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Can hormesis of plant-released phytotoxins be used to boost and sustain crop production?

Tasawer Abbas [a, *], Muhammad Ather Nadeem [a], Asif Tanveer [a], Bhagirath Singh Chauhan [b]

[a] Department of Agronomy, University of Agriculture, Faisalabad, 38040, Pakistan
[b] The Centre for Plant Science, Queensland Alliance for Agriculture and Food Innovation (QAAFI), The University of Queensland, Gatton/Toowoomba, Queensland 4343/4350, Australia

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ABSTRACT

A great deal of work has been done to explore the hormetic potential of various herbicides to enhance crop growth and yield. However, the growth stimulatory potential of plant-released phytotoxins at low rates to enhance crop yield has not yet been realized, as most of the research has focused on the herbicidal potential of these phytotoxins. However, hormesis of plant-released phytotoxins is a more practical aspect, as these are present at low concentrations in field conditions. These phytotoxins are biodegradable and safe for the environment, and have the potential for crop enhancement both under controlled and field conditions. Low doses of plant-released phytotoxins have been reported to enhance crop growth by up to 50% under controlled conditions, and crop yield by up to 42% under field conditions. In this review, we have discussed hormesis of plant-released phytotoxins with examples. In addition, we discuss the potential for crop enhancement, the influence of different factors on the expression of hormesis, as well as the potential for both undesirable (in weeds) and desirable hormesis (in crop plants). The use of plant-released phytotoxins as growth regulators is also discussed, focusing on sustainable crop production. In future, phytotoxins may be utilized as a crop stimulator to enhance crop yield, especially in organic crop production systems.

Contents

1. Introduction . . . 69
2. Hormetic potential of natural plant phytotoxins . . . 70
   2.1. Maximum stimulation caused by natural plant phytotoxins . . . 70
   2.2. Phytotoxin-specific differences in stimulatory response . . . 70
   2.3. Plant and trait-specific differences in stimulatory response . . . 71
   2.4. Time-specific differences in stimulatory response . . . 72
3. Role of hormesis in plant enhancement under stress conditions . . . 72
4. Undesirable hormesis of natural phytotoxins in weeds . . . 73
5. Hormesis in crops: caused by use of plant phytotoxins as natural herbicides . . . 73
6. Application of plant phytotoxins as growth regulators . . . 73
7. Conclusions . . . 74
References . . . 75

1. Introduction

Low dose stimulatory responses of toxicants have long been

* Corresponding author.
E-mail address: tagondaluaf@gmail.com (T. Abbas).

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observed. Paracelsus, who is widely considered to be the father of toxicology, said that "poison is in everything, and no thing is without poison; the dosage makes it either a poison or a remedy" (Duke et al., 2006). The low dose stimulatory effect of toxicants is known as hormesis (Calabrese, 2005). It is important to note that this definition of hormesis does not state whether the hormetic effect is beneficial or harmful to the organism, only that it is stimulatory for the parameter that is being measured (Calabrese and Baldwin, 2002). Although stimulatory responses of toxicants were acknowledged earlier, the term hormesis was first used in 1943, for the stimulatory effect of low doses of an extract of western red-cedar heartwood (*Juniperus virginiana* L.) on certain fungi (Southam and Erlich, 1943). The extract was inhibitory at higher doses. Stimulatory responses to low doses of toxicants (hormesis) have been observed in almost all groups of organisms, including fungi, bacteria, higher plants, and animals (Calabrese, 2005).

Plant phytotoxins (allelochemicals) are secondary metabolites released by a variety of organisms, including fungi, viruses, and plants, which influence the surrounding organisms (Torres et al., 1996). Effects of these phytotoxins may be stimulatory or inhibitory (Torres et al., 1996). Most plant phytotoxins (allelochemicals) produce inhibitory effects at higher concentration and stimulate growth when used at lower concentration (Li Liu et al., 2003). These substances are non-nutritional in nature and can be produced in any plant part, such as bark, leaves, stems, roots, and seeds. Many plants have high phytotoxic potential to successfully manage crop pests, including weeds, insects, and diseases (Farooq et al., 2011a). Considerable literature is available to prove the phytotoxic potential of natural plant-released phytotoxins (Farooq et al., 2011a, 2013).

