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### Mini Review

## Hormetic Dose Response as the Paradigm of Plant Response to Stress

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### Abstract

The paradigm of the response of a biological organism to exposure to stressor agents is hormetic dose response, in which high doses of a stressor are toxic or harmful but low doses are beneficial. The exploitation of this biological characteristic could enable the efficient use of plants in the fields of phytoremediation and agriculture.

### INTRODUCTION

Life on earth is surrounded by many challenges constantly creating disturbances in the sensitive, dynamic equilibrium a living organism inherently possesses and the delicate mutual relationship between the living being and its environment. The challenges may come in the form of biotic stressors such as pathogenic microorganisms or abiotic factors such as drought arising from environmental perturbations. Thanks to cellular homeostasis, the internal system of an organism is well designed to sense changes in its environment, to adapt to stress situations and to restore the stable internal environment.

Unlike animals, higher plants, cannot escape from their surroundings, as they are sessile, thereby their interactions with their growth environment which may present stress factors such as water deficiency and toxicity and how the plants respond to the stress conditions are critical. In order to grow

under stressful conditions, plants need to adapt themselves to their growth environment that exposes them to stress factors, through a series of molecular responses to cope with the adverse conditions. The integration of many transduced events into a comprehensive network of signalling pathways forms the basis of the physiological processes for the molecular responses, which enable the plants to adapt to the adverse conditions. Plant hormones may act in conjunction with other signals to regulate cellular processes such as division, elongation and differentiation. Since stress factors are also major ecological factors influencing the ecosystem, the mutual concerted relationship between plants and the environment which presents the cues or stimuli for the plants to evolve molecular mechanisms of stress signalling pathways is fundamental. The plant signalling pathways and sensor network as adaptive mechanisms to environmental stress are crucial in the contexts of agricultural environment and sustainable development [1,2].

Reactive oxygen species (ROS) are produced in the presence of oxygen as a product of cellular metabolism, but exposure to any stress factor results in the excessive production of ROS which may result in oxidative stress which is a deleterious process. Despite their destructive activity, ROS are also able to trigger a cascade of events that leads to conferment of tolerance to various environmental stresses [3]. More often than not, this renders an organism the capability to resist tougher challenges. Here dose is the criterion that determines whether exposure to stress promotes destruction or resilience [4]. Biphasic dose-response (hormesis), in which high doses of a substance/stressor agent are toxic/harmful but low doses are beneficial, forms the basis for the adaptive responses of a living organism to stress conditions [4-6]. Biphasic responses have been reported in organisms ranging from bacteria to human, but to date, 'hormesis' has been primarily associated with only human toxins [4]. To date, only a limited number of studies on the occurrence of hormesis in plants have been conducted. An understanding of the relationship between hormesis and biological plasticity of plants is of importance in improving crop yield under stressful conditions and the efficiency of phytoremediation, which is a low input biotechnology approach to clean up contaminated soils and waters. This paper reviews the potential and newly emerging application of hormesis underpinning the adaptive responses of plants to stressful conditions, in the fields of agriculture and phytoremediation.

## OXIDATIVE STRESS RESPONSES IN PLANTS

Under normal conditions ROS are formed in plant cells during the electron transport activities in the chloroplast and mitochondria or as a by-product of various metabolic activities localized in different cellular compartments [7-11]. Environmental stresses such as drought, salinity, chilling, chemical toxicity, UV radiation and pathogens disrupt cellular homeostasis and lead to an excessive production of ROS in plant cells. At high concentrations ROS are harmful to plants and would lead to oxidative stress and programmed cell death [3]. In a study carried out on *Arabidopsis thaliana*, cell death was demonstrated in leaves of the plants grown on Murashige and Skoog (MS) medium supplemented with 0.5mM phenanthrene [12]. The exposure of *Arabidopsis* leaves to phenanthrene was shown to induce localized hydrogen peroxide ( $H_2O_2$ ) production [12] which is known to mediate cell death. Additionally, Zacchi *et al.* (2000) [13] had shown that the greater abundance of ROS than that of the reducing equivalents in fungal cells caused gross disorganisation of cellular ultra-structure. On the other hand, the electron micrographs of the roots of tall fescue (*Festuca arundinacea*) grown in drought and naphthalene-contaminated ( $0.8 \text{ g kg}^{-1}$  sand dw [dry weight]) environment illustrated distortions in the root cortex [14]. While these also suggest either programmed cell death or gross disorganization of cellular structure in stressed plant roots, the distorted cortex cells were similar in appearance to lysigenous aerenchyma formation. Here lysigenous aerenchyma denotes air spaces in a soft plant tissue formed by lysis triggered by deficiency of oxygen to facilitate gas diffusion within the tissue.

