Heavy agricultural use of fertilizers has been implicated in degradation of the environmental quality of lakes, rivers and aquifers. There is also widespread public concern about the use of pesticides, including fungicides, on farms and their potential effect on our environment and food. However, it is certain that the use of fungicides as part of intensive agriculture has stabilized our food supply and permitted millions of people to live longer lives. Data from our laboratory and others have indicated that foliar sprays of phosphate and potassium salts can induce systemic protection against foliar pathogens in various crops such as cucumber, maize, rose, grapevine, apple, mango and nectarine. Expression of disease tolerance is dependent on a number of factors including use of fertilizers and pesticides. Therefore, the possible dual role of NPK fertilizers in activation of the mechanism(s) which induce plant protection against pathogens was studied. Data from the application of this concept to various host-pathogen interactions are presented in the present review. A single phosphate spray of 0.1 M solution induced a systemic protection against powdery mildew in cucumber caused by *Sphaerotheca fuliginea* and against common rust in maize caused by *Puccinia sorghi*, and northern leaf blight (NLB) caused by *Exserohilum turcicum*. This systemic protection against powdery mildew in cucumber, common rust or NLB in maize was obtained on upper leaves after NPK fertilizer application on the lower leaves. In both the latter host-pathogens interactions, growth increase was also observed in maize plants as a result of one foliar spray of phosphates. In addition, it was evident throughout all the experiments that a single application of phosphates was effective in suppressing the lesions of powdery mildew on the diseased foliage of cucumber, greenhouse-grown roses, field grown mango, nectarine and grapevine. This phenomenon was investigated in combination with fungicides. © 1998 Elsevier Science Ltd. All rights reserved

**Keywords:** cucumbers; grapes; systemic induced resistance (SIR); maize; phosphates; roses; mango; nectarine

**Introduction**

Plant diseases continue to play a major limiting role in agricultural production, particularly in intensively managed crops. Concerns about food safety, environmental quality and pesticide resistance have dictated the need for alternative pest management techniques. Breeding for resistance, and plant immunization are among the possible alternatives and can be promoted as possible strategies for inclusion in an Integrated Pest Management (IPM) program. IPM is a combination of crop protection practices, designed to keep pests below a designated economic threshold; these practices fall into the categories of chemical, cultural and biological (including host-plant) resistance. It is becoming increasingly evident that plant disease resistance is, many times, an induced response to the pathogen. Recent reports strongly indicate that the mechanisms for disease tolerance are multicomponent (Reuveni, 1995). Environmental factors such as the increased use of fertilizers and pesticides, the appearance of new virulent phytopathogenic races, and cultural factors, such as irrigation and other environmental stresses, can modify disease resistance reactions. Moreover, it is well established that resistance can be systemically induced in plants by inoculation with non-pathogens, restricted inoculation with pathogens, or treatment with chemicals, including phosphate salts (Doubrava et al., 1988; Descalzo et al., 1990; Kuc, 1995; Ye et al., 1995).

The relation between fertilizer amounts and combinations, and the expression of resistance or susceptibility to plant pathogens has been thoroughly investigated and has received increased attention in recent years. Over 2440 studies concerning the relationship between potassium, alone or combined with other elements, and plant health have been reported by Perrenoud (1990). More than 400 diseases and pests were included in this report. However, results were often contradictory. There are a number of factors that might explain these variations including rates and types of fertilizer applied, soil NPK status, and data interpretation. In general, elements P and K tend to improve plant health.
According to Perrenoud's report (1990), most authors agree that N generally increases crop susceptibility to pests and diseases. It was also indicated that the balance between various nutrients is as important as their absolute rates. For instance, increased N rates reduce crop resistance less when K fertilization is adequate (Lee, 1966; Harper and Will, 1968; Webb and George, 1968; Herlihy and Caroll, 1969; Singh, 1978; Jensen and Munk, 1997). P or K application reduced diseases in 65% of cases and increased diseases or insect pest in 28% of cases (Perrenoud, 1990). P and K may affect the reaction of a plant to pests in one or more of the following ways:

1. Direct effects on the pathogen multiplication, development and survival.
2. Direct effects on the internal metabolism of the plant, thus affecting food supply for the pathogen; and
3. Effects on the establishment of the pathogen and its spread within the plant, through the influence of the elements on plant defence responses and cell-wall ultrastructures and function of stomata.