Recently, various reports have been published that explore the hormetic responses of different crops to lower doses of herbicides (Belz et al., 2011; Abbas et al., 2015). However, very little information is available on the hormetic effects of plant phytotoxins (allelochemicals). Most of the existing studies explore the inhibitory effects of plant phytotoxins against various crops and pests (Farooq et al., 2011a; Abbas et al., 2014). This is because of dose-response designs that rarely include the dose of plant phytotoxins expected to create hormesis. The inhibitory effects of plant phytotoxins occur at higher concentrations (Cheema and Khaliq, 2000; Farooq et al., 2011a; Abbas et al., 2014). Under field conditions, plant phytotoxins are present at very low concentrations. Hormesis of plant phytotoxins has higher practical potential as compared to their inhibitory potential. Concentrations that are normally used in bioassays cannot be produced under field conditions, even after the incorporation of allelopathic crop residues into the soil. Therefore, it is probable that plant phytotoxins exist at very low concentrations in agricultural fields to produce hormesis (Belz et al., 2005). Thus, it is practical to study low dose responses of plant phytotoxins, rather than artificially high concentrations. Furthermore, plant phytotoxins offers a valuable alternative to herbicides for use in crop production, as these are natural products, highly degradable and safe for human health and the environment (Dayan et al., 2009; Roeleveld and Bretveld, 2008).

Although stimulatory effects (hormesis) of plant phytotoxins on crops and weeds have been researched for years, and for different traits, such as plant growth, biomass production, protein content, and stress resistance, the stimulatory potential of plant phytotoxins to boost plant growth and yield has received comparatively little attention. Because of the predicted gap between global food demand and the availability of agricultural land, the importance of crop enhancement is increasing, and so too the need for new technologies like toxicant-induced hormesis (Cedergreen et al., 2009). Although allelopathy is known to have a significant role in crop protection, weed invasion, and the structure of plant communities, contemporary approaches that explore natural plant phytotoxin-induced crop stimulation are limited. In this review, we present the hormetic potential of plant phytotoxins, factors influencing hormetic stimulation, and current examples of hormesis caused by low doses of plant phytotoxins that are toxic at higher doses. Additionally, we discuss the role of plant-released phytotoxins in enhancing crop growth under various stress conditions (temperature, nutrient, salt, drought, and plant competition stresses), possibilities for undesirable hormesis in weeds, and desirable hormesis in crop plants. The use of plant-released phytotoxins as growth regulators is focused on sustainable crop production. The results presented are from experiments conducted under controlled laboratory and glasshouse conditions, as well as under uncontrolled field conditions. This is the first review article written on the hormetic potential of plant-released phytotoxins, and it may provide new research directions for use of these phytotoxins in sustainable crop production.

2. Hormetic potential of natural plant phytotoxins

In considering the potential of plant phytotoxins for crop enhancement, the key questions are a) whether the maximum stimulatory response is large enough to be considered, and b) whether linking crop enhancement with crop protection has additional advantages for crop production.

2.1. Maximum stimulation caused by natural plant phytotoxins

Across all fields of science, types of organisms and toxins investigated, hormesis produces on average 30–60% stimulation in the control (Calabrese, 2008, 2010; Belz et al., 2011). The literature reveals that plant phytotoxins can cause up to 50% growth stimulation in different crops under controlled conditions (Table 1), and significant stimulation of growth and yield under field conditions (Table 2). For example, leaf extracts of moringa (*Moringa oleifera* L.) enhanced the growth of tomato, peanut, corn and wheat at the early vegetative growth stage, and increased their yields by 20–35% (Fuglie, 2000). The magnitude of hormetic growth stimulation for various measured crop traits depends upon the time of application, type and concentration of plant phytotoxins (Table 1).

2.2. Phytotoxin-specific differences in stimulatory response

Few studies are available on stimulatory responses of plant-released phytotoxins. However, various studies on inhibitory effects of different plant phytotoxins reveal that the inhibitory response of tested plants was dependent on the type of plant phytotoxins (Manandhar et al., 2007; Farooq et al., 2011a,b). In the studies reviewed, the magnitude of growth inhibition varied between toxic compounds, with some having no significant impact on growth. For example, Abbas et al. (2014) studied inhibitory effects of five aquatic weeds against wheat (*Triticum aestivum* L.). It was concluded that the phytotoxins released by these weeds elicited specific responses in wheat, and a differential rate of inhibition was shown in wheat. In a recent study, a 3% water extract of sorghum (*Sorghum bicolor* L.), maize (*Zea mays* L.), rice (*Oryza sativa* L.) and moringa was applied alone, and in combination, to enhance growth of maize (Kamran et al., 2016). It was observed that the phytotoxins released by these crops were not equally effective in the initiation of stimulatory responses in morphological and yield traits (Table 3). The explanation for this differential potential of plant phytotoxins to induce crop stimulation (hormesis) is most probably associated with the mechanism of action through which the growth stimulants are produced. Studies addressing phytotoxin-specific hormetic responses of plant-released phytotoxins are absent in the