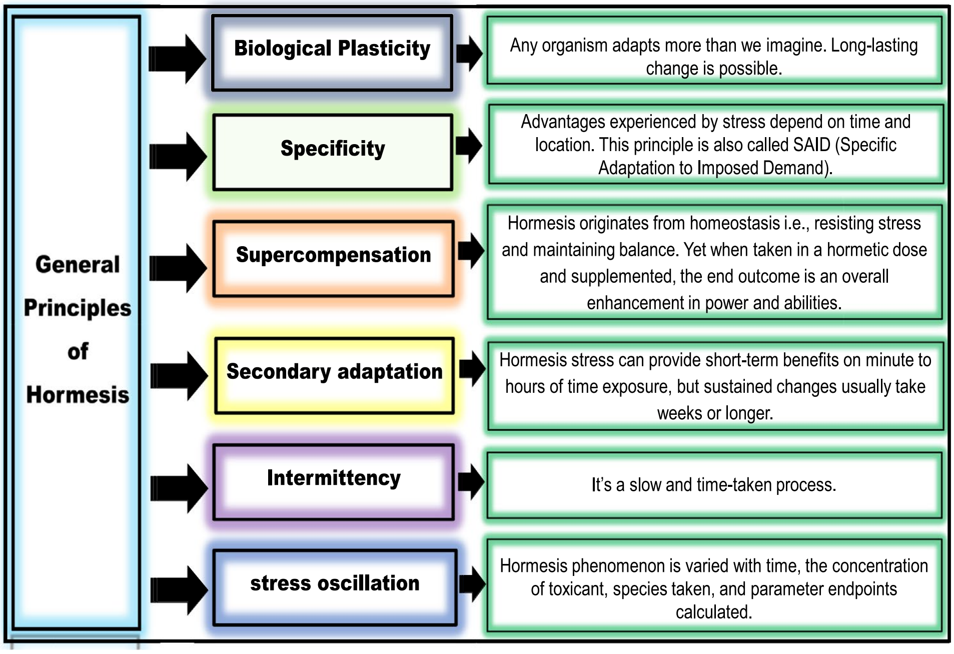
S. no.	Plant species (belong to family)	Heavy metal (HMs)	Hormesis doses	Exposure time	Endpoint evaluated	Hormetic response	References
	Zea mays L. cv. KOSMO 230 (Poaceae)	Pb	0.5, 1,5 and 10 µM Pb	14 days old seedling treated with Pb for the last 4 days	Flavanol content	Significant increase in flavanol content with increase in metal ion concentration	Małkowski et al. (2020)
	Triticum astivum (cv. Bahara) (Poaceae	Sm	2500 and 5000 µM	21 days	Total phenol content and anthocyanin content	Continuous increase in phenol and anthocyanin content up to 5000 µM Sm	Haghighi et al. (2023)
	Triticum astivum (cv. Bahara) (Poaceae)	Sm	2500 µM	21 days	Flavonoid content	Increased in flavonoid content as compared to control	Haghighi et al. (2023)
	Triticum astivum (cv. Arta &Bahara) (Poaceae)	Ce	2500, 5000, 7500,10,000 µM	21 days	Anthocyanin content	*Triticumastivum* cv. Arta showed continuous increase in anthocyanin content up to 5000 µM, while *Triticumastivum*cv. Bahara showed continuous increase in anthocyanin content up to 10,000 µM	Haghighi et al. (2023)
	Triticum astivum (cv. Arta & Bahara) (Poaceae)	Ce	2500 µM	21 days	Total phenol content and Flavonoid content	Increased in phenol and flavonoid content in both the wheat cultivars were observed	Haghighi et al. (2023)
	Brassica oleracea var. *italica* L. (Brassicaceae)	W	1,5,10 mg kg^{-1}	30 days	Phenolic compounds and Flavonoids	Significant increase up to a concentration 10 mg tungstate per kg of soil in 30 days old plants as compared to control	Dawood and Azooz (2019)
	Fagopyrum esculentum (Polygonaceae)	Al (nanscales)	250, 500, 750 and 1000 mgL^{-1}	21 days	Phenol content	Shows a sharp rise at 250mgL^{-1} Al nanoscale, then the increase becomes steady and remains almost 145% as compared to the control group	Smirnov et al. (2019)
	Camellia sinensis (Theaceae)	Al	300 µM	8 weeks (56 days)	Flavonoids and phenolic compounds	Increased in flavonoids and phenolic content as compared to control	Hajiboland et al. (2013)

Table 7 Hormesis effects on osmolyte content of various plants species under low doses of heavy metals stress

S. no.	Plant species (belong to family)	Heavy metal (HMs)	Hormesis doses	Exposure time	Endpoint evaluated	Hormetic response	References
	Capsicum annuum (Solanaceae)	Si	60 mg L^{-1}	28 days	Free amino acid	Significant increase in amino acid content as compared to control and other treatments groups	Trejo-Téllez et al. (2020)
	Brassica oleracea var. *italica* L. (Brassicaceae)	W	1,5,10 mg kg^{-1}	30 days	Amino acids and soluble sugar	Significant increase in the Amino acids and soluble sugar contents in 30 days old plant	Dawood and Azooz (2019)
	Capsicum annuum (Solanaceae)	V	5 µM	28 days	Free amino acids and total soluble sugar content	The maximum increase in total soluble content and free amino acid as compared to the control treatment	García-Jiménez et al. (2018)
	Glycine max (Fabaceae)	La	0.40 mM and 1.20 mM	7 days	Amino acid content	Increased in amino acid content as compared to control	Zhang et al. (2017)
	Capsicum annuum (var. Sven, Sympathy & Zidenka) (Solanaceae)	La	10 µM	30 days	The total amino acid content	Increased in soluble amino acid content as compared to control	Garcia-Jimenez et al. (2017)
	Capsicum annuum (Solanaceae)	La	10 µM	30 days	Soluble sugar	Increased in soluble sugar as compared to control	Garcia-Jimenez et al. (2017)
	Zea mays (Poaceae)	Ni	180 mg kg^{-1}	28 days	Sucrose content	Significantly increased in sucrose content as compared to the control	Nie et al. (2015)
	Camellia sinensis (Theaceae)	Al	300 µM	8 weeks (56 days)	Amino acids	Increased amino acids content	Hajiboland et al. (2013)

Table 8 Hormesis effects on plant mineral nutrient content after low doses of metal uptake

S. no.	Plant species (belong to family)	Heavy metal (HMs)	Hormesis doses	Exposure time	Endpoint evaluated	Hormetic response	References
	Dianthus carthusianorum (Caryophyllaceae)	Cd	1 µM	24 weeks (168 days)	Nutrient uptake (Fe and Zn)	Fe and Zn accumulation increased in shoot parts	Muszyńska et al. (2018)
	Glycine max (Fabaceae)	La	5 and 10 µM	28 days	Nutrient uptake (Zn, Cu, and Fe)	Zn, Cu, and Fe accumulation increased in shoot parts and Cu in root parts	de Oliveira et al. (2015)
	Glycine max (Fabaceae)	La	5, 10, 20, 40, 80, 160 µM	28 days	Nutrient uptake	levels of K, Ca, P, Mg, and Mn in roots and shoots increased considerably	de Oliveira et al. (2015)
	*Pisumsativum (*Leguminosae (Fabaceae)	Cr (VI)	20 mg L^{-1}	28 days	Nutrient uptake (Mg, Zn, Cu, and Fe)	Application of Cr (VI) to pea raised the content of Mg, Zn, Cu, and Fe in the roots and shoot parts	Rodriguez et al. (2012)
	Vicia faba (Fabaceae)	La, Cd	6 µM Cd, 2 and 8 µM La	15 days	Mg content	Combined treatment of 6 µM Cd and 2 or 8 µM La showed stimulation in Mg levels from 2 to 8 µM La dosage range along with 6 µM Cd treatments	Wang et al. (2012a)
	Vicia faba (Fabaceae)	La, Cd	6 µM Cd, 8 and − 240 µM La	15 days	Ca, Zn, Cu and K content	Combine treatment of 6 µM Cd and 8–240 µM La showed that Calcium, zinc, copper and potassium levels generally dropped initially, then increased (max. increased at 6 µM Cd along with 240 µM La), and then dropped again as HMs Cd and La treatment progressed to the high concentration	Wang et al. (2012a)
	Vicia faba (Fabaceae)	La, Cd	6 µM Cd, 8–60 µM La	15 days	Mo content	Combine treatment of 6 µM Cd and 8–60 µM La revealed significant stimulation, with significant hormetic effects being shown in the low dosage area in 8–60 µM La with 6 µM Cd	Wang et al. (2012b)
	Vetiveria zizanioides (L.) Nash (Poaceae)	Cd	1 mg L^{-1} Cd	15 days	Root activity (capacity to absorb nutrients and water)	Enhancement in root activity as compared to control	Aibibu et al. (2010)



General Principles of Hormesis

Biological Plasticity – Any organism adapts more than we imagine. Long-lasting change is possible.

Specificity – Advantages experienced by stress depend on time and location. This principle is also called SAID (Specific Adaptation to Imposed Demand).

Supercompensation – Hormesis originates from homeostasis i.e., resisting stress and maintaining balance. Yet when taken in a hormetic dose and supplemented, the end outcome is an overall enhancement in power and abilities.

Secondary adaptation – Hormesis stress can provide short-term benefits on minute to hours of time exposure, but sustained changes usually take weeks or longer.

