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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.

Contents

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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.

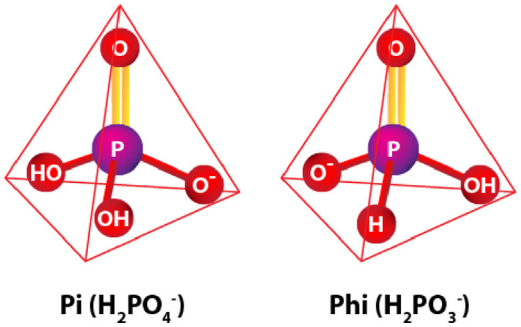

Fig. 1. Three-dimensional chemical structures of phosphate ($H_2PO_4^-$; Pi) and phosphite ($H_2PO_3^-$; Phi) forming tetrahedral structures.

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

signal transduction pathway responsible for the detection of, and response to internal Pi levels. If so, Phi could potentially be used as a tool to manipulate and study the regulation of this pathway in higher plants, which indeed has been demonstrated by Schroetter et al. (2006) and López-Arredondo and Herrera-Estrella (2012).

Phosphorous acid (H_3PO_3) and its Phi-salts contain higher concentrations of P (39%) than traditional phosphate-based (H_3PO_4) fertilizer (32% P). Phi-salts are usually more soluble than their analogous Pi-salts, making leaf and root Phi-uptake more efficient. This fact must be taken into consideration in order to tightly regulate Phi applications, since excessive dosages of Phi can be toxic to plants.

Phosphite undergoes a gradual transformation after addition to soil, either by biological or non-biological oxidation. Soil microorganisms (i.e., bacteria and cyanobacteria) are able to assimilate Phi and release Pi, gaining energy and nutrients during this biological conversion (Varadarajan et al., 2002). Thanks to soil microbial activity, Phi oxidation to Pi lasts approximately 3–4 months. In fact, Lovatt and Mikkelsen (2006) reported that the conversion of phosphite to phosphate after foliar applications may result from slow chemical oxidation or by oxidizing bacteria and fungi that have been found in plant leaves, while non-biological oxidation of phosphite may also occur gradually, but at a slower rate.

Therefore, since soil microorganisms are able to assimilate and metabolize phosphite, the impact on plant physiology of Phi applied to the soil solution in field crops is affected by such biological processes and Phi may not directly impact plant metabolism as a proper P-source.

Just recently, Loera-Quezada et al. (2015) revealed that three microalgae species (*Chlamydomonas reinhardtii*, *Botryococcus braunii* and *Ettlia oleoabundans*) are unable to use Phi as a sole P-source. Therefore, these findings demonstrate that both lower and higher plants lack the mechanisms to metabolize Phi. The only way that plants can use Phi as a P-source is through the expression of a bacterial phosphite dehydrogenase, as has been reported for *Arabidopsis* and tobacco (López-Arredondo and Herrera-Estrella, 2012), which open up new opportunities to use Phi as a P-source in P-nutrition approaches. However, this approach has not been applied in crop fields at commercial level yet.

For many years, studies of the biogeochemistry of P have been hampered by a lack of analytical tools to delve into the speciation of phosphorus at environmental concentrations (Benitez-Nelson, 2015). Fortunately, new methodologies and instruments are now providing insights into this nutrient cycle (Kizewski et al., 2011; Karl, 2014; Van Mooy et al., 2015), and will ultimately further our understanding of the contribution of phosphonate and phosphite to the global P cycle.

3. Uptake, transport and compartmentalization of phosphite in plant cells

Both phosphate (Pi) and phosphite (Phi) are considered to be acquired by plants via Pi transporters (Varadarajan et al., 2002; Jost et al., 2015). Though Pi transporters are primarily involved in Pi uptake (Guest and Grant, 1991; Ullrich-Eberius et al., 1981), they also participate in Phi acquisition, most probably through both high- and low-affinity transport systems (d'Arcy-Lameta and Bompeix, 1991; Danova-Alt et al., 2008; Jost et al., 2015).