Although P and K fertilizers improve plant health in the majority of cases (Perrenoud, 1990), disease cannot be controlled by the use of fertilizers alone. In many cases, economic control requires periodic applications of fungicides. However, optimal fertilization can be an important, and often underappreciated component of an integrated program for disease management.

We are currently investigating the use of foliar fertilizer applications for induction of plant resistance. Data from the application of this concept to various host–pathogen interactions are presented below.

**Systemic induced resistance (SIR) by foliar NPK fertilizers**

An early report by Chester (1933) described the development of systemic induced resistance (SIR) to diseases in plants following infection. One explanation of SIR is that an immunity signal(s), released or synthesized at the induction site of the inducer leaf, is systemically translocated to the challenged leaves, where it activates a mechanism(s) for defence (Kuc', 1989; Fought and Kuc', 1996). Salicylic acid (SA) has been hypothesized as a possible signal and its exogenous application induces resistance and direct or of an indirect influence of the phosphate on conidial germination or development is not clear. The signal itself is unlikely to be phytoxic or antifungal, and host responses are clearly required for protection (Kuc', 1995; Ye et al., 1995). In spite of the accumulated data on acquired systemic resistance in various hosts the mechanisms remain unclear (Kessmann et al., 1994; Hammerschmidt and Smith Becker, 1997).

We were led to investigate the possible use of NPK foliar fertilizers as agents for induction of systemic protection. Foliar fertilizers have been used on many crops for at least 40 years. In recent years, foliar application of essential nutrients has increased and has served to improve the quality and increase yields of muskmelon (Giskin and Nerson, 1984; Nerson et al., 1985), maize (Bare' and Black, 1979; Giskin et al., 1984; Giskin and Efron, 1986), soybean (Garcia and Hanway, 1976; Bare' and Black, 1979), peanuts (Malakondiah and Rajeswararao, 1979, 1980) rice (Debata and Murty, 1983), barley (Afridi and Samiullah, 1973; Qaseem et al., 1978), and wheat (Sherchand and Paulsen, 1985). The ability of a crop variety to absorb large amounts of nutrients and to convert them into plant biomass on highly enriched soils, where less efficient cultivars reach a yield plateau, has been described as the 'effectual response' to fertilizer application. In this approach to plant nutrition, the emphasis is placed solely on plant uptake from the soil. One of the most immediate, obvious effects of applying mineral nutrients, especially nitrogen, to the soil is an increase in leaf area. It has been argued that this is agronomically the most important result of fertilizer application because an increase in leaf area results in more radiation intercepted by the crop. The above-mentioned studies have shown that foliar fertilization is a potential alternative to soil application for increasing foliar area.

**SIR in cucumbers**

A single phosphate spray induced a high level of systemic protection against powdery mildew caused by *Sphaerotheca fuliginea* in cucumbers (Reuveni et al., 1993, 1995b). In this study, SIR against powdery mildew was obtained on the leaves of 2, 3 and 4 of 5-leaf-stage cucumber plants (leaves 2, 3 and 4) in response to a foliar spray of phosphate on leaf 1 as early as 2 h before inoculation with conidial suspensions of *S. fuliginea*. In these experiments, the best protection was observed on leaf 2 and declined acropetally. Induced resistance is effective for a long time and at locations distant from the place of application. Whether these findings are the results of a direct or of an indirect influence of the phosphate on conidial germination or development is not clear. The initiation of such signal(s) by phosphate salts was proposed as an important factor in immunization of cucumbers against various diseases, including powdery mildew (Gottstein and Kuc', 1989; Mucharromah and Kuc', 1991). A direct response to foliar fertilization was noted. A single spray of K$_2$HPO$_4$ on leaf 1, applied 1 or 2 days before inoculation, stimulated plant growth, regardless of disease (Reuveni et al., 1993).