Intermittency – It's a slow and time-taken process.

stress oscillation – Hormesis phenomenon is varied with time, the concentration of toxicant, species taken, and parameter endpoints calculated.

Fig. 2 Illustration of the general principle involved in hormesis (a concept derived from reference sources: Furrer et al. 2023; Kim et al. 2018; Calabrese 2015; Calabrese and Mattson 2011)

Heavy Metal-Induced Alteration in Plant Morphology

The interaction of heavy metals (HMs) with plant morphological traits tells a complicated story that goes beyond toxicity. As noted by Cândido et al. (2020), HMs have a harmful effect on plant morphological characteristics (like plant height, root or shoot length, fresh or dry weight, leaf number/area, total biomass, etc.). This discovery is aligned with the knowledge that heavy metals (HMs), which serve no biological purpose in plants, are mostly responsible for unfavorable consequences (Mengel and Kirkby 2001). These all-morphological characteristics are well observable through the naked eye (as shown in Fig. 10). The majority of HMs accumulation occurs inside various plant parts, which predominantly interferes with essential biological processes including plant growth and cell division. Particularly, it is recognized that metals such as Cd, Hg, Cr, and Se have the ability to accumulate within plant components, thereby hindering growth via diverse mechanisms.

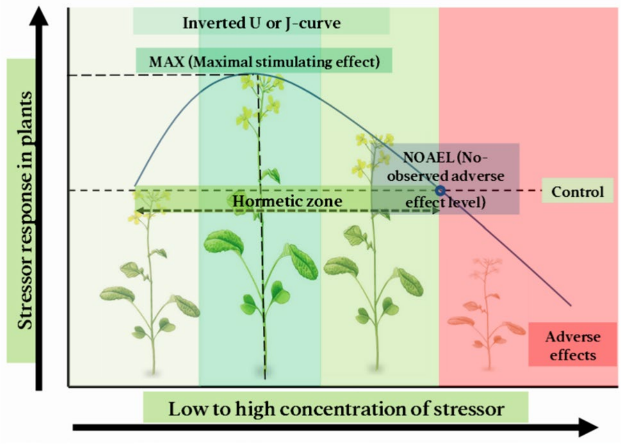


Fig. 3 Heavy metal or other toxic chemical-induced plant hormesis showing common global quantitative characteristics (adapted from reference source: Agathokleous et al. 2019a)

On the other hand, the relationship between plants and HMs is not entirely antagonistic. According to the research, hormetic stimulation in morphological parameters (plant height, root or shoot length, fresh or dry weight, leaf number/area, total biomass, etc.) was also observed in plants treated with a low concentration of heavy metals as compared to the untreated plants (as shown in Fig. 10 and Table 1). Table 1 shows the heavy metal-induced hormetic effect on the morphological parameters of various plant species. This hormesis effect points to a complex interaction in which HMs, at amounts below what is considered toxic, may cause adaptive responses that lead to an increase in certain growth parameters. The hormetic response shows that plants can tolerate and possibly benefit from low-level HM exposure by upregulating stress response pathways or improving nutrient uptake (Singhal et al. 2023). This duality emphasises the relevance of context in analyzing HM on plant physiology (Muszyńska and Labudda 2019). Therefore, it is essential to have a full understanding of the particular conditions in which HMs shift from being hormetic to poisonous to conduct an in-depth analysis of their impact on the environment and to devise measures to alleviate the

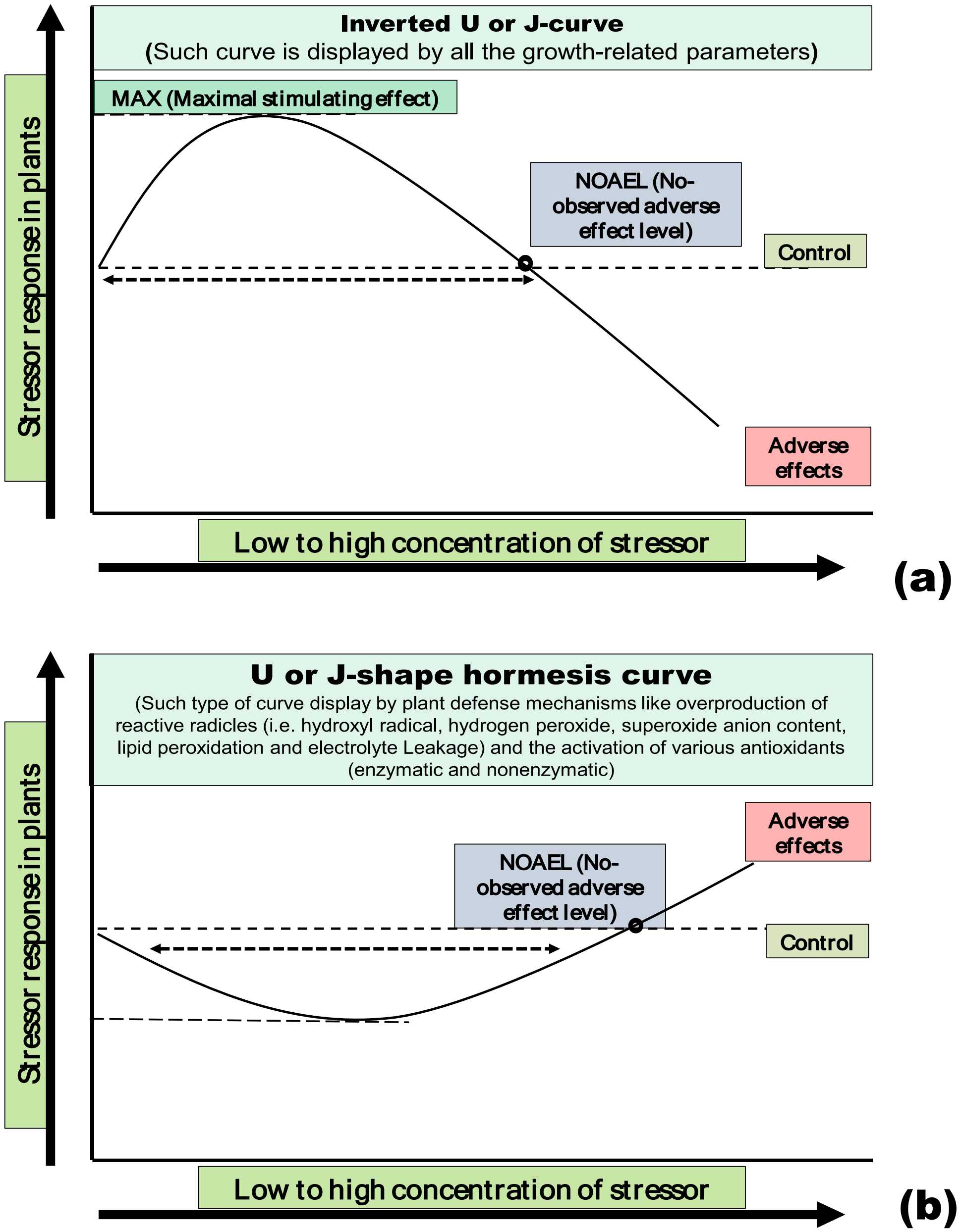


Fig. 4 Heavy metal or other toxic chemicals induced: **a** inverted U- or J-shape hormesis curve; **b** U- or J-shape hormesis curves. The *Y*-axis shows the percent change (maximum stimulatory response (MAX) value) of the response variable (i.e. the parameter measure) as compared to the untreated control. *X*-axis shows the different concentrations of the heavy metal or any other stressor

negative impacts that they have on plant life (Muszyńska and Labudda 2019).

Plant Photosynthetic Hormesis

The complex interaction between different concentrations of heavy metals (HMs) and plant photosynthetic machinery is an important field of research in plant physiology and environmental stress biology. It has been known that higher concentrations of HMs stress can cause damage to photosynthetic apparatus (Parmar et al. 2013). Since then, numerous experimental studies have revealed a decrease in a variety of photosynthetic parameters [like pigment (chlorophyll, carotenoid, xanthophyll) content, gas exchange parameters (photosynthetic rate, intercellular carbon, transpiration rate, stomatal conductance), and various other chlorophyll fluorescence parameters] in plants under high doses of HMs stress (Cunha Neto et al. 2020; Souri et al. 2019).

