

Silicon and Rice Disease Management

Fabício A. Rodrigues¹ & Lawrence E. Datnoff²

¹Universidade Federal de Viçosa, Departamento de Fitopatologia, Laboratório da Interação Patógeno-Hospedeiro, Viçosa, MG, CEP 36570-000, e-mail: fabricio@ufv.br; ²University of Florida, Department of Plant Pathology, Gainesville, FL 32611-0680, e-mail: ledatnoff@ifas.ufl.edu

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Corresponding author: Fabrício A. Rodrigues

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ABSTRACT

The element silicon (Si) is not considered an essential nutrient for plant function. Nevertheless, Si is absorbed from soil in large amounts that are several fold higher than those of other essential macronutrients in certain plant species. Its beneficial effects have been reported in various situations, especially under biotic and abiotic stress conditions. The most significant effect of Si on plants, besides improving their fitness in nature and increasing agricultural productivity, is the restriction of parasitism. There has been a considerable amount of research showing the positive effect of Si in controlling diseases in important crops. Rice (*Oryza sativa*), in particular, is affected by the presence of Si, with diseases such as blast, brown spot and sheath blight becoming more severe on rice plants grown in Si-depleted soils. The hypothesis underlying the control of some diseases in both mono- and di-cots by Si has been confined to that of a mechanical barrier resulting from its polymerization *in planta*. However, some studies show that Si-mediated resistance against pathogens is associated with the accumulation of phenolics and phytoalexins as well as with the activation of some PR-genes. These findings strongly suggest that Si plays an active role in the resistance of some plants to diseases rather than forming a physical barrier that impedes penetration by fungal pathogens.

Additional keywords: mechanisms of host resistance, electron microscopy, PR-genes, phenolic-like compounds, phytoalexins.

RESUMO

Uso do silício no manejo de doenças em arroz

O elemento silício (Si) não é considerado um nutriente essencial para o funcionamento das plantas. Todavia, em certas espécies de plantas, o Si é absorvido do solo em quantidades superiores a alguns macronutrientes. O efeito benéfico do Si às plantas tem sido relatado em várias situações especialmente sob condições de stress biótico e abiótico. O efeito mais significativo do Si às plantas, além de melhorar a adaptação delas ao solo e aumentar a produção, é a restrição ao parasitismo. Existe na literatura uma considerável quantidade de informações mostrando o efeito positivo do Si no controle de doenças em importantes culturas. O arroz (*Oryza sativa*), em particular, é afetado pela presença do Si, uma vez que doenças como a brusone, a mancha parda e a queima-das-bainhas tornam-se mais severas em plantas cultivadas em solos deficientes nesse elemento. A hipótese para o controle das doenças pelo Si, tanto em mono quanto em dicotiledôneas, tem sido atribuída à barreira mecânica resultante da polimerização desse elemento na planta. Entretanto, outros estudos revelaram que a resistência mediada pelo Si contra patógenos está associada com a acumulação de compostos fenólicos e fitoalexinas, além da ativação de alguns genes PR. Esses resultados revelam que o Si tem um papel ativo na resistência de algumas plantas às doenças e não exerce apenas uma barreira mecânica que impede o ingresso dos fitopatógenos.

Palavras-chave adicionais: mecanismos de resistência de plantas, microscopia eletrônica, PR genes, compostos fenólicos, fitoalexinas.

The Element Silicon

Silicon (Si) is the second most abundant mineral element in soil, comprising approximately 28% of the earth's crust (Elawad & Green, 1979; Singer & Munns, 1987; Epstein, 1991). In warm sub-humid and humid tropical ecoregions (Inokari & Kubota, 1930), a high degree of weathering, mainly as desilication, has resulted in the development of soil orders rich in iron and aluminum oxides and low in nutrient bases and Si (Juo & Sanchez, 1986).

Some of these soil orders such as Ultisols and Oxisol, which account for 34% of the area of major soil orders in the tropics, occupy great expanses of land in Africa and South and Central America on the order of about 1,666 million hectares. Highly-organic Histosols that contain little mineral matter also may contain low levels of Si (Savant *et al.*, 1997b). As a result of Si leaching, the soluble Si content of tropical soils such as Ultisols and Oxisols is generally five-ten times less than in most temperate soils (Foy, 1992). This

might be one of the unidentified causes of lower rice (*Oryza sativa* L.) productivity in many tropical and subtropical soils compared with those from temperate areas (Savant *et al.*, 1997a). Although most soils can contain considerable levels of Si, repeated cropping can reduce the levels of plant-available Si to the point that supplemental Si fertilization is required for maximum production.

Many plants are able to uptake Si. Depending upon the species, the content of Si accumulated in the biomass can range from 1% to greater than 10% (Elawad & Green, 1979; Epstein, 1991). Plant species are considered Si accumulators when the concentration of Si (in dry weight basis) is greater than 1% (Epstein, 1999). Relative to monocots, dicots such as tomato (*Lycopersicon esculentum* Mill.), cucumber (*Cucumis sativa* L.), and soybean [*Glycine max* (L.) Merrill] are poor accumulators of Si with values of less than 0.1% of Si in their biomass. Dryland grasses such as wheat (*Triticum aestivum* L.), oat (*Avena sativa* L.), rye (*Secale cereale* L.), barley (*Hordeum vulgare* L.), sorghum [*Sorghum bicolor* (L.) Moench], corn (*Zea mays* L.), and sugarcane (*Saccharum officinarum* L.) contain about 1% of Si in their biomass, while aquatic grasses have up to 5% Si content (Jones & Handreck, 1967; Epstein, 1991, 1999; Rodrigues *et al.*, 2001b).

Silicon is accumulated at levels equal to or greater than essential nutrients in plant species belonging to the families Poaceae, Equisetaceae, and Cyperaceae (Savant *et al.*, 1997b). In rice, for example, Si accumulation is about 108% greater than nitrogen. It is estimated that a rice crop producing a total grain yield of 5 ton.ha⁻¹ will remove 0.23 to 0.47 ton Si ha⁻¹ from the soil (Savant *et al.*, 1997b). Therefore, applications of 5 ton slag ha⁻¹ (1 ton Si ha⁻¹) appear to be sufficient for supplying enough Si to the plant so that the tissue content will be 3% or greater (Snyder *et al.*, 1986). Concentrations between 3 - 5% may be the minimum tissue levels needed for disease control in rice (Datnoff *et al.*, 1997).

Silicon is considered a plant nutrient “anomaly” because it is presumably not essential for plant growth and development (Epstein, 1991). However, soluble Si has enhanced the growth, development and yield of several plant species including *Equisetum* spp., rice, sugarcane, wheat, and some dicotyledons (Jones & Handreck, 1967; Elawad & Green, 1979; Bélanger *et al.*, 1995; Savant *et al.*, 1997b). Plants absorb Si exclusively as monosilicic acid, also called orthosilicic acid (H₂SiO₄), by diffusion and also by the influence of transpiration-induced root absorption known as mass flow (Elawad & Green, 1979). Plant species from the family Poaceae accumulate Si at levels equal to their transpiration rate (Jones & Handreck, 1967).

Silicon is deposited in the form of silica gel or biogenetic opal as amorphous SiO₂•nH₂O in cell walls and intercellular spaces of root and leaf cells as well as in bracts (Yoshida, 1962, 1965; Lanning, 1963). Silicon can also be found in the form of monosilicic acid, colloidal silicic acid, or organosilicone compounds in plant tissues (Yoshida, 1962;

Inanaga *et al.*, 1995). Silicon is distributed basipetally and accumulates greater amounts in the epidermal cells than in any other types of leaf cells (Elawad & Green, 1979). Once deposited, silica gel is immobile and is not redistributed to actively growing tissues (Elawad & Green, 1979; Ma *et al.*, 1989; Epstein, 1991).