It is important to note that ROS also have a role as secondary messengers/ signalling molecules promoting adaptive response

in biological organisms. The delicate equilibrium between ROS production and scavenging determines whether ROS will act as damaging or signalling molecule [3]. Evolving effective antioxidant defence responses is critical in resisting oxidative stress that inversely correlates with lifespan in a variety of organisms [15] including plants.

The protective effects of soluble sugars against oxidative stress have been widely reported in the literature [16-19]. In addition to functioning as antioxidants, sugars at high concentrations (sucrose, fructans, sugar-like compounds) may directly scavenge ROS derived from excess  $H_2O_2$  entering the vacuole [19], producing sugar radicals. A study conducted by Balasubramaniyam and Harvey (2014b) [20] on tall fescue showed that the abundance of glucose, galactose, UDP-glucose, ribose, sucrose and trehalose was significantly higher in naphthalene-treated roots when compared to the controls. The high increase of glucose concentration in contaminated plant roots shown in the study of Balasubramaniyam and Harvey (2014b) [20] particularly highlight the importance of glucose signalling and ROS scavenging in plant defence against oxidative stress. Sucrose is required for the production of anthocyanins which play an important role in ROS scavenging and antioxidant defence [15]; hence the increased levels of sucrose in treated roots would effectively contribute to the stress tolerance [20].

ROS also plays a role in gravitropism and it has been demonstrated that scavenging of ROS by antioxidants inhibited gravitropism [21]. In a study conducted by Balasubramaniyam and Harvey (2014 a) [22] and Balasubramaniyam *et al* (2015) [14], tall fescue roots grown in sand contaminated with petroleum crude oil ( $10.8 \text{ g kg}^{-1}$  sand dw) or naphthalene ( $0.8 \text{ g kg}^{-1}$  sand dw) showed deviations from normal root orientation response to gravity, turning away from the contaminated soil matrix back into the top layer of clean sand, indicating scavenging of ROS by antioxidants.

A strong dependence of plants on photosynthesis when the roots are exposed to stress has been illustrated in the study of Balasubramaniyam *et al* (2015) [14] that showed that the shoot growth was not affected in 3 weeks old tall fescue grown in naphthalene-contaminated sand ( $0.8 \text{ g kg}^{-1}$  sand dw) whereas their root growth was severely inhibited when compared to the controls. The roots exposed to the toxic chemicals were able to grow into the contaminated matrix without restrictions at later stages and the scanning electron and fluorescence micrographs of these roots revealed enhanced thickening in the endodermis and greater suberization [14,20], whereas the expression of the tentatively identified compound indole acetic acid (IAA) was subdued in the stressed root and shoot tissues [20]. Since  $H_2O_2$ , an ROS, is a substrate for enhanced lignification that leads to enhanced thickening and greater suberization [3] as well as peroxidase catalysed IAA oxidation [23-26], the results of these studies demonstrate adaptive responses of plants to oxidative stress. Here the greatly thickened endodermis and suberized exodermis could also be plant root adaptations, helping with prevention of toxic contaminants from reaching the inner core of the roots [14], whereas the IAA oxidation could be related to a contaminant-detoxification pathway [25].