In plant systems, the photosynthesis process mainly relies on chlorophyll. Plants, under high doses of HMs stress, undergo chlorophyll breakdown, which is a catabolic process. It happens when dying cells need to get rid of potentially phototoxic pigments and recycle nutrients. Besides this, chlorophyll catabolites were reported to have a physiological role in plant defence against plant stressors (Hörtensteiner and Kräutler 2011). It was reported that chlorophyllase, an enzyme that catalyses the degradation of chlorophyll to create chlorophyllide (which is more hydrophilic,

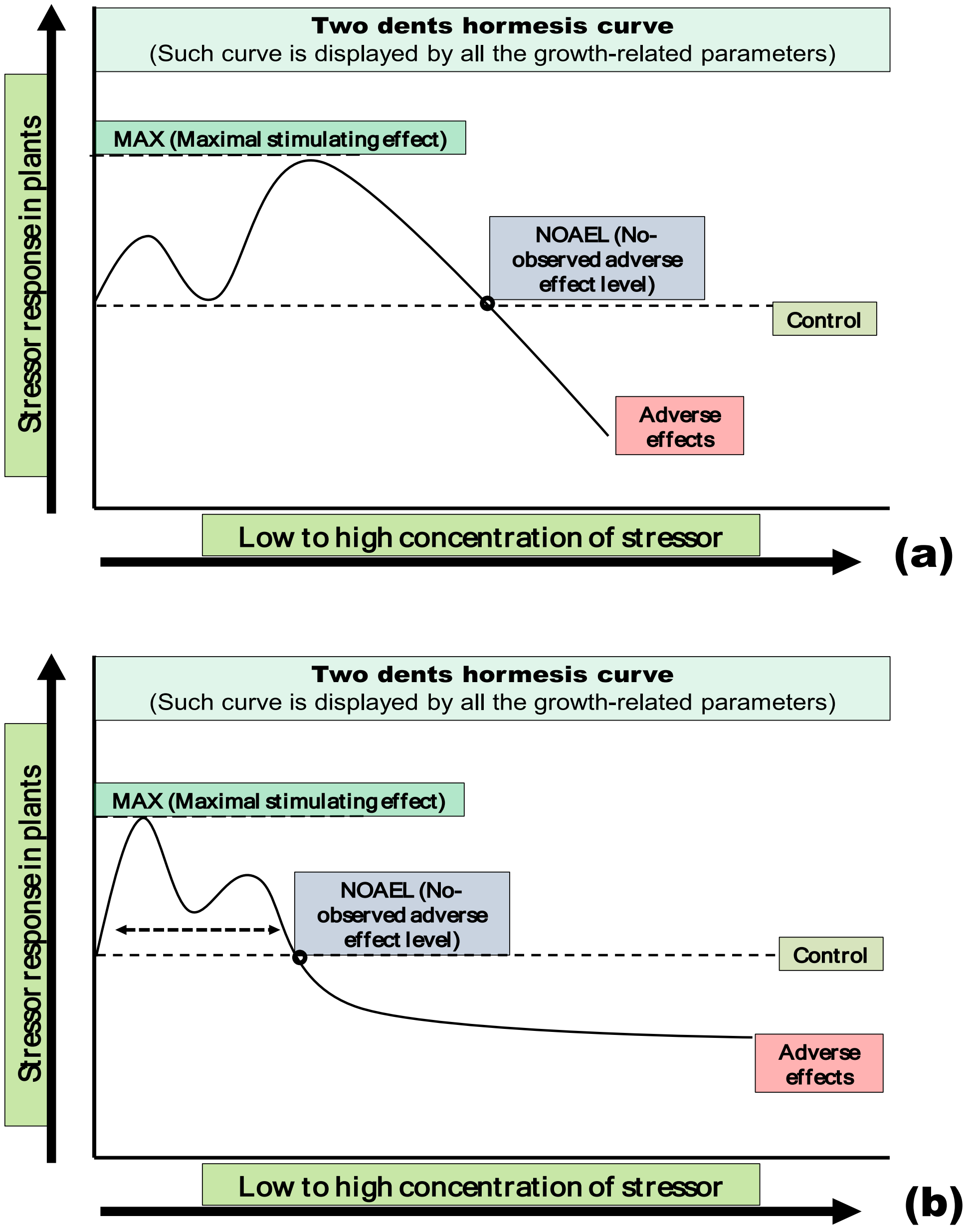


Fig. 5 Heavy metal or other toxic chemical induced (**a**) and (**b**) two dents hormesis curves. The *Y*-axis shows the percent change (maximum stimulatory response (MAX) value) of the response variable (i.e. the parameter measure) as compared to the untreated control. *X*-axis shows the different concentrations of the heavy metal or any other stressor

i.e. water loving in nature) plays an essential part in plant defensive mechanism against herbivores (Hu et al. 2015).

It is interesting to note that the interaction between HMs and the process of photosynthesis is not solely a negative one. Scientific investigations have also revealed a hormetic response, in which modest amounts of HM improve photosynthesis and general plant health (Table 2). Investigatory reports have also shown that chloroplasts are redox sensors that trigger acclamatory or stress-resistant hormetic responses in plants (Stamelou et al. 2021). Inside plant's chloroplast, during the process of photosynthesis, photosystem II (PS II) utilizes light energy to convert water (H_2O) into molecular oxygen (O_2) and provides electrons (e−) and protons (H+). Under low doses of HMs, PS II initiates a hormetic response through the non-photochemical fluorescence quenching (NPQ) mechanism (Moustakas et al. 2022). This mechanism serves to safeguard the photosynthetic apparatus from photo-oxidative damage by dispersing surplus light energy in the form of heat instead of creating reactive oxygen species (ROS). Moreover, under lower doses of HMs, an increase in NPQ will lower the electron transport rate (ETR), which will limit the production of ROS (Li et al. 2002; Takahashi and Badger 2011). Thus, the lower to moderate production of ROS levels inside the cells are regulated by NPQ's photoprotective mechanism (Adamakis et al. 2020a, b; Agathokleous et al. 2019b; Czarnocka and Karpiński 2018; Mittler 2017).

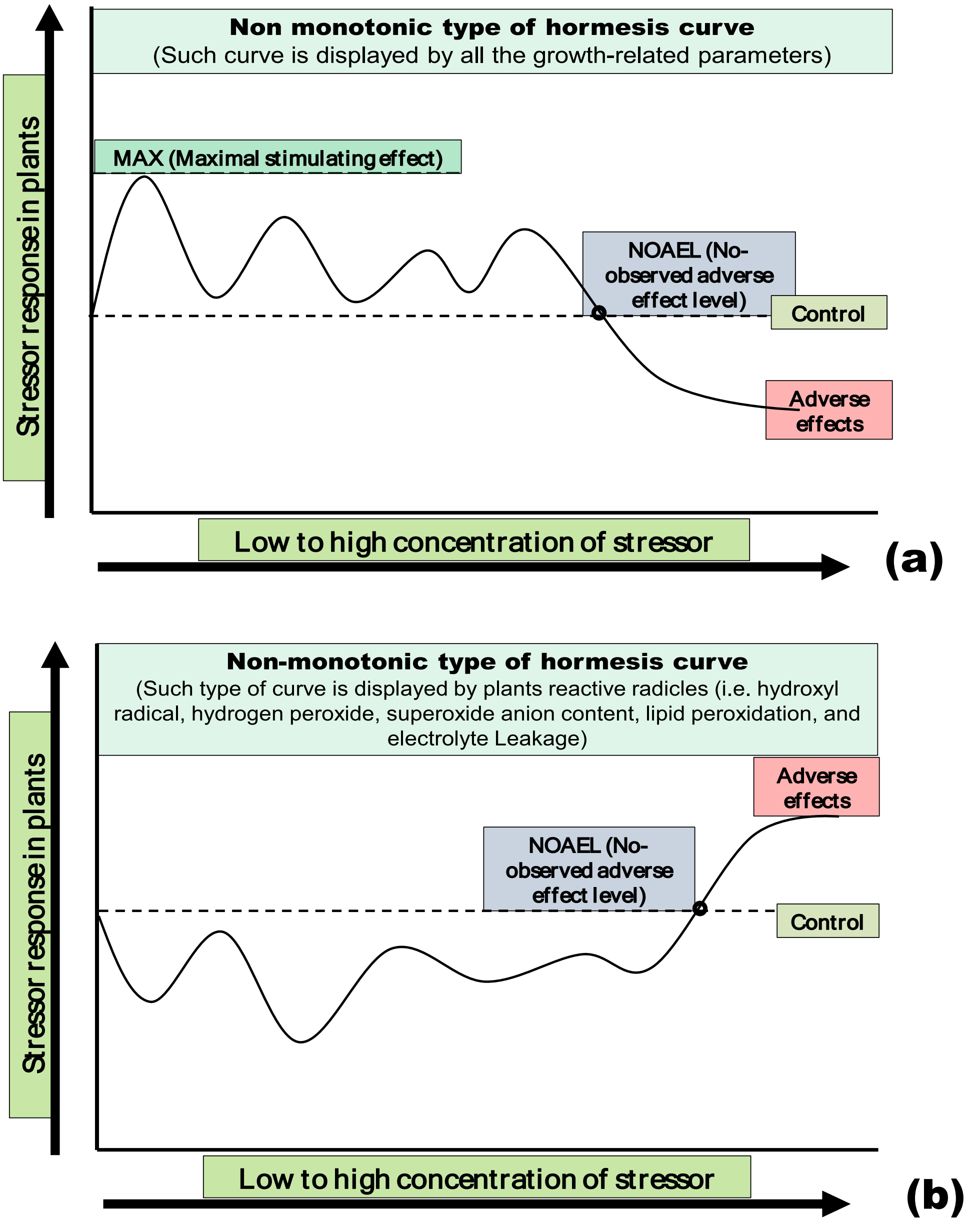


Fig. 6 Heavy metal or other toxic chemical induced (**a**) and (**b**) non-monotonic types of hormesis curves. The *Y*-axis shows the percent change (maximum stimulatory response (MAX) value) of the response variable (i.e. the parameter measure) as compared to the untreated control. *X*-axis shows the different concentrations of the heavy metal or any other stressor (adapted from reference source: Erofeeva 2014)

The photoprotective effectiveness of NPQ, which is dependent on the xanthophyll cycle, particularly zeaxanthin, and the PsbS (PSII subunit S) protein, highlights the ability of the plant to adapt and alleviate the potentially detrimental consequences of HMs (Ruban and Wilson 2021; Welc et al. 2021). Furthermore, the utilization of pulse amplitude-modulated (PAM) chlorophyll fluorometers provides a sophisticated method of monitoring PSII performance under stress, which in turn provides insights into the distribution of energy within the photosystem (Murchie and Lawson 2013; McAusland et al. 2019).

