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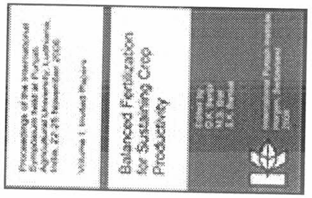

Balanced Chloride, Potassium and Silicon Nutrition for Plant Disease Management

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Abstract

Balanced plant nutrition is important since essential and even non-essential elements play key roles in the function, development and growth of plants. This fact becomes even more apparent when the plants are under some environmental stress, and the element in question is either low or limiting. As such, the plant may become even more susceptible to disease caused by a number of microorganisms. Chloride, potassium and silicon have been shown to reduce a number of plant diseases in a wide variety of crops. Each element has a different mode of action for plant disease suppression. Chloride appears to reduce the cell osmotic potential, increase manganese uptake, and enhance the activity of beneficial microbes via altered root exudation. Potassium acts on a number of processes that include alterations in protein or amino acid availability, decreased cell permeability, or decreased susceptibility of tissue to maceration and penetration. Silicon affects plant disease resistance by either an accumulation of absorbed silicon in the epidermal tissue, or expression of pathogenesis-induced host defense responses. This paper provides a general overview on the nutrient/host relationships of chloride/wheat, potassium/rice and silicon/rice, and how each influences plant disease development.

Keywords: Nutrients, plant diseases, plants-nutrition, silica minerals

Mineral nutrition plays a number of essential and functional roles in the development and growth of plants (Datnoff, 1994). They are involved in many physiological and biochemical processes that include enzyme activators, structural components, metabolic regulators, and substrates (Huber, 1990). These nutrients are supplied to the plant in organic or inorganic forms, and their availability to the plant depend on a number of factors such as soil texture, pH, moisture, temperature, mineral solubility, soil retention, soil microbial activity and the ability of the plant to use each nutrient efficiently. As such, the nutritional status of a plant will affect its inherent disease resistance, and the ability of the pathogen to infect and survive. This becomes even more apparent when the plant is under an environmental stress and the nutrient in question is low or limiting. This paper provides a general overview of the influences of chloride on diseases of wheat, and potassium and silicon on diseases of rice.

Chloride

In nature, chlorine exists mostly as chloride in rock salt (common salt, halite, NaCl), carnallite ($KMgCl_3.6H_2O$), and sylvite (KCl), which is mined and marketed as muriate of potassium. It was not until the late 1940's when the essentiality of chlorine as a micronutrient in photosynthesis was conclusively shown (Arnon and Whatley, 1949; Broyer *et al*., 1954). Since then a number of studies have suggested that the benefits of chloride applications may be maximized when plants are under stress by disease or drought (Trolldenier, 1985). In fact, most of the reported benefits of chloride application on crop production have been made in environments where considerable environmental stress or disease pressure was present. Such observations suggest that chloride fertilization may improve defense mechanisms against stress factors and may explain the lack of response when disease or stress factors are absent. Although reports of growth enhancement in asymptomatic non-stressed plants have been made, it may not rule out the suppression of minor pathogens or a correction of chloride deficiency.

The majority of reports demonstrating disease suppression with chloride fertilization have been made on monocots such as asparagus, barley, corn, coconut, date palm, millet, and wheat (Table 1). However, dicots like beets, celery, cotton, potato, and soybean have shown considerable benefit from chloride fertilization (Maas, 1986; Fixen, 1993). All plants that show growth responses to chloride nutrition are usually ranked as moderately tolerant/tolerant to both chloride and salinity (Maas, 1986). These plants have acquired a high level of tolerance or even preference for chloride in their nutrition.

Effect of chloride on controlling wheat diseases

The effects of chlorides on wheat diseases have been studied more thoroughly than on any other crop. Both root and foliar disease suppression has been documented along with reports that found no response to chloride. Powelson and Jackson (1978) first demonstrated the effect of chloride on take-all root disease caused by *Gaeumannomyces graminis* (Sacc.) Arx & D. Olivier var. *tritici* J. Walker. Banding wheat at planting with chloride fertilizers led to increased vigor and less take-all. Their findings stimulated many other studies on take-all of wheat (Christensen *et al*., 1981; Christensen *et al*., 1982; Engel and Mathre, 1988; Powelson, *et al*., 1985; Taylor *et al*., 1981; Trolldenier, 1985). Rates of approximately 350 kg Cl ha^{-1} as NH_4Cl were shown to increase grain yield from 11% to 40% over using NH_4SO_4 in plots where take-all disease had been confirmed. In another report, Christensen and Brett (1985) found chloride applied as NH_4Cl did not affect disease incidence, but disease severity was significantly reduced in acid soils. In contrast,

Table 1. Host plants, diseases, and pathogens suppressed by chloride[a]

Host plant	Disease	Pathogen(s)
Asparagus	Fusarium crown and root rot	*Fusarium oxysporum, F. proliferatum*
Barley	Common root rot	*Bipolaris sorokiniana, Fusarium culmorum*
Barley	Powdery Mildew	*Erysiphe graminis* f. sp. *hordei*
Barley	Rust	*Puccinia hordei*
Beets (Table)	Rhizoctonia root and crown rot	*Rhizoctonia solani*
Celery	Fusarium yellows	*Fusarium oxysporum* f. sp. *apii*
Coconut	Leaf spot	*Bipolaris incurvata*
Corn	Stalk rot	*Gibberella zeae, G. fujikuori*
Corn	Smut	*Ustilago maydis*
Cyclamen	Fusarium wilt	*Fusarium oxysporum* f. sp. *cyclaminis*
Date Palm	Fusarium wilt	*Fusarium oxysporum* f. sp. *albedinis*
Pearl Millet	Downy Mildew	*Sclerospora graminicola*
Sorghum	Stalk rots	*Gibberella thapsinum, Gibberella zeae, Macrophomina phaseolina*
Soybeans	Soybean cyst nematode	*Heterodera glycines*
Soybeans	Sudden death	*F. solani* f. sp. *glycines*
Wheat	Take-all	*Gaeumannomyces graminis* var. *tritici*
Wheat	Root rot	*Fusarium culmorum, Gibberella zeae* *Bipolaris sorokinian*
Wheat	Stripe (yellow) rust	*Puccinia striiformis*
Wheat	Leaf rust	*P. recondite* f. sp. *tritici*
Wheat	Powdery mildew	*Erysiphe graminis* f. sp. *tritici*
Wheat	Tanspot	*Pyrenophora tritici-repentis*
Wheat	Glume blotch	*Septoria tritici*
Wheat	Stagonospora blotch	*Phaeosphaeria avenaria*

[a]See Elmer (2006) for more inclusive information

Gardner *et al.* (1998) compared chloride application to several other treatments for reducing take-all disease in South Australia and found chloride was ineffective. Gardener *et al.* (1998) suggested that the naturally high chloride concentration in the soil and the late application led to its ineffectiveness. Trolldenier (1985) demonstrated that take-all disease suppression observed with chloride was influenced by drought stress. Wheat grown in pot experiments under low soil moisture conditions and inoculated with *G. graminis* var *tritici* grew better when fertilized with KCl rather than K_2SO_4. However, when sufficient moisture was added and/or the plants were not inoculated, the ameliorating effects of chloride were marginal.

Other root rot diseases on wheat have been investigated as well. Engle and Grey (1991); Engel *et al.* (1994) evaluated whether chloride could increase yield of wheat and affect root disease caused by *Fusarium culmorum* (W.G. Smith) Sacc. Chloride applied under NH_4-N regime increased yield of hard spring wheat, but chloride had no effect on root rot severity rating when wheat cultivars were artificially inoculated with *F. culmorum*. Subsequent studies confirmed these findings at six different sites in Montana, where an average 7% increase in yield was recorded following chloride application without significant reductions in disease severity (Engle *et al.*, 1994). Alternatively, Tinline *et al.* (1993) found chloride reduced the severity of common root rot (*Bipolaris sorokiniana* (Sacc.) Shoemaker) without affecting yield. In a series of chloride experiments conducted in Saskatchewan, Canada, (4 out of 11 trials) chloride applied as KCl or NaCl significantly reduced the severity of common root rot. No yield benefits were noted. Buchenau and Rizvi (1990) found that wheat seedlings grown in sand infested with *Gibberella zeae* (Schwein) Petch had significantly less root lesions when irrigated with water containing 60 mg liter^{-1} chloride. Windels *et al.* (1992), however, found no association between chloride applications and common root rot or wheat yields over five separate trials in Minnesota.

Before Powelson and Jackson (1978) had made their report on chloride suppression of take-all, Russell (1978) had demonstrated in greenhouse pot trials in England that applications of KCl and/or NaCl reduced the severity of stripe (yellow) rust of wheat caused by *Puccinia striiformis* Westend. In field plots, Russell (1978) found that application of KCl and NaCl at 1130 kg ha^{-1} reduced disease incidence by an average of 63%. The effect was observed on six cultivars of wheat. Christensen *et al.* (1981; 1982); Scheyer *et al.* 1987) also noted that application of chloride salts reduced the apparent infection of stripe rust in chloride-treated plots in Oregon. Accordingly, Rizvi *et al.* (1988) found potted wheat plants had 42% less wheat leaf rust than untreated controls when treated with $CaCl_2$. Reductions in both powdery mildew and leaf rust in chloride-treated plots were observed by Engel *et al.* (1994), but the effect was dependent on the location. Grybauskas *et al.* (1988) observed on winter wheat treated with KCl, but not with $CaCl_2$, marginal reductions in the severity of powdery mildew (*Erysiphe graminis* DC. f. sp. *tritici* Em. Marchal). Yields were greater in chloride treated plants, but yield increases were not associated with reduction in powdery mildew. In studies from 1984-1987, Buchenau *et al.* (1988a) recorded reductions in the number and pustule size of leaf rust (*P. recondita* Roberge ex Desmaz. f. sp. *tritici* (Eriks. & E. Henn.) D.M. Henderson) following applications of KCl and $CaCl_2$. They also noted chloride-treated plants had less tan spot (*Pyrenophora tritici-repentis* (Died.) Drechs. and Stagonospora blotch (*Phaeosphaeria avenaria* (G.F. Weber) O. Eriksson). Controlled pot studies with $CaCl_2$ with wheat seedlings inoculated with *P. tritici-repentis* revealed smaller and fewer lesions than on nontreated seedlings (Buchenau *et al.*, 1988b). Gelderman *et al.* (1999) reported chloride applied as KCl had marked effects in reducing tan spot and rust on 15 spring wheat cultivars. Chloride decreased the diseased portion of the flag leaf from 25% to 13%, and reduced the mean decrease in leaf rust infection from 33 to 12%. Chloride did not affect scab caused by various species of *Fusarium*. Findings by Sweeney *et al.* (2000) were in agreement with those above and found KCl reduced leaf rust severity and increased yield. Miller and Tucker (1999); Miller and Jungman (1998) in Texas explored the option of reducing costly fungicide sprays to reduce leaf rusts caused by *P. recondita* f. sp. *tritici* by integrating chloride nutrition on wheat. After demonstrating that KCl significantly reduced overall injury from leaf rust in six wheat cultivars, studies were initiated to include the fungicide propiconazole with KCl. Interestingly, the fungicide offered no added benefit indicating the chloride applications might replace costly fungicides at a fraction of the cost.

Several workers such as Kettlewell *et al.* (1990; 2000); Cook *et al.* (1993); Mann *et al.* (2004) have explored the use of spraying chloride salts on wheat to suppress leaf diseases. Field studies were established in Shropshire, England. Late-season application of KCl suppressed glume blotch of wheat caused by *Septoria nodorum* (Berk.) Berk. in Berk. & Broome. Kettlewell *et al.* (1990) reported leaf blotch (*Septoria tritici* Roberge in Desmaz) and powdery mildew (*E. graminis* sp. *tritici*) were similarly suppressed by late season foliar sprays of KCl.

How chloride suppresses plant diseases?

A complete understanding of how chloride affects disease has not been resolved, but there have been many attempts to decipher its role in suppressing plant disease (Elmer, 2006). With a few exceptions, a general consensus is that chloride provided suppression of plant disease because it has a minor toxic effect on the pathogen. However, most soilborne pathogens grow better in culture as chloride concentrations are increased to 0.5-1.0% (Firdous and Shahzad, 2001; Suleman *et al.*, 2001). Although it is conceivable that soil application of granular NaCl or KCl would initially cause a concentrated and perhaps inhibitory plume to percolate through the soil system, this effect would likely be short lived and could not explain the long lasting suppression observed in many of the host-pathogen systems listed in Table 1.

The major overall influence of chloride fertilization on plant disease appears to be related to a reduction in cell osmotic potential, increased manganese uptake, and enhancement of beneficial microbes via altered root exudation (Elmer, 2006). While the reduction of cell osmotic potential would be a direct physiological result of chloride uptake, there are chemical and/or microbial methods for achieving a chloride-mediated increase in manganese uptake. Soil pH may have a governing effect on whether manganese uptake is mediated chemically or microbiologically. In acid soils (<pH 6.6), chloride suppresses nitrification. The persistence of nitrogen in the ammonical form facilitates the chemical reduction of manganese oxides, whereas in neutral to alkaline soils, chloride may enhance manganese by altering nutritional composition of the root exudates that, in turn, favors microbes that possess the manganese reduction trait. Chloride acts as a nitrification inhibitor that forces the wheat plant to take-up more of the nitrogen as ammonium than as nitrate when ammonical fertilizers are applied. The plant roots then give off hydrogen ions that result in an increase in acidity at the root surface. As a consequence, disease severity decreases due to inhibition of the take-all pathogen by microorganisms which thrive in a more acidic root zone environment.

At present, the current understanding would implicate these two processes, the reduction in cell osmotic potential and the increased uptake of manganese, as acting in concert to suppress disease. These mechanisms would seemingly have far-reaching effects on both foliar and root diseases. Furthermore, one should recognize that the root-mediated alteration in the rhizobacteria that occurs may also include added benefits delivered by these microbes in conferring biological control, plant-growth-promotion and systemically-acquired-resistance.

Potassium

Potassium (K) plays many essential roles in plant nutrition Although K is not structurally bound in the plant, it increases root growth, improves water and nutrient uptake, increases cellulose and protein content, reduces lodging, enhances and regulates at least sixty different plant growth enzymes, and can affect plant disease (Ishizuka, 1978).

Plants readily absorb available K in the soil and once inside the plant, K moves readily from older to younger tissue so that its deficiency first appears in older leaves and can be easily confused with nitrogen deficiency. The difference between rice plants deficient or not in K is the color of the lower leaves. Symptoms of K deficiency include stunting with little or no reduction in tillering, droopy and dark green upper leaves and chlorosis of interveinal areas and margins of the lower leaves starting at the leaf tip. In severe cases, the affected leaves show scorching or firing along leaf margins. Plant growth and root development are reduced in K-deficient plants (Fageria and Barbosa Filho, 1994), seed and fruit are small and shriveled, and K-deficient plants may be predisposed to disease.

Effect of potassium on controlling rice diseases

Potassium alone or its combination with N, P and other nutrients can alter the disease severity of many soil-borne and foliar plant pathogens (Kiraly, 1976; Fageria *et al*., 1997). These have been extensively reviewed before on a number of crops, diseases, and pathogens (Prabhu and Fageria, 2006; Huber, 1980; Huber and Arney, 1985, Huber, 1990; Datnoff, 1994). Even though no generalization can be made on the effect of K on disease development, this element is reported to decrease the intensity of many diseases (Table 2). As mentioned above with Cl, many investigators have failed to give adequate consideration to the companion anions, nutrient balance, and nutrient status in order to determine a definitive role of K (Prabhu and Fageria, 2006). Thus, there may be a greater response to K in deficient than fully sufficient plants or with an excess of K beyond that required for nutrient sufficiency (Huber and Arny, 1985). This suggests that K may affect host resistance more as opposed to a direct effect on the pathogen.

Table 2. Reported effects of potassium on fungal diseases[a]

Host	Disease	Pathogen	Effect[b]
Alfalfa	Leaf spot	Pseudopeziza medicaginis	⊕
Apple	Gleosporium fruit rot	*Pezicula malicorticis*	⊗
Apricot	Brown rot	*Sclerotinia fructicola*	⊕
Aspen	Canker	*Hypoxylon mammatum*	⊕
Aster	Wilt	*Phialophora asteris*	⊗
Avocado	Root rot	*Phytophthora cinnamomi*	⊕
Banana	Fusarium wilt	*Fusarium oxysporum* f.sp. *cubenses*	⊕
Barley	Net blotch	*Helminthosporium teres*	⊕
	Powdery mildew	*Erysiphe graminis*	⊕
Bean (*Phaseolus vulgaris*)	Root rot	*Rhizoctonia solani*	⊗
Bean (*Phaseolus mung*)	Leaf spot	*Mycospherella cruenta*	⊗
Beet	Damping off	*Pythium ultimum.*	⊕
Bermuda grass	Leaf blight	*Helminthosporium cynodontis*	⊕
Broadbean (*Vicia faba*)	Chocolate spot	*Botrytis fabae*	∅
Cabbage	Club root	*Plasmodiophora brassicae*	⊗
	Downy mildew	*Peronospora parasitica*	⊗
	Gray mold	*Botrytis cinerea*	⊕
	Yellows	*Fusarium oxysporum* f.sp. *conglutinans*	⊕

Carnation	Stem rot, stub dieback	*Gibberella zeae*	⊗
	Wilt	*Fusarium* spp.	⊕
Castor bean	Capsule browning and maceration	*Botrytis* spp.	⊗
Cedar, red	Blight	*Phomopsis juniperovora*	⊗
Celery	Yellows	*Fusarium oxysporum* f.sp. *apii*	⊕
Cereals	Rust	*Puccinia* spp.	⊕
	Powdery mildew	*Erysiphe graminis*	⊕
Chrysanthemum	Root rot	*Phoma chrysanthemicola*	⊕
Citrus	Brown rot gummosis	*Phytophthora parasitica*	⊗
Clover, red	Wilt and root rot	*Fusarium* spp.	⊕
Conifers	Root rot	*Armillariella mellea*	⊗
Cotton	Wilt	*Fusarium oxysporum* f.sp. *vasinfectum*	⊕
	Root rot	*Phymatotrichum omnivorum*	⊕
	Wilt	*Verticillium albo-atrum*	⊕
	Wilt	*Verticillium dahliae*	∅
	Wilt	*Fusarium oxysporum* f.sp. *vasinfectum*	∅/⊕
	Seedling blight	*Rhizoctonia solani*	⊗/⊕
	Leaf blight	*Cercospora gossypina*	⊕
	Leaf blight	*Alternaria solani*	⊕
Cowpea (*Vigna sinensis*)	Damping-off	*Rhizoctonia solani*	⊗
	Rust	*Uromyces phaseoli*	∅
Flax	Wilt	*Fusarium lini*	⊕
	Rust	*Melampsora lini*	⊕
Grape	Fruit rot	*Botrytis cinerea*	⊕
Hemp, sunn	Root rots	*Rzhizoctonia solani*	⊕
	Root rots	*Pythium butleri*	⊕
	Root rots	*Sclerotium rolfsii*	⊕
Jute	Anthracnose	*Collectotrichum corchorum*	⊕
	Root rot	*Rhizoctonia solani*	⊕
	Stem rot	*Macrophomina phaseoli*	⊕
Maize	Northern leaf blight	*Exserohilum turcicum*	⊕
	Root rot	*Gibberella saubinetti*	⊕
	Stalk rot	*Fusarium moniliforme*	⊕

	Stalk rot	*Gibberella zeae*	⊕
	Stalk rot	*Diplodia zeae*	⊕
	Stem rot	*Fusarium culmorum*	⊕
Mangolds	Leaf spot	*Pleospora herbarum*	⊕
Melon	Wilt	*Fusarium oxysporum* f.sp. *melonis*	⊕
	Gummy stem blight	*Mycophaerella melonis*	⊗
Millet	Downy Mildew	*Sclerospora graminicola*	∅
Muskmelon	Downy mildew	*Pseudoperonospora cubensis*	⊗
Narcissus	Basal rot	*Fusarium oxysporum* f.sp. *narcissi*	⊕
Onion	Purple blotch	*Alternaria porri*	⊗
Palm	Wilt	*Fusarium oxysporum* f.sp. *elaeidis*	⊕
	Boyomi	*Fusarium bulbigenum*	⊗
Pea	Root rot	*Aphanomyces euteiches*	⊕
	Wilt	*Fusarium oxysporum* f.sp. *pisi*	⊕
Peanut	Pod rot	*Rhizoctonia solani*	⊗
	Leaf spot	*Mycospherella arachadis*	⊕
Pine (*Pinus* sp.)	Wood rot	*Fomitopsis annosa*	⊕
Pine (*P. elliottii* and *P. taeda*)	Fusiforme rust	*Cronartium fusiforme*	⊗
Pine (*P. radiata*)	Root rot	*Phythopthora* spp.	⊗
Pine, white (*P. strobus*)	Rust	*Peridermium* spp.	⊕
Pineapple	Root rot	*Phytophthora cinnamomi*	⊕
Potato	Canker	*Rhizoctonia solani*	⊕
	Canker	*Rhizoctonia solani*	⊗
	Late blight	*Phytophthora infestans*	⊕
	Scab	*Streptomyces scabies*	⊗
	Scab	*Streptomyces scabies*	∅
	Stem end rot	*Fusarrium* spp.	⊕
Prune	Canker	*Cytospora leucostoma*	⊕
Pumpkin	Stem rot	*Sclerotinia sclerotiorum*	⊕
Rice	Leaf spot	*Cercospora oryzae*	⊕
	Leaf spot	*Helminthosporium* spp.	⊕
	Brown leaf spot	*Cochliobolus miyabeanus*	⊕
	Sheath blight	*Corticium sasakii*	⊕
	Stem rot	*Leptosphaeria salvinii*	⊕
	Stem rot	*Helminthosporium sigmoideum*	⊕

	Brown spot	*Ophiobolus miyabeanus*	⊕
	Leaf blast	*Pyricularia oryzae*	⊕
	Sclerotial disease	*Sclerotium oryzae*	⊕
	Sheath rot	*Sarocladium oryzae*	⊕
Rose	Mildew	*Phyllactinia guttata*	⊕
Rye	Stalk smut	*Urocystis occulta*	⊕
Snapdragon	Wilt	*Verticillium dahliae*	⊕
Soybean	Pod rot	*Diaporthe sojae*	⊕
	Root rot	*Phytophthora megasperama*	⊗
	Pod rot	*Diaporthe sojae*	∅
	Purple seed stain	*Cercospora kikuchii*	⊕
Squash	Foot rot	*Fusarium solani* f.sp. *cucurbitae*	⊕
Sugarcane	Eye spot	*Helminthosporium sacchari*	⊕
Timothy	Leaf spot	*Heterosporium phlei*	⊕
Tobacco	Leaf blights	*Alternaria, Cercospora,* and *Sclerotinia*	⊕
Tomato	Wilt	*Fusarium oxysporum* f.sp. *lycopersici*	⊗/⊕
Turf	Fuarium patch	*Fusarium ivale*	⊕
	Ophiobolus patch	*Ophiobolus graminis*	⊕
	Leaf spot	*Helminthosporium* spp.	⊕
Walnut, black	Anthracnose	*Gnomonia leptostyla*	⊗
Watermelon	Wilt	*Fusarium oxysporum* f.sp. *niveum*	⊗
Wheat	Leaf blotch	*Septoria tritici*	⊕
	Glume blotch	*Septoria nodorum*	⊕
	Root rot	*Fusarium* spp.	⊗
	Take-all	*Gaeumannomyces graminis*	⊗/⊕
	Stem rust	*Puccinia graminis*	⊕
	Leaf rust	*Puccinia recondita*	⊕
	Leaf rust	*Puccinia trticina*	⊕
	Stripe rust	*Puccinia striiformi*	⊕
	Bunt	*Tilletia* spp.	⊗/⊕
	Flag smut	*Uromyces tritici*	⊗
	Powdery mildew	*Erysiphe graminis*	⊕

[a] Data compiled from Huber and Arny (1985) with additional articles. See Prabhu and Fageria (2006) for K effects on bacteria, nematodes and viruses

[b] Potassium can decrease (⊕), increase (⊗), or has no effect (∅) on disease intensity

Rice blast (*Magnaporthe grisea* (Hebert) Barr) (anamorph *Pyricularia grisea* Sacc. = *P. oryzae* Cavara) has been classified as a high sugar disease and a well-nourished plant is prone to greater susceptibility. There was a highly significant positive ($P < 0.01$) relationship between leaf blast and K applied to lowland rice (Fig 1). All plants received 52 kg P ha^{-1} and 60 kg N ha^{-1} at sowing and an additional 60 kg N ha^{-1} at the active tillering stage. However, resistant plants frequently contained more K in plant tissues than those that are susceptible. Panicle blast severity was negatively correlated with K and Ca, but positively correlated with N, P, and Mg levels in panicle tissues (Filippi and Prabhu, 1998). The effect of K was confined to the deficiency range and no further increase in resistance was achieved beyond an optimal supply of this element.

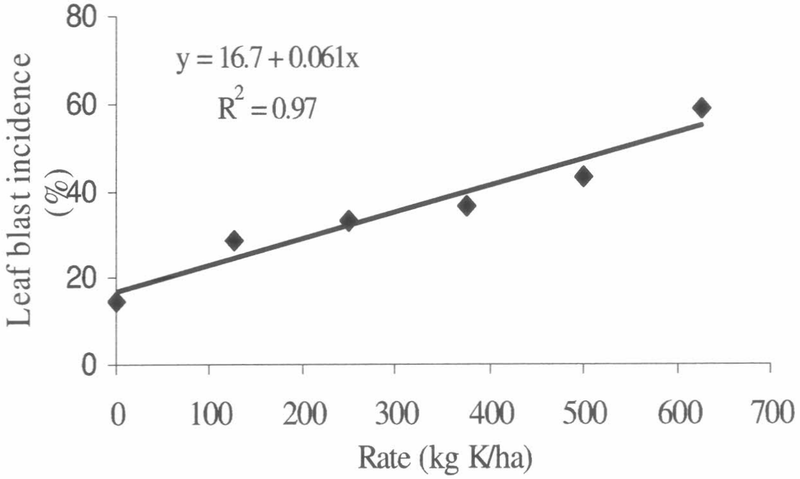

Fig 1. Effect of potassium rates on leaf blast of irrigated rice cultivar Epagri 109 grown on an Inceptisol in Brazil (Prabhu and Fageria, 2006)

Some genotypes are more efficient than others in K uptake, and this may contribute to their increased disease resistance and higher grain yield (Fageria *et al.*, 1990). Distinct differences in grain yield of upland rice cultivars susceptible and resistant to rice blast at different K levels have been reported (Table 3). The wide differences in yield were mainly due to blast incidence. In the blast resistant line, CNA 418, a significant linear yield response to applied K was attributed to enhanced blast resistance and possibly K uptake since the relationship between tissue K and disease severity was negative and linear.

Table 3. Effect of potassium rates on the yields of susceptible and resistant rice blast cultivars

K applied	Susceptible			Resistant		
	Dourado Precoce	IAC 47	IAC 164	CNA 466	CNA 4476	CNA 418
	kg ha^{-1}					
0	622	625	563	2.277	2.118	2.050
25	708	650	647	2.403	2.302	2.183
50	700	647	662	2.285	2.352	2.245
75	716	657	683	2.317	2.368	2.482
100	740	640	675	2.332	2.010	2.447
Linear	*	ns	*	ns	ns	**
Quadratic	ns	ns	ns	ns	ns	ns

* and ** = significant at 5 and 1% probability level, respectively; ns = non significant
Source: Fageria *et al.* (1990)

Several diseases increase with an increase in N and the effect of K can be directly correlated with the level of N. The critical factor affecting rice leaf blast is the N:K ratio in leaves. Blast severity is low when there is a high tissue K:N ratio while a high N:K ratio increases blast (Ou, 1985). When the concentration of N is low, the addition of K suppresses rice blast. On the other hand, when the level of N is high, the addition of K increases blast. The K and N ratio greatly influences plant growth as well as disease development, and the ratio may change with growth of the plant.

The relationship between K_2O and panicle blast in rice at three different N rates was studied in a field experiment conducted on Dark Red Latosol (Oxisol) using a susceptible upland rice cultivar (Prabhu *et al.*, 1999). Potassium fertilization in the absence of additional N greatly decreased panicle blast. The response was significantly linear and negative with increasing levels of K (Fig 2). On the other hand, the response of panicle blast to different levels of K was quadratic at 30 kg ha^{-1} of N. Disease severity increased as the N rate increased from 0 to 60 kg ha^{-1} and decreased at rates above 60 kg N ha^{-1}. In contrast to lower N rates, K fertilization did not affect panicle blast when 60 kg N ha^{-1} was applied. These results are consistent with earlier reports that excess K results in more severe blast under high N conditions (Kozaka, 1965). Thus, K fertilization may increase, decrease or have very little effect on rice blast depending on the N rate. Soave *et al.* (1977) reported that both N and K increased the percentage of leaves with blast lesions. Because the critical factor affecting blast development is the K:N ratio, the results of K fertilization on blast incidence and development have been contradictory when the ratio is not considered (Ou, 1985).

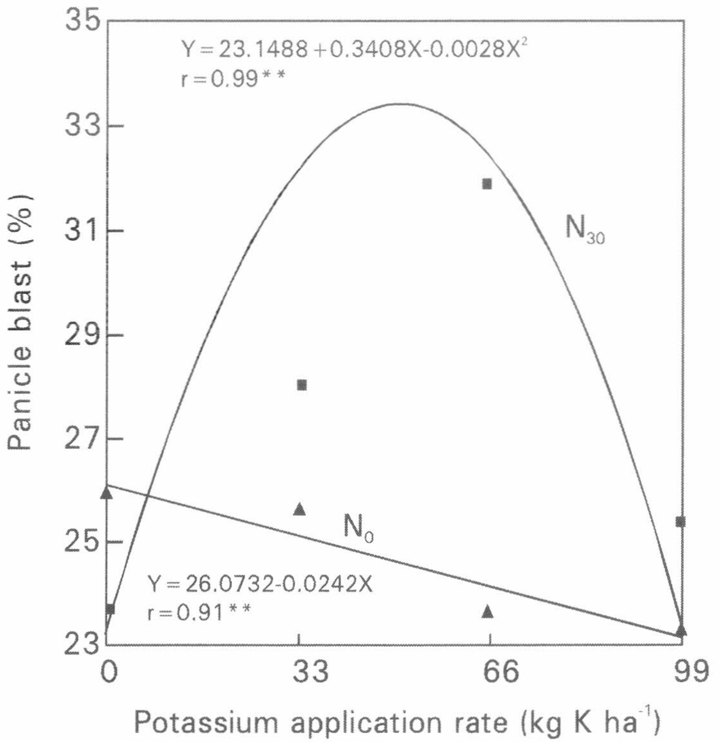

Fig 2. Effect of potassium fertilization on panicle blast at two nitrogen (N) levels in upland rice (N_0 = ▲; N_{30} = ■). The regression equations were calculated using fertilizer application rates expressed as K_2O

Certain plant growth stages are more susceptible to disease and the yield loss greatly depends on the stage at which plants are attacked. Rice is more susceptible to leaf blast during the vegetative phase of growth that occurs 30 to 45 days after seeding, and to panicle blast at the milky dough stage (Prabhu and Morais, 1986). Both leaf and panicle blast increase in upland rice with increasing rates of N applied all at planting (Faria *et al.*, 1982).

Brown spot of rice (*Cochliobolus miyabeanus* (Ito and Kuribayashi) Drechs. ex Dastur (anamorph: *Bipolaris oryzae* (Breda de Haan) Shoemaker) is usually associated with a K:N imbalance, and K amendments decrease the intensity of brown spot (Baba *et al.*, 1951). Although a low N:K ratio (0:30) resulted in high brown spot incidence, brown spot severity decreased when the N:K ratio was 45:30 (Faria and Prabhu, 1983).

Fertilizer sources of K include various salts from which the anion may also manifest an effect on disease in combination with or independent of the K ion. The more common sources of K fertilizers include the chloride (muriate) or sulphate salts; however, carbonate, nitrate, phosphate (mono and dibasic), silicon, and various organic salts are also used. It is difficult to distinguish between the effect of the K or the anion in the fertilizer salt used on disease unless many combinations are studied. It is well known that the Cl anion can affect various diseases independent of K (Elmer, 2003; Huber and Arny, 1985; Huber, 1991) and that K influences plant uptake of nitrate, Ca, and other mineral elements. Similar interactions are observed with phosphate salts of K (Lopez and Lucas, 2002).

The level of K in plants depends on the availability of Mg and Ca. Calcium alters the Ca:K ratio and interacts with other elements. The function of K in cellular organization and permeability is complimented by large Ca reserves in mature plant tissue. Calcium enhances K availability in neutral soils, but not in acid soils. An interaction between K and Mg was demonstrated on rice leaf blast (Sako and Takamore, 1958; Kozaka, 1965). Disease increased when K was applied alone but could be reduced by adding Mg. In addition, a negative correlation between tissue K and Mg was observed.

A combination of Si and K reduced rice blast (Winslow, 1992; Prabhu *et al.*, 2001). Potassium deficiency reduces the accumulation of Si in epidermal cells and increases susceptibility of rice to blast (Nogushi and Suagawara, 1966). Predisposition of upland rice to blast under low moisture conditions could be attributed to reduced K and Si uptake by the rice plant (Baba *et al.*, 1951). Integration of Si and K application is important for disease management and sustainable upland rice yields (Savant *et al.*, 1997).

How potassium suppresses plant diseases?

Although the physiological function of K in disease resistance mechanisms is not well understood, nutritional factors favoring host plant resistance have been attributed to alterations in protein or amino acid availability, decreased cell permeability, or decreased susceptibility of tissue to maceration and penetration. Potassium and Mg in potato extracts inhibited the macerating action of some enzymes (Huber, 1980). Arginine increases as the level of K increases and resistance of potato plants to late blight increases as the levels of K increases due to the accumulation of fungistatic levels of arginine in leaves. Exudates of arginine inhibit germination of sporangia of *P. infestans* and exudation is lowest in the absence of K when N and P are high (Alten and Orth, 1941). The ability of various soil or foliar applied K salts such as potassium phosphonate, K_2HPO_4, KH_2PO_4, and KNO_3 to

stimulate systemic acquired resistance (SAR) in susceptible plants against powdery mildews, anthracnose, rust and several other pathogens suggests fundamental changes in physiological pathways are probably important in disease resistance (Reuveni *et al.*, 1995; Reuveni and Reuveni, 1998; Reuveni *et al.*, 2000; Becot *et al.*, 2000; Orober *et al.*, 2002). Interestingly, a partially purified extract from barley seedlings referred to as the papilla-regulating extract (PRE) that induced resistance to penetration by the powdery mildew fungus was shown to be a potassium phosphate (Inoue *et al.*, 1994).

Anatomical changes affected by K nutrition may also play an important role in disease resistance. Enhanced silicification of cell walls by K is one explanation for increased disease resistance. A deficiency of K decreases Si accumulation in epidermal cells and increases the susceptibility of rice to leaf blast (Nogushi and Sugawara, 1966). Potassium, in combination with P, induces the development of thicker cuticles and cell walls that function as mechanical barriers to infection by several pathogens or limit the growth of some pathogens as a result of a higher proportion of sclerenchyma tissue (Huber, 1980).

Silicon

Silicon (Si) is the second most abundant mineral element in soil and comprises approximately 28% of the earth's crust (Elawad and Green, 1979; Singer and Munns, 1987; Epstein, 1991). Many plants are able to uptake Si and, most recently, a Si transporter gene, Lsi1, was identified and characterized in rice (Ma *et al.*, 2006). Depending upon the species, the content of Si accumulated in the biomass can range from 1 to greater than 10% (Elawad and Green, 1979; Epstein, 1991). Plant species are considered Si accumulators when the concentration of Si (on dry weight basis) is greater than 1% (Epstein, 1999). Relative to monocots, dicots such as tomato and soybean are considered poor accumulators of Si with values less that 0.1% of Si in their biomass. Dryland grasses such as wheat, oat, rye, barley, sorghum, corn, and sugarcane contain about 1% of Si in their biomass, while aquatic grasses have Si content up to 5% (Jones and Handreck, 1967; Epstein, 1991; 1999; Rodrigues *et al.*, 2001). Silicon is taken up at levels equal to or greater than essential nutrients such as nitrogen and potassium in plant species belonging to the families Graminaeae, Equisetaceae, and Cyperaceae (Savant *et al.*, 1997). The Si:Ca ratio is another criterion used to determine if a plant species is a Si accumulator (Ma and Takahashi, 2002). Although Si has not been considered an essential element for crop plants for lack of supportive data, species such as *Equisetum* and some diatomaceaes cannot survive without an adequate level of Si in their environment (Epstein, 1991; 1999).

The beneficial effects of Si, direct or indirect, to plants under biotic and/or abiotic stresses occur in a wide variety of crops such as rice, oat, barley, wheat, cucumber, and sugarcane (Datnoff *et al.*, 2001; Ma and Takahashi, 2002). Leaves, stems, and culms of plants grown in the presence of Si show an erect growth, especially for rice. This suggests that the distribution of light within the canopy is greatly improved (Elawad and Green, 1979; Ma and Takahashi, 2002; Epstein, 1991; Savant *et al.*, 1997). Silicon increases rice resistance to lodging and drought and dry matter accumulation in cucumber and rice (Lee *et al.*, 1985; Adatia and Besford, 1986; Epstein, 1991). Silicon can positively affect the activity of some enzymes involved in the photosynthesis in rice and turfgrass (Savant *et al.*, 1997; Schmidt *et al.*, 1999) as well as reduce rice leaf senescence (Kang, 1980). Silicon can lower the electrolyte leakage of rice leaves promoting greater photosynthetic activity in plants grown under water deficit or heat stress (Agarie *et al.*, 1998). Silicon increases the oxidation power of rice roots, decreases injury caused by climate stress, such as typhoons and cool summer damage in rice, alleviates frost damage in sugarcane and other plants, and favors super cooling of palm leaves (Savant *et al.*, 1997; Hodson and Sangster, 2002). Silicon reduces the availability of toxic elements such as Mn, Fe and Al to roots of plants such as rice and sugarcane and increases rice and barley resistance to salt stress (Horiguchi, 1988; Liang *et al.*, 1996; Savant *et al.*, 1997). Moreover, the most significant effect of Si to plants, besides improving their fitness in nature and increasing plant productivity, is the suppression of plant disease development (Bélanger *et al.*, 1995; Datnoff *et al.*, 1997; Savant *et al.*, 1997).

Effect of silicon on controlling rice diseases

The majority of research using Si to control plant disease(s) has been conducted with rice; however, this element has reduced the intensity of several diseases in a number of important crops (Table 4). Suzuki (1935) reported that Si application to paddy soils enhanced rice resistance to blast (*M. grisea*). Volk *et al.* (1958) observed that the number of blast lesions on leaves of Caloro rice cultivar decreased linearly as the Si content in leaf blades increased. Rabindra *et al.* (1981) found that the content of Si in leaf and neck tissues varied among four rice cultivars grown under similar climatic conditions; and that those cultivars accumulating more Si in shoots showed less incidence of leaf and neck blast. Interestingly, the susceptibility to blast was negatively correlated with the content of Si accumulated in shoots for specific rice cultivars grown at different Si rates (Kozaka, 1965; Ou, 1985). However, other reports have revealed that rice cultivars accumulating higher levels of Si in shoots are not always more resistant to blast than cultivars accumulating lower levels of Si when grown under the same cultural and environmental conditions (Kozaka, 1965; Ou, 1985; Winslow, 1992).

Table 4. Host, disease and plant pathogen response to silicon applications

Host	Disease	Pathogen	Effect[a]
Rice	Leaf and neck blast	*Magnaporthe grisea*	⊕
	Brown spot	*Cochliobolus miyabeanus*	⊕
	Sheath blight	*Thanathephorus cucumeris*	⊕
	Leaf scald	*Monographela albescens*	⊕
	Stem rot	*Magnaporthe salvinii*	⊕
	Grain discoloration	Many fungi species	⊕
	Bacterial leaf blight	*Xanthomonas oryzae pv. oryzae*	⊕
	Root knot nematodes	*Meloidogyne* spp.	⊕
Wheat	Powdery mildew	*Blumeria graminis*	⊕
	Septoria leaf blotch	*Septoria nodorum*	⊕
	Foot rot	*Fusarium* spp.	⊕
	Leaf spot	*Phaeosphaeria nodorum*	⊕
	Eye spot	*Oculimacula yallundae*	⊕
	Brown foot rot	*Fusarium culmorum*	∅
	Brown rust	*Puccinia recondita*	∅
Sorghum	Anthracnose	*Colletotrichum graminicola*	⊕
Barley	Black point	*Alternaria* spp.	⊕
	Powdery mildew	*Erysiphe graminis* f.sp. *hordei*	⊕
Rye	Powdery mildew	*Erysiphe graminis*	⊕
Sugarcane	Rust	*Puccinia melanocephala*	∅
	Ring spot	*Leptosphaeria sacchari*	⊕
Zoysiagrass	Leaf blight	*Rhizoctonia solani*	⊕
Creeping bentgrass	Root rot	*Pythium aphanidermatum*	⊕
	Brown patch	*Rhizoctonia solani*	⊕
	Dollar spot	*Sclerotinia homoeocarpa*	⊕
Kentucky bluegrass	Powdery mildew	*Sphaerotheca fuliginea*	⊕
Bermudagrass	Leaf spot	*Bipolaris cynodontis*	⊕
St. Augustinegrass	Gray leaf spot	*Magnaporthe grisea*	⊕

Corn	Stalk rot	*Pythium aphanidermatum* and *Fusarium moniliforme*	⊕
	Corn smut	*Ustilago maydis*	⊕
Dicots			
Tomato	Fusarium wilt	*Fusarium oxysporum* f.sp. *lycopersici* (races 1 and 2)	∅
	Fusarium crown and root rot	*Fusarium oxysporum* f.sp. *radicis-lycopersici*	∅
	Powdery mildew	*Oidiopsis sicula*	⊕/∅[b]
	Bacterial wilt	*Ralstonia solanacearum*	⊕
Cucumber	Powdery mildew	*Sphaerotheca xanthii*	⊕
	Anthracnose	*Colletotrichum orbiculare*	⊕
		Colletotrichum lagenarium	∅
	Leaf spot	*Corynespora citrullina*	⊕
	Crown and root rot	*Pythium ultimum* and *Pythium aphanidermatum*	⊕
	Gray mold rot	*Botrytis cinerea*	⊕
	Black rot	*Didymella bryoniae*	⊕
	Fusarium wilt	*Fusarium oxysporum* f.sp. *cucumerinum*	⊕
Muskmelon	Powdery mildew	*Sphaerotheca xanthii*	⊕
Zucchini squash	Powdery mildew	*Erysiphe cichoracearum*	⊕
Pumpkin	Powdery mildew	*Sphaerotheca xanthii*	⊕
Rose	Powdery mildew	*Sphaerotheca pannosa*	⊕
	Black spot	*Diplocarpon rosae*	⊕
Morning gloria	Anthracnose	*Colletotrichum gloeosporioides*	⊕
Pea	Leaf spot	*Mycosphaerella pinodes*	⊕
Paper daisies	Anthracnose	*Colletotrichum gloeosporioides*	⊕
Grape	Powdery mildew	*Uncinula necator*	⊕/∅[b]
Soybean	Stem canker	*Diaporthe phaseolorum* f.sp. *meridionalis*	⊕
Tobacco	BdMV	*Belladonna mottle virus*	⊗
Strawberry	Powdery mildew	*Sphaerotheca macularis* f.sp. *macularis*	⊕
Lettuce	Pythium root rot	*Pythium* spp.	

[a] Silicon can decrease (⊕), increase (⊗), or has no effect (∅) on disease intensity.
[b] Silicon decreases disease intensity if sprayed onto the leaves, but has no effect on disease if added to the nutrient solution (Datnoff *et al.*, 2006)

The source and rate of Si used can strongly affect the magnitude of disease(s) control in rice. According to Aleshin *et al.* (1987), the incidence of rice blast was reduced by nearly 50% in rice plants amended with various inorganic and organic silicon sources relative to plants not receiving Si. In Nigeria, the application of sodium silicate to a Si-depleted soil cultivated with upland rice decreased the severity of neck blast on three cultivars around 40% (Yamauchi and Winslow, 1989). Winslow (1992) reported that the addition of sodium metasilicate to Si-deficient soils in Nigeria reduced by over 50% the severity of neck blast on eight different genotypes of rice. Datnoff *et al.* (1991) noted a significant reduction of neck blast in rice plants growing in a Si-deficient Histosol in southern Florida amended with 5, 10, and 15 tonne ha^{-1} of calcium silicate slag. The authors found significant linear and quadratic relationships among the rates of slag and the severity of neck blast and yield, respectively. Additional studies conducted with calcium silicate slag revealed that finely ground grades were more effective than more coarsely ground grades at reducing the intensity of neck blast (Datnoff *et al.*, 1992). The use of finely ground grades of slag was also correlated with higher silicon content in rice shoots and increased yield. Datnoff and Snyder (1994) demonstrated that reductions in the severity of neck blast brought about by the application of 0.4 tonne Si ha^{-1} did not differ significantly from those achieved by applying a labeled rate of the fungicide benomyl. In their studies, disease severity was negatively correlated with the content of Si that accumulated in plant tissue. Studies conducted by Seebold *et al.* (2004) revealed that Si alone at 0.1 tonne ha^{-1} was as effective as labeled rates of fungicides, edifenphos and tricyclazole, for the control of leaf and neck blast at low intensity levels. Furthermore, application of Si plus a 10-25% rate of fungicide provided control equal to the full rate of fungicide under conducive environmental conditions for leaf and neck blast development. Indeed, a single soil application of Si had a significant effect in controlling leaf and neck blast in the next rice season. The effect of Ca on disease development was avoided by adding lime to the plots to achieve equivalent levels of Ca throughout the treatments. It has been reported that Si was the only element that significantly increased in tissues of rice grown over a 3-year period in organic soil amended with calcium silicate slag (Snyder *et al.*, 1986). Silicon uptake may depress the absorption of Ca and its accumulation in shoots (Ma *et al.*, 1989; Inanaga *et al.*, 1995). It appears that Si can be used to augment inherent levels of resistance of some rice cultivars to blast. At one experimental area in eastern Colombia, Seebold *et al.* (2000) found that application of Si reduced the severity of rice blast in a partially resistant cultivar to levels of severity observed in a resistant cultivar not amended with Si.

Silicon also reduced the intensity of sheath blight (*Thanatephorus cucumeris* (A.B. Frank) Donk (anamorph *Rhizoctonia solani* Kühn)) even though there was no significant difference between the high and low rates of Si applied (Mathai *et al.*, 1977). Winslow (1992) reported that Si reduced the severity of sheath blight in irrigated *indica* rice genotypes, but not on *japonica* upland rice and intermediate genotypes. However, Rodrigues *et al.* (2001) showed that Si can decrease the severity of sheath blight in both tropical *japonicas* and an *indica* type rice cultivar, which indicates that enhanced disease resistance by Si is not limited to *indica* types. Indeed, the authors noted that Si reduced the intensity of sheath blight of two susceptible (Lemont and Labelle) and two moderately susceptible (Drew and Kaybonnet) rice cultivars to levels of intensity observed in two cultivars (Jasmine and LSBR-5) with high partial resistance to sheath blight but not amended with Si. In Brazil, application of Si to a Si-deficient typic acrustox Red Yellow Latosol (Oxisol) reduced significantly the total number of sheath blight lesions on sheaths, the total area under the relative lesion extension progress curve, the severity of sheath blight, and the highest relative lesion height on the main tiller by 37%, 40%, 52%, and 24%, respectively, in six rice cultivars as the rate of Si increased from 0 to 8 tonne ha^{-1} (Rodrigues *et al.*, 2003c). Rodrigues *et al.* (2003b) also studied the effect of Si and rice growth stages on tissue susceptibility to sheath blight and observed that as the rates of Si increased in the soil, the intensity of sheath blight was significantly reduced at all rice growth stages.

Brown spot (*C. miyabeanus*), stem rot (*Magnaporthe salvinii* (Cattaneo) R. Krause & Webster), leaf scald (*Monographella albescens* (Thuem.) and grain discoloration (caused by a complex of insects and fungal species) are other diseases controlled by Si (Gangopadhyay and Chatopadhyay, 1974; Datnoff *et al.*, 1990; 1991; 1992; Correa-Victoria *et al.*, 1994; Deren *et al.*, 1994; Savant *et al.*, 1997; Korndörfer *et al.*, 1999; Seebold *et al.*, 2000). Regarding bacterial diseases, Chang *et al.* (2002), reported a significant reduction in lesion length of bacterial leaf blight (*Xanthomonas oryzae* pv. *oryzae* (Ishiyama). The reduction in lesion length was positively correlated with a decrease in the content of soluble sugar in leaves of plants amended with Si. Rice cultivars accumulating high content of Si in roots also showed increased resistance to the root-knot nematode *Meloidogyne* spp. (Swain and Prasad, 1991).

How silicon suppresses plant diseases?

The effect of Si on plant resistance to disease is considered to be due to either an accumulation of absorbed Si in the epidermal tissue or an expression of pathogenesis-induced host defense responses (Datnoff and Rodrigues, 2005). Accumulated monosilicic acid polymerizes into polysilicic acid and then transforms to amorphous silica, which forms a thickened Si-cellulose membrane. By this means, a double cuticular layer protects and mechanically strengthens plants. Silicon also might form complexes with organic compounds in the cell walls of epidermal cells, therefore increasing their resistance to degradation by enzymes released by fungi. Research also points to the role of Si *in planta* as being active and this suggests the element might be a signal for inducing defense reactions to plant diseases (Belanger *et al.*, 2003; Rodrigues *et al.*, 2003a). Silicon has been demonstrated to stimulate chitinase activity and rapid activation of peroxidases and polyphenoxidases after fungal infection. Glycosidically bound phenolics extracted from Si amended plants when subjected to acid or B-glucosidase hydrolysis displayed strong fungistatic activity (Cherif *et al.*, 1994). More recently, flavonoids and momilactone phytoalexins, low molecular weight compounds that have antifungal properties, were found to be produced in both dicots and monocots, respectively, fertilized with Si and challenged inoculated by the pathogen in comparison to non-fertilized plants also challenged inoculated by the pathogen (Fawe *et al.*, 1998; Rodrigues *et al.*, 2004). These antifungal compounds appear to be playing an active role in plant disease suppression. In addition, an increase in superoxide (O_2^-) generation was observed in rice leaves of plants treated with Si 15 minutes after inoculation with *M. grisea* (Maekawa *et al.*, 2002). More recently, Prabhu *et al.* (2005) demonstrated that silicon will suppress the sugar content of rice plants (Fig 3) while Rodrigues *et al.* (2005) showed that B 1-3 glucanase, peroxidase and PR-1 proteins are associated with rice blast suppression. Both these studies further suggest other additional mechanisms may be involved in Si mediated resistance to plant diseases.

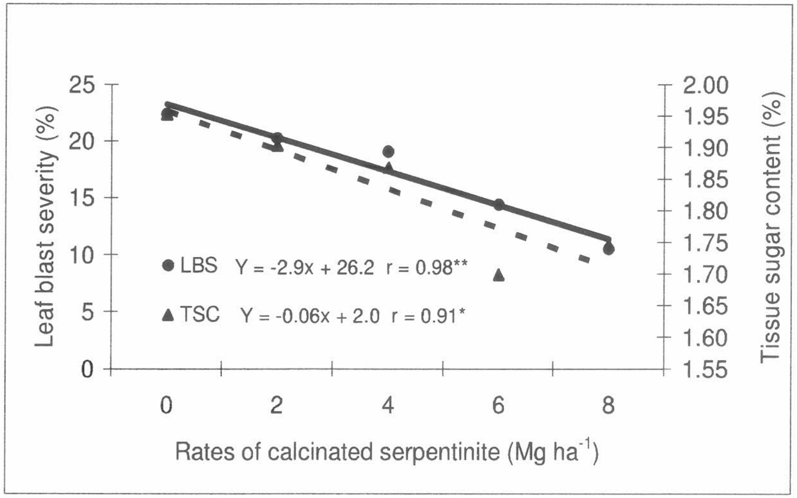

Fig 3. Relationships of leaf blast severity and tissue soluble sugar content to rates of calcinated serpentinite applied as a silicon source to irrigated rice (Prabhu *et al.*, 2005)

Conclusion

The Cl, K, and Si nutrient-host relationships outlined above demonstrate well how important each one of these elements can be for plant health, especially when the plant is low or deficient and/or under some adverse environmental stress. Although K may fluctuate in its ability to suppress plant disease, Cl and Si clearly play important roles in plant disease defense. Large gaps still exist in growers' awareness for these two elements in improving plant health. Large gaps also still exist for all three elements in understanding their ratio to other key elements in plant tissue, and subsequent effects on plant diseases and their mechanism (s) in disease suppression. More research is warranted in understanding adequate rates and application times for these three elements to improve plant utilization and subsequently plant production and health.

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