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Phosphite for control of Phytophthora diseases in citrus: model for management of *Phytophthora* species on forest trees?†

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Abstract

Phosphite (PO_3^{3-}) is well known for its ability to induce pathogen and host-mediated resistance to *Phytophthora* spp. in a wide range of plants. This review addresses how phosphite moves in citrus trees, fate of phosphite when applied to soil, how phosphite controls Phytophthora infection of citrus tissues, phosphites as fungicides for control of Phytophthora diseases in citrus and their applicability for management of *Phytophthora* species on forest trees. Experimental data from citrus is presented to illustrate these properties. As an example, phosphite is rapidly taken up by leaves and highly systemic enabling phosphite applied to the tree canopy to move to fruit and provide protection against citrus brown rot of fruit caused by *Phytophthora palmivora* (Butler) Butler for several months after application. Foliar-applied phosphite also moves readily to the trunk and roots for control of collar and root rot caused by *P. nicotianae* Breda de Haan for several weeks after application. Soil application of phosphite is more effective for control of root rot than foliar applications due to higher concentrations of phosphite in roots, but soil-applied phosphite may be oxidised to phosphate by soil bacteria before root uptake. Because phosphite moves readily to metabolically active root-, shoot- and reproductive tissues, foliar-, stem- or soil applications are highly effective for the long-term, above- and below-ground protection of trees against Phytophthora infection.

Keywords: host-mediated induced resistance; phosphate nutrition; phosphite fungicides; *Phytophthora nicotianae; Phytophthora palmivora*

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Introduction

This paper reviews phosphites, their movement *in planta*, their fate in soil and their use as fungicides, particularly on citrus. Experimental data for citrus is used to illustrate these properties of phosphite and the applicability for management of *Phytophthora* species on forest trees.

What are phosphites?

Phosphorus (P) is an essential macronutrient required by all living organisms. In nature, P exists in a fully oxidised form as phosphate anion (PO_4^{3-}, Pi) and with one less oxygen as phosphite anion (PO_3^{3-}, Phi). The conjugate acid of the Phi anion is phosphorous (or phosphonic) acid (H_3PO_3). In this review, the term Phi is used to refer to the inorganic salts of phosphorous acid, and the term phosphonate is used to designate

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a Phi ester containing a carbon-phosphorus (C-P) bond. In fertiliser, P is normally found in the form of phosphoric acid (H_3PO_4) or its salts, such as triple super phosphate, ammonium phosphate, and potassium phosphate. All of these forms readily release hydrogen phosphate anions (HPO_4^{2-}) and dihydrogen phosphate anions ($H_2PO_4^-$) used by plants. In the early 1950s, Phi was evaluated as a phosphate fertiliser replacement (Rickard, 2000), and subsequently recognised as a source of slow release P as evidence developed that common soil microorganisms (bacteria, fungi, actinomycetes) use Phi as a P source and oxidise Phi to Pi (Adams & Conrad, 1953; Casida, 1960). In the 1980s, interest in Phi grew rapidly as disease control attributes of the phosphonate fungicide, aluminum tris ethyl phosphonate) (fosetyl-Al, Aliette, Bayer Crop Science, Research Triangle Park, NC, USA) and phosphorous acid were studied for induction of plant resistance, blockage of pathogen induction of disease, and direct inhibition of the pathogen (Fenn & Coffey, 1984). Renewed interest in Phi as a plant nutrient increased in the early 1990s when Lovatt (1990) discovered that P deficiency caused changes in nitrogen metabolism and that foliar application of potassium Phi to P-deficient citrus restored normal plant growth. Lovatt and Mikkelsen (2006) emphasised the balance between Phi and Pi supply to avoid plant toxicity. Furthermore, Lovatt (1999) and Albrigo (1999) reported that Phi increases floral intensity, yield, fruit size, and total soluble solids of citrus which led to the first commercialisation of potassium Phi as a fertiliser (Lovatt, 1996) under the tradename, Nutri-Phite (Biagro Western Sales, Visalia, CA, USA). Improvement in citrus fruit set and quality in response to Phi sprays are benefits accepted widely by citrus growers. However, using Phi as a source of fertiliser P continues to be controversial because of the slow conversion of Phi to Pi *in planta* (Zambrosi et al. 2011; Carswell et al., 1996). Nevertheless, many Phi fertilisers and fungicides are marketed throughout the world (Thao & Yamakawa, 2009). This review discusses the role of Phi as a fungicide that elicits pathogen and host plant responses resulting in control of Phytophthora infection of citrus and other horticultural tree crops (Guest & Grant, 1991).