Further supporting photosynthetic hormesis, evidence suggests that low-level HMs stress can boost plant performance and photosystem II activity (Adamakis et al. 2020b; Agathokleous 2018, 2021; Agathokleous et al. 2020b), which in turn is responsible for increasing the various plant photosynthetic parameters (such as pigments (chlorophyll, carotenoid, xanthophyll) content, gas exchange parameters (photosynthetic rate, intercellular carbon, transpiration rate, stomatal conductance), and various other chlorophyll fluorescence parameters) (Table 2). The fact that chlorophylls are frequently stimulated by low-level stressors suggests that they are important constituents of stress biology, and their higher concentration under low-level stress suggests that they are necessary for normal plant functioning (Agathokleous et al. 2020b). Increased chlorophyll content in response to low-level stress may provide plant systems with a greater capacity to defend

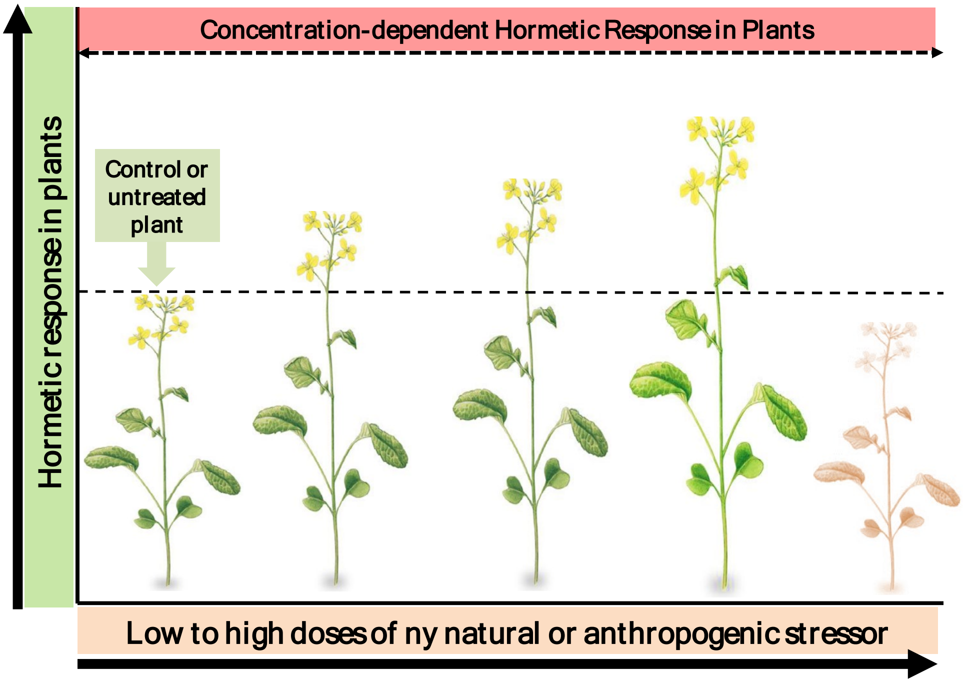


Fig. 7 Illustration of concentration-dependent hormetic response in plants. *Y*-axis shows the percentage change in the hormetic response as compared to the untreated or control plant. *X*-axis shows the low to high concentrations of the heavy metal or any other stressor as compared to the untreated or control plant

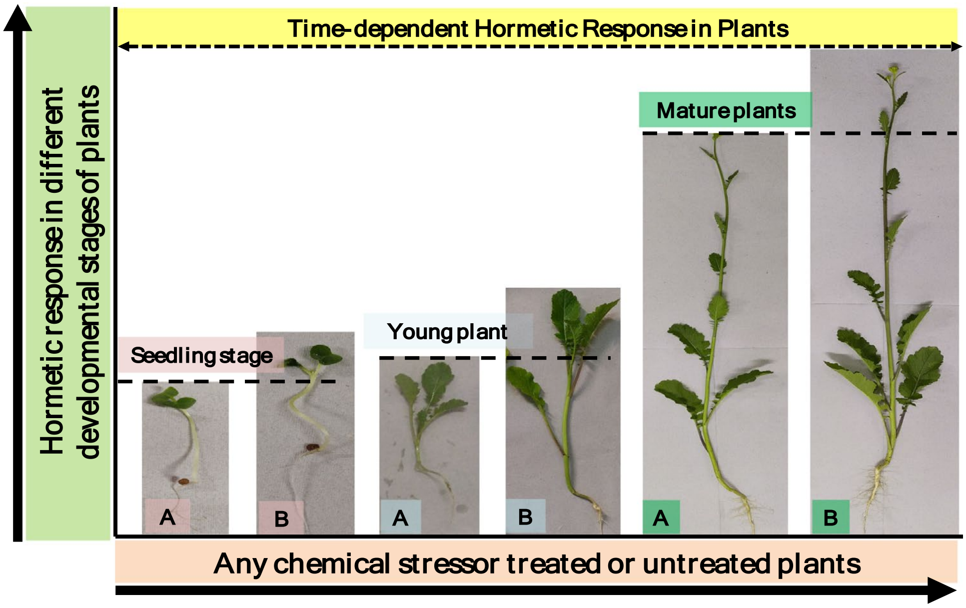


Fig. 8 Illustration of time-dependent hormetic response in plants. *Y*-axis shows the percentage change in the hormetic response as compared to the untreated or control plant of different developmental stages (seedling stage, young plant, or mature plant). *X*-axis shows the low concentrations of the heavy metal or any other chemical stressor-treated or -untreated plants of different developmental stages. **A** Untreated or control plant and **B** plant subjected to any kind of low amount of stress, such as heavy metal exposure, pesticide or herbicide treatment, etc.

against high level of HMs threats within specified time periods (Agathokleous 2021).

Oxidative Stress Markers-Induced Hormesis

Plants produce ROS immediately after being exposed to HMs. Plant cells either survive or die, and such fate of the plant cell under heavy metal stress is decided by the amount of reactive oxygen species (ROS) generated inside the plant cells. A low amount of ROS in plant's cell is essentially important for plant's appropriate cellular functioning. Furthermore, hormetic responses can be triggered by a slightly elevated level (i.e. low to moderate amount) of ROS in the plant cell, which induces potentially positive beneficial effects in plants (Moustakas et al. 2022).

Additionally, to stop HMs from producing ROS, which is further harmful, a sophisticated network of antioxidant enzymes situated in various plant cell organelles is activated. This system allows plants keep up balances and harmless ROS gradients, which further act as powerful warning signals to turn on more defence systems and stress-related genes (Mittler et al. 2004). ROS, and particularly hydrogen

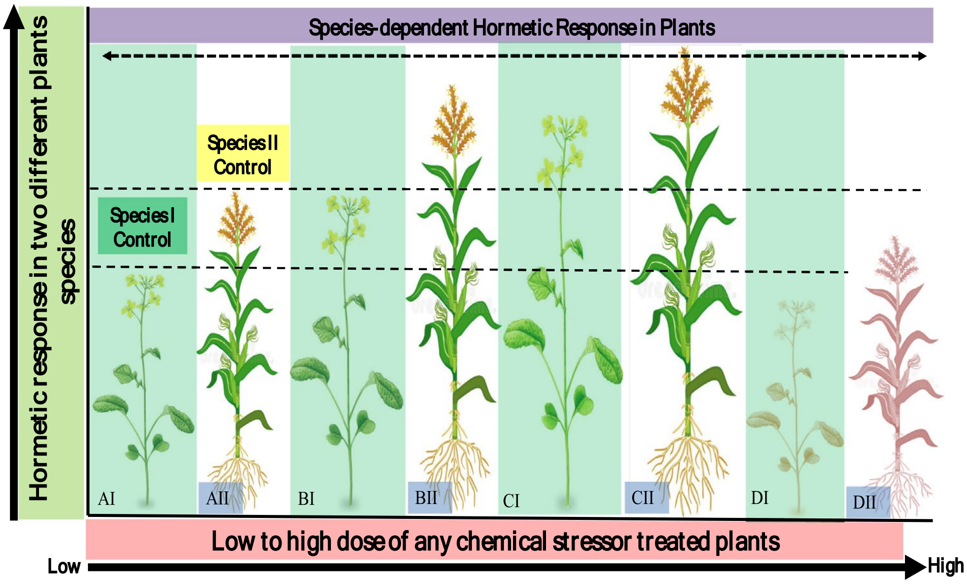


Fig. 9 Illustration of species-dependent hormetic response in two different plant species showing each species has a different hormetic response. *Y*-axis shows the percentage change in the hormetic response of two plant species, i.e. plant species I and II as compared to the untreated or control plant species I and II. *X*-axis shows the low to high concentrations of the heavy metal or any other stressor-treated plants species I and II. **AI** Untreated or control plant of species I, **AII** untreated or control pPlant of species II, **BI** and **CI** Plant species I subjected to any kind of low amount of stress, such as heavy metal exposure, pesticide or herbicide treatment, etc. **BII** and **CII** Plant species II subjected to any kind of low amounts of stress, such as heavy metal exposure, pesticide or herbicide treatment, etc. **DI** Plant species I subjected to any kind of higher dose of stress, such as heavy metal exposure, pesticide, or herbicide treatment, etc. **DII** Plant species I subjected to any kind of higher dose of stress, such as heavy metal exposure, pesticide. or herbicide treatment, etc.