Diseases Suppressed by Silicon Application

The most significant effect on plants of maintaining adequate levels of Si in the soil is the restriction of grazing and parasitism (Bélanger *et al.*, 1995; Datnoff *et al.*, 1997; Savant *et al.*, 1997b). Kawashima (1927) first demonstrated, under controlled conditions, that application of Si to rice plants increased resistance to blast (*Pyricularia grisea* Sacc. Cavara [teleomorph: *Magnaporthe grisea* (Hebert) Barr]). Silicon content in rice tissues also increased upon application of silica gel or solid silica to the soil. The results showed Si content in rice straw and husks were proportional to the amount of Si applied to the soil, and that the severity of blast on panicles was inversely proportional to the amount of the Si in rice tissues. Ito & Hayashi (1931) and Miyake & Ikeda (1932) also showed that the application of Si increased resistance to blast. Inokari & Kubota (1930) demonstrated that application of Si to peat land paddy fields reduced blast incidence. Many other Japanese researchers demonstrated that applications of 1.5 to 2.0 ton.ha⁻¹ of various Si sources to Si-deficient paddy soils significantly reduced the intensity of blast (Suzuki, 1935; Kozaka, 1965). Volk *et al.* (1958) also reported that the number of blast lesions on leaves of rice cultivar Caloro decreased linearly as the Si content in leaf blades increased. Rabindra *et al.* (1981) found that the Si content 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, blast susceptibility of some rice cultivars grown in soil receiving different rates of Si was negatively correlated with the content of Si in shoots (Kozaka, 1965; Ou, 1985). Miyaki & Adachi (1922) compared the Si content of two rice cultivars. They used a susceptible and a resistant cultivar at three different growth stages. The silicon contents of Akage (susceptible) at heading, flowering, and milky dough stages were 1.68, 2.27, and 2.92% (per fresh weight), respectively, and that of Bozu, the resistant cultivar, were 1.93, 2.53, and 3.32%, respectively. The highest values for Si content observed in Bozu lead the authors to conclude that more resistant rice cultivars contain more Si than susceptible ones. However, rice cultivars accumulating higher levels of Si in shoots are not always more resistant to blast than cultivars accumulating lower levels of Si (Kozaka, 1965; Ou, 1985; Winslow, 1992).

The source and rate of Si used can strongly affect the magnitude of rice blast control. According to Aleshin *et al.* (1987), the incidence of rice blast on rice plants amended with various inorganic and organic silicon sources was reduced by nearly 50% 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 by approximately 40% (Yamauchi & Winslow, 1987). Winslow (1992) reported that the addition of sodium metasilicate to Si-deficient soils in Nigeria greatly reduced the severity of neck blast by over 50% on eight different rice genotypes.

Datnoff *et al.* (1991) reported a significant reduction in the severity of brown spot caused by *Cochliobolus miyabeanus* (Ito & Kuribayashi in Ito) Drechs. ex Dastur [anamorph *Bipolaris oryzae* (Breda de Haan) Shoemaker] and incidence of neck blast in rice plants growing in a Si-deficient Histosol in southern Florida after an application of calcium silicate. In 1987, applications of calcium silicate slag reduced neck blast by 30.5% and brown spot by 15.0% over the control. In 1988, neck blast and brown spot were reduced by 17.4 and 32.4%, respectively, over the control.

In 1988, brown spot was reduced by 14.5% in the plots with residual calcium silicate slag, compared to a 17.6% reduction for plots newly fertilized in 1988. Plots with residual Si plus the additional 5 ton.ha⁻¹ of calcium silicate slag application had 16.5% less brown spot than the control.

Other investigators have also reported a reduction in brown spot severity by Si application (Takahashi, 1967; Gangopadhyay & Chatopadhyay, 1974; Lee *et al.*, 1981; Nanda & Gangopadhyay, 1984). Neck blast incidence at the highest slag rate decreased 29.1, 27.0, and 32.4% over the control for residual 1987 slag effects on the 1988 crop, 1988 slag applications, and residual 1987 slag rates each receiving 5 ton.ha⁻¹ of slag in 1988, respectively. Although the application of slag in 1988 suppressed neck blast more than the 1987 residual applications on the 1988 rice crop, the residual applications were very effective.

The analysis of rice straw samples in this study showed that Si content alone significantly increased with increasing slag rates over the control, indicating that the reduction in neck blast severity can be accounted for only by Si, not calcium. As previously reported by Snyder *et al.* (1986), Si was the only element that significantly increased in tissues of rice grown over a three-year period in organic soil amended with calcium silicate slag. Indeed, it has been also known that Si uptake may depress the absorption of Ca and its accumulation in shoots (Ma *et al.*, 1989; Inanaga & Okasaka, 1995).

Application of Si has also been shown to reduce the intensity of sheath blight caused by *Thanatephorus cucumeris* (A. B. Frank) Donk. (anamorph *Rhizoctonia solani* Kühn) anastomosis group 1 IA. Mathai *et al.* (1977) reported that Si had a significant effect in reducing sheath blight intensity at 75 days after sowing, but the difference between high (500 kg.ha⁻¹ of sodium silicate) and low (250 kg.ha⁻¹ of sodium silicate) rates of Si was not statistically significant. Rodrigues *et al.* (2003b) studied the effect of Si on rice tissue susceptibility to sheath blight by inoculating plants on the following days after emergence: 45 (four-leaf

stage), 65 (eight-leaf stage), 85 (tillering), 117 (booting), and 130 (panicle exertion). The authors observed that for plants inoculated with *R. solani* at all growth stages, Si concentration in straw increased as application rates of Si increased from 0 to 1.92 g.pot⁻¹. The level of Ca in soil was equilibrated for each rate of wollastonite (Si source) by using dolomitic lime. Concentration of Ca in the straw did not differ among plant growth stages; therefore, only variations in Si levels could account for the difference in the components of host resistance evaluated. The incubation period was not affected by the amount of Si added to the soil, but it was shorter at booting and panicle exertion stages. Plants grown in pots without Si amendments and inoculated with *R. solani* at any growth stage exhibited the highest values for severity of sheath blight. Severity of sheath blight reached lower values on inoculated plants at 117 (booting) and 130 (panicle exertion) days after emergence as the rates of Si increased from 0 to 1.92 g.pot⁻¹. Overall, plants grown in pots without Si amendment and inoculated at any growth stage, but particularly at 45 days after emergence, exhibited the highest values for total number of sheath blight lesions on sheaths as well as total area under the relative lesion extension curve, than inoculated plants amended with Si.

Grain discoloration caused by a complex of fungal species such as *Bipolaris oryzae*, *Curvularia* sp., *Phoma* sp., *Microdochium* sp., *Nigrospora* sp., and *Fusarium* sp., is another important constraint for irrigated and upland rice production worldwide. Prabhu *et al.* (2001) showed that the severity of grain discoloration in several irrigated and upland rice genotypes linearly decreased as the soil rates of SiO₂ increased. The severity of grain discoloration was reduced by 17.5%, on average, at the rate of 200 kg.ha⁻¹ of SiO₂ while grain weight increased 20%. Correa-Victoria *et al.* (2001) also reported a reduction in grain discoloration for the cultivar Oryzica Llanos 5 upon Si application. Under African upland conditions, Si application decreased husk discoloration in both *indica* and *japonica* type rice cultivars (Winslow, 1995).

