



# ROS and Oxidative Response Systems in Plants Under Biotic and Abiotic Stresses: Revisiting the Crucial Role of Phosphite Triggered Plants Defense Response

Mohammad Aqa Mohammadi<sup>1,2,3,4</sup>, Yan Cheng<sup>1,5</sup>, Mohammad Aslam<sup>2,3</sup>, Bello Hassan Jakada<sup>2</sup>, Myat Hnin Wai<sup>2,6</sup>, Kangzhuo Ye<sup>2,5</sup>, Xiaoxue He<sup>2</sup>, Tiantian Luo<sup>2,5</sup>, Li Ye<sup>2,5</sup>, Chunxing Dong<sup>2,6</sup>, Bin Hu<sup>2,5</sup>, S. V. G. N. Priyadarshani<sup>2,7</sup>, Gefu Wang-Pruski<sup>1,8\*</sup> and Yuan Qin<sup>2,3\*</sup>

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### \*Correspondence:

Yuan Qin  
yuanqin001@foxmail.com  
Gefu Wang-Pruski  
Gefu.Wang-Pruski@Dal.Ca

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<sup>1</sup> Joint FAFU-Dalhousie Lab, College of Horticulture, Fujian Agriculture and Forestry University, Fuzhou, China, <sup>2</sup> State Key Laboratory of Ecological Pest Control for Fujian and Taiwan Crops, Fujian Provincial Key Laboratory of Haixia Applied Plant Systems Biology, College of Life Sciences, Center for Genomics and Biotechnology, Fujian Agriculture and Forestry University, Fuzhou, China, <sup>3</sup> State Key Laboratory for Conservation and Utilization of Subtropical Agro-Bioresources, Guangxi Key Lab of Sugarcane Biology, College of Agriculture, Guangxi University, Nanning, China, <sup>4</sup> Department of Horticulture, College of Agriculture, Alberoni University, Kohistan, Afghanistan, <sup>5</sup> College of Plant Protection, Fujian Agriculture and Forestry University, Fuzhou, China, <sup>6</sup> College of Agriculture, Fujian Agriculture and Forestry University, Fuzhou, China, <sup>7</sup> National Education Commission, Nugegoda, Sri Lanka, <sup>8</sup> Department of Plant, Food, and Environmental Sciences, Faculty of Agriculture, Dalhousie University, Truro, NS, Canada

Phosphite (Phi) is a chemical analog of orthophosphate [ $\text{HPO}_4^{3-}$ ]. It is a systemic pesticide generally known to control the prevalence of oomycetes and soil-borne diseases such as *Phytophthora*, *Pythium*, and *Plasmopora* species. Phi can also control disease symptoms and the spread of pathogenic bacteria, fungi, and nematodes. Phi plays critical roles as a fungicide, pesticide, fertilizer, or biostimulator. Overall, Phi can alleviate the severity of the disease caused by oomycete, fungi, pathogenic bacteria, and nematodes (leave, stem, fruit, tuber, and root) in various plants (vegetables, fruits, crops, root/tuber crops, ornamental plants, and forests). Advance research in molecular, physiological, and biochemical approaches has approved the key role of Phi in enhancing crop growth, quantity, and quality of several plant species. Phi is chemically similar to orthophosphate, and inside the cells, it is likely to get involved in different features of phosphate metabolism in both plants and pathogens. In plants, a range of physiobiochemical alterations are induced by plant pathogen stress, which causes lowered photosynthesis activities, enzymatic activities, increased accumulation of reactive oxygen species (ROS), and modification in a large group of genes. To date, several attempts have been made to study plant-pathogen interactions with the intent to minimize the loss of crop productivity. Phi's emerging function as a biostimulant in plants has boost plant yield and tolerance against various stress factors. This review discusses Phi-mediated biostimulant effects against biotic and abiotic stresses.

**Keywords:** phosphite, oomycete, plant pathogens, biotic stress, abiotic stress, reactive oxygen species, oxidative stress, gene modification

## INTRODUCTION

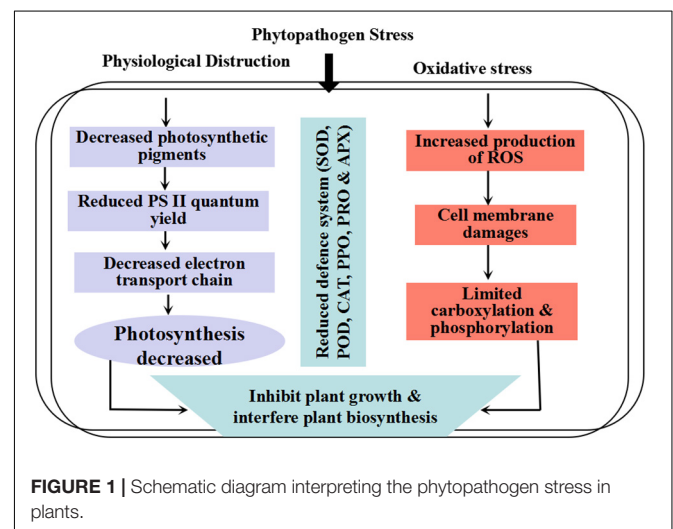
Pesticides and fungicides are used extensively during crop production, but these chemical agents are toxic to the environment and health. Therefore, the choice of environmentally friendly agents, which can be used as pesticides and fungicides, is essential. Salts of phosphorous acid, Phi (phosphite), are less harmful to the environment and have been used as a fungicide for over 40 years and still attract attention to be used as fungicides. Several chemical and biological compounds, known as resistance inducers, can persuade plant defense response commotion (Silva et al., 2011). Since the discovery of its protective effects in 1977, Phi (known as fostyl-Al Fosjet/Agri-fos) has been applied widely on various crops to control both disease symptoms and the spread of fungi. The active ingredient in these chemicals is Phi ( $\text{H}_2\text{PO}_3^{2-}$ ) (Guest et al., 1995). The chemical similarity of Phi to phosphate (Pi) indicates that the center of mechanism relies on disordering of some desperate aspects of Pi metabolism (McDonald et al., 2001). Still, no molecular template has been proposed which qualified to count for all the remarkable effects that Phi have on *Phytophthora* spp. and on a major set of plant hosts.

Phi are generally applied as a pesticide (fungicide), fertilizer, and biostimulator for plant defense responses (McDonald et al., 2001; Han et al., 2021). As a biostimulator, Phi has been proven to boost nutrient absorption and assimilation and enhance product quality and biotic and abiotic stress tolerance. Phi also improves plant growth, nutritional value, and production (Ávila et al., 2013). Besides, Phi is extensively applied to prevent pathogen spreads, and in many countries, it is registered as a pesticide (Wu et al., 2019). Although, Pi analogs applications are as fertilizers and its effects limited to phosphorus (P) nutrition. Phi effectively prevents plant pathogens caused by oomycetes, particularly *Peronospora*, *Plasmopara*, *Phytophthora*, and *Pythium* genus (Silva et al., 2011; Olivieri et al., 2012; Burra et al., 2014; Groves et al., 2015). Phi can directly inhibit oxidative phosphorylation of pathogen metabolism (Lobato et al., 2008; Norton and Swinton, 2018), and indirectly alleviate plant defense mechanisms, ultimately inhibiting the pathogenesis (Daniel and Guest, 2005). The pathogenesis-related genes increase resistance against diseases and increase soluble protein accumulations in *Arabidopsis*, potatoes, and tomatoes (Silva et al., 2011; Chandrasekaran et al., 2017). Besides, Phi increases systemic acquired resistance (SAR) signaling activities in various plants against oomycetes, for instance, *Phytophthora* (Lim et al., 2013), *Pythium* (King et al., 2010), and *Pseudoperonospora* species (Ramezani et al., 2017b).

*In planta*, the sensitivity to oxidative stress could result in the entire balance between factors that increase the production of antioxidants and cellular compounds. The interaction between plants and pathogens leads to physiochemical alteration in host plants. For example, photosynthesis reaction, respiration rate, and carbon uptake can be highly affected during pathogen infection (Raggi, 1978; Gonçalves et al., 2019). Damages to chlorophyll, photosystem II (PS II), and other components of the electron transport chain lead to a remarkable decrease in transport of photosynthetic electron chains. Therefore,

considerable light energy is released as heat or fluorescence (Roháček et al., 2008). Previous reports suggest that several resistance inducers with low or minimum health risks can be used as an alternative to chemical fungicides (Thakur and Sohal, 2013; Tajik et al., 2019). During biotic and abiotic stresses, a high amount of reactive oxygen species (ROS) concentrations are induced, which could damage several intracellular macromolecules (Forouzanfar et al., 2016; Ramezani et al., 2018). These ROS with high oxidation rate cause damages to plant tissues, DNA mutation, cell organelle disordering, and decay of lipid, protein, and photosynthetic apparatus. It has been shown that a high level of resistance to the Phi-treated plants against biotic stresses is due to stimulation of antioxidant and defense enzymes in plant cells (Figure 1) (Oyaburo et al., 2015).

Plant oxidative response system, which includes non-enzymatic and enzymatic productions, have interfered with an aerobic process to neutralize oxidative cleavage due to ROS production (Figure 1). Protective enzymes include catalase (CAT), ascorbate peroxidase (APX), guaiacol peroxidase (GPX), superoxide dismutase (SOD), and polyphenol oxidase (PPO), while glutathione peroxidase (GR), ascorbate (AsA), proline (Pro), and carotenoids (Car) have non-enzymatic protection functions (Figure 5) (Jung et al., 2000; Lombardi and Sebastiani, 2005; Singh et al., 2009; Forouzanfar et al., 2016; Debnath et al., 2018; Ramezani et al., 2018). Like other biological tensions, fungal infections produce excessive free radicals, such as hydroxyl radical ( $\cdot\text{OH}$ ), hydrogen peroxide ( $\text{H}_2\text{O}_2$ ), and superoxide radicals ( $\cdot\text{O}_2^-$ ), in cytosol, chloroplast, and mitochondria (Mofidnakhai et al., 2016). It has been well documented that following antioxidant enzyme activation, plant tolerance to biotic stresses significantly increased (Lobato et al., 2011). The balance between ROS that resulted from loss to PS II and the alteration of oxidative stress can limit plant health and normal physiological process (Figure 1) (Dias et al., 2014). Changes in the expression of ROS molecules are a vital step in activation of plant response to phytopathogens. The antioxidant enzyme activities have been reported to prevent the release of oxidative molecules and permit



**FIGURE 1** | Schematic diagram interpreting the phytopathogen stress in plants.

cells to resist against the penetration of *Aphanomyces euteiches* and *Sclerotinia sclerotiorum* in plant tissues (Ali et al., 2006; Peluffo et al., 2010; Djébalí et al., 2011).

## Invasion and Phytopathogenesis-Colonization of Plant Pathogens in Hosts

Vegetative hyphae can infect plant tissues in the same way as other infectious organelles (Hardham, 2007). Mycelia infection may occur due to root-to-root contact at the site (McCarren et al., 2005). The primary multiplication of zoospore pathogen infection is motile, and it is suggested that these have a radius of infection of 1–3 cm and can float for hours or even days (Hardham, 2007). The spores are often absorbing and encyst by tiny roots and are preferably located in the elongated area behind the meristems. The encystment may be caused by physical irritation, cold or increased calcium concentration, and the contents of the cytoplasmic vesicles secreted in the first few minutes after contact with the roots, forming a tape that binds to the plant cell wall (Hardham, 2007; Hardham and Blackman, 2018). The cyst then induces a germ tube that makes a hole into the cell wall outside or around the edge of the plant root cells by forming an aspersorium and then produces haustoria-like structures inside the cell that can absorb nutrients from the plant's cell (Hardham, 2001). After getting into the plant cell, the phytopathogen obtains energy from glycolysis of plant rather than beta-oxidation (Torto-Alalibo et al., 2007) and grows asexually (Savidor et al., 2008).