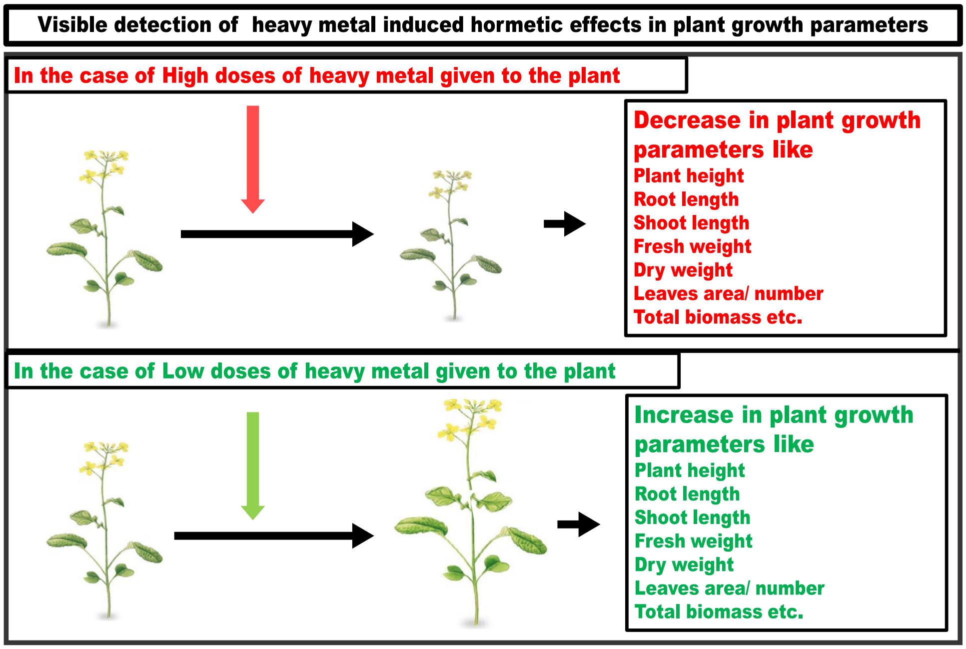


Fig. 10 Illustration of visible detection of heavy metal-induced hormetic effects on plant growth parameters

peroxide, act as powerful signals that initiate the activation of genes mainly involved in the production of antioxidants and other stress-related genes. ROS may have a hormetic effect by stimulating antioxidant defences in an organism (plants and animals) (Poschenrieder et al. 2013; Pastori and Foyer 2002; Ye and Gressel 2000). It has been claimed that the mitochondria of animal cells are the sites where hormetic responses are induced in response to mild oxidative stress (Li et al. 2012). PUMPs, which stand for mitochondrial uncoupling proteins, have also been found in plants.

The PUMP genes can be activated in response to a number of different stimuli, both biotic and abiotic (Vercesi et al. 2006). However, till date, plant hormetic responses have not been linked to uncoupling proteins by any plant researcher. Besides this, presently, there is abundant experimental proof demonstrating the specificity of ROS generation in response to stress and signalling caused by the absolute control and regulation of the synthesis and activity of respiratory burst oxidase (Rboh) homologous genes. Several developmental processes and stress responses are under the control of the various isoforms of the respiratory burst oxidases (Rboh) gene (Suzuki et al. 2011). Rboh gene isoforms D and F (AtRbohD, F) are reported to be involved in *Arabidopsis thaliana*'s pathogen response and leaf stomatal control and regulation. However, AtRbohD seems to be activated by injury, systemic attacks, or abiotic stress (Poschenrieder et al. 2013; Suzuki et al. 2011). On the other hand, high concentrations of HMs in the plant tissues (much above the toxicity limit) cause a large amount of ROS to get accumulate inside plant cells, i.e. outside acceptable limits. This will cause deleterious effects on the plant cell's ability to function normally (Moustakas et al. 2022), deactivated antioxidant system, plant growth suppression, and finally lead to plant programmed cell death.

However, the minor concentration of HMs leads to the production of a low to moderate amount of ROS, which further causes the activation of various stress signalling pathways like hormonal defence signalling pathways, antioxidant defence system, and various other stress-related genes that finally help the stressed plant to induce hormetic adaptive growth responses (Fig. 11). Therefore, in plants' reactions to heavy metal stress, ROS plays a multifaceted function. They can be agents of cellular damage in situations of extreme stress or crucial signalling molecules for stress adaptation. It is essential for the plant to have the capacity to finely adjust ROS production and signalling to successfully navigate the thin line that separates survival and death when exposed to HM. Table 3 shows the low to moderate production of various oxidative stress markers in various plant species under low doses of heavy metals stress.

Hormetic Effects on Proteins

In plants, an excessive amount of HMs exposure for an extended period of time causes metal homeostasis disruptions that lead to the development of stress and toxicity symptoms, which will finally lead to lowering the protein content. The mechanism underlying this reduction involves protein oxidative modification, in which ROS can damage protein functioning by direct oxidation of amino acid side chains or through secondary interactions with aldehydic products of lipid peroxidation (Reinheckel et al. 1998). to further elucidate this mechanism, Palma et al. (2002) discovered that HM-induced oxidative stress causes protein oxidation to occur more quickly, which in turn leads to proteolysis and fragmentation. This finding highlights the detrimental effect that HMs have on the proteome. On the other hand, researchers have not done much research on plant hormesis, especially when it comes to how proteins react to low levels of HMs. However, there are many

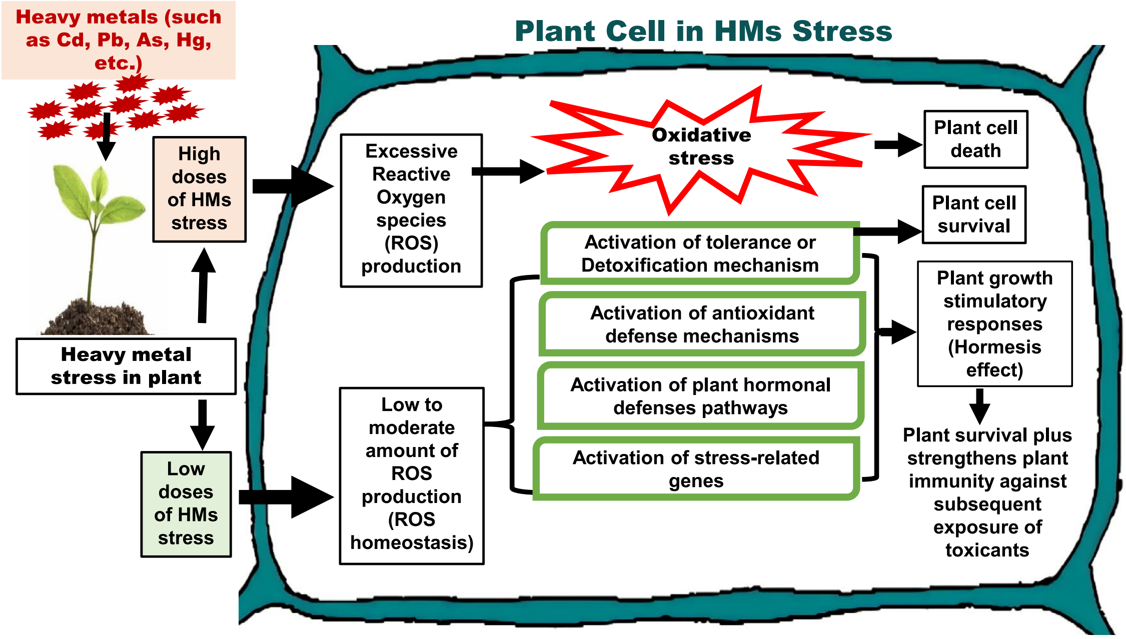


Figure. 11 Stress signalling cross talk involved in HMs-induced hormesis

investigatory reports showing lower doses of HMs-induced hormetic stimulation in plant protein in various plant species (Table 4). The lower doses of HMs trigger the production of a variety of plant stress-associated proteins that might be responsible for increasing the protein content (Di Toppi and Gabbrielli 1999). Demple (1991) showed that roughly 40 proteins were activated in prokaryotes when they were under oxidative stress. Stress-associated proteins are mainly made up of antioxidant enzymes, phytochelatins (PCs) and glutathione (GSH)-producing enzymes and heat shock proteins. Additionally, soluble proteins have the potential to serve as osmoprotective agents that help to keep the structure and function of cells stable under stress conditions (Wei et al. 2022; Abbas and Mobin 2016). The plants' ability to tolerate metals at lower concentrations and initial exposure times is evidence of defence adaptation facilitated by these kinds of stress-associated proteins. Table 4 shows the various experimental reports of hormesis effects on protein stimulation in various plant species under low doses of heavy metal stress. Therefore, undoubtedly, elevated levels of HMs disrupt protein functionality and diminish protein content, resulting in symptoms of toxicity and stress. Conversely, reduced HMs concentrations may stimulate hormetic responses that stimulate stress-associated proteins. These proteins protect the plant against HM exposure and boost its defences, allowing it to survive and adapt under sub-toxic stress (Di Toppi and Gabbrielli 1999). This dual role of proteins under HM stress highlights the complexity of plant responses to environmental challenges, emphasizing the relevance of dose, exposure length, and plant adaptability in crossing the delicate line between stress and survival.