Seebold *et al.* (2000) reported that the severity of leaf scald caused by *Monographella albescens* (Thümen) Parkison, Sivanesan & Booth was reduced by Si application at two locations in Colombia. The severity of leaf scald on Oryzica Llanos 5, Linea 2SR, and Oryzica 1 rice cultivars was significantly different at each rate of Si. Leaf scald severity was reduced at Santa Rosa by 23% at 500 kg.ha⁻¹ of Si, and by 41% at 1000 kg.ha⁻¹ (Table 1). At La Libertad, scald severity was reduced by 32 and 42%, respectively, at 500 and 1000 kg.ha⁻¹ (Table 1). Correa-Victoria *et al.* (2001) also reported that the severity of leaf scald on rice cultivar Oryzica Llanos 5 was significantly reduced by 17.4% as the rates of Si increased from 0 to 3 ton.ha⁻¹. Prabhu *et al.* (2001) showed that leaf scald was suppressed with increasing rates of Si from 0 to 4 ton.ha⁻¹ of SiO₂ applied in the form of wollastonite. The relationship between rates of Si and leaf scald severity was quadratic negative. The lesion length was

reduced from 0.6 cm to 0.4 cm at the rate of 1 ton.ha⁻¹ of SiO₂.

Stem rot caused by *Magnaporthe salvinii* Cattaneo has also been efficiently suppressed by Si (Elawad & Green, 1979).

Regarding bacterial diseases, Chang *et al.* (2002) reported a significant reduction in lesion length of bacterial leaf blight caused by *Xanthomonas oryzae* pv. *oryzae* (Ishiyama) Swings *et al.* from 5 to 22% among four rice cultivars supplemented with Si. 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 reduced levels of incidence of the root-knot nematode *Meloidogyne* spp. (Swain & Prasad, 1988).

Silicon and Interactions with Fungicides

Kitani and co-authors (1960) probably were the first scientists ever to demonstrate the influence of Si and fungicides alone and in combination for controlling blast. In their study, Si applied as calcium silicate slag reduced neck blast severity almost as effectively as foliar application of a mercurial fungicide, 12% vs. 10% and 11.2% vs. 7.4%, respectively, depending on the level of nitrogen (N) applied.

Silicon alone was associated with a gain in grain weight over the control of 37% (50 kg N ha⁻¹) to 40% (75 kg N ha⁻¹). The mercurial fungicide applications increased weights by 28 to 34%, respectively, for the two different N treatments. Combined Si/fungicide treatments were the most effective for the reduction of neck blast severity (below 3%) and increased grain weight (40 to 48%). Hashimoto & Hirano (1976) conducted similar studies on neck blast development but included other factors such as rice cultivars and nitrogen. They demonstrated that calcium silicate alone reduced rice blast 13%, fungicide alone (edifenfos) by 22% and the fungicide + calcium silicate by 27% in comparison to the non-amended control. They concluded that the fungicide effect in reducing blast was supplemented by the addition of calcium silicate.

In Florida, an evaluation of Si fertilization in combination with benomyl or propiconazole was undertaken to determine if Si could control diseases such as blast or brown spot as effectively as a fungicide (Datnoff & Snyder, 1994; Datnoff *et al.*, 1997). A rice crop was treated with Si at 0 and 2 ton Si ha⁻¹ and benomyl at 0 and 1.68 kg.ha⁻¹ and propiconazole at 0 and 0.44 l.ha⁻¹. Fungicide sprays were applied at panicle differentiation, boot, heading and heading plus 14 days. Blast incidence was 73% in the non-Si, non-fungicide control plots and 27% in the benomyl treated plots. Where Si was applied, blast incidence was 36% in the non-fungicide plots and 13% in the benomyl treated plots. The same degree of blast control was generally obtained when either benomyl or Si were applied individually. Brown spot responses were similar to those observed with blast (Table 2; Figure 1). Brown spot severity, number of lesions, and area under the disease progress curve were reduced more by

Si in combination with propiconazole and Si alone than with propiconazole itself. For both diseases, the greatest reduction in disease development was obtained by integrating Si fertilization with fungicides. Thus, Si provided a great degree of control than fungicides for two economically important diseases. Mathai *et al.* (1977) evaluated Si applied as sodium silicate alone and in combination with two fungicides, edifenfos and mancozeb, in the control of sheath blight. All treatments were effective in reducing sheath blight intensity (SBI) and in increasing yields in comparison to the control; Si (SBI=48% and yield=4.6%), mancozeb (SBI=68% and yield=9.5%), edifenfos (SBI=99% and yield = 16.8%), mancozeb + Si (SBI=84% and yield=13.1%) and edifenfos + Si (SBI=100% and yield=37.2%). The combination of Si and a fungicide was the best treatment for dramatically reducing disease. The increase in grain yield was synergistic when the fungicide edifenfos was used in combination with Si.

Considering that Si can control several rice diseases to the same general degree as a fungicide, it is possible that Si might help reduce the number of fungicide applications or the rate of active ingredients. This hypothesis was tested by Seebold (1998) under field experiments of upland rice in

TABLE 1 - Severity of leaf scald on rice (*Oryza sativa*) cultivars treated with silicon at 500 or 1,000 kg.ha⁻¹ at Santa Rosa and La Libertad, Colombia, in 1996

Silicon rate (kg.ha ⁻¹)	Severity of leaf scald (% DLA) ^{a,b}	
	Santa Rosa	La Libertad
0	8.3 a	4.0 a
500	6.4 b	2.7 b
1,000	4.9 c	2.3 c

^a Percent of diseased leaf area (DLA) was estimated visually on all leaves of five tillers per subplot.

^b The interaction between rates of Si and cultivar was not significant ($P < 0.05$); therefore Si treatment means were averaged across the cultivars Oryzica Llanos 5, Linea 2SR, and Oryzica 1.

TABLE 2 - Effect of propiconazole and silicon on brown spot caused by *Cochliobolus miyabeanus* development

Treatment	Lesion number per cm ²	AUDPC ^a	Brown spot severity ^b
Control	2.5 a ^c	2772 a	87 a
Propiconazole (P)	2.0 b	1124 b	61 b
Silicon (Si)	1.6 c	583 c	37 c
P+Si	0.6 d	284 d	14 d

^a AUDPC = area under disease progress curve.

^b Brown spot severity based on a 0-9 scale, where 0 = no disease and 9 = 76% or more of leaf area affected. The percent mean affected area of leaf for each numerical rating was used for estimating differences between treatments.

^c Means followed by a different letter are significantly different based on Fisher Least Significant Difference ($P \leq 0.05$).

the savannahs of Colombia. Silicon was applied as wollastonite at 400 kg Si ha⁻¹ and the rice cultivar *Oryzica Sabana 6* was seeded at 80 kg.ha⁻¹. Treatments included a non-treated control, Si applied alone, and Si plus fungicides (edifenfos at 1 l.ha⁻¹ and tricyclazole at 300 g ha⁻¹) applied at the following growth stages: tillering (T), panicle initiation (PI), booting (B), 1% panicle emergence (1%), 50% panicle emergence (50%), PI, B, 1%, and 50%; B, 1% and 50%; 1% and 50%; B and 1%; PI and 1%; T (Figure 2). Incidence of neck blast was significantly reduced using either Si alone or Si plus fungicides in comparison with the nontreated control.