How does phosphite move in citrus?

Several reports verify that Phi is readily absorbed by leaves and roots (Carswell et al., 1996; Forster et al., 1998; Schroetter et al., 2006). When applied to citrus foliage, Phi moves through the cuticle into leaves within hours and is translocated downward in the phloem to the roots within days. An example of this process is illustrated for grapefruit (Figure 1). There was little Phi in the leaves prior to foliar spray treatment but high levels were found in the leaves 25 days later. The high level of Phi in fruit 25 days after treatment indicates that Phi was moving rapidly into expanding fruit tissues. Over time, the level in Phi decreased in fruit and leaves but increased in roots. Foliar Phi does not increase Pi status or growth of P-deficient citrus seedlings over the course of 16 weeks, confirming that Phi is only slowly oxidised to Pi *in planta* (Orbovic et al., 2008; Zambrosi et al., 2011).

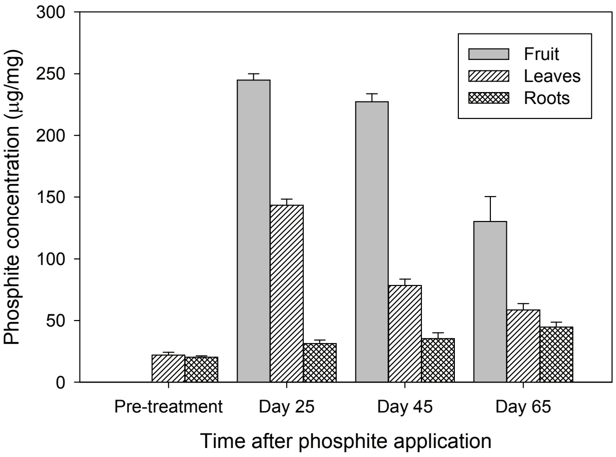

FIGURE 1: Increase in level of phosphite (Phi) in fruits, leaves and roots of 8-year-old ‘Rio Red’ grapefruit (*Citrus paradisi* Macf.) trees before and for 65 days after foliar application of potassium phosphite at a rate of 6 g a.i./1.9 L spray volume per tree in April (spring). Error bars represent the standard error of the means of 6 replicate trees. Elevated Phi in the pretreated root and leaf tissues was due to residual Phi from applications to the trees in the previous season. Thereafter, residual level of Phi in non-treated control trees was at or near zero throughout the 65-day sampling period. Tissue Phi was determined following the method described by Ouimette and Coffey (1988).

Based on the observed longevity of fungicidal activity, the rate of conversion of Phi to Pi depends on the metabolic activity of the plant, occurring over months in subtropical citrus and avocado (Guest & Grant, 1991) and up to several years in slow growing Australian woody perennials (Shearer et al., 2006). Perhaps because of long residual activity, application of Phi may result in phytotoxicity of P-deficient plants (Orbovic et al., 2008; Thao et al., 2008a,b; Zambrosi et al., 2011). Phytotoxic symptoms in citrus seedlings are associated with impaired Pi and nitrogen utilisation efficiency for growth as well as lower nutrient use efficiency in the photosynthetic process (Zambrosi et al., 2011). In contrast, Phi does not inhibit root colonization by mycorrhizal fungi and but slightly enhances phosphate uptake activity by citrus mycorrhizas (Graham & Drouillard, 1999).