Several pathogens that may be involved in plant inoculation have been isolated and identified as oomycetes. They consist of cell wall-destroying enzymes like endocellulase,  $\beta$ -1,3-glucanase (GLU),  $\beta$ -glucosidase, chitinase (CHI), pectinesterase, galactinase, and endopolygalacturonases (van West et al., 2003; Mohammadi et al., 2019). The majority of oomycetes generate extracellular RNAase, DNase, phosphatases, lipases, amylases, proteases, and cellulase, which can all be associated with phytopathogenesis (Kamoun, 2006; Win et al., 2007). *Phytophthora* spp. also produces factors that enhance or suppress host defense by producing enzymes that chemically attack the host. Sequencing of *Phytophthora infestans* genome and comparison with other stramenopiles including diatoms and other oomycetes like *Phytophthora*, *Hyaloperonospora*, *Arabidopsis*, and *Pythium ultimum* has revealed plenty of hydrolases. The ABC transports proteinase inhibitors and a combination of a wonderful family of 700 proteins with homology to the hormonal avirulence oomycete genes (Taylor et al., 2011). Plant defense responses are induced and stained by plant pathogens, to some extent, pathogenicity relies on protein-targeting patterns (Govers and Gijzen, 2006). New features of oomycete genomes contain the proliferation of genes that encode secretory effectors, plant cell wall-destroying enzymes in *Phytophthora*, and the over-representation of genes involved in photolytic degradation and signal transduction in *Pythium* spp. (Adhikari et al., 2013). Plant defense responsive cutters are induced and secreted by *Phytophthora* to some extent; it can be said that pathogenesis relies on protein-targeting motifs

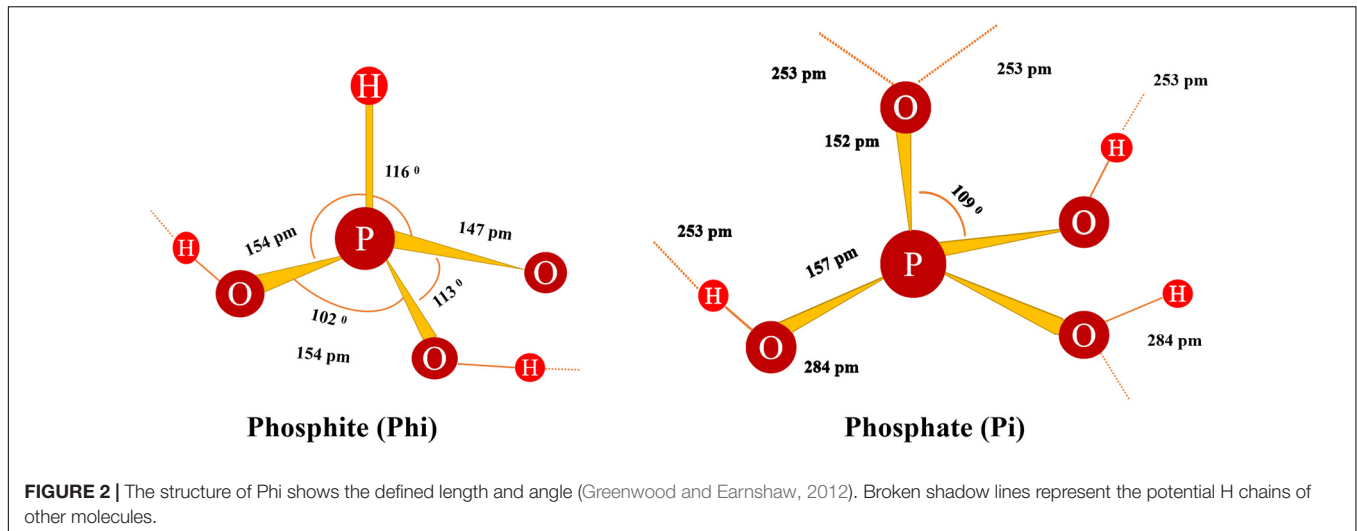
(Bengyella et al., 2019). A necrosis-inducing protein isolated from *P. cinnamom* facilitates the colonization of host tissues during the necrotrophic stage by stimulating plant cell death by facilitating nutrient uptake by pathogens (Martins et al., 2019). Effects of fungal and oomycete proteins have been shown to play an important role in apoplasts for adaptation, with recent advances in understanding the role of these proteins in escaping chitin-induced immunity (Rocafort et al., 2020). In this study, they also demonstrated the ability of apoplastic-affecting proteins to be incompatible with detection by different plant cell surface immune receptors and to use their effectiveness to rapidly detect protein-cell immune receptor interactions and apoplastic cells (Rocafort et al., 2020).

## ENVIRONMENTALLY FRIENDLY AGROCHEMICAL OHOSPHITE

Phi is an alkali metal salt of phosphoric acid (McDonald et al., 2001), and it should not be confused with Pi, which is derived from phosphoric acid ( $\text{H}_3\text{PO}_4$ ). Phi salts contain a metal cation such as  $\text{K}^+$ ,  $\text{Na}^+$ , or  $\text{Mg}^+$  and any of the following non-metal anions: Phi ( $\text{PO}_3^{3-}$ ), hydrogen Phi ( $\text{HPO}_3$ ), or dihydrogen Phi ( $\text{H}_2\text{PO}_3$ ). When phosphorous acid ( $\text{H}_3\text{PO}_3$ ) reacts with water, it forms phosphonic acid, which is highly acidic and is neutralized by potassium hydroxide (KOH) to potassium dihydrogen Phi ( $\text{KH}_2\text{PO}_3$ ) or dipotassium hydrogen Phi ( $\text{K}_2\text{HPO}_3$ ). These two compounds are active ingredients in several fungicides, pesticides, and fertilizers (Landschoot and Cook, 2005). Inorganic  $\text{H}_3\text{PO}_3$  salts can be found under various names in the literature. Phi (preferred here) and phosphonates are widely used, followed by the synonyms hydrogen phosphonates, ortho-Phi, phosphonic acid, and phosphorous acid (Hardy et al., 2001). They emphasized that the use of the term (Phi) clearly distinguishes inorganic salts of  $\text{H}_3\text{PO}_3$  from phosphonates because the latter contains an organic group that binds to the P ion and is found in conventional chemical fungicides. The comparative advantage of Phi over phosphate (Pi) is that Phi can have direct toxic effects on fungi. The side effect of Phi is high-risk chemical toxicity when use at doses above 5 g/L or 36 kg/ha (Barrett et al., 2003). The utility of Phi in agriculture has been studied in relation to its influence on disease prevention than to be a plant fertilizer. The latter is possible when Phi is used to the soil and comes in contact with certain soil bacteria, which can oxidize them to Pi and absorb as P (Figure 6) (McDonald et al., 2001; Barrett et al., 2003). However, this process is long and may take 4 months; therefore, it has no actual significance (McDonald et al., 2001; Lovatt and Mikkelsen, 2006).

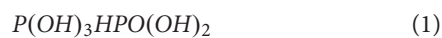
## The Chemistry of Phi

In an aqueous solution, ( $\text{H}_3\text{PO}_3$ ) is in equilibrium with tautomer  $\text{H}_3\text{PO}_4$  (Equation 1) (Guthrie, 1979), but it turns into a quadrilateral form (Kraszewski and Stawinski, 2007). At neutral pH, the solution also contains a mixture of mono- and dianionic forms of phosphonate ions, known here as Phi (Figure 2; Equations 2 and 3). In Phi,  $\text{P}^+$  was oxidized, and the oxygen

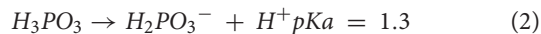


atom ( $O_2^{2+}$  was replaced by a non-ionized hydrogen atom (Greenwood, 1984; Greenwood and Earnshaw, 1997).

Tautomeric equilibrium:



Phi dissociation:



### Phi as an Alternative Fungicide

Phi, a reduced form of Pi, is the oxyanion of phosphoric acid ( $H_3PO_4$ ). When the Phi are dissolved in water, a strong acid form called phosphonic acid is produced. The addition of alkaline metal salts, such as  $K^+$ ,  $Ca^+$ ,  $Mg^+$ , and  $Al^+$ , preserves neutral pH; low pH itself is harmful to plant tissues. KOH is added to form the resulting solution, which is referred to as potassium mono or di-salt of phosphorous acid ( $KH_2PO_3/K_2HPO_3$ ). Another solution, fosetyl-Al, was created by adding  $Al^+$  (Guest and Grant, 1991).

In the 1970s, Phi was discovered as an anti-fungal agent in the laboratory of Ron Polink in France. It is absorbed by membranes on the leaves and stems of plants and has good solubility and mobility. Phi is a phloem-mobile molecule that can be applied by spraying on leaves or injecting the trunk. Thus, foliar application of Phi based on fungicide was found with systemic properties to reduce the tumor and root diseases (Guest and Grant, 1991). Also, Phi fungicides are safe and environmentally friendly pesticides, according to the US Environmental Protection Agency (Lobato et al., 2017). Also, the fungicides resistance action committee (FRAC) classified Phi as grouped 33, as a low-risk fungicide<sup>1</sup>. Integrated pest management (IPM) is the safest and most effective

way for pest control while minimizing pesticide use on plants. In the IPM program, Phi is an alternative product for promoting the reduction of toxic fungicides application (Mayton et al., 2008).

### Phi Mode of Actions

Phi's mode of action in plants is divided into direct and indirect modes. The Phi direct mode of action is complicated (Massoud et al., 2012). Studies have shown that the direct mode of action depends on Phi concentration: higher levels of Phi have a direct inhibitory effect on various fungal and fungal-like organisms such as oomycetes and other species (Fo et al., 1990). The direct mode of action is related to the inhibition growth of zoospores and mycelia production (Cohen and Coffey, 1986; Wilkinson et al., 2001; Liu et al., 2020). After the addition of Phi in the culture plates, changes in gene expression levels were reported in *P. cinnamom* (King et al., 2010). Genes involved in the biosynthesis of the pathogen cell wall, like cellulose and glycan synthases, were inhibited in Phi (40  $\mu\text{g/ml}$ ) medium, and gene expression was not significantly altered in the medium containing relatively low (5  $\mu\text{g/ml}$ ) Phi. After adding Phi (40  $\mu\text{g/ml}$ ) for 4 days, about 70% of the *P. cinnamom* culture growth in the medium was inhibited. These results indicate that Phi directly inhibits the cell wall biosynthesis of pathogens and relatively low Phi concentration (5  $\mu\text{g/ml}$ ) may not be enough to directly prevent its growth (King et al., 2010).

In contrast to Phi's direct mode of action, Phi's low concentrations are associated with indirect action to boost plant defense responses as induced resistance (IR) (Coffey and Joseph, 1985; Jackson and Andrews, 2000). Phi-induced resistance (IR) studies suggest that Phi operates in more than one way in plants. Indirect actions of Phi are more useful to suppress pathogens than the direct effects (Daniel and Guest, 2005). Previous studies have revealed the biochemical changes that led to the suppression of pathogens (Guest and Grant, 1991; Jackson and Andrews, 2000; Bengtsson, 2013). Expression of many genes in plants was

<sup>1</sup>www.frac.info



studied, and defense-related genes against *P. infestans* resistance were found to be upregulated (Eshraghi et al., 2011). The indirect molecular mechanism of Phi which inhibits *P. infestans* has been determined (Daniel and Guest, 2005; Massoud et al., 2012).