Spraying of a 1:1 mixture of both P and K fertilizer salts did not improve the systemic protection against....
powdery mildew over that obtained by use of each compound alone (Reuveni et al., 1995b). This study showed that systemic protection was not reduced when inoculum concentration increased. Evidently, post-inoculation application of phosphate on the first leaf of cucumber plants induced systemic protection against powdery mildew on upper leaves, even when it was sprayed 4 days after inoculation. However, it should be noted that the efficacy of phosphate in inducing resistance against powdery mildew in cucumbers and in maize against other pathogens is highly related to time of induction before challenge inoculation. The best protection was always obtained when phosphate salts were sprayed as early as 2 h before inoculation, suggesting that these chemicals rapidly trigger the plant’s response. Our findings confirm earlier reports that resistance to cucumber anthracnose caused by *C. lagenarium* can be induced by chemical treatments and phosphates (Gottstein and Kuc’, 1989), and that these compounds induce systemic resistance to *S. fuliginea* (Mucharromah and Kuc’, 1991). A single phosphate spray induced a systemic protection against common rust on maize plants (Reuveni and V. Agapov, unpublished data). Importantly, this protection can be observed in maize plants as a result of one foliar spray of various phosphates on the first 1 to 3 leaves as early as 2–4 h before inoculation with spore suspensions (Reuveni et al., 1994a, 1994c, 1996b). In addition, protection was observed when the phosphate was sprayed 10 days before the pathogen challenge and was persistent up to leaf 7. No signs of physiological change were seen in SIR leaves of maize (1, 2 and 3) that would eventually suggest accumulation of peroxidase, chitinase, or other host compounds that might be damaging to the pathogen. Inoue et al. (1994) identified potassium phosphate as the active component in the enhancement of papilla formation and resistance of barley to powdery mildew.

As in cucumbers, growth increase was also observed in maize plants as a result of one foliar spray of phosphates (Reuveni et al., 1994c). This phenomenon was not reported in other studies (Gottstein and Kuc’, 1989; Descalzo et al., 1990; Mucharromah and Kuc’, 1991). However, Tuzun et al. (1986) reported that immunization of tobacco plants against blue mould disease by stem injection of a sporangial suspension of *Peronospora tabacina* into stem tissue increased the marketable yield (greater height and fresh weight) of tobacco.

Because of the rapidity of induction of protection by various chemicals, it may be that a non-specific mechanism is involved in this phenomenon. Although it is tempting to assume that phosphates accumulate in the upper protected leaves after spray induction on the lower leaves and may have a direct role in the defence reaction against the pathogens, no accumulation of total P or K elements was detected in the upper protected maize leaves against rust (Reuveni et al., 1994b). Therefore, it seems that ‘release of an existing active signal’ as a result of the foliar spray of the chemicals on the lower leaves of the susceptible plants, is responsible for the activation of the defence mechanism.

**SIR by microelements**

Trace elements also may play an important role in plants by affecting their susceptibility to fungal or bacterial phytopathogens (Graham, 1983). There are reports that some trace elements increase susceptibility of bean leaves to tobacco mosaic virus (Yarwood, 1954). Trace elements also increased or decreased resistance of asparagus bean to tobacco necrosis virus (TNV) (Pennazio and Roggero, 1988). Addition of Mn reduced natural resistance of asparagus bean to TNV, whereas Cu, Co and Ni increased resistance. The induction of SIR to foliar pathogens by a foliar spray of trace element solutions has not been extensively investigated. Our studies clearly indicated that a single foliar spray of 0.005 M H3BO3, CuSO4, MnCl2 or KMnO4 separately on the upper surface of the lower leaves of cucumber plants induced systemic protection against powdery mildew on cucumber plants (Reuveni et al., 1997) and against common rust on maize plants (R. Reuveni, M. Reuveni and V. Agapov, unpublished data).

We have found similar levels of protection when trace elements were applied 2 h (day 0), and 2, 4 and 5 days before challenge inoculation with fungal pathogens. The application of these solutions provided a significant level of systemic protection that was similar and comparable with that achieved by the use of K2HPO4 or KH2PO4. The systemic protection was observed on leaves 2, 3 and 4 when the first true leaf was induced. It was also evident that the systemic protection induced by micronutrient solutions was similar when the first true leaf was induced 2 h before inoculation (day 0) or 1 or 3 days before inoculation. A 1:1 mixture of phosphate and micronutrient solutions did not improve the systemic protection compared with that for either solution applied alone.