In higher plants, four families of Pi transporter genes (named *Pht1*, *Pht2*, *Pht3*, and *Pht4*) encoding 19 protein products (i.e., Pht enzymes) have been identified and some of them characterized (López-Arredondo et al., 2014; Shen et al., 2014). For instance, the Pht1 family includes plasma membrane proteins involved in the uptake of Pi from the soil solution and the redistribution of Pi within the plant, and members of this family function as $H_2PO_4^-/H^+$ symporters (Smith et al., 2003) and as Phi transporters too (Ticconi et al., 2001; Varadarajan et al., 2002; Nussaume et al., 2011).

Pht enzymes catalyze processes of Pi uptake, translocation and homeostasis and are found not only in roots but also in above ground parts of the plants. Indeed, Nussaume et al. (2011) indicated that the Pi transporter gene families are active both in root and leaf tissues, and therefore Pi and Phi can be taken up both via nutrient solutions applied to the roots in hydroponic systems and sprays applied to the leaves. In fact, Ruthbaum and Baille (1964) found that Phi is highly water soluble and less prone than Pi to adsorb to soil particles, which makes it more accessible to plants (Jost et al., 2015). Because of its higher solubility, Phi is more rapidly absorbed and translocated within the plant than Pi (Ratjen and Gerendas, 2009).

Of the 19 Pht Pi transporters, those encoded by the *Pht1* gene family are predominantly active in epidermal cells and in the outer cortex of the root. These proteins are part of the so-called direct Pi uptake pathway and transport P as Pi anions, mainly $H_2PO_4^-$ and HPO_4^{2-}, against a concentration gradient between the soil solution (which typically contains 0.1–10 μM Pi) and the cytoplasm of the root epidermal cell (which typically contains 5–10 mM Pi) (Raghothama and Karthikeyan, 2005).

Though most *Pht1* transcripts have been located in root epidermal cells and root hairs, some of them have also been found in leaves, stems, cotyledons, pollen grains, seeds, flowers, and tubers in different plant species, suggesting their involvement not only in Pi uptake by roots but also in internal root-to-shoot distribution (Nussaume et al., 2011; López-Arredondo et al., 2014).

In contrast to *Pht1* genes, members of the *Pht2*, *Pht3*, and *Pht4* gene families have been mainly associated with Pi distribution within sub-cellular compartments, and their gene products are specifically located in the plastid inner membrane (Cubero et al., 2009), mitochondrial inner membrane (Guo et al., 2008), and Golgi compartment (Versaw and Harrison, 2002), respectively. In *Arabidopsis*, the chloroplast-located low-affinity transporter Pht2;1, a protein product encoded by a member of the *Pht2* gene family, is involved in the Pi transport into the plastids and Pi allocation throughout the whole plant. Although the Pht2 family of transporters is also present in crop plants, compelling evidence of its function in those plants is still in its infancy. Interestingly, mitochondrial Pi transporter genes have also been identified in soybean, maize, and rice (Takabatake et al., 1999). Nevertheless, further research is also needed to determine their particular physiological functions and to evaluate their potential as biotechnological tools to improve the use of both Pi and Phi.

According to López-Arredondo et al. (2014), the concerted action of Pht proteins ensures Pi distribution to specific sites within the plant. Consequently, naturally occurring or engineered alterations of Pht proteins expression provide an opportunity to optimize uptake and proper distribution of Pi within the plant to improve yield. Since Phi is an analogue of Pi and is considered to be transported by Pht enzymes, those alterations of Pht expression may also stimulate given metabolic pathways, including a more efficient use of Phi as an alternative metabolic inductor either applied to the roots in the nutrient solution or in the form of foliar sprays. Interestingly, López-Arredondo and Herrera-Estrella (2012) developed a dual fertilization and weed control system by generating transgenic plants that can use Phi as a sole P-source. Under greenhouse conditions, these transgenic plants demanded up to 50% less P-input when fertilized with Phi to bring about similar productivity to that achieved by the same plants using Pi-fertilizer; moreover, when competing with weeds, biomass accumulation was up to 10 times greater than when fertilized with Pi. The use of this novel system could be considered as an integrative approach to be implemented in the low-Pi-tolerant genotypes that have already been developed (López-Arreadondo et al., 2014).