Phi applied to foliage in the spring moves in the phloem from the leaves to the developing fruit and then down to roots in late spring (Figure 1). As illustrated in Valencia oranges trees (Figure 2), foliar Phi applied in

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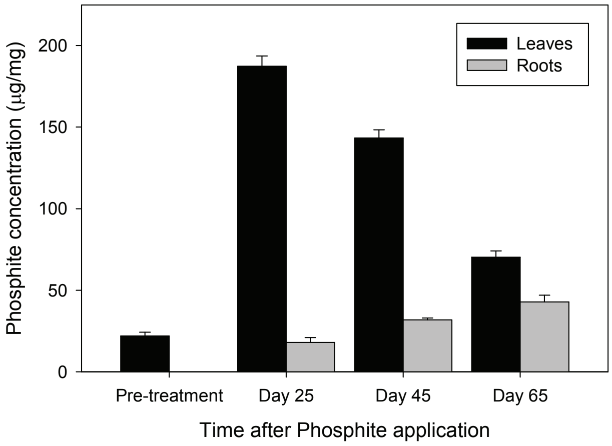

FIGURE 2: Increase in level of phosphite (Phi) in leaves and roots of 5-year-old Valencia orange (*Citrus sinensis* [L.] Osbeck) trees after foliar application of potassium phosphite (Phi) at 6 g a.i./1.9 L spray volume per tree in October (autumn). Error bars represent the standard error of the means of 6 replicate trees. Elevated Phi in the pretreated leaf tissues was due to residual Phi from applications to the trees in the previous season. Thereafter, residual level of Phi in non-treated check trees was at or near zero throughout the 65-day sampling period. Tissue Phi was determined following the method described by Ouimette and Coffey (1988).

the summer and autumn moves from leaves to roots coincident with allocation of carbohydrates to the fall root flush (Duncan et al., 1993). The reduction of Phi in leaves is much greater than the increase in roots so Phi is presumed to move into other tissues such as the bark. Hence, Phi is an ideal systemic compound, moving from shoots to trunk to roots depending on seasonal movement of carbohydrate to tissues (Graham & Drouillard, 1999).

What is the fate of phosphite in soil?

Phi applied to a P-deficient soil at an equivalent rate to Pi, incubated for days or weeks, stimulates growth of sour orange seedlings in the same way as soil-applied Pi (Orbovic et al., 2008). Phi is readily oxidised to Pi by soil microorganisms and taken up by roots as Pi (McDonald et al., 2001; Orbovic et al., 2008). Because of the risk of microbial oxidation, soil application of Pi is only recommended under specified conditions. Soil application of Phi may have positive effects on the growth and health of citrus trees as a result of the fungicidal properties of this compound and some conversion of Phi into Pi by soil microorganisms (Orbovic et al., 2008). Although Phi can be converted to Pi by soil microbes capable of oxidising Phi (Casida, 1960; Malacinski & Konetzka, 1966), they preferentially use Pi over Phi as a source of P (Adams & Conrad, 1953). Hence, the application of Phi to soil, while ineffective as a source of P compared with Pi fertilisers, can be effective as a soil fungicide (Orbovic et al., 2008). However, Phi applied too frequently or at high rates may increase risk of toxicity to citrus roots because of the slow conversion of Phi to Pi *in planta* (Zambrosi et al., 2011).

How does phosphite control Phytophthora infection?