## HORMETIC RESPONSES IN PLANTS

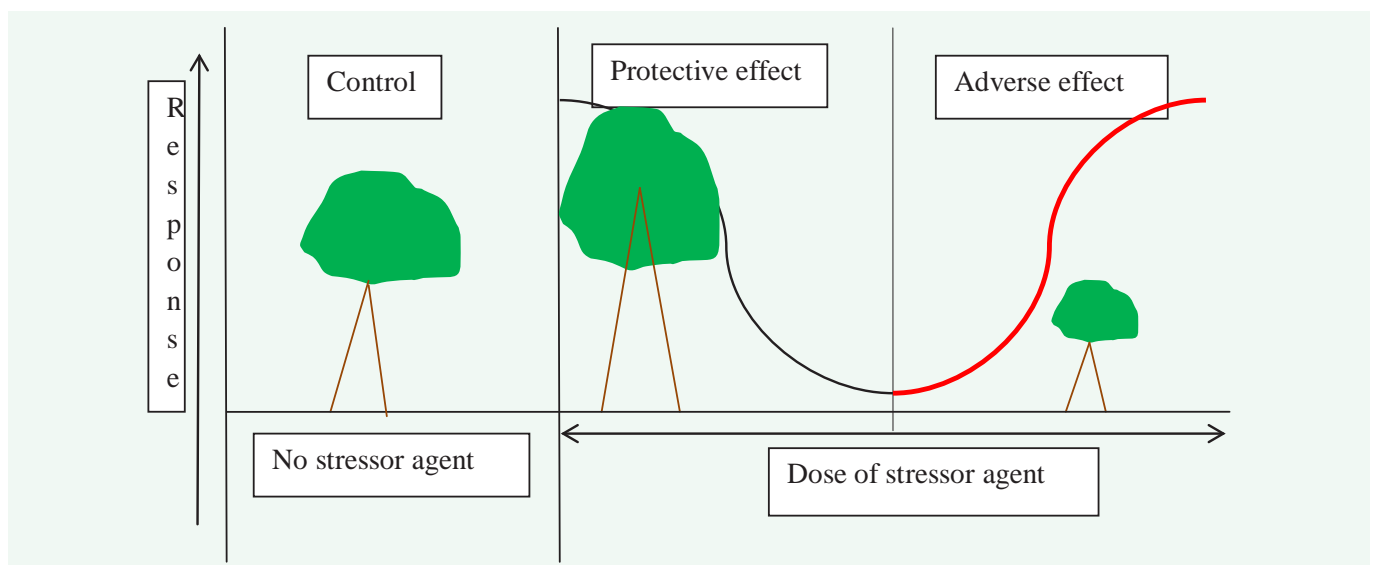
Herbicide-related hormesis has been demonstrated by many authors [27-36]. Cedergreen *et al.* (2007) [36] demonstrated hormesis in four species: the aquatic plant **Lemna minor**, the micro-alga **Pseudokirchneriella subcapitata** and the two terrestrial plants **Tripleurospermum inodorum** and **Stellaria media** exposed to nine herbicides and one fungicide and a mixture of both. Their study demonstrated that both the frequency and the magnitude of the hormetic response depended on the endpoint being measured: dry weight at harvest showed a higher frequency and a larger hormetic response compared to relative growth rates. Viewed from an evolutionary perspective, a trade-off between traits to minimise fitness reduction could be expected of hormetic responses in plants [36]. Limiting the extent of cell wall thickening in response to contaminant exposure by developing alternative contaminant barriers such as shedding root hairs and possessing an increased cortex zone was evident in tall fescue roots exposed to crude oil contamination in the study of Balasubramaniyam and Harvey (2014a) [22], reflecting a balance between prevention of contaminant entry and admittance of the desired substances such as water and nutrients across the endodermis into the steel, which is the central core of the root consisting of the vascular tissue and associated supporting tissue, and this too demonstrates a trade-off between traits.

Furthermore, Huang *et al.* (1991) [37] demonstrated smaller and fewer metaxylem vessels in seminal wheat roots exposed to high temperature (40°C) and showed that the stressed plants resisted drought stress at later stages, and this count as a hormetic response. Moreover, the study of Balasubramaniyam *et al.* (2015) [14] showed that tall fescue grown in naphthalene-treated sand which presented a drought environment for the plants resisted drought stress after the acclimatisation period of three months better than the control plants. In this study, the naphthalene-treated roots contained a well-developed

exodermis which was absent in control roots at the same position behind the root tip, and this could have conferred drought resilience to naphthalene-treated plants [14]. Jupp and Newman (1987) [38] reported that a well-developed exodermis, if in place in grass roots, prevents cortex cells from drying out from water deficit conditions. Additionally, tall fescue roots exposed to naphthalene contamination that also confers drought stress to plants contained a greater abundance of trehalose [20], a disaccharide that retains water retention properties and is accountable for the resurrection of *Selaginella* which grows in desert and mountainous areas [39]. Furthermore, a microcosm study carried out to determine the effect of oil sands effluent on cattail and clover showed an accumulation of novel dehydrins, stress proteins that protect plants against drought in the plants grown in the impacted site [40].