Table 1
Beneficial effects of phosphite (Phi) as a biostimulator in vegetable crops.

Crop	Phosphite source (dosage)	Method of application	Improved trait/s	Reference
Celery	Phosphorous acid	Foliar spray	Yield	Rickard (2000)
Lettuce	Phosphorous acid (50% of total P as Phi)	Nutrient solution in hydroponics	Biomass dry weight, foliar area and P content in the whole plant	Bertsch et al. (2009)
Onion	Phosphorous acid	Foliar spray and soil application	Percentage of jumbo size onions	Rickard (2000)
Potato	Phosphorous acid	Foliar spray	Size and yield of US No. 1 grade potatoes	Rickard (2000)
Potato	Potassium phosphite	Foliar application	Phytoalexin and chitinase content, and yield maintenance	Lobato et al. (2011)
Potato	Potassium phosphite	Sprays applied to seed tubers and foliage	Reinforcement of the cell wall and defense response	Olivieri et al. (2012)
Potato	Potassium phosphite	Liquid solution applied to tubers	Emergence, early growth and mycorrhizal colonization	Tambascio et al. (2014)
Potato	Potassium phosphite	Foliar spray	Chlorophyll content, protection against UV-B light and activation of the antioxidant system	Oyarburo et al. (2015)
Sweet pepper	Phosphorous acid	Drip irrigation and foliar spray	Size and yield of US No. 1 grade peppers	Rickard (2000)
Tomato	Phosphorous acid (50% of total P as Phi)	Nutrient solution in hydroponics	Biomass dry weight, foliar area and P content in the whole plant	Bertsch et al. (2009)

Note: Most studies were based on the application of commercial Phi-containing products without clear indication on the labels of their precise Phi content. Therefore, Phi dosage in the table is only indicated when precise data are available in the cited articles.

Schroetter et al. (2006) reported that foliar applications of KH_2PO_3 caused higher Pi contents in the whole plants, which may be due to a partial oxidation of incorporated Phi to Pi in plant tissues. Non-biological oxidation of Phi to Pi may also occur gradually *in planta*, although at a slower rate in comparison to Phi applied to the soil during fertilization (Adams and Conrad, 1953; Orbovic et al., 2008).

Phosphite has been found to display systemic effects and high chemical stability in plant tissues, though it also shows great mobility throughout the whole plant. This mobility facilitates the penetration and transport of the foliar-applied Phi to the rest of the plant, including the roots (Smillie et al., 1989; Brunings et al., 2015).

Once Pht proteins are activated, Phi is rapidly absorbed and translocated within the plant (Guest and Grant, 1991) and uptake kinetics reveals a swift acquisition and translocation of Phi in all plant tissues (Schroetter et al., 2006). The uptake of Phi is pH dependent and subject to competition by Pi (Ouimette and Coffey, 1990). Furthermore, mobility of Phi in both xylem and phloem is similar to that of Pi (Ouimette and Coffey, 1989).

Remarkable progress has also been made in characterizing the Pi transporters in several economically important plant species, including tomato, potato, soybean, rice, barley, and maize (López-Arredondo et al., 2014). The properties of these transporters have been studied in several expression systems and significant divergence among genotypes has been found. The different reported affinities and expression patterns probably reflect diverse functional roles such as uptake from the soil as opposed to translocation or remobilization of stored Pi within the plant (Nussaume et al., 2011; Ceasar et al., 2014).