Unlike traditional fungicides, Phi protects plants against *Phytophthora* spp. through a complex mode of action that includes direct and indirect responses resulting in enhanced defence responses following pathogen challenge (Guest & Grant, 1991; Daniel & Guest, 2006). Some evidence suggests that Phi induces a Pi-starvation stress in the pathogen, causing the release of stress metabolites that elicit more vigorous defence responses in the host plant (Perez et al., 1995; Smith et al., 1997; McDonald et al., 2001). Host plant recognition of *Phytophthora* spp. triggers a signalling cascade that coordinates defence responses, leading to activation of the phenylpropanoid pathway (Dixon et al., 2002). This pathway synthesises a range of structural polyphenolics, such as lignin, as well as other plant-defence compounds called phytoalexins. Phenylalanine ammonia lyase (PAL), responsible for the deamination of L-phenylalanine to cinnamic acid, is a key enzyme in this pathway. Increases in PAL activity and the accumulation of phenolic compounds have been associated with resistance to *P. cinnamomi* in less susceptible selections of *Eucalyptus marginata* and *E. calophylla* (Cahill & McComb, 1992), whereas more susceptible plants show comparatively smaller changes in PAL activity following pathogen challenge. Another example is the greater resistance in roots of *Lambertia formosa*, an Eastern Australian shrub, to *P. cinnamomi* associated with more rapid and intense release of superoxide at the penetration site, and activation of the phenylpropanoid pathway, than in the more susceptible Western Australian species, *L. inermis* (Suddaby et al., 2008). Similarly in citrus, differential response of the phenylpropanoid metabolite, scoparone, is observed in resistant and susceptible species to *P. citrophthora* (R.E.Smith & E.H.Smith) Leonian (Afek & Sztejnberg, 1988). Treatment of citrus species with fosetyl-Al or phosphorous acid increases scoparone in bark tissue inoculated with *P. citrophthora* compared with non-treated tissue (Afek & Sztejnberg, 1989).

How does phosphite control citrus diseases?

Control of root rot and collar rot of citrus occurs through trunk or soil applications of Phi; whereas, foliar

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applications control brown rot of fruit as well as root rot and collar rot caused by *P. palmivora* or *P. citrophthora* (Le Roux, 2000). Phi formulations are most commonly potassium (K) salts, although formulations with other cations (e.g. sodium; Na) are also available. An example of the effectiveness of Phi salts in controlling *P. palmivora* in 'Hamlin' oranges is shown in Figure 3. One foliar application of Phi provides 8 – 13 weeks of disease control. While Phi products at equivalent active ingredient (a.i.) are similar in their effect on brown rot severity (Figure 3A), K salts may be more efficacious for preventing the disease (Figure 3B). Likewise, the fungicide formulations Aliette and Phostrol (K Phi) at the same concentration of Phi are equivalent for control of root rot caused by *P. nicotianae* and brown rot caused by *P. palmivora* on citrus (Graham unpublished data). Foliar sprays of Phi can cause phytotoxicity to citrus leaves and rapidly growing fruit later in the season if applied at high rates, at high temperatures, or if the tree is under drought stress (Le Roux, 2000). Other factors, in addition to Phi dosage, may increase the risk of phytotoxicity. These include mixing of Phi in spray tanks and pH shifts due to insufficient buffering or chemical modification by other materials (e.g. copper fungicides and other metals, petroleum oil, sulfur) in the tank (B. McLean and R. Adair, unpublished observations).

Soil drenches of Phi fungicides are more effective for root control than foliar sprays due to do the delivery of more active ingredient as Phi to the target tissue (Table 1 and Orbovic et al., 2008). Application to the soil surface must be practised only when the area under the tree canopy is weed-free and application can be followed with adequate irrigation area coverage to move Phi into the root zone. If these conditions for application are not met, an extended residence time of the Phi in the soil may risk microbial conversion of Phi to Pi and loss of fungicide efficacy for root rot control.

Best management practices for use of phosphite for management of citrus Phytophthora diseases

Control failures with post-epidemic applications of Phi for brown rot confirm that Phi is only effective when used preventatively for control of fruit infection. For control of endemic Phytophthora root rot, foliar or soil treatments should be timed in advance of root flushes (late spring , summer and autumn) to protect them from root infection (Graham & Kosola, 2000). With repeated application for root rot control, rate of application should decrease from spring to autumn to minimise risk of phytotoxicity due to build-up in tissue Phi.

