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Review

Biostimulant activity of phosphite in horticulture

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ABSTRACT

Phosphite (Phi), a reduced form of phosphate (Pi), is emerging as a novel biostimulator in horticulture. Though there is still no consensus on its physiological function as a P-source for plant nutrition, experimental evidence has shown that Phi can act as a biocide and affect plant production and productivity. Positive effects of Phi on plant metabolism are more evident when applied to the roots in hydroponic systems or to the leaves in the form of foliar sprays in the presence of sufficient Pi. Published research conclusively indicates that Phi functions as an effective pesticide against various species of pathogenic bacteria and Oomycetes. Nonetheless, the use of Phi as a sole P-source for plant nutrition is still at issue. When Phi is applied to the soil, it comes into contact with microorganisms, which mediate the oxidation of Phi to Pi. Thus, by this indirect method, Phi can become available to the plant as a P nutrient after microbial oxidative reactions. Interestingly, efforts to generate transgenic plants harboring microbial genes that enable plants to use Phi as a sole P-source have opened up new avenues for the use of this P-containing compound for plant nutrition. Nowadays, Phi is emerging as a potential inductor of beneficial metabolic responses in plants, as it has demonstrated its effectiveness against different stress factors and has improved crop yield and quality. Advances in molecular, biochemical, and physiological approaches have confirmed the role of Phi in improving both yield and quality of different horticultural species. Although important progress has been made in the field of Phi uptake, transport and subcellular localization, a more in-depth understanding of the fundamental processes behind the effects of Phi on plant metabolism is still lacking. In this review, we outline the current advances in research on the impact of Phi as a novel biostimulant for horticultural production and discuss some strategies being used to improve the yield and quality of important crop species. Moreover, we address the challenges and opportunities related to Phi use in horticulture.

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1. Introduction

As part of the nucleic acids DNA and RNA, the phospholipids in cell membranes, and the key energy nucleoside ATP, phosphorus (P) plays a pivotal role in genetic heredity, membrane structure, signal transduction pathways, and metabolism, and is therefore considered essential to all forms of life existing on Earth, including both lower and higher plants (Ashley et al., 2011; Butusov and Jernelöv, 2013). In agriculture, P, compared to other major nutrients, is by far the least mobile and least available to crop plants under most soil conditions (Ramaekers et al., 2010).

It has been widely demonstrated that phosphate (Pi) is the sole P-containing nutrient important for optimal plant growth and development (López-Arredondo et al., 2014). Nevertheless, over the past three decades, phosphite (Phi; $H_2PO_3^-$) or its conjugate phosphorous acid (H_3PO_3), a reduced form of Pi, has increasingly been used as a pesticide, supplemental fertilizer, and biostimulant. As a biostimulant, Phi has been proved to improve nutrient uptake and assimilation, abiotic stress tolerance and product quality. Moreover, Phi promotes root growth, yield and nutritional value of horticultural crops. Furthermore, Phi is largely used for controlling pathogens and in many countries it is registered as a fungicide and bactericide. Though this Pi analogue is used as an alternative fertilizer, its contribution to P nutrition is limited and it has been the subject of controversy.

The extensive use of Phi and its related products in agriculture has raised considerable debate in the technical and scientific worlds (McDonald et al., 2001; Thao and Yamakawa, 2009), especially since its effects are not fully understood yet. While Phi has proved to be effective in controlling important plant diseases caused by Oomycetes, particularly the genera *Peronospora*, *Plasmopara*, *Phytophthora* and *Pythium* (Lobato et al., 2008, 2010; Silva et al., 2011; Burra et al., 2014; Dalio et al., 2014; Brunings et al., 2015; Groves et al., 2015) and some bacteria (Lobato et al., 2010, 2011; Aćimović et al., 2015), it does not provide P nutrition for higher plants (Thao and Yamakawa, 2009; Loera-Quezada et al., 2015), and therefore cannot be used as a proper fertilizer in agriculture. Instead, recent evidence points to Phi having a role as an enhancer of different metabolic processes in plants, such as improvement of yield and quality, as well as responses to environmental cues. Some processes mediated by Phi as a biostimulator are shown in Tables 1 and 2.

Moor et al. (2009) found that the application of Phi does not affect strawberry growth or yield compared to traditional Pi fertilization, although it does increase the quality of the fruits by activating the synthesis of ascorbic acid and anthocyanins. Similarly, Estrada-Ortiz et al. (2013) found beneficial effects of Phi on strawberry fruit quality and induction of plant defense mechanisms (Estrada-Ortiz et al., 2011, 2012), which has also been reported by Rickard (2000) in several crop species and cultivars. Likewise, Glinicki et al. (2010) reported beneficial effects of Phi on the growth parameters of three strawberry cultivars.