According to Danova-Alt et al. (2008), Phi accumulates in both the cytosol and an acidic compartment, most likely the vacuole. Interestingly, the presence of Pi enhances Phi sequestration in the vacuole. Therefore, as postulated by Thao and Yamakawa (2009), plants with an adequate P status can tolerate moderate Phi exposure without visible toxicity symptoms. Nonetheless, it has to be taken into account that such tolerance depends not only on the P nutrient status of the plant, but also on the Phi level applied. In contrast, Pratt et al. (2009) showed that Phi accumulates massively in the cytosol and prevents Pi efflux from the vacuole, while subsequent incorporation of Pi into the cells triggered a massive transfer of Phi from the cytosol to the vacuole. This inhibition of Pi efflux from the vacuole may worsen Pi-starvation symptoms and lead to accelerated programmed cell death in Pi-starved plants (Singh et al., 2003; Jost et al., 2015). Moreover, Berkowitz et al. (2013) observed a constant combined tissue concentration of Phi + Pi in Phi-treated plants across a wide range of external concentration ratios, suggesting a mechanism integrating Pi and Phi concentrations and regulating the homeostasis in both shoot and root tissues.

Pi-starved cells predominantly accumulate Phi in the cytoplasm, and it appears that Phi import into the vacuole is a non-favored process under such conditions. Conversely, in Pi-preloaded cells, Phi accumulates almost exclusively in vacuoles. This condition favors the vacuolar uptake of both Pi and Phi. However, with the same extracellular concentration of both substances, the vacuolar signal intensities of Pi and Phi show a much greater accumulation of Pi than Phi (Danova-Alt et al., 2008). Consequently, different regulatory elements responsible for the transport of Pi and Phi from the cytoplasm to the vacuole may be postulated. While the reason for vacuolar uptake of Pi is Pi storage, Phi uptake could be representing a pathway for detoxification of xenobiotic Phi. Thus, it became clear that the metabolic state of the cells and the Pi supply had a strong influence on the subcellular localization of Phi (Martinoia et al., 2000). This could also affect the mechanisms of interaction between Phi and Pi signaling and possibly the Pi-starvation response under different P-feeding conditions (i.e., sufficiency, starvation, resupply, or preloading) (Danova-Alt et al., 2008).

Recently, Zhao et al. (2013) revealed that application of inorganic P solution (56% phosphorous oxyanion and polyoxyanion solution, containing mono- and dipotassium salts of phosphorous acid) alleviated P limitations and improved the appearance and fruit production of huanglongbing (*Candidatus Liberibacter* spp.) infected citrus trees. In this study, new molecular mechanisms involving small RNAs (sRNA) and microRNAs (miRNA) related to P metabolism were discovered.

4. Phosphite interactions with P nutrition in plants

The similarity between Pi and Phi appears to end at the level of translocation. Because Phi is not converted into Pi in plants, it fails to enter the biochemical pathways in which Pi

Table 2
Beneficial effects of phosphite (Phi) as a biostimulator in fruit crops.

Crop	Phosphite source (dosage)	Method of application	Improved trait/s	Reference
Avocado	Phosphorous acid	Foliar spray	Yield of commercially valuable sized fruit	Lovatt (2013)
Banana	Phosphorous acid (50% P as HPO_4^{2-} and 50% as $H_2PO_3^-$)	Nutrient solution in hydroponics	Biomass dry weight, foliar area and P content in the whole plant	Bertsch et al. (2009)
Citrus	Phosphorous acid	Foliar spray	Yield and acid content in fruits	Lovatt (1998, 1999)
Citrus	Phosphorous acid	Foliar spray	Yield	Albrigo (1999)
Citrus	Phosphorous acid	Foliar spray	Yield	Rickard (2000)
Peach	Phosphorous acid	Foliar spray	Sugar and soluble solids content	Rickard (2000)
Raspberry	Phosphorous acid	Foliar spray	Fruit firmness	Rickard (2000)
Strawberry	Potassium phosphite	Plants soaked and irrigated	Fruit acidity, ascorbic acid and anthocyanin content	Moor et al. (2009)
Strawberry	Potassium phosphite (6.7% of total P as Phi)	Root application through a controlled watering system	Growth of roots and shoots	Glinicki et al. (2010)
Strawberry	Phosphorous acid (30% of total P as Phi)	Nutrient solution applied to the roots	Concentrations of chlorophylls, amino acids and proteins in leaves	Estrada-Ortiz et al. (2011)
Strawberry	Phosphorous acid (20% of total P as Phi)	Nutrient solution applied to the roots	Sugar concentration and firmness of fruits	Estrada-Ortiz et al. (2012)
Strawberry	Phosphorous acid (20–30% of total P as Phi)	Nutrient solution applied to the roots	pH, EC and anthocyanin concentration in fruits	Estrada-Ortiz et al. (2013)