For brown rot control under subtropical climate conditions (such as those found in the citrus-growing area of Florida, USA), a single application

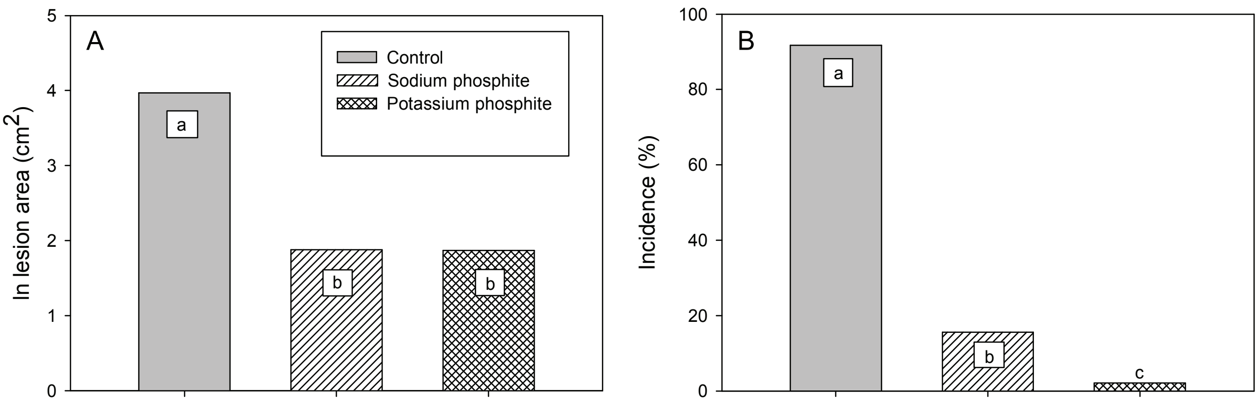

FIGURE 3: Control of fruit brown rot caused by *Phytophthora palmivora* in 'Hamlin' orange (*Citrus sinensis*) after foliar spray with potassium or sodium phosphite (Phi) at 13.3 g a.i./4.2L spray volume per tree. (A) Brown rot severity (percentage lesion area); and (B) Incidence (percentage of infected fruit). Phi activity in fruiting trees was assayed for 12 fruit per tree at 90 days after foliar spray application by inoculation of fruit harvested from treated trees. Each sample consisted of 12 fruit placed in a humid chamber with the stem end down. A 0.5 cm^3 aliquot of pasteurized Candler fine sand infested with chlamydospores of *P. palmivora* (100 propagules per cm^3 soil) was placed on the stylar end of each fruit and periodically wetted with a zoospore suspension of *P. palmivora*. Fruit were incubated at 27 – 30 °C. Fruit were measured at 8 – 11 days after inoculation. Percentage incidence was calculated as the number of infected fruit/total fruit × 100; Percentage area infected was calculated as lesion area/fruit area × 100. The means of 5 replications per treatment with different letters are significantly different at $P < 0.05$ according to Student Newman Keuls multiple range test.

TABLE 1: Comparison of soil drench vs. foliar application of the phosphonate fungicide fosetyl-Al (Aliette, Bayer Crop Science) and potassium phosphite (Phostrol, Nufarm, Inc.) at 1.0/2.39 g Phi a.i./L (drench/foliar) per plant for control of root rot caused by *Phytophthora nicotianae* on sweet orange (*Citrus sinensis*) seedlings.

Treatment	**Fibrous root dry weight (g)**	**Root rating (1 – 5)**[1]	***P. nicotianae* positive roots (%)**[2]
Control	1.09 a[3]	1.10 c	0.00 c
Fosetyl-Al foliar	0.80 b	2.00 b	21.50 b
Potassium phosphite foliar	0.76 b	2.20 b	11.50 bc
Fosetyl-Al drench	0.69 b	2.00 b	7.50 bc
Potassium phosphite drench	0.63 b	1.90 b	1.50 c
P. nicotianae inoculated control	0.23 c	4.10 a	74.00 a

[1] *Visual rating for symptoms of water-soaking and sloughing of the root cortex on a scale of 1 to 5, where 1 = no visible symptoms of root rot and 5 = no visible healthy roots.*

[2] *Percentage of twenty 1-cm root pieces positive for* P. nicotianae.

