Plant Science 212 (2013) 15–25

Contents lists available at ScienceDirect

Plant Science

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

Review

Do toxic ions induce hormesis in plants?

Charlotte Poschenrieder*, Catalina Cabot, Soledad Martos, Berta Gallego, Juan Barceló

Lab. Fisiología Vegetal, Facultad Biociencias, Universidad Autónoma de Barcelona, E-08193 Bellaterra, Spain

ARTICLE INFO

Article history:
Received 17 April 2013
Received in revised form 14 July 2013
Accepted 30 July 2013
Available online 8 August 2013

Keywords:
Acclimation
Antioxidant
Defense
Hormesis
Metal ion
Toxicity

ABSTRACT

The concept of hormesis in plants is critically reviewed, taking growth stimulation by low concentrations of toxic trace elements as a reference. The importance of both non-adaptive and adaptive mechanisms underlying ion-induced hormetic growth responses is highlighted. The activation of defense mechanisms by metal ions and pathogenic elicitors and the cross talk between the signals induced by metal ions and biotic stressors are considered. The production of reactive oxygen species and, consequently, the induction of stress-induced antioxidants, are key mechanisms in metal ion-induced hormesis in plants. It is concluded that in the current scientific literature, hormesis is used as an "umbrella" term that includes a wide range of different mechanisms. It is recommended that the term hormesis be used in plant toxicology as a descriptive term for the stimulated phase in growth response curves that is induced by low concentrations of toxic metal ions without evidence of the underlying mechanisms. If the mechanisms underlying the stimulated growth phase have been identified, specific terms, such as *amelioration*, *defense gene activation*, *priming* or *acclimation*, should be used.

Contents

1. Introduction

As early as the 16th Century, Paracelsus recognized that the toxicity of a substance depends on the dose and that low doses of toxic substances can have therapeutic effects. An illustrative example of this was the use of small quantities of mercury to treat syphilis, although unsuccessfully. The positive actions of low doses of poisons were further explored in the 19th century by the psychiatrist Rudolph Arndt, the pharmacologist Hugo Schulz, and the bacteriologist Ferdinand Hueppe; the phenomenon was introduced into the scientific literature under the name of "Arndt-Schulz law" or "Hueppe's rule". The first record of the word hormesis is a manual annotation in the Ph.D. thesis of Chester Southam in 1941. The word comes from the ancient Greek word hormesis meaning "setting into motion" or "to boost something". Southam and Ehrlich [1] then used the term hormesis in an article published in the journal *Phytopathology* to describe the increased growth rates of wood-decaying

* Corresponding author at: Lab. Fisiología Vegetal, Edificio C, Facultad Biociencias, Universidad Autónoma de Barcelona, 08193 Bellaterra, Spain. Tel.: +34 935812163.
E-mail address: charlotte.poschenrieder@uab.es (C. Poschenrieder).

0168-9452/$ – see front matter © 2013 Elsevier Ireland Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.plantsci.2013.07.012

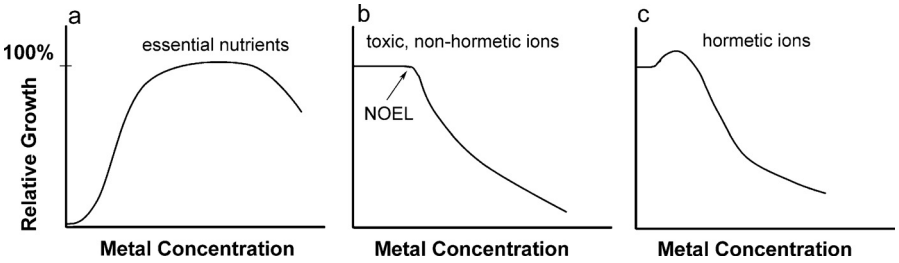

Fig. 1. Concentration–growth response curves: (a) response to essential elements displaying growth stimulation for increasing concentrations in the deficient range, followed by optimal performance under sufficient supply and reduced performance when exposed to supraoptimal concentrations; this is typical for both macro and micronutrients, (b) for non-essential elements with a tolerable concentration range; beyond the threshold for toxicity growth is inhibited, and (c) hormetic response in the form of an inverted U-shaped growth curve for low concentrations of a non essential, toxic, trace element. Ions of non essential elements (e.g. Hg, Cd, Cr, Al, As) can originate either type *b* or type *c* curves, depending on the experimental conditions.

fungi when treated with diluted extracts of cedar heartwood. They further provided a general definition of hormesis as follows: "The term hormesis (adj. hormetic) is proposed to designate such a stimulatory effect of sub-inhibitory concentrations of any toxic substances on any organism" [2]. Later, the concept was sporadically used in other contexts, mainly human toxicology, medicine, or radiation biology, to describe the stimulatory effects of low doses of toxic substances. Multiple investigations have indeed shown such effects in many different biological systems, including plants [3,4].