Note: Most studies were based on the application of commercial Phi-containing products without clear indication on the labels of their precise Phi content. Therefore, Phi dosage in the table is only indicated when precise data are available in the cited articles.

is involved (Varadarajan et al., 2002) and, therefore, accumulation of non-metabolizable Phi in plant tissues may either cause deleterious effects (Loera-Quezada et al., 2015) or induce potentially beneficial responses. Indeed, Phi prevents the activation of many genes involved in Pi-starvation responses (Ticconi et al., 2001; Varadarajan et al., 2002), thus altering P nutrition. According to Danova-Alt et al. (2008), Phi inhibits phosphate uptake in a competitive manner and induces a range of physiological and developmental responses by disturbing the homeostasis of Pi (Kobayashi et al., 2006; Berkowitz et al., 2013). In turn, Phi uptake is strongly and competitively inhibited in the presence of Pi (Pratt et al., 2009; Jost et al., 2015). Once Phi is within the plant cell, it preferentially accumulates in sink tissues (Nartvaranant et al., 2004; Jost et al., 2015).

Plants grown in P-limited conditions are highly sensitive to Phi and display toxicity symptoms such as leaf chlorosis and stunted growth (McDonald et al., 2001; Ratjen and Gerendas, 2009; Thao and Yamakawa, 2009). Moreover, Phi can cause arrest of primary root growth, yellowing of the leaf lamina of young leaves, and a patchy accumulation of anthocyanins in older leaves (Varadarajan et al., 2002; Hanserud et al., 2014), while the respiration rates decline upon Phi treatment under P-limited conditions (Pratt et al., 2009). Furthermore, the accumulation of Phi affects the metabolism in *Arabidopsis*, leading to changes in the levels of central metabolites, most predominantly those of aspartate, asparagine, glutamate and serine (Berkowitz et al., 2013; Jost et al., 2015).

Beneficial effects of Phi on plant nutrition may be a result of soil microbial activity that oxidizes Phi to Pi (Lovatt and Mikkelsen, 2006; Loera-Quezada et al., 2015). According to Varadarajan et al. (2002), this biological conversion certainly makes Phi an important component of the global P cycle but not a direct source of P-nutrient for plants. Furthermore, Lovatt and Mikkelsen (2006) reported that soil microorganisms are able to assimilate Phi and release Pi, gaining energy and nutrient during this biological conversion.

Once in the plant, only a small part of the Phi appears to be oxidized to Pi (Schroetter et al., 2006). This is because the Phi molecule is quite stable and persists within plant tissues for months (Ouimette and Coffey, 1990), as plants lack the biochemical mechanisms to rapidly assimilate Phi.

As Phi is more soluble than Pi, the challenge now is to design efficient molecular and biotechnological approaches to enable plants to metabolize Phi. A promising system has been reported by López-Arredondo and Herrera-Estrella (2012), in which they developed transgenic plants capable of using Phi as a Pi-source. Since plants in nature lack the ability to metabolize Phi, and Phi has been proved to have negative effects in plants when applied without considering the P status, the employment of a single compound could achieve both phosphorous fertilization and weed control (López-Arredondo et al., 2014), which could be of great use in horticulture.

5. Biostimulant effects of phosphite on horticultural crops

Some of the most prominent findings on the effect of phosphite in improving horticultural crop responses, especially focused on yield, fruit quality, and tolerance to abiotic stress factors, are summarized in Tables 1 and 2.