Protection on the upper leaves was obtained even under high inoculum pressure (1.6 x 104 conidia per ml) of *S. fuliginea* which was used to challenge the protected plants. Importantly, this protection can be expressed as a delay in colony development which can affect the spread and progress of the disease epidemic in the field or the greenhouse.
Although the mechanism for SIR development is still unknown, we suggest that these chemicals trigger a release and rapid movement of the 'immunity signal' from challenged leaves to unchallenged ones. The mechanism might be related to the enhancement in both soluble and ionically bound components of peroxidase activity and β-1,3-glucanase content in protected leaves above those sprayed with MnCl₂. Mn and Cu probably act as cofactors of metallo-protein enzymes such as peroxidase, for which Mn ions serve as inducing agent (Fowler and Morgan, 1972). Peroxidase and β-1,3-glucanase are related to cross-linking of cell-wall components, polymerization of lignin and suberin monomers, and subsequent resistance to pathogens in several host-pathogen interactions (Reuveni, 1995). In addition, it appears that levels of β-1,3-glucanase and chitinase and the activity of peroxidase are elevated in immunized cucumber plants as a result of phosphate treatment (Irving and Kuc', 1990; Dalisay and Kuc', 1995).

Salicylic acid has been hypothesized to be a trans-locatable signal compound in SIR (Yalpani et al., 1991). It interacts with intracellular Ca²⁺ in the induction of chitinase in carrot suspension culture (Schneider-Muller et al., 1994). Application of cations such as Mn, Cu and B can exchange and therefore release Ca²⁺ cations which interact with salicylic acid and activate SIR mechanisms (Reuveni et al., 1997).

The above findings support the hypotheses that the mechanism for resistance is present in susceptible plants (Dean and Kuc', 1987), that SIR can be induced by simple inorganic or organic chemicals, and that this induced resistance is not pest-specific (Mucharromah and Kuc', 1991; Fought and Kuc', 1996).

**Suppression and integrated control of foliar pathogens by NPK salts and fungicides**

Foliar fungal pathogens, such as the powdery mildew fungi, are widely distributed and cause serious diseases of a large number of greenhouse- and field-grown crops. In grapevine, powdery mildew, caused by Uncinula necator (Schw.) Burr., may attack flowers, leaves, stems and fruits and cause considerable crop loss (Bulit and Lafon, 1978; Pearson, 1988) and deterioration in juice quality (Ouge and Berg, 1979). Significant damage has been reported on nectarine and on mango infected with powdery mildew (Keil and Wilson, 1961).

Fungicides are important in the control of many diseases. Sulphur and compounds belonging to the sterol biosynthesis inhibitor group are widely used to control powdery mildews. The development of fungicide resistance has hampered efforts to control mildew on cucurbits and grapes (Schroeder and Proovidenci, 1969; Schepers, 1983; Steva and Clerjeau, 1990; McGrath, 1996). Once resistant strains appear, many can survive for long periods. For example, the resistance of S. fuliginea to benzimidazoles can persist for 10 years after withdrawal of the fungicides from use (Schepers, 1984). Powdery mildew resistance to pyrazophos persisted for as long as 7 years in cucumber greenhouses.

Our recent studies clearly demonstrated that phosphates and potassium salts effectively suppressed and controlled powdery mildew diseases on various crops (Reuveni et al., 1994b, 1995a, 1995b; Reuveni and Reuveni, 1995a, 1995b). It was evident throughout all the experiments that a single application of phosphates was effective in direct suppression of the lesions and eradication of the conidia on the diseased foliage of cucumber that had not been sprayed previously with phosphate (Figure 1) and on rose plants (Figure 2) (Reuveni et al., 1994b, 1995a). The data showed that the effectiveness was improved when they were applied in combination with Tween 20, which aided the retention of phosphate ions on foliar surfaces and penetration of stomata. Similarly, Horst et al. (1992) reported improved powdery mildew black spot control in rose when sodium bicarbonate and Tween 20 or horticultural oils were applied. A similar effect of bicarbonates was reported on curcubit powdery mildew (Ziv and Zitter, 1992). A collapse of hyphal walls and shrinkage of conidia and conidiophores of S. fuliginea exposed to potassium bicarbonate has been observed (Homma and Arimoto, 1990). In addition, an inhibitory influence on sclerotial germination of Sclerotium rolfsii and on conidial formation and germination of S. fuliginea has been reported (Homma et al., 1981; Punja and...
Grogan, 1982). The mode of action of foliarly applied phosphate salts in suppression of pustules of powdery mildew fungus has not been clearly determined. Phosphonate — the hydrolysis product of H₃PO₃ in plants — is extremely mobile within plant tissues. It can move both upward and downward within plants. Phosphonate, when applied after infection, reduced the incidence of downy mildew disease and sporulation of Plasmopara viticola (Wicks et al., 1991). Antifungal activity following foliar sprays of phosphates or commercial systemic fungicides such as Dorado Pyrifeno (Dorado), 480 EC, penconazole, and benomyl, was observed on field-grown Chardonnay winegrapes. Both phosphates and systemic fungicides inhibited development of U. necator on fruit clusters (Figure 3). Phosphate-treated vines had higher fruit yields than untreated controls (Reuveni and Reuveni, 1995b). Alternating treatments of phosphate salts with diniconazole (Marit), myclobutanil (Sistane) and penconazole (Ophir) were more effective than phosphate alone in controlling powdery mildew on inflorescences of mango and fruits of nectarine, respectively (Reuveni and Reuveni, 1995a). In these cases the number of fungicides applications was reduced by 50% by alternating phosphate sprays with systemic fungicides without reducing the efficacy of disease control (Figure 4).