Silicon alone significantly reduced the incidence of neck blast by 40%. The treatment Si plus one fungicide reduced neck blast 75 to 90% while Si + two applications reduced neck blast 76 to 94%. Silicon plus three to five applications reduced neck blast 94 to 98%. However, no significant differences in yield were observed among Si alone or Si plus fungicide applications, regardless of timing. All treatments significantly increased yield in comparison to the control. In another experiment, Si was incorporated prior to seeding at 0 and 1000 kg.ha⁻¹ (80). Two foliar sprays of edifenfos were applied at 0, 10, 25 and 100% of recommended rates. Ratings of leaf blast for Si alone and Si plus edifenfos at various rates were 54-75% lower than in the nontreated control.

For neck blast, Si alone and Si plus edifenfos and tricyclazole at various rates were 28-66% lower in comparisons to the non-treated control. The greatest leaf and neck blast reductions were observed when Si plus the full rate of fungicide were applied. Silicon and lower rates of fungicides (10% and 25%) were able to reduce leaf and neck blast as effectively as a full rate of the fungicide. Silicon alone was just as effective as the fungicides alone in comparison to the control treatment for reducing leaf blast severity and promoting plant growth.

Fungicides improved yields ranging from 22 to 28% over the control. Interestingly, Si alone improved yields by 51%, and this increase was significantly greater than the fungicide contribution. The effect of Si on reducing a disease such as blast unquestionably contributed to an increase in yield, but Si also has been shown to increase yields in the absence of disease (Ou, 1985). Increase in grain yield can be attributed to an increase in the number of grains per panicle (Deren *et al.*, 1994). Spikelet fertility also has been associated with Si concentration in rice (Savant *et al.*, 1997b). Therefore, Si alone could improve grain yields of rice cultivars without further genetic improvements.

In 1995 and 1996, Si was incorporated prior to seeding at 0 and 1000 kg.ha⁻¹ (Seebold *et al.*, 2004). In order to study the residual effects, plots that were treated in 1995 (residual Si) were compared with plots receiving a fresh or current year application of Si in 1996. Two foliar applications of edifenfos were applied at 20 and 35 days after planting, followed by three applications of tricyclazole. Leaf blast was evaluated as the percentage of the area on individual leaves

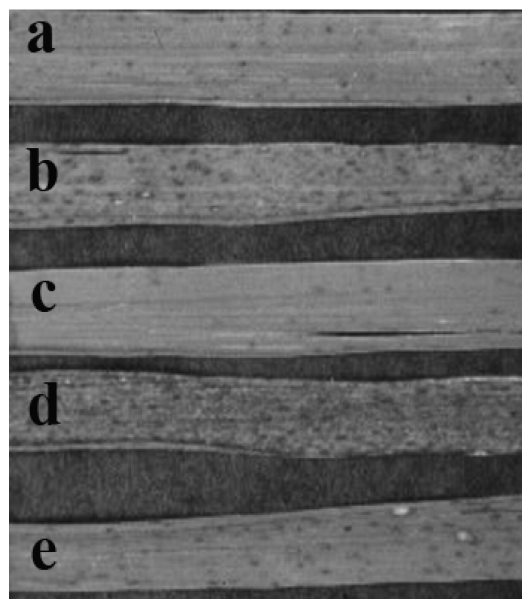


FIG. 1 - Symptoms of brown spot caused by *Cochliobolus miyabeanus* on rice (*Oryza sativa*) as influenced by applications of silicon (a and e), propiconazole (b), the combination of silicon + propiconazole (c), and the nontreated control (d). Reprinted from Crop Protection, vol. 16, Datnoff, L. E., Deren, C. W., and Snyder, G. H., Silicon fertilization for disease management of rice in Florida, p.529, 1997, with permission from Elsevier.

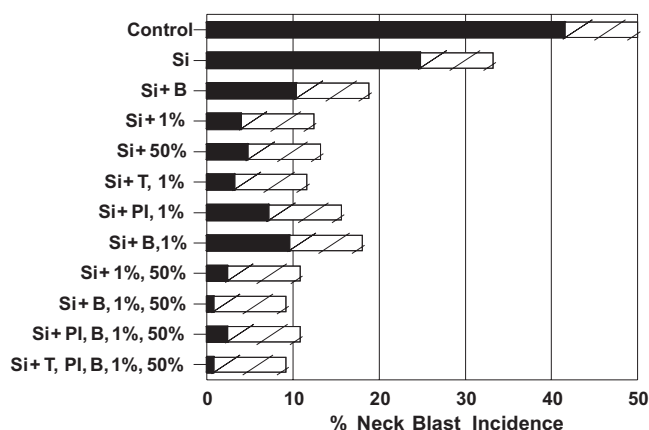


FIG. 2 - Effect of silicon and fungicide timings on neck blast incidence caused by *Magnaporthe grisea* on rice (*Oryza sativa*). Fungicides timings are at: tillering (T), panicle initiation (PI), booting (B), 1% heading (1%), 50% heading (50%) and various combinations. Stripe bars represent Fisher Least Significant Difference value ($P \leq 0.05$).

and neck blast was rated as percentage of incidence on 100 panicles. In both 1995 and 1996, ratings of leaf blast for Si alone (residual and fresh applications) and Si plus edifenfos (residual and fresh applications) were 50-68% lower than in comparison to the nontreated control.

The greatest reductions in leaf blast were observed where Si plus fungicide had been applied. The one year residual Si application was as effective as a fresh application, and these treatments were not significantly different for leaf blast control in comparison to edifenfos alone or in combination with a one year residual. Silicon alone reduced leaf blast to the same level as the edifenfos applied with Si in 1995. In 1996, ratings of leaf blast for Si alone were significantly lower (35%) than for the full rate of fungicide. Incidence of neck blast was reduced 28 to 66% with applications of Si and Si plus tricyclazole. A one year residual application of Si applied in 1995 was as effective in reducing neck blast incidence as a fresh application in 1996. However, these treatments were not as effective as fungicide applied alone or in combination with Si. The fungicide tricyclazole alone or in combination with Si effectively reduced neck blast incidence. Silicon alone and in combination with tricyclazole applied in 1995 or in 1996 increased yields 28 to 51% over the non-treated control. The 1995 residual Si application was as effective in increasing yields and not significantly different from tricyclazole alone or tricyclazole applied in combination with Si applied in 1995 or 1996.

Silicon enhances rice resistance to diseases

Kozaka (1965) made a comprehensive review in English of the research done in Japan on the effects of Si on rice resistance to diseases. The author cited the research of several Japanese scientists dating from 1917 to 1959. General observations indicated that rice plants treated with Si had fewer blast lesions, a large number of silicified epidermal cells and an increased resistance to blast.

A positive correlation between Si content in rice tissues and blast resistance within a given rice cultivar occurred; however, this correlation was not observed between different rice cultivars. Winslow (1992) and Deren *et al.* (1994) have made similar observations for blast and several other diseases. Nevertheless, Kozaka (1965) showed that the susceptible cultivar Kurusmochi amended with Si had lower number of blast lesions at a level comparable to the resistant cultivar Ishikrishiroke which was not amended with this element.