Hormetic Effects on the Antioxidant System

Plant adaptation to heavy metal (HM) stress requires sophisticated modulation of antioxidative systems, which are essential for managing the oxidative stress caused by fluctuating HM concentrations. The plant responses to low and high doses of HMs were frequently connected with the up or downregulation of adaptation mechanisms, particularly those involving antioxidative (enzymatic and non-enzymatic) processes. These associations were observed in a number of different plant species (Table 5). Recent studies confirmed moderate activation of antioxidant enzymes (catalase, superoxide dismutases, peroxidases, etc.) and an increase in non-enzymatic antioxidative compounds (such as alpha-tocopherol, flavonoids, phenolic compounds, reduced glutathione, ascorbic acid, etc.) (Erofeeva 2022b). However, the degree to which these antioxidative enzymes showed inhibition or stimulation depends directly on the proportion of HM concentration present in the plant sample (Sardar et al. 2007). However, it has been noted that the activity of antioxidant enzymes is affected not only by the type of HMs, but also by the contamination method and incubation period (Fang et al. 2017). Catalase activity was reported to be boosted by low HMs concentration, but decreased when the HM concentration was increased beyond the tolerance limit of the plants (Table 5). The increase in catalase activity at the lowest HMs concentration in plants was considered to have an associated link with the higher plant growth and development observed at the low doses of HMs treatments (Calabrese and Agathokleous 2021). Catalase may play an essential role in early triggered adaptive responses that occur in lower concentrations of HMs-treated plants that do not show any visible symptoms of toxicity. In addition to this, other antioxidants (enzymatic and non-enzymatic) such as superoxide dismutase (SOD), ascorbate peroxidase (APOX), glutathione peroxidase (GPOX), reduced glutathione (GSH), ascorbic acid, and α-tocopherol have also shown an increase. An increase in these antioxidants under lower doses of HMs alleviates the damaging effects by causing the removal of ROS, whereas a higher concentration of HMs might cause damage to the antioxidative system, thus inhibiting enzymatic or non-enzymatic activity and therefore lead to minimizing the resistances against ROS production (Zhao et al. 2019). Glutathione reductase (GR), ascorbate peroxidase (APX), reduced glutathione (GSH), and ascorbate are major components of the ascorbate–glutathione cycle and are responsible for the elimination of H_2O_2 from different parts of cells (Rodríguez-Serrano et al. 2009). On the other hand, interestingly, several recent investigations found growth hormesis in the absence of alterations or even a reduction in various antioxidant enzymatic activities, for example, in the case of wheat plants' exposure to graphene oxide (Ren et al. 2020) or Ag@CoFe2O4 nanoparticles (López-Luna et al. 2020). Further, cadmium metal makes soybeans grow faster, but it also causes enzyme antioxidant defence to go down and non-enzyme antioxidant levels to go up (Francischini et al. 2020). Similarly, hormetic dosages of atmospheric Hg reduced SOD (superoxide dismutase) activity, while increasing glutathione levels in the moss *Tillandsia usneoides* (Sun et al. 2021). Such kind of previous investigation reveals that non-enzyme antioxidants might play a prominent role in certain types of hormesis as compared to enzymatic antioxidants.

Moreover, research has clearly shown that the majority of cellular GSH is found in the mitochondria, where it plays an essentially important role in maintaining the redox equilibrium and homeostasis of metal ions (Koffler et al. 2013). Ascorbic acid (AsA) and glutathione (GSH) are reported to be one of the essential antioxidants that can maintain intracellular redox equilibrium as well as safeguard the plasma membrane from oxidation (Wei et al. 2022; Apel and Hirt 2004). Glutathione not only functions as a stress signalling molecule and an essential component of the antioxidant defence system, but also chelates metals and acts as a precursor for the synthesis of phytochelatins (Jozefczak et al. 2012).

GSH is crucially important for the production of phytochelatins (PC), which are capable of combining with heavy metals to form PC–HM complexes and play a key part in the process of HMs detoxification through vacuolar sequestration of the PC–HM complexes (Shi et al. 2021). All of these actions of GSH make GSH a crucial component in the regulation of proteins that shield plants from the damaging effects of HMs. Table 5 describes the antioxidative defence response in various plant species under low doses of heavy metal stress. In summary, the way in which plants react to HM stress involves a nuanced equilibrium between the induction of antioxidative defence mechanisms and the avoidance of toxicity thresholds. The ability of plants to respond to different levels of HM is based on the complex regulation of enzymatic and non-enzymatic antioxidants. This shows how adaptable and resilient plants are in the face of environmental stressors.

Hormetic Effect on Phenolic Compounds

Plants' phenolic compounds display antioxidative behaviours under HM stress (Michalak 2006). The antioxidant action of the phenolic compound is mainly due to the presence of hydroxy (–OH) and carboxyl (–COOH) groups in their chemical structures which are able to bind metals (Michalak 2006). Flavonoids are ubiquitous in plant kingdoms and are the most common type of phenolic compound (Michalak 2006). Phenylalanine ammonia-lyase (PAL) is the primary enzyme involved in regulating the conversion of phenylalanine into secondary metabolites such as phenolic substances, flavonoids, anthocyanin, etc. (Dong et al. 2010). Activation of phenylalanine ammonia-lyase (PAL) may account for the greater phenolic and flavonoid contents at lower HMs doses, which may account further for scavenging the ROS to counterbalance the direct harmful impact of HMs on plant growth. Chen in 2015 reported the highest PAL enzymatic activity under low to moderate Ce doses (0.5–1.0 mM), which is in line with the fact that the amount of flavonoids or other secondary metabolites in Ginkgo suspension cells increased. Thus, HMs can raise the concentration of phenolic or flavonoid compounds by boosting PAL activity. These phenolic or flavonoid compounds may represent a self-protective mechanism employed by the plants for itself to cope with metallic stress. Numerous researchers have shed light on the phenols' and flavonoids' antioxidant potential by demonstrating their ability to chelate metal ions, sequestration, metal uptake, and reduction of ROS production through the transfer of electrons to free radicals (Haghighi et al. 2023). Moreover, HMs have the ability to reduce lipid hydroperoxide (LOOH) by breaking the (O–O) bond through haemolysis. This leads to the formation of lipid alkoxyl radicals and free-radical oxidized chains that ultimately cause lipid peroxidation, which finally results in plant cell and membrane damage. Flavonoids and phenolic substances have the ability to encapsulate these lipid alkoxyl radicals, which stops the process of lipid peroxidation (Michalak 2006). Additionally, HMs encourage the transcription of important metabolic genes, which results in an increase in the production of secondary metabolites that support the plant's entire defence mechanism. Despites this insight, the whole molecular level process by which HMs are taken up by plants, its effects inside the plant cell, and biochemical physiology of stress plant cells under the lower concentration of HMs remain to be further investigated. Table 6 shows the hormesis effect on plant phenolic compounds in various plant species under low doses of heavy metal stress.

Hormetic Effect on Osmoprotectants

Low doses of HMs treatments contribute to osmoregulation by enhancing amino acid biosynthesis and carbohydrate metabolism. Hormetic doses of various stressors, such as veterinary antibiotics, silicon, etc., increase the levels of soluble sugars like glucose (Tasho et al. 2018; Trejo-Téllez et al. 2020). This investigatory report showed the possibility of glucose signalling being involved in the process of hormesis and also suggesting its central role in modulating plant growth and stress response. Sugar signalling works through complex networks that interact with growth-promoting phytohormones (such as auxins, cytokinins, brassinosteroids, etc.) either through Hexokinase 1-dependent or -independent mechanism pathways (Saksena et al. 2020). Prado et al. (2010) also discovered that mild concentrations of heavy metals boosted carbohydrate metabolic processes. Both hexoses and sucrose were reported to increase the activity of genes involved in growth and decrease the activity of genes involved in stress (Rosa et al. 2009).

Moreover, increased amino acid synthesis, like proline, contributes mainly to the osmotic homeostasis of stress plant cells (Trejo-Téllez et al. 2020). However, there are few experimental reports that also show a decrease in proline content at lower doses of heavy metals (Haghighi et al. 2023). This might be due to the fact that in some plant species, an appropriate quantity (low to moderate amount) of proline has been shown to improve plant stress tolerance, but in large quantities, it can produce phytotoxicities (Hayat et al. 2012). On the other hand, some plants use an increase in their proline content as a form of defence against stressors. Some of the functions that proline can perform are functioning as a carbon–nitrogen source, ROS scavenger, minimizing electrolytic leakage, hydraulic buffer, osmoprotectant, a powerful antioxidant, and membrane stabilizer (Hare and Cress 1997). Plants exposed to higher concentrations of

HMs have been shown to have more proline, which may be related to their improved ability to inhibit reactive oxygen species (ROS) and protect their cells from oxidative stress (Haghighi et al. 2023). Table 8 shows hormesis effects on the osmolyte content of various plant species under low doses of heavy metals stress. These findings highlight the relevance of understanding plant species' metabolic and physiological responses to HM stress to improve plant resilience and growth under environmental constraints.