### Phi Uptake and Mobility Within Plants

Plants absorbed Phi easily and transport it in xylem and phloem as the same mechanism of Pi (Borza et al., 2017). Evidence suggests that Phi is actively mobile into plants and controls fungal development (Borza et al., 2014) or indirectly can become available to the plant as a P-source for plant nutrition after microbial oxidative reactions and improved the growth parameter in the host plants (Constán-Aguilar et al., 2014). The microorganisms in the soil and rhizosphere oxidize the Phi to Pi, which is easily absorbed by the roots of plants through the normal Pi channels. However, the process is slow and may take several months. Transportation, classification, biostimulant effects, and Phi fungicide effects were recently investigated in potato leaves using gas chromatography/time-of-flight mass spectrometry (GC-TOF-MS) (Wu et al., 2019). GC-TOF-MS showed that the Phi program modified some metabolite libraries. Phenylalanine (PAL) treatment is associated with higher levels of pathway accumulation of phenylpropane, chlorogenic acid, caffeic acid, and salicylic acid (SA). In Pi-starved tobacco cells, it was found that Phi competitively inhibits the influx of Pi through multiple transport mechanisms and accumulates in the cytoplasm, preferably vacuoles. In contrast, Phi-treated preloaded cells almost exclusively collected Phi in the vacuole (Danova-Alt et al., 2008). Depending on Pi status of the plants, the compartmentalization of Phi in either the cytosol or vacuole may explain why Phi is more effective in controlling oomycete diseases in low Pi soils and conversely requires more frequent application in plants grown on high Pi soils such as in potato fields (Wang-Pruski et al., 2010). Previously, it was reported that intracellular orthophosphate is acting as an inductor of adaptive response to stresses and is stimulated for better plant performance (Trejo-Téllez and Gómez-Merino, 2018).

### The Effects of Phi on Plant Chemistry

Phi seems to have a minor effect on tobacco cell processes and respiration (Danova-Alt et al., 2008). Unlike *Phytophthora* spp., treatment of tobacco cells with Phi did not reduce nucleoside triphosphates or glucose-6-phosphate, nor did it stimulate nucleoside diphosphates or pyrophosphate and adenylate pools. However, these results were obtained only in 20 h of incubation after Phi application. Whereas, Gent et al. (2020) documented that the occurrence of *Pseudoprosopura humoli* isolates was at a higher level of sensitivity to fosetyl-Al and other Phi fungicides. Plant tissues contain pyrophosphate values in the range of 0.5–40 nmol/g of fresh weight (FW) (equal to 0.5–40  $\mu$ M) (Heinonen, 2001). No measurable changes in pyrophosphate concentration were observed in *Brassica nigra* seedlings grown at 10 mM Phi concentration (Carswell et al., 1997). In comparison, the concentration of pyrophosphate in *Phytophthora palmivora* increases from the control concentration of 0.2 to 1.5 mM in the

presence of Phi. In *Brassica*, *Arabidopsis thaliana* contained high pyrophosphate levels (Heinonen, 2001).

### Phi-Mediated Improvement of Plant Health

Depending on the concentrations applied, Phi has been documented to prevent Pi starvation response, alter physiology metabolism and growth, and enhance plant defenses against infection by various fungi (Table 1). Research on the effects of fosetyl-Al and Phi indicated that in general, high exogenous Phi dosage can be associated with a decline in plant normal growth and development (Carswell et al., 1997; Trejo-Téllez and Gómez-Merino, 2018). In addition, Phi reduced tiny root growth and decreased colonization of mycorrhizal fungi in onion (Sukarno et al., 1998). Phi application on healthy plants affects pollen fertility and seed germination of some annual species of *Eucalyptus* trees (Fairbanks et al., 2001). It seems that repeated use of Phi, in long term, can limit the diversity of plants in the ecosystem, and this effect can be lessened by proper timing of Phi programs. Avocado plant pollen tube germination and growth seemed to be sensitive to Phi treatment, although relatively high concentrations of Phi were used in these experiments and performed *in vitro* (Nartvaranant et al., 2004). Phi could have detrimental effects on plant growth and overall health, especially in P deficiency in plants (Carswell et al., 1997). Phi's long-term effect relies on both type and time of plant inoculation with pathogens (Wilkinson et al., 2001). Injection of 50–100 g Phi/L protects *Banksias* and *Eucalyptus* plant infection for a minimum of 4 years, and the lesion is often present with callus (Shearer et al., 2006). However, 3 weeks after root inoculation with *P. cinnamom*, stem injection with Phi could not control *Escherichia marginata* growth. In *Banksia coccinea*, there is a U-shaped relationship between stem injection of Phi concentration and the effectiveness of Phi in preventing the spread of *Phytophthora cinnamomi*, belt formation, and growth retardation (Shearer et al., 2006; Shearer and Fairman, 2007). The results of Phi applied on citrus plants showed that Phi not only enhanced plant growth but also increased fruit nutrient and yield (Lovatt and Mikkelsen, 2006). Unlike orthophosphate; Phi was readily taken when citrus-deficient leaves were applied. Phi application improved various horticultural plant's agronomical traits, for example, yield, growth, quality, and biomass stimulation (Gómez-Merino and Trejo-Téllez, 2015). Phi application on strawberry improves growth, root, and quality of fruits compared with control (Glinicki et al., 2010; Estrada-Ortiz et al., 2011). Pretreatment of isolated chickpea leaves with Phi and later on infection with *Phytophthora cryptogea* controlled growth of the pathogen. This effect was entirely back set by preapplication of Phi on plant leaves as a PAL pathway inhibitor (Saindrenan et al., 1990). Phi prevents stem canker in *Persea americana* and *Persea indica* caused by *Phytophthora citricola* (El-Hamalawi et al., 1995) and moldy core rot in apple fruits caused by the causal agent *Alternaria alternata* (Reuveni et al., 2003).

The similarity between the response of plants to Pi and the application of Phi, especially in long-term field trials,

**TABLE 1** | Effects of Phi on enhancement on plant growth and physiological and biochemical attributes of different plants grown under different pathogen stressed.

Effect of Phi	Plant species, organism	References
Diseases suppression in plants	Incidence of diseases caused by <i>Phytophthora</i> spp., <i>Verticillium</i> spp., <i>Fusarium</i> spp., <i>Armillaria luteobubalina</i> , and <i>Plasmoparaviticola</i> is controlled by Phi treatment in host plants; Phi suppressed <i>P. infestans</i> , <i>F. solani</i> , and <i>R. solani</i> inoculation in <i>Solanum tuberosum</i> . Phi alleviated apical necrosis in <i>Mangifera indica</i> caused by <i>P. syringae</i> . Plants also revealed a delay in senescence after the Phi application.	Mohammadi et al. (2020); Borza et al. (2019); Ramezani et al. (2018); Lobato et al. (2008); and Torés Montosa (2006)
Phi-enhanced plants to Pi starvation	Phi enhanced the expression of Pi starvation-induced gene expression, improving the growth and defense system in tomato plants. Phi applied to Pi-sufficient white lupin elicited a complete Pi starvation response (PSR) by (enhancing root development and enzyme activity alleviation) whereas application of Phi to Pi-deficient plants enhanced PSR. Phi enhanced the PSR in Pi-deficient turnip.	Vinas et al. (2020); Gilbert et al. (2000); and Carswell et al. (1997)
Prevention of Pi uptake	Phi boosted Pi absorption by root protection in <i>Hakea sericea</i> .	Sousa et al. (2007)
Decrease pollen fertility and seed germination	Phi application decreased pollen fertility and seed germination in a concentration-dependent manner in several plants. Fosetyl-Al on field-treated apple, pear, and cherry orchards has been revealed to be very effective on flowering the year following treatment, and a positive effect was noticed both on the number and quality of flower buds.	Eshraghi et al. (2011) and Peyrard et al. (2015)
Improved phytoalexin and phenolic accumulation	Foliar application of Phi enhanced phytoalexin and phenolic stimulation by 12–24 h in potato slices after inoculation with <i>P. infestans</i> . Phi caused defense response and an accumulation of ROS and ethylene in pepper after pathogen challenged by <i>P. capsici</i> . Phi treatment reduced <i>Sclerotinia sclerotiorum</i> lesion development in common bean and was associated with triggered ROS and MDA accumulation and increase in host defense enzymes and limitation of pathogen growth.	Mohammadi et al. (2019); Liu et al. (2016); and Fagundes-Nacarath et al. (2018)
Improved hypersensitive reaction	Phi application increased high accumulation of plant defense response system on suppression of pathogens in apple after apple scab ( <i>Venturia inaequalis</i> ) after infection.	Felipini et al. (2016)
Prevention of the plant's root elongation	Phi prevents root elongation under Pi stress in <i>A. thaliana</i> .	Varadarajan et al. (2002)
Inhibition of pathogen growth and development	Inhibited growth of the pathogen <i>in vitro</i> culture, enhanced vesicle formation within hypha, and inhibited zoosporogenesis in <i>Phytophthora</i> spp. Phi setback development in nematode species. Phi inhibited growth <i>in vitro</i> in <i>Verticillium</i> spp. Phi caused stunted growth under suboptimal also optimal Pi absorption in maize. Phi increased growth, fruit quality, and production in strawberries.	Belhaj (2017); Oka et al. (2007); Borza et al. (2019); Schroetter et al. (2006); and Estrada-Ortiz et al. (2011)
Phytotoxicity	The side effects of Phi are phytotoxic symptoms in several plant species including foliar necrosis, defoliation, abnormalities growth, chlorosis, reduced root growth, at high-dosage rates, and plant death.	Scott et al. (2016) and Shearer et al. (2006)

has led us to believe that Phi can act as a biological fertilizer or biostimulant. However, Thao and Yamakawa (2009) concluded that increasing plant health attribution due to Phi being a source of Pi is misleading, because the half-life of Phi to Pi is several months due to oxidation of soil microorganisms, and those test plants can become infected again with pathogenic oomycetes, which are highly decreased by Phi (Adams, 2004). Although the effects of Phi on plant health may vary, in most cases, the use of Pi fertilizers, in general, can increase plant performance and reduce disease susceptibility (Walters and Bingham, 2007). Phi application increased cucumber plant resistance to downy mildew by creating a rapid generation of antioxidants and a high reduction sensitivity to ROS production that programmed cell death (Ramezani et al., 2017a). Induction of wheat resistance

to Russian aphid (*Diuraph isnoxia*) mediated by Phi was associated with increased PAL and enzymatic activity levels (Venter et al., 2014).