Foliar applications of potassium chloride reduced rust and powdery mildew diseases in barley (Kettlewell et al., 1992). Application of over 17 mM of silicon as potassium silicate has been shown to reduce the number of powdery mildew colonies on cucurbit species and grape leaves (Bowen et al., 1992; Menzies et al., 1992). These compounds may have a direct effect against the fungus, promote antagonistic phylloplane organisms, or stimulate host defence reactions.

Figure 3. The effect of foliar application of phosphate on the control of Uncinula necator on clusters of vines. Top phosphate application; bottom control. (For details see: Reuveni and Reuveni, 1995a)

<table>
<thead>
<tr>
<th>Disease rating (0 - 4)</th>
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<tbody>
<tr>
<td>Leaves</td>
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<tr>
<td>3</td>
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<tr>
<td>2</td>
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<td>1</td>
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Control Altern. Myclobutanil

Figure 4. The effect of foliar application of the systemic fungicide myclobutanil and spraying in alternation with phosphate on control of powdery mildew on fruits and leaves of nectarine trees. Six foliar sprays were applied at various intervals during the growing season starting at bloom on 28 March 1993. Additional sprays were applied on 4, 18 and 29 April and 7 and 17 May. The alternating (Altern.) treatment was sprayed three times with phosphate (K,H₃PO₄+KOH (40 mM) and three times with myclobutanil (0.05%). (For details see: Reuveni and Reuveni, 1995a)
Acknowledgements

Applications of other nutritional elements have also been shown to influence the development of powdery mildew. Kent (1941) showed that lithium, a common component of soil, increased resistance to disease and stimulated growth, at low concentrations, however, it was phytotoxic at higher concentrations. Abood et al. (1991) showed that application of 1 mM lithium chloride solution to cucumber plants via the root system gave protection against powdery mildew infection of the leaves by S. fuliginea. It was suggested that lithium treatment may partially suppress or delay the maturation of fungal germ tubes. This effect becomes increasingly important during development of mycelium and conidiophores. Since lithium chloride is readily mobile, it was suggested that it could be effective as a systemic fungicide.

The effectiveness of foliar fertilization is limited by a number of factors, including nutrient-specific element type and degree of mineral uptake, or inability to supply the required amounts (Karhadkar and Kannan, 1984). Foliar-applied phosphate, on the other hand, appears to be effective as a nutritional supplement and an SIR stimulant over a broad range of conditions.

The use of foliar fertilizers as SIR agents in conjunction with the use of resistant varieties, improves overall control of certain diseases. In studies of powdery mildew of cucumber, a significantly higher percentage of control was consistently obtained by the application of NPK fertilizers to resistant varieties compared with susceptible ones (Reuveni and Reuveni, unpublished data). There is a promising future for the use of macro- and micronutrients in the management of plant diseases through the mechanism of SIR.

Prospects for the future

Resistant varieties can be combined with specific cultural management techniques to efficiently manage plant diseases. Systemic induced resistance is one strategy that can be used to further the integrated management approach. The ideal SIR agent is a chemical with minimum adverse effects on the host and high levels of efficacy. NPK fertilizers that induce SIR, in combination with resistant varieties, are particularly attractive.

Reduction in the expense of crop production, conservation of beneficial biological enemies of pests, preservation of environmental quality and slowing the rate of development of pesticide-resistant strains represent the immediate beneficial impact of the use of ‘foliar-fertilizer’ therapy in the future.

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