The study by Balasubramaniyam *et al.* (2015) [14] also showed that tall fescue roots exposed to naphthalene stress withstood uptake of Nile red, a hydrophobic, fluorescent dye beyond the endodermis, demonstrating resistance to hydrophobic xenobiotic uptake into the xylem that represent the predominant route for shoot-ward movement of contaminants. The ability of plant roots to withhold harmful substances from entering the root xylem protects the process of photosynthesis from being disturbed.

Moreover, the results of the study by Balasubramaniyam and Harvey (2014b) [20] indicate that the shoot tissues of naphthalene-treated plants are protected from chemical toxicity, whilst echoing some of the oxidative stress responses of their roots such as under-expression of IAA and the presence of fructans. Vacuolar fructans has the function of stabilising cell membranes under stress conditions [15], hence stabilizing leaf cell membrane against oxidative stress whereas foliar IAA degradation in treated plants could suggest response to ROS accumulation in treated shoots, presumably due to the root to shoot communication via stress-mediated sugar signalling pathways [20].



**Figure 1** Illustration of hormetic responses of plants. Exposure to low-doses of a stressor agent produces a postulated protective response, enabling the plant to resist tougher challenges (middle). Increased-doses produce an oppositely postulated adverse response (right). Adapted from Hayes, 2007 [1].

Calabrese et al. [4] documented that low levels of toxins or other stressors produce beneficial effects by triggering the production of defence molecules within the organism and once formed, these defence molecules not only deal with the immediate threat but also increase resistance to other threats. Tall fescue grown in naphthalene-contaminated sand showed remarkably well-expressed hormetic responses such as resilience to drought stress and restrictions to the entry of xenobiotic uptake [14], indicating promising applications of 'hormesis' to the fields of phytoremediation and agrochemistry.

The application of 'hormesis' can be of use in overcoming drought which is one of the most serious world-wide problems for agriculture and is looming by day. Intermittent exposure to moderate water stress could induce changes in the biochemical pathways in plants, making them adapted to grow effectively in drought conditions. Allowing plants to evolve changes in biochemical pathways and gene composition to suit the drought conditions will take time, and some plants may not be able to survive the stress. Still, the surviving plants could become greatly adapted to not only moderate drought stress but other severe stresses too.

However, the genetic composition, i.e. the species of plant is crucial in taking advantage of 'hormesis' in phytoremediation and agriculture. This is evident in the study of Balasubramaniyam (2012) [41] that showed the dose of petroleum hydrocarbon contamination (10.8 g kg<sup>-1</sup> sand dw) that triggered adaptive/stimulatory responses in tall fescue was damaging for parsnip, carrot, beetroot and brown top bent.

## CONCLUSIONS

Plants are exposed to many challenges arising from exposure to stressors in their growth environment. Certain plants are able to overcome the stress below a certain threshold level. The hormetic responses of plants to stress help overcome not only the stress the plants are exposed to, but help the plants withstand tougher challenges as well. The application of hormesis merits attention in making plants more drought resistant and in the safe and efficient use of plants in phytoremediation.