On the other hand, applying Phi to plant roots in the presence of sufficient Pi may result in synergic effects between Pi and Phi, promoting the absorption of phosphorus into plants (Bertsch et al., 2009), and suppressing the negative effects of Phi itself (Varadarajan et al., 2002), which confirms that the effects of Phi depend strongly on the phosphorus state of the plant (Thao and Yamakawa, 2009). Herein, we review the current status of the knowledge concerning the use of Phi as a biostimulant in horticulture, including its role as a novel elicitor of molecular, biochemical, and physiological responses to stress agents, with special focus on yield, harvest quality, and abiotic stress responses.

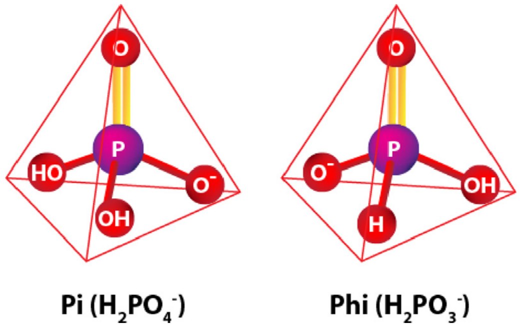

Fig. 1. Three-dimensional chemical structures of phosphate ($H_2PO_4^-$; Pi) and phosphite ($H_2PO_3^-$; Phi) forming tetrahedral structures.

2. Chemical properties and characteristics of phosphite (Phi)

At pH values near neutrality, the dominant P species according to equilibrium calculations are: $H_2PO_4^-$ and HPO_4^{2-} for phosphate, $H_2PO_3^-$ and HPO_3^{2-} for phosphite, and $H_2PO_2^-$ for hypophosphite. This speciation is based on the following pK_a values: for phosphate, pK_a1 = 2.1, pK_a2 = 7.2, and pK_a3 = 12.7; for phosphite, pK_a1 = 1.3 and pK_a2 = 6.7; and for hypophosphite pK_a1 = 1.1 (Corbridge, 1995; Hanrahan et al., 2005). The charge of each species defines the reactions that in turn may affect its mobility and distribution. Furthermore, the detection of a given chemical species is determined by its level of protonation (McDowell et al., 2004; Hanrahan, 2012).

Phosphite ($H_2PO_3^-$) is an isostere of the phosphate anion ($H_2PO_4^-$), in which one of the oxygen atoms bonded to the P atom is replaced by hydrogen (Varadarajan et al., 2002) (Fig. 1). Phi may also be referred to as phosphorous acid or phosphonate, though the term phosphonate is used to mean a wide range of compounds containing carbon–phosphorus (C—P) bonds like fosetyl-Al (McDonald et al., 2001; Metcalf and van der Donk, 2009).

In the Phi molecular structure, a hydrogen atom replaces an oxygen one. This substitution results in significant differences affecting the behavior of both molecules in plants. According to McDonald et al. (2001), in Pi, the P atom is located at the center of a tetrahedral molecular geometry, with the oxygen atoms distributed at the points of the structure. The charge on the ion is distributed evenly among these four oxygen atoms so that the whole structure is entirely symmetrical from the four faces of the 3D structure. In Phi, the P atom is also at the center of a tetrahedron, although the molecule loses the symmetry observed in Pi. Both the shape of the molecule and the charge distribution seem to influence the binding of Pi to its interacting enzymes. Once Pi has bound to an enzyme, the remaining oxygen emerges from the surface, and thus becomes available to react with other molecules in the reaction catalyzed by the enzyme. Phi only has one face of the tetrahedron relatively similar to all the faces of the Pi 3D structure, so if it is to bind to the surface of an enzyme that normally binds Pi, it must bind at this face. When Phi binds to the enzyme surface in this orientation, it is the hydrogen atom bonded to the P atom that emerges from the enzyme surface, not an oxygen atom as in Pi. Thus, Phi cannot participate in the same biochemical reactions as Pi. Therefore, due to these unique structures and considering the difference in charge distribution of the two anions, most enzymes involved with phosphoryl transfer reactions readily discriminate between Phi and Pi (Plaxton, 1998). However, some plant and yeast proteins appear to recognize Phi as Pi. These proteins include membrane Pi transporters, as well as the Pi-sensing-machinery (McDonald et al., 2001), which allow plants and yeasts to detect and respond to cellular Pi depletion at the molecular level (Varadarajan et al., 2002). According to Plaxton and Carswell (1999), Phi might modulate the