Interestingly, we were unable to find any study in the literature identifying positive effects of Phi on flowers and ornamental species, other than controlling diseases (Banko and Hong, 2001; Shearer and Fairman, 2007; Shearer and Crane, 2012).

5.1. Vegetables

In a series of field and greenhouse trials, Rickard (2000) reported that foliar phosphite increased the yield and quality of several species, including celery, onion, potato, and pepper. For instance, celery yield was significantly increased by Phi treatment. Furthermore, the percentage of jumbo size onions was significantly greater when a combination of soil- and foliar-applied Phi was used. Similarly, the size and yield of potato was significantly greater when Phi was applied. Moreover, sweet pepper yield was significantly increased when Phi was applied either by drip irrigation or foliar spray. However, data showing that the effectiveness of Phi-derived P fertilizer is equal to or better than that of conventional Pi fertilizers may be considered uncommon (Thao and Yamakawa, 2009).

By contrast, other studies on *Brassica nigra* seedlings and *Brassica napus* culture cells (Carswell et al., 1996, 1997), as well as hydroponically-cultivated tomato and pepper (Förster et al., 1998; Varadarajan et al., 2002), indicated that Phi is not an appropriate P-source, as plants treated with Phi exhibited significant growth reduction and phytotoxicity. Therefore, more in-depth studies on

this issue are needed in order to improve our understanding of the role of Phi as a potential biostimulator of plant metabolism.

Lovatt and Mikkelsen (2006) mentioned that Phi may influence sugar metabolism, cause internal hormonal and chemical changes, and induce the shikimic acid pathway, resulting in increased floral intensity, and fruit yield and quality, such as soluble solid content, in various species including onions, potatoes and tomatoes.

In lettuce, tomato and banana, the application of Pi plus Phi (50% as HPO_4^{2-} and 50% as $H_2PO_3^-$) in a hydroponic system improved biomass dry weight, foliar area, and P content in the whole plant (Bertsch et al., 2009). However, when foliar treatments (100% P as Phi) were applied to those crops, a dramatic reduction of plant growth was observed, which was accompanied by evident deleterious effects such as worsened foliage and root deterioration.

The application of potassium Phi to seed potato tubers and foliage resulted in increased pectin content in both periderm and cortex tissue in tubers. The content and activity of polygalacturonase and proteinase inhibitors also increased in tubers from Phi-treated plants, while a new isoform of chitinase was detected in the tuber periderm of treated plants. These results suggest that Phi applied to seed tubers and foliage induces defense responses in tuber periderm and cortex and that these reactions are associated with structural and biochemical changes in these tissues (Olivieri et al., 2012).

Foliar applications of potassium Phi induced a systemic defense response in potato tubers, including an increase in phytoalexin and chitinase contents as well as enhanced peroxidase and polyphenoloxidase activities as part of the Phi-induced defense mechanism. Interestingly, no negative effects were observed in potato yield at harvest, which suggests that the energetic cost involved in the defense response activation would not be detrimental to plant growth (Lobato et al., 2011).

Tambascio et al. (2014) reported that the application of potassium Phi reduced the period between planting and emergence, and increased leaf area and dry matter. Moreover, indigenous mycorrhizal colonization increased after Phi application to seed tubers, which suggests that Phi application in crop production would be advantageous, especially for potatoes.

Similar to other plant inductors, it is assumed that Phi is effective against different types of biotic and abiotic stress, while the underlying signaling pathways probably overlap and interact. Indeed, Oyarburo et al. (2015) evaluated the effect of potassium Phi pre-treatment on UV-B stress tolerance in potato leaves and demonstrated that Phi had a beneficial effect on chlorophyll content and expression of the *chloroplast-encoded D1 polypeptide of photosystem II* gene (*psbA* gene), which encodes a key photosynthetic protein. Oxidative stress caused by UV-B was also prevented by Phi, which demonstrates that phosphite mediates UV-B stress tolerance in potato plants.