Systemic resistance induced against rust in *Vici faba* is shown by treating the leaf with 10 mM Phi (Walters and Bingham, 2007). This reaction is very close to the response observed in chestnut after its trunk is being injecting with different Phi dosages (Daniel and Guest, 2005). It was shown that plants treated with Phi after inoculation with *P. cinnamomi* responded quickly to the disease severity in injected trees than plants untreated with Phi. Recently, experiments were conducted in the greenhouse to study the effects of Ca-Phi (38 kg P/ha 1) on the soil characteristics and growth parameters of four kinds of soil green manures, three superphosphates (TSP), and control (no fertilization). After 8 weeks of planting, the soil biomass yield, Phi concentration

in plant biomass, various soil P pools, and microbial biomass nutrients were measured. In addition, with the exception of lupin in the control (*Lupinus albus* L.), Phi has no negative effect on green manure performance (Fontana et al., 2021). The Phi concentration in plant biomass varies with species and soil types. The maximum concentration of mustard (*Brassica juncea* L.) in clay is about 400 mg Phi/kg. Compared with the control, the fertilization of TSP and Phi had similar effects on different P pools and microbial biomass nutrients (C, N, and P), although the response depended on the soil type. In sand, after adding Phi, the amount of P ( $P_{NCHO_3}$ ) much increased in TSP treatment, indicating that Phi is partially oxidized. Among clays with high P stabilization ability, Phi  $P_{NaHCO_3}$ , which is higher than TSP, may promote the chemical P form due to different solubility (Fontana et al., 2021). The Phi-treated roots of avocado obtained protection from zoospores of *P. cinnamomi*, Phi enhanced the root resistance to pathogen invasion (van der Merwe et al., 1992). Besides, Phi application enhanced mycorrhizal formation in American chestnut and various other responses in plants (Table 1).

## PHI-TRIGGERED PLANT DEFENSE RESPONSE AGAINST BIOTIC STRESSES

Phi-treated plants accumulate phytoalexin, phenolic, flavonoids, proline, hydrazine,  $H_2O_2$ , MDA, and SOD. Tobacco cultivar (cv.) NC2326 becomes resistant to *Phytophthora nicotianae* by rapidly inducing accumulation of sesquiterpenoid phytoalexin (antimicrobial substance) at the penetration site. After treating tobacco cultivar NC2326 with mevinolin, an inhibitor of sesquiterpene biosynthesis, the plants became sensitive to *P. nicotianae*. However, pretreatment with Phi in NC2326 followed by mevinolin exposure did not increase its resistance. Also, the application of Phi on tobacco cv. Hick is susceptible to *P. nicotianae*, and Phi applications increased phytoalexin levels, suggesting that Phi activated more than one defense response (Guest et al., 1995).

Phenolic compounds play a crucial role in providing physical and chemical barriers to pathogen growth at the site of infection. This compound is produced by the phenylpropane pathway and is derived from the amino acids phenylalanine and tyrosine (Candela et al., 1995; Jiang et al., 2019). To study the phenylpropane pathway for Phi protection (Jackson and Andrews, 2000), the activities of two enzymes involved in the phenylpropanoid pathways, 4-coumarate coenzyme A ligase (4-CL) and cinnamyl alcohol dehydrogenase (CAD), and concentration of soluble phenolic and Phi were measured. They found that when the Phi concentration in the root is low, it interacts with the pathogen at the entry site to stimulate host defense enzymes. At high concentrations of Phi, it can directly affect the pathogen before it can communicate with the host to prevent it from growing, and the host defense remains unchanged. In potato *P. infestans* pathosystems, Phi-treated potato leaves had an increased amount of phenolic and phytoalexin after pathogen infection. The antioxidant enzyme compounds after Phi treatments were also

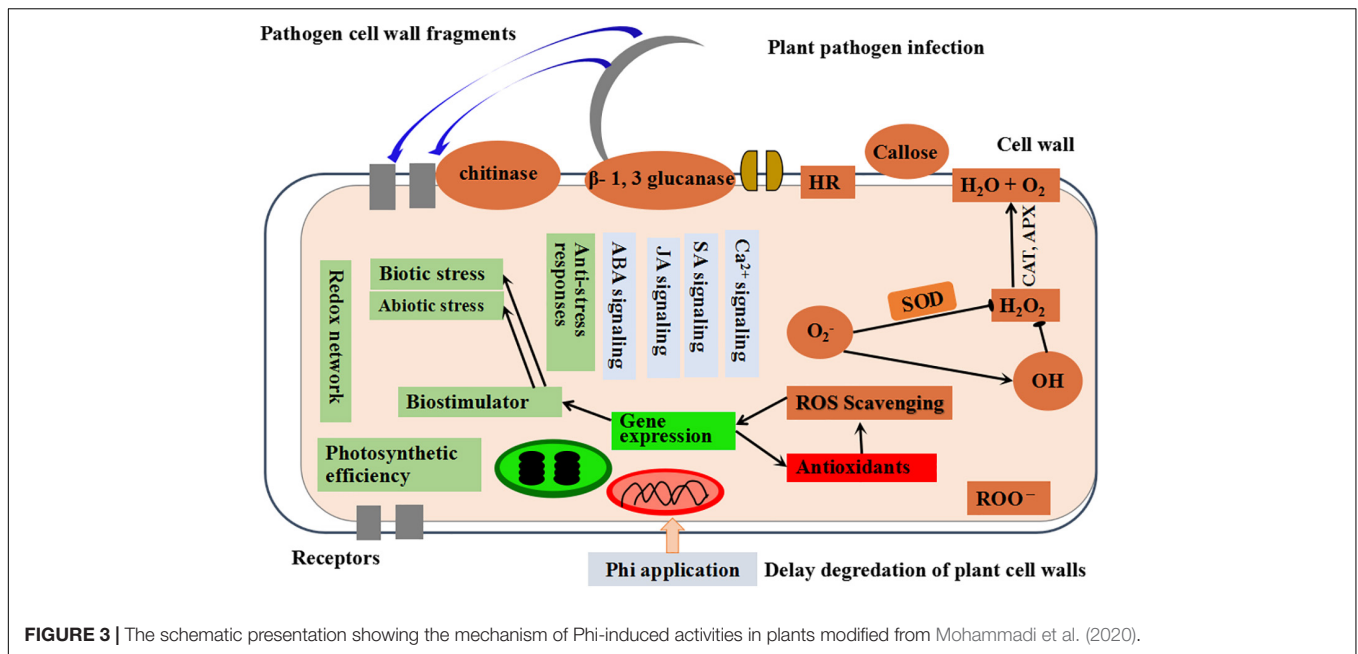
increased (Machinandiarena et al., 2012; Mohammadi et al., 2019).

In addition to the accumulation of phytoalexins and phenolic, after KPhi application on potatoes sensitive to *P. infestans* increased antioxidant enzyme activities levels in potato tubers (Mohammadi et al., 2019). Under the light microscope, SOD release, rapid cytoplasmic aggregation, and nuclear migration were observed in Phi-treated tobacco against *P. nicotianae* and Phi-treated *Arabidopsis* against *P. palmivora* (Guest and Grant, 1991; Daniel and Guest, 2005). Recently, Phi-treated *Arabidopsis* leaves showed faster and intense callus deposition and  $H_2O_2$  production than untreated leaves after infection with *P. cinnamomi* (Eshraghi et al., 2011). Olivieri et al. (2012) reported increased pectin in the cortex of tubers obtained from Phi-treated plants.

Current knowledge about plant defense responses has been extensively reviewed (Boller and He, 2009; Gimenez-Ibanez et al., 2019). The defensive response of plants to pathogens can be divided into two categories: the initial response to initial resistance that occurs within minutes and the response to resistance to specific host-pathogen genes that lasts for several days. To infect plants, the pathogen must first penetrate the physical barrier of the cell wall and neutralize any pre-prepared antimicrobial compounds, such as phytoalexins. The next hurdle is preventing plants from recognizing pathogen-related molecular patterns (PAMP) by non-self-aware systems (Nejat and Mantri, 2017). Examples of PAMP are fungal chitin and bacterial flagella; PAMP forms a non-specific basic immune response, including ion penetration, protein phosphorylation cascade including mitogen-activated protein kinase (MAPK) and ROS, and signaling molecules such as salicylic acid (SA) and jasmonic acid (JA) ethylene (ET) production. Induction of genes related to defense (such as hydrolase), phytoalexin biosynthesis, callus production, cell wall expansion, and possibly programmed cell death (Boller and He, 2009; Mohammadi et al., 2020).

In case of attack by pathogens, germinating plants show rapid defense responses. Natural or synthetic compounds can be used to chemically induce the onset of plant defense, and plants with previous experience of pathogen contamination show an initial defense response (Martinez-Medina et al., 2016). Saffron leaves that have been pretreated with different concentrations of SA under greenhouse conditions accumulated high levels of phenolics and flavonoids; activity and gene expression of PAL enzymes increased profiled proteins before and after Phi treatments in potato leaves (Lim et al., 2013; Tajik et al., 2019). These findings strongly demonstrate that priming plant leaves for 3 days induced the production of a large number of defense proteins against *P. infestans*.

Several crop species that had been sprayed with Phi and inoculated with different pathogens showed protection functions to the plants; such protection is related to the rapidly increased amounts of phytoalexin and ROS than untreated, infected plants (Ramezani et al., 2017a; Borza et al., 2019; Mohammadi et al., 2019). Cucumber plants infected with *Pythium ultimum* and treated with Phi-evidenced induction of antioxidant enzymes decreased ROS and alleviated damping-off symptoms (Mofidnakhai et al., 2016). Saindrenan et al. (1990) reported



**FIGURE 3** | The schematic presentation showing the mechanism of Phi-induced activities in plants modified from Mohammadi et al. (2020).

that the resistance induced by Phi treatment to the isolated leaves of cowpea after inoculation with *P. cryptogea* could be setback by pre-application of the leaves with aminooxyacetate (AoA) and PAL ammoniolyase inhibitor in the phenylpropanoid pathway. This suggests that phytoalexin biosynthesis is responsible for mediating the effects of Phi. Several changes in the host-pathogen interface have been observed after the treatment of plants with Phi. For example, Jiang and Hartung (2008) showed that Phi increases in the development of electron deposits are formed in uninfected neighboring cells. However, in the extraction of enhanced defense response, the indispensable factor is the presence of Phi and pathogens (Figure 3) (Jackson et al., 2000).

Pathogens also produce defense-inducing effects, such as viral gene product (AVR) proteins, lecithin, and elicitors. Pathogen molecules can be specifically identified by plant host resistance proteins (R proteins), which can determine the resistance between specific pathogens and hosts (Cui et al., 2015). The detection of pathogen AVR protein through plant dependence and R protein is more complicated than the simple interaction proposed by the gene-gene concept and can be described more accurately by the guard hypothesis (Jones and Dangl, 2006) or the decoy model (van der Hoorn and Kamoun, 2008). The guard hypothesis says that plant R-proteins (protectors) are associated with endogenous host proteins that are common-target proteins for pathogens. The interaction of effective pathogen proteins with host proteins changes their structure, which is then recognized by protective proteins. R-protein activation is highly regulated in plants because it ultimately leads to programmed cell death. However, early detection is important to successfully defend against plants. Any model of the effect of Phi on plants requires an increase in defense responses in the treated plants. However, if Phi has a direct effect on pathogens, it is essential. The low Phi activity *in vitro* indicates that the plant immune response is involved to a certain extent, so it is concluded that plants

without a dynamic immune response are not protected by Phi (Arfaoui et al., 2020). Based on a 2-year field experiment, Borza et al. (2019) documented that a mixed-mode of Phi affects both plant defense and pathogen growth *in vitro*. However, the results were consistent with the site of Phi operation in *Verticillium* spp.; these studies indicate that plant defense plays a vital role in preventing fungi development.