## REFERENCES

- Hayes DP. Nutritional hormesis. *Eur J Clin Nutr.* 2007; 61: 147-159.
- Wu G, Shao HB, Chu LY, Cai JW. Insights into molecular mechanisms of mutual effect between plants and the environment. A review. *Agron Sustain Dev.* 2007; 27: 69-78.
- Sharma P, Jha AB, Dubey RS, Pessarakli M. Reactive oxygen species, oxidative damage, and antioxidative defense mechanism in plants under stressful conditions. *J Bot.* 2012.
- Calabrese EJ, Bachmann KA, Bailer AJ, Bolger PM, Borak J, Cai L, et al. Biological stress response terminology: Integrating the concepts of adaptive response and preconditioning stress within a hormetic dose-response framework. *Toxicol Appl Pharmacol.* 2007; 222:122-128.
- Rattan SIS, Le Bourg E. Hormesis in Health and Disease. Rattan SIS, Le Bourg E, editors. CRC Press; 2014.
- Le Bourg E, Rattan SI. "Is hormesis applicable as a pro-healthy aging intervention in mammals and human beings, and how?" Introduction to a special issue of Dose-Response. *Dose Response.* 2009; 8: 1-3.
- Foyer CH, Harbinson J. Oxygen metabolism and the regulation of photosynthetic electron transport. In: Causes of photooxidative stresses and amelioration of defense systems in plants. Foyer CH, Mullineaux P, editors. Boca Raton (Fla): CRC Press; 1994.
- Foyer CH. Oxygen metabolism and electron transport in photosynthesis. In: Molecular biology of free radical scavenging systems. Scandalios J, editor. (NY): Cold Spring Harbor Laboratory Press; 1997. pp. 587-621.
- del Río LA, Sandalio LM, Corpas FJ, Palma JM, Barroso JB. Reactive oxygen species and reactive nitrogen species in peroxisomes. Production, scavenging, and role in cell signaling. *Plant Physiol.* 2006; 141: 330-335.
- Blokhina O, Fagerstedt KV. Reactive oxygen species and nitric oxide in plant mitochondria: origin and redundant regulatory systems. *Physiol Plant.* 2010; 138: 447-462.
- Heyno E, Mary V, Schopfer P, Krieger-Liszka A. Oxygen activation at the plasma membrane: relation between superoxide and hydroxyl radical production by isolated membranes. *Planta.* 2011; 234: 35-45.
- Alkio M, Tabuchi TM, Wang X, Colón-Carmona A. Stress responses to polycyclic aromatic hydrocarbons in Arabidopsis include growth inhibition and hypersensitive response-like symptoms. *J Exp Bot.* 2005; 56: 2983-2994.
- Zacchi L, Morris I, Harvey PJ. Disordered ultrastructure in lignin-peroxidase-secreting hyphae of the white-rot fungus *Phanerochaete chrysosporium*. *Microbiology.* 2000; 146 : 759-765.
- Balasubramaniyam A, Chapman MM, Harvey PJ. Responses of tall fescue (*Festuca arundinacea*) to growth in naphthalene-contaminated sand: xenobiotic stress versus water stress. *Environ Sci Pollut R.* 2015.
- Bolouri-Moghaddam MR, Le Roy K, Xiang L, Rolland F, Van den Ende W. Sugar signalling and antioxidant network connections in plant cells. *FEBS J.* 2010; 277: 2022-2037.
- Weber AP, Schwacke R, Flügge UI. Solute transporters of the plastid envelope membrane. *Annu Rev Plant Biol.* 2005; 56: 133-164.
- Solfanelli C, Poggi A, Loreti E, Alpi A, Perata P. Sucrose-specific induction of the anthocyanin biosynthetic pathway in Arabidopsis. *Plant Physiol.* 2006; 140: 637-646.
- Ritsema T, Brodmann D, Diks SH, Bos CL, Nagaraj V, Pieterse CM, et al. Are small GTPases signal hubs in sugar-mediated induction of fructan biosynthesis? *PLoS One.* 2009; 4: e6605.
- Van den Ende W, Valluru R. Sucrose, sucrosyl oligosaccharides, and oxidative stress: scavenging and salvaging? *J Exp Bot.* 2009; 60: 9-18.
- Balasubramaniyam A, Harvey PJ. Changes in the abundance of sugars and sugar-like compounds in tall fescue (*Festuca arundinacea*) due to growth in naphthalene-treated sand. *Environ Sci Pollut Res Int.* 2015; 22: 5817-5830.
- Joo JH, Bae YS, Lee JS. Role of auxin-induced reactive oxygen species in root gravitropism. *Plant Physiol.* 2001; 126: 1055-1060.
- Balasubramaniyam A, Harvey PJ. Scanning electron microscopic investigations of root structural modifications arising from growth in crude oil-contaminated sand. *Environ Sci Pollut Res Int.* 2014; 21: 12651-12661.
- Fry SC. Cross-linking of matrix polymers in the growing cell walls of angiosperms. *Annu Rev Plant Physiol Plant Mol Biol.* 1986; 37:165-186.
- Grambow HJ. Pathway and mechanism of the peroxidase catalysed degradation of indole-3-acetic acid. In: Greppin H, Penel C, Gaspar T, editors. Molecular and physiological aspects of plant peroxidases. University of Geneva (Switzerland): 1986; 31-41.
- Machackova I, Ullmann J, Krekule J, Opatrny Z. Comparison of in