5.2. Fruit crops

Phosphite has also been used as an enhancer of fruit quality. Lovatt (1990) discovered that foliar application of potassium-Phi (K_3PO_3) to P-deficient citrus seedlings caused a biochemical response equal to that of calcium phosphate feeding and also restored plant growth. Additionally, Lovatt (1998) showed that foliar applications of K_3PO_3 to Navel orange trees significantly increased the number of commercially valuable large size fruit, while both total soluble solids and the ratio of soluble solids to acid were improved, as compared to control fruits (Lovatt, 1999). Similarly, Albrigo (1999) reported that winter pre-bloom foliar applications of Phi to Valencia oranges increased flower number, fruit set and yield, plus increased total soluble solids. Interestingly, Graham (2011) reported that Phi does not inhibit root colonization by mycorrhizal fungi but slightly enhances phosphate uptake activity by citrus mycorrhizas (Graham and Drouillard, 1999). Moreover, in citrus and avocado, a single foliar application of phosphite has been proven to increase floral intensity, yield, fruit size, total soluble solids, and anthocyanin concentrations Lovatt and Mikkelsen (2006).

Rickard (2000) summarized the results of various studies on the effect of Phi on fruit production and quality. For instance, citrus trees showed benefits in orange yield from Phi fertilization using foliar sprays. In Navel orange trials, soluble solid content and acidity, as well as fruit yield, were both improved by the use of the Phi treatment. Stone fruits also showed improvement in quality as a result of Phi foliar sprays. In peaches, both sugar and soluble solids were significantly higher in the treated fruit compared to the control. Raspberry fruit quality was also enhanced by the Phi treatment, based on measurements of greater firmness in dark red berries, a factor related to premium pricing.

According to Lovatt and Mikkelsen (2006), phosphite is most effective when the rate and the application are properly timed to match the needs of the crop, which depend on the plant genotype, phenological stages and environmental conditions (Lovatt, 2013). Furthermore, considering the differences in chemical properties between Phi and Pi, phosphite applications must be tightly regulated to avoid plant damages as a consequence of Phi toxicity.

In strawberry, Moor et al. (2009) found that Phi irrigation increased the quality of the fruits by activating the synthesis of ascorbic acid and anthocyanins. Indeed, biochemical adaptations to Pi-starvation include increased synthesis of anthocyanins (Hernández and Munné-Bosch, 2015). These water-soluble vacuolar pigments act as light attenuators, presumably to adjust photosynthetic light reactions to the Pi-dependent Calvin cycle (Ticconi et al., 2001). Additionally, anthocyanins may also act as powerful antioxidants with beneficial effects not only on plant physiology but also on human health (Zafra-Stone et al., 2007; Lo Piero, 2015). Importantly, the rate of accumulation, amount, and composition of anthocyanins vary greatly with the region of cultivation, agronomic management, and seasonal changes and their effects on growth patterns, and also with developmental patterns of different species, varieties, and plant cultivars (Steyn et al., 2002; Lo Piero, 2015). Increased synthesis and accumulation of anthocyanin in plants have been observed in response to many stress factors, such as nutrient deficiency and pathogen attack (Routray and Orsat, 2011). Accordingly, Estrada-Ortiz et al. (2011) reported that Phi applied into the nutrient solution increased free amino acids and protein contents in leaves, sugar content (Estrada-Ortiz et al., 2012) and anthocyanin content (Estrada-Ortiz et al., 2013) in strawberry fruits.

6. Commercial products containing phosphorous acid or phosphite-salts

The list of Phi products that are available in the international market includes a large number of different brands. Experimentally, the most used Phi-containing compounds have been aluminum-, ammonium- and potassium-Phi as well as phosphorous acid (Schreiner, 2010; Ávila et al., 2012, 2013; Berkowitz et al., 2013; Borza et al., 2014), whereas the active ingredients of most commercial products include aluminum-Phi, phosphorous acid, and potassium-Phi (Leymonie, 2007; Thao and Yamakawa, 2009; Kromann et al., 2012).