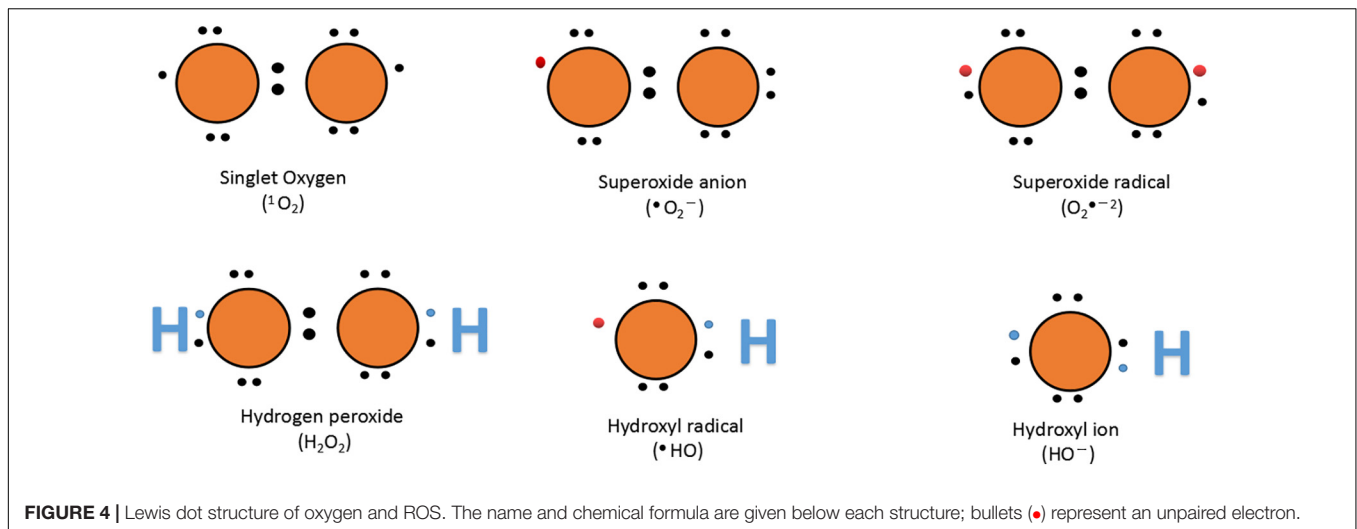
### Phi Mediated Improvement in Alleviation of Adverse Effects of ROS in Plants After Being Challenged by Plant Pathogens

Atmospheric oxygen ( $O_2$ ) is a free molecule, and triple oxygen ( $3O_2$ ) exists on earth. The two electrons of parallel and unpaired rotation have the same number of rotations and lose their reactivity. However, the extra energy from other biochemical reactions, electron transfer chains, ultraviolet B, and ionizing radiation helps to release  $3O_2$  from the limitation of rotation and convert it to ROS (Figure 4) (Mailloux, 2016).

Many reports have shown that during several stresses, a large amount of ROS is produced that can damage intracellular macromolecules (Forouzanfar et al., 2016; Ramezani et al., 2018). The balance between ROS due to PS II damages and antioxidant enzyme activity can determine plant safety (Dias et al., 2014). Preliminary reports indicated that Phi induces high resistance on pretreated plants to pathogenic stresses and is mainly related to the high accumulation of defense enzymes in host plant (Oyarburo et al., 2015).

Plant antioxidants and oxidative enzyme production are enhanced by aerobic change, balancing the oxidative damage caused by ROS. Defense enzymes including CAT, APX, SOD, and various molecules including GR, Prl, AsA, and Car have non-enzymatic protective function (Jung et al., 2000; Lombardi and Sebastiani, 2005; Singh et al., 2009; Forouzanfar et al., 2016;





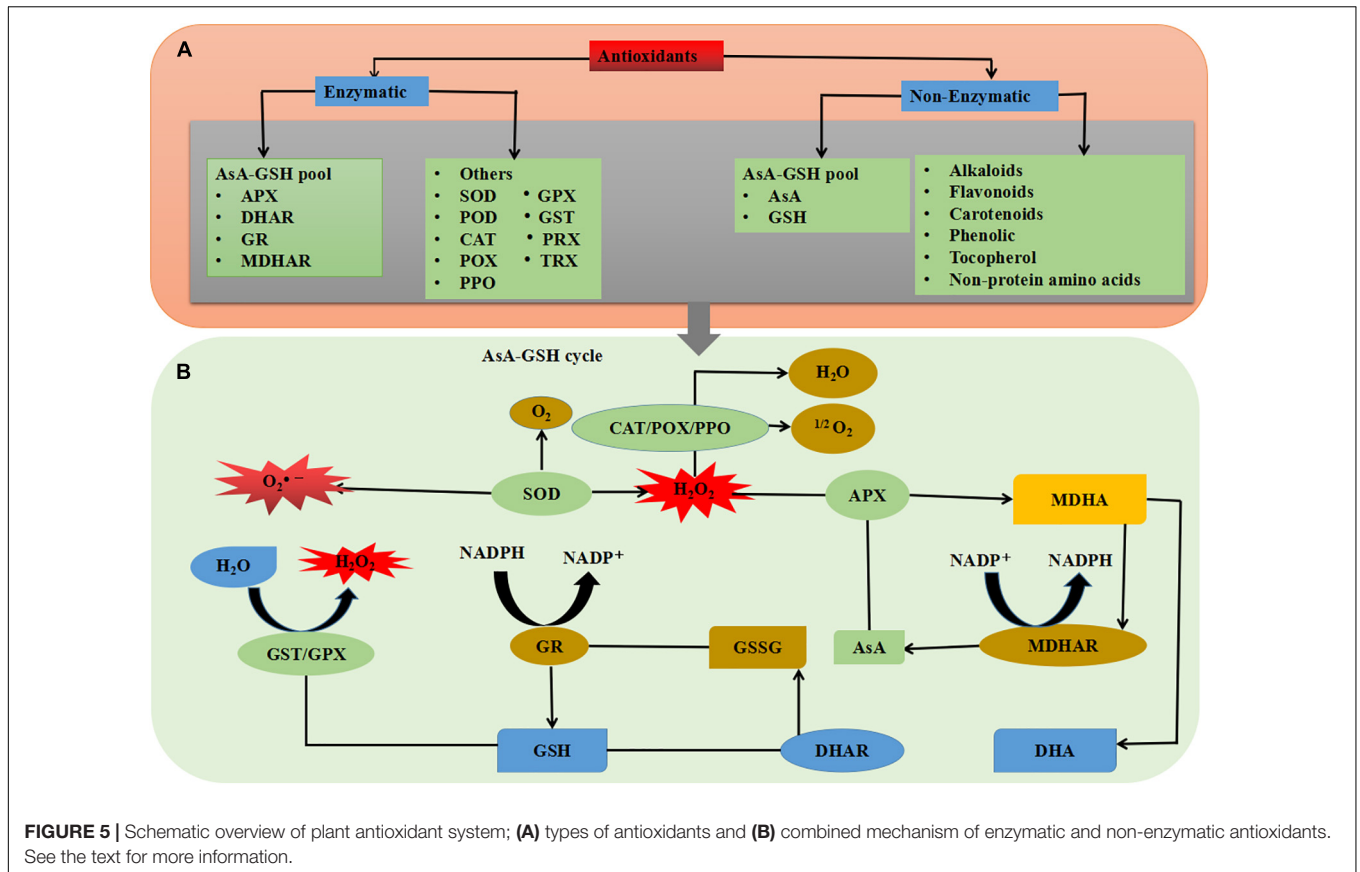
Debnath et al., 2018; Ramezani et al., 2018). Similar to other biological stresses, fungal infections cause the excess production of free radicals, such as hydroxyl radicals ( $\text{OH}^\bullet$ ),  $\text{H}_2\text{O}_2$ , and SOD production (Mofidnakhai et al., 2016). It is well described that after activation of antioxidant enzymes, the plant's tolerance to biotic stress significantly increased (Lobato et al., 2011). Phi has a significant influence on various enzymatic processes (CAT, POD, SOD, APX, PPO, and GPX) and non-enzymatic processes (phytoalexins, phenolics, flavonoids, and anthocyanins), which support the fight in the overproduction of ROS caused by pathogens in stimulating the integration of plant cells (Figure 3).  $\text{O}_2$  acts as an electron receptor with subsequent accumulation of ROS such as singlet oxygen ( $^1\text{O}_2$ ), hydroxyl radical ( $\text{OH}^\bullet$ ), superoxide radical ( $^\bullet\text{O}_2^{-2}$ ), and  $\text{H}_2\text{O}_2$  under stressful conditions. Low concentrations of Phi (0.005%) have been shown to help protect plants against ROS-induced oxidative damage; however, higher concentrations of Phi act as a per oxidant, causing ROS stimulation and oxidative stresses (Liu et al., 2016).

Many researchers have described Phi for increasing ROS inhibitory activity, decreasing MDA concentration, membrane damage, and triggered gene expression (Mofidnakhai et al., 2016; Feldman et al., 2020). Besides, reduced production of  $\text{H}_2\text{O}_2$  under Phi treatment has also been confirmed (Novaes et al., 2019). Under fungi stress, lowered  $\text{H}_2\text{O}_2$  contents were observed in Phi-treated soybean (Batista et al., 2020). Meanwhile, plants treated by Phi showed fewer amounts of MDA under heat stress, indicating that Phi is critical in reducing lipid peroxidation by increasing antioxidant enzymes and protecting the membrane structures of potato seedlings (Xi et al., 2020), *Cucumis sativus* L. (Ramezani et al., 2017a), and *Glycine max* L. (Batista et al., 2020). Also, it was observed that the production of lipid MDA decreases with increasing Phi concentration under pathogen stress (Mohammadi et al., 2020). The comprehensive effect of MDA on plant cells is to reduce membrane fluidity to increase membrane leakage and to prevent damage to proteins, enzymes, and membrane in ion channels (Saed-Moucheshi et al., 2014). Appropriate concentrations of Phi are useful

for reducing lipidoxygenase overexpression to maintain the formation of fatty acids in addition to the reduced generation of ROS, which is driven by the regulation of antioxidant systems (Ahanger and Agarwal, 2017).

### Phi Mediated Improved Plant Resistance by Modulation of Enzymatic and Non-enzymatic Antioxidants

The antioxidant defense system including both non-enzymatic antioxidants and some antioxidant enzymes consists of lower molecular weight (Hasanuzzaman et al., 2019). Non-enzymatic antioxidants like AsA, reduced glutathione (GSH),  $\alpha$ -tocopherol, phenolic, flavonoids, alkaloids, and non-protein amino acids work in a coordinated path with antioxidant enzymes such as SOD, CAT, POD, PPO, APX, monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), GR, GPX, glutathione-S-transferase (GST), thioredoxin (TRX), and peroxireductinase (PRX) to control ROS production (Figure 5) (Nath et al., 2018; Laxa et al., 2019). *In planta*, SOD is directly related to the stress that initiates the first line of defense, by converting  $\text{O}_2^-$  to  $\text{H}_2\text{O}_2$  (Table 2) (Biczak, 2016; Luis et al., 2018). Produced  $\text{H}_2\text{O}_2$  can be further converted to  $\text{H}_2\text{O}$  by CAT, APX, and GPX enzymes or catalyzed by the AsA-GSH cycle. In a plant cell, the AsA-GSH is the main antioxidant defense pathway in  $\text{H}_2\text{O}_2$  detoxification, which consists of non-enzymatic antioxidants AsA and GSH, as well as the four important enzymes APX, MDHAR, DHAR, and GR. In antioxidant defense system, the AsA-GSH cycle plays a key role in minimizing  $\text{H}_2\text{O}_2$  homeostasis and redox (Hasanuzzaman et al., 2019). Furthermore, the GPX-GST is also an essential enzyme for  $\text{H}_2\text{O}_2$  and xenobiotic detoxification (Figure 5) (Hasanuzzaman et al., 2018). Among the non-enzymatic antioxidants, AsA and GSH are the most abundant soluble antioxidants in higher plants, which play an important role as electron donors, and capture ROS directly in the AsA-GSH cycle (Hasanuzzaman et al., 2019). Furthermore,  $\beta$ -carotene reacts with  $^\bullet\text{OH}$ ,  $^\bullet\text{O}_2^-$  and  $\text{ROO}^\bullet$  radicals which



**FIGURE 5 |** Schematic overview of plant antioxidant system; **(A)** types of antioxidants and **(B)** combined mechanism of enzymatic and non-enzymatic antioxidants. See the text for more information.