Numerous vivid discussions about the importance of hormetic responses in toxicology and risk assessment can be followed in scientific papers and in the media, particularly during the last 15 years. It is assumed that hormesis is an adaptive response to stress. According to Calabrese and Baldwin [4], the stimulation response can be seen as "an adaptive compensatory process following an initial disruption in homeostasis" In addition to this adaptive overcompensatory hormesis, Calabrese et al. also defined so-called direct stimulation hormesis [5,6]. This direct stimulation does not imply a disruption of homeostasis, but rather, according to the authors, can be considered adaptive and may be due to toxicant–receptor interactions. In contrast, others considered that receptor-mediated biphasic growth responses that do not correspond to a disruption in homeostasis and overcompensation should not be related to hormesis [7]. The term hormesis has been stretched even further when focused on medicine and human toxicology to include the terms autoprotection and physiological and chemical preconditioning [5]. Recently, hormesis has been implicated as a means of retarding age-related effects. According to this theory, aging of an organism or cell is associated with decreased function of the maintenance and repair mechanisms. Challenging or entraining these mechanisms by mild stress can delay aging. The authors apply the term hormesis to describe this stimulating or strengthening effect of the mild stress treatment [8]. The term eustress has been used in both human or animal and plant stress physiology to designate mildly stressful treatments with positive stimulatory effects [9]. Short periods of eustress clearly contribute to the fitness of plants under subsequent, more severe stress (priming or acclimation) and reduce mortality. However, particularly in monocarpic plants, even mild stress is frequently related to escape strategies that advance flowering followed by programmed senescence [10].

Recently, in a further attempt to convert the classical descriptive term of hormesis into a mechanistically based concept, it was proposed that hormesis be considered an adaptive response that is "providing a quantitative estimate of biological plasticity" [11]. The continuous evolution of the term hormesis, particularly in the context of medicine and human health, has strayed from the original concept of hormesis in plant research, where it was initially coined. Extracting the term hormesis from its descriptive context of a dose–response curve and attempting to fit it into a mechanistic context by assimilating the term to the concepts of adaptive and receptor-mediated responses may give the false impression that the mechanisms underlying all hormetic growth responses are clearly identified and that all of the stimulatory effects of low concentrations of toxic substances are due to adaptive mechanisms.

Hormetic growth stimulation has frequently been observed in plants exposed to low concentrations of non-essential, toxic metal ions [3]. Dose–response curves (Fig. 1) of the hormetic type have been reported for Cd, Cr, Al, and Pb, among others, as well as for non-metallic trace elements, such as As and Se. The view that this growth stimulation is due to an adaptive compensatory process is highly attractive in view of the current knowledge in the field of stress signaling cross talk. Metal ions can act as elicitors of defense responses that in turn can stimulate the growth of plants, particularly under stress conditions. However, in most of the studies in which stress-induced growth stimulation was observed and hormesis in the sense of an adaptive response was claimed, the molecular and physiological mechanisms responsible for the stimulatory response were not analyzed. This is particularly the case in studies of metal ion toxicity in plants.

Not all of the growth-stimulating effects of low concentrations of toxic trace elements imply an adaptive response. This review provides a critical examination of the different mechanisms that may underlie the growth stimulation by toxic metals and trace elements without an essential function in higher plants. Three main modes of actions will be distinguished (Fig. 2), as follows:

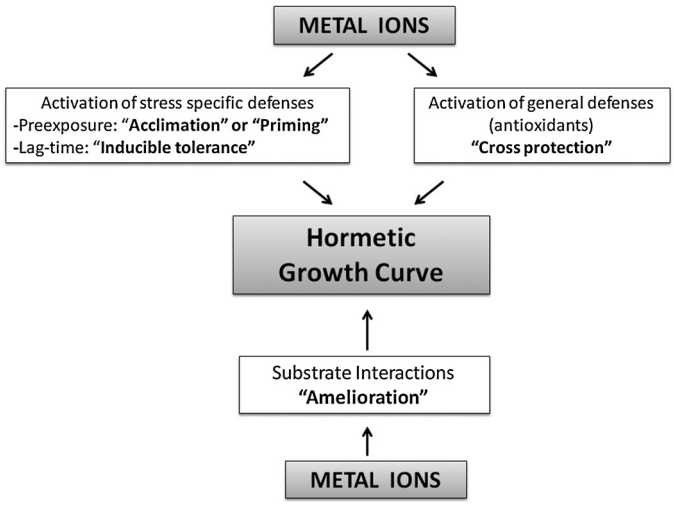

Fig. 2. Main mode of actions of toxic metal ions leading to hormetic growth responses.