Hormetic Effects on Plant Mineral Nutrient Content After Low Doses of Metal Uptake

Since the late nineteenth and early twentieth centuries, scientists have been able to get a lot of information about the relationship between the availability of plant macronutrients (Mg, Ca, N, K) and micronutrients (Mn, Cu, Fe, Zn) and plant growth and development (Calabrese and Baldwin 2000). These elements are critical to plant development, regulating a variety of physiological and biochemical processes. Subsequent investigations (Table 8) confirmed that plant micro- and macronutrients could elicit hormesis in many plants under lower doses of HMs. Essential micro/macronutrients at lower doses of HMs boosted plant growth markers, root/shoot ratios, yield, and chlorophyll content relative to controls while decreasing lipid peroxidation rates (Erofeeva 2021). Mineral nutrient content rises inside various plant species under HMs exposure might be the reason for hormetic enhancement in plant morphology and various plants' photosynthetic parameters (Tables 1, 2). This shows that under HM stress, plants can use higher mineral resources to boost their physiological capabilities, resulting in enhanced root activity, as seen in *Vetiveria zizanioides* with lower cadmium (Cd) levels (Aibibu et al. 2010). Enhanced root activity is an indicator of a plant's ability to absorb nutrients and water more efficiently. Specifically, Fe content increase in plants exposed to lower concentrations of HM is notable for its roles in heme and chlorophyll production, because this nutrient regulates the rate of aminolevulinic acid creation, a universal precursor of these biosynthetic processes (Cakmak et al. 2010). This biological process helps plants maintain and improve photosynthetic capacity (Cakmak et al. 2010). Furthermore, the increase in copper content may cause a rise in the concentration of plastocyanin, which in turn stimulates the activity of photosystem I (PS I) and the synthesis of quinine. This, in turn, leads to an increase in the activity of photosystem II (PS II) and the transfer of electron energy between the two photosystems (Cakmak et al. 2010), highlighting the interconnectedness between the supply of nutrients and the efficiency of photosynthesis. Table 8 shows various investigatory reports of the hormesis effects on plant mineral nutrient content after low doses of metal uptake. Here, the hormesis phenomenon demonstrates the potential of subtle concentrations of HMs to elicit favourable physiological reactions that further highlight the ability of plants to employ stressors as signals to improve growth and activate defence mechanisms. It shows how plants balance nutrient absorption, metabolic changes, and stress mitigation to maximize growth and development under lower doses of HMs.

Hormetic Effects on Other Biochemical Compounds

Hormesis also seems to alter the amounts of endogenous stress hormone levels inside the plant body. *Lactuca sativa* plants exposed to low amounts of wastewater stimulated root development and reduced the amount of ABA (Abscisic acid), which is a growth inhibitor (McGinnis et al. 2019). This drop in ABA, a stress hormone that stops plants from growing when they are under a lot of stress, shows how hormesis might be able to lessen stress reactions and help plants grow (McGinnis et al. 2019). In addition, a higher amount of auxin, which acts as a growth stimulant, was found in maize plants that had been subjected to lead and cadmium metal (Małkowski et al. 2020). Auxins, especially indole-3-acetic acid (IAA), are very important for cell growth, division, and differentiation. This means that HM-induced stress can actually help plants grow in some ways by changing the amounts of phytohormones (Małkowski et al. 2020). Bisphenol A has also been reported to stimulate plant growth by increasing IAA (indole-3-acetic acid) and zeatin content as well as a decrease the ratios of ABA/IAA, ABA/GA (gibberellic acid), ABA/zeatin, ethylene/IAA, ethylene/GA and ethylene/zeatin (Li et al. 2017; Qiu et al. 2013). This emphasizes the significance of altering the ratio of endogenous phytohormones for growth hormesis, which refers to the predominance of growth-stimulating factors over growth-inhibiting factors.

Furthermore, non-protein thiols (NP-SH), a type of metal chelator, are also known to exhibit hormetic response under lower doses of Cd (10, 20, and 40 µM) exposure (14 days) in *Brassica juncea* plants, where the content of NP-SH decreases after a considerable increase up to 40 µM Cd (Seth et al. 2008). Phytochelatin content also displays hormetic response under lower doses of Cd (10, 20, 40, and 80 µM) exposure (14 days) in *Brassica juncea* plants, where the content of phytochelatin decreases after a significant increase up to 80 µM Cd (Seth et al. 2008). Therefore, plants may utilize low-level stress exposures to drive favourable growth responses by fine-tuning phytohormone balances and activating specific biochemical pathways, demonstrating the complicated strategies plants use to flourish in stress situations. Overall, high doses of HMs were reported to reduce the plant morpho-physio-biochemical compounds, while lower doses of HMs also called beneficial elements (especially Cd, Hg, Pb, or As) increased the plant morpho-physio-biochemical compounds that further causes the activation of various cellular signalling pathways responsible for the hormetic effect (Fig. 12).

Omics-Based Exploration of Hormesis in Plants

To fully understand, how hormesis improves the growth, quality, and productivity of any plant's species, especially crop plants, is attained mainly by becoming aware of the importance of reading, understanding, and processing experimental data and literature about gene expression, protein biosynthesis, metabolites biosynthesis, genome and so on (Rico-Chávez et al. 2022). Therefore, we can learn all we need to know about how plants react to modest levels of heavy metal stress by studying hormesis mainly via the prism of omics technologies, which mainly include genomics, miRNAomics, transcriptomics, proteomics, metabolomics, and phenomics (Raza et al. 2023; Rico-Chávez et al. 2022).

Genetic and expression-level alterations in plants can be better understood with the use of genomics and transcriptomics, which show how stress modulates particular genes and pathways (Xu et al. 2023; Wang et al. 2023; Ma et al. 2022). Xu et al.'s (2023) experimental study reveals that quantitative real-time PCR and transcriptomic analysis revealed that the photosynthesis–antenna proteins pathway was essential for the hormesis effect and that LHCB7 (light-harvesting complex B7) and LHCP from this pathway were the most responsive to acephate hormesis. Additionally, according to physiological and transcriptomic analyses, juvenile peppermint plants exposed to low levels of cadmium experienced hormesis due to the constant activation of antioxidant activity. (Wang et al. 2023). Another transcriptomic analysis revealed that plant hormone signalling and secondary metabolism, particularly glucosinolate homeostasis, ethylene, and auxin signalling pathways, react in a manner that is opposite to that of low vs high levels of cadmium, indicating that these pathways are involved in the process of hormesis and the detoxification of cadmium (Ma et al. 2022). In addition to this, research into microRNAs' function in post-transcriptional regulation (miRNAomics) adds another layer to our understanding of how plants adapt their gene expression to environmental stress (Raza et al. 2023).

Proteomics takes this omics research a step further by revealing which proteins are involved in detoxification, the plant's reaction to stress, and its metabolic pathways, among other important functions (López-Bucio et al. 2022; Anani et al. 2022; Gressel and Dodds 2013; Randić and Estrada 2005). According to the findings of one study, heavy metal chromium (Cr (VI)) has two different effects on plants: low levels make them grow faster and better handle stress, while high levels stop them from growing and cause oxidative stress (López-Bucio et al. 2022). In this research, proteomic studies revealed changes in proteins linked to reactive oxygen species (ROS) detoxification, metabolism, and defence whereas transcriptomic studies revealed activation of genes involved in transport, detoxification, and stress response (López-Bucio et al. 2022).

Further, metabolomics supplements these omics approaches by analysing the tiny molecule metabolites

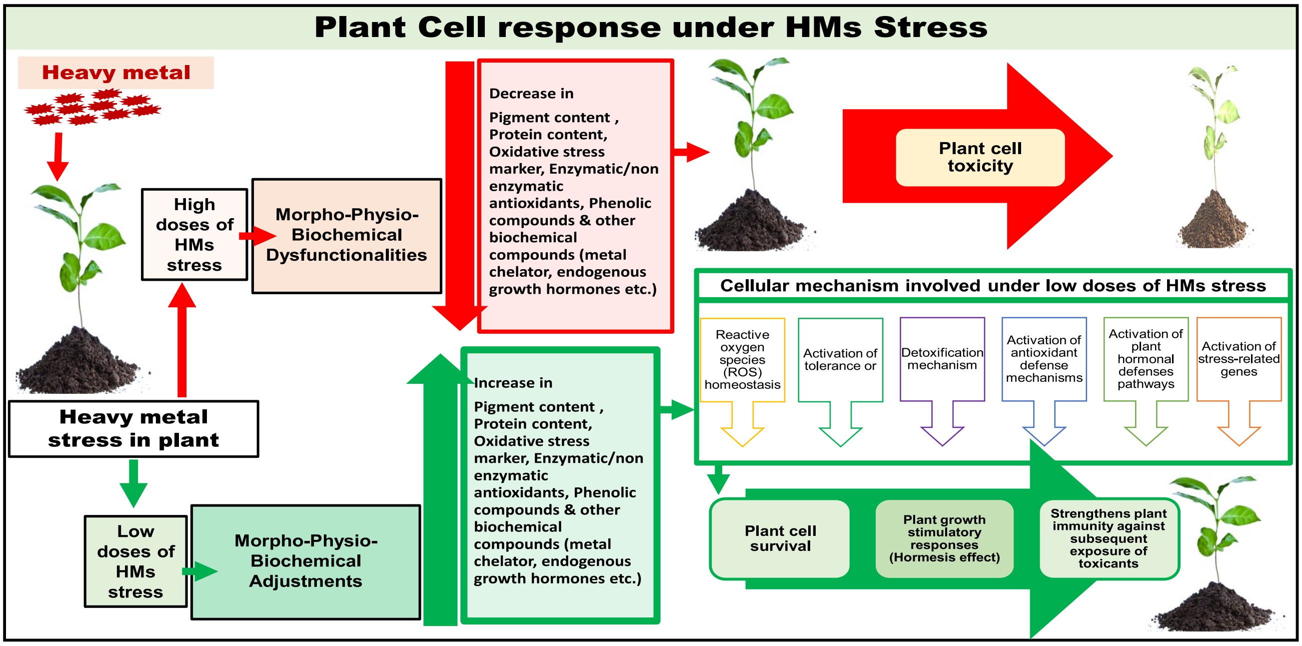


Fig. 12 Plant cell morpho-physio-biochemical response under low and high doses of heavy metals stress

produced by stressed plants, which can reveal physiological states and adaptive responses (Anani et al. 2022; Gressel and Dodds 2013). According to the findings of one investigation based on plant proteomic and metabolomic responses to metal stress that mainly highlight the processes that crop plants use to withstand and detoxify metal stress, such as the overexpression of certain proteins and metabolites that chelate metals, boost antioxidant defences, and maintain cellular balance (Anani et al. 2022). This research also highlights that phytochelatins, metallothioneins, and certain transporter proteins are some of the methods that are used to keep metals out of cellular processes that are sensitive and make it easier for them to be stored or thrown out of the cell (Anani et al. 2022).