**TABLE 2 |** Phosphite mitigates pathogen stress-induced oxidative damage by changes in different antioxidant enzyme activities in several plant species.

Plant species	Diseases	Causal agent	Method application of	Antioxidant activity	References
<i>Avena sativa</i> L.	White mold	<i>Sclerotinia sclerotiorum</i>	Foliar application	CHI ↓ GLU ↓ PPO ↓ SOD ↑ APX ↑	Fagundes-Nacarath et al. (2018)
Common bean	Without inoculation	Normal condition	Root application	CAT ↑ POD ↑	Ávila et al. (2013)
<i>Cucumis sativus</i> L.	Damping off	<i>Pythium ultimum</i> var.	Foliar spray	SOD ↑ POD ↑ CAT ↑	Mofidnakhaei et al. (2016)
<i>Cucumis sativus</i> L.	Downy mildew	<i>Pseudoperonospora cubensis</i>	Foliar spray	CHI ↑ GLU ↑ PPO ↓	Ramezani et al. (2018)
<i>Glycine max</i> L.	White mold	<i>Sclerotinia sclerotiorum</i>	Foliar spray	CHI ↑ GLU ↑ SOD ↓ POD ↓ CAT ↑ PAL ↑	Novaes et al. (2019)
<i>Malus pumila</i>	Apple scab	<i>Venturia inaequalis</i>	Foliar spray	POD ↑ GLU ↓	Felipini et al. (2016)
<i>Solanum tuberosum</i> L.	Late blight	<i>Phytophthora infestans</i>	Foliar application	SOD ↑ POD ↑ CAT ↑ APX ↑	Mohammadi et al. (2020)

cause a decrease in ROS production in plant cells (Figure 5) (Kapoor et al., 2019).

Plants produce a set of antioxidant enzymes after exposure to various stresses, and it is interesting to note that the use of Phi has been shown to increase the antioxidant enzyme activities and decrease the ROS overproduction to cope with stress (Mohammadi et al., 2020; Xi et al., 2020). In pathogen stress, ROS can be detoxifying by antioxidant compounds (Table 2). Antioxidant enzymes, such as SOD, POD, APX, CAT, PPO, CHI, and GLU, are believed to positively react to Phi application in order to induce pathogen tolerance in plants (Mohammadi et al., 2019; Novaes et al., 2019). The researchers hypothesized that increasing the level of Phi-mediated antioxidant defense is one of the key mechanisms which can protect the plant from oxidative stress stimulated by the phytopathogens (Machinandiarena et al., 2012). SOD, APX, and CAT activities were significantly enhanced by Phi treatment in potato and cucumber seedlings under *P. infestans* and *Pseudoperonospora cubensis* stress, respectively (Mofidnakhai et al., 2016; Ramezani et al., 2018; Mohammadi et al., 2020). In another study, the accumulation of antioxidants in cucumber due to Phi mediated increased levels of SOD, POD, APX, and CAT activities in plants (Mofidnakhai et al., 2016). An increase in activities of the SOD, CAT, POD, APX, and PAL enzymes is observed in different crops like potato, common bean, *Avena sativa* L., and *Solanum lycopersicum* L. (Fagundes-Nacarath et al., 2018; Mohammadi et al., 2019), as seen in Table 2. One of the first changes after Phi application on *P. palmivora* mycelium treatment is the size of adenylate nucleotides (Griffith et al., 1993). Adenylate is involved in the synthesis of purines, pyrimidines, aromatic amino acids, nicotinamide adenine dinucleotides (NAD<sup>+</sup>), and nicotinamide adenine dinucleotide phosphate (NADP<sup>+</sup>) (Nelson et al., 2008). The evidence of the increases in enzyme activity observed in the body can be explained as a secondary effect of Phi. This is because transcriptional induction is a homeostatic reaction that limits the inhibitory effect of Phi on the enzyme. The organism tries to increase the metabolism through a pathway (Nelson et al., 2008). Besides, the increase in SOD accumulation is caused by the rapid conversion of  $\bullet\text{O}_2^-$  to  $\text{H}_2\text{O}_2$ , which is produced in the chloroplast electron transport chain of the mitochondria. Evolving  $\text{H}_2\text{O}_2$  was neutralized by CAT in the cytoplasm or by APX in the ASA-GSH pathway. In addition, increased SOD activity in Phi-treated seedlings, following optimum defense of chloroplast yield, altered the likelihood of  $\bullet\text{OH}^-$  synthesis (Nouet et al., 2011). Inhibition of  $\text{H}_2\text{O}_2$  and MDA to water and lipid alcohol is performed by two important enzymes: GSH-POX and GR (Lim, 2012). GSH-PX is considered a vital enzyme, which is strongly activated by Phi in different plants under different environmental stresses (Xi et al., 2020). Increasing the activity of antioxidants reduces the levels of  $\text{H}_2\text{O}_2$  and MDA and improves pepper and cucumber plants by overcoming oxidative damage stimulated by ROS under pathogen stress (Liu et al., 2016; Mofidnakhai et al., 2016). Phi supplementation in citrus byproducts regulates the antioxidant system by increasing the activity of SOD, CAT, and APX after four treatments on coffee seedlings. In addition, increasing the antioxidant content

continuously evolves in defense of the PS electron transport chain by maintaining better levels of the NADP<sup>+</sup> and inhibiting the composition of toxic radicals (Fernandes et al., 2014). These results show that proper use of Phi can be useful to improve the antioxidant defense mechanism of plants under pathogen stress.

## Phi Suppresses Adverse Effects of Oomycete Pathogens

The use of Phi-based fungicides can strengthen plants for a rapid and vigorous defense response to many diseases, fungi, and oomycetes, such as the genera *Phytophthora*, *Fusarium*, and *Rhizoctonia* (Machinandiarena et al., 2012; Alexandersson et al., 2016). Johnson et al. (2004) evaluated the effectiveness of the commercial prescription of Phi Phostrol (containing 53.6% of sodium and potassium salts of Phi and ammonium) to control tuber rot caused by *P. infestans* and *Phytophthora erythroseptica*. The mean prevalence and intensity of late potato disease and facial rot in tubers obtained from two treatments at 7.49 kg/ha were lower than control tubers. Miller et al. (2006) reported that the application of twice phostrol (8 pints/acre) for late blight and three times (10 pints/acre) for pink rot was significant to protect tubers from these diseases. Moreover, postharvest application of 14% phostrol for late blight and pink rot suppression after 77 days in storage was examined; Phi was able to control 90% of late blight and 61% of pink rot symptoms when compared with untreated potato tubers (Şandor and Opruța, 2012).

Seed tubers and potato leaves pretreated with Ca and K salts of phosphorous acid were examined (Lobato et al., 2008). With a ratio of 1% (V/V) as a commercial product equal to 3 L/ha, Phi provided tubers with a protective level from *P. infestans*, while excellent protection of foliage was provided in four application rates of 2% of the product. In contrast, systemic fungicides, such as chlorothalonil (Bravo) or mancozeb (Dithane or Manzate), were applied on potato plants in combination with Phi during the growing season in Canada (Wang-Pruski et al., 2010). In a greenhouse study, foliar sprays of 1%  $\text{KH}_2\text{PO}_3$  three times with an interval of 15 days significantly reduced the severity of late blight in potato tubers of two Chinese potato cultivars Xinjia No. 2 and Zhongshu No. 3, 50% and 40%, respectively, on the tubers of untreated potato plant (Mohammadi et al., 2019). In another experiment by Wang-Pruski et al. (2010), a 3-year field trial was conducted to evaluate Phi's efficacy (Confine<sup>TM</sup> containing 45.8% mono- and di-potassium salts of phosphorous acid) on potato late blight of Prince Edward Island, Canada. Analysis of the severity of the disease indicated that the leaves of the potato plants were pretreated five times in 2007 and 2008 at a ratio of 58 L product/ha, and the disease was significantly less than that of the untreated plants. The combined use of Phi and chlorothalonil provided better disease inhibition compared with the use of Phi or chlorothalonil alone. Also, by using Phi alternately with Bravo, the usage of Bravo was decreased by 50%. The late blight pressure was high in both field seasons, but Phi alone or in combination with Bravo provided complete control of late blight (Wang-Pruski et al., 2010).

**TABLE 3** | Suppression of oomycetes/*Phytophthora* spp. diseases by different sources of phosphite on several plant species.

Plant	Disease	Causal agent	Experimental details	Phosphite source (dosage)	References
Avocado	Root rot	<i>P. cinnamomi</i>	Trunk injection	Potassium phosphite	McLeod et al. (2018)
Banksia	<i>P. cinnamomi</i>	<i>P. cinnamomi</i>	Glasshouse	Mono-dipotassium phosphite	Barrett et al. (2003)
Citrus	Brown rot	<i>P. citrophthora</i>	Pot culture (soil and foliar application)	Potassium phosphite	Oren and Yogev (2002)
Orange	Brown rot	<i>P. citrophthora</i>	Soiless media culture	Potassium phosphite	Orbović et al. (2008)
Papaya	Fruit rot	<i>P. palmivora</i>	Growth	Potassium phosphite	Smillie et al. (1989)
Pepper	Crown rot	<i>P. capsici</i>	Chamber (pot culture) hydroponic culture	Phosphorous acid	Förster et al. (1998)
Potato	Pink rot	<i>P. erythroseptica</i>	Field trial	Phosphorous acid	Taylor et al. (2011)
Potato	Late blight	<i>P. infestans</i>	Pot culture Peat, perlite, and vermiculite	Potassium phosphite	Mohammadi et al. (2020)
Strawberry	Leather rot	<i>P. cactorum</i>	Pot culture (peat, steam disinfected soil and sand)	Phosphorous acid	Rebollar-Alviter et al. (2007)
Tobacco	Black shank	<i>P. nicotianae</i>	Growth chamber (pot culture)	Potassium phosphite	Guest et al. (1995)
Vinca	Shoot blight	<i>P. nicotianae</i>	Containers (pine bark medium)	Potassium phosphonate	Banko and Hong (2004)

In addition, Phi is effective as protectant fungicides against Dieback disease in indigenous plant species in Australia, like *Banksia brownie* (Hardy et al., 2001; Barrett et al., 2003), Brown rot in two citrus plants, *Citrus volkameriana* and *Citruslimonia* (Förster et al., 1998; Oren and Yogev, 2002). The incidence of *Phytophthora capsici* in tomato and pepper plants grown hydroponically by adding Phi was significantly reduced. On the other hand, foliar application of Phi in strawberry (*Fragaria ananassa*) plants effectively protects fruits against *Phytophthora cactorum* leather rot for up to 7 days and also has a therapeutic activity of at least 36 h (Rebollar-Alviter et al., 2007). Likewise, foliar application of Phi decreased the prevalence of *P. infestans* and *P. erythroseptica*, although Phi did not affect the suppression of *Pythium ultimate* (Johnson et al., 2004). By combining foliar and postharvest treatment of Phi, potato tubers were effectively controlled against *P. erythroseptica*, which induced pink rot during storage (Taylor et al., 2011). Similarly, the postharvest application of Phi effectively controlled the spread of potato tubers during storage (Lobato et al., 2011; Mohammadi et al., 2019). Also, when the leaves were treated with Phi, the susceptibility of the tubers to *P. infestans* was reduced significantly (Liljeroth et al., 2016). Whereas, the use of Phi on harvested tubers effectively controlled oomycete during storage (Lobato et al., 2008). Moreover, combining Phi with a wide range of non-systemic fungicides like chlorothalonil showed the most effective control against potato late blight disease (Liljeroth et al., 2016). In vinca, 0.5 mM foliar application of Phi in 3–6 days meantime highly protects plants against *P. nicotianae*, as performed by spraying 3 g/L Aliette at 14-day intervals (Banko and Hong, 2004). In *Banksia brownii*, Phi gave high resistance to *P. cinnamomi* in the initial infection stage (Barrett et al., 2003). In *Banksia grandis*, *B. coccinea*, and *Eucalyptus marginata*, Phi's trunk injection gave reasonable control of *P. cinnamomi* and provides efficient control of the endangered native flora against this pathogen (Shearer et al., 2006). Also, Phi used on leaves alleviate death of four *P. cinnamomi*-infected *Banksia* spp. (Shearer and Fairman, 2007; Shearer and Crane, 2009). In the species of *Banksia* (Shearer

and Crane, 2012), the changes in genotype observed follow the Phi treatment to control this oomycete, and (Eshraghi et al., 2014) Phi has been reported to induce resistance to those pathogen in *Arabidopsis*, which also has been confirmed in *Banksia grandis* and *Eucalyptus marginata* plant as seen in Table 3 (Scott et al., 2015).