[3] *Means followed by unlike letters are significantly different at the P < 0.05 according to Student Newman Keuls multiple range test.*

in midsummer is completely effective for protection of fruit throughout the autumn season of highest fruit susceptibility (Graham & Timmer, 2011). Phi is safe for use on fresh fruit, with a short preharvest interval and no standard for maximum residue level (MRL) in fruit. Some precautions for making applications to the tree canopy are required in order to reduce phytotoxicity risk to fruit for fresh market. These include: not tank-mixing Phi with other chemicals and avoiding Phi application during hot periods (>35 °C).

Does the citrus model apply to forest trees?

Citrus is a horticultural crop with known Phytophthora pathogens, host susceptibility, and well-characterised phenological cycles of roots, shoots, and fruiting (Graham & Kosola, 2000). In native plant ecosystems several variables may reduce the efficacy of Phi as a fungicide (Hardy et al., 2001). These factors include: (1) multiple hosts with varying susceptibility; (2) unique plant phenology/physiological activity; (3) variable uptake into aboveground tissues; (4) variable sensitivity to Phi toxicity depending on plant genotype or exacerbation of toxicity due to plant P deficiency; (5) differing rate of metabolism of Phi (i.e. residual activity); and (6) variable efficacy against *Phytophthora* spp. and the diseases they incite (e.g. blights, cankers, and root rots).

Trunk injection of Phi has been used effectively to protect avocado (Darvas et al., 1984; Pegg et al., 1987), cocoa (Guest et al., 1994), citrus (Schutte et al., 1991), pome (Long et al., 1989), and stone fruits (Wicks & Hall, 1988) against several *Phytophthora* spp. However, large differences between agricultural crops and different species in native plant communities do not allow extrapolation of results from one plant to another. Stem injection of Phi has been widely practiced for control of *P. cinnamomi* spread in native plant communities in Western Australia (Shearer et al., 2006). One injection of 50 – 100 g/L Phi protected *Banksia* and *Eucalyptus* trees for at least 4 years and reduced extension of a *P. cinnamomi* disease front for 5 years (Shearer et al., 2004, 2006). Periods of protection following one injection of Phi in native woody plants are much longer than those found for horticultural trees. Pegg et al. (1987) controlled *P. cinnamomi* infection of avocado with annual injections, whereas, injections were repeated at 6-month intervals for control of Phytophthora diseases of cocoa (Guest et al., 1994). Schutte et al. (1991) recommended that citrus be treated with repeated applications of Phi regardless of the method of application. Differences in the longevity of action of Phi between native plant and horticulture hosts depend on the dynamics of competing carbohydrate source-sink relationships at the time of injection, the presence of active defence responses to *P. cinnamomi* invasion, and environmental interactions (Shearer et al., 2006). Little is known of how the factors influencing Phi effectiveness will interact in native plant versus horticultural situations.

Advantages of phosphites for control of Phytophthora diseases of forest and native plants

Methods for wide-scale aerial and trunk application of Phi fungicides have been validated through their use for control of Phytophthora disease epidemics in forest and native plant systems (Hardy et al., 2001; Shearer et al., 2007). Phi has several particular advantages compared to other fungicides: (1) applications can be effective for both aerial- and root-infecting *Phytophthora* spp. because of systemic movement up and down in the tree; (2) long residual activity particularly in slow-growing native forest species with demonstrated longevity of control on 2 to 3-year cycles; (3) realistic cost of Phi fungicides for wide-scale application; (4) breakdown products of Phi that are acceptable in sensitive ecosystems; and (5) ecosystem-scale applications that have been accepted after considering risks and benefits. Despite these positive attributes, limited trials of Phi applications to candidate hosts should be performed before conducting large-scale applications to determine the efficacy of Phi in a given plant ecosystem (e.g. Shearer & Fairman, 2007; Shearer et al., 2006; Garbelotto & Schmidt, 2009).

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