Kim & Lee (1982) investigated the effects of Si soil amendments on the susceptibility of several rice cultivars (Tongil or *Japonica* types) to neck blast development in Korea. Their study revealed that Tongil types were the most susceptible to neck blast with incidence ranging from 37 to 79% in the controls vs. 4.6 to 6.3% for the *Japonicas*. Disease control of Tongil types in response to Si amendments was 56 to 60% as compared with 6 to 46% in the *Japonica* types. Yield increases among all the cultivars due to Si amendments ranged from 9 to 22%. Interestingly, the cultivar Akibare, which might be considered the most resistant to rice blast in their study, had yield increases of 10% over the non-amended control even though its resistance was little improved with the addition of Si. These findings suggest that cultivars that have complete genetic

resistance to blast or any other disease might still have their yields augmented without further genetic improvements by using Si.

Rice cultivars that have lost resistance to a disease such as blast, but show some good agronomic traits, might be redeployed simply by using Si fertilization for disease management. Winslow (1992) reported that African *japonica* upland rice genotypes had 50 to 100% higher Si concentration in mature flag leaves, and were more resistant to neck blast than Asian *indica* upland genotypes.

Seebold *et al.* (2000) conducted an extensive study on the interaction of Si rates with rice cultivars with different levels of resistance to blast. Blast resistant, Oryzica Llanos 5, partially resistant, Linea 2, and susceptible Oryzica 1 cultivars were planted in soil amended with Si at 0, 500 or 1000 kg.ha⁻¹. Although blast disease intensity was low (> 1 to 6%), leaf blast was reduced by Si at the highest rate by 50 and 73% on Linea 2 and Oryzica 1, respectively, as compared to the control. The level of resistance to leaf blast in Linea 2 amended with 500 or 1000 kg.ha⁻¹ of Si was augmented to the same level of Oryzica Llanos 5 without Si. Similar results were obtained by Osuna-Canizalez *et al.* (1991). The authors conducted experiments with nutrient solutions of Si and three IR cultivars varying in levels of blast resistance. The IR36 and IR50 were lowland cultivars, and IR36 contained a higher level of partial resistance to blast than IR50. The IAC165 was an upland cultivar with almost complete resistance to the race of *M. grisea* used in this study. They demonstrated significant reductions in number of lesions per cm² of leaf tissue (30 to 35 lesions for IR50 and IR36 cultivars non-amended with Si versus 2 to 4 lesions on amended Si plants). The resistance of these two cultivars was greatly improved with the addition of Si. In addition, the level of resistance of these two cultivars amended with Si was equivalent to that of IAC165 without Si fertilization.

Seebold *et al.* (2000) also investigated neck blast incidence in blast resistant Oryzica Llanos 5, partially resistant, Linea 2, and susceptible Oryzica 1 cultivars of rice. Neck blast incidence was significantly different among the cultivars and varied according to the rate of Si applied. Silicon reduced the incidence of neck blast for Linea 2 and Oryzica 1. No detectable changes were recorded for Oryzica Llanos 5. For Linea 2 and Oryzica 1, neck blast incidence decreased by 37 and 28%, respectively, as the rate of Si increased from 0 to 1000 kg.ha⁻¹. Cultivars Linea 2 and Oryzica 1 had higher blast incidence at 500 or 1000 kg of Si ha⁻¹ as compared to the non amended blast resistant cultivar Oryzica 5. However, the addition of 1000 kg of Si ha⁻¹ reduced the incidence of neck blast on Oryzica 1 as effectively as partially resistant Linea 2 without Si. Rough rice yields of Oryzica 1 amended with 500 and 1000 kg.ha⁻¹ Si did not differ from either the non amended Oryzica Llanos 5 or Linea 2. The increase of Si rates from 0 to 1000 kg.ha⁻¹ increased yields by 20% for both Oryzica Llanos 5 and Linea 2.

Effective disease control strategies for agronomic crops include the incorporation of genetically controlled

resistance into cultivars. Since genotypes vary in disease resistance, the relationship between Si content among genotypes and disease resistance needs to be investigated. In a test of 18 rice cultivars grown at three locations representing high (116 mg Si l⁻¹ soil), typical (40 mg Si l⁻¹ soil), and low (6 mg Si l⁻¹ soil) Si status, cultivars varied significantly for tissue concentration (Deren *et al.*, 1992). Certain genotypes consistently ranked high or low in Si concentration across locations. This suggests that the acquisition of Si may be an inherited trait. Selected genotypes were further evaluated for Si accumulation and brown spot development on a low-Si soil (Histosols) amended with 0 and 10 ton.ha⁻¹ of calcium silicate slag (Deren *et al.*, 1994). Results indicated that genotypes differed for Si concentration and brown spot severity at each location and for each Si treatment, but the ranking remained fairly consistent. Most genotypes had a 30 to 40% relative decrease in brown spot severity when Si was added. Rico 1, which is known to be brown spot susceptible, was severely diseased at two locations, whereas Katy and Experimental Line 1 were consistently the least diseased. Genotypes with intermediate ranks shifted ranking with location and treatment, which was reflected in the significant genotype x Si treatment interaction in the analysis of variance. This variation in cultivar susceptibility with either high or low Si content simply may reflect variability within the pathogen population. However, resistance may be controlled by other factors inherent within a genotype as well as by plant accumulation of Si. Among genotypes, brown spot severity was negatively correlated (mean $r = -0.58$) with Si concentration in plant tissue. The correlation obtained in this experiment is based upon a small number of genotypes; a larger population would merit further investigation. Furthermore, Rico 1 and Della X2 had the greatest Si concentrations, yet were also consistently the most severely diseased genotypes. This also has been observed with blast; some cultivars with low Si were more resistant whereas others with high Si concentration were more susceptible (Ou, 1985). Rice genotypes accumulating higher levels of Si are not necessarily more resistant to diseases in comparison to genotypes accumulating low levels of Si when grown under the same Si fertility level (Kozaka, 1965). Hence, although Si concentration varied among genotypes and is negatively correlated with brown spot severity, the strength of this association may be mitigated by other genotypic factors which also affect response to disease.

Winslow (1992) reported that *indica* upland rice genotypes had a great reduction in the severity of sheath blight in response to Si application in comparison to African *japonica* and intermediate genotypes. Rodrigues *et al.* (2001a) showed that high Si content in rice tissues of tropical *japonicas* (LSBR-5, Drew, Kaybonnet, Lemont, and Labelle) and an *indica* type (Jasmine) rice cultivar contributed to a reduction in sheath blight severity. This clearly indicates that enhanced resistance to sheath blight conferred by Si was not limited to *indica* types as previously reported by

Winslow (1992). To determine whether the application of Si to moderately susceptible and susceptible cultivars could suppress the severity of sheath blight to those cultivars with high levels of partial resistance, which had not been treated with Si, Rodrigues and collaborators (2001a) selected cultivar-Si combinations and compared them by single degree of freedom contrasts. The statistical analysis showed that the combination of Drew and Kaybonnet (moderately susceptible) and Lemont and Labelle (susceptible) grown with Si reduced the severity of sheath blight to the same statistical level as the cultivars (Jasmine and LSBR-5) containing high levels of partial resistance. The level of sheath blight resistance for Jasmine and LSBR-5 was also further enhanced when these cultivars were supplemented with Si.

Effects of Silicon on Components of Host Resistance

Seebold *et al.* (2001) evaluated the effect of Si on several components of resistance in four rice cultivars with different levels of resistance to race IB-49 of *M. grisea* grown in Si-deficient soil amended with 0, 2, 5, and 10 ton calcium silicate ha⁻¹. The cultivar M201 has no known major or minor genes for resistance to race IB-49 of *M. grisea* and is highly susceptible. The cultivars Rosemont and Lemont are partially resistant and Katy is highly resistant. For each cultivar tested, the incubation period was extended by increased rates of Si while lesion length, rate of lesion expansion and disease leaf area were dramatically decreased.