Phenomics, one of the important omics analyses in the field of hormesis which examines phenotypic qualities at different scales (from the cell to the whole plant), is crucial because it allows us to see and measure these reactions, connecting the dots between the molecular alterations and the visible traits (Rico-Chávez et al. 2022). A study that was based on phenomic and metabolomic analysis discovered that the low-Cd rice cultivar (TY816) improved its tolerance to Cd-induced oxidative stress through a number of different strategies (Liu et al. 2021). These strategies included adjusting the architecture of the root system, modifying the turnover of membrane lipids, and releasing secondary metabolites for the purpose of preventing lipid peroxidation and metal chelation (Liu et al. 2021). By employing image-based phenotyping and sophisticated sensors, scientists are capable of identifying hormetic fluctuations in growth patterns, physiological processes (e.g. photosynthesis and transpiration), and morphology (Raza et al. 2023; Rico-Chávez et al. 2022). This integrative omics approach provides a holistic understanding of plant hormetic effects and suggests ways to improve crop resilience and yield under environmental stress (Raza et al. 2023).

Future Prospective

Environmental agencies such as the World Health Organization (WHO), the United States Environmental Protection Agency (US EPA), and the Bureau of Indian Standards (BIS) establish a threshold limit for each heavy metal beyond which these heavy metals are considered toxic (Dhiman et al. 2023; Karthik et al. 2022; Shuja 2016). However, these non-essential HMs, such as cadmium, lead, mercury, and arsenic, which were once thought toxic but are nowadays included in the group of beneficial elements. These beneficial elements have been emerging as a surprising source for growth and development and also in regaining the ability to assist the plant in withstanding a variety of stresses, both biotic and abiotic. Non-essential HMs such as arsenic, lead, mercury, cadmium, etc., are relatively new to the list of beneficial elements, yet, research indicating their favourable influence has been available for quite some time. Despite this, their use is not as valuable and widely acceptable as essential HMs. However the results of these recent studies have encouraged scientists and researchers to learn more about these beneficial HMs and keep looking for other unusual toxic elements that might also be beneficial. Such kinds of toxicants will probably join the group of beneficial elements in the future. In addition, there are many new areas of focus in the field of phyto-hormesis research, such as trace element-induced phyto-hormesis, molecular mechanisms of phyto-hormetic responses, chemical genomics, plant chemical biology, and microbial phyto-hormesis.

The implementation of the hormesis phenomena in the agriculture sector has the potential to transform future methods for increasing the productivity and resilience of food crops. The more we learn about how low doses of stressors affect plants, the more we will understand and accept controlled stress as a useful tool in crop management. Hormetic dosages of heavy metals and other agricultural chemicals have the ability to improve crop quality and productivity while simultaneously making crops more resistant to pests and diseases (Vázquez-Hernández et al. 2019; Vargas-Hernandez et al. 2017). By carefully monitoring the exposure of crops to these stressors, we are able to harness the eustress, also known as the beneficial stress, to induce desirable traits or advantageous features in food crops (Vázquez-Hernández et al. 2019). These traits include the synthesis of specialized metabolites or improved stress tolerance in plants, which allows us to optimize the growth conditions and output of these crops (Aguirre-Becerra et al. 2021).

To better understand hormesis, future research should aim to increase our understanding of the underlying genomic, transcriptomic, proteomic, phenomic, miRNAomics, and metabolomic alterations under lower doses of stressors. To figure out such complicated molecular processes that allow plants to do well in controlled stress situations, we will need to use advanced data analysis and interpretation (Rico-Chávez et al. 2022). To improve crop performance in a sustainable way, we need to learn how to activate the plant's natural defensive systems by applying specific stress levels. To summarize, the future of research on plant hormesis holds a great deal of potential for the revolutionary transformation of agricultural methods. We can improve food security and sustainability on a global scale by discovering innovative ways to make stress work for our crops, through the strategic use of stressor components or chemicals. This will lead to higher yields, better quality, and greater resilience.

The exact and complete detailed explanatory mechanism through which HMs generate plant hormesis is still in its infant stages. It is necessary to clarify the mechanistic regulatory processes in which these milder concentrations of

HMs or other chemical toxicants are involved in plant condition, growth, photosynthesis, and development to determine their potential stress-relieving effects. Such a goal will not be attainable without additional research done on the morphological, physiological, and biochemical parameters. If such additional research is not done, then it will not be possible to completely explore these HMs'/metalloids'/any other chemical toxicant's regulatory molecula- level mechanistic processes with respect to enhancing plant growth, resistance, and productivity. In the same way, we do not fully understand how different plant species can tolerate different HMs or any other chemical toxicants, as the HMs or toxicants concentration varies greatly between plant species and also there is a variation in the plant morpho-physio-biochemical end points evaluated. For this reason, morphological, physiological, biochemical, and finally molecular-level detailed study is essentially important for a better understanding of the mechanisms behind HMs-induced plant hormesis. In addition to this, the exact levels of these hazardous HMs that are beneficial/stimulatory to the plant body are not completely understood. Moreover, this beneficial/stimulatory level in plants can also be affected by the features of the substrate (soil or any other media) on which they are grown.

The importance of ROS in plants' various biological processes and stress responses is widely understood. However, not much is known about ROS homeostasis or induced levels of ROS in particular kinds of cells, organelles, or tissues when they are exposed to low levels of toxicants. To help better understand the mechanisms of phyto-hormesis, the development of new methods that are capable of effectively analysing ROS levels under low levels of HMs will be of immense help. Also, sensitive redox proteomics methods are being developed to shed light on how proteins control the production and removal of ROS in living beings.

Conclusion

In this review, an ample number of reports have been examined, and the majority of those scientific reports have produced positive results, but there are still certain knowledge gaps that need to be filled to cultivate a complete understanding of HMs or other toxicants-induced plant hormetic responses. Moreover, the available literature on HM-induced hormetic response is quite limited. This is because in the past (during the first half of the twentieth century), scientific communities only partially correctly characterized the dose–response concept (Calabrese 2005a, b). They were right about how plants responded to high doses of HMs, but wrong about the most important plant response at low doses of HMs. Although in the current scenario, some progress has been made, further research is needed to clearly and completely understand the lower doses of HMs or other toxicants-induced plant responses at all levels (i.e. morphological, physiological, biochemical, and molecular). Furthermore, laboratory-based morphological, biochemical, and physiological methodologies were considered the basis of studying the details of plant hormesis and its mechanistic aspects. Thus, there is still a great deal of work to be done in this area to understand the morphological, physiological, biochemical, and, finally, molecular mechanisms of HM-induced phytohormetic responses under lower dosages of HMs. Furthermore, these HMs, now included in the category of beneficial elements, will continue to be a contentious issue until additional literature information showing their absolute significance in improving the plant's chance of survival is released publicly. Until then, the topic will remain contentious.

Environmental Implication

HMs are hazardous in nature, but the lethality of HMs was determined by how much concentration of HMs was consumed by the organism. Additionally, as a matter of fact, low to moderate levels of heavy metal contamination more frequently occurs in nature than unrealistically high to excessive higher concentrations, which are often impractical. So, studying how plants react to low levels of heavy metals, i.e. hormetic growth stimulatory mechanism, is crucial. Plant morphological, physiological, and biochemical experimental studies can help to achieve this goal. These studies further help in understanding a complete picture of the molecular mechanistic pathways that are linked with a minor dosage of heavy metal-induced plant hormetic responses.

The effects and risks on the environment of heavy metal-induced hormesis are big, and they change how we evaluate risks to both human health and the environment. Hormesis is biphasic, which makes ecological risk assessments more complicated because the good effects of low doses may hide the risks of higher doses, which makes it harder to set regulatory threshold limits (Schalie and Gentile 2000). Additionally, as a result of species-specific responses, even low concentrations of heavy metals can upset ecological balances, which in turn impacts biodiversity and the dynamics of ecosystems (Poschenrieder et al. 2013). It is necessary to give careful consideration to environmental management and public health policies to properly reduce potential dangers due to the dual nature of hormetic reactions, which are beneficial at low concentrations and dangerous at large doses.

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Declarations

Conflict of interest The authors declare that they have no competing interests.

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