- vivo IAA decarboxylation rate with in vitro peroxidase, IAAoxidase activities. Bandurski RS, Krekule J, Kutacek R, editors. In: Physiology and biochemistry of auxins in plants. Academia (Praha): 1988; 87-91.
26. Gaspar T, Penel C, Hagege D et al. Peroxidases in plant growth, differentiation and development processes. Lobarzewski J, Greppin H, Penel C, Gaspar T, editors. In: Biochemical, molecular and physiological aspects of plant peroxidases. University of Geneva (Switzerland). 1991; 249-280.
27. Ries SK, Chmiel H, Dille DR, Filner P. The increase in nitrate reductase activity and protein content of plants treated with simazine. Proc Natl Acad Sci U S A. 1967; 58: 526-532.
28. Wiedman SJ, Appleby AP. Plant growth stimulation by sublethal concentrations of herbicides. Weed Res. 1972; 12: 65-74.
29. Pulver EL, Ries SK. Action of simazine in increasing plant protein content. Weed Sci. 1973; 21: 233-7.
30. Strbac VD, Ayers GS, Ries SK. Protein fractions in chemically induced high-protein wheat seed. Cereal Chem. 1974; 51:316-323.
31. Schabenberger O, Kells JJ, Penner D. Statistical test for hormesis and effective dosage in herbicide dose-response. Agron J. 1999; 91: 713-721.
32. Nelson A, Renner KA, Hammerschmidt R. Effects of protoporphyrinogen oxidase inhibitors on soybean (*Glycine max* L.) response, *Sclerotinia sclerotiorum* disease development, and phytoalexin production by soybean. Weed Technol. 2002; 16: 353-359.
33. Davies J, Honegger JL, Tencalla FG, Meregalli G, Brain P, Newman JR, et al. Herbicide risk assessment for non-target aquatic plants: sulfosulfuron--a case study. Pest Manag Sci. 2003; 59: 231-237.
34. Wagner R, Kogan M, Parada AM. Phytotoxic activity of root absorbed glyphosate in corn seedlings (*Zea mays* L.). Weed Biol Manag. 2003; 3: 228-232.
35. Cedergreen N, Streibig JC, Spliid NH. Species specific sensitivity of aquatic macrophytes towards herbicides. Ecotoxicol Environ Safety. 2004; 58: 314-23.
36. Cedergreen N, Streibig JC, Kudsk P, Mathiassen SK, Duke SO. The occurrence of hormesis in plants and algae. Dose Response. 2006; 5: 150-162.
37. Huang BR, Taylor HM, McMichael BL. Effects of temperature on the development of metaxylem in primary wheat roots and its hydraulic consequence. Ann Bot. 1991; 67:163-166.
38. Jupp AP, Newman EI. Morphological and anatomical effects of severe drought on the roots of *Lolium-perenne* L. New Phytol. 1987; 105: 393-402.
39. Higashiyama T. Novel functions and applications of trehalose. Pure Appl Chem. 2002; 74:1263-1269.
40. Crowe AU, Han B, Kermode AR, Bendell-Young LI, Plant AL. Effects of oil sands effluent on cattail and clover: photosynthesis and the level of stress proteins. Environ Pollut. 2001; 113: 311-322.
41. Balasubramaniyam A. Root adaptive responses of tall fescue (*Festuca arundinacea*) growing in sand treated with petroleum hydrocarbon contamination [dissertation]. University of Greenwich (Kent): University of Greenwich, 2012.

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