## General Characteristics and Economic Values of Oomycetes

According to Dick's classification in 2001, the oomycetes belong to the Chromista/Stramenopile kingdom and are commonly referred to as water mold and downy mildew. Miscellaneous algae (including brown algae and golden algae) originated from Stramenopiles. Sparrow reported the taxonomic classification of oomycetes in 1960 and 1976 and Dick's scientific work and research in 2001 (Birch and Whisson, 2001). They divided all oomycetes into two main groups, the first group containing water molds (Eurychasmiales, Leptomitales, and Saprolegniales) and the second group belonging to the Peronosporalean order (Rhipidiales, Pythiales and Peronosporales). Rhipidiales and Albuginea belong to the Peronosporalean branch like Peronosporales (Birch et al., 2012). According to Blum et al. (2012), the cell wall of the true fungi consists of chitin, but the oomycete cell wall is formed of cellulose and  $\beta$ -1,3-glucan. Therefore, it is classified as pseudo-fungi. However, due to some unique biological characteristics, the difference between oomycetes and other eukaryotic microorganisms is still in discussion. The vegetative growth of oomycetes in the filaments produces mycelium and can go through sexual and asexual spore replications. Oomycetes contain tubular forms of mitochondria to synthesize lysine (Vogel et al., 1970). Zoospores are formed by the cleavage of cytoplasmic membranes of asexual spores (Latijnhouwers et al., 2003). Zoospores include two flagella, one's tinsel anterior flagellum, and another whiplash flagellum. It contributes to the movement of mononuclear nucleated cells (Walker and van West, 2007). Oomycetes belong to a diploid trophic stage, but genetic recombination was not known in homologous diploid cells of other fungi. Due to the lack of



**TABLE 4** | Plant diseases are suppressed by different sources of phosphite.

Plant	Disease	Causal agent	Experimental details	Phosphite source	References
Apple	Apple scab	<i>Venturia inaequalis</i>	Pot culture Bovine manure campus Vermiculite Sand	Potassium phosphite	Felipini et al. (2016)
Apple	Fire blight	<i>Erwinia amylovora</i>	Trunk injection (fiel d trial)	Potassium phosphite	Aćimović et al. (2015)
Apple	Blue mold	<i>Penicillium expansum</i>	<i>In vitro</i> and postharvest treatment	Potassium phosphite	Amiri and Bompeix (2011)
Apple	Moldy-Core	<i>Alternaria alternata</i>	Field trial	Potassium phosphite	Reuveni et al. (2003)
Bok Choy	Club rot	<i>Plasmodiophor abrossicae</i>	Field trial	AG3 Phosphonate	Abbasi and Lazarovits (2006)
Bristle oat	Nematode	<i>Meloidogyne marylandi</i>	Soil drenches	Phosphonic acid	Oka et al. (2007)
Cabbage	Club rot	<i>Plasmodiophor abrossicae</i>	Field trial	AG3 Phosphonate	Abbasi and Lazarovits (2006)
Corn	Foliar disease	<i>Phaeosphaeria maydis</i> <i>Cercosporazea emaydise</i>	Field trial	Potassium phosphite	Da Silva et al. (2020)
Corn	Root lesion nematode	<i>Exserohilum turcicum</i> <i>Pratylenchus brachyurus</i>	Pine bark, coconut fiber, and vermiculite	Manganese phosphite	Puerari et al. (2015)
Corn	Downy mildew	<i>Peronosclerospora sorghi</i>	Pot culture (peat, vermiculite, and soil)	Phosphonic acid	Panicker and Gangadharan (1999)
Cucumber	Downy mildew	<i>Pseudoperonos pora cubensis</i>	Pot culture Peat, perlite, and coco peat	Potassium phosphite	Ramezani et al. (2018)
Cucumber	Damping off	<i>Pythium ultimum</i> var.	Pot culture Peat, perlite, and coco peat	Potassium phosphite	Mohammadi et al. (2020)
Grape	Downey mildew	<i>Plasmopara viticola</i>	Field trial	Potassium phosphite	Speiser et al. (2000)
Pecan	Pecan scab	<i>Fusicladium effusum</i>	Trunk injection	Potassium phosphite	Bock et al. (2013)
Pinus spp.	Pitch canker	<i>Fusarium circinatum</i>	Pot culture, peat, and perlite	Potassium phosphite	Cerqueira et al. (2017)
Potato	Tuber rot	<i>Rhizoctonia solani</i> <i>Fusarium solani</i> <i>Streptomyces scabies</i>	<i>In vitro</i> culture	Calcium phosphite Potassium phosphite Copper phosphite	Lobato et al. (2010)
Rice	Stem rot	<i>Nakataea oryzae</i> (Catt.)	Field trial	Potassium phosphite	Martinez-Medina et al. (2016)
Soybean	Charcoal root rot	<i>Macrophomina phaseolina</i>	<i>In vitro</i> assay	Manganese phosphite	Scott et al. (2015)
Soybean	White mold	<i>Sclerotinia sclerotiorum</i>	Pot culture Peat, pine bark, and vermiculite	Manganese phosphite	Novaes et al. (2019)
Wheat	Nematode	<i>Heterodera avenae</i>	Soil drenches	Phosphonic acid	Oka et al. (2007)

homologous recombination, few species of genus *Phytophthora* have been reported, such as *P. infestans*, *Phytophthora ramorum*, and *Phytophthora sojae* (Tyler, 2007; Schornack et al., 2009). The genome size of oomycetes varies from 18 to 37 Mb (Judelson, 2012). Molecular research revealed that the oomycete genome consists of repetitive sequences, and some genes such as *Cytb* are much conserved among *Phytophthora* spp. (Mao and Tyler, 1996; Lamour et al., 2007). However, many researchers are still working on the genome of *Phytophthora* spp. to study its unique characteristics.

The habitat of saprophytic oomycetes is primarily humid and wet soil. Recycling and rotting organic matter is one of the positive effects of saprophyte (Margulis et al., 2000; Kamoun et al., 2003). Oomycete plant pathogens are the source of many types of destructive diseases in crops. The genus of *Phytophthora* contained more than 60 species, most of which vigorously attack dicotyledon crops. Crops like potato, tomato, pepper, alfalfa, and soybeans were facing devastating problems by *Phytophthora* spp. (Agrios, 2005). *Phytophthora infestans* is the most critical disease-causing late blight of

potatoes (Birch and Whisson, 2001; Kamoun, 2003). Worldwide, approximately US\$6.7 billion annual loss occurs from the late blight of potatoes (Judelson, 2012). Many other economic-related diseases are caused by *Phytophthora* spp., such as *P. sojae* causing root rot disease in soybeans, *P. palmivora* and *Phytophthora megacarya* cause destructive disease in a black pod in cocoa, *P. cinnamomi* causes cranberry root rot and dieback of eucalypts, *P. ramorum* causes sudden death of the oak fish. *Albugo* and *Bremia* which cause white rust, mild mold caused by binding biotrophs *Plasmopara viticola* are not included in the *Phytophthora* genus. *Pythium* is another genus that is not included in *Phytophthora*, which comprises more than 100 species that cause many economic diseases.

## Phi Mediated Enhancement of Plant Resistance to Various Plant Pathogens

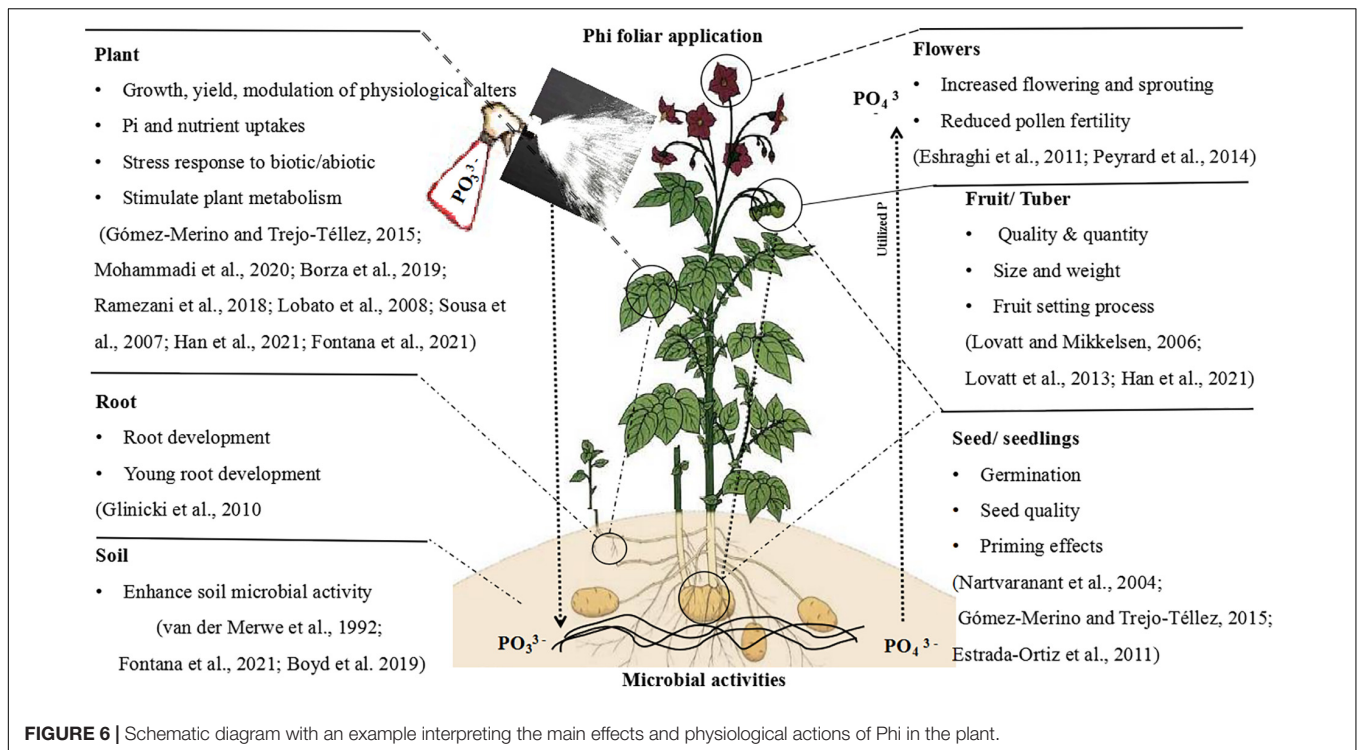
Phi has been documented as an effective pesticide to control several phytopathogenic organisms, such as nematode, fungi, and bacteria (Deliopoulos et al., 2010; Percival and Banks, 2014; Puerari et al., 2015). Phi induces a wide range of resistance to plant pathogens (Jost et al., 2015) and plays a vital role as the initial molecule of plant defense responses (Machinandiarena et al., 2012; Burra et al., 2014). In the occurrence of pathogenic bacteria, the use of 1.0 or 0.67 (v/v) Phi inhibits approximately 80% and 60% growth of *Streptomyces scabies* in potatoes, respectively (Lobato et al., 2010). When Phi is applied to the leaves of field-grown potato, the collected tubers showed less susceptibility to *Erwinia carotovora* inoculation, indicating that Phi induced systemic immune resistance (Lobato et al., 2011). In apples, the use of Phi highly decreased the prevalence of a blue mold caused by *Penicillium expansum* in injured and infected fruits (Amiri and Bompeix, 2011), while trunk injection was useful in the management of fire blight caused by *Erwinia amylovora* in apple trees (Aćimović et al., 2015). It was also used as a fungicide to control *Pseudoperonospora humuli*, which causes mold production in grapes (Salmon and Ware, 1925). In *Cucumis sativus*, Phi effectively contains *Pythium* spp. and suppresses disease by increasing the Phi concentration (Mofidnakhai et al., 2016; Mofid Nakhai et al., 2018). Researchers reported that Phi control *Plasmopara viticola*, but not *Oidium tuckeri* and *Pseudopezicula tracheiphila* in grape (Speiser et al., 2000). In their study, the use of Phi resulted in Phi residues in wine, which were nevertheless assessed toxic and safe. According to Reuveni et al. (2003), Phi treatment on apple fruits or trees gives a sufficient reduction of moldy core caused by *Alternaria alternate* and KPhi trunk injection in apple trees decreased *Erwinia amylovora* causal agent fire blight (Aćimović et al., 2015). In turnip, Chinese cabbage, and cabbage, the Phi treatment reduced disease severity of clubroot casual agent of *Plasmodiophora brassicae* (Abbasi and Lazarovits, 2006). In *Pinus* and *Pseudotsuga menziesii*, Cerqueira et al. (2017) reported that Phi prohibited *Fusarium circinatum* mycelium grown in a dose-dependent path. In corn, there is an efficient reduction in the occurrence and severity of *Peronosclero sporasorgi*, at the same time, yield increased by 73% (Panicker and Gangadharan, 1999).