The relative infection efficiency of *M. grisea*, determined as the number of sporulating lesions per square millimeter of leaf area, was highest on M201 and Rosemont and lowest on Katy. The relationship between the number of sporulating lesions per leaf area and the rate of calcium silicate was linear for all cultivars. The cultivar Lemont had 92% fewer sporulating lesions per leaf area than M201. Relative infection efficiency was 97% lower on Katy compared with M201 and was significantly lower when compared with Rosemont or Lemont, except at the highest rate of Si. The number of sporulating lesions counted on Lemont treated with 10 ton.ha⁻¹ was not significantly different from Katy, but there was no significant change in the number of sporulating lesions on Katy at any rate of calcium silicate. When the rate of calcium silicate was increased from 0 to 10 ton.ha⁻¹, the number of sporulating lesions per leaf area decreased by 71% on M201, Rosemont, and Lemont. By reducing relative infection efficiency, the number of sporulating lesions that can produce inoculum for secondary cycles is curtailed, and reductions in size of lesions further limit production of inoculum. The effect of Si on this component of resistance was more apparent on partially resistant or susceptible cultivars and was rate-responsive. In the case of blast-resistant Katy, the number of sporulating lesions found on plants that did not receive calcium silicate was near zero. Osuna-Canizales *et al.* (1991) also found no differences in the number of sporulating lesions between resistant cultivars grown in a solution

containing Si and those that had not received Si. The number of spores per square millimeter of lesion was different among all four cultivars. Sporulation per square millimeter of lesion was over three times higher on M201 than on Rosemont and ten times higher than Lemont. The relationship between rate of calcium silicate and the number of spores per square millimeter of lesion was linear for all cultivars, but significant only at $P = 0.10$. Sporulation per square millimeter of lesion on all cultivars was reduced by 47% as the rate of calcium silicate increased from 0 to 10 $\text{ton}\cdot\text{ha}^{-1}$. Only M201 showed a decrease in spores per square millimeter of lesion as the rate of Si increased. The effect of Si on the number of conidia per lesion was not clear. Although a general decline in number of conidia was observed across all cultivars, an examination of means by cultivar shows that, in reality, sporulation per lesion area was reduced by Si on M201 only. Despite having nearly the same content of Si in leaf tissue as M201, no change in sporulation occurred on Rosemont or Lemont at 0, 5, and 10 ton of calcium silicate per hectare, and no conidia were recovered from lesions on Katy. It is important to note that the total number of lesions available for estimation of number of conidia was smaller on the partially resistant and resistant cultivars than on the susceptible cultivar, and the number of lesions decreased as the rate of Si increased. Thus, the small sample sizes and inherent resistance in some cultivars contributed to erratic estimates of the number of conidia per square millimeter of lesion. In the case of Katy, sporulating lesions were rare at any rate of Si. Sporulation per lesion is probably of less epidemiological importance than the reduction in lesion number. Regardless of the rate of Si, the daily rate of lesion expansion was significantly higher on M201 than on Rosemont, Lemont, or Katy.

Rate of lesion expansion was 42 and 59% slower on Rosemont and Lemont, respectively, compared with M201 and did not differ significantly between these two cultivars. Rate of lesion expansion was slower on Katy than on Rosemont, Lemont, or M201. For all cultivars, rate of lesion expansion decreased from 0.8 to 0.43 mm per day (49%) as the rate of calcium silicate increased from 0 to 10 $\text{ton}\cdot\text{ha}^{-1}$ ($P \leq 0.07$). The effect of rate of Si on lesion length was less significant than for relative infection efficiency. Unlike relative infection efficiency, lesion length was reduced on all cultivars by an average of 46% with increasing rates of Si. The reduced lesion size with Si application enhanced the blast resistance exhibited by the cultivars tested in this study. The rate of lesion expansion was closely associated with the length of lesions. Lesions caused by *M. grisea* are determinate in size and reached maximum size at roughly the same time for all cultivars and rates of Si, resulting in measurements similar to those for length of lesion. Of these two components, lesion length appears to be a more important component of resistance to leaf blast than rate of lesion expansion because sporulation was not observed on lesions from any treatment until maximum size was reached.

Rodrigues *et al.* (2003c) investigated the effect of Si

on sheath blight development in Brazil. The predominant commercial rice cultivars BR-Irga 409, Metica-1, EPAGRI-109, Rio Formoso, Javaé, and CICA-8 were grown in pots containing soil from a Si-deficient typical acrustox red yellow latosol amended with 0, 0.48, 0.96, 1.44, and 1.92 g Si pot^{-1} . Plants were inoculated at the maximum tillering stage by placing a *R. solani* colonized toothpick into the lowest inner sheath of the main tiller. For all cultivars, Si concentration in straw increased more than 60% as the rate of Si increased from 0 to 1.92 $\text{g}\cdot\text{pot}^{-1}$. Incubation period of *R. solani* was slightly prolonged with increasing Si rates and ranged from 53 to 64 h depending upon the cultivar. Total number of sheath blight lesions, total area under the relative lesion extension progress curve, severity of sheath blight, and the highest relative lesion height on the main tiller decreased

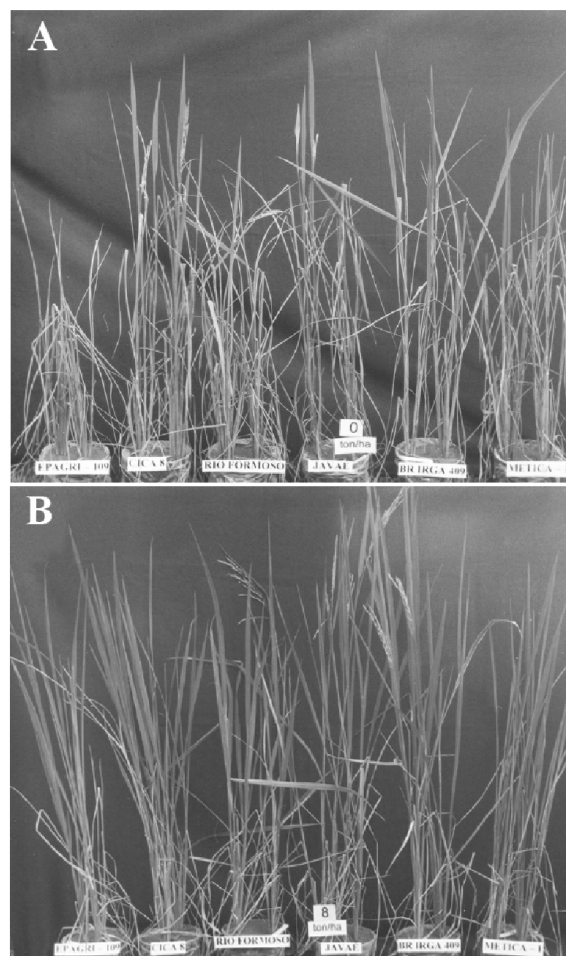


FIG. 3 - Symptoms of sheath blight caused by *Rhizoctonia solani* on six Brazilian cultivars of rice (*Oryza sativa*). **A** - Nontreated control plants (0 g Si pot^{-1} or 0 $\text{ton calcium silicate ha}^{-1}$); **B** - plants grown at the highest rate of Si (1.92 g Si pot^{-1} or 8 $\text{ton calcium silicate ha}^{-1}$). Reprinted from Crop Protection, Vol. 22, Rodrigues, F. Á., Vale, F. X. R., Korndörfer, G. H., Prabhu, A. S., Datnoff, L. E., Oliveira, A. M. A., and Zambolim, L. Influence of silicon on sheath blight of rice in Brazil, p. 27, 2003, with permission from Elsevier.

by 37, 40, 52, and 24%, respectively, as the rate of Si increased in the soil. Overall, rice cultivars grown at highest Si rate had sheath blight intensities that were greatly reduced as compared with cultivars grown in pots not amended with Si (Figure 3).