All of these products are formulated as alkali salts of phosphorous acid and have been registered either as pesticides, fertilizers, or stimulators of biological processes in plants. However, experimental evidence indicates that Phi's primary role is as a biostimulant and biocide, rather than as a fertilizer.

In spite of that, farmers worldwide apply Phi formulations marketed as fertilizers rather than as pesticides. This is especially profitable for the agrochemical companies selling Phi fertilizer products, as they appear to avoid spending the considerable time and budget associated with registering an agricultural pesticide (i.e., by labeling their Phi products as a P fertilizer).

Recently, the Minor Crop Farmer Alliance in the United States (MCFA, 2014) warned that the European Union (EU) has reclassified phosphite-containing compounds as pesticides only rather than as fertilizers. This evolution impacts international exports of foods to the EU that have been treated with Phi and certainly will influence the future use of Phi in horticulture worldwide.

In the case of the US, growers primarily use phosphite products as foliar fertilizers or soil drenches, rather than as a pesticide. Furthermore, the EU is relying on Maximum Residual Level (MRL) for fosetyl-Al to cover any Phi residues, regardless of the Phi source. Consequently, crops on which Phi-containing compounds are used as fungicides or fertilizers are now at risk of not complying with EU-MRL requirements. This could occur if those growers do not have registered uses of fosetyl-Al where their crops are produced, or established MRLs equivalent to current EU regulations. While the EU set a temporary MRL of 75 ppm Phi through December 2015, it will revert to low default MRLs beginning in 2016 (EFSA, 2014). Therefore, crop producers that use phosphite-containing products and ship their horticultural products to the EU should review the EU's MRLs for fosetyl-Al to assess whether they are in compliance.

7. Conclusions and perspectives

In spite of the similarities between phosphate (Pi) and phosphite (Phi), Phi is not metabolized by plant cells and may not be used as a main source of P nutrition. The reported effects of Phi as an alternative fertilizer on plant growth and yield are still at issue. Phosphite's deleterious effect on growth and production is strongly determined by the Pi status of the plants. In this paper, we have strengthened the claim that Phi can be used as a biostimulator that improves plant performance by activating molecular, biochemical and physiological responses, especially when applied in the presence of sufficient Pi. Therefore, while in some species negative effects have been reported, these effects have proved to be attenuated by administering sufficient phosphate.

The combination of phosphite with traditional phosphate fertilization may increase fruit quality, for instance, by activating the synthesis of antioxidant metabolites. Importantly, in addition to its well-recorded biocide effects against Oomycetes and bacteria, phosphite may bring to bear additional physiological effects in the plant, including increased flower and fruit set as well as better fruit quality and improved responses to environmental stimuli and stress agents. Apart from considering the Pi status of the plant, Phi efficiency is more evident when its rate and application are properly scheduled to fulfill the requirements of crop plants in order to stimulate physiological processes, which in turn depend on plant genotypes, environmental conditions, agronomic management, source and dosage of Phi to be used.

Interestingly, transgenic plants over-expressing bacterial enzymes capable of metabolizing Phi have been generated, which open up new avenues in P nutrition, including the use of Phi as a P-source for plants. Nonetheless, no commercial biotech crop harboring such recombinant proteins is available in the market. Hence, further research and innovations are needed before this approach can be introduced into the market.

A better understanding of the local and systemic signals and the mechanisms that perceive and transduce Phi signals into metabolic and morphologic responses is expected to provide novel avenues to improve horticultural production using Phi as a potential biostimulator. The molecular machinery underlying these effects remains to be elucidated.

In conclusion, Phi can provide outright stimulation to plants that might not occur with Pi. This positive effect is a certainty if an appropriate combination of Phi and Pi ions is used. However, finding the right method of application (i.e., hydroponic solution or foliar spray), source, rate, and phenological stage of Phi application for different horticultural genotypes deserves further attention.

Finally, how Phi is used as a novel biostimulant must be decided in close consultation with professionals in order to reach goals related to food quality and yields. International requirements and new regulations on the use of Phi must be taken into consideration for a proper use of Phi in horticulture.

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