In *Glycine max* L. Silva et al. (2011) documented that the Phi decreased spot losses due to *Peronospora manshurica* incidence, while for the first time (Scott et al., 2015) witnessed an effective reduction of *Macrophomina phaseolina* by using a combination treatment with plant growth rhizobacteria (PGPR) grown under glasshouse conditions. Therefore, Phi can be a reasonable pesticide to prevent the incidence and prevalence of such pathogens in crops (Shafique et al., 2016). Because it is a global pathogen that causes many diseases including root rot, stem rot, and dry root stem rot around 500 plant species such as vegetables, fruits, and crops, for detailed information, see **Table 4** (Khan, 2007).

Plant-parasitic nematodes are highly economic important parasites. In maize, Phi application was useful for controlling *Pratylenchusbra chyrurus* (Dias-Arieria et al., 2012). Phi's capacity to accumulate plant defense response primed plants by phytoalexins synthesis (Dercks and Creasy, 1989). In addition, manganese Phi was effective against *Meloidogyne javanica* prevention in *Glycine max* and decreased the number of eggs/gram of root when applied 7 days prior to infection of nematodes in pest-resistant cultivar (Puerari et al., 2015). Similarly, Oka et al. (2007) found that the use of Phi in wheat and oats significantly suppressed *Heterodera avenae* and *Meloidogyne marylandi*, which stimulated Phi's ability to confirm the synthesis of phytoalexins in plants (Dercks and Creasy, 1989; Han et al., 2021). Since nematodes are prevalent in some vegetables and crops, Phi is a highly effective bactericide to manage such pathogens in agriculture. The general response of plants to Phi application is shown in **Figure 6**.

## Phi-Mediated Gene Expression Modification Under Pathogen Stress

Previously, microarray analysis determined the changes in gene expression after Phi application and pathogen infection (Feldman et al., 2020). Their findings indicate a differential expression of 172 genes after Phi treatment and 22 Phi genes after pathogen infection, mainly the genes involved in signal transduction and defense responses, expressed (Feldman et al., 2020). Plant hormones play a central role in the expression of defense-related genes. Phi elevated the transcription of the genes involved in abscisic acid (ABA), ethylene biosynthesis, and mitogen-activated protein kinase cascade (MAPK) under *P. capsici* stress, which in turn elevated H<sub>2</sub>O<sub>2</sub>, stimulating expression and activities of antioxidant enzyme genes in pepper (*Capsicum annum* L.) (Liu et al., 2016). Also, the NAD kinase-2 mutation (NADK2) attenuates the disruption of ABA orifice closure and the ABA inhibition of light orifice opening. NADK2 disruption also disrupts ABA-stimulated H<sub>2</sub>O<sub>2</sub> accumulation (Sun et al., 2018). Phi primed the expression of salicylic acid (SA) and pathogenesis-related protein transcripts, mobilized essential components of basal resistance, enhanced disease susceptibility, isolated phytoalexin deficiency, and negatively regulated MAPK in *Arabidopsis*, thus triggering SA-dependent defense responses following inoculation by *Hyaloperonospora arabidopsidis* (Massoud et al., 2012). Profiled proteins before and after Phi treatments in potato leaves demonstrated that priming



**FIGURE 6 |** Schematic diagram with an example interpreting the main effects and physiological actions of Phi in the plant.

plant leaves for 3 days induced the production of a large number of defense proteins against *P. infestans* (Lim et al., 2013).

In *Arabidopsis*, PR1, PR5, and NPR are marker genes involved in salicylic acid pathways, while THI2.1 and PDF1.2 are involved in jasmonic acid/ethylene pathways (Turner et al., 2002). Investigation includes the expression of the five defense-related genes at the transcription level by using quantitative real-time reverse transcription-polymerase chain reaction (qRT-PCR) (Eshraghi et al., 2011). Phi-treated *Arabidopsis* showed enhanced expression of these five genes via SA- or JA/ET-dependent pathways. In contrast, it was SA dependent rather than JA or ET dependent, and PR1 expression was induced, indicating a similarity to SAR with SA-dependent priming (Massoud et al., 2012).

## PHI-MEDIATED ENHANCEMENT OF PLANT RESISTANCE TO ABIOTIC STRESSES

Phi also stimulates tolerance mechanisms against many abiotic stresses. In maize, the replacement of 1/4 Pi by Phi induced POD activity (Avila et al., 2011). Besides, Phi reduced the biomass stimulation of plants under low Pi supply, while no effect was observed in plants grown under efficient Pi supplement (Avila et al., 2011). In Phi-treated potato leaves exposed to ultraviolet stress, Phi increases photosynthetic pigments and psbA gene expression, which encodes the PS II reaction center protein D1 than control (Oyarburo et al., 2015). In addition, potatoes have been shown to prevent UV-B oxidative stress, thus mediating

UV-B stress tolerance (Oyarburo et al., 2015). In our previous publication, we reported that Phi application significantly increased heat resistance in potato seedlings by evaluating morphological characteristics, photosynthetic apparatus, PS II efficiency, oxidative stress, and DNA damage level. Also, RNA sequencing was performed to investigate the role of Phi signals and mechanisms of basic heat resistance (Xi et al., 2020). The findings showed that Phi treatment is not only essential for better plant performance but also improves plant heating by reducing oxidative stress and DNA damage and improving the biological synthesis of osmolytes and defense metabolites in case of exposure to adverse thermal conditions. RNA-Seq showed that Phi's immune responses to heat stress were regulated by reprogramming global gene expressions (Xi et al., 2020). Recently, it was noticed that the Phi application enhanced the PS pigments and proline accumulation in leaves under water-deficit stress with a value equal to those observed in irrigated control plants (Gonçalves et al., 2019). After the plant's exposure to abiotic stress, Phi increases the large number of proteins involved in cell wall formation as tolerance inducers. Thus, Phi, as resistance or tolerance inducer is not limited only to trigger plant defense process against pathogens but also interact to abnormal condition and incuse abiotic stress resistance.

## CONCLUSION

Phi compounds in various plant species suppress most omycete pathogens. Currently, in agriculture systems, Phi is being used as a plant biostimulant to boost nutritional efficiency, yield, crop quality, production, and tolerance to biotic and abiotic

stresses. Phi is also used as a highly useful resistance or defense inducer against several plant pathogens. Although, in nature, plants do not have the mechanisms to utilize Phi as a suitable P-source fertilizer. If not properly administered, its use can have devastating effects on plants. Because Phi appears as an effect of internal secretion, it may increase effective responses when used in low doses. However, when applied at high levels, adverse effects can result in cell damage or death. Therefore, its dosage and usage must be monitored to ensure a better response in a range of products. Here, we presented evidence that Phi can be used as biological stimulants in plant resistance. Phi as a plant biostimulant may activate several micro- and macromolecules and biochemical and physiological mechanisms that lead to the induction of plant tolerance response to biotic and abiotic stress factors and improve crop growth parameters and productivity. To confirm the efficiency of Phi application and prohibit adverse effects, the plant condition must first be considered. Besides, the details of testing and dosing of Phi for use must be timed appropriately to meet crop needs, which depends on crop genetic background, environmental signs and soil status, culture performance, chemical source, and Phi dosage. Using a new technology facilitated by science provides us this possibility to explore how and what extent Phi alters the molecular mechanism that triggers defense responses in several plant species. A piece of better knowledge on the molecular mechanisms of P utilization efficiency can be achieved. In crops, the proper application of Phi could allow plants to grow in soil with low Pi existence while addressing P degradation and herbicide resistance challenges.

As a result, Phi can stimulate positive effects on plants if appropriately combined with other protectant fungicides. Phi can act as biocellular stimulants in conventional cropping systems that increase crop yield, quality, and agronomic performance under stress conditions. Phi may also improve postharvest application on fruit quality. Also, it can be used to control pathogenic organisms, including bacteria, oomycete, fungi, and nematodes. Interestingly, Phi can be used in various methods, for example, as foliar spraying, trunk injection, postharvest treatment, hydroponic systems, and through fertilization, soil, and soil paints. However, the most influential method of application for different agricultural species and cultivars still

needs to be studied. There are several other factors to consider regarding the global application of Phi in agriculture, including the development of pathogen resistance to Phi, the effect of Phi on soil microorganisms, its potential threat to public health, etc. Therefore, there is a need to study and document all these phenomena soon. Environmental impacts and new trends in international food markets regarding Phi's residual level must be considered and ensured.

## AUTHOR CONTRIBUTIONS

MM conceived the idea, wrote the manuscript, and drafted the figures and tables. YC and MA revised the manuscript. BJ and MW organized the tables. KY, TL, XH, LY, CD, BH, and SP organized the figures. GW-P conceived the idea and revised the manuscript. YQ conceived, organized, and financially supported the manuscript.

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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