Possible Mechanisms for Silicon-Mediated Rice Resistance

In the rice-*M. grisea* pathosystem, increased resistance through Si treatment has been associated with the density of silicified buliform, long, and short cells in the leaf epidermis that act as a physical barrier to impede penetration by *M. grisea* (Ito & Hayashi, 1931; Suzuki, 1940; Hemmi *et al.*, 1941). This physical barrier hypothesis is strengthened by the findings of Yoshida *et al.* (1962), who reported the existence of a layer of silica of approximately 2.5 µm thick beneath the cuticle of rice leaves and sheaths. This cuticle-Si double layer can impede *M. grisea* penetration and, consequently, decrease the number of blast lesions on leaf blades. According to Volk *et al.* (1958), Si might form complexes with organic compounds in the cell walls of epidermal cells, therefore increasing their resistance to degradation by enzymes released by *M. grisea*. Indeed, Si can be associated with lignin-carbohydrate complexes in the cell wall of rice epidermal cells (Inanaga *et al.*, 1995).

Kim *et al.* (2002) investigated some of the cellular features of Si-mediated resistance to blast. The authors observed that the epidermal cell wall thickness was not significantly affected by Si. However, the thickness ratios of silica layers to epidermal cell walls were much higher in the resistant cultivar than in the susceptible cultivar. Although the fortification of epidermal cell walls was considered the main cause for the reduced number of leaf blast lesions, no evidence in relation to the physical impedance offered by the fortified cell wall was given to the penetration peg of *M. grisea*. Interestingly, Ito & Sakamoto (1939) studied the puncture resistance of rice epidermal cells to a needle tip from beneath a torsion balance using leaves collected from rice plants grown under different Si rates. Their results showed that the puncture resistance was not explained solely by the leaf epidermis silicification; rather, it was attributed mainly to the nature of the protoplasm of epidermal cells. In another study, it was reported that rice cultivars resistant to blast had lower lesion numbers and silicified epidermal cells than susceptible cultivars (Kawamura & Ono, 1948). As reported by Hashioka (1942), the density of silicified cells in rice leaf epidermis is not always proportional to the level of resistance of some rice cultivars to blast. Altogether, these observations suggest that resistance of Si-treated plants to *M. grisea* is much more complex than a physical resistance against penetration due to the silicified cells or to the cuticle-Si double layer.

Seebold *et al.* (2001) made some inferences about the mechanisms by which Si acts to reduce blast. The authors noted that the reduced number of sporulating lesions (relative infection efficiency) on partially resistant and susceptible cultivars fertilized with calcium silicate indicated there were

fewer successful infections established per unit of inoculum, lending support to the physical barrier hypothesis. The reductions in the total number of lesions as the rates of Si increased, clearly indicated that Si manifested its effect before the penetration peg of *M. grisea* actually entered the epidermis, or soon thereafter, indicative of blockage to ingress by the fungus.

In an attempt to gain further insight into the role of Si in rice blast resistance, Rodrigues *et al.* (2003a) investigated the ultrastructural outcome of the rice-*M. grisea* interaction upon Si application. The authors provided the first cytological evidence that Si-mediated resistance to *M. grisea* in rice correlated with specific leaf cell reaction that interfered with the development of *M. grisea*. Ultrastructural observations of samples collected from plants grown in soil unamended with Si revealed that some host cells were devoid of organelles and that some host cell walls were no longer discernible in the massively colonized mesophyll and vascular bundle (Figure 4A and B). A light deposition of osmiophilic material with a granular texture, occasionally interacting with fungal walls, was seen in some epidermal cells (Figure 4C, arrows). In plants amended with Si, empty fungal hyphae were evenly surrounded by a dense layer of granular osmiophilic material partially occluding the epidermal cells (Figure 4D, arrows), the vascular bundle (Figure 4E, arrowheads), and the mesophyll cells (Figure 4F, arrows). The possibility that this amorphous material constitutes phenolic compounds appears realistic, considering not only its staining with toluidine blue and its texture and osmiophilic properties, but also the occurrence of marked fungal hyphae alterations. Cytochemical labeling of chitin revealed no difference in the pattern of chitin localization over fungal cell walls of either samples from plants amended or not with Si at 96 h after inoculation with *M. grisea*, indicating limited production of chitinases as one mechanism of rice defense response to blast. On the other hand, the occurrence of empty fungal hyphae, surrounded or trapped in amorphous material, in samples from plants amended with Si suggested that phenolic-like compounds or phytoalexin(s) played a crucial role in rice defense response against infection by *M. grisea*. Therefore, Si could be acting as a modulator to positively amplify rice defense response(s), namely by influencing the synthesis of antifungal compounds after the penetration peg of *M. grisea* enters the epidermal cell.

In a further study, Rodrigues *et al.* (2004) tested the hypothesis that an alteration in the development of *M. grisea* in leaf tissues of rice plants amended with Si could be associated with an enhanced production of phytoalexin(s). Analysis of the ethyl ether fraction (FII) obtained from leaf extracts of plants amended with (+Si) or without (-Si) and inoculated with *M. grisea* revealed that of the five sub-fractions (SF) collected, only SF5, which corresponded to compounds eluting after 90 min in the HPLC chromatograms, displayed antifungal activity against *M. grisea*. The SF5 from Si⁺ treatment showed higher

fungitoxicity against *M. grisea* than SF5 from Si⁻ treatment. Sub-fractions 1, 2, 3, and 4 had no apparent antifungal activity against *M. grisea* regardless of Si treatment. Based on these observations, SF5 from FII was further analyzed by HPLC. This allowed separation of the two momilactones on the basis of their ultraviolet spectra and retention time (R_t) (momilactone A R_t 46 min and momilactone B R_t 47

min). These compounds were present in minute or small quantities in non-inoculated plants amended or not with Si. By contrast, both products showed a two to three-fold increase in leaf extract from plants grown in soil amended with Si and inoculated with *M. grisea* treatment compared to the lower levels observed in leaf extract from inoculated plants non-amended with Si. Rice plants not amended with

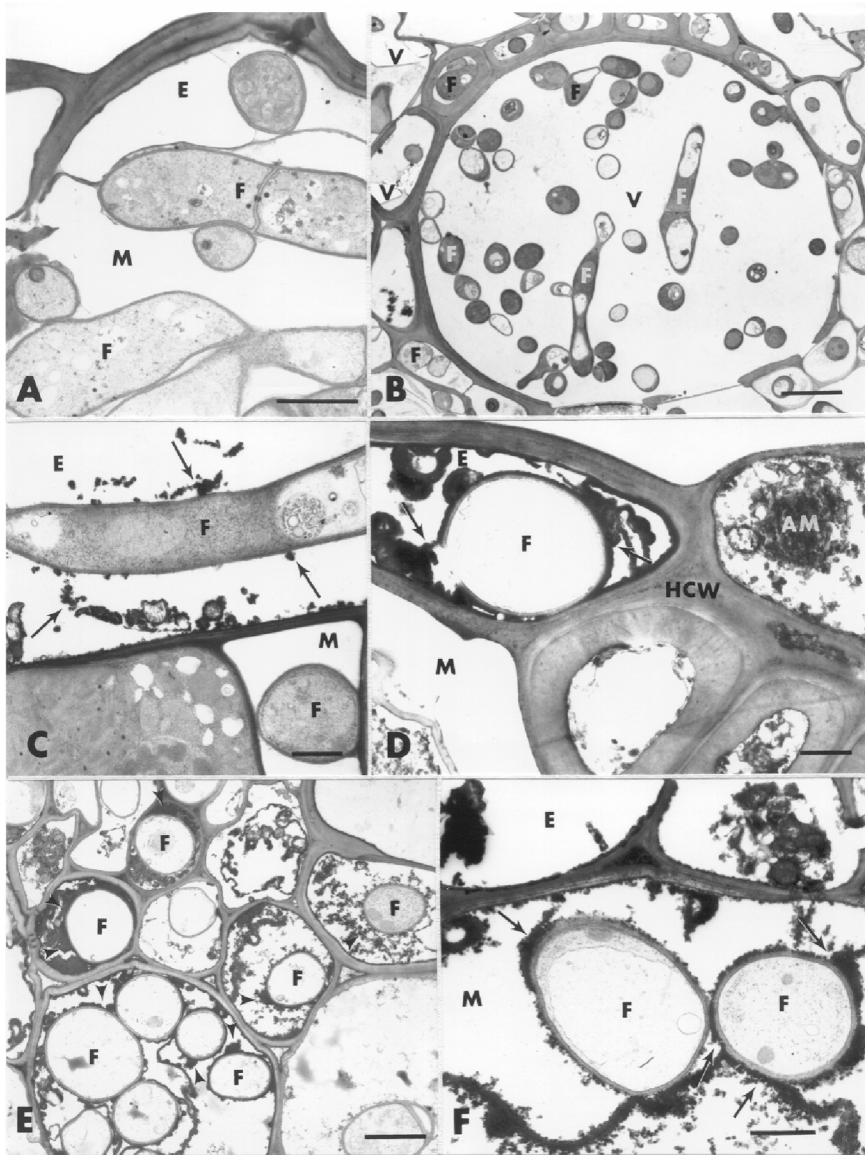


FIG. 4 - Transmission electron micrographs of leaf samples collected from -Si and +Si rice (*Oryza sativa*) plants 96 h after inoculation with *Magnaporthe grisea*. **A** - Ultrastructurally normal fungal hyphae colonize both the epidermis and mesophyll. Host cell walls are no longer discernible in the mesophyll (-Si). Bar = 2 μ m. **B** - The vascular bundle is massively colonized by the fungal hyphae (-Si). Bar = 5 μ m; **C** - Some amorphous material (arrows) accumulates in an epidermal cell and irregularly interacts with a fungal cell wall (-Si). Bar = 1 μ m; **D** - A dense amorphous material (arrows) accumulates around an empty fungal hyphae in the epidermal cell and also is found in an epidermal cell neighbouring the colonized one (+Si). Bar = 1 μ m; **E** - Fungal hyphae invading the vascular bundle are often surrounded by dense amorphous material and often reduced to empty shells (+Si; arrowheads). Bar = 2 μ m; **F** - Two fungal hyphae in a mesophyll cell are evenly coated by the amorphous material (+Si; arrows) Bar = 1 μ m. Amorphous material (AM), fungal hyphae (F), epidermis (E), mesophyll (M), host cell wall (HCW), and vascular bundle (V).

Si and inoculated with *M. grisea*, in spite of releasing antifungal compounds including momilactones, were obviously not protected efficiently against fungal colonization. By contrast, rice plants amended with Si and inoculated with *M. grisea*, releasing higher amounts of momilactones probably earlier in the infection process, benefited from a lower level of rice blast severity (Figure 5).

While little is known about the mechanism(s) of resistance of rice plants amended with Si in response to *M. grisea* infection, two mutually agreeable hypotheses must be considered. On the one hand, it is possible that in certain areas of heavy Si deposition, delayed fungal ingress and colonization provides the rice plant enough time for momilactones, synthesized in response to infection by *M. grisea*, to accumulate to considerable levels and express their fungitoxicity within the zone of the infection site. On the other hand, as proposed by Fawe *et al.* (2001), the soluble Si present in the plant cells may mediate some defense responses that are functionally similar to systemic acquired resistance. The results of this study, together with the ultra structural observations, strongly suggest that Si plays an active role in the resistance of rice to blast rather than simply forming a physical barrier in leaf epidermis to avoid fungal penetration.

Outlook and Future Silicon Research Needs

Silicon fertilization of rice grown in soil orders with less than optimum Si levels, offers promising results with respect to reducing rice susceptibility to fungal, bacterial, and nematode diseases and improving yields. This sustainable practice ideally fits in with the concept of environmentally friendly strategies for management of rice

diseases. Interestingly, Si can control rice diseases to the same general degree as obtained by using fungicide applications and also contributes to reducing the amount of fungicides needed. Consequently, sources of Si and their management practices should be developed and practiced in integrated pest management programs for those crops where Si has been demonstrated to have a positive effect.

Some Si sources have residual activity that persists over time, raising the possibility that applications need not be applied annually. Also, after the first initial Si amendment, subsequent application rate requirements might be considerably lower due to these residual effects. However, silicate slags are considered to be expensive Si sources, so there is a need to find or develop cheaper and more efficient Si sources. Recycling of rice hulls and/or straw may be one possible alternative.

Silicon genotypes differ in their Si content, responding differently to Si application. Genetics definitely plays an important role in Si accumulation and merits further consideration while selecting genotypes for other important agronomic traits. The strategic combination of fine-grade Si formulation with 'Si-accumulator' cultivar/genotypes would also reduce application rate requirements, thereby minimizing the cost of the Si amendment program.

That Si plays an important role in the mineral nutrition of many plant species is not in doubt, nor is its ability to efficiently control several plant diseases. Effective, practical means of application and affordable sources of Si are needed for use in row crop agriculture in particular. As researchers and growers become aware of Si and its potential in agriculture, it is likely that this often overlooked element will be recognized as a viable means of sustainably managing important plant diseases worldwide.

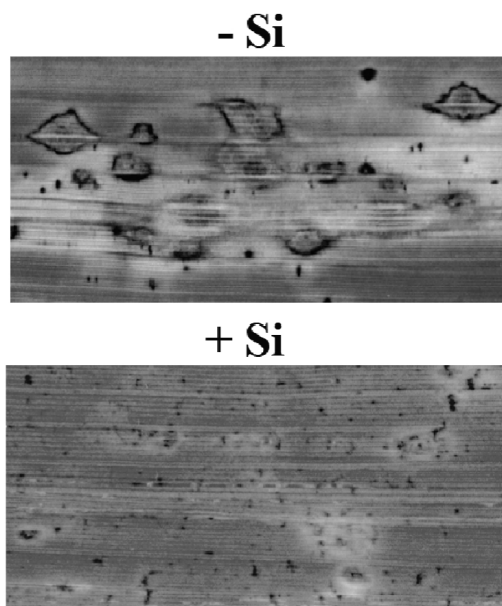


FIG. 5 - Development of leaf blast symptoms at 96 h after inoculation with *Magnaporthe grisea* in rice plants nonamended (-Si) or amended (+Si